# CASSIDULOIDS

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The cassiduloids are a distinctive group of medium-sized echinoids having a generally plane oral surface and gently to strongly rounded aboral surface. The outline of the test seen from below or above is nearly perfectly circular in some genera, but even to somewhat uneven ovoid outlines are most common. The ambulacra are distinctly petaloid adapically and the periproct invariably is located outside of the apical system. The surface of the test usually is marked by the presence of phyllodes and bourrelets. Oldest known cassiduloids have been collected from Jurassic strata, and representatives of the order are distributed through post-Jurassic formations to the Recent. Various living kinds are widespread and abundant.

Mortensen (1948) revised this order, even though he saw few fossil species and worked primarily from illustrations and descriptions by previous workers. Unfortunately, many of the old illustrations are inaccurate. For example, Cotteau's artist always showed double pores in the phyllodes, regardless of whether they were double or single. Of hundreds of species of irregular echinoids figured in *Paléontologie Française, Terrain Tertiaire* (Cotteau, 1885-94), all are shown with double pores in the ambulacral plates beyond the petals, despite the fact that double pores occur in none of them.

These defects became apparent early in the five-year period spent by me on the cassiduloid section of the *Treatise* and hence further research was undertaken to perfect the systemization. In this connection, two visits financed by grants from the National Science Foundation were made to Europe, where many of the primary types are located. The type-species of almost all genera were studied and photographed. As a result, a revision of the cassiduloids was published (Kier, 1962), and it is from this work that most of the following information has been abstracted.

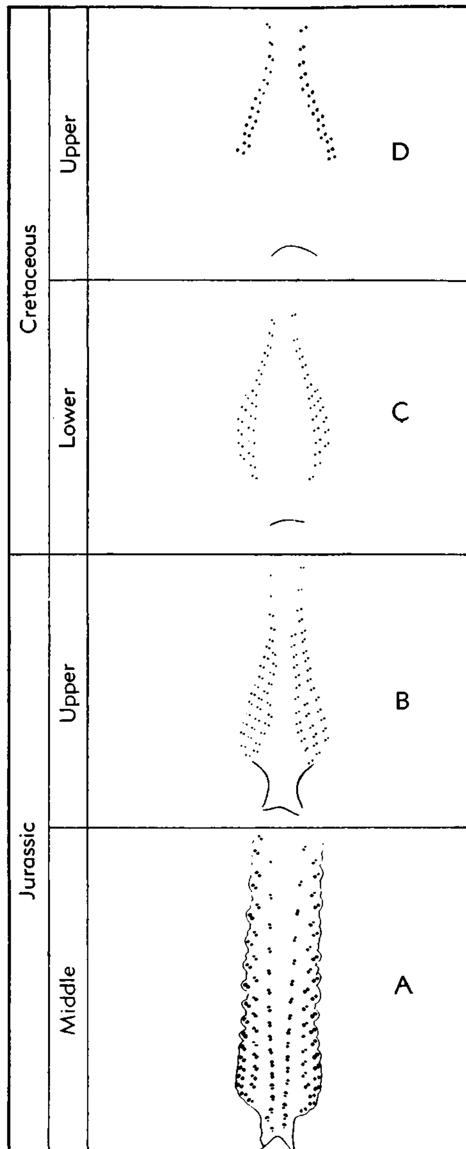



Fig. 378. Evolution of pygurid type of phyllode, trend toward decrease in number of pores, widening of phyllodes, and increase in distance between pores and edge of peristome shown in four species of *Pygurus* (not to scale) (Kier, n).

## EVOLUTION

### AMBULACRAL PORES

Pore pairs occur in all ambulacral plates of pre-Cenomanian cassiduloids, but in post-Senonian species only single pores are present in ambulacral plates beyond the petals. This abrupt change occurs in all families of the order. Reduction from a pore pair to a single pore probably was caused by a functional change of tube feet beyond the petals from breathing to food gathering.

### PHYLLODES

Phyllodes of the cassiduloids can be divided into two types: nucleolitid and pygurid. The pygurid type (Fig. 378) is characterized by a large number of pore pairs in the more primitive species. The trend in evolution of the pygurid phyllodes is toward broadening them, reducing the number of pore pairs, and increasing the distance between pores and edge of the peristome. Primitive species with the nucleolitid phyllode (Fig. 379) have fewer pore pairs than the pygurid type. From Bajocian to Cenomanian time little change occurred in the phyllodes but during and after the Cenomanian the number of pores in each plate was reduced from two to one, and buccal pores appeared. Subsequently the phyllodes widened and the number of pores in each inner series was reduced.

### PETALS

The petals of earliest cassiduloids extend to margins of the test, with only a small area below the petals (Fig. 380). In later species, the test became higher, and the area below the petals increased in size. Apparently this change enabled the echinoid to burrow deeper into the substratum.

### APICAL SYSTEM

The apical system underwent considerable evolution, changing from a tetrabasal system in the Jurassic, commonly with complimentary and catenal plates, to a monobasal system without any extra plates. This change is quite abrupt; no species with a monobasal apical system is known from sources older than Senonian, and none with a tetrabasal system from sources younger than Senonian.

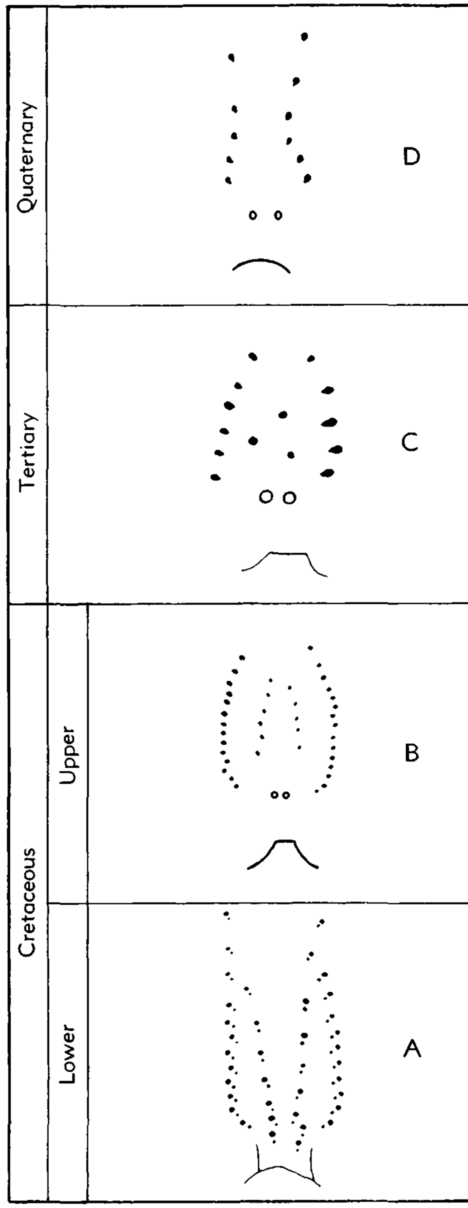



Fig. 379. Evolution of nucleolitid type of phyllode, trend toward widening of phyllodes, reduction from pore pairs to single pores, and introduction of buccal pores shown in four species (*A, Pygorhynchus obovatus* (Agassiz); *B, Petalobrissus lefebvrei* (Fourtau); *C, Pliolampas gauthieri* (Cotteau); *D, Cassidulus cariboearum* Lamarck (not to scale) (Kier, n).

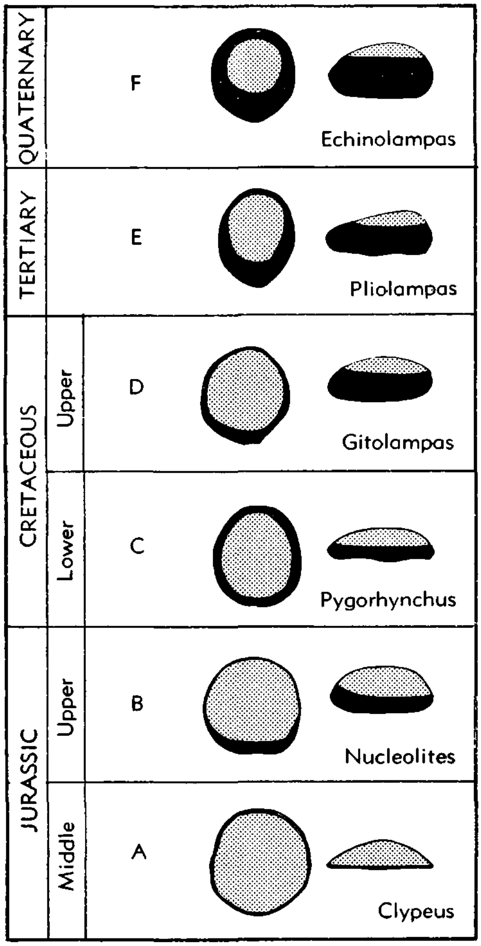



FIG. 380. Aboral and side view of some important cassiduloid genera showing change in shape of test and length of petals (petaloid area shaded, area below petals solid black) (Kier, n).

#### BOURRELETS

The bourrelets are slightly to moderately developed in earliest cassiduloids, but by the Cenomanian Epoch they were more prominent, reaching the zenith of their development in the Senonian, when in some species they were large and toothlike. After the Maastrichtian, the bourrelets usually were not as well developed.

#### PERIPROCT

The periproct normally is supramarginal in earliest cassiduloids, and may be in contact with the apical system. By Early Cretaceous time it had shifted marginally in many genera, and by the Turonian it was marginal or inframarginal in most genera. Many species again had supramarginal periprocts in the Senonian and Tertiary, but in none of them was the periproct as far forward and near the apical system as in earlier species.

#### TUBERCULATION

Specialized adoral tuberculation differing from adapical tuberculation was developed in the later cassiduloids. Adoral and adapical tuberculation are very similar in Jurassic species, both sets of tubercles being approximately the same in size. By the Neocomian, adoral tubercles near the peristome were slightly larger than adapical ones. In the Cenomanian, the adoral tubercles were considerably larger, and for the first time a naked, granular, normally pitted sternal area was developed in interambulacrum 5. Large adoral tubercles commonly have eccentric bosses. Most Upper Cretaceous and Tertiary genera have larger adoral tubercles and many have naked sternal areas. Probably the larger adoral tubercles and the naked sternal area aided the animals in burrowing.

#### SHAPE

The test of later cassiduloids is more elongate than that of earlier species. The outline is circular or wider than long in many of the oldest genera, but by the Early Cretaceous time and from then until the present, most genera are elongate, with a few exceptions, such as circular Maastrichtian species of *Hardouinia.* Generally, post-Jurassic species with circular tests are highly inflated, as in some of the larger species of *Echinolampas,* whereas many circular tests of Jurassic species are rather low. Presumably, the trend toward elongation reflects a change in living habits, where the elongate test would be better suited for burrowing through sediment.

### PHYLOGENY

The evolutionary trends summarized in Figure 381 suggest phylogeny of cassiduloid genera (Fig. 382).

The Galeropygidae are the earliest of all cassiduloids and the most primitive in that

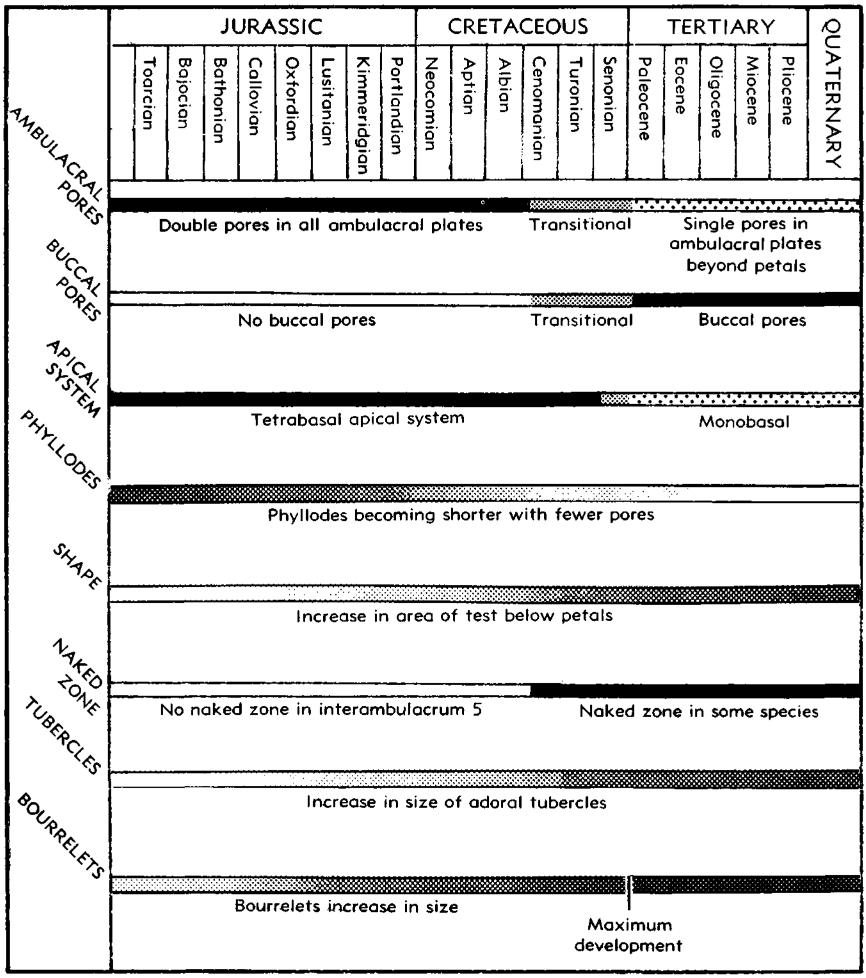



FIG. 381. Evolutionary trends in Cassiduloida (Kier, n).

they have a supramarginal periproct in contact with the apical system, petals very slightly developed, test low and wide, and phyllodes long and narrow.

The Clypeidae descended from the Galeropygidae or from a close ancestor of the Galeropygidae. They are more advanced, with their petals well developed and the periproct usually more marginal or inframarginal.

The Nucleolitidae, like the Clypeidae, descended from the Galeropygidae or a close ancestor of the Galeropygidae. They are more advanced in having more pronounced petals and normally have fewer pore pairs in the phyllodes. All genera in the family, excepting possibly *Pseudosorella*, apparently are derived from *Nucleolites*. Their phyllodes are very similar, with two series of pore pairs in each half-ambulacrum, and most have similarly elongate tests and open petals with narrow poriferous zones.

The Faujasiidae appear to have descended from the Nucleolitidae, probably from a form similar to *Phyllobrissus*. Evolutionary trends in this family are toward decrease in number of pores in the phyllodes, increase in the development of the bourrelets and

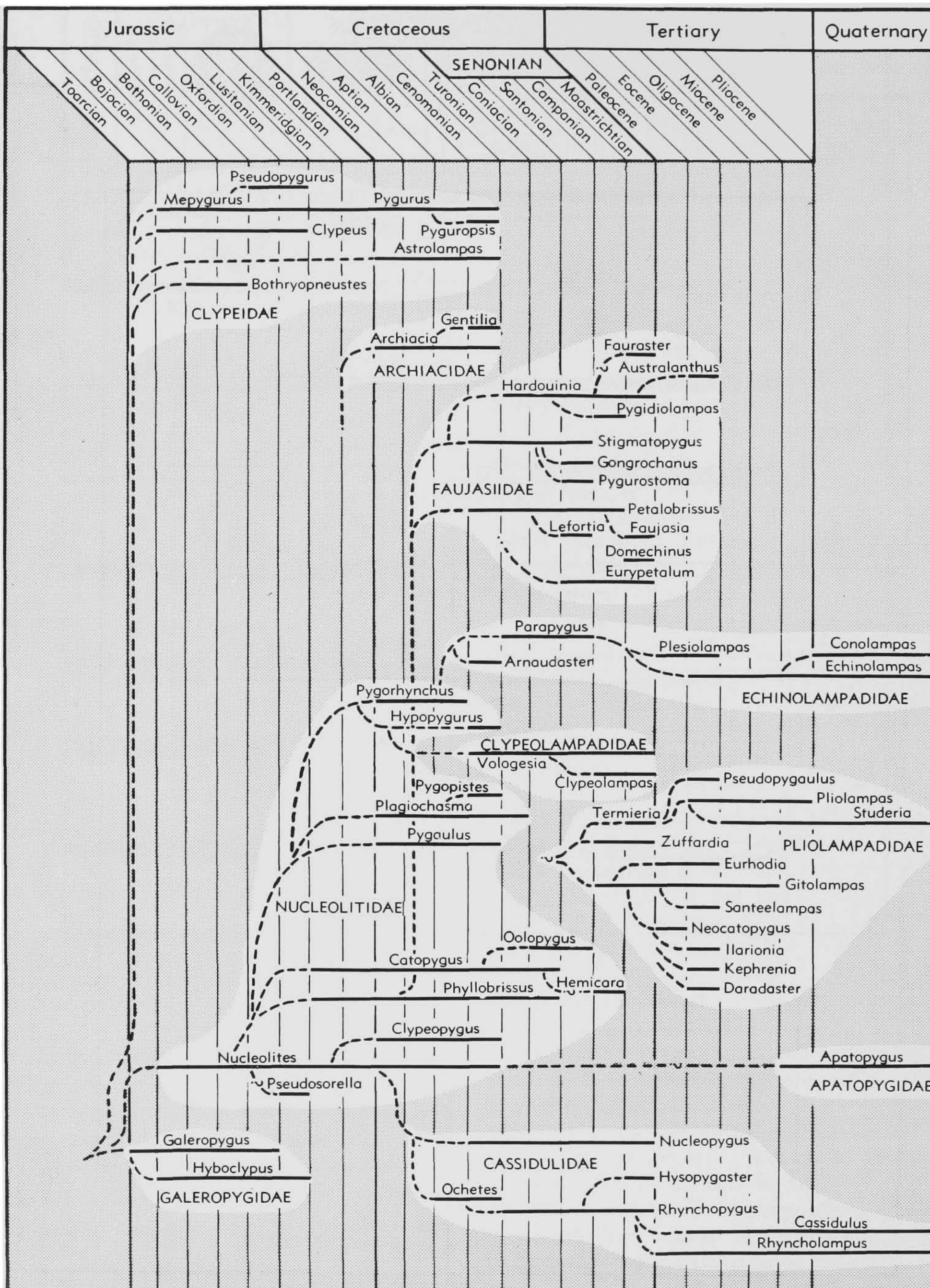



FIG. 382. Phylogeny of Cassiduloida (98).

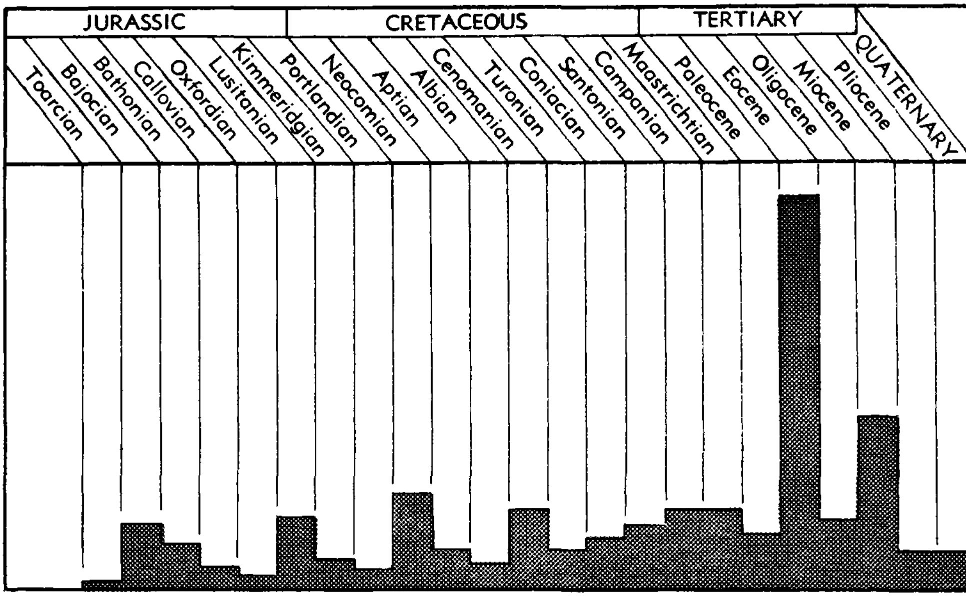



FIG. 383. Relative abundance of cassiduloid species in successive divisions of Jurassic and post-Jurassic time (scale arbitrary) (98).

petals, and change from a tetrabasal to monobasal apical system.

The Cassidulidae probably evolved from the Nucleolitidae, with *Nucleopygus* originating from *Nucleolites.* These two genera are similar in having the periproct supramarginal and petals straight and open, with narrow poriferous zones; *Nucleopygus* is more advanced in having single pores in its ambulacral plates beyond the petals, and in having buccal pores.

The Echinolampadidae descended from the Nucleolitidae, probably from a genus like *Pygorhynchus.* The two oldest genera in the family, *Arnaudaster* and *Parapygus,* are similar to *Pygorhynchus,* their only important difference being the single pores in the ambulacral plates beyond the petals of *Arnaudaster* and *Parapygus,* and their buccal pores. Because both of these characters are advanced features and because both genera occur later than *Pygorhynchus,* it is apparent that the *Pygorhynchus*-like form is the ancestor.

The Pliolampadidae are not homogeneous and may not be a natural grouping. They originated from the Nucleolitidae, but it is not clear from what genus. They are distinguished from the Echinolampadidae in having petals with poriferous zones of equal length and in lacking a naked zone adorally in interambulacrum 5 of most species. They differ from the Faujasiidae in their smaller, more rounded bourrelets and narrower phyllodes. The family can be divided into two morphological (perhaps phylogenetic) stocks: one with open petals and very broad poriferous zones (e.g., *Pliolampas*), and the other having closed petals with narrow poriferous zones (e.g., *Gitolampas*).

The Clypeolampadidae arose from some genus of the Nucleolitidae. Their petals are similar to those of *Hypopygurus.*

The Archiacidae have two series of pores in the phyllodes of each half-ambulacrum, and therefore probably originated from some genus in the Nucleolitidae.

The Apatopygidae probably descended from the Nucleolitidae, as evidenced by their straight petals with narrow, open poriferous zones, supramarginal periproct, slightly developed bourrelets, and phyllodes with two series of pores in each half-ambulacrum. Absence of buccal pores in a

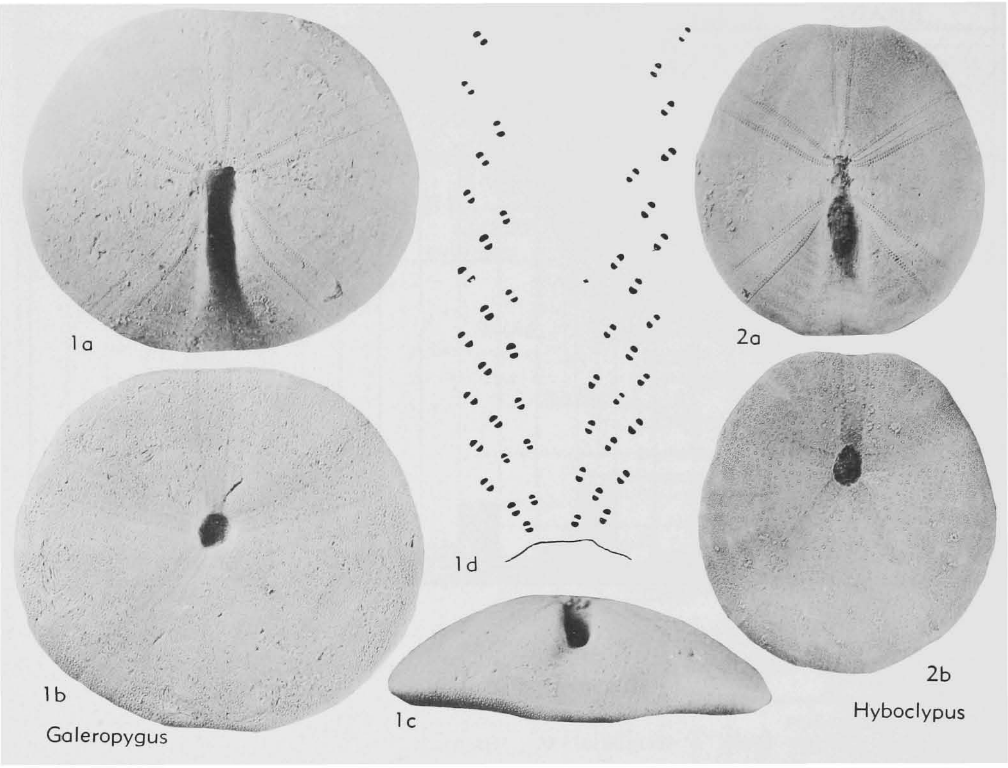



FIG. 384. Galeropygidae (p. U499).

single-pored phyllode and presence of "pyrinid" plating in the ambulacra beyond the petals distinguish the Apatopygidae from all other cassiduloids and cast some doubt on their affinities.

## DISTRIBUTION IN TIME

The relative abundance of known cassiduloid species is shown in Figure 383. One of the most striking features of this distribution is the occurrence of extraordinarily numerous species in the Eocene and subsequent decrease of their numbers in the late Tertiary and Quaternary. More than 500 species have been reported from the Tertiary, but only 16 species are living today. This great decline may have been caused by a cooling of the seas and an increase in competition from other echinoids.

## ECOLOGY

The ecology of extant species of the cassiduloids has not been studied. Morphological evidence suggests that they live partially buried up to their petals. The absence of fascioles probably prevents them from completely burying themselves.

## Order CASSIDULOIDA Claus, 1880

Ambulacra petaloid adapically; periproct outside of apical system; phyllodes and bourrelets usually present; no jaws or gill slits in adult. *Jur.-Rec.*

### Family GALEROPYGIDAE Lambert, 1911

Large; apical system central, tetrabasal; ambulacra subpetaloid, long; all ambulacral plates double-pored; periproct supramarginal, in contact with apical system; peristome anterior; bourrelets absent or slightly developed; phyllodes narrow with 2 or 3 series of pore pairs in each half-ambulacrum; no buccal pores. *Jur.*

**Galeropygus** Cotteau, 1856, p. 648 [**Hyboclypus agariciformis* Wright, 1851, p. 99; OD] [=*Galeopygus* Desor, 1857 *(nom. null.)*; *Ressopygus* Pomel, 1883, p. 56 (type, *Clypeus constantini* Cotteau, 1873, p. 228)]. Low circular; broad apical system with genital plates arranged in semicircle; bourrelets slightly developed. *L.Jur.(Toarc.)-U.Jur.(Oxford.)*, Eu.——Fig. 384,*1*. **G. agariciformis* (Wright), M.Jur.(Inferior Oolite), G.Brit.; *1a-c,* aboral, oral, post., ×1; *1d,* amb. V phyllode, ×10 (98).

**Hyboclypus** L. Agassiz, 1839, p. 75 [**H. gibberulus*; OD, M] [=*Hyboclypeus* Gray, 1840 *(nom. null.)*; *Hyboclipus* Desor, 1842 *(nom. null.)*; *Hyboclybus* Sismonda, 1842 *(nom. null.)*; *Hybodyhus* Ebray, 1859 *(nom. null.)*; *Aulacopygus* Pomel, 1883 (type, *Hyboclypus caudatus* Wright, 1851, p. 100)]. Elongate apical system, oculars II and IV usually in contact; bourrelets absent or slightly developed. *Jur.*, Eu.——Fig. 384,*2*. **H. gibberulus,* M. Jur. (Bajoc.)-U. Jur. (Kimmeridg.), Fr.; *2a,b,* aboral, oral, ×1 (98).

## Family CLYPEIDAE Lambert, 1898

Medium-sized to large, low; apical system tetrabasal; petals broad, outer pores slitlike, all ambulacral plates double-pored; periproct usually longitudinal; peristome anterior, bourrelets usually well developed; phyllodes in early species with 3 series of pore pairs in each half-ambulacrum, in later only one; no buccal pores. *Jur.-U.Cret.*

**Clypeus** Leske, 1778, p. 93 [**C. plotii*; SD, Kier, 1958, p. 30] [=*Echinoclypeus* de Blainville, 1830 (obj.); *Auloclypeus* Pomel, 1883, p. 60 (type, *Nucleolites michelini* Wright, 1851, p. 23); *Crotoclypeus* Pomel, 1883, p. 60 (type, *Nucleolites agassizi* Wright, 1851, p. 368); *Dactyloclypeus* Maccagno, 1947, p. 126 (type, *Clypeus wylliei* Currie, 1925, p. 63)]. Broad; petals long, broad; periproct supramarginal; bourrelets well developed; phyllodes with many pore pairs. *M. Jur. (Bajoc.)-U. Jur. (Kimmeridg.),* Eu.-Afr.——Fig. 386,*4*. **C. plotii,* M.Jur.(Inferior Oolite), G. Brit. aboral, ×0.5 (98).——Fig. 385,*1*. *C. sinuatus* Leske, M.Jur.(Gr. Oolite), Fr.; amb. I phyllode, ×4 (98).

**Astrolampas** Pomel, 1883, p. 63 [**Pygurus productus* L. Agassiz, 1836; OD]. Elongate; bourrelets slightly developed, not inflated; phyllodes long, narrow. *Cret.(Valangin.-Cenoman.),* Eu.-Syria.——Fig. 386,*3*. **A. productus* (L. Agassiz), L.Cret., Switz.; *3a,b,* aboral, oral, ×1 (98).

**Bothryopneustes** Fourtau, 1924, p. 27 [**B. lamberti*; SD Currie, 1927, p. 425] [=*Clypeobrissus* Currie, 1925, p. 69 (type, *C. somaliensis*)]. Medium-sized, margin well rounded; periproct marginal to inframarginal; bourrelets well developed; phyllodes slightly broadened, with many pore pairs. *Jur.(Bathon.-Callov.),* Afr.——Fig. 386,*2a-c*. **B. lamberti,* Egypt; *2a-c,* aboral, lat., oral, ×2 (98).——Fig. 386,*2d*. *B. somaliensis* (Currie), U.Jur., Somaliland; aboral, ×1 (98).


Fig. 385. Clypeidae (p. U499).

**Pseudopygurus** Lambert, 1911, p. 184 [**P. letteroni*; OD, M]. Large; petal III absent or slightly developed; periproct inframarginal; bourrelets well developed; phyllodes with many pore pairs. *U.Jur.(Sequan.),* Eu.-Afr.——Fig. 386,*1*. **P. letteroni,* Fr.; *1a-c,* aboral, oral, lat., ×1; *1d,* adapical, ×4 (98).

**Pygurus** L. Agassiz, 1839, p. 68 [**Echinolampas montmollini* L. Agassiz, 1836, p. 134; SD Savin, 1902, p. 271] [=?*Echinanthites* Leske, 1778 (no type-species)]. Large, petals broad; periproct inframarginal; bourrelets well developed; phyllodes varying from broad with few pore pairs to narrow with many pore pairs. *M. Jur.(Bajoc.)-U. Cret. (Cenoman.),* cosmop.

**P. (Pygurus)** [=*Echinopygus* d'Orbigny, 1856, p. 303 (type, *Clypeaster oviformis* Lamarck, 1816, p. 15)]. Slightly elongate; apical system anterior; broad phyllodes. *U.Jur.(Oxford.)-U.Cret. (Cenoman.),* Eu.-Afr.-N. Am.——Fig. 385,*2*; 387,*1*. **P. montmollini* (L. Agassiz), L.Cret. (Neocom.), Fr.; 385,*2,* phyllode, enlarged; 387,*1,* aboral, ×1 (98).

**P. (Mepygurus)** Pomel, 1883, p. 65 [**Pygurus michelini* Cotteau, 1849, p. 70 (=*Pygurus depressus* Agassiz, 1847, p. 162); SD Lambert & Thiéry, 1921, p. 356]. Low, broad; central apical system; narrow phyllodes with many pore pairs. *Jur.(Bajoc.-Oxford.)*, Eu.-Afr.——FIG. 388,*1*. **P. (M.) depressus* (AGASSIZ), M.Jur.(Callov.), Fr.; *1a,b*, aboral, oral, ×0.5 (98).

**P. (Pyguropsis)** DE LORIOL, 1902, p. 32 [**P. noetlingi* DE LORIOL, 1899, p. 4; OD]. Test thick, sides steep. *U. Cret. (Cenoman.)*, Lebanon.——FIG. 387,*2*. **P. (P.) noetlingi*; *2a-c*, aboral, oral, lat., ×2 (98).

## Family NUCLEOLITIDAE L. Agassiz & Desor, 1847

Apical system tetrabasal; petals moderately developed, usually open, with narrow poriferous zones; usually double pores in all ambulacral plates; phyllodes narrow; bourrelets moderately developed. *M.Jur.-U.Cret.*

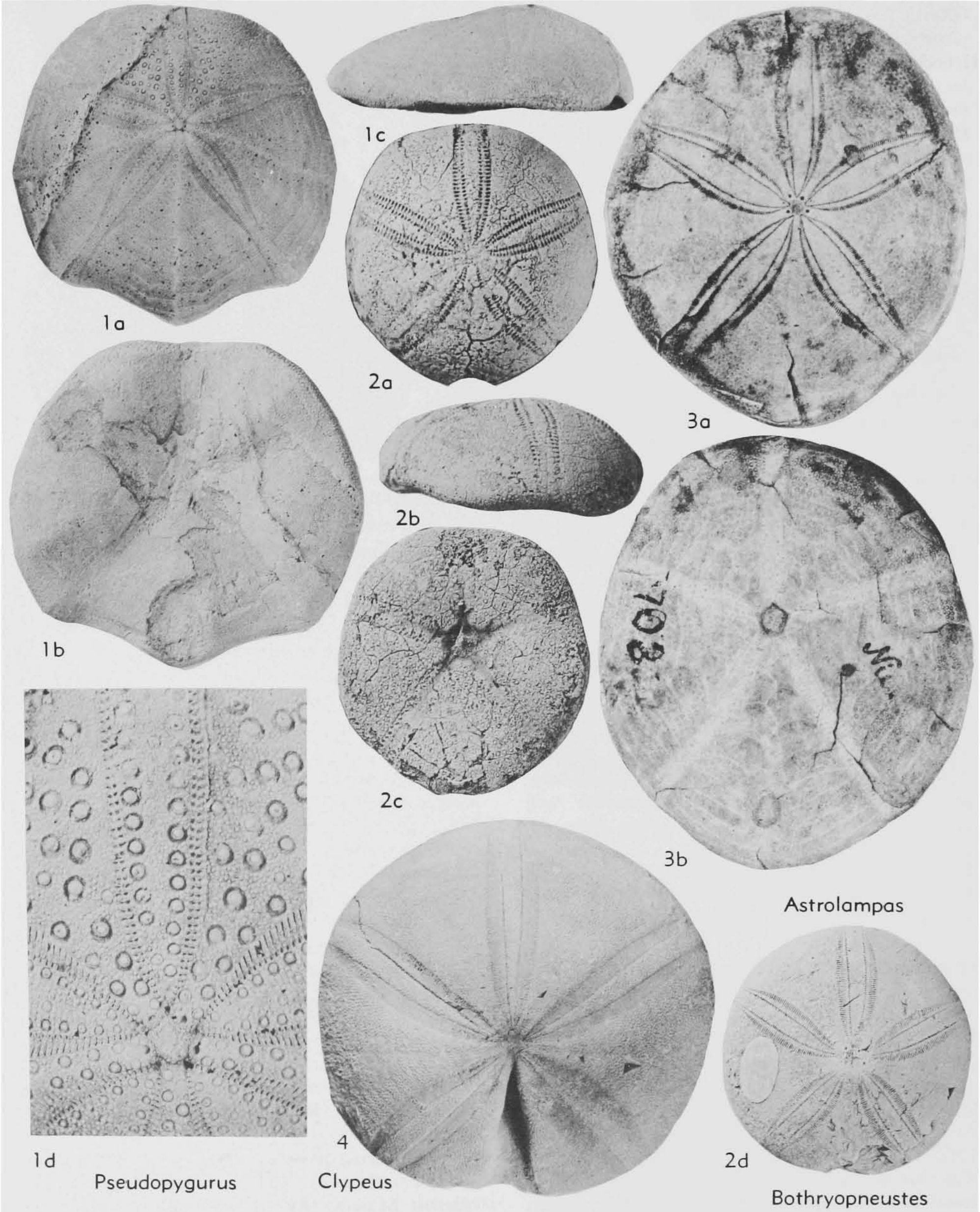



FIG. 386. Clypeidae (p. U499).

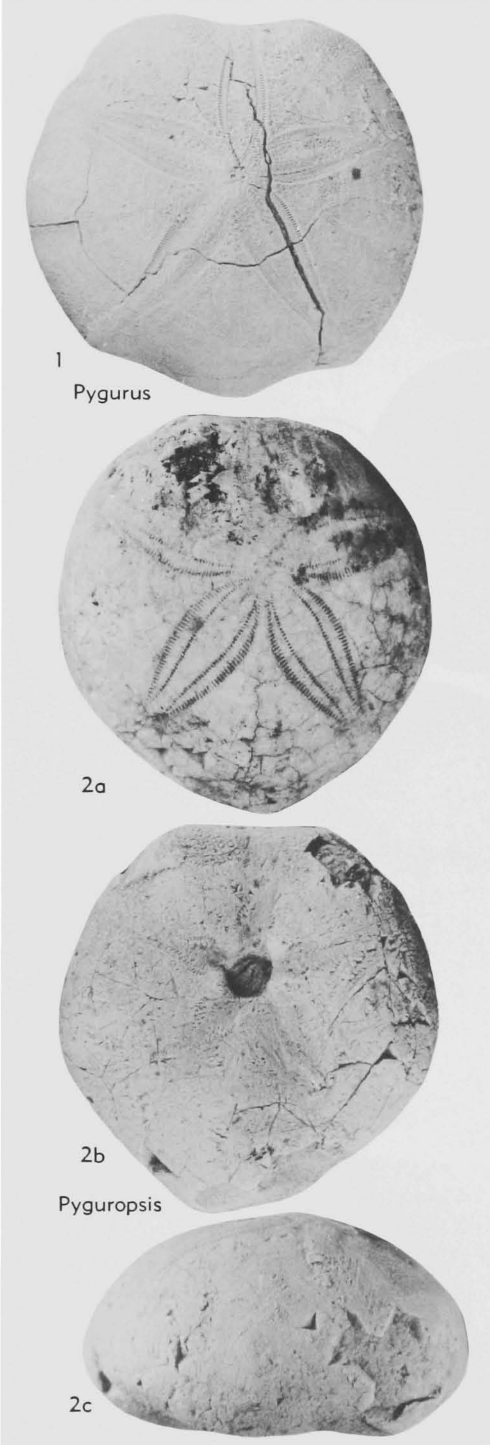



FIG. 387. Clypeidae (p. U499-U500).

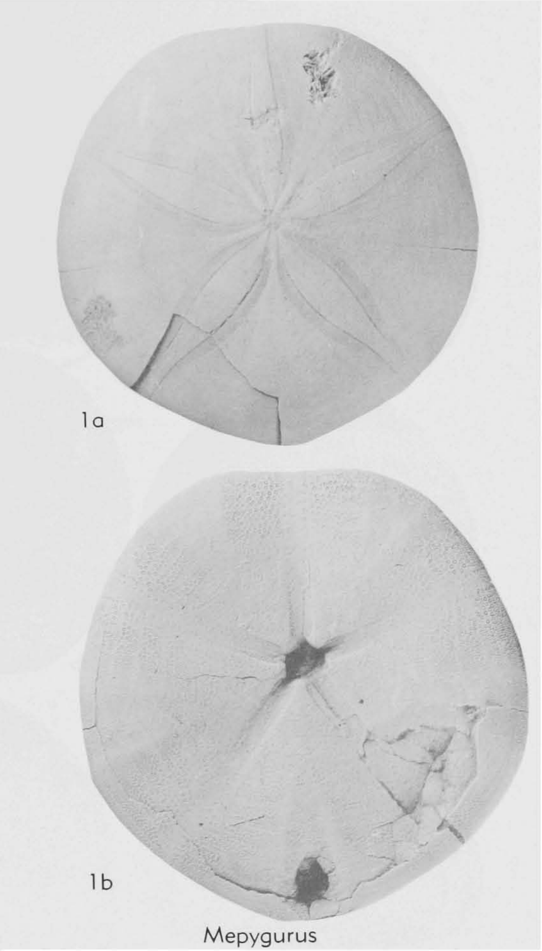



FIG. 388. Clypeidae (p. U499-U500).

**Nucleolites** LAMARCK, 1801, p. 347 [*N. scutatus LAMARCK, 1816, p. 36; SD LAMBERT, 1889] [=*Echinobrissus* GRAY, 1825, p. 429 (obj.); *Acromazus* POMEL, 1883, p. 58 (type, *Echinobrissus burgundiae* COTTEAU, 1871, p. 259); *Clitopygus* POMEL, 1883, p. 58 (type, *Echinobrissus lorioli* COTTEAU, 1871, p. 236); *Cluniculus* POMEL, 1883, p. 57 (type, *Nucleolites gracilis* L. AGASSIZ, 1840, p. 44); *Holcoepygus* POMEL, 1883, p. 58 (type, *Nucleolites elongatus* L. AGASSIZ, 1840, p. 4); *Lophopygus* POMEL, 1883, p. 57 (type, *Nucleolites cordatus* GOLDFUSS, 1826, p. 142); *Notopygus* POMEL, 1883, p. 58 (type, *Nucleolites amplus* L. AGASSIZ in AGASSIZ & DESOR, 1847, p. 96); *Taphropygus* POMEL, 1883, p. 59 (type, *Nucleolites subquadratus* L. AGASSIZ, 1839, p. 41); *Thigopygus* POMEL, 1883, p. 59 (type, *Echinobrissus humilis* GAUTHIER, 1875, p. 79); *?Heteronucleus* LAM-

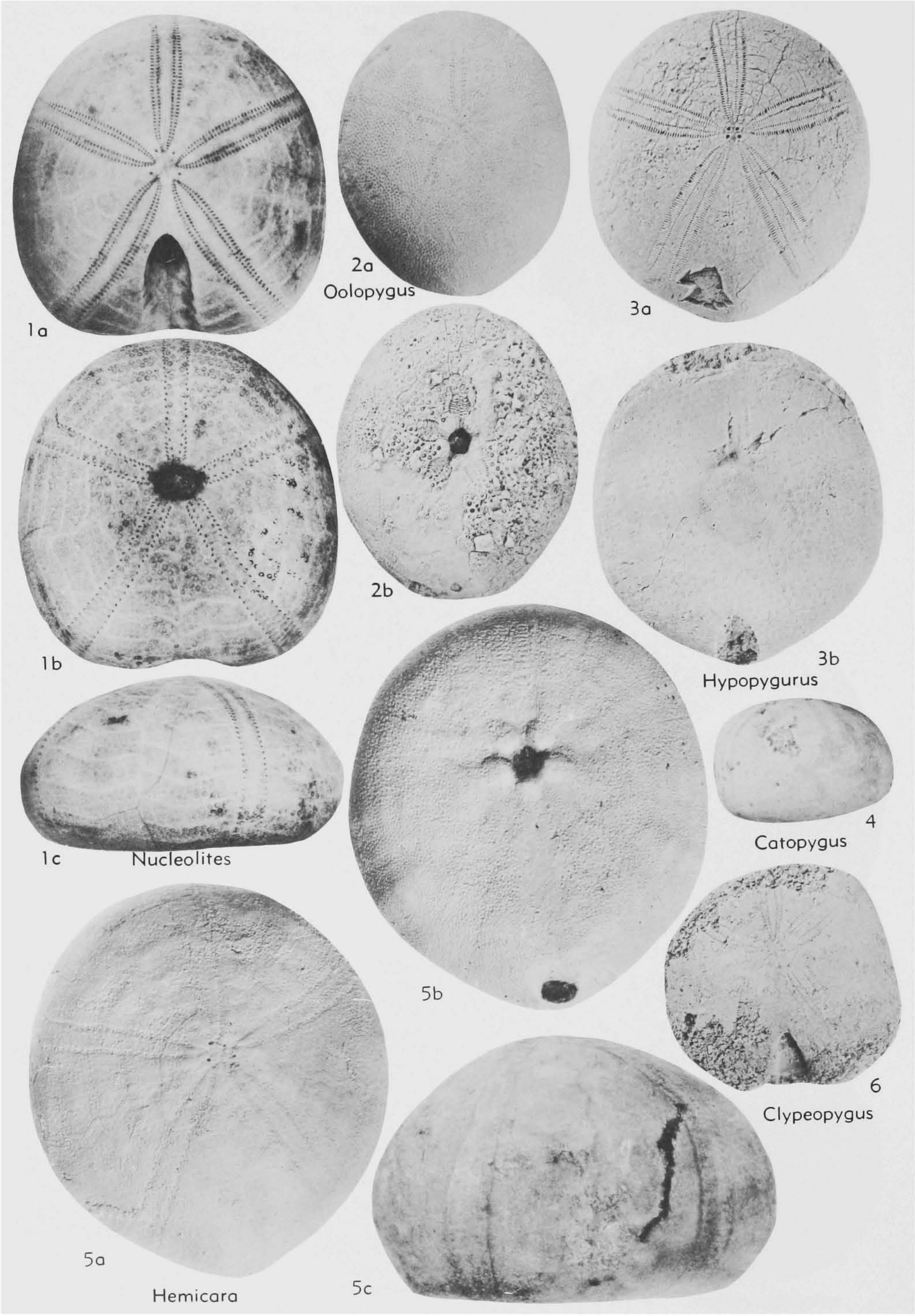



FIG. 389. Nucleolitidae (p. U501, U503, U505).

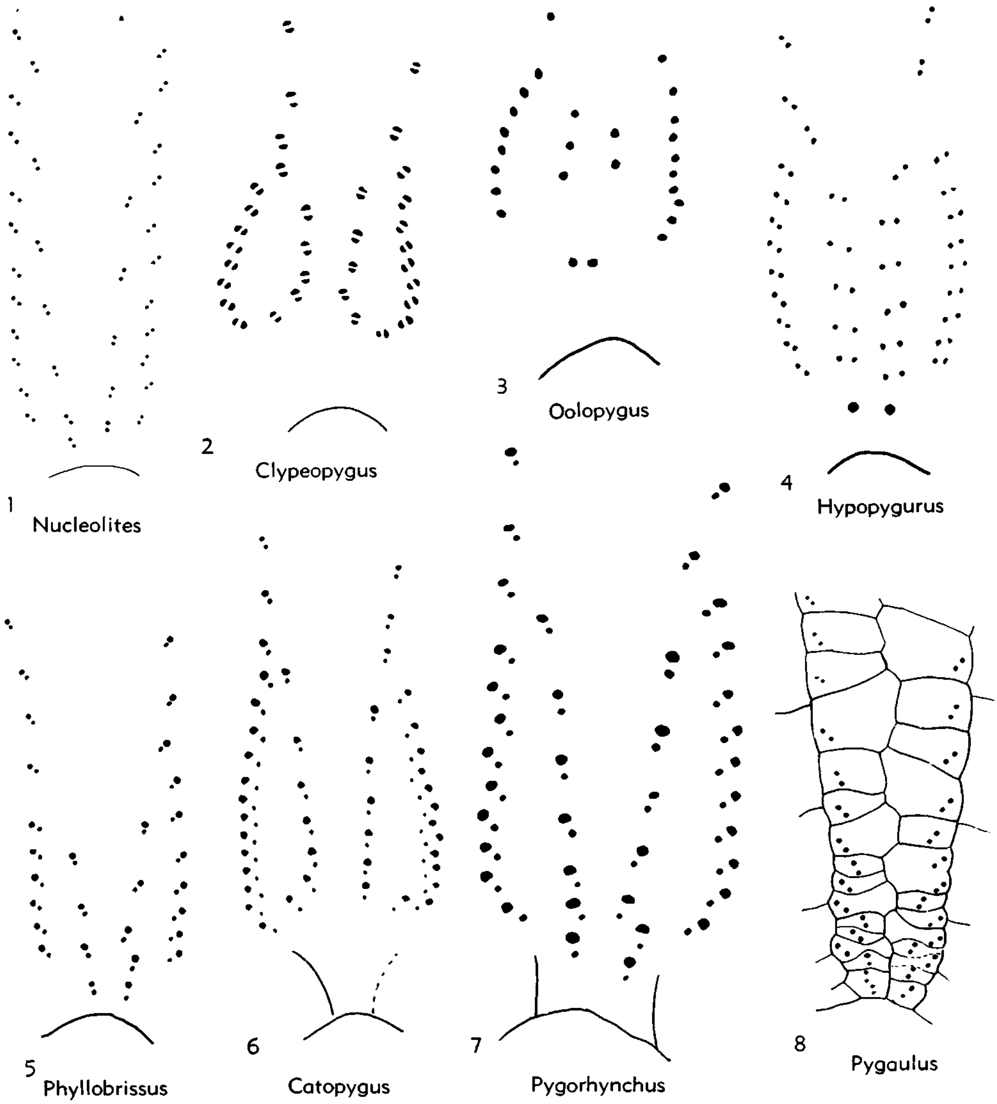



FIG. 390. Nucleolitidae (p. *U501*, *U503*, *U505-U506*).

BERT, 1911, p. 184 (type, *H. peroni*)]. Small to medium-sized, usually with greatest width posterior to center, thick margins; all ambulacral plates double-pored; no buccal pores. *M.Jur.(Bajoc.)-U. Cret.(Cenoman.)*, Eu.-Afr.——FIG. 389,*1*; 390,*1*. **N. scutatus* LAMARCK, U.Jur.(Oxford.), Fr.; 389,*1a-c*, aboral, oral, lat., ×2; 390,*1*, amb I phyllode, ×10 (98).

**Catopygus** L. AGASSIZ, 1836, p. 185 [**Nucleolites carinatus* GOLDFUSS, 1826, p. 142; SD COTTEAU, 1869, p. 121] [=*Penesticta* POMEL, 1883, p. 64 (type, *Oolopygus bargesii* D'ORBIGNY, 1856, pl. 976)]. Small, oval, highly inflated; 3 or 4 genital pores; petals flush, all ambulacral plates double-pored; periproct marginal; bourrelets well developed; phyllodes with 2 series of pore pairs in each half-ambulacrum, inner pore usually smaller than outer; no buccal pores. *U.Jur.(Kimmeridg.)-U. Cret.(Senon.)*, cosmop.——FIG. 389,*4*; 390,*6*; 391, *4*. **C. carinatus* (GOLDFUSS), U.Cret.(Cenoman.), Fr.; 389,*4*, lat., ×1; 390,*6*, amb V phyllode; 391, *4a,b*, aboral, oral, ×2 (98).

**Clypeopygus** D'ORBIGNY, 1856, p. 201 [**Clypeus paultrei* COTTEAU, 1851, p. 291; SD D'ORBIGNY,

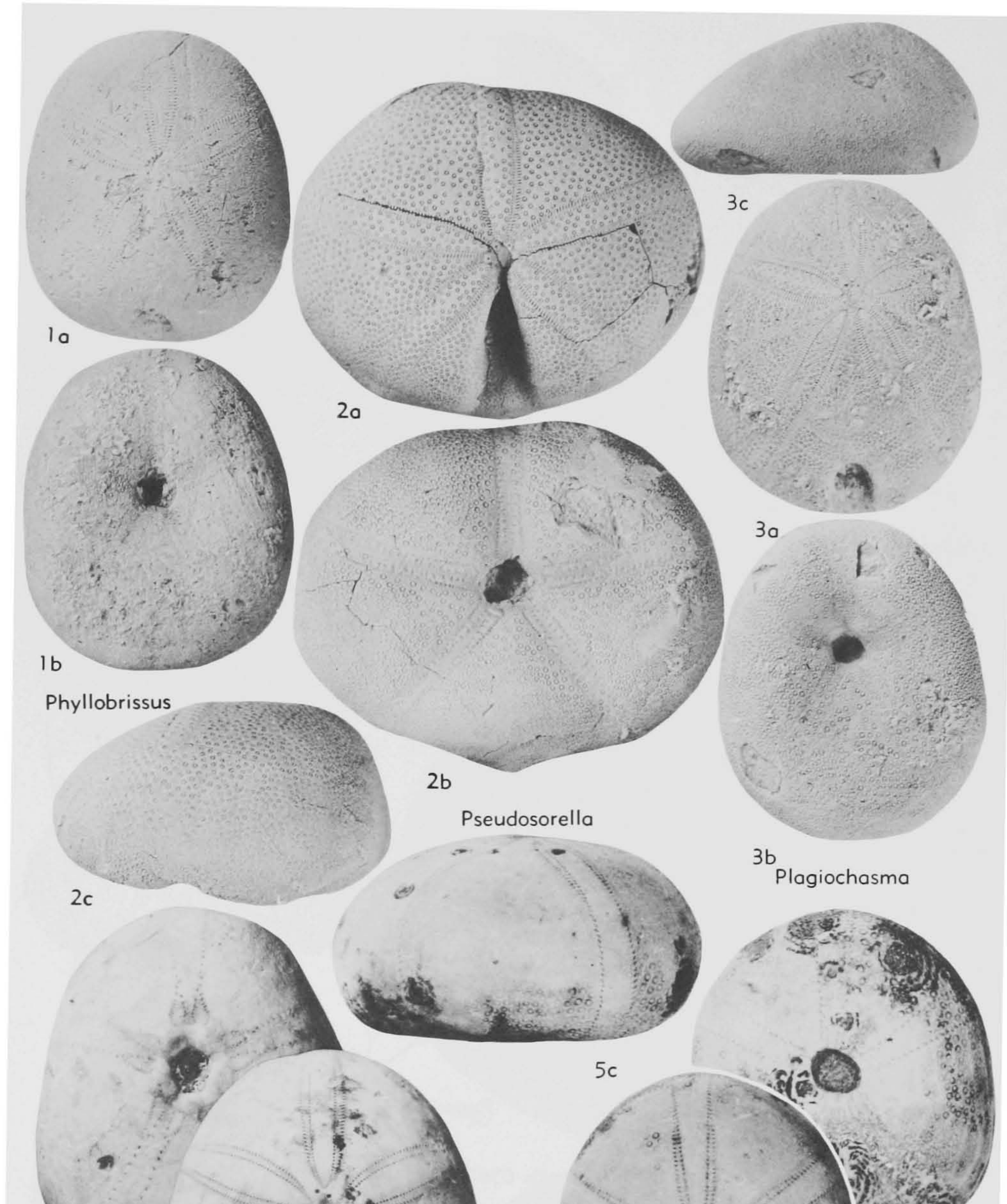



FIG. 391. Nucleolitidae (p. U503, U505-U506).

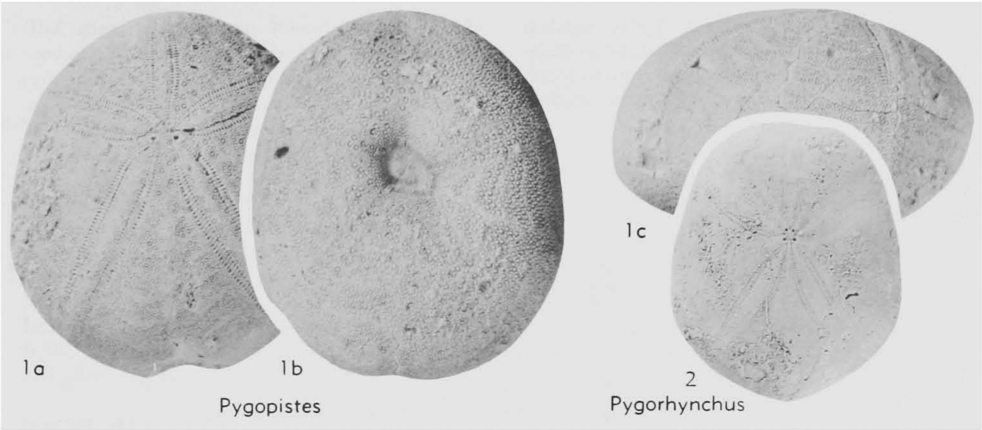



FIG. 392. Nucleolitidae (p. U506).

1858, p. 422]. Medium-sized, flat; all ambulacral plates double-pored; periproct supramarginal; bourrelets well developed; phyllodes broad, with 2 series in each half-ambulacrum; no buccal pores. *Cret.(Neocom.-Cenoman.)*, Eu.-Afr.——FIG. 389, *6*; 390,*2*. **C. paultrei* (COTTEAU), L.Cret.(Neocom.), Fr.; 389,*6*, aboral, ×1; 390,*2*, amb II phyllode (98).

**Hemicara** SCHLÜTER, 1902 [**H. pomeranum*; OD]. Medium-sized, petals very slightly developed, narrow; all ambulacral plates double-pored; periproct inframarginal; phyllodes widened; no buccal pores. *U.Cret.*, Eu.——FIG. 389,*5*. **H. pomeranum*, U. Cret., Pol.; *5a-c*, aboral, oral, post, ×2 (98).

**Hypopygurus** GAUTHIER, 1889, p. 37 [**H. gaudryi*; OD, M]. Low, elongate, pointed posterior margin; petals broad, open, straight poriferous zones, all ambulacral plates double-pored; periproct inframarginal; bourrelets well developed; phyllodes broadened, with pore pairs in 2 series in each half-ambulacrum; buccal pores. *U.Cret.(Cenoman.)*, Tunisia.——FIG. 389,*3*; 390,*4*. **H. gaudryi*; 389, *3a,b*, aboral, oral, ×1; 390,*4*, amb III phyllode, ×5 (98).

**Oolopygus** D'ORBIGNY, 1856, p. 976 [**O. pyriformis* D'ORBIGNY, 1856 (*non Echinites pyriformis* LESKE, 1778=*O. gracilis* LAMBERT, 1909, p. 20; SD COTTEAU, 1860)] [=?*Pseudonucleus* LAMBERT, 1920, p. 17 (type, *Pseudonucleus malladai* LAMBERT, 1920, p. 17)]. Small to medium-sized; elongate, highly inflated; 3 or 4 genital pores; petals slightly developed, flush, ambulacral plates beyond petals single-pored; periproct marginal; broad phyllodes; well-developed bourrelets; buccal pores. *U.Cret. (Senon.)*, Eu.——FIG. 389,*2*; 390,*3*. **O. gracilis* LAMBERT, Fr.; 389,*2a,b*, aboral, oral, ×2; 390,*3*, amb V phyllode, ×15 (98).

**Phyllobrissus** COTTEAU, 1859, p. 81 [**Catopygus gresslyi* L. AGASSIZ, 1839, p. 49; SD COTTEAU, 1860, p. 553] [=*Anthobrissus* POMEL, 1883, p. 60 (type, *Nucleolites cerceleti* DESOR in AGASSIZ & DESOR, 1847, p. 155); *Trochalia* POMEL, 1883 (type, *Echinobrissus requieni* DESOR in AGASSIZ & DESOR, 1847, p. 96) (*non* SHARPE, 1850); *Asterobrissus* DE LORIOL, 1888, p. 104 (*nom. van. pro Trochalia*)]. Small, slightly depressed adapically; petals of approximately equal length, all ambulacral plates double-pored; periproct slightly visible dorsally; bourrelets fairly well developed; phyllodes slightly broadened, inner pore of each pair reduced in size; no buccal pores. *U.Jur. (Kimmeridg.) - U. Cret.(Senon.)*, Eu.-India-USA. ——FIG. 390,*5*; 391,*1*. **P. gresslyi* (L. AGASSIZ), L.Cret.(Neocom.), Fr.; 390,*5*, amb IV phyllode, ×15; 391,*1a-c*, aboral, oral, ×2 (98).

**Plagiochasma** POMEL, 1883, p. 59 [**Nucleolites olfersii* L. AGASSIZ, 1836, p. 133; SD MELVILLE, 1952, p. 1] [=*Trematopygus* D'ORBIGNY, 1857, p. 374 (obj.); *Dochmostoma* DUNCAN, 1891, p. 176 (obj.)]. Small to medium-sized, elongate; petals usually unequal with petals V and I longer than others, all ambulacral plates double-pored; periproct supramarginal, longitudinal; bourrelets slightly developed; phyllodes slightly widened; no buccal pores. *Cret.(Neocom.-Senon.)*, Eu.-Afr.-USA.——FIG. 391,*3*. **P. olfersii* (L. AGASSIZ), L. Cret.(Hauteriv.), ?Fr.; *3a-c*, aboral, oral, lat., ×2 (98).

**Pseudosorella** ÉTALLON, 1859, p. 415 [**Desoria orbignyana* COTTEAU, 1855, p. 227; OD, M] [=*Neoclypeus* DE LORIOL, 1901, p. 33 (type, *N. syriacus*)]. Medium-sized to large, broad, inflated; petals broad, long, all ambulacral plates double-pored; periproct supramarginal, in contact with apical system; phyllodes slightly broadened, 2 series of pore pairs in each half-ambulacrum; no buccal pores. *U.Jur.(Raurac.)*, Eu.-Syria.——FIG. 391,*2*. **P. orbignyana* (COTTEAU), Fr.; *2a,b*, aboral, oral, lat., ×2 (98). [=*Pseudodesorella* COTTEAU, 1862, p. 124 (*nom. null.*).]

**Pygaulus** L. AGASSIZ, 1847, p. 158 [**P. desmoulinsii*; SD COTTEAU, 1869, p. 124]. Medium-sized;

elongate, sides usually parallel, highly inflated; petals broad, poriferous zones narrow, all ambulacral plates double-pored; periproct inframarginal; bourrelets slightly developed; phyllodes slightly developed, 2 series of pore pairs in each half-ambulacrum; no buccal pores. *Cret.(Neocom.-Cenoman.)*, Eu.——FIG. 390,*8*; 391,*5*. **P. desmoulinsii*, L.Cret.(Barrem.), Fr.; 390,*8*, phyllode, ×10; 391,*5a-c*, aboral, oral, lat., ×2 (98).


FIG. 393. Echinolampadidae (p. *U*506-*U*508).

**Pygopistes** POMEL, 1883, p. 56 [**Catopygus floridus* COQUAND *(nom. nud.)* (=*Pygaulus coquandi* COTTEAU, 1869, p. 243); OD, M]. Highly inflated; apical system very far forward; petals long, all ambulacral plates double-pored; periproct marginal; peristome oblique; bourrelets slightly developed; phyllodes slightly broadened, 2 series of pore pairs in each half-ambulacrum; no buccal pores. *U.Cret.(Cenoman.)*, Afr.——FIG. 392,*1*. **P. coquandi* (COTTEAU); *1a-c*, aboral, oral, lat., ×2 (98).

**Pygorhynchus** L. AGASSIZ, 1839, p. 53 [**Catopygus obovatus* L. AGASSIZ, 1836, p. 136; SD LAMBERT, 1898, p. 162] [=*Botriopygus* D'ORBIGNY, 1856, p. 334 (type, *Catopygus obovatus* L. AGASSIZ, 1836, p. 136; *Bothriopygus* GAUTHIER in MORGAN, 1902 *(nom. null.)*]. Medium-sized to large, greatest width posterior to center; petals well developed, all ambulacral plates double-pored; periproct marginal to inframarginal; peristome regular or oblique; bourrelets well developed; phyllodes slightly broadened, 2 series of pore pairs in each half-ambulacrum; no buccal pores. *L.Cret.(Neocom.-Alb.)*, Eu.-Afr.-N.Am.——FIG. 390,*7*; 392,*2*. **P. obovatus* (L. AGASSIZ), L.Cret.( Neocom.), Switz.; 390,*7*, amb III phyllode, ×15; 392,*2*, aboral, ×1 (98).

## Family ECHINOLAMPADIDAE Gray, 1851

Medium-sized to large, usually highly inflated; apical system tetrabasal or monobasal; petals long, open, usually with unequal poriferous zones, single pores in ambulacral plates beyond petals; periproct marginal to inframarginal, transverse or longitudinal; bourrelets well developed; phyllodes widened, with few or many pores; narrow, naked, granular zone in interambulacrum 5; buccal pores. *Cret.(Cenoman.)-Rec.*

**Echinolampas** GRAY, 1825, p. 429 [**Echinus oviformis* GMELIN, 1789, p. 3187; SD POMEL, 1883, p. 62] [=*Hypsoclypus* POMEL, 1869, p. 25 (type, *Conoclypus lucae* DESOR in AGASSIZ & DESOR, 1847, p. 168 =*C. plagiosomus* L. AGASSIZ, 1840, p. 5); *Palaeolampas* BELL, 1880, p. 43 (type, *P. crassa*); *Merolampas* POMEL, 1883, p. 63 (type, *Echinolampas mattsensis* QUENSTEDT, 1830, p. 489); *Miolampas* POMEL, 1883, p. 62 (type, *Echinolampas depressa* GRAY, 1851, p. 448); *Sphelatus* POMEL, 1883, p. 54 (type, *Caratomus lehoni* COTTEAU, 1880, p. 25); *Euechinolampas* POMEL, 1887,

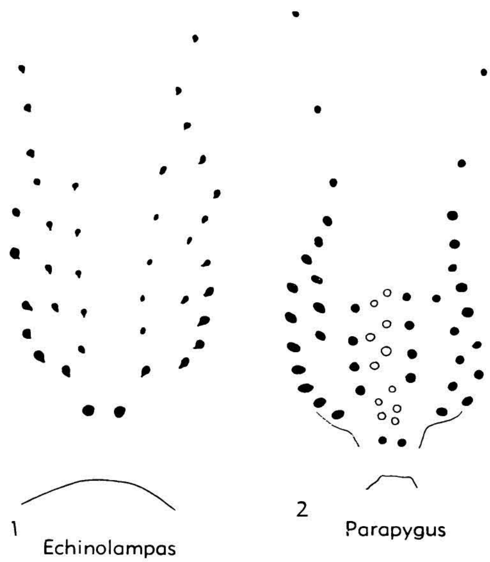



FIG. 394. Echinolampadidae (p. U506-U508).

p. 127 (type, *Echinolampas florescens* POMEL, 1883, p. 26); *Palaeolampas* POMEL, 1887 (*non* BELL, 1880); *Craterolampas* COTTEAU, 1891, p. 186 (type, *Echinolampas raulini* COTTEAU, 1863, p. 107); *Heteroclypeus* COTTEAU, 1891, p. 104 (type, *Galerites semiglobus* LAMARCK, 1816, p. 311); *Progonolampas* BITTNER, 1892, p. 357 (type, *P. novae hollandae* =*Echinolampas posterocrassus* GREGORY, 1890, p. 483); ?*Aplolampas* LAMBERT, 1906, p. 32 (type, *Echinolampas montevialensis* SCHAUROTH, 1865, p. 191); *Cypholampas* LAMBERT, 1906, p. 33 (type, *Clypeaster stelliferus* LAMARCK, 1816, p. 16); *Isolampas* LAMBERT, 1906, p. 33 (type, *Echinolampas goujoni* POMEL, 1888, p. 376); *Macrolampas* LAMBERT, 1906, p. 33 (type, *Clypeaster hemisphericus* LAMARCK, 1816, p. 293); *Scutolampas* LAMBERT, 1906, p. 33 (type, *Conoclypus plagiosomus* L. AGASSIZ, 1840, p. 5); *Psammolampas* LAMBERT, 1913, p. 136 (type, *Echinolampas scutiformis* DESMOULINS, 1837, p. 348); *Libyolampas* LAMBERT, 1914, p. 112 (type, *Echinolampas africanus* DE LORIOL, 1888, p. 34); *Cylindrolampas* LAMBERT, 1918, p. 44 (type, *Echinolampas subcylindricus* DESOR, 1853, p. 277); *Oeidolampas* LAMBERT, 1918, p.

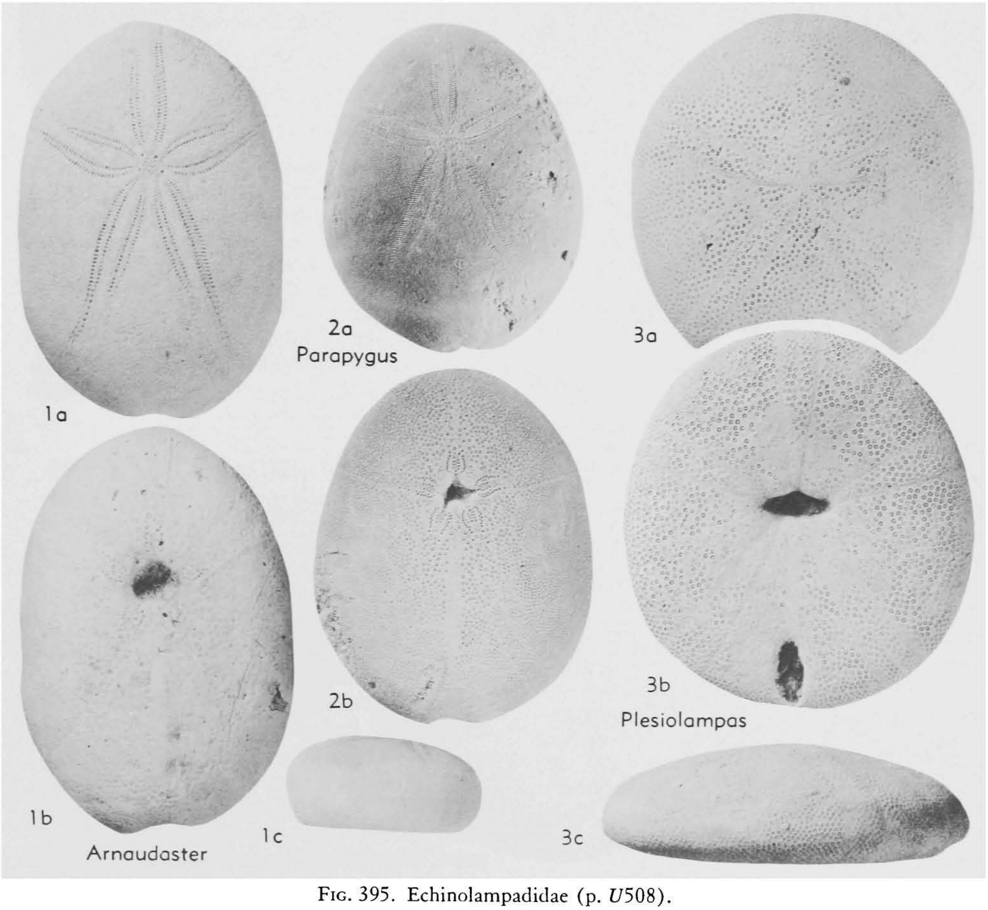
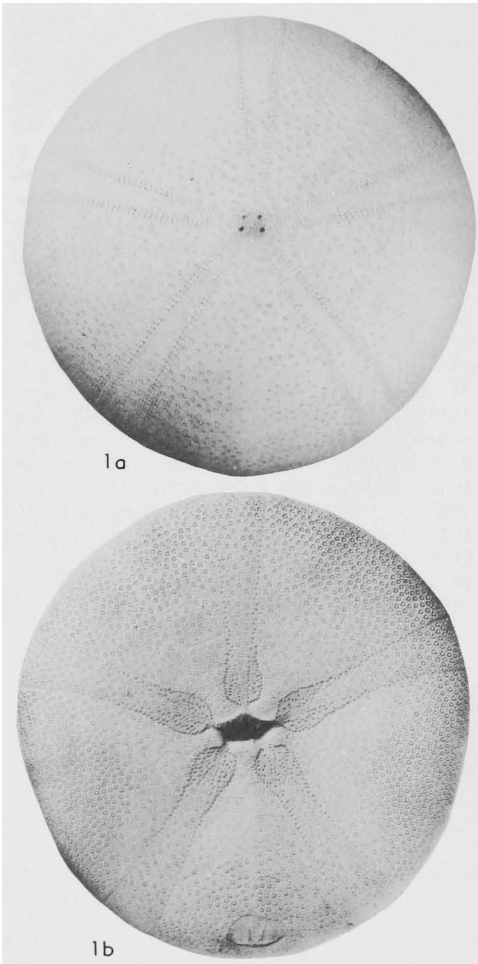



FIG. 395. Echinolampadidae (p. U508).




Conolampas

FIG. 396. Echinolampadidae (p. U508).

44 (type, *Echinolampas ataxensis* COTTEAU, 1890, p. 80); *Politolampas* LAMBERT, 1918, p. 45 (type, *Clypeaster politus* LAMARCK, 1816, p. 293); *Planilampas* MORTENSEN, 1948, p. 297 (type, *Echinolampas sternopetala* AGASSIZ & CLARKE, 1907, p. 130); *Hypsoheteroclypeus* SZÖRÉNYI, 1953, p. 76 (type, *Hypsoclypus doma* POMEL, 1887, p. 163)]. Medium-sized to large, usually inflated; apical system monobasal; poriferous zones usually unequal, wide interporiferous zones. *Eoc.-Rec.*, cosmop.——FIG. 393,*1*; 394,*1*. **E. oviformis* (GMELIN), Rec., Ind.Ocean; 393,*1a-c*, aboral, oral, lat., ×1; 394,*1*, amb IV phyllode, ×8 (98). [=*Conolampas* POMEL, 1883, p. 63 (*non* AGASSIZ, 1883) (type, *Echinolampas fraasi* DE LORIOL, 1880); *Pachylampas* LAMBERT, 1918 (*nom. van. pro Macrolampas*, obj.)]

**Arnaudaster** LAMBERT, 1918, p. 32 [**A. gauthieri* LAMBERT, 1920, p. 152; SD LAMBERT, 1920, p. 152]. Medium-sized, elongate, cylindrical; petals well developed, unequal poriferous zones; periproct marginal, longitudinal; phyllodes slightly broadened. *U.Cret.(Cenoman.)*, Fr.——FIG. 395, *1*. **A. gauthieri* LAMBERT; *1a,b*, aboral, oral, ×2; *1c*, lat., ×1 (98).

**Conolampas** A. AGASSIZ, 1883, p. 48 [**Conoclypus sigsbei* A. AGASSIZ, 1878, p. 190; OD, M]. Large, high, circular; apical system monobasal; petals long, straight, with narrow poriferous zones; periproct inframarginal; bourrelets well developed; phyllodes with many pores. *Rec.*, W. Indies.——FIG. 396,*1*. **C. sigsbei* (A. AGASSIZ), Rec., W. Indies; *1a,b*, aboral, oral, ×1 (98).

**Parapygus** POMEL, 1883, p. 61 [**Botriopygus cotteauanus* D'ORBIGNY, 1856, p. 341; SD LAMBERT, 1898, p. 162] [=*Pseudocatopygus* COTTEAU & GAUTHIER, 1895, p. 62 (type, *P. longior*); *Rostropygus* SZÖRÉNYI, 1955, p. 66 (type, *R. annae*)]. Medium-sized to large, with well-rounded margin; apical system tetrabasal; petals well developed; periproct marginal, longitudinal; bourrelets well developed; phyllodes broadened. *U.Cret.(Turon.-Senon.)*, Eu.-Afr.——FIG. 394,*2*; 395,*2*. **P. cotteauanus* (D'ORBIGNY), Fr.; 394,*2*, amb IV phyllode, ×5; 395,*2a,b*, aboral, oral, ×1 (98).

**Plesiolampas** DUNCAN & SLADEN, 1882, p. 9 [**P. elongata*; OD, M] [=*Oriolampas* MUNIER-CHALMAS, 1882 (type, *Amblypygus michelini* COTTEAU, 1856, p. 335)]. Medium-sized to large, low; apical system monobasal; petals long, open, unequal poriferous zones; periproct inframarginal, longitudinal; bourrelets well developed. *Paleoc.-Eoc.*, India-Afr.-Eu.-Tasmania.——FIG. 395,*3*. *P. placenta* DUNCAN & SLADEN, Paleoc., India; *3a-c*, aboral, oral, lat., ×1 (98).

?**Pygastrides** LOVÉN, 1888 [**P. relictus*; OD, M]. Based on immature specimen; generic characters not known.

## Family FAUJASIIDAE Lambert, 1905

[*nom. correct.* KIER, herein (*pro* Faujasidae LAMBERT, 1905, p. 13)]

Small to large, commonly broad, flat oral surface; apical system monobasal or tetrabasal; periproct supramarginal or inframarginal; petals equal, broad, closed (except in *Australanthus*), outer pore slitlike; single pore in all ambulacral plates beyond petals; bourrelets strongly developed; phyllodes very wide; buccal pores; naked granular zone in interambulacrum 5. *U.Cret.-Eoc.*

**Faujasia** D'ORBIGNY, 1856, p. 290 [**Pygurus apicalis* DESOR, 1847, p. 162; SD LAMBERT & THIÉRY, 1921, p. 273]. Small to medium-sized, blunt anterior, pointed posterior; apical system monobasal,

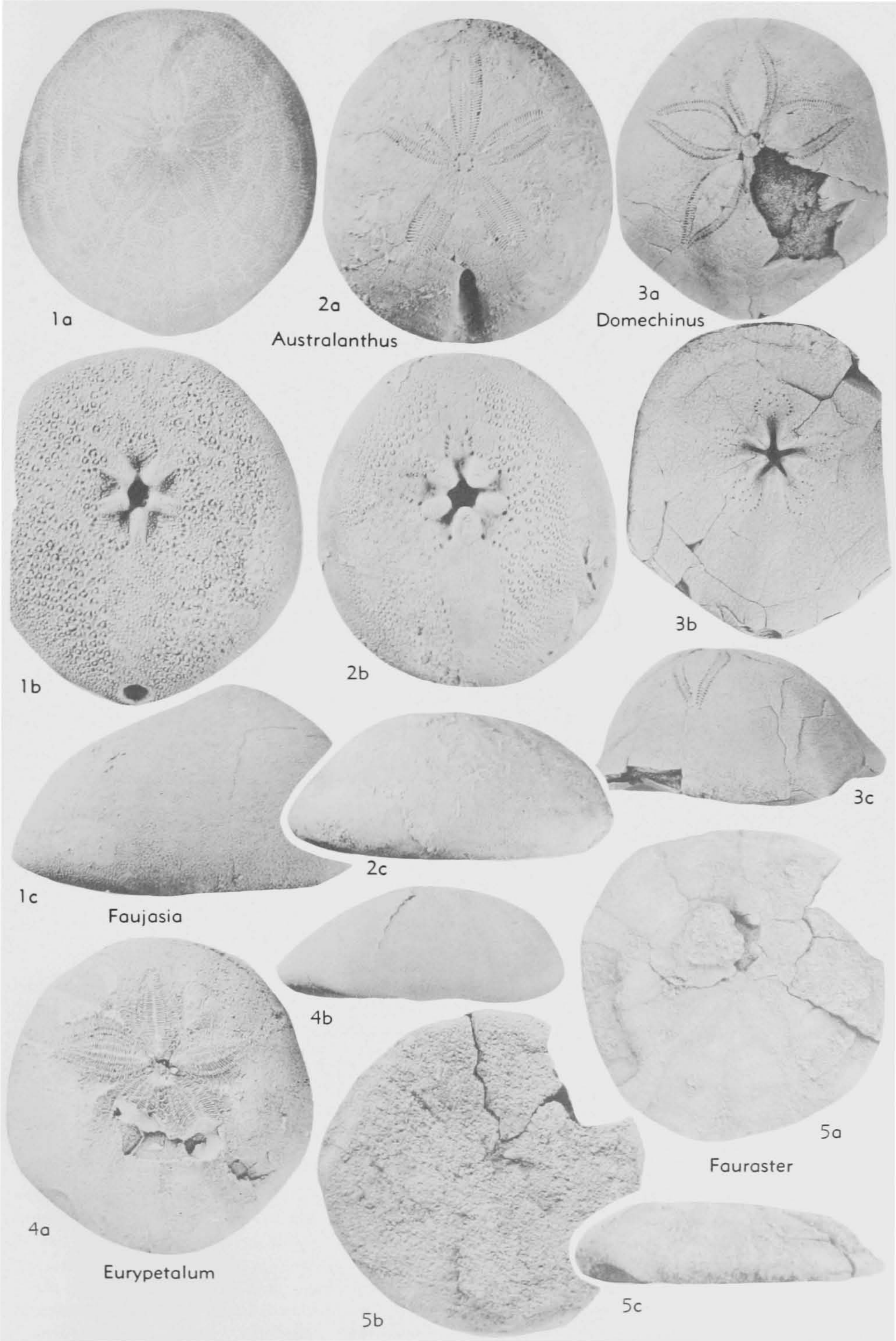



FIG. 397. Faujasiidae (p. U510, U512).

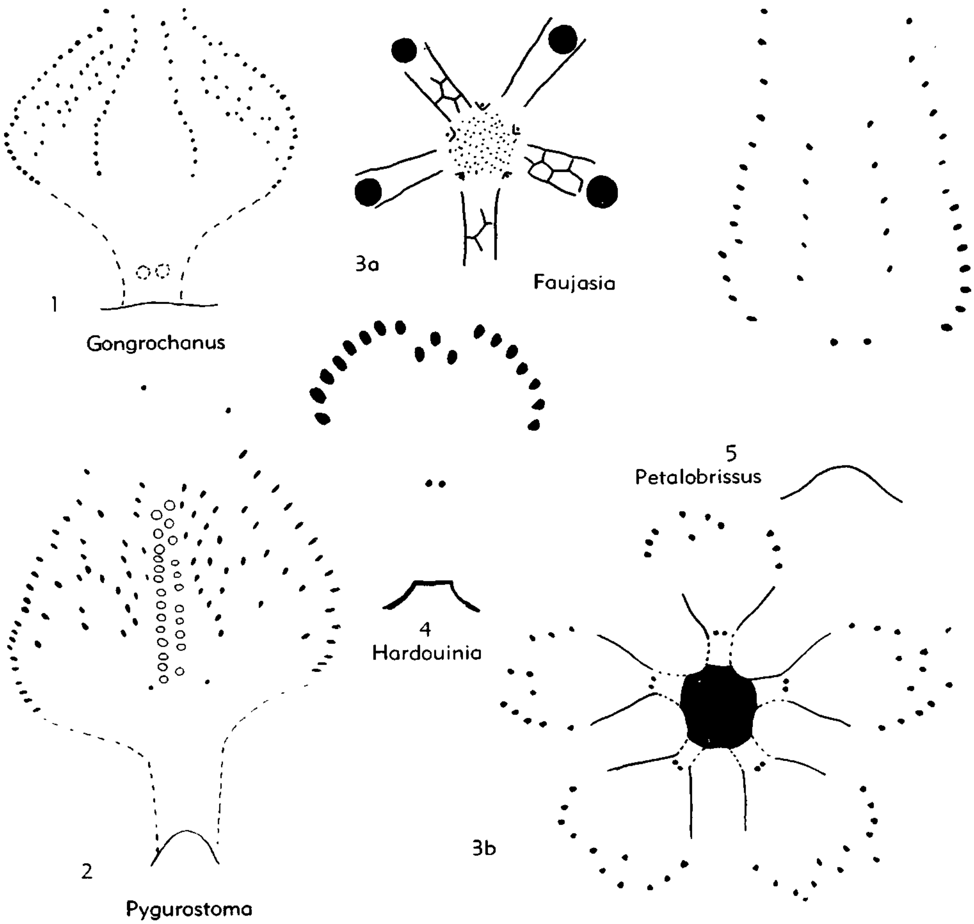



FIG. 398. Faujasiidae (p. U510, U512).

genital pores in interambulacra; petals short, broad, equal, closed; periproct inframarginal, transverse; phyllodes with pores arranged in arc. *U.Cret.* *(Maastricht.),* Eu.——FIG. 397,*1*; 398,*3*. **F.* *apicalis* (DESOR), Belg.; 397,*1a-c,* aboral, oral, lat., ×2; 398,*3a,b,* apical system, phyllodes, ×15, ×6 (98).

**Australanthus** BITTNER, 1892, p. 350 [**Cassidulus longianus* GREGORY, 1890, p. 482; OD]. Medium-sized, oval, moderately inflated; apical system monobasal; petals broad, short, open, pores strongly conjugate with equal poriferous zones, periproct supramarginal, longitudinal; phyllodes with few pores; adorally tubercles much larger. *U.Eoc.,* Australia.——FIG. 397,*2*. **A. longianus* (GREGORY), Janjukian; *2a-c,* aboral, oral, lat., ×1 (98).

**Domechinus** KIER, 1962, p. 141 [**Faujasia chelonium* COOKE, 1953, p. 14; OD]. Medium-sized, highly inflated; apical system monobasal; petals broad, equal, closed; periproct marginal to inframarginal, transverse; phyllodes with two series of pores in each half-ambulacrum. *U. Cret.* *(Maastricht.),* USA.——FIG. 397,*3*. **D. chelonium* (COOKE), USA(Tex.); *3a-c,* aboral, oral, lat., ×1.5 (98).

**Eurypetalum** KIER, 1962, p. 140 [**Echinolampas faujasia* DESMOULINS, 1837, p. 346; OD]. Medium-sized, blunt anterior, pointed posterior, aboral surface moderately inflated, flat adoral; apical system tetrabasal, genital pores in genital plates; petals broad, closed, equal; periproct inframarginal, transverse; phyllodes broad. *U. Cret.(Senon.-*

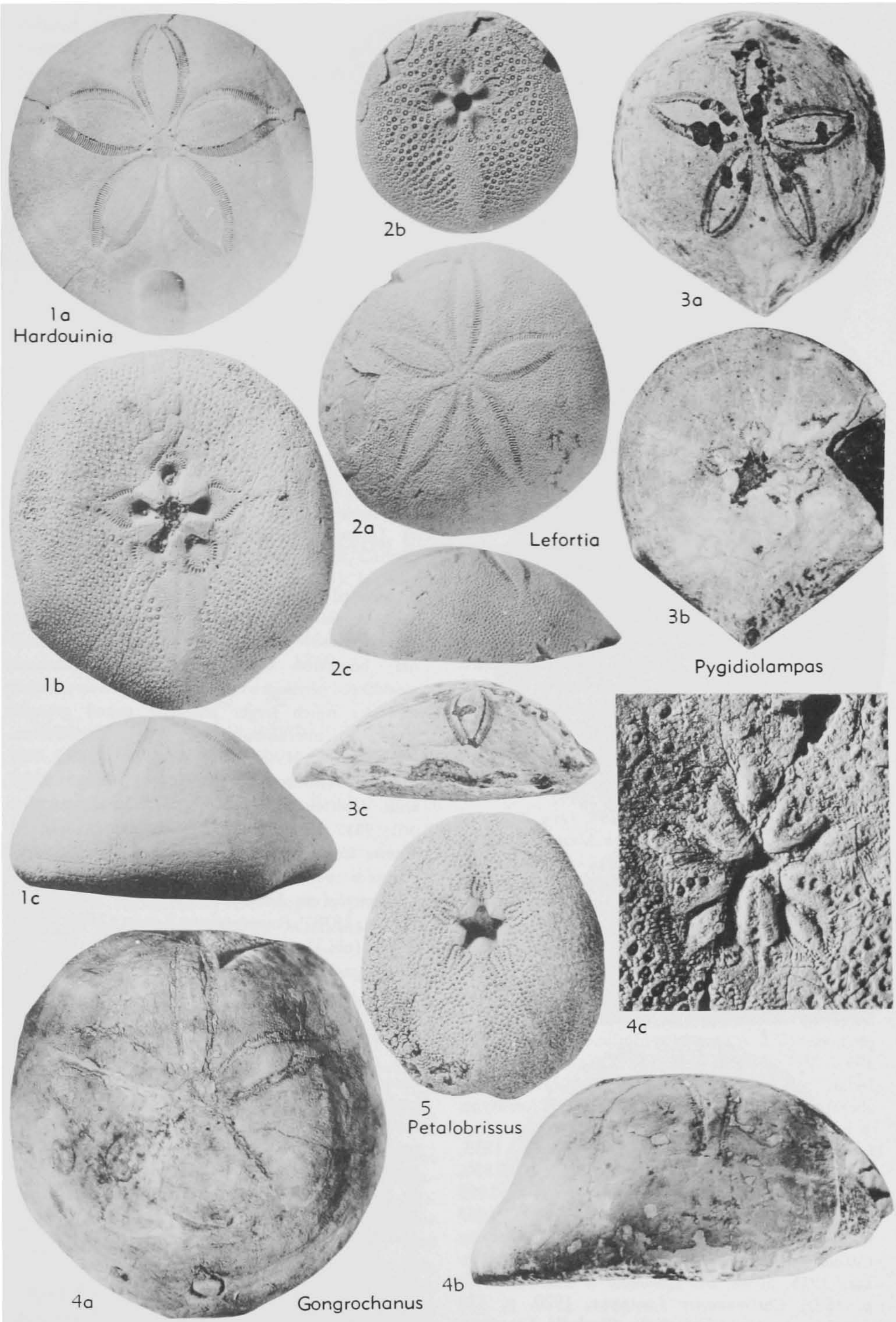



FIG. 399. Faujasiidae (p. U512-U513).

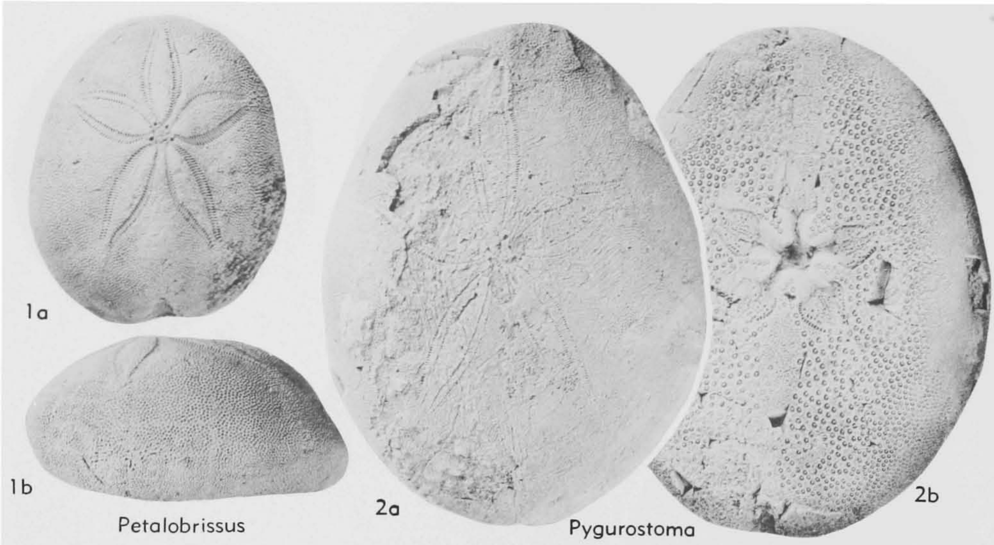



FIG. 400. Faujasiidae (p. U512-U513).

*Maastricht.),* Eu.——FIG. 397,*4*. **E. faujasii* (DESMOULINS), Maastricht., Belg.; *4a,b,* aboral, lat., ×1.5 (98).

**Fauraster** LAMBERT in LAMBERT & THIÉRY, 1924, p. 396 [**F. priscus*; OD]. Small, flattened; apical system tetrabasal; petals broad, equal, wide interporiferous zones; periproct supramarginal, broad bourrelets strongly developed, toothlike. *U.Cret. (Maastricht.),* Spain.——FIG. 397,*5*. **F. priscus,* Spain; *5a-c,* aboral, oral, lat., ×2 (98).

**Gongrochanus** KIER, 1962, p. 131 [*pro Cyrtoma* M'CLELLAND, 1840, p. 185 (*non* MEIGEN, 1824)] [**Cyrtoma herscheliana* M'CLELLAND, 1840, p. 185; OD]. Large, broad, aboral surface highly inflated with posterior truncated, oral surface flat; apical system tetrabasal, 3 genital pores in type-species; petals broad, outer pore slitlike; periproct supramarginal, longitudinal, in notch; phyllodes very broad with many pores; prominent bulge in median area of each ambulacrum in phyllode. *U.Cret.(Senon.),* India.——FIG. 398,*1*; 399,*4*. **G. herscheliana* (M'CLELLAND), Senon., India; 398,*1,* amb V phyllode, ×?; 399,*4a,b,* aboral, lat., ×1; 399,*4c,* floscelle of paratype, ×1 (98).

**Hardouinia** HAIME in D'ARCHIAC & HAIME, 1853, p. 214 [**Pygorhynchus mortonis* MICHELIN, 1850, p. 240; OD, M] [=*Gonioclypeus* EMMONS, 1858 (type, *G. subangulata*); *Harduinia* POMEL, 1883 *(nom. null.)*; *Clarkiella* LAMBERT, 1916 (type, *Cassidulus conoideus* CLARK in CLARK & TWITCHELL, 1915, p. 80; SD LAMBERT & THIÉRY, 1921, p. 369); *Cossmanaster* LAMBERT, 1920, p. 138 *(nom. van. pro Clarkiella)*; *Clarkella* LAMBERT, 1920 (*non* WALCOTT, 1908) *(nom. null.)*]. Medium-sized to large, commonly highly inflated, oral side flat; apical system tetrabasal; petals very broad, closed; periproct supramarginal, longitudinal; bourrelets strongly developed, commonly toothlike; phyllodes moderately to very wide; tubercles much larger adorally; naked granular zone in interambulacrum 5. *U.Cret.(Turon.-Maastricht.),* N.Am.——FIG. 398,*4*; 399,*1*. **H. mortonis* (MICHELIN), Maastricht., Miss.; 398,*4,* amb V phyllode, ×6; 399,*1a-c,* aboral, oral, lat., ×1 (98).

**Lefortia** COSSMANN, 1901 (Jan.), p. 58 [**Pomelia delgadoi* DE LORIOL, 1900, p. 67; OD, M] [=*Pomelia* DE LORIOL, 1900, p. 66 (obj.) (*non* ZITTEL, 1878); *Pomelopsis* DE LORIOL, 1901 (May), p. 45 (obj.)]. Small, low, broad, flat, oral surface; apical system tetrabasal, genital pores in genital plates; petals long, broad, closed; periproct marginal, longitudinal; phyllodes broad. *U.Cret. (Senon.),* Eu.-India-Afr.-N.Am.——FIG. 399,*2*. **L. delgadoi* (DE LORIOL), Senon., Port.; *2a-c,* aboral, oral, lat., ×2 (98).

**Petalobrissus** LAMBERT, 1916, p. 82 [**Echinobrissus setifensis* COTTEAU, 1866, p. 267; OD]. Small to medium-sized; apical system tetrabasal, 4 genital pores; petals broad, equal; periproct supramarginal to marginal, longitudinal; phyllodes broad; naked median zone in interambulacrum 5. *U.Cret. (Cenoman.-Maastricht.),* Afr.-N.Am.——FIG. 398, *5*; 399,*5*; 400,*1*. **P. setifensis* (COTTEAU), Maastricht., Algeria; 398,*5,* amb I phyllode, ×15; 399,*5,* oral, ×2; 400,*1a,b,* aboral, lat., ×2 (98).

**Pygidiolampas** CLARK, 1923, p. 345 [**P. eurynota*; OD]. Medium-sized, broad, circular except for pointed posterior extremity; aboral surface inflated, oral side flat; apical system tetrabasal; petals broad, equal, closed, with very wide interporiferous zones; periproct inframarginal, longitudinal; bourrelets strongly developed, toothlike; phyllodes very broad. *U.Cret.(Campan.),* N.Am.——FIG. 399,*3*. **P. eurynota*, Campan., USA(S.Car.); *3a-c,* aboral, oral, lat., ×1 (98).

**Pygurostoma** COTTEAU & GAUTHIER, 1895, p. 51 [**P. morgani*; OD, M]. Medium-sized to large, low; apical system tetrabasal; periproct marginal to inframarginal, longitudinal; petals broad, equal, closed; phyllodes broad, with many pores. *U.Cret. (Senon.),* S.Am.-Asia(Iran).——FIG. 398,*2*; 400, *2*. **P. morgani,* Senon., Iran; 398,*2,* amb V phyllode, ×6; 400,*2a,b,* aboral, oral, ×1 (98).

**Stigmatopygus** D'ORBIGNY, 1856, p. 331 [**S. galeatus*; SD LAMBERT & THIÉRY, 1921, p. 363]. Medium-sized to large, aborally inflated, orally flattened; apical system tetrabasal; petals broad, equal, closed; periproct supramarginal, longitudinal, high on oblique posterior truncation with deep transverse groove ventral to opening; phyllodes very broad. *U.Cret.(Cenoman.-Senon.),* Eu.-Afr.——FIG. 401,*1*. *S. lamberti* BESAIRIE, Campan., Madag.; *1a-d,* aboral, oral, lat., post., ×1 (98).

## Family ARCHIACIIDAE Cotteau & Triger, 1869

[*nom. correct.* KIER, herein (*pro* Archiacidae COTTEAU & TRIGER, 1869, p. 426)]

Medium-sized, highly inflated; apical system tetrabasal, very anterior; periproct inframarginal, longitudinal; peristome very eccentric anteriorly, longitudinal; petals broad, closed, petal III absent or very short, with doubling of pores; single or double pores in ambulacral plates beyond petals; bourrelets moderately developed; phyllodes slightly widened; with or without buccal pores. *Cret.*

**Archiacia** L. AGASSIZ, 1847, p. 159 [**A. sandalina*; SD D'ORBIGNY, 1856, p. 284]. Medium-sized, high, oral surface flat; double pores in ambulacral plates beyond petals. *Cret.(Neocom.-Cenoman.),* Eu.-Afr.——FIG. 402,*1a-c*. **A. sandalina,* Cenoman., Fr.; *1a-c,* aboral, oral, lat., ×2 (98).——FIG. 402, *1d*. *A. saadensis* PERON & GAUTHIER, Cenoman., Tunisia; amb II phyllode, ×8 (98).

**Gentilia** LAMBERT, 1918, p. 35 [**G. tafileltensis*; SD LAMBERT, 1920, p. 154] [=*Thomasia* LAMBERT, 1918 (type, *Archiacia araidahensis* GAUTHIER, 1889, p. 18) (*non* POCHE, 1908); *Thomasaster* LAMBERT, 1920, p. 138 (*nom. van. pro Thomasia*)]. Medium-sized, high, oral surface flat; single pores in phyllodes beyond petals. *U.Cret. (Cenoman.),* Afr.——FIG. 402,*2*. *G. syriensis* KIER, Syria; *2a-c,* aboral, oral, lat., ×1.5; *2d,* amb IV phyllode, ×10 (98).

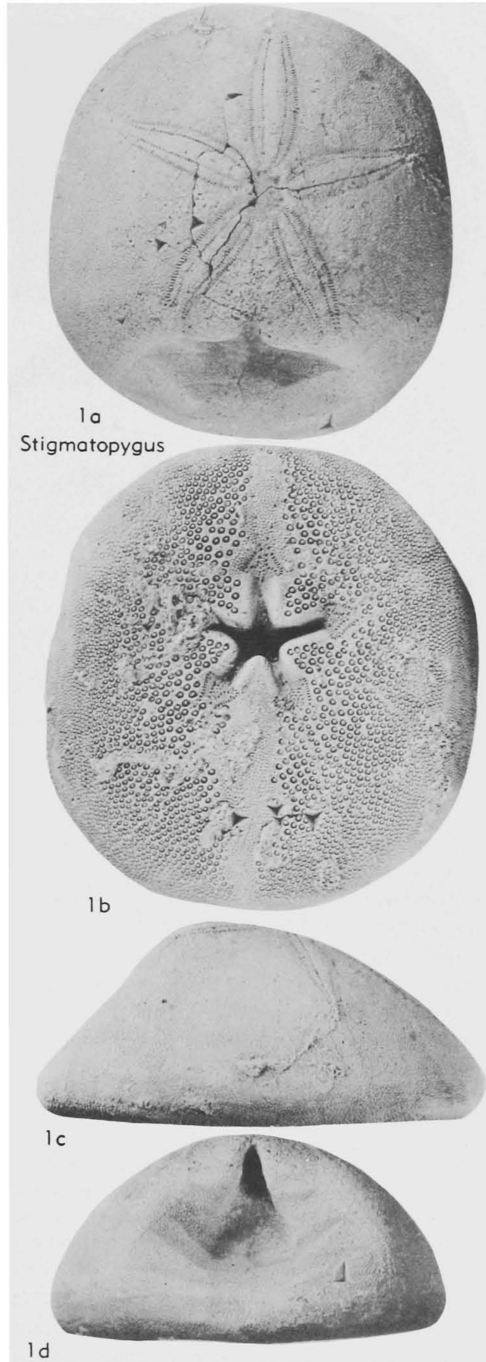



FIG. 401. Faujasiidae (p. U513).

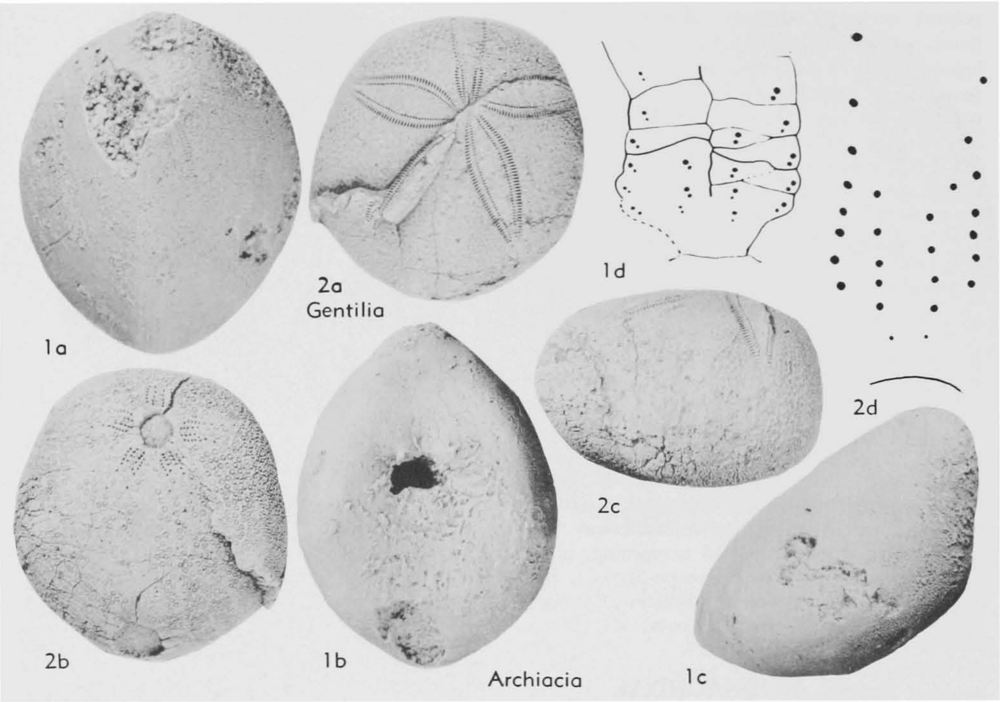



FIG. 402. Archiaciidae (p. U513).

## Family CASSIDULIDAE L. Agassiz & Desor, 1847

Small to large, oral surface flat; apical system monobasal or tetrabasal; periproct supramarginal to marginal, longitudinal or transverse; peristome transverse; petals broad, usually equal, commonly inconspicuous, ambulacral plates double-pored in pre-Senonian species; bourrelets well developed; buccal pores absent in pre-Senonian species; tubercles much larger adorally, naked zone in interambulacrum 5 adorally. *L.Cret.-Rec.*

**Cassidulus** LAMARCK, 1801, p. 348 [**C. cariboearum*; OD, M] [=*Glossaster* LAMBERT, 1918, p. 39 (type, *Cassidulus sorigneti* COTTEAU, 1887, p. 512)]. Small; apical system monobasal; petals straight, open, ambulacral plates beyond petals single-pored; periproct supramarginal; phyllodes with few pores; buccal pores present. *Eoc.-Rec.*, cosmop.——FIG. 403,*1*; 404,*2*. **C. cariboearum*, Rec., W.Indies; 403,*1a-c*, aboral, oral, lat., ×2; 404,*2*, amb I phyllode, ×13 (98).

**Hypsopygaster** BAJARUNAS, 1915, p. 230 [**H. ungosensis*; OD, M]. Small, posterior margin truncated with periproct high on truncation; apical system monobasal with three genital pores, no pore in left anterior genital plate; petals slightly developed, ambulacral plates single-pored beyond petals; bourrelets toothlike; phyllodes broad with few pores; buccal pores present. *Paleoc.(Danian)*, USSR.——FIG. 403,*4*. **H. ungosensis; 4a,b,* aboral, oral, ×4 (98).

**Nucleopygus** L. AGASSIZ, 1840, p. 7 [**N. minor* DESOR, 1842, p. 33; SD LAMBERT, 1898, p. 165] [=*Lychnidius* POMEL, 1883, p. 55 (type, *Nucleolites scrobiculatus* GOLDFUSS, 1826, p. 138); *Porobrissus* LAMBERT, 1916, p. 169 (type, *Echinobrissus angustatus* CLARK, 1915, p. 69)]. Small; apical system tetrabasal; petals inconspicuous, ambulacral plates beyond petals single-pored; periproct supramarginal, longitudinal; bourrelets not pointed, slightly to moderately developed; phyllodes narrow; buccal pores present. *U.Cret.(Cenoman.-Maastricht.)*, Eu.-Afr.-N.Am.——FIG. 403,*3*; 404,*4*. **N. minor* DESOR, Senon., Fr.; 403, *3a,b*, aboral, oral, ×3; 404,*4*, amb V phyllode, ×15 (98).

**Ochetes** POMEL, 1883, p. 57 [**Nucleolites morrisii* FORBES, 1849, p. 8; SD KIER, 1962, p. 170]. Small; apical system tetrabasal; petals slightly developed; double pores in all ambulacral plates; periproct supramarginal, in deep groove; bourrelets well developed; spheridia in 2 rows in each ambulacrum; no buccal pores. *Cret.(Alb.-Cenoman.)*, G.Brit.——FIG. 404,*3*; 405,*1*. **O. morrisii*, Alb.: 404,*3*, amb III phyllode, ×20; 405,*1a*, lat., ×2; 405,*1b,c*, aboral, oral, ×4 (98).

**Rhyncholampas** A. AGASSIZ, 1869, p. 270 [**Pygor-*

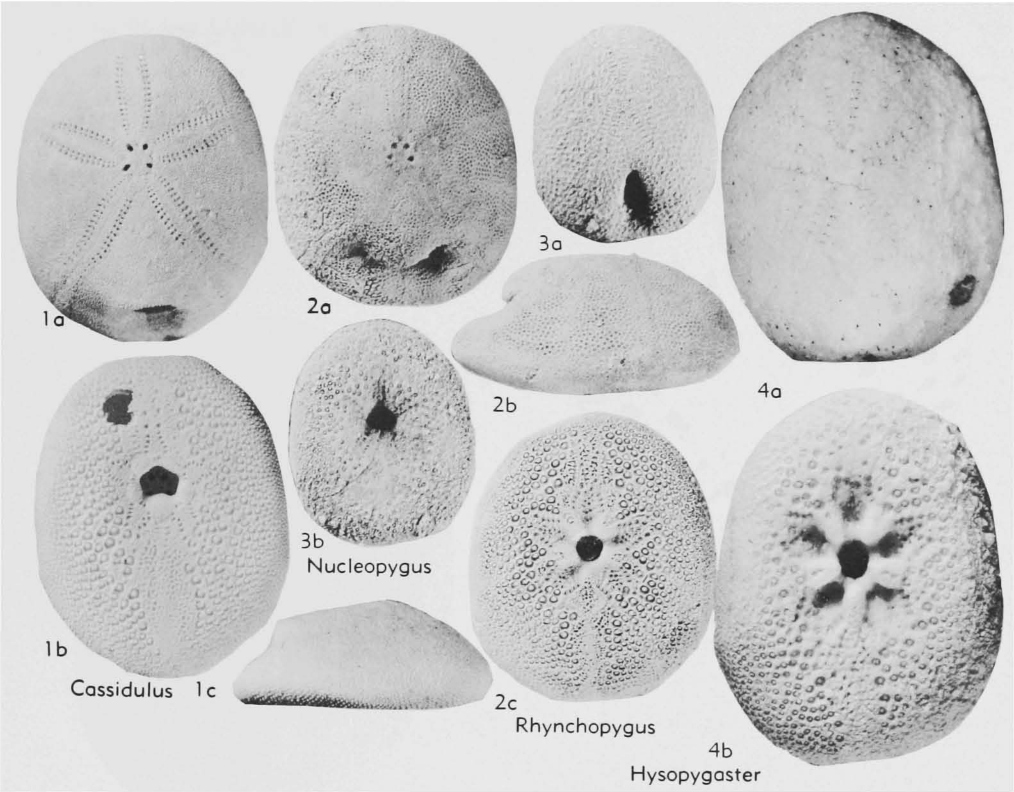



FIG. 403. Cassidulidae (p. *U*514-*U*515).

*hynchus pacificus* A. AGASSIZ, 1863, p. 27; SD LAMBERT, 1918, p. 41] [=*Galerolampas* COTTEAU, 1889, p. 1 (type, *G. sorigneti*); *Plagiopygus* LAMBERT, 1898, p. 162 (type, *Nucleolites grignonensis* DEFRANCE, 1825, p. 214); *Gisopygus* GAUTHIER, 1889, p. 648 (type, *Rhynchopygus navillei* DE LORIOL, 1880, p. 29); *Pleuropygus* LAMBERT & THIÉRY, 1913 (*nom. van. pro Plagiopygus*); *Anisopetalus* ARNOLD & CLARK, 1927, p. 44 (type, *A. ellipticus*)]. Medium-sized to large, greatest width posterior to center; apical system monobasal; petals lanceolate, equal, closed, with unequal poriferous zones; periproct slightly supramarginal, marginal, or slightly inframarginal, transverse; bourrelets moderately developed; phyllodes widened. *Paleoc.-Rec.*, cosmop.——FIG. 404, *1*; 406,*1*. **R. pacificus* (A. AGASSIZ), Rec., N.Am. (W.Coast); 404,*1*, amb II phyllode, ×10; 406, *1a-c*, aboral, lat., oral, ×1 (98).

**Rhynchopygus** D'ORBIGNY, 1856, p. 323 [**Cassidulus marmini* L. AGASSIZ in AGASSIZ & DESOR, 1847, p. 157; OD, M] [=?*Paralampas* DUNCAN & SLADEN, 1882, p. 72 (type, *P. pileus*); *Procassidulus* LAMBERT, 1918, p. 33 (type, *Echinites lapiscaneri* LESKE, 1778, p. 256)]. Small, greatest width posterior to center, oral surface flat, apical system tetrabasal; ambulacral plates beyond petals with single pores; periproct supramarginal, transverse or longitudinal; bourrelets well developed; phyllode wide, few pores. *U.Cret.(Turon.-Maastricht.)*, Eu.——FIG. 403,*2*; 404,*5*. **R. marmini* (L. AGASSIZ), Maastricht., Neth.; 403,*2a-c*, aboral, lat., oral, ×2; 404,*5*, floscelle, ×6 (98).

## Family CLYPEOLAMPADIDAE Kier, 1962

Large, highly inflated, oral surface flat; apical system tetrabasal or monobasal; petals broad, straight, open, long, poriferous zones of same petal of equal length, ambulacral plates beyond petals single-pored; periproct inframarginal, transverse; bourrelets moderately to strongly developed; buccal pores present; narrow, naked granular zone in interambulacrum 5 adorally. *U.Cret.(Cenoman.-Maastricht.)*.

**Clypeolampas** POMEL, 1869, p. 25 [**Clypeaster leskei* GOLDFUSS, 1829, p. 132 (=**Galerites ovatus* LAMARCK, 1816, p. 22; OD, M] [=*Phylloclypeus*

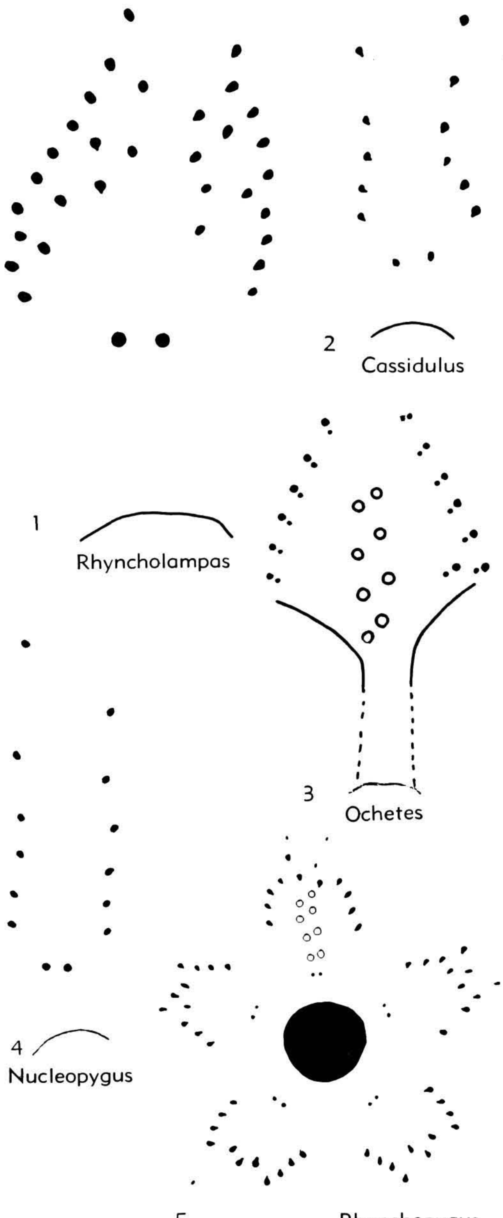



FIG. 404. Cassidulidae (p. U514-U515).

DE LORIOL, 1880, p. 79 (obj.)]. Petals very large with broad poriferous zones; apical system monobasal; bourrelets strongly developed; phyllodes broad, crowded; large tubercles on aboral surface. *U. Cret. (Campan. - Maastricht.),* Eu. - Asia (India).——FIG. 407,*1*; 408,*1*. **C. ovatus* (LAMARCK), Maastricht., Fr.; 407,*1*, amb III phyllode, ×6; 408,*1a-c*, aboral, oral, lat., ×1 (98).

**Vologesia** COTTEAU & GAUTHIER, 1895, p. 65 [**V. tataosi*; OD, M] [=*Hungaresia* SZÖRÉNYI, 1955, p. 76 (type, *H. hungarica*); *Pseudovulechinus* SZÖRÉNYI, 1955, p. 79 (type, *P. rotundatus*)]. Apical system tetrabasal; floscelle moderately developed; no large tubercles adapically. *U.Cret. (Cenoman.-Maastricht.),* Eu.-Asia (Iran).——FIG. 408,*2*. *V. ovum* (GRATELOUP), Senon., Switz.; aboral, ×1 (98).

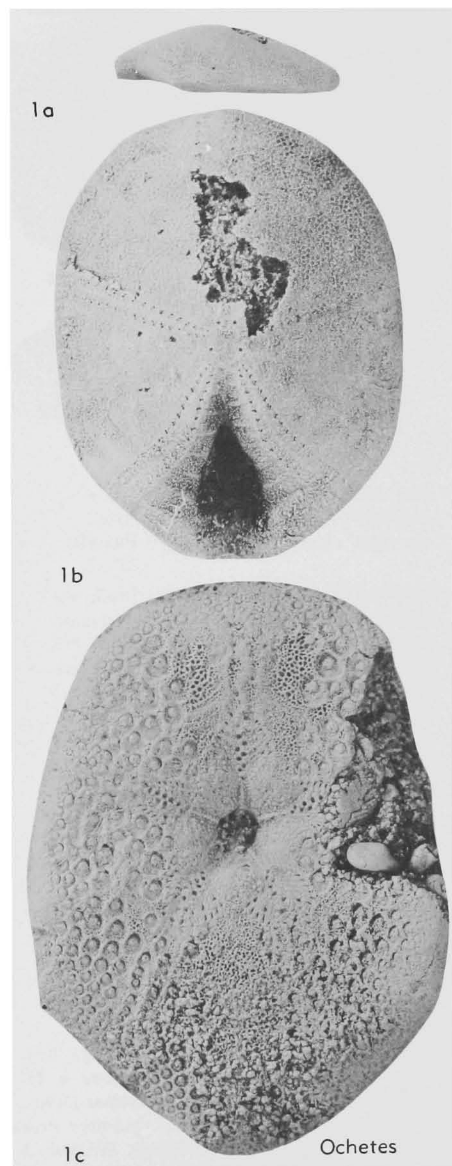



FIG. 405. Cassidulidae (p. U514).

**Family PLIOLAMPADIDAE Kier, 1962**

Medium-sized to large, apical system monobasal, 3 or 4 genital pores; petaloid pores strongly conjugate, single pore in all ambulacral plates beyond petals; periproct marginal, inframarginal or supramarginal, usually longitudinal; bourrelets usually well developed; buccal pores; usually no naked zone in interambulacrum 5 adorally. *U.Cret.(Senon.)-Rec.*

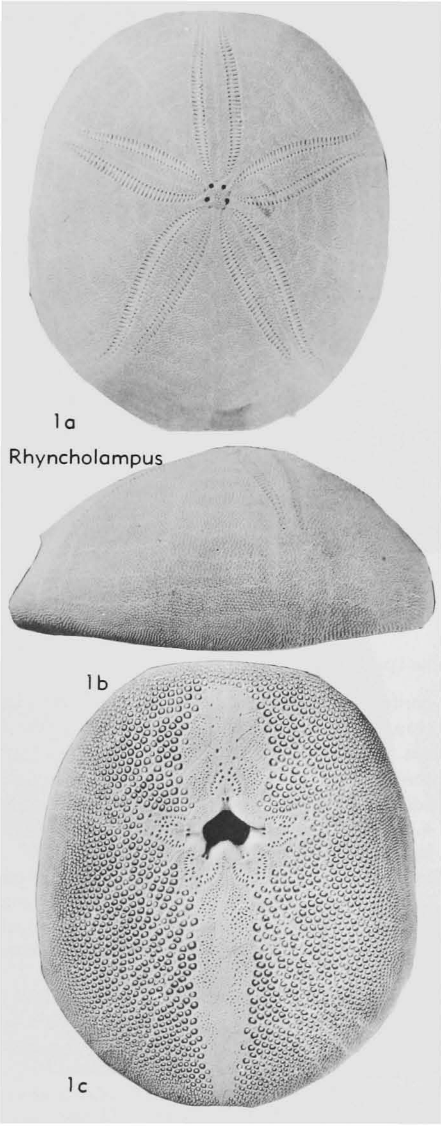



FIG. 406. Cassidulidae (p. U515).

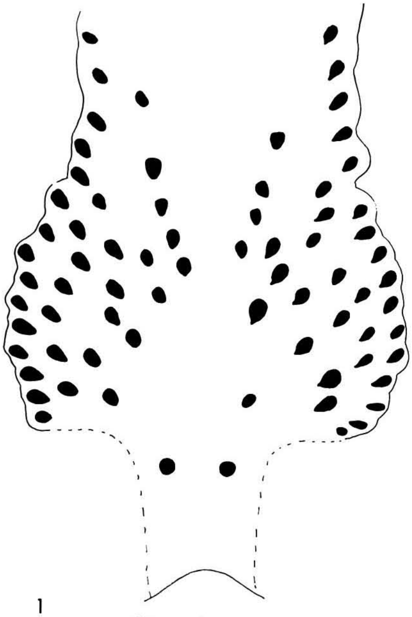



FIG. 407. Clypeolampadidae (p. U515-U516).

**Pliolampas** POMEL, 1888, p. 446 [**Echinolampas gauthieri* COTTEAU, 1880, p. 446; OD, M] [=*Breynella* GREGORY, 1891, p. 600 (type, *Pygorhynchus vassalli* WRIGHT, 1855, p. 271); *Milletia* DUNCAN, 1891, p. 191 (type, *Echinolampas elegantulus* COTTEAU, 1883, p. 458)]. Medium-sized, apical system with 3 or 4 genital pores; petals well developed; phyllodes broad with large pores. *Eoc.-Plio.*, Eu.-Afr.-Malaya.——FIG. 409,*3*; 410,*6*. **P. gauthieri* (COTTEAU), Mio., Fr.; 409,*3a,b*, aboral, oral, ×2; 410,*6*, amb I phyllode, ×15 (98). [=*Plesiolampas* POMEL, 1883 (*non* DUNCAN & SLADEN, 1882) (type, *Echinolampas gauthieri* COTTEAU, 1880, M).]

**Daradaster** TESSIER, 1952, p. 295 [**D. peroni*; OD, M]. Adapical system with genital pores widely separated from each other; petals extremely broad, closed, with poriferous zones of same petal widely separated near apical system; interiporiferous zones extremely wide; periproct marginal; phyllodes very wide; bourrelets strongly developed, tooth-like. *Eoc.*, Afr.(Senegal).

**Eurhodia** HAIME, 1853, p. 213 [**E. morrisi*; OD, M] [=*Ravenelia* MCCRADY, 1859, p. 283 (type, *Pygorhynchus rugosa* RAVENEL, 1848, p. 4)]. Elongate, low, oral side flattened; petals equal, broad; periproct supramarginal; peristome higher than wide; bourrelets strongly developed. *Paleoc.-Eoc.*, Asia(India)-Eu.-Afr.-N.Am.——FIG. 409,*2*; 410,*1*. **E. morrisi*, Paleoc., India; 409,*2a,b*, aboral, oral, ×1; 410,*1*, amb III phyllode, ×10 (98).

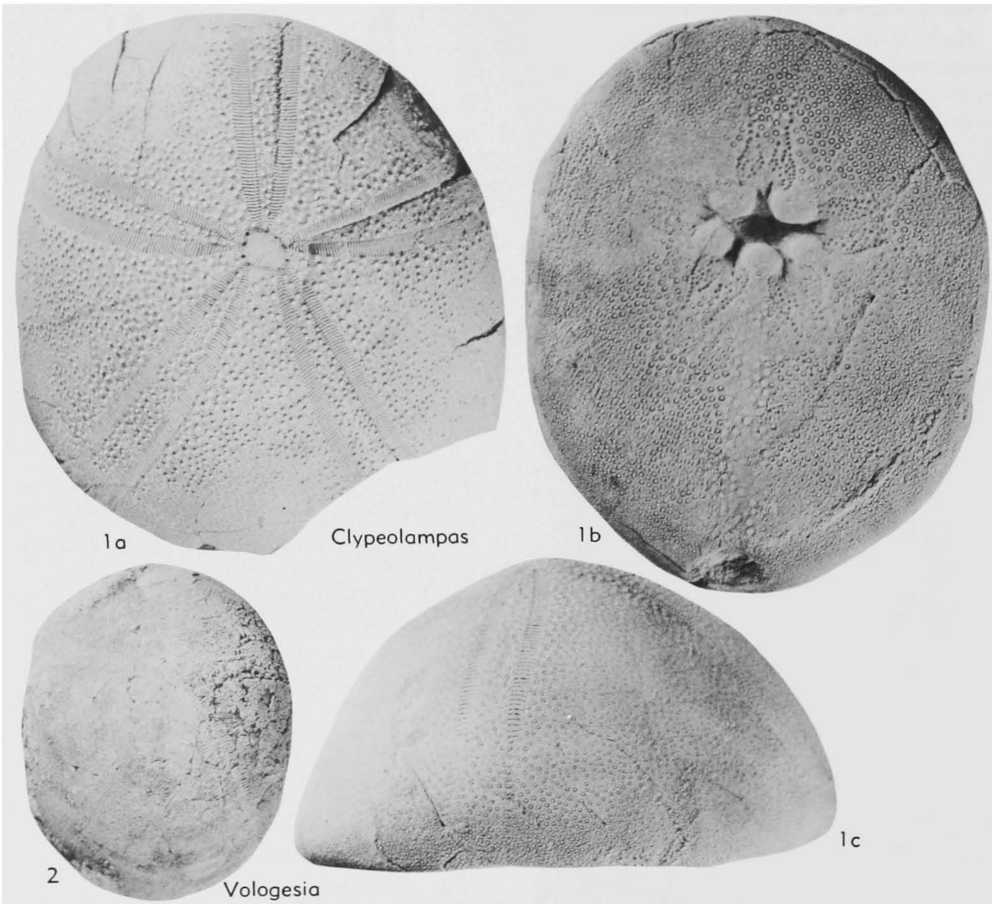



FIG. 408. Clypeolampadidae (p. U515-U516).

**Gitolampas** GAUTHIER, 1889, p. 98 [**Pliolampas tunetana* GAUTHIER, 1889, p. 99; OD, M] [=*Bothriolampas* GAUTHIER, 1899, p. 652 (obj.); *Gitolampopsis* CHECCHIA-RISPOLI, 1921, p. 18 (type, *Gitolampas lamberti* CHECCHIA-RISPOLI, 1921, p. 18); *Echanthus* COOKE, 1942, p. 37 (type, *Echinanthus georgiensis* TWITCHELL, 1915, p. 139)]. Poriferous zones of same petal of equal length; periproct marginal, longitudinal; peristome transverse; bourrelets well developed; phyllodes broad. *U.Cret.(Senon.)-Mio.*, Eu.-Afr.-N.Am.-Asia (India).——FIG. 409,*1*; 410,3. **G. tunetana* (GAUTHIER), Campan., Tunisia; 409,*1a-c*, oral, aboral, lat., ×1.5; 410,*3*, amb II phyllode, ×15 (98).

**Ilarionia** DAMES, 1878, p. 34 [**Echinanthus beggiatoi* LAUBE, 1868, p. 22; OD, M]. Inflated, with steep sides, oral side flat; petals closed, narrow poriferous zones; periproct marginal, longitudinal; peristome usually with rim; bourrelets vertical, not inflated; phyllodes narrow, with few pores; very narrow naked zone in interambulacrum 5 adorally. *Eoc.*, Eu.-Asia(India)-Afr.——FIG. 409, *4*. **I. beggiatoi* (LAUBE), Italy; *4a-c*, aboral, oral, lat., ×1 (98).

**Kephrenia** FOURTAU, 1909, p. 138 [**K. lorioli*; OD]. Petals closed, narrow poriferous zones; periproct marginal, transverse; peristome higher than wide. *Eoc.*, Egypt.——FIG. 409,*5*. **K. lorioli*; *5a-d*, oral, aboral, lat., post., ×2 (98).

**Neocatopygus** DUNCAN & SLADEN, 1882, p. 76 [**N. rotundus*; OD, M]. Broad, highly inflated; periproct inframarginal; bourrelets well developed; phyllodes widened; no naked sternal region. *Paleoc.*, India.——FIG. 410,*5*; 411,*1*. **N. rotundus*; 410,*5*, amb I phyllode, ×15; 411,*1a-c*, aboral, oral, lat., ×1 (98).

**Pseudopygaulus** Coquand, 1862, pl. 31 (expl.) [**Catopygus trigeri* Coquand, 1862, p. 274; OD, M] [=*Eolampas* Duncan & Sladen, 1882, p. 61 (type, *E. antecursor*); *Ottiliaster* Penecke, 1885, p. 350 (type, *O. pusillus*); *Petalaster* Cotteau, 1885, p. 330 (type, *P. maresi*)]. Inflated; ambulacrum III not petaloid; periproct inframarginal, transverse; bourrelets slightly developed. *Paleoc.*-

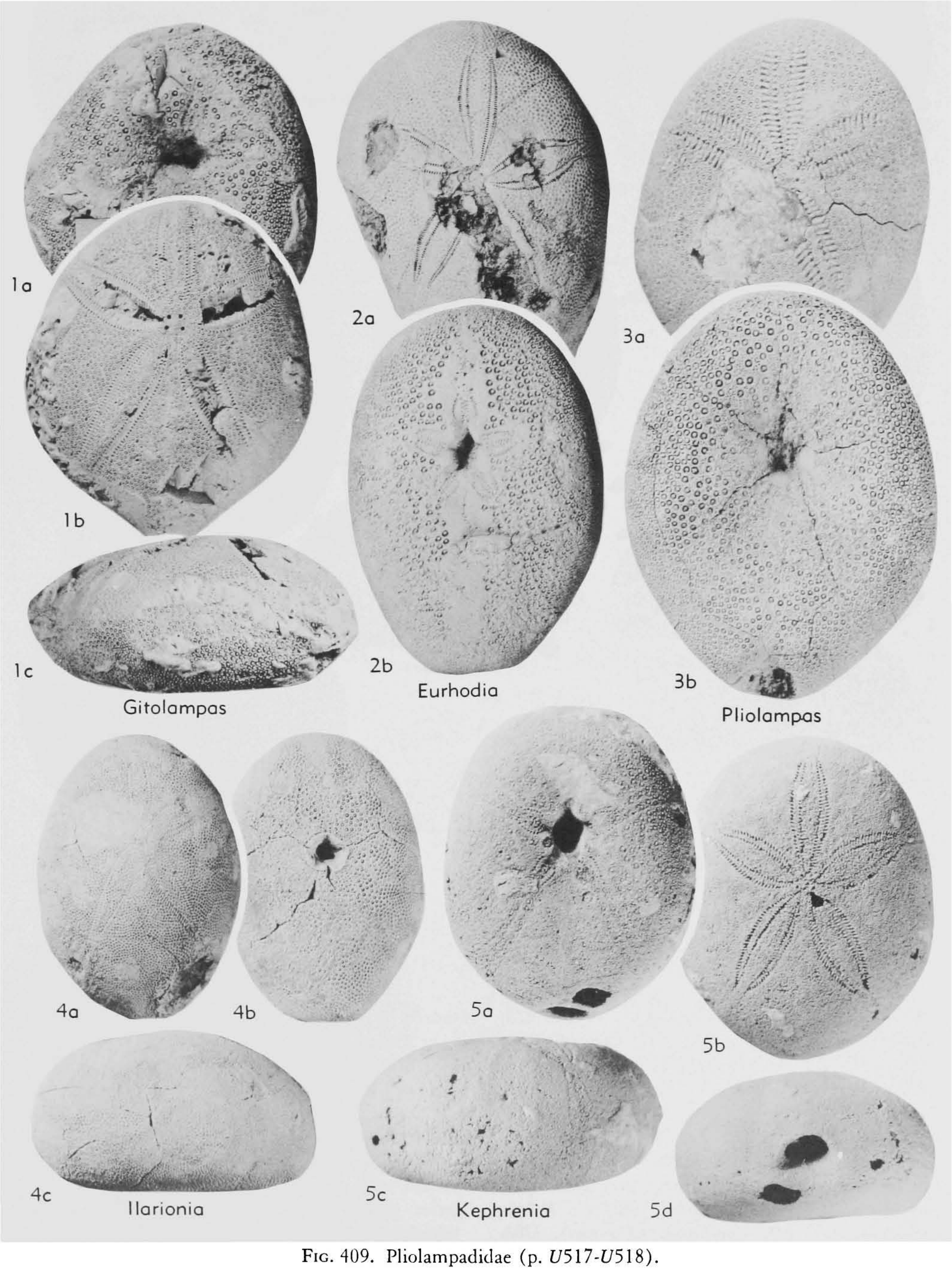



Fig. 409. Pliolampadidae (p. *U*517-*U*518).

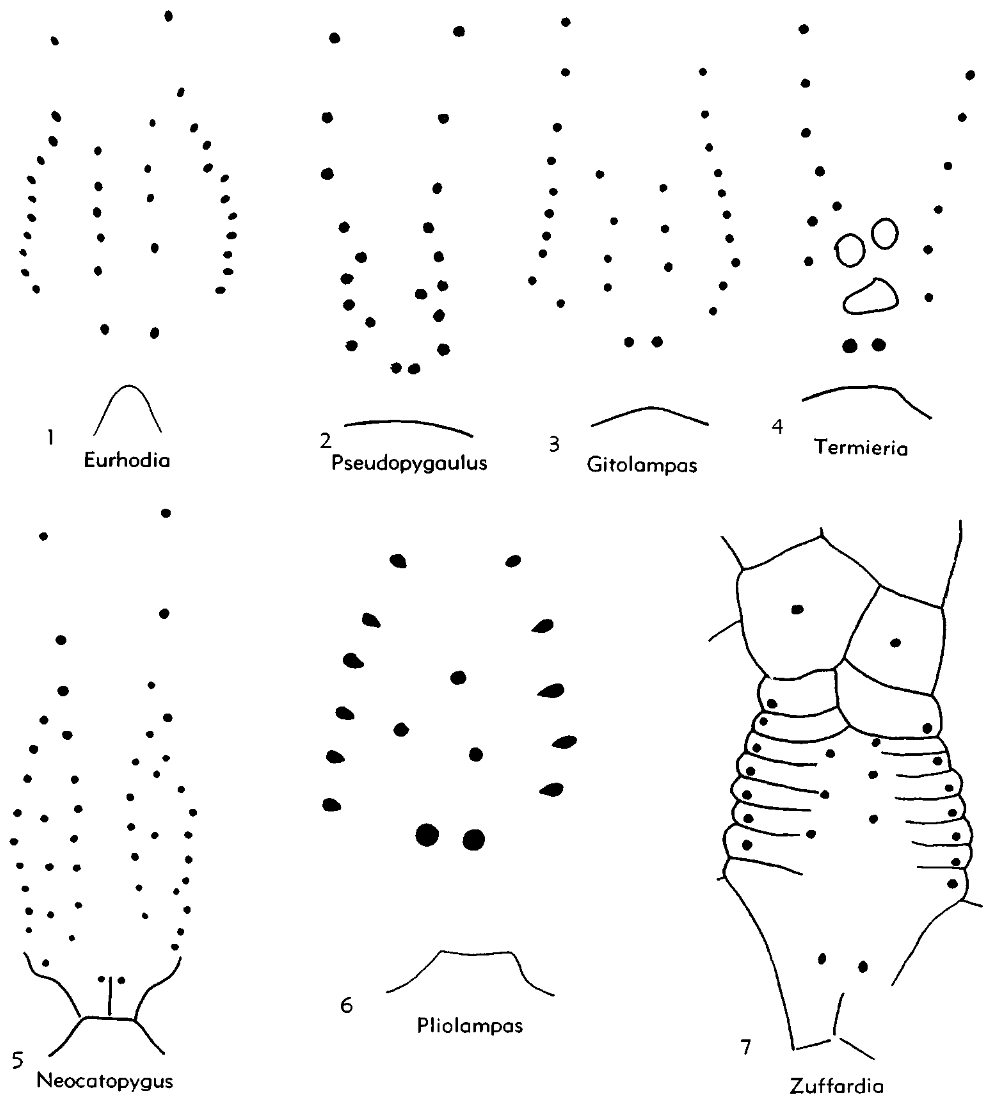



Fig. 410. Pliolampadidae (p. *U*517-*U*520, *U*522).

*Eoc.*, Eu.(Fr.-Aus.)-Afr.-Asia(India).——Fig. 410, *2*; 411,*2*. **P. trigeri* (Coquand), Eoc., Tunisia; 410,*2*, amb I phyllode, ×15; 411,*2a-c*, aboral, oral, lat., ×2 (98).

**Santeelampas** Cooke, 1959, p. 61[**Catopygus oviformis* Conrad, 1850, p. 39; OD]. Apical system very eccentric anteriorly; petals straight, narrow; periproct marginal, longitudinal; no naked zone in interambulacrum, 5 adorally. *M.Eoc.*, N.Am. ——Fig. 411,*5*. **S. oviformis* (Conrad), USA (S.Car.); *5a-c*, aboral, oral, lat., ×1 (98).

**Studeria** Duncan, 1891, p. 185 [**Catopygus elegans* Laube, 1869, p. 8; OD, M] [=*Tristomanthus* Bittner, 1892, p. 355 (type, *Nucleolites subcarinatus* Goldfuss, 1826, p. 142); *Phaleropygus* de Loriol, 1902, p. 15 (type, *P. oppenheimi*); *Hypselolampas* Clark, 1917, p. 104 (type, *Studeria recens* A. Agassiz, 1879, p. 204)]. Apical system with 3 genital pores; no pore in left anterior genital plate; petals long, straight, open, adjacent pore pairs widely spaced; periproct marginal, longitudinal; bourrelets very strongly devel-

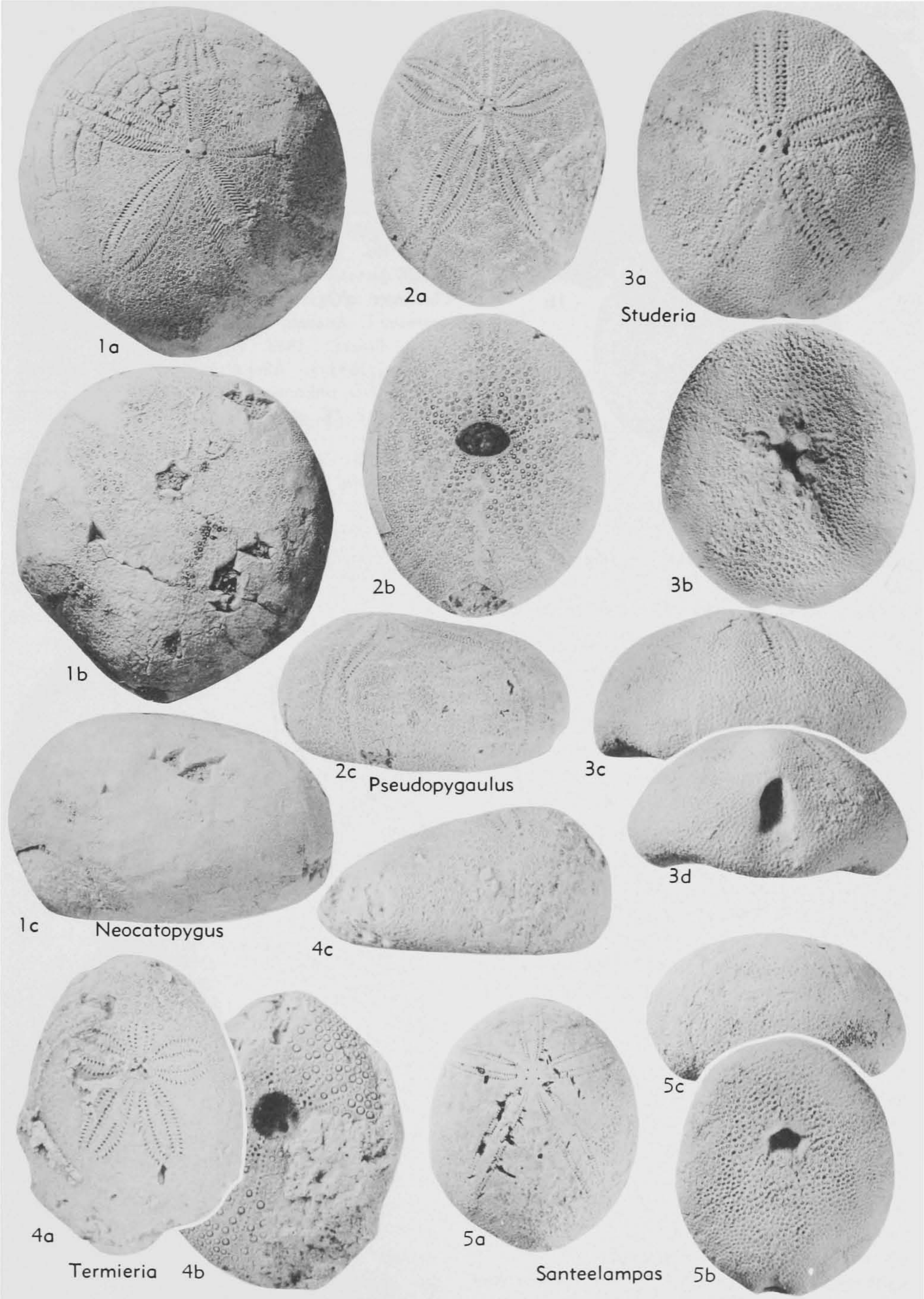



FIG. 411. Pliolampadidae (p. U517-U520, U522).

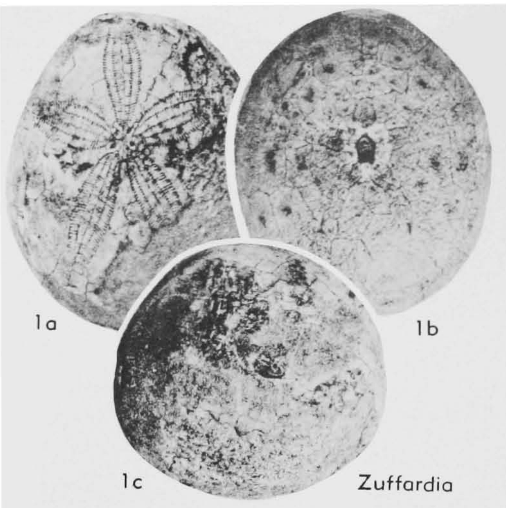



FIG. 412. Pliolampadidae (p. U522).

oped; phyllodes slightly widened. *Oligo.-Rec.*, Eu.-Afr.-Australia.——FIG. 411,*3*. **S. subcarinatus* (GOLDFUSS), Oligo., ?Ger.; *3a-d*, aboral, oral, lat., post., ×1.5 (98).

**Termieria** LAMBERT, 1931, p. 30 [**T. henrici*; OD]. Small, apical system monobasal; petals broad, unequal, petal III short, periproct inframarginal, round; bourrelets and phyllodes slightly developed. *U.Cret.(Maastricht.)*, Morocco.——FIG. 410,*4*; 411,*4*. **T. henrici*; 410,*4*, amb III phyllode, ×21; 411,*4a-c*, aboral, oral, lat., ×3 (98).

**Zuffardia** CHECCHIA-RISPOLI, 1917, p. 492 [**Pseudocatopygus sanfilippoi* CHECCHIA-RISPOLI, 1914, p. 5; OD]. Medium-sized, highly inflated; apical system monobasal; petals well developed; periproct marginal, longitudinal; peristome higher than wide; bourrelets well developed. *U.Cret.(Senon.)*, Afr.——FIG. 410,*7*; 412,*1*. **Z. sanfilippoi* (CHECCHIA-RISPOLI), Tripoli; 410,*7*, amb IV phyllode, ×8, 412,*1a-c*, aboral, oral, post., ×1 (98).

## Family APATOPYGIDAE Kier, 1962

Medium-sized, apical system tetrabasal in young, monobasal in adult; petals moderately developed; ambulacral plates beyond petals single-pored; periproct supramarginal; bourrelets slightly developed; no buccal pores. *Neog.*

**Apatopygus** HAWKINS, 1920, p. 393 [**Nucleolites recens* EDWARDS, 1836; OD]. Characters of family. *U.Tert.-Rec.*, N.Z.-Australia.——FIG. 413,*1*. **A. recens* (EDWARDS), Rec., N.Z.; *1a,b*, aboral, oral, ×1; *1c*, amb. IV phyllode, ×6 (98).

## Family UNCERTAIN

**Astropygaulus** CHECCHIA-RISPOLI, 1945, p. 2 [**A. trigonopygus*; OD, M]. Low, wide; closed petals; peristome oblique; based on one fragment. *U. Cret.*, Afr.

**Centropygus** EBRAY, 1858, p. 483 [**Antropygus guetinicus* EBRAY, 1859, p. 759; SM EBRAY, 1859, p. 759] [=*Centroclypus* EBRAY, 1858 *(nom. null.)*]. Similar to *Hyboclypus* but differing in having smaller oculars II and IV; never figured. *Jur.*, Eu. [=*Antropygus* EBRAY, 1859 *(nom. null.)*.]

**Claviaster** D'ORBIGNY, 1856, p. 281 [**Archiacia cornuta* L. AGASSIZ, 1847, p. 101; OD] [=?*Passalaster* POMEL, 1883 (type, *Claviaster costatus* POMEL, 1883)]. Aboral surface highly inflated; oral surface unknown. *U.Cret.*, Afr.-Eu.(Fr.).——FIG. 413,*2*. **C. cornutus* (L. AGASSIZ), Egypt; lat., ×2 (98).

**Clypeanthus** COTTEAU, 1894, p. 354 [**Toxaster pentagonalis* FRAAS, 1878, p. 93; OD, M]. Small, subcircular, slight anterior groove; apical system central; petal III short, pores conjugate; peristome anterior; periproct marginal, higher than wide; floscelle unknown. *Cret.*, Lebanon.

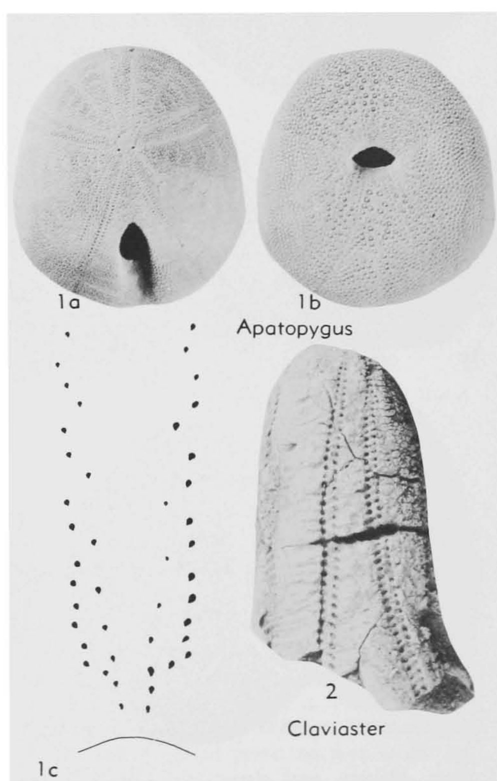



FIG. 413. Apatopygidae *(1)*; Family Uncertain *(2)* (p. U522).

[**Echinanthopsis** MUNIER-CHALMAS, 1889 *(nom. nud.)*].

**Echinanthus** LESKE, 1778, p. 121 [**E. ovatus* LESKE (*op. cit.*, p. 127); SD KIER, 1962, p. 226]. LESKE's figure is too poor to permit determination of characters of the species. *Rec.*, loc. uncertain.

**Jolyclypus** LAMBERT, 1918, p. 26 [**Galeropygus jolyi* GAUTHIER, 1898, p. 836; OD]. Small, elongate; apical system tetrabasal, in contact with periproct; ambulacral arrangement and floscelle not clear. Probably related to *Galeropygus*. Age uncertain, Eu.(Fr.).

**Lovenilampas** MAURY, 1934a, p. 3 [**Lovenia baixadoleitensis* MAURY, 1934b, p. 156; OD]. Based on fragment of an external cast of the peristomial region. *U.Cret.*, Brazil.

**Ovulechinus** LAMBERT, 1920, p. 148 [**O. pilula*; OD]. Based on 2 very poorly preserved and probably immature specimens; impossible to determine generic characters of this species from these specimens. *U.Cret.*, Fr. [Transfer from p. *U*448.]

**Platipygus** DE LORIOL, 1902, p. 17 [**Cyrtoma posthumum* ORTMANN, 1901, p. 369; OD, M]. Large, low; petals equal, broad, closed; periproct supramarginal, notched; bourrelets strongly developed; phyllodes unknown. *Mio.*, S.Am.

# HOLASTEROIDS

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## INTRODUCTION

Echinoids of the order Holasteroida display wide variation in development of most major morphological characters. The adult test ranges in size from very small to moderately large (approx. 100 mm.) and in shape from round, subglobular, elongate or heart-shaped to bottle-shaped, with the vertex consisting of either the apical system (e.g., *Hagenowia*) or the adoral area (e.g., *Echinosigra*).

The apical system typically is elongate or disjunct, with separation of anterior and posterior segments very marked in some. The system is disjunct in the Collyritidae and Disasteridae, in which the anteroapical segment consists of ocular plates II, III, and IV and genital plates 1, 2, 3, and 4, and the posteroapical segment consists of oculars I and V (genital plate 5 invariably absent). A series of catenal plates may be present between the two segments and one or more complemental plates may appear in the anteroapical system. The Holasteridae are characterized by an elongate apical system in which the large oculars II and IV meet at the mid-line, separating genital plates 2 and 3 from 1 and 4. In the families Urechinidae and Calymnidae the apical system is similar to that of the Holasteridae, but only three, or rarely two, genital pores may occur, rather than the usual four. The apical system in the Pourtalesiidae is irregular in that the genital plates may be partly coalesced, the anterior pair not being differentiated from the posterior pair, and there may be three or four genital pores. The three anterior oculars may be well separated from the posterior pair and not easily recognizable as discrete plates. Where the genital plates are coalesced, the madreporic pores may be distributed over the entire complex. In the Stenonasteridae and Somaliasteridae the apical system is ethmophract and not elongate.

Dissimilarity between ambulacrum III and the paired ambulacra is notable throughout the order. The difference may involve size, shape, and number of plates, as well as size and shape of pores. The frontal ambulacrum is commonly sunken, in some forms deeply so, whereas the paired ambulacra are flush with the test. Early members of the order have plates with double pores; later species may have a single pore in each plate either in part of an ambulacrum or throughout its entire length. Incipient phyllodes or bourrelets may be present but no well-developed floscelle.

The interambulacra display some distinct specializations, particularly in the adoral portion of interambulacrum 5. Development of the plastron, or sternum, is of major classificatory importance. Earlier taxa have a primitive plastron in which the adoralmost plate, the **labrum,** is succeeded by simple alternating plates of equal size. This type of plastron is termed **protosternous.** In a **meridosternous** plastron the labrum is followed by a single large **episternal** and a varying number of plates in a single column. It is believed that the meridosternous type is developed as a result of increasing pressure between the double columns finally producing a single column made up of alternate plates from the original two. The plastron may be raised or keeled or flush with the test; it commonly bears tubercles of different size and distribution than those on the paired interambulacra, suggesting the development of spines for special functions. In the paired interambulacra, the first post-primordial plates may be single (**meridoplacous**) or double (**amphiplacous**).

The periproct may be marginal, supramarginal, or inframarginal. In most holasteroids it is situated on the usually truncate posterior end of the test. Interambulacrum 5 is so developed in many pourtalesiids as to form an adapically placed hood over the periproct accompanied by an adoral anal rostrum, so that the periproct lies in a cavity.

The peristome is usually central or anterior on the underside of the test and may be more or less rounded or semilunar in outline. Specialized development of the oral area in some forms, particularly the pourtalesiids, has altered orientation of the mouth so greatly that the peristomial membrane is vertical.

Primary tubercles are usually more or less uniformly developed except on the plastron; they are perforate and crenulate. Earlier representatives may have distinctly larger primaries and smaller miliaries, in some genera disposed in a distinct pattern but in none regularly arranged over the entire corona, as in the Holectypoida. Most living species have more or less uniform, slender spines with evenly rounded or spatulate tips. A subanal fasciole is common in the Holasteridae, Urechinidae, and Pourtalesiidae, and an ambulacral or peripetalous fasciole in the Somaliasteridae. Pedicellariae, observed in various living forms, have been described in detail by AGASSIZ (1881) and MORTENSEN (1907).

Earliest known representatives of the order are recorded from the Lower Jurassic, probably arising from a stirodont ancestor. The Collyritidae and Disasteridae are well represented in Europe and North Africa throughout the Jurassic and into the Early Cretaceous when both families disappear. The Holasteridae appear in the Valanginian and diversify greatly throughout the Cretaceous and into the Tertiary, attaining almost worldwide distribution; only one living genus (*Stereopneustes*), found in the Indo-Pacific region, is known. The Stenonasteridae are recorded from Cretaceous of the Mediterranean region. The Somaliasteridae are known from the Cretaceous and Paleocene of Iran and Somalia. The remaining three families appear to be most closely related to the Holasteridae; the Urechinidae first appear in the Miocene and have wide distribution in present seas; the Calymnidae and Pourtalesiidae are known only from the Recent.

Most living representatives are deep-water inhabitants with exceedingly thin and fragile tests. *Stereopneustes* has been taken from depths of 250-900 m., urechinids from 110-4,163 m., *Calymne* from approximately 4,845 m., and pourtalesiids from ?50-7,000 m. Fossil members are, on the whole, associated with fine sediments, many of them chalky in nature.

Detailed studies of groups within the Holasteroida include those of BEURLEN, 1934, on the Collyritidae, A. AGASSIZ, 1881, on the Pourtalesiidae, Urechinidae and Calymnidae, T. MORTENSEN, 1907, on the Pourtalesiidae, and LOVÉN, 1883, on the genus *Pourtalesia*.

## Order HOLASTEROIDA Durham & Melville, 1957

Apical system typically elongate or disjunct, no genital 5; plastron feebly differentiated or meridosternous; petals not always differentiated, paired petals typically not impressed; no floscelle; apical system and peristome may be opposite to one another; fascioles variable. *L.Jur.-Rec.*

### Family COLLYRITIDAE d'Orbigny, 1853

Oculars II and IV juxtaposed; apical system disjunct; plastron protosternous. *L.Jur.-L.Cret.*

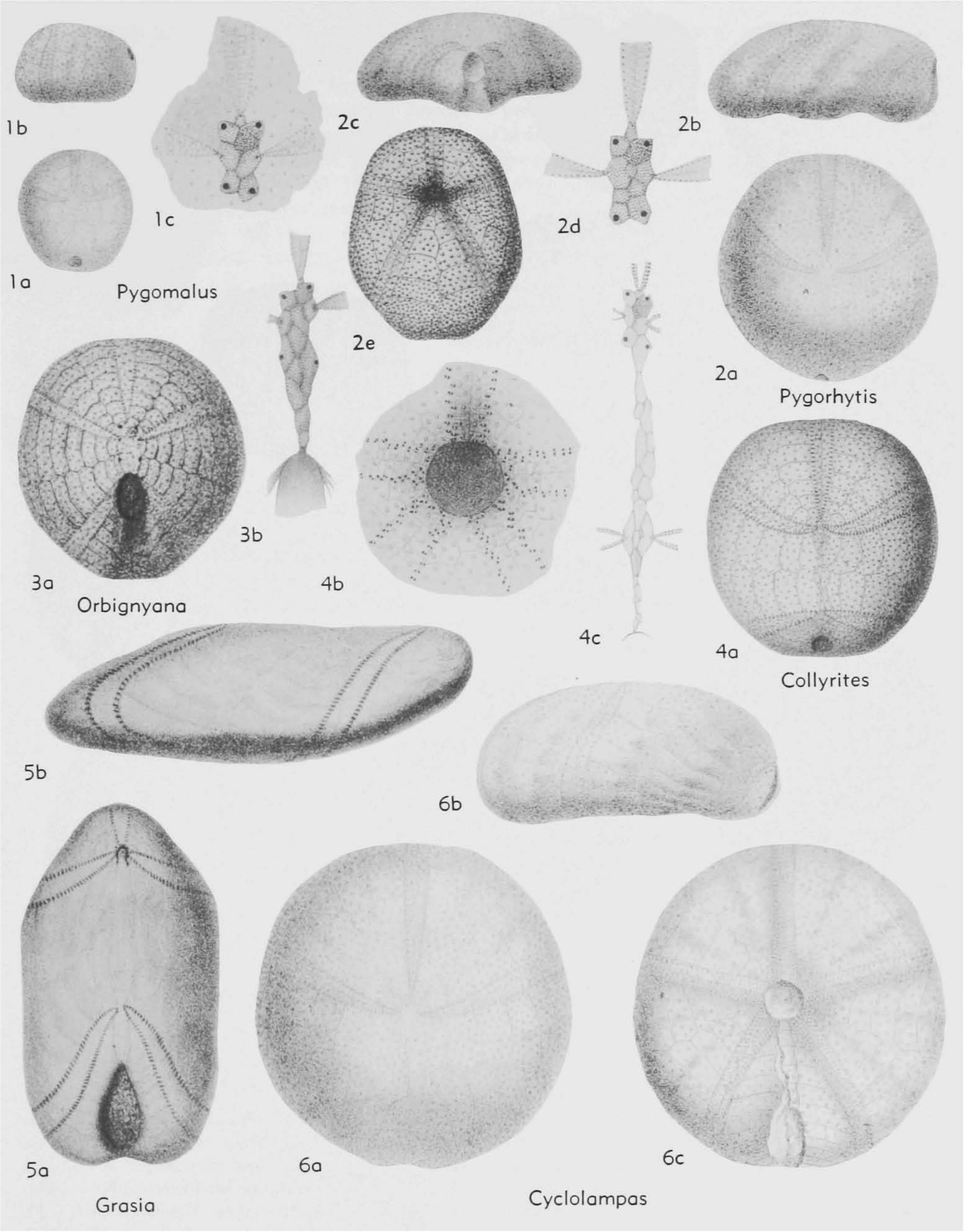


FIG. 414. Collyritidae (p. *U525-U527*).

**Collyrites** DESMOULINS, 1835, p. 212 [**Ananchytes elliptica* LAMARCK, 1816, p. 318; OD]. Ambulacral pores crowded adorally, may be arranged in triads; anteroapical system central or posterior, oculars I and V near posterior margin; periproct marginal, not in groove, not contiguous to oculars; peristome round, anterior, not sunken; ambulacrum III may be slightly depressed; tubercles on oral side larger, with excentric boss. *Jur.(Bathon.-Tithon.)*, Eu.-N.Afr.——FIG. 414,*4*. **C. elliptica*

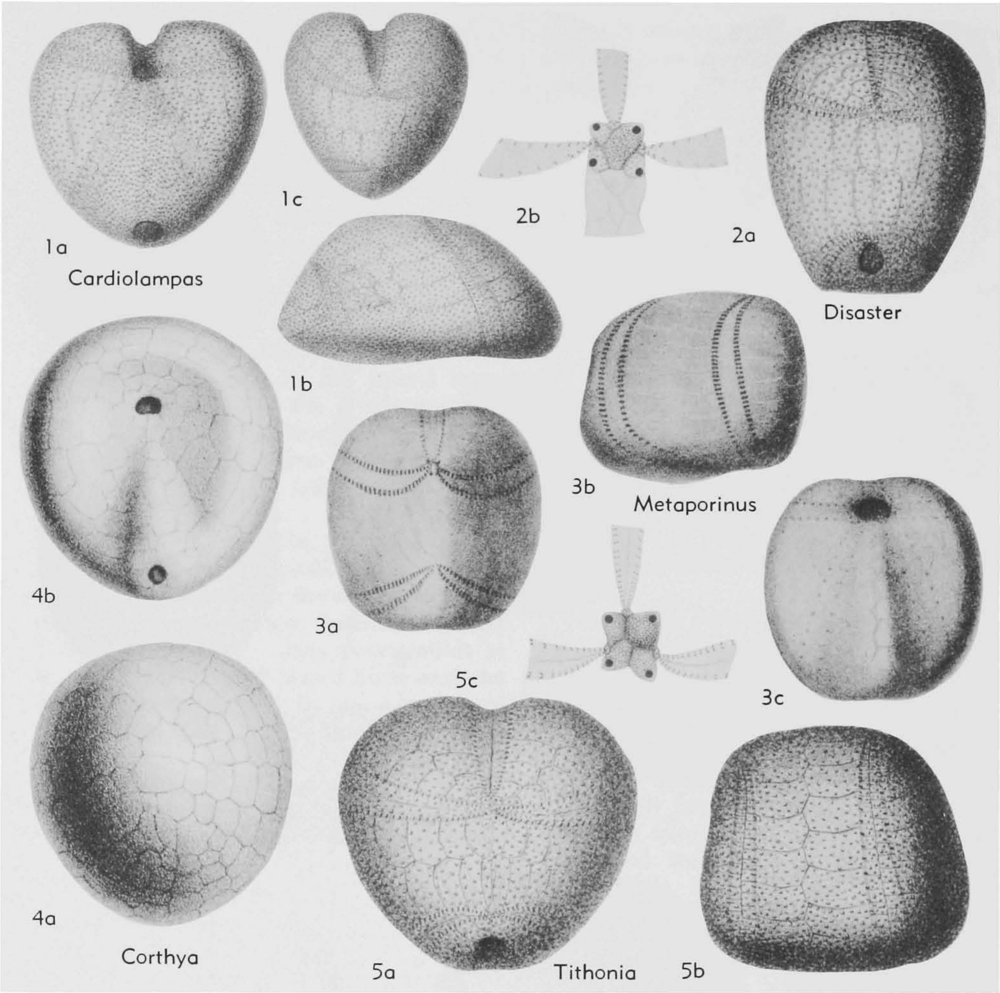


FIG. 415. Disasteridae (p. U527-U528).

(LAMARCK), Bathon., Fr.; *4a,* apical, ×0.7; *4b,* adoral, enlarged; *4c,* apical system, enlarged (27b).

**Cardiopelta** POMEL, 1883, p. 50 [**Collyrites trigonalis* DESOR in DESOR & DE LORIOL, 1872; SD SAVIN, 1903, p. 50]. Test as in *Collyrites* except outline cordate, catenal plates connecting anteroapical system, and posterior oculars rudimentary or lacking. *U. Jur. (Callov.)-L. Cret. (Valangin.),* Eu.

**Cyclolampas** POMEL, 1883, p. 51 [**Disaster voltzii* AGASSIZ, 1839, p. 8; SD LAMBERT & THIÉRY, 1924, p. 391]. Ambulacra faintly petaloid, pores small, round; adorally pores increase in abundance, arranged in oblique series of 3; anteroapical system central or slightly posterior, oculars I and V at posterior end of test; periproct not contiguous to oculars, may be inframarginal. *U.Jur.(Callov.-Tithon.),* Eu.——FIG. 414,6. **C. voltzii* (AGASSIZ), Oxford., Switz.; *6a-c,* apical, lat., oral, ×1 (186).

**Grasia** MICHELIN, 1854, p. 439 [**Hyboclypus elongata* GRAS, 1852, p. 49; OD]. Test subcylindrical, posteriorly concave; ambulacral pores slightly unequal; anteroapical system near anterior end of test; periproct large, not contiguous to oculars, in deep groove; peristome distinctly sunken, slightly elongate along III-5 axis. *U.Jur.(Oxford.),* Fr. ——FIG. 414,5. **G. elongata* (GRAS); *5a,b,* aboral, lat., ×0.7 (27b).

**Orbignyana** EBRAY, 1860, p. 56 [**Collyrites ebrayi* COTTEAU, 1873, p. 168; SD LAMBERT & THIÉRY, 1924, p. 389] [=*Spatoclypus* POMEL, 1883, p. 51 (obj.)]. Ambulacra narrow, nonpetaloid, pores small; anterolateral ocular plates separated by complemental plates, also with catenal plates between anterior apical system and posterior oculars, distance between apical poles not great; periproct contiguous with posterior oculars, at adapical end of deep groove; peristome distinctly sunken. *M.Jur.(Bajoc.-Bathon.)*, Eu.(Fr.-Caucasus).——FIG. 414,*3*. **O. ebrayi* (COTTEAU), Bajoc., Fr.; *3a*, aboral, ×1.5; *3b*, apical system, enlarged (27b).

**Proholaster** GAUTHIER, 1896, p. 17 [**P. auberti*; OD]. Ambulacrum III depressed, sternum slightly raised; petals unequally developed, pores of ambulacrum III small, round; paired ambulacra with larger, transversely oval, oblique pores; anteroapical system central, posterior oculars subcentral; no complemental plates; periproct on truncate posterior face, relationship to posterior oculars unknown, peristome anterior. *U. Jur.(Tithon.)*, Tunisia.

**Pygomalus** POMEL, 1883, p. 51 [**Spatangites ovalis* LESKE, 1778, p. 253; SD BUERLEN, 1934, p. 65 (Zool. Code, 1961, Art. 69a, iv)]. Aboral side highly inflated; anteroapical system anterior, without complemental plates, oculars I and V near posterior margin; periproct contiguous to oculars, not in groove; peristome anterior, rounded; tubercles somewhat larger on oral side, sternum incipient. *Jur.(Sinemur.-Oxford.)*, Eu.——FIG. 414, *1*. **P. ovalis* (LESKE), Bathon., Fr.; *1a,b*, apical, lat., ×1 (186); *1c*, apical system, enlarged (27b).

**Pygorhytis** POMEL, 1883, p. 50 [**Disaster ringens* AGASSIZ, 1836, p. 183; SD LAMBERT & THIÉRY, 1924, p. 390]. Oculars I and V more posterior than in *Orbignyana;* periproct contiguous with posterior oculars, in faint groove; anteroapical system central or slightly posterior, complemental plates present or absent. *Jur.(Bajoc.-Oxford.)*, Eu. (Fr.-Caucasus).——FIG. 414,*2*. **P. ringens* (AGASSIZ), Bajoc., Switz. *(2a-c)*, Fr. *(2d,e)*; *2a-c*, apical, lat., post., ×1 (186); *2d*, anteroapical system, enlarged (27b); *2e*, oral, ×1 (27b).

## Family DISASTERIDAE A. Gras, 1848

Oculars II and IV separated by genital 2; apical system disjunct; plastron protosternous. *M.Jur.-L.Cret.*

**Disaster** AGASSIZ, 1836, p. 16 [**Nucleolites granulosus* GOLDFUSS, 1826, p. 138; SD DESOR, 1858, p. 201] [=*Dysaster* AGASSIZ, 1839, p. 95 *(nom. van.)*]. Test small, posterior obliquely or squarely truncate; ambulacral pores small, round, pores of ambulacrum III may be slightly larger; anteroapical system anterior, genital 2 conspicuously larger than other genital plates, posterior oculars widely separated from anteroapical system; periproct small, oval, not in groove, contiguous to oculars. *U.Jur.(Bathon.)-L.Cret.(Neocom.)*, Eu.-N. Afr.——FIG. 415,*2*. **D. granulosus* (GOLDFUSS), U.Jur.(Oxford.), Fr. *(2a)*, U.Jur.(Kimmeridg.), Fr. *(2b)*; *2a*, aboral, ×1; *2b*, ant. apical system, enlarged (27b).

**Acrolusia** LAMBERT, 1920, p. 13 [**A. gauthieri*; OD]. Only known specimen incomplete; apparently closely related to *Metaporinus* but elongate pores present in all ambulacra. *L.Cret.(Neocom.)*, Alg.

**Cardiolampas** POMEL, 1883, p. 50 [**Collyrites friburgensis* OOSTER, 1865, p. 55; SD GAUTHIER, 1896, p. 21]. Test cordate, aboral side may have median keel; ambulacrum III deeply sunken; anteroapical system slightly anterior, widely separated from posterior oculars; periproct inframarginal, transversely elongate, not contiguous to oculars; peristome transversely elongate, near anterior edge. *U.Jur.(Tithon.)*, Eu.-N.Afr.——FIG. 415,*1*. **C. friburgensis* (OOSTER), Oxford., Fr.; *1a-c*, oral, lat., apical, ×0.7 (27b).

**Collyropsis** GAUTHIER, 1896, p. 22 [**Spatangites carinatus* LESKE, 1778, p. 245; SD LAMBERT & THIÉRY, 1924, p. 392][=*Procollyropsis* BEURLEN, 1934, p. 129 (type, *Disaster platypygus* QUENSTEDT, 1874, p. 565)]. Test heart-shaped, aboral side highly inflated, may be keeled, sternum slightly raised; ambulacral pores small, posterior petals somewhat broader than anterior; anteroapical system anterior, genital plates contiguous, oculars small; oculars I and V posterior, no complemental plates; periproct on posterior end of test, not contiguous to oculars; peristome anterior. *U.Jur.(Callov.)-L.Cret.(Valangin.)*, Eu.

**Corthya** POMEL, 1883, p. 51 [**Disaster hemisphaericus* GRAS, 1848, p. 66; OD]. Oral side slightly concave, sternum raised; ambulacral pores very small, indistinct; ambulacral plates nearly as high as interambulacral plates; anteroapical system central, posterior oculars posterior; periproct inframarginal; peristome anterior, transversely elongate. *L.Cret.(Neocom.)*, Fr.——FIG. 415,*4*. **C. hemisphaerica* (GRAS); *4a,b*, aboral, oral, ×1 (142).

**Dialyaster** POMEL, 1883, p. 46 [**Metaporinus gueymardi* GRAS, 1848, p. 69; OD]. Like *Metaporinus* except narrower, more elongate and lower; anteroapical system closer to posterior oculars; periproct in deep groove continuing onto oral side; margin of plastron raised to form prominent keels. *L.Cret. (Valangin.)*, Fr.

**Metaporinus** AGASSIZ, 1844, p. 730 [**M. michelini*; OD] [=*Metaporhinus* MICHELIN, 1847 *(nom. null.)*; *Thesaporhinus* EBRAY, 1859 *(nom. nud.)*, *Thecaporinus* EBRAY, 1859 *(nom. null.)*; *Perioxus* POMEL, 1883, p. 49 (type, *Collyrites censoriensis* COTTEAU, 1849-56, p. 262)]. Test high, slightly elongate, slight frontal depression; paired ambulacra with elongate, comma-shaped pores, ambulacrum III with small, round pores; posterior ambulacra concave frontally; anteroapical system close to anterior margin, oculars I and V close to posterior margin, no complemental plates; periproct not contiguous with oculars; peristome anterior, transversely elongate, not sunken. *U.Jur.(Oxford.)*, Eu.——FIG. 415,*3*. **M. michelini*, Oxford., Fr.; *3a-c*, apical, lat., oral, ×0.7 (27b).

**Oustechinus** LAMBERT, 1931, p. 92 [**O. bassae*; OD]. Test small, cordate; ambulacra of high hexagonal plates, pores small, round; anteroapical system central, posterior oculars at posterior margin; periproct small, round, inframarginal, apparently contiguous to oculars; peristome semilunar, near anterior margin; plastron apparently large, strongly tuberculate, adjoining ambulacral plates narrow, elongate. *U.Jur.*, Tunisia.

**Tithonia** POMEL, 1883, p. 49 [**Nucleolites convexus* CATULLO, 1827, p. 28; OD]. Test as in *Metaporinus* except petals of bivium convex frontally, their adapical tips pointing backward; periproct closer to posterior oculars; ambulacrum III not conspicuously different from paired petals. *M.Jur.(Bathon.)-L.Cret.(Neocom.)*, Eu.-N.Afr.——FIG. 415,*5*. **T. convexus* (CATULLO), Neocom., Fr.; *5a,b*, apical, lat., ×1; *5c*, apical system, enlarged (27b).

## Family HOLASTERIDAE Pictet, 1857

Plastron meridosternous; oculars II and IV juxtaposed; ambulacra with double pores; interambulacra typically amphiplacous; apical system not disjunct. [Subfamilies Holasterinae (MORTENSEN, 1950) and Stegasterinae (LAMBERT, 1917) not recognized.] *L.Cret.-Rec.*

**Holaster** AGASSIZ, 1836, p. 183 [**Spatangus nodulosus* GOLDFUSS, 1829, p. 149; SD SAVIN, 1905, p. 26] [=*Holasteropsis* ELBERT, 1902, p. 115 (type, *H. credneriana*); *Ananchothuria* FOSSA-MANCINI, 1919, p. 3 (type, *A. tesselata*)]. Outline cordate, interambulacrum 5 raised orally; ambulacrum III nonpetaloid, pores small, paired ambulacra subpetaloid, pores elongate, not conjugate; apical system central, elongate; periproct on truncate posterior end; plastron meridosternous; peristome anterior, semicircular, usually not labiate; no fascioles. *L.Cret.(Valangin.)-Paleog.(Eoc.)*, cosmop.——FIG. 416,*5*. **H. nodulosus* (GOLDFUSS), U.Cret.(Cenoman.), Fr.; *5a-c*, apical, oral, post., ×0.7 (142).

**Aurelianaster** LAMBERT & THIÉRY, 1925, p. 589 [**Leiocorys valettei* LAMBERT in VALLETTE, 1913, p. 9; OD] [=*Leiocorys* LAMBERT in VALLETTE, 1913, p. 8 (obj.); *Vallettaster* LAMBERT & THIÉRY, 1924, p. 405 (obj.)]. Test as in *Sternotaxis* except ambulacral pores microscopical, round, those of ambulacrum III smaller than in paired ambulacra. *U.Cret.(Turon.)*, Fr.

**Basseaster** LAMBERT, 1936, p. 23 [**B. rostratus*; OD]. Small, faintly cordate; ambulacra nonpetaloid, plates high, pores microscopical; ambulacrum III apparently with single pores; apical system ?fused, 4 genital pores; plastron unknown, labrum large; ?anal fasciole. *U.Cret.(Maastricht.)*, Madag.

**Cardiaster** FORBES, 1850, p. 422 [**Spatangus cordiformis* WOODWARD, 1853, p. 50 (=**S. granulosus* GOLDFUSS, 1826, p. 148); OD]. Test cordate; ambulacrum III deeply sunken, adjoining interambulacra forming sharp keels, pores smaller than in paired ambulacra; paired ambulacra not sunken, pores comma-shaped; apical system central, elongate, 4 genital pores; periproct on posterior end, elongate-oval; peristome anterior, slightly labiate; a marginal fasciole passing under periproct. *U.Cret.(Cenoman.-Senon.)*, *?Tert.*, cosmop.(nearly worldwide).——FIG. 416,*4*. **C. granulosus* (GOLDFUSS), Cenoman., Eng.; *4a,b*, apical, oral, ×0.5 (191b).

**Cardiotaxis** LAMBERT, 1917, p. 25 [**Cardiaster peroni* LAMBERT, 1887, p. 268; OD]. Like *Cardiaster* except plastron with regular series of single plates. *U.Cret.(Turon.-Senon.)*, Eu.

**Cibaster** POMEL, 1883, p. 48 [**Cardiaster bourgeoisanus* D'ORBIGNY, 1853, p. 129; SD LAMBERT, 1892, p. 96]. Ambulacra not depressed, pores small, round, those of ambulacrum III slightly smaller; apical system elongate, 4 genital pores; peristome not labiate; periproct above marginal fasciole. *U.Cret.(Santon.-Senon.)*, Fr.——FIG. 416, *6*. **C. bourgeoisanus* (D'ORBIGNY), Senon.; *6a,b*, aboral, post., ×1; *6c*, apical system, enlarged (142).

**Duncaniaster** LAMBERT, 1896, p. 317 [**Holaster australiae* DUNCAN, 1887, p. 51; OD]. Ambulacra petaloid, slightly sunken on oral side, all similar; pores small, round, conjugate; apical system elongate; peristome slightly labiate; plastron raised; no fascioles. *Eoc.*, Australia.——FIG. 416,*1*. **D. australiae* (DUNCAN); *1a,b*, aboral, oral, ×0.7 (15).

**Echinocorys** LESKE, 1778, p. 175 [**E. scutatus* (=*E. vulgaris* BREYNIUS, 1732, pre-Linnean, cited by LESKE, p. 177, as synonym of *E. scutatus*); SD LAMBERT, 1898, p. 179] [=*Echinocorytes* LESKE, 1778, p. 178 (obj.); *Ananchites* LAMARCK, 1801, p. 347 (=*Ananchytes* LAMARCK, 1816, p. 23 (type, *A. ovatus*); *Galea* SMITH, 1817, p.21 (obj.); *Oolaster* LAUBE, 1869, p. 451 (type, *O. mattseensis*); *Spatagoides* BAYLE, 1878, p. 152 (obj.); *Corculum* POMEL, 1883, p. 48 (type, *Anachytes corculum* GOLDFUSS, 1826, p. 147)]. Subconical aborally; ambulacra nonpetaloid; pores round or outer pore slightly elongate, near center of plates; periproct inframarginal; no labrum; no fascioles. *U. Cret.(Turon.)-Paleog.(Dan.)*, Eu.-Asia Minor-Madag.-N.Am.——FIG. 416,*8*. **E. scutatus*, Senon., Eng.; *8a,b*, oral, lat., ×0.7; *8c*, apical system, enlarged (173). [=*Galeola* QUENSTEDT, 1874, p. 585 (type, *G. papillosa*, p. 595; OD).]

**Entomaster** GAUTHIER, 1888, p. 532 [**E. rousseli*; OD]. Like *Guetarria* except oculars II and IV with supplemental genital pores; peristome more anterior, transversely elongate; large tubercles scattered on aboral surface; no marginal fasciole. *U.Cret.(Senon.)*, Alg.——FIG. 416,*9*. **E. rousseli*; view of peristome, ×2 (136h).

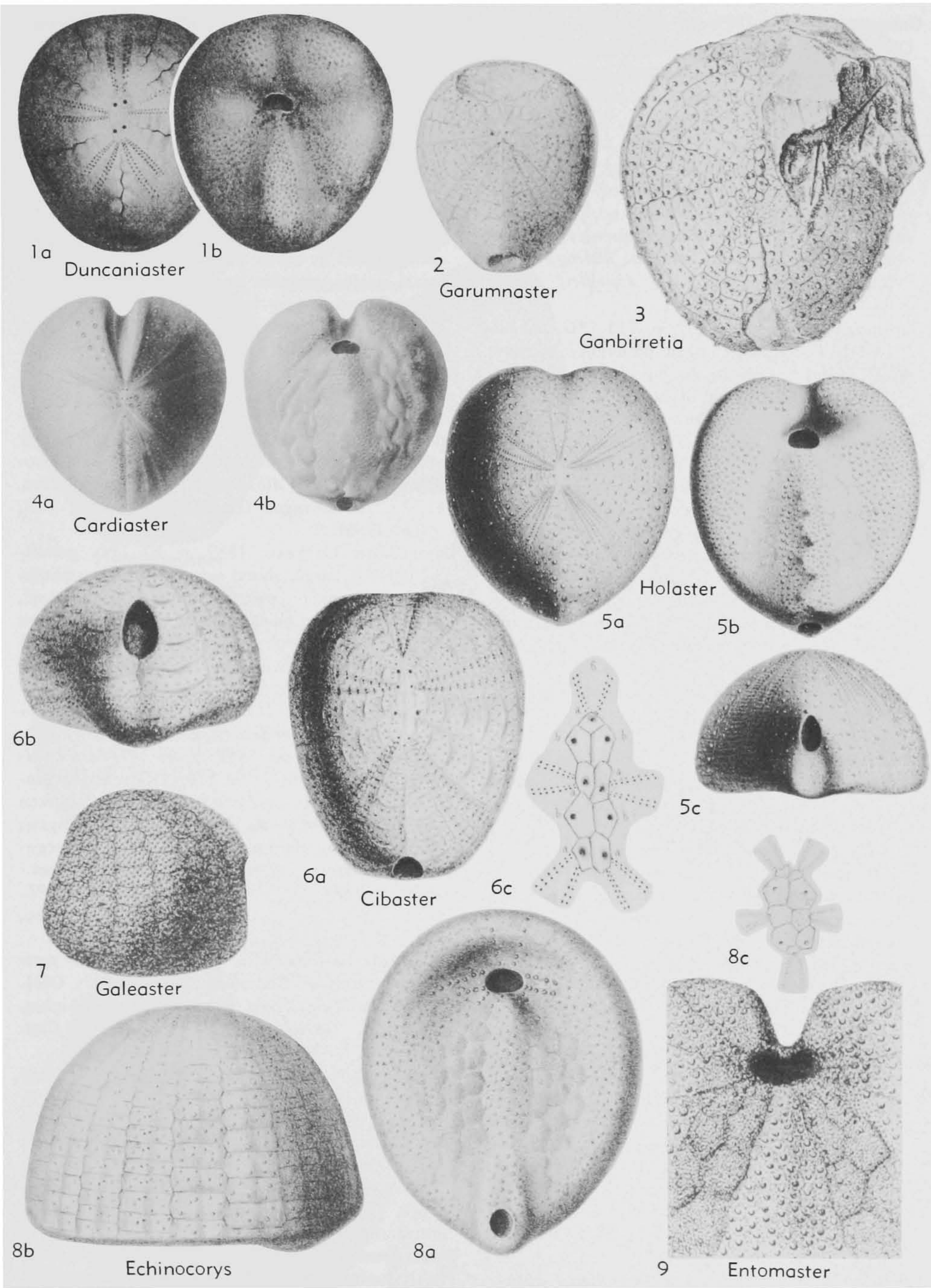


FIG. 416. Holasteridae (p. U528, U530).

**Galeaster** SEUNES, 1889, p. 821 [*G. bertrandi; OD]. Like *Stegaster* but globular, keeled posteriorly; plates of ambulacrum III lower, pores crowded; plastron narrower, sharply raised. *U.Cret. (Campan.),* Fr.——FIG. 416,*7*. *G. bertrandi; lat., ×1 (219b).

**Ganbirretia** GAUTHIER, 1903, p. 19 [*G. douvillei; OD]. Ambulacra similar, not sunken, nonpetaloid, plates high, pores small, round; ocular plates II and IV large; large crenulate tubercles scattered over aboral side; ?no fascioles. *Paleog.(Dan.),* Pyrenees.——FIG. 416,*3*. *G. douvillei; aboral, ×0.67 (195c).

**Garumnaster** LAMBERT, 1907, p. 718 [*G. michaleti; OD]. Test small, elongate posteriorly; sternum raised to form rostrum; ambulacra similar, nonpetaloid, pores in center of plates; indistinct subanal fasciole. *Paleog.(Dan.),* Fr.——FIG. 416,2. *G. michaleti; aboral, ×1.3 (203c).

**Guettaria** GAUTHIER, 1888, p. 532 [*G. angladei; OD]. Frontal notch very deep, posterior concavely truncate; ambulacrum III deeply sunken adorally, pores small, separated by granule, pairs oblique; paired ambulacra subpetaloid, anterior pore series small, round, posterior series larger, elongate; ocular plates II and IV each with 2 supplemental genital pores; plastron orthosternous; marginal fasciole. *U. Cret. (Cenoman.-Senon.),* N. Afr.-Madag.; *Senon.,* Timor.——FIG. 417,*8*. *G. angladei, Senon., Alg.; *8a,b,* aboral, oral, ×0.7; *8c,* apical system, ×2 (136h).

**Hagenowia** DUNCAN, 1889, p. 210 [*Cardiaster rostratus FORBES, 1852, p. 3; OD] [=*Martinosigra* NIELSON, 1942, p. 163 (obj.); *Hagenovia* GREGORY, 1900, p. 321 *(nom. null.)*]. Similar to *Infulaster* but with vertex forming slender rostrum; apical system at vertex, genital pores in genital plates 2 and 4; ambulacrum III sharply sunken, plates high. *U.Cret.(Santon.-Campan.),* N.Eu.——FIG. 417,*3*. *H. rostrata (FORBES), Santon., Eng.; *3a,* oblique lat., ×1 (211b); *3b,* apical system (expanded), ×10 (225).

**Hemipneustes** AGASSIZ, 1836, p. 183 [*Spatangus radiatus LAMARCK, 1840, p. 331 (=*Spatangus striatoradiatus LESKE, 1778, p. 234); OD]. Ambulacrum III sunken, pores small, round; paired ambulacra subpetaloid, anterior pore series small, round, posterior pore series with inner pore small, round, and outer pore elongate; peristome semilunar, labrum well marked; prominent phyllodes; plastron of large, cuneiform, alternating plates; no fascioles. *U.Cret.(Senon.-Maastricht.),* Eu.-N.Afr.-Madag.-India.——FIG. 417,*1*. *H. striatoradiatus (LESKE), Senon., Fr.; *1a,b,* aboral, oral, ×0.5 (142).

**Infulaster** DESOR, 1858, p. 347 [*Cardiaster hagenowi D'ORBIGNY, 1853, p. 143 (=*Spatangus excentricus WOODWARD, 1833, p. 37); SD LAMBERT, 1917, p. 29]. Conical, vertex anterior; ambulacrum III sharply depressed, ambulacra nonpetaloid, pores minute; periproct, at top of posterior concavity; peristome anterior; plastron metasternal; marginal fasciole. *U.Cret.(Turon.-Coniac.),* Eu.——FIG. 417,*4*. *I. excentricus (WOODWARD), Turon., Ger.; *4a-c,* oral, lat., frontal, ×1 (142).

**Ismidaster** BOEHM, 1927, p. 194 [*I. toulai; OD]. Like *Echinocorys* except ambulacra subpetaloid, pores conjugate. *U.Cret.(Senon.),* Asia Minor.

**Jeronia** SEUNES, 1888, p. 809 [*J. pyrenaica; OD]. Large, posterior end pointed; ambulacra similar, not sunken, nonpetaloid; pores small, round, in oblique pairs at center of adoral border of plates; apical system irregular, no pore in genital plate 2, plates 2 and 3 may be fused, some species with complemental plate in center; periproct inframarginal; peristome deeply sunken; plastron narrow; no fascioles. *Paleog.(Dan.),* Pyrenees.——FIG. 417,*5*. *J. pyrenaica; aboral, ×0.7 (219a).

**Labrotaxis** CASEY, 1960, p. 260 [*Holaster (Labrotaxis) cantianus; OD]. Like *Holaster* except plastron primitive meridosternous, almost protosternous. *Cret. (Alb.-Cenoman.),* Eu.——FIG. 417,*7*. *L. cantianus (CASEY), Alb., Eng.; oral, ×0.6 (179a).

**Lampadaster** COTTEAU, 1889, p. 87 [*L. grandidieri; OD]. Large, aboral side subconical; ambulacrum III sunken: paired ambulacra subpetaloid, outer pore more elongate than inner pore, pores of pair in circumflex; genital plates 2 and 4 usually with 2 genital pores; periproct inframarginal; peristome at end of deep frontal furrow; no fascioles. *U.Cret.(Senon.),* Madag.——FIG. 417,*2*. *L. grandidieri; aboral, ×0.4 (203a).

**Lampadocorys** POMEL, 1883, p. 46 [*Holaster sulcatus COTTEAU, 1873, p. 170; OD]. Highly inflated aborally; ambulacrum III deeply sunken adorally, all pore zones alike, outer pore elongate, inner pore round; plates of plastron low, regularly alternating; no fascioles. *U.Cret.(Cenoman.-Senon.),* Eu.(Fr.-Italy)-N.Afr.——FIG. 417,*6*. *L. sulcatus (COTTEAU), Cenoman., Alg.; *6a,b,* lat., oral, ×1 (26).

**Messaoudia** LAMBERT, 1917, p. 4 [*Holaster pyriformis PERON & GAUTHIER, 1878, p. 87; OD]. Similar to *Zumoffenia* but smaller and higher, and both ambulacral pores round. *U.Cret. (Cenoman.),* Alg.

**Offaster** DESOR, 1858, p. 333 [*Ananchytes pilula LAMARCK, 1816, p. 27; SD QUENSTEDT, 1874, p. 606]. Test small, subglobular; ambulacra alike, not depressed, nonpetaloid, plates high, pores small, round; periproct above marginal fasciole. *U. Cret. (Campan.)-Paleog. (Dan.),* Eu.——FIG. 418,*1*. *O. pilula (LAMARCK), Senon., Fr.; *1a-c,* aboral, oral, lat., ×1 (142).

**Opisopneustes** GAUTHIER, 1889, p. 2 [*O. cossoni; OD]. Ambulacrum III deeply sunken, pores small, round, obliquely arranged, pores of each pair separated by granule; paired ambulacra petaloid, curved, anterior series of pores small, round, equal, posterior series with inner pore round, outer pore elongate; periproct in deep depression; peristome

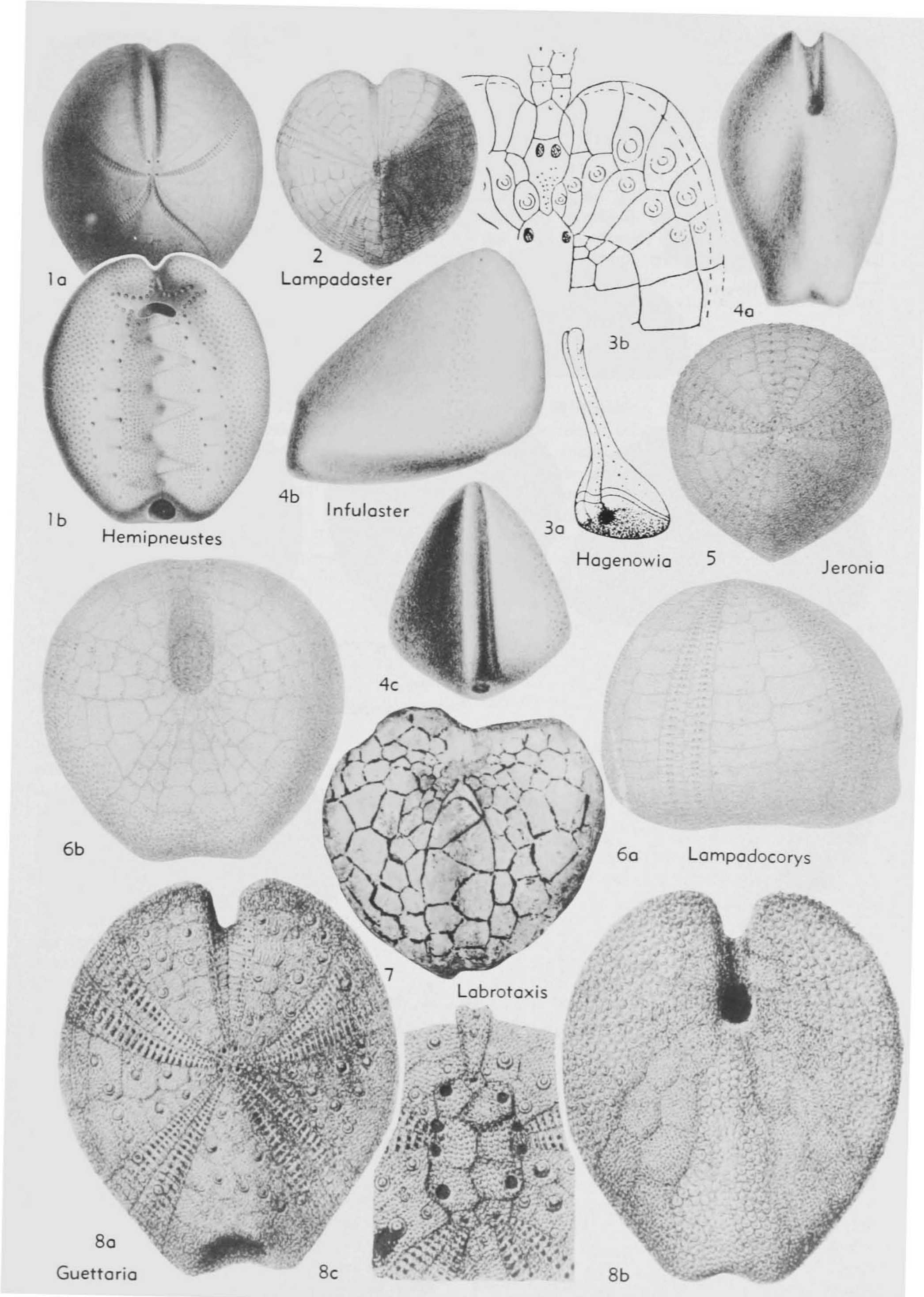


FIG. 417. Holasteridae (p. U530).

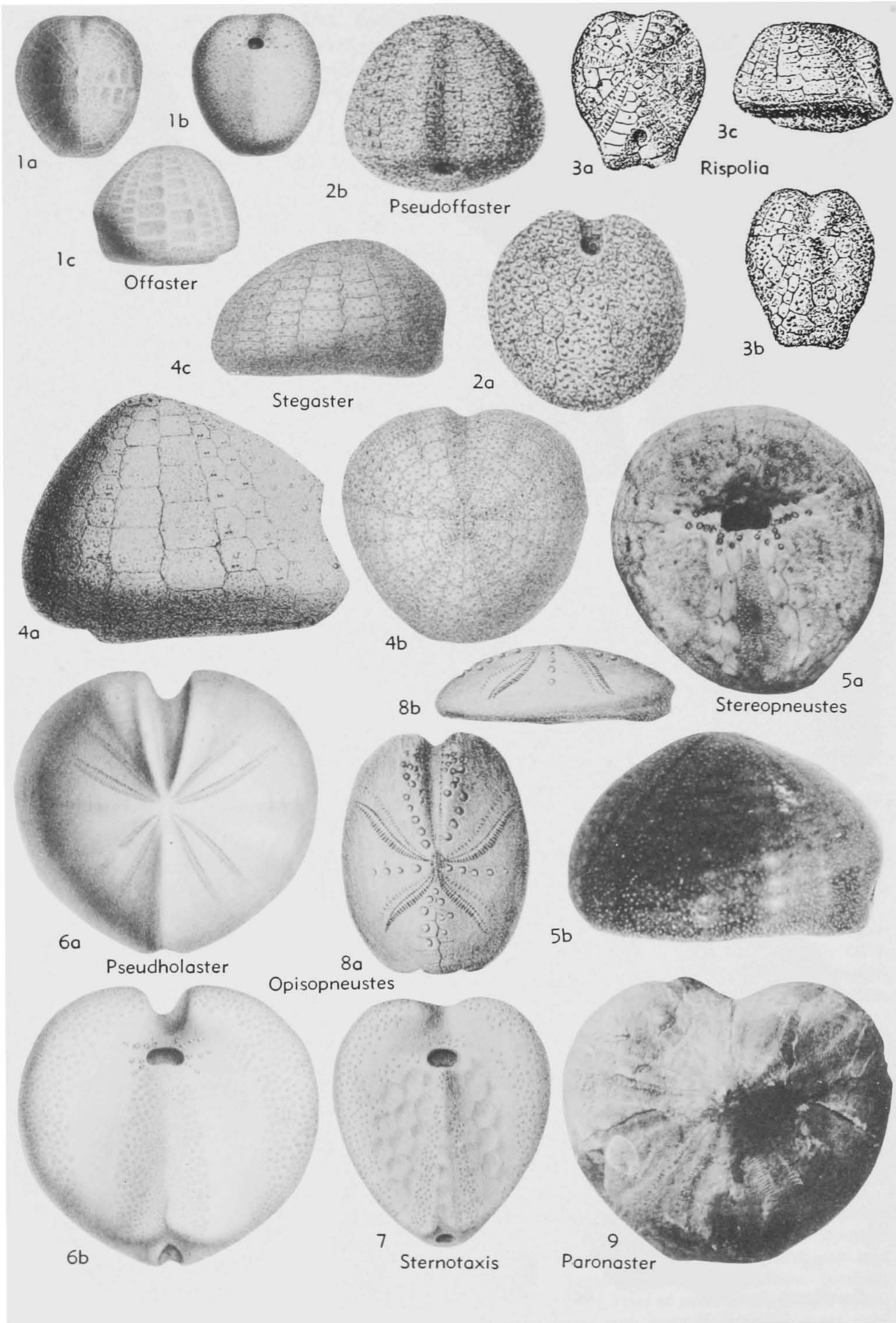


FIG. 418. Holasteridae (p. U530, U533).

anterior, broad, labrum prominent; large scrobiculate tubercles on each side of ambulacrum III, similar large tubercles at mid-line of other interambulacra; marginal fasciole. *U.Cret.(Senon.)*, Tunisia.——FIG. 418,*8*. **O. cossoni*; *8a,b*, aboral, lat., ×0.7 (66).

**Paronaster** AIRAGHI, 1906, p. 107 [**P. cupuliformis*; OD]. Test large, cordate, apical area sharply raised; ambulacrum III narrower than paired ambulacra, pores of outer series transversely elongate; peristome anterior, labiate; fascioles unknown. *Cret.*, Italy.——FIG. 418,*9*. **P. cupuliformis*; aboral, ×0.5 (176).

**Pseudananchys** POMEL, 1883, p. 45 [**Ananchytes algiris* COQUAND, 1862, p. 240; OD] [=*Craginaster* LAMBERT, 1903, p. 219 (type, *Holaster completa* CRAGIN, 1893, p. 155)]. Like *Echinocorys* except pores of ambulacra transversely elongate, outer pore longest, ambulacral plates lower; peristome may be labiate. *Cret.(Alb.-Senon.)*, Medit.-Iran.

**Pseudholaster** POMEL, 1883, p. 45 [**Holaster bicarinatus* AGASSIZ, 1847, p. 29; SD LAMBERT, 1917, p. 20]. Test large, as in *Holaster* except outer pores of posterior series of petals transversely elongate, petals broad; ambulacrum III deeply sunken, adjoining interambulacra forming sharp keels. *Cret.(Apt.-Senon.)*, Medit.-Madag.——FIG. 418,*6*. **P. bicarinatus* (AGASSIZ), Senon., Fr.; *6a,b*, apical, oral, ×0.5 (142).

**Pseudoffaster** LAMBERT, 1924, p. 413 [**Holaster caucasicus* DRU, 1884, p. 63; OD]. Small; ambulacrum III deeply depressed adorally, pores small, round; pores of paired ambulacra larger, subelliptical; plastron unknown; some larger, scrobiculate tubercles orally and on ambulacrum III; marginal fasciole. *U.Cret.(Maastricht.)*, Spain-Caucasus.——FIG. 418,*2*. **P. caucasicus* (DRU), Caucasus; *2a,b*, oral, frontal, ×1.5 (188).

**Rispolia** LAMBERT, 1917, p. 27 [**Nucleolites subtrigonatus* CATULLO, 1827, p. 226; OD]. Ambulacrum III sunken, pores small; paired ambulacra not sunken, pores transversely elongate, anterior pore series smaller than posterior; peristome labiate; marginal fasciole. *U.Cret.(Campan.-Maastricht.)*, Italy-N.Afr.(Alg.-Tunisia)-Madag. —— FIG. 418,*3*. **R. subtrigonata* (CATULLO), Campan., Tunisia; *3a-c*, aboral, oral, lat., ×1 (195b).

**Scagliaster** MUNIER-CHALMAS, 1891, p. 11 [**Ananchytes concavus* CATULLO, 1827, p. 6; OD]. Like *Echinocorys* except ambulacrum III sunken; some larger tubercles above ambitus; aboral side low, arched, orally flat or concave; *U.Cret.*, Italy.

**Stegaster** POMEL, 1883, p. 48 [**Cardiaster gillieroni* DE LORIOL, 1873, p. 4; OD] [=*Seunaster* LAMBERT in BLAYAC, 1912, p. 385 (type, *Holaster bouillei* COTTEAU in DE BOUILLE, 1873, p. 24); *Synochitis* LAMBERT, 1917, p. 30]. Ambulacra nonpetaloid, plates fairly high, pore pairs at adoral center of plates, ambulacrum III deeply sunken; peristome at end of deep frontal sulcus; plastron ?orthosternous; no fascioles. *U.Cret.(Senon.)*, Eu.-N.Afr.-Madag.——FIG. 418,*4a*. **S. gillieroni* (DE LORIOL), Switz.; lat., ×1 (119). ——FIG. 418,*4b,c*. *S. cotteaui* SEUNES, Fr.; aboral, lat., ×0.7 (219b).

**Stereopneustes** DE MEIJERE, 1902, p. 9 [**S. relictus*; OD]. Ambulacra not sunken, ambulacrum III narrower than paired ambulacra; pores equal, obliquely arranged in ambulacrum III; labrum not well developed; phyllodes distinct; subanal fasciole; globiferous, tridentate, ophicephalous, and triphyllous pedicellariae. *Rec.*, Japan-E.Indies.——FIG. 418,*5*. **S. relictus*, E.Indies; *5a,b*, oral, lat., ×0.7 (*5a*, 136h; *5b*, 208).

**Sternotaxis** LAMBERT, 1893, p. 95 [**Spatangus planus* MANTELL, 1822, p. 192; OD] [=*Plesiocorys* POMEL, 1883, p. 45 (type, *Holaster placenta* AGASSIZ in AGASSIZ & DESOR, 1847, p. 27)]. Aboral side highly inflated, frontal depression slight; pores of ambulacrum III small, round; pores of paired ambulacra smaller; 4 genital pores; periproct elongate oval, on posterior end; peristome anterior, semicircular; plastron as in *Cardiotaxis*; no fascioles. *U.Cret.(Turon.-Senon.)*, Eu.(Fr.-Eng.).——FIG. 418,*7*. **S. planus* (MANTELL), Turon., Eng.; oral, ×0.7 (173).

**Taphraster** POMEL, 1883, p. 46 [**Holaster campicheanus* (D'ORBIGNY); *1a,b*, aboral, oral, ×1; irregularly ovoid, sternum raised; ambulacra sunken on oral and aboral side, ambulacrum III more deeply depressed; pores small, round, pores of pair separated by granule; ?no fascioles. *L.Cret.(Neocom.)*, Switz.——FIG. 419,*1*. **T. campicheanus* (D'ORBIGNY); *1a,b*, aboral, oral, ×1; *1c*, detail of ambulacrum, enlarged (142).

**Tholaster** SEUNES, 1890, p. 23 [**Gibbaster munieri* SEUNES, 1889, p. 819; OD] [=*Gibbaster* SEUNES, 1889, p. 819 (obj.) (*non* GAUTHIER, 1887)]. Ambulacrum III deeply sunken; ambulacra nonpetaloid, pores small, round; plastron apparently orthosternous; some large, crenulate tubercles on interambulacra aborally; no fascioles on type-species. *U.Cret.(Maastricht.)*, Eu.(Fr.-Belg.).——FIG. 419,*3*. **T. munieri* (SEUNES), Fr.; *3a-c*, aboral, oral, lat., ×1 (219c).

**Titanaster** SZÖRÉNYI, 1929, p. 19 [**T. labiostoma*; OD]. Diagnosis unknown, referred to Holasteridae. *Eoc.*, Eu.——FIG. 419,*5*. **T. labiostoma*, Hung.; aboral, ×0.5 (136h, after Szörényi).

**Toxopatagus** POMEL, 1883, p. 30 [**Hemipneustes italicus* MANZONI, 1878, p. 156; OD] [=*Heteropneustes* POMEL, 1883, p. 46 (type, *H. deletrei*)]. Ambulacrum III deeply sunken, pores small, round, not conjugate; paired ambulacra petaloid, posterior pair shorter than anterior pair; posterior pore series larger than anterior pore series, pores transversely elongate, conjugate; labrum highly developed; no fascioles. *U.Cret.(Senon.)-Neog.(Mio.)*, Eu.-Iran-Madag.-W.Indies.——FIG. 419,*4*. **T. italicus* (MANZONI), Mio., Italy; *4a-c*, aboral, lat., oral, ×0.7 (206a).

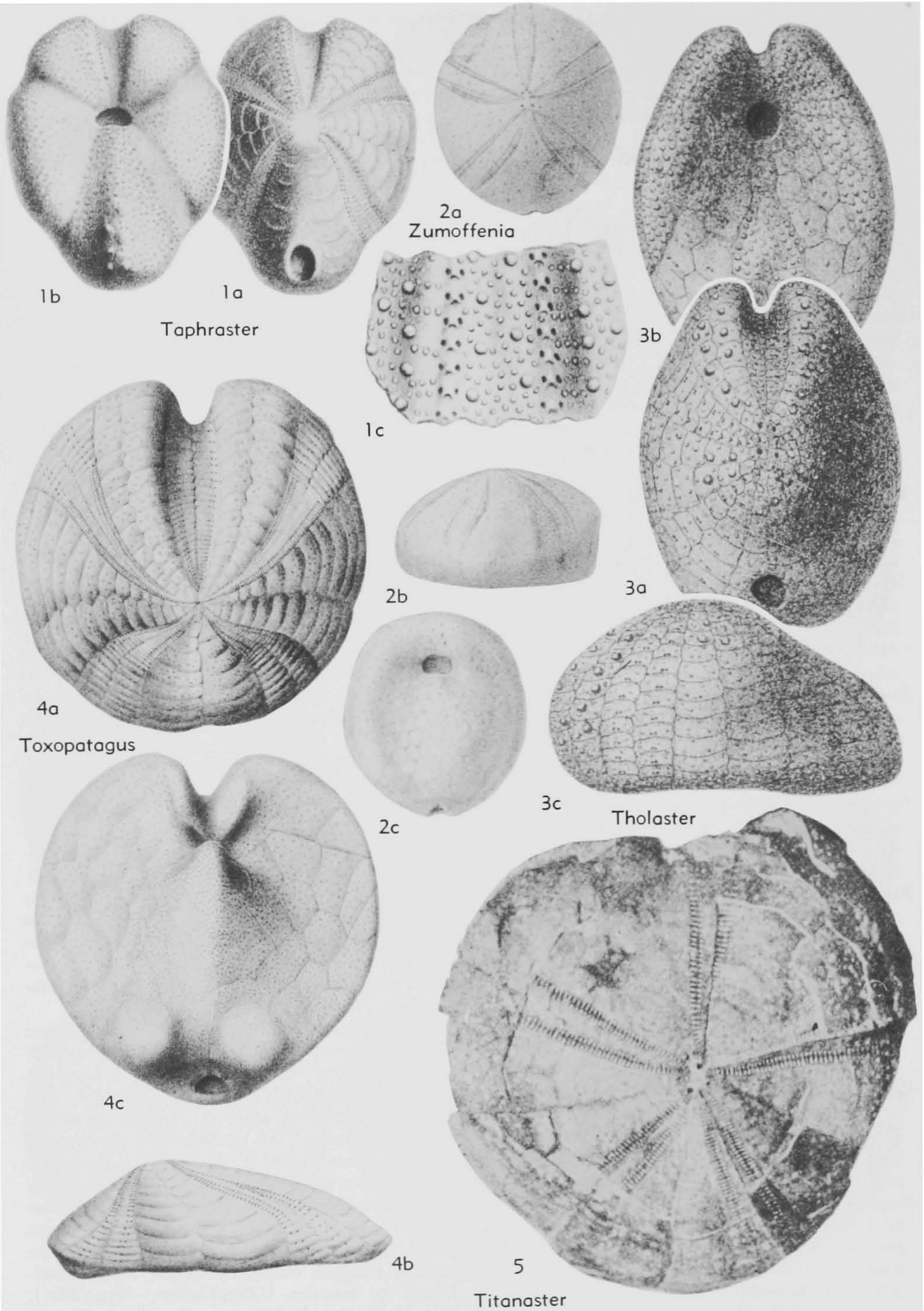


Fig. 419. Holasteridae (p. U533, U535).

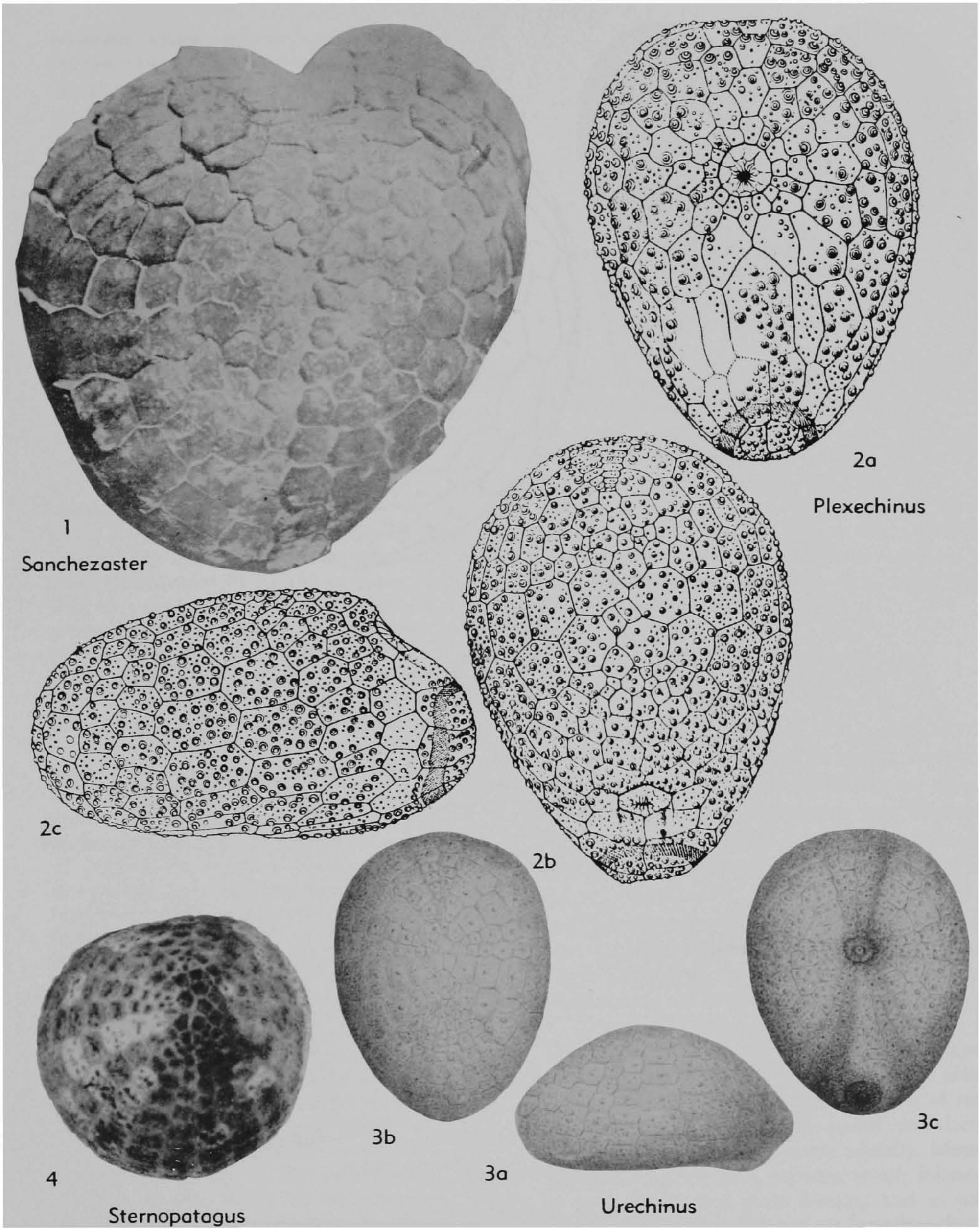


FIG. 420. Urechinidae (p. *U536-U537*).

**Zumoffenia** FOURTAU, 1912, p. 50 [**Z. ludovici*; OD]. Test small; ambulacra similar, pores conjugate, outer pore elongate, not sunken; periproct on truncate posterior; apparently no fascioles. *U.Cret.(Cenoman.)*, Syria.——FIG. 419,*2*. **Z. ludovici*; *2a-c*, aboral, lat., oral, ×1 (192).

## Family URECHINIDAE Duncan, 1889

Test thin, plastron meridosternous; oculars II and IV juxtaposed; paired ambulacra with single pores adapically; first postprimordial interambulacral plate single; mostly

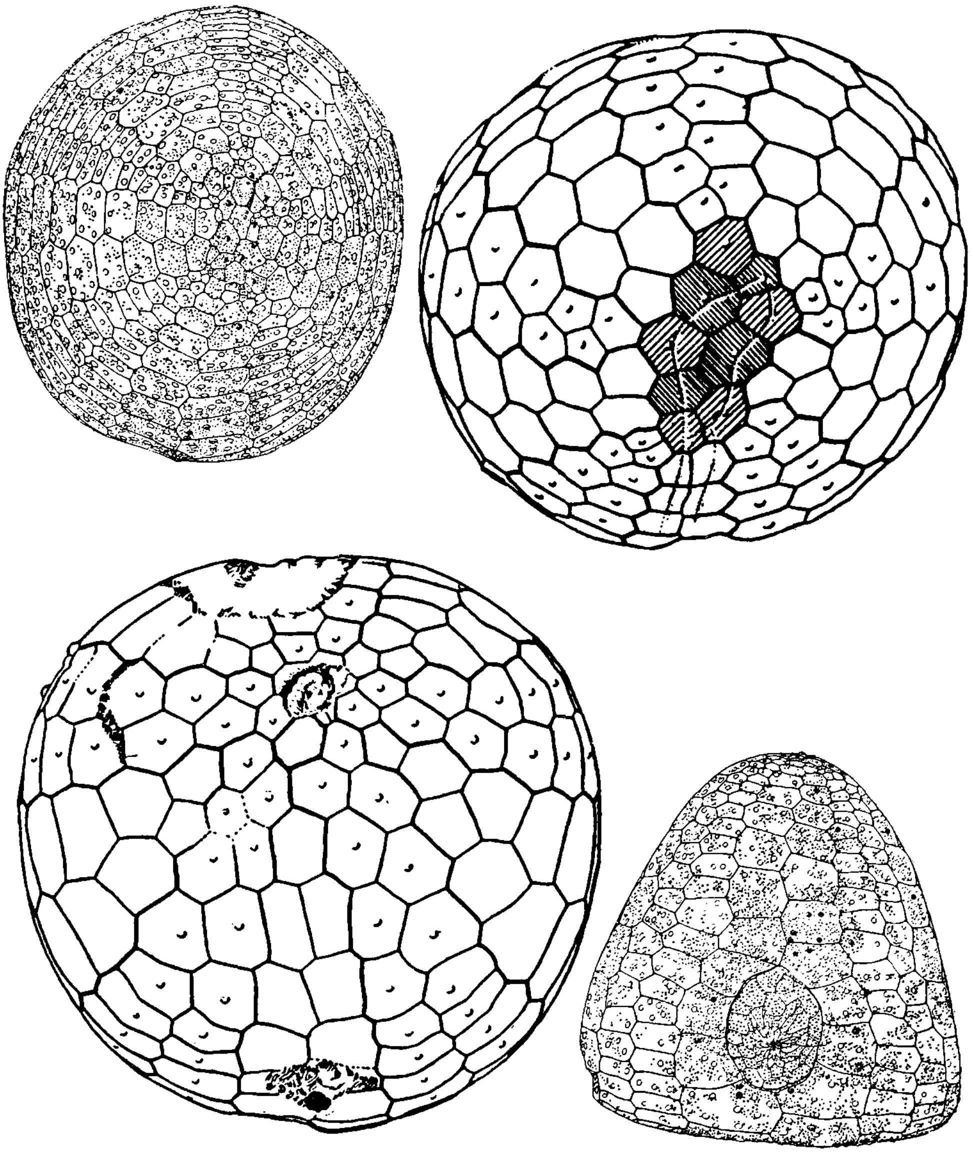

FIG. 421. Urechinidae (p. U536-U537).

with subanal or marginal fasciole. *?U.Eoc., Mio.-Rec.*

**Urechinus** A. AGASSIZ, 1879, p. 207 [**U. naresianus*; OD] [=*Cystechinus* A. AGASSIZ, 1879, p. 207 (type, *C. wyvillei*)]. Ambulacra similar, non-petaloid, anterior and posterior genital plates widely separated, 3 or 4 genital pores; periproct round or elongate, with numerous small plates; peristome not labiate; phyllodes inconspicuous, bourellets incipient; subanal fasciole indistinct, may be lacking; spines short, simple, irregularly arranged; one primary tubercle on each plate; globiferous, tridentate, ophicephalous, and triphyllous pedicellariae. [Bathyal.] *Rec.,* Atl.-N.Pac.-Antarctic.——FIG. 420,*3*. **U. naresianus*, Antarctic; *3a-c,* lat., apical, oral, ×0.7 (2).

**Chelonechinus** BATHER, 1934, p. 799 [**C. suvae*; OD]. Plates very large, mostly high, hexagonal ambulacral plates nearly as tall as interambulacrals, pores small, apparently single, in center of plates; apical system elongate, oculars II and IV not meeting, madreporite minute; periproct marginal;

peristome round, anterior; primordial plates of interambulacra 1, 4, and 5 separated from following plates by enlargement of adjacent ambulacra; no large primary tubercles; no fascioles. *Mio.*, Fiji-Java-Barbados.——FIG. 421,*2*. **C. suvae*, Fiji; *2a,b*, aboral, oral, ×1 (178).

**Pilematechinus** A. AGASSIZ, 1904, p. 163 [**Cystechinus rathbuni* A. AGASSIZ, 1898, p. 79; OD]. Test large, thin, flexible; ambulacra simple, plates high; 3 or 4 genital pores, anterior genital plates separated from posterior by oculars II and IV; periproct supramarginal; phyllodes present; plastron not well developed; tubercles irregularly arranged; no fascioles; globiferous, tridentate, ophicephalous and triphyllous pedicellariae; auricles moderately developed. [Bathyal.] *Rec.*, Panama-Antarctica.——FIG. 421,*1*. **P. rathbuni* (A. AGASSIZ), Malpelo Is.; *1a,b*, apical, post., ×0.7 (3).

**Plexechinus** A. AGASSIZ, 1896, p. 78 [**P. cinctus*; OD]. Interambulacrum 5 with adapical keel extending into subanal snout; periproct supramarginal; ambulacrum III with more plates adapically than in paired ambulacra; 2 or 4 genital pores, genital plates 2 and 4 may be fused; labrum may be separated from succeeding plate by enlargement of adjacent ambulacra; rudimentary phyllodes; subanal fasciole; primary and secondary tubercles irregularly arranged; globiferous, tridentate, ophicephalous, and triphyllous pedicellariae. *Rec.*, N.Atl.-Antarctica-Sulu Sea-Gulf Calif. ——FIG. 420,*2*. **P. cinctus*, Gulf Calif.; *2a-c*, oral, apical, lat., ×3 (3).

**Sanchezaster** LAMBERT in SÁNCHEZ ROIG, 1924, p. 13 [**S. habanensis*; OD]. Corona very large, cordate; aboral ambulacral and interambulacral plates high hexagonal; ambulacra nonpetaloid, pores minute, round, in center of plates; structure of apical system unknown; periproct sunken, inframarginal; peristome anterior, transversely elliptical; plastron orthosternous; tuberculation fine; marginal fasciole. *?U.Eoc.*, Cuba.——FIG. 420,*1*. **S. habanensis*; aboral, ×0.5 (216a).

**Sternopatagus** DE MEIJERE, 1902, p. 10 [**S. sibogae*; OD]. Test very fragile; ambulacra similar, nonpetaloid, plates large, pores single; apical system elongate, 4 genital pores; peristome anterior, at end of frontal furrow, labiate, buccal membrane vertical; plastron small, labrum separated from succeeding plates by enlargement of adjacent ambulacra; all tubercles small, perforate, crenulate; "submarginal" fasciole. *Rec.*, Timor Sea.——FIG. 420,*4*. **S. sibogae*; aboral, ×0.5 (208).

## Family CALYMNIDAE Mortensen, 1907

Plastron meridosternous; ambulacra with single pores; interambulacra 2 and 3 with first postprimordial plates paired; peristome not in groove. *Rec.*

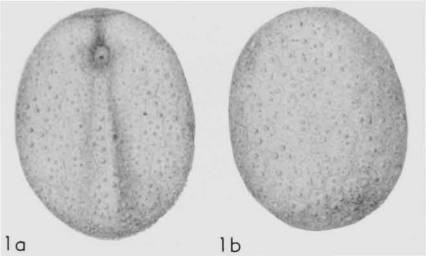


FIG. 422. Calymnidae (p. U537).

**Calymne** THOMSON, 1877, p. 396 [**C. relicta*; OD]. Ovoid, test thin, plastron raised; ambulacra similar, plates as large as interambulacral plates; 2 genital pores; apical system apparently disjunct, exact structure unknown; peristome not labiate; spatulate spines on plastron, around periproct and posteriorly; marginal fasciole on oral side anteriorly, above periproct posteriorly; pedicellariae rostrate, of 2 types. *Rec.*, Bermuda.——FIG. 422,*1*. **C. relicta*; *1a,b*, oral, aboral, ×0.5 (2).

## Family POURTALESIIDAE A. Agassiz, 1881

Bottle-shaped; plastron meridosternous; ambulacra with single pores except adorally in some genera; frontal ambulacrum forming deep groove to peristome; interambulacra 1 and 4 meeting adapically; subanal fasciole. [Sublittoral to hadal, mostly bathyal.] *Rec.*

**Pourtalesia** A. AGASSIZ, 1869, p. 272 [**P. miranda*; OD] [=*Phyale* POMEL, 1883, p. 40 (type, *Pourtalesia jeffreysi* THOMSON, 1873, p. 108) (*non Phyale* KOCH, 1847); *Phyalopsis* POMEL, 1883, p. 40 (type, *Pourtalesia laguncula* AGASSIZ, 1879, p. 205)]. Test small to medium-sized, bottle-shaped posterior rostrate, very fragile; ambulacral plates almost as high as interambulacrals; plates of ambulacrum III lower than in paired ambulacra, ambulacra I and V discontinuous adorally, labrum separated from sternum, sternum small, followed by pair of episternal plates forming keel to subanal rostrum, adapical plates of interambulacrum 5-paired; genital plates usually compact, 4 genital pores; ambulacrum III without spheridia; spines uniform or long, curved, stout and may be serrate; tubercles perforate, crenulate; fasciole around anal rostrum; tridentate, globiferous, rostrate, and ophicephalous pedicellariae; tube feet simple. *Rec.*, cosmop.——FIG. 423,*2a*. **P. miranda*, Florida Str.; lat., ×2.3 (1).——FIG. 423,*2b,c*. *P. jeffreysi* THOMSON, off Norway; *2b,c*, aboral, oral, ×3 (123).

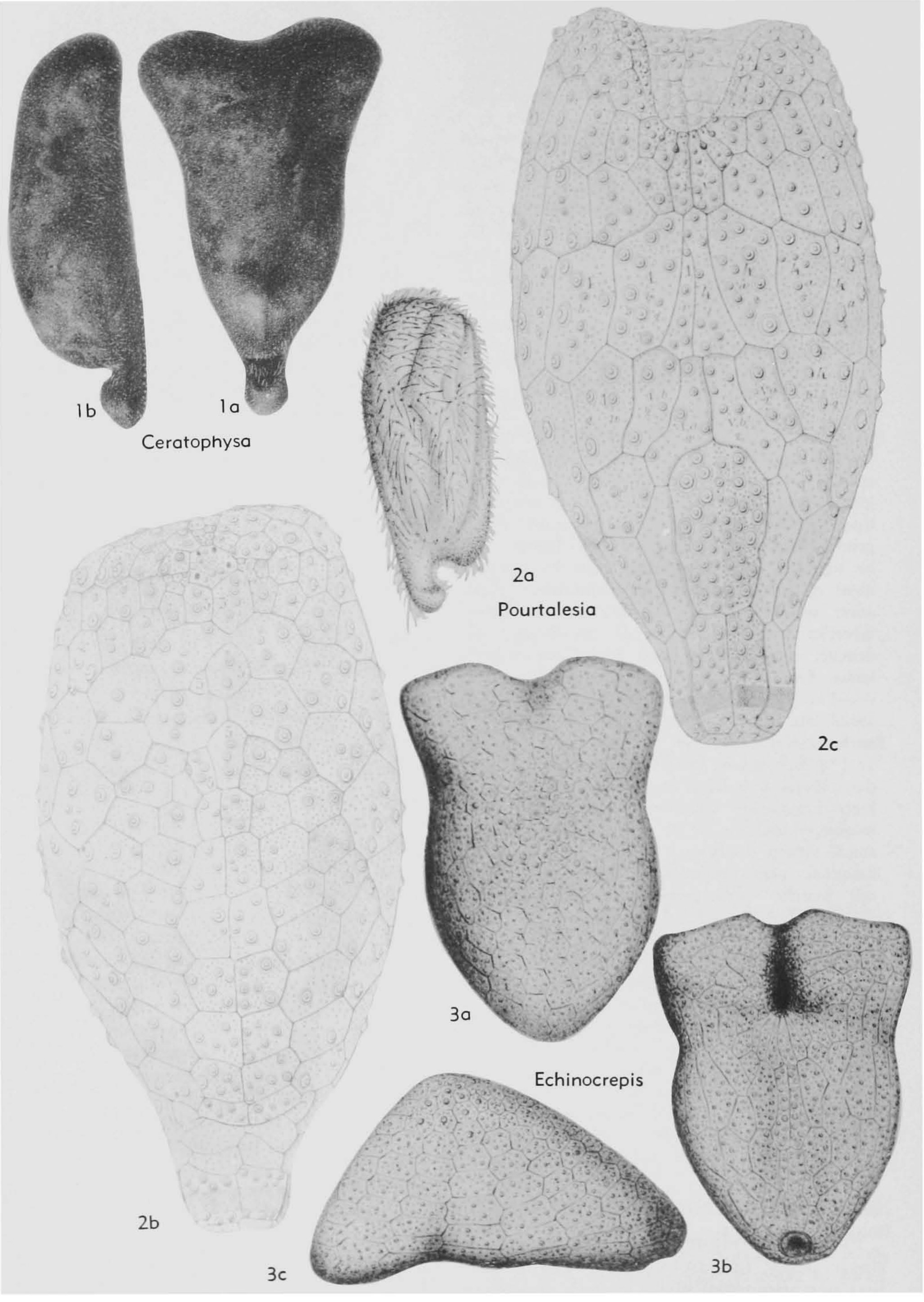


Fig. 423. Pourtalesiidae (p. U537, U539).

**Ceratophysa** Pomel, 1883, p. 40 [**Pourtalesia ceratopyga* A. Agassiz, 1879, p. 205; SD Mortensen, 1907, p. 82] [=*Rodocystis* Lambert & Thiéry, 1924, p. 424 (obj.)]. Large, outline triangular, orally flattened; genital plates partly coalesced, 4 genital pores; periproct posterior, above rostrum; peristome anterior; adoral structure of bivial ambulacra unknown; labrum large, sternum faintly raised, plates of interambulacrum 5 alternating aborally; spines small, dense; subanal fasciole; globiferous, tridentate, and ophicephalous pedicellariae. *Rec.,* Antarctic-S. Ind. O.-Chile.——Fig. 423,*1*. **C. ceratopyga* (A. Agassiz), S.Pac.; *1a,b,* aboral, lat., ×0.7 (2).

**Cystocrepis** Mortensen, 1907, p. 84 [**Echinocrepis setigera* A. Agassiz, 1898, p. 78; OD]. Similar to *Echinocrepis* but outline elongate oval; interambulacra 1 and 4 meet at mid-line adorally; labrum rudimentary; posterior genital plates not coalesced with anterior pair; long spines aborally; tridentate, rostrate, and ophicephalous pedicellariae. [Bathyal.] *Rec.,* Panama.

**Echinocrepis** A. Agassiz, 1879, p. 206 [**E. cuneata*; OD]. Large, outline irregularly triangular, aboral side pyramidal, vertex anterior, anterior irregularly truncate; ambulacra of trivium somewhat sunken, bivial ambulacra apparently continuous on oral side; labrum separated from sternum; apical system compact, three genital pores; plates of interambulacrum 5 alternating aborally; numerous fine spines, few adapical interambulacral plates each with single larger spine; no subanal fasciole; tridentate pedicellariae. *Rec.,* Antarctic.——Fig. 423, *3*. **E. cuneata*; *3a-c,* aboral, oral, lat., ×0.7 (2).

**Echinosigra** Mortensen, 1907, p. 82 [**Pourtalesia phiale* Thomson, 1873, p. 90; OD]. Similar to *Pourtalesia* but more elongate; ambulacra I and V continuous; labrum large, conspicuous; primary spines short, partly spatulate. [Bathyal.] *Rec.,* cosmop.——Fig. 424,*2*. **E. phiale* (Thomson), N.Atl.; *2a-c,* aboral, lat., oral, ×5 (135).

**Helgocystis** Mortensen, 1907, p. 82 [**Pourtalesia carinata* A. Agassiz, 1879, p. 205; OD]. Large; ambulacra of bivium continuous, adoral ambulacral plates with 2 pores each; labrum large, widening posteriorly, separated from sternum; plates of interambulacrum 5 alternating; 4 genital pores, genital plates not compact; globiferous, rostrate, tridentate, and ?ophicephalous pedicellariae. *Rec.,* Antarctic-Subantarctic-Chile.

**Spatagocystis** A. Agassiz, 1879, p. 206 [**S. challengeri;* OD]. Very fragile; posterior pointed; plastron keeled, forming subanal rostrum, periproct submarginal; genital plates separate, 4 genital pores; ambulacra I and V discontinuous; labrum small, separated from sternum; plates of interambulacrum 5 small, alternating; subanal fasciole; rostrate and two types of tridentate pedicellariae. *Rec.,* Antarctic-S.Ind.O.——Fig. 424,*1*. **S. challengeri,* Antarctic; *1a,* lat., ×0.7 (2); *1b,* oral, ×1 (3).

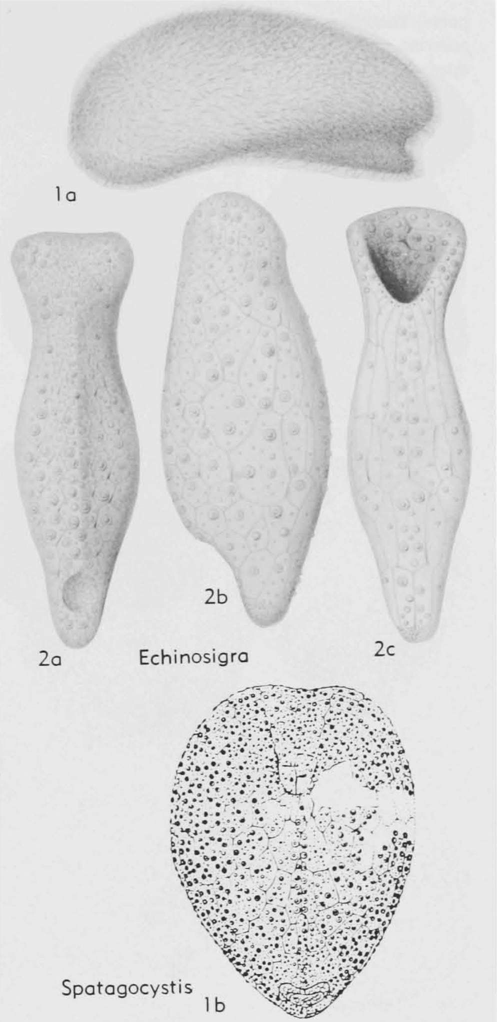


Fig. 424. Pourtalesiidae (p. *U*539).

## Family STENONASTERIDAE Lambert, 1922

Interambulacrum V protosternous; ambulacra with double pores, not petaloid; apical system without complemental plates, ethmophract, not elongate. *U.Cret.*

**Stenonaster** Lambert, 1922, p. 114 [**Ananchytes tuberculata* Defrance, 1816, p. 41; OD] [=*Stenonia* Desor, 1858, p. 333 (obj.) (*non* Gray, 1853); *Stenocorys* Lambert & Thiéry, 1917, p. 3 (obj.)]. Subconical aborally, flattened orally, with sunken peristome; ambulacra similar, pores somewhat elongate, those of pair arranged in circumflex, pores of oral side large, single, vertically elongate; apical system with 4 genital pores, central; periproct inframarginal; peristome anterior, subpentagonal; labrum not well developed; no fascioles. *U.Cret.*, Medit.——Fig. 425,4. **S. tuberculata* (Defrance), Italy *(4a-c)*, Tunisia *(4d,e)*; *4a-c*, aboral, oral, lat., ×0.7 (142); *4d,e*, apical system, plastron, enlarged (136h).

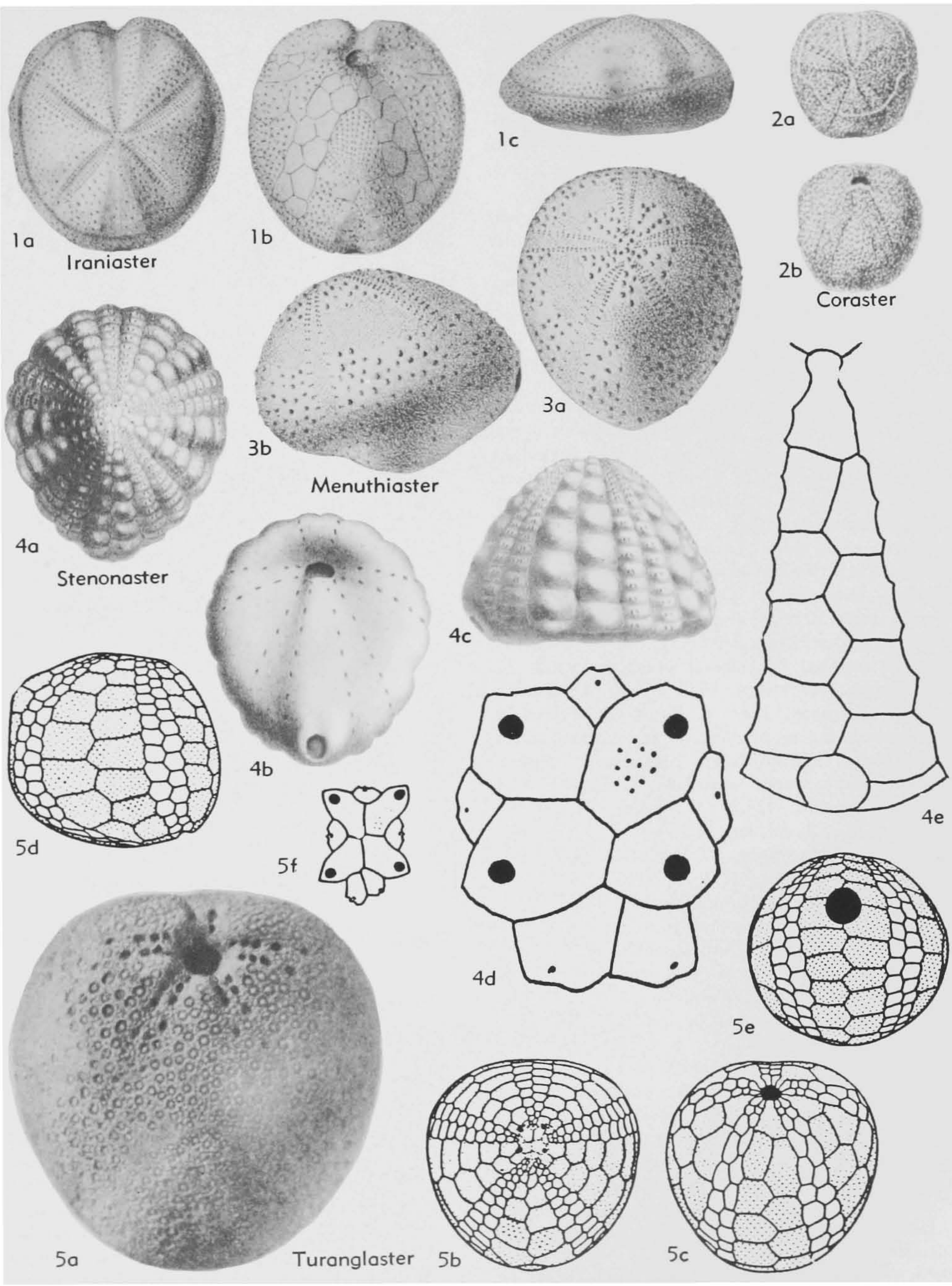


Fig. 425. Stenonasteridae *(4)*; Somaliasteridae *(1)*; Family Uncertain *(2-3,5)* (p. U539-U543).

## Family SOMALIASTERIDAE Wagner & Durham, n. fam.

Plastron meridosternous, labrum typically separated from succeeding interambulacral plates by meeting of adjacent ambulacra at mid-line adorally; paired ambulacra petaloid; apical system ethmophract or ethmolytic, not elongate; peripetalous fasciole present. *U.Cret.(Senon.)-Paleoc.*

**Somaliaster** Hawkins, 1935, p. 53 [**S. magniventer*; OD]. Test inflated aborally, plastron raised, outline subcircular, with faint frontal depression, test commonly asymmetrical with right anterior quadrant extended anteriorly; petals well developed, open, flush with test but with interporiferous zone somewhat sunken, pores of pairs equal, rounded; pores of anterior ambulacrum round, in single series; labrum with lip moderately well developed, sternal plate large, subtriangular, succeeding plastronal plates in regular alternating series, interambulacrum 1 meridoplacous, interambulacra 2, 3, and 4 amphiplacous; apical system slightly posterior, commonly tending toward ethmolytic condition, 4 genital pores; periproct horizontally elongate, on short posterior slope; peristome anterior, semilunar; primary tubercles crenulate, not arranged in regular pattern. *U.Cret.(Senon.)*, Somal.-Iran.——Fig. 425A, *2. *S. magniventer*, Somal.; *2a,b*, aboral and post. views, ×1.5; *2c*, arrangement of plates on oral side, ×0.75 (*2a,b*, 136h; *2c*, 91b).

**Brightonia** Kier, 1957, p. 871 [**B. macfadyeni*; OD]. Test small, subglobular, widest anteriorly; anterior ambulacrum slightly sunken, petals narrow, straight, pores slightly elongate, conjugate; labrum separated from succeeding interambulacral plate by meeting of adjacent ambulacra at midline, interambulacrum 1 meridoplacous, interambulacra 2, 3, and 4 amphiplacous; apical system anterior, 2 genital pores; tubercles small, crenulate, not arranged in pattern. *Paleoc.*, Somal. ——Fig. 425A,*1*. **B. macfadyeni*; *1a,b*, aboral and lat. views, both with peripetalous fasciole marked, ×1; *1c*, arrangement of plates on oral side, ×1 (94a).

**Iraniaster** Cotteau & Gauthier in Morgan, 1895, p. 26 [**I. morgani*; OD]. Test slightly longer than wide, aboral side inflated, plastron raised, anterior ambulacrum depressed, faint double keel present on aboral side in interambulacra; pores of petals transversely elongate, interporiferous zones of petaloid ambulacra depressed; pores of anterior ambulacrum small, round; apical system central, 4 genital pores; periproct on short posterior slope; labrum commonly separated from succeeding interambulacral plate by meeting of adjacent ambulacra at mid-line; peripetalous fasciole passing at some distance from tips of petals; tubercles scattered except on adoral-most area of plastron where they are arranged in more or less longitudinal rows. *U.Cret.(Senon.)*, Iran. ——Fig. 425,*1*. **I. morgani*; *1a-c*, aboral, oral, and lat. views, ×0.7 (210).

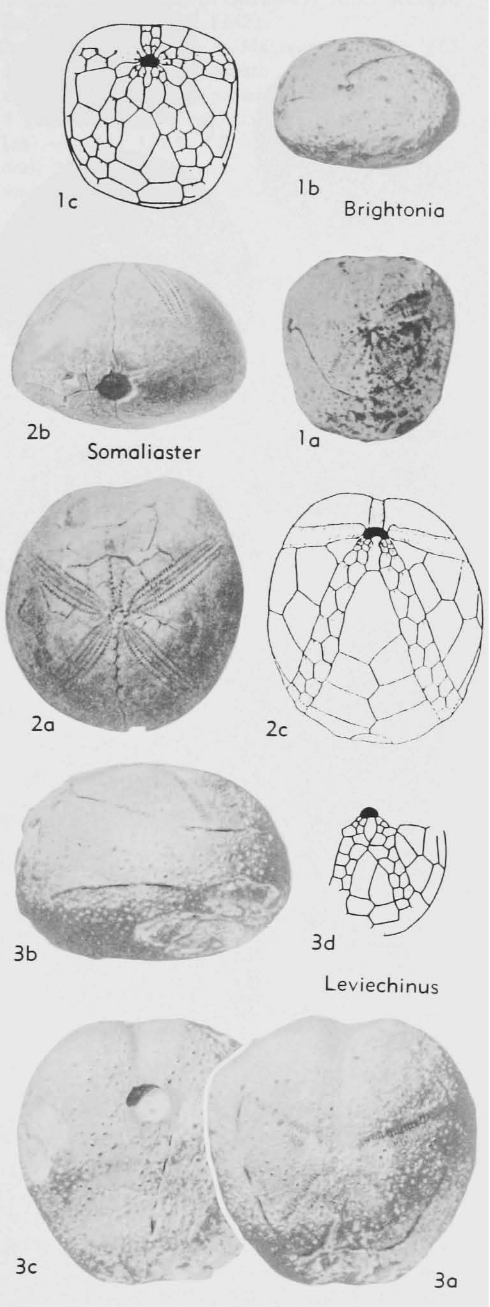


Fig. 425A. Somaliasteridae (p. U541-U542).

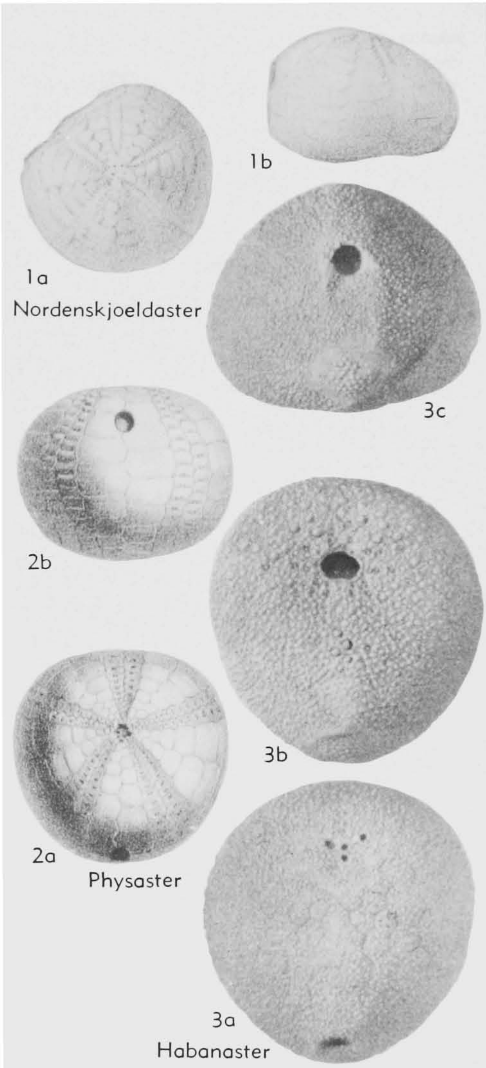


FIG. 426. Family Uncertain (p. U542-U543).

**Leviechinus** KIER, 1957, p. 873 [**Pericosmus gregoryi* CURRIE, 1927, p. 430; OD]. Test subglobular, greatest width anterior, greatest height posterior; ambulacrum III slightly sunken anteriorly, nonpetaloid, paired ambulacra petaloid, faintly depressed in large specimens; pores very elongate, conjugate, interporiferous zones narrow, anterior paired petals longer than posterior pair; second postlabrum plate of plastron extending almost as far adorally as first, labrum separated from first postlabrum plate by meeting at midline of one ambulacral plate from each adjacent column; peristome anterior, semicircular, slightly depressed; periproct elongate along III-5 axis, situated on high posterior slope partially visible from apical side; peripetalous fasciole not well developed, possibly not continuous, evidence of marginal fasciole present on some specimens; tubercles small, not arranged in regular pattern. *Paleoc.*, Somal.——FIG. 425A,*3*. **L. gregoryi* (CURRIE); *3a-c,* aboral, lat., and oral views, ×1; *3d,* plate arrangement of plastron, ×0.5 (94a).

## Family UNCERTAIN

**Coraster** COTTEAU, 1886, p. 69 [**C. vilanovae*; OD]. Small, subglobular, faint frontal depression; pores of ambulacrum III small, round; pores of paired ambulacra small, comma-shaped; apical system compact, 4 genital pores; peristome anterior, labrum well developed; periproct posterior; structure of plastron unknown; peripetalous fasciole. *U.Cret.-Paleog.(Dan.),* Medit.——FIG. 425, *2*. **C. vilanovae,* Dan., Spain; *2a,b,* aboral, oral, ×1 (136h).

**Corechinus** KONGIEL, 1936, p. 8 [**C. pulaviensis*; OD]. Test small; aboral side inflated, oral side convex; ambulacrum III deeply sunken; pores small; paired ambulacra nonpetaloid, pores larger; apical system anterior; periproct apparently inframarginal; peristome near anterior margin; fascioles not observable. *U.Cret.*, Pol.

**Habanaster** LAMBERT in SÁNCHEZ ROIG, 1924, p. 11 [**H. sanchezi*; OD]. Small, aborally highly inflated; ambulacra similar, nonpetaloid, pores minute; interambulacrum 5 discontinuous adapically; structure of apical system unknown, 2, 3, or 4 genital pores; periproct high on truncate posterior end; peristome anterior, labrum not distinct. *Eoc.*, Cuba.——FIG. 426,*3*. **H. sanchezi*; *3a-c,* aboral, oral, post., ×1 (136h).

**Menuthiaster** LAMBERT, 1896, p. 322 [**M. cotteaui*; OD]. Aborally inflated, orally slightly convex, plastron raised; apical system compact, ethmophract, 4 genital pores; periproct inframarginal; peristome rounded, labrum poorly developed; wide ambulacral fasciole; interambulacra with some large crenulate, perforate tubercles both within and without fasciole. *U.Cret.(Senon.),* Madag.——FIG. 425,*3*. **M. cotteaui*; *3a,b,* aboral, lat., ×1 (203a).

**Nordenskjoeldaster** LAMBERT, 1910, p. 9 [as *Nordenskjöldaster*] [**N. antarcticus*; OD]. Small; pores of ambulacrum III minute; pores of paired ambulacra larger, conjugate, interporiferous zones narrow; petals of bivium shorter than in trivium; apical system ethmophract, elongate; periproct posterior, high; peristome transversely elliptical, not distinctly labiate; ?no fascioles. *U.Cret. (Cenoman.),* Antarctic.——FIG. 426,*1*. **N. antarcticus*; *1a,b,* aboral, lat., ×1 (108).

**Physaster** POMEL, 1883, p. 47 [**Echinospatagus in-*

*flatus* d'Orbigny, 1854, p. 171; OD] [=*Inflataster* Anthula, 1899]. Small, subglobular; ambulacra simple, pores of ambulacrum III small, round; pores of paired ambulacra comma-shaped, 4 genital pores; periproct small, round, high up on broad ambitus; peristome subpentagonal, labrum not distinct; interambulacrum 5 simple, no plastron. *Cret. (Alb.-Senon.),* Medit.-W. Afr. (Senegal).——Fig. 426,2. **P. inflatus* (d'Orbigny), Alb., Senegal; *2a,b,* aboral, post., ×1 (142).

**Turanglaster** Solovyev & Melikov, 1963, p. 107 [**T. mazkii*; OD]. Small, subglobular, orally convex; periproct high posteriorly, subanal fasciole; 4 genital pores. *U.Cret.,* USSR(Turkmen-Azerbaijan).——Fig. 425,5. **T. nazkii,* Azerbaijan; *5a,* oral, ×3; *5b-e,* apical, oral, lat., post., ×2; *5f,* apical system, enlarged (219a).

# SPATANGOIDS

By Alfred G. Fischer
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## INTRODUCTION

Spatangoids comprise the heart urchins, *sensu stricto.* All are classed as **amphisternous,** inasmuch as their posterior ambulacral areas begin at the peristome with a single plate, the **labrum,** which is bilaterally symmetrical except in most primitive forms and followed by a pair of **sternal plates.** The sternal plates are asymmetrical and only slightly differentiated in most primitive spatangoids but symmetrically placed and quite distinct in more advanced ones, which also have succeeding plates of the plastron well differentiated and arranged in bilateral pairs.

Like some, but not all, irregular echinoids, structure of the spatangoid test follows Lovén's law, which observes that among the ten ambulacral plates adjoining the peristome five carry the normal complement of a single tube foot and the remaining five each bear two tube feet. The pair-pored plates invariably occupy positions which in Lovén's scheme of reference are designated by the symbols Ia, IIa, IIIb, IVa, and Vb (Fig. 427).

Despite their lack of jaws, spatangoids (as well as disasterids) possess internal projections on the peristomial margin (Devriés, 1960). In spatangoids these apophyses occur mainly in the posterolateral ambulacra, that on the left side (amb I) being invariably larger than the corresponding one on the right (amb V). In advanced forms the larger apophysis is developed as a long blade or tooth projecting backward. The function of this structure has not been described, but Kier (personal communication) suggests that it supports the esophagus.

As a group, spatangoids are specialized for a burrowing existence. Some live on the

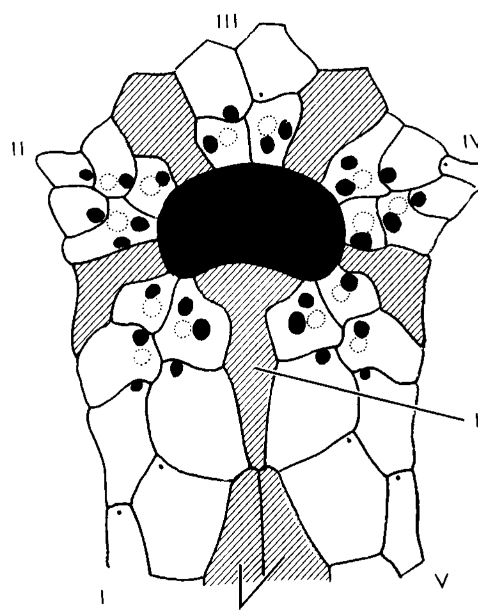



Fig. 427. Peristomial region of *Lovenia elongata* (mod. from Mortensen). [Explanation: peristome (large black area) with peristomial plates omitted; interambulacral plates shaded; *l,* labrum; *s,* sternal plates. Ambulacral plates near peristome with large feeding tube feet set into pits (black) and with spheridia set into pits (dotted); more distant ambulacral plates with thin tube feet emerging through very small pores (dot); 5 larger ambulacral plates each bearing 2 tube feet, constant in asymmetrical placement around peristome (Lovén's law).]

surface of sea-bottom sediment, but most burrow downward into it, a few descending to depths below the water-sediment interface amounting to several times their own height (Fig. 205, 206).

## FORM AND FUNCTION RELATED TO HABITAT

Life in burrows presents special problems for echinoids, and most features characteristic of spatangoid families are adaptive toward solution of these problems. One involves construction and maintenance of the burrow, which is somewhat larger in diameter than that of the animal and commonly provided with extensions. The extensions include a respiratory canal or funnel for transport of oxygenated water into the burrow and a single or double sanitary canal that functions for disposal of stale water and waste products (Fig. 205, 206). A simple burrow in coherent sediment can be excavated and maintained by a cover of short spines on the echinoid test, but burrows in loose sediment require a lining of mucus in order to remain open, and for the construction and maintenance of respiratory and sanitary canals a requirement is the presence of long prehensile tube feet or extremely long primary spines, or both.

Another problem concerns respiration. Even partial burial of the echinoid in mud or fine sand reduces the area of contact with oxygen-rich sea water and this has led to specialization of the adapical tube feet for functioning as respiratory structures, an adaptation which is reflected in the petaloid nature of nearly all spatangoid tests. Completely buried individuals presumably live in environments that range from mildly oxidizing to highly reducing, which has required development of various means for bringing oxygen to the right spots. The construction of respiratory and sanitary canals contributes to this end, and depression of the petaloid areas below the general surface of the test undoubtedly aids in channeling the flow of water over the respiratory tube feet. Most of all, the burrowing echinoid needs to find a means of drawing water into the burrow in front of the animal and of expelling waste water to the surface of sediment in which it is buried or into the sediment at rear of the test. Echinoids are normally provided with cilia which can produce water currents flowing over the surface of the test, but the greater demand of spatangoids for such circulation has led in advanced forms to the development of fascioles (Fig. 185), which are bands on the outer surface of the test characterized by closely crowded tiny spines covered with cilia. These cilia can produce currents much stronger than those developed elsewhere on the test. Different groups of spatangoids developed distinct types of fascioles.

Knowledge of the life habits of spatangoids has been advanced greatly by the recent observations of NICHOLS (140) on British shallow-water species. His studies have provided a rational basis for interpreting many fossil representatives of the group—for example, those occurring in the well-known evolutionary lineage of *Micraster* found in the English chalk. Successive forms in this lineage appear to depict adaptation to gradual deeper-burrowing habits. Understanding of fossil spatangoid assemblages is severely limited by the paucity of present knowledge as to the mode of life and general biology of living forms.

## ORIGIN AND EVOLUTIONARY TRENDS

The earliest known spatangoids are members of the Toxasteridae, occurring in rocks of Early Cretaceous (Berriasian) age of the Mediterranean region. BEURLEN (13) visualized these as descendants of Late Jurassic holasteroids of his Collyritidae (including the Disasteridae and Collyritidae of present classification), specifically of the genus *Metaporinus*; MORTENSEN (136h, p. 12) concurred in this judgment.

This hypothesis meets with an obstacle in that the Disasteridae and Collyritidae show a progressive disjunction of the apical system, bivium and trivium. If spatangoids are derived from them, this evolutionary trend was reversed, and the compact apical system of spatangoids is a secondary reacquisition. DURHAM & MELVILLE (52) therefore sought the origin of spatangoids in the Galeropygidae, and DURHAM now suggests, as the most conservative view,

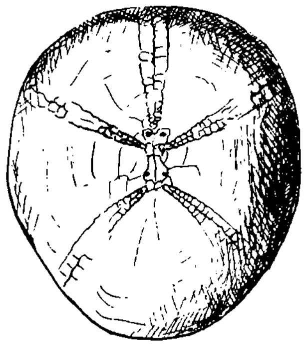


FIG. 428. *Toxaster laffittei* DEVRIÈS, possible link between collyritid holasteroids and toxasterid spatangoids. L.Cret.(Berrias.), N.Afr., ×2 (after Devriès).

that the Holasteroida, Cassiduloida, and Spatangoida arose from a common ancestor at the beginning of the Jurassic.

However, *Toxaster laffittei* DEVRIÉS, from the Berriasian, appears to be a connecting link between the Collyritidae and Toxasteridae, and thus gives new support to the general views of BEURLEN and MORTENSEN. The general form of *T. laffittei* resembles that of the early toxasterids, but the bivium and trivium are clearly disjunct (Fig. 428), and the apical system is elongate (Fig. 429,*A*), resembling that of *Collyrites,* but catenal plates are lacking. *T. africanus* COQUAND (Berriasian-Hauterivian) has an apical system intermediate between that of *T. laffittei* and the compact system of typical toxasterids. Unlike toxasterids in general, *T. laffittei* is nonpetaloid, having high ambulacral plates and rather round pores. Its plastron (Fig. 430,*2a*) is protamphisternous, intermediate between those of *Collyrites* and typical toxasterids. In summary, *T. laffittei* does not appear to be properly referable to *Toxaster,* and does not fit very well in the family Toxasteridae, but DEVRIÉS' conclusion that it is a connecting link between the Collyritidae and Toxasteridae seems reasonable to me.

The **apical system** of spatangoids (Fig. 429) is characterized by lack of the posterior genital plate. As just mentioned, this system is elongate in *Toxaster laffittei,* interpreted as most primitive, with its anterolateral oculars side by side so as to separate the anterior genital plates from the posterior ones. In primitive spatangoids generally, the apical system is compact, with four genital plates meeting medially and thus forming the so-called **ethmophract** condition. In advanced spatangoids of various families, the madreporite extends farther to the rear and separates the posterior ocular plates (**ethmolytic** condition). Gonopores normally are four but may be reduced to three or two.

Fascioles (Fig. 185) are lacking in primitive spatangoids such as most members of the Toxasteridae. More advanced forms developed a basic **fasciole** pattern, which is **peripetalous** in the hemiasterid branch, peripetalous with added **marginal fasciole** in the Pericosmidae, and peripetalous with added **lateroanal fasciole** in the Schizasteridae. Basic in the micrasterid branch is the **subanal fasciole,** to which the Brissidae and some Loveniidae added a peripetalous fasciole, thus indicating convergence with the hemiasterid assemblage, and the Loveniidae as a whole added an **internal fasciole.** *Echinocardium* has also an **anal fasciole.** Finally, some advanced spatangoid groups gave rise to stocks lacking fascioles (e.g., many Asterostomatidae).

Specialization in characters of **spines** marks another evolutionary trend. Primitive spatangoids possessed a fairly uniform cover of short spines. Progressive differentiation of these is marked by development of (1) small cilia-bearing spines termed **clavules** within the fascioles, (2) oar-shaped spines on the plastron, adapted to aid in locomotion, (3) small spines over the peristome and ambulacral petals, suited to shield the

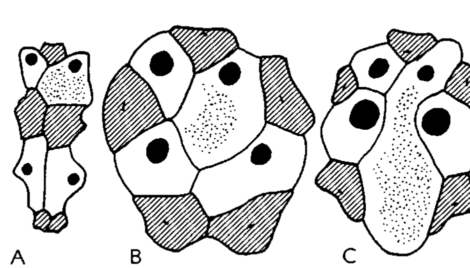



FIG. 429. Three evolutionary stages of spatangoid apical system.——*A.* Primitive elongate condition (*Toxaster lafittei*) (after Devriès).——*B.* Ethmophract condition (*Hemiaster*) (after Mortensen).——*C.* Ethmolytic condition (*Brissus*) (after Mortensen).

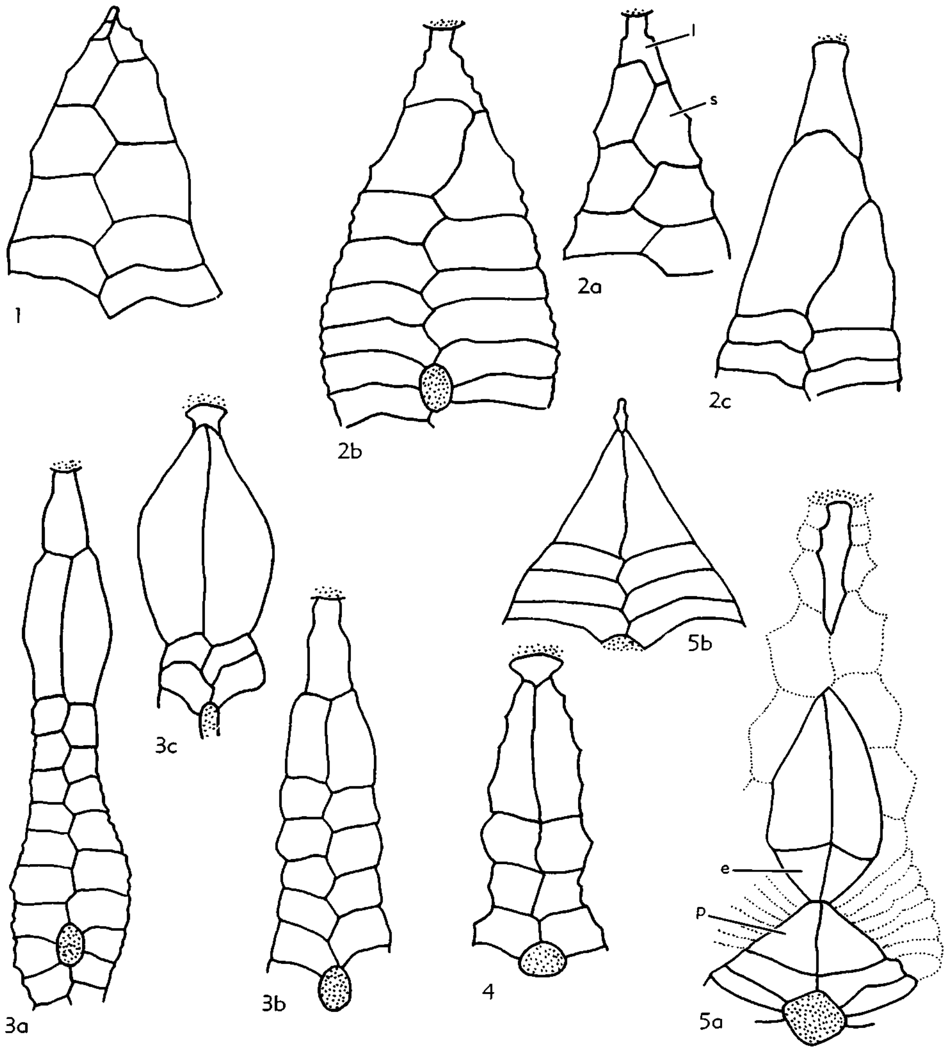



FIG. 430. Evolution of plastron in spatangoids.——*1.* Protosternatous plastron, *Collyrites dorsalis,* of Disasteridae, family ancestral to Spatangoida.——*2.* Protamphisternous plastrons; *2a, Toxaster laffittei,* gradational to protosternous type; *2b, T. africanus,* more advanced; *2c, Hemiaster texanus,* typical.——*3.* Mesamphisternous plastrons; *3a, Ovulaster lamberti,* micrasterid; *3b, Leiostomaster gentili,* palaeostomatid; *3c, Schizaster* sp.——*4.* Holamphisternous plastron, *Spatangus purpureus.*——*5.* Ultramphisternous plastrons; *5a, Eupatagus (Gymnopatagus) antillarum,* brissid; *5b, Asterostoma excentricum* (all after Mortensen, except *2a,* after Devriès, and *5a,* after Fischer). [Explanation: *l,* labrum; *s,* sternal; *e,* episternal; *p,* pre-anal.]

mouth and respiratory tube feet, and (4) large **primary spines,** generally curved longitudinally, concerned with functions of the respiratory and sanitary canals. In several spatangoid groups the large spines came to be based in deeply recessed **scrobicules** consisting of skeletal pouches that project as bulges on the inner surface of the test. These pouches are here termed **camellae.** Largely unstudied additional aspects of spine specialization are the development of strongly curved spines, highly excentric scalelike spine bases, and mamelons of a type which restricts motion of the spines to certain directions.

Specialization of **tube feet,** reflected in

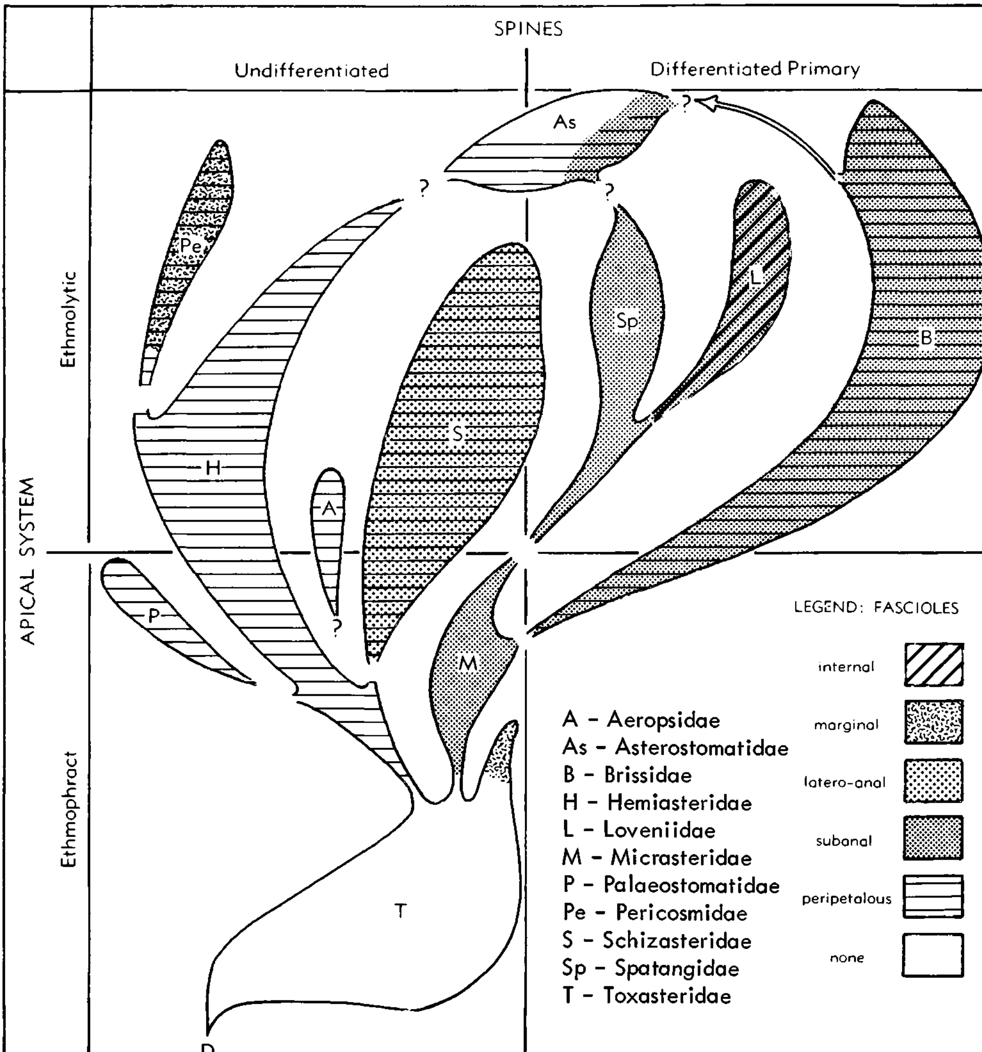



FIG. 431. Spatangoid family tree indicated by structure of apical system and differentiation of spines and fascioles. Primitive Toxasteridae are inferred to have given rise to two main branches, distinguished as the hemiasterid stock (suborder Hemiasterina) at left and the micrasterid stock (suborder Micrasterina) at right. The family Asterostomatidae (suborder Asterostomatina) appears to represent a polyphyletic group derived from several families (Fisher, n).

fossils by the nature and distribution of ambulacral pores, is well demonstrated in spatangoids. Among regular echinoids the tube feet primitively serve a variety of functions, such as respiration, locomotion, sensory perception, food gathering, and fixation. In spatangoids some or all tube feet of the adapical surface are modified for respiration, being broadened and closely crowded to produce the familiar petals. All five ambulacral areas may be petaloid, but commonly only the paired areas comprise petals and bear respiratory tube feet. In the aberrant Aeropsidae the frontal unpaired ambulacrum is petaloid, whereas the paired ambulacra are nonpetaloid. In normal spatangoids the frontal ambulacrum generally carries round pores which serve for egress of large penicillate tube feet that function in maintaining a respiratory funnel and in food gathering. Tube feet of the ambital area beyond the petals generally are very small and emerge through tiny pores. NICHOLS (140) considered these to be specialized for sensory functions. According to KIER (98), most Cretaceous spatangoids have these pores arranged in pairs, which is the normal condition in echinoids as a whole, with each tube foot penetrating an ambulacral plate in two branches. KIER's observations indicate that in post-Cretaceous spatangoids the tube feet are undivided beyond the petals; hence each plate in such areas shows only a single pore (many published figures being erroneous in this respect). Double pores persist in the subanal and peristomial region of at least some spatangoid groups, however.

Tube feet of the peristomial region have become large and penicillate in spatangoids. They are specialized for picking up sediment or food-laden mucus passed down from above and for transmitting such material to the mouth. Pores near the peristome of advanced spatangoids tend to be large, single, and located in depressions, which, with spheridial pits, may form a more or less conspicuous floscelle (Fig. 427).

**Increasing bilateral symmetry** of the plastron constitutes still another evolutionary trend (Fig. 430). In collyritids (Fig. 430,*1*) the plastron is **protosternous.** Toxasterids, however, show differentiation of the plate adjacent to the peristome as a distinct labrum, with a pair of succeeding sternal plates more or less side by side, thus attaining the **amphisternous** condition. In primitive amphisternous forms (e.g., *Hemiaster texanus*), these sternal plates are far from symmetrical and accordingly their plastrons here are termed **protamphisternous** (Fig. 430,*2*; 449). On the other hand, the sternal plates of advanced Hemiasteridae, Micrasteridae, and some other families are almost mirror images of each other (e.g., *Ovulaster, Schizaster*), with succeeding plates arranged alternately—a condition here termed **mesamphisternous** (Fig. 430,*3*; 453; 465). The next stage, represented by *Spatangus,* has plates beyond the labrum arranged in bilateral pairs but not differentiated otherwise. This condition is defined here as **holamphisternous** (Fig. 430,*4*; 489). The most specialized development of plastrons is distinguished by paired sternal plates of markedly dissimilar shape and size and in some by the greatly narrowed or interrupted nature of the plastron. This stage, which is shown by loveniids, brissids, and asterostomatids (Fig. 430,*5*; 468; 496; 501), is here termed **ultramphisternous.**

## CLASSIFICATION

Among numerous proposed classifications of spatangoids (named Amphisternata by MORTENSEN, 1950), the most significant have been published by LOVÉN (1883), POMEL (1883), CLARK (1917), LAMBERT & THIÉRY (1924-25), MORTENSEN (1950), and DURHAM & MELVILLE (1957). The differentiation and arrangement of families adopted in the *Treatise* essentially agree with MORTENSEN's classification, but on the basis of priority, Asterostomatidae is accepted in place of Palaeopneustidae. Main morphological features of recognized suborders and families are summarized in Table 1 (p. *U*628). All but Asterostomatidae are judged to be natural phylogenetic assemblages. Their relationships indicated by evolutionary trends shown mainly in features of fascioles, apical systems, and spines are illustrated diagrammatically (Fig. 431). Geological distribution and diversity through time expressed in terms of genera also are indicated graphically (Fig. 432).

The picture of spatangoid echinoids here presented differs from earlier views particularly in one respect, namely, that previously the Asterostomatidae have been considered by most students to be primitive forms. This is because of their overall appearance, with tendency to have weakly developed petals (some genera entirely nonpetaloid), with absence of fascioles in many, and with lack of spine differentiation in some. In terms of the apical system and plastronal symmetry, however, the asterostomatids are highly developed spatangoids, with a known fossil record reaching back only to the Eocene. Further, their connecting links with the Brissidae, Spatangidae, and Hemiasteridae seemingly mean that the Asterostomatidae are not a primitive group but a polyphyletic assemblage derived from highly specialized ancestors. Members of

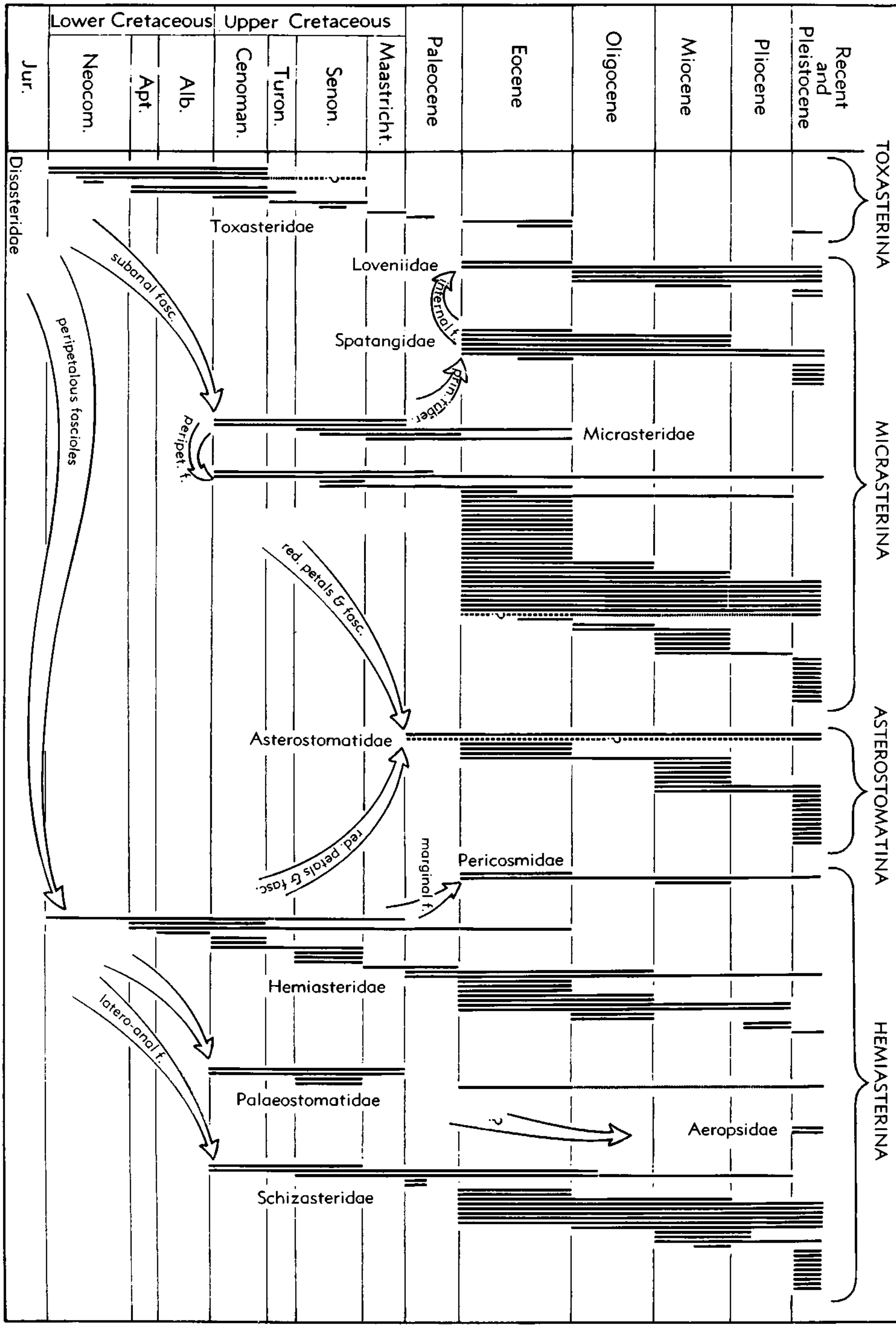



FIG. 432. The spatangoid family tree plotted on a time base (Fischer, n). [Explanation: vertical lines represent individual genera; total number of genera per stage and per 40-million-year intervals plotted at right.]

the group resemble one another mainly because of a reduction or loss of characters that function in burrowing.

The evolutionary scheme here visualized provides for four main groups of spatangoids ranked as suborders. The Toxasterina are inferred to comprise the primitive rootstock, which ranges from Late Jurassic to Recent, with greatest success attained in Early and Middle Cretaceous time. The suborder is represented by the single family Toxasteridae, characterized by an ethmophract apical system, small spines only, and lack of fascioles in most genera. The group gave rise to two branches, which respectively comprise the suborders Hemiasterina and Micrasterina.

The Hemiasterina are characterized by presence of a peripetalous fasciole, with which others (except subanal fasciole) may occur also. Main families are the Hemiasteridae, with only a peripetalous fasciole, and the Schizasteridae, which may possess a lateroanal fasciole in addition. Advanced members of both families evolved ethmolytic apical systems and some schizasterids evolved primary spines. The Palaeostomatidae, which developed a pentagonal peristome with five triangular peristomal plates, may be an early offshoot of the hemiasterids. The Aeropsidae are another possible offshoot, which lacks a fossil record. This group is characterized by a petaloid anterior ambulacrum and nonpetaloid paired ambulacra. The Pericosmidae are a small third offshoot marked by the presence of a marginal fasciole.

The Micrasterina have a subanal fasciole as basic feature. The family Micrasteridae, mainly of Cretaceous age, grades into the Toxasteridae. The mainly Cenozoic families Spatangidae, Loveniidae, and Brissidae are inferred to be derivatives of the Micrasteridae. They are wholly ethmolythic, possess highly differentiated spines, exhibit advanced types of plastron, and have added other fascioles (peripetalous in Brissidae, internal in Loveniidae), though some have lost the subanal fasciole.

As previously noted, the Asterostomatina seem to be a polyphyletic assemblage which has lost burrow-adaptive structures (e.g., petals, fascioles, and primary spines) in some degree. Ultimately it may be possible to reclassify the genera of this group, but for the present recognition of the suborder fills a taxonomic need.

Although some spatangoid families have been divided by authors into subfamilies (e.g., Spatangidae and Loveniidae by MORTENSEN), little seems to be gained by such procedure. The families are so small that division of them in arbitrary manner serves no practical end, and knowledge of morphological relationships is yet insufficient to define subfamilies having evolutionary significance.

## GEOLOGIC HISTORY

From small beginnings in the Neocomian the spatangoids became moderately diversified in Cretaceous time. They were then established as a successful group of echinoids which flourished especially in warm-water environments of the neritic zone where they were buried chiefly in calcareous sediment. The advanced families Schizasteridae and Brissidae originated during the Cretaceous Period. Others, marked by such specializations as reduction of many ambulacral pores to a single-pore condition and development of primary spines, arose in Eocene time. The diversity of spatangoids attained an all-time maximum in the Eocene (Fig. 432), since which epoch the number of spatangoid genera has declined steadily, though not rapidly. Allowing for vastly greater knowledge of modern faunas of the world than of fossil assemblages, we may conclude that each family of spatangoids passed its peak of diversity at some time in the Tertiary. The apparent Recent climax of the asterostomatids is attributable to their preference for abyssal and bathyal environments, which are very scantily represented in the fossil record. Whether the decline of spatangoids denotes a losing-out by them to some group of competing organisms or decimation of the great Mediterranean and Caribbean echinoid faunas of Early Tertiary time caused by climatic deterioration which culminated in the Pleistocene cold spells is undetermined.

## Order SPATANGOIDA Claus, 1876

[Spatangoida CLAUS, 1876, p. 295 (*emend.* DURHAM & MELVILLE, 1957, p. 276)] [=Amphisternous Spatangidae LOVÉN, 1883, p. 93; Amphisternata LAMBERT, 1893, p. 63, MORTENSEN, 1907, p. 90]

Apical system compact, ethmophract or

ethmolytic, not opposite peristome, with 4 or fewer gonopores. Oral side of posterior interambulacral area normally differentiated into amphisternous plastron with bilateral pair of sternal plates behind terminal labrum. Ambulacral plates primitively bearing pair of pores for egress of each tube foot but many forms with sensory and circumoral (phyllodal) tube feet emerging from single pore, and specialized forms with pores on aboral side partly reduced to single state; all or some ambulacral areas of aboral side generally petaloid and all (in agreement with Lovén's law) with peristome adjoining plate of ambulacral rows Ia, IIa, IIIb, IVa, and Vb, perforated by 2 pores or pore pairs, thus providing for 2 tube feet. Peristome generally anteriorly eccentric and labiate, but some forms with centrally placed round or pentagonal peristomes. Phyllodes generally present but bourrelets lacking. Mouth devoid of teeth. Periproct located near posterior extremity. Spines of fossil forms poorly known other than on basis of their corresponding tubercles; approximately half of spatangoid families characterized by rather uniform cover of small spines, other families showing differentiated primary and secondary spines, curved, bristle-like primary spines occurring on aboral surface, where they serve to maintain breathing shaft extended to surface, and in subanal region, where they function in sanitation. Most spatangoids, other than Toxasteridae, possessing fascioles, classified according to position as peripetalous, marginal, subanal, latero-anal, anal, and internal, and occurring singly or in combination. *L.Cret.(Berrias.)-Rec.*

## Suborder TOXASTERINA A. G. Fischer, new suborder

[=Adetes Duncan, 1889 *(partim)*]

Petaloid spatangoids generally lacking fascioles and primary spines, and having primitive (ethmophract) apical system. These forms represent the rootstock of spatangoids. Restricted to family Toxasteridae. *L.Cret.(Berrias.)-Rec.*

### Family TOXASTERIDAE Lambert, 1920

[Toxasteridae Lambert, 1920, p. 16] [=Palaeostominae Zittel, 1879, p. 359]

Apical system normally ethmophract (posterior genital plates mutually contiguous), gonopores 3 or 4; paired ambulacra petaloid, generally open, frontal ambulacrum petaloid or not; ambital and circumoral ambulacral pores double, even in living species (in contrast to all other modern spatangoids); fascioles normally lacking; no primary spines; plastron protamphisternous to mesamphisternous. *L.Cret.(Berrias.)-Rec.*

*Toxaster laffittei* Devriès (Berrias., N. Afr.) (Fig. 428; 429,*A*; 430,*2*) (not truly a *Toxaster*) forms link to *Collyrites* in the holasteroid family Collyritidae, retaining the disjunct bivium and trivium and the elongate apical system of *Collyrites* but lacking catenal plates and possessing a plastron which stands on the borderline between protosternous and protamphisternous types. *Enallopneustes,* with a marginal fasciole, stands alone; species with traces of peripetalous fascioles form a bridge to the Hemiasteridae.

**Toxaster** L. Agassiz, 1840, p. 25 [**Spatangus retusus* Lamarck, 1816, p. 33; SD Cotteau, 1878, p. 117] [=*Echinospatagus* Breynius, 1732 (type, *E. cordiformis* Breynius, *nom. nud.*); *Echinospatagus* d'Orbigny, 1853, p. 30 (obj.); *Hypsaster* Pomel, 1883, p. 44 (type, *Spatangus argilaceus* Phillips, 1829; *Miotoxaster* Pomel, 1883, p. 44 (type, *Echinospatagus breyniusi* d'Orbigny, 1859, p. 173); *Pliotaxaster* Fourtau, 1907, p. 140 (type, *P. lyonsi*, OD)]. Test ovoid to heart-shaped, posterior extremity truncated, front depressed; frontal ambulacrum subpetaloid; paired ambulacra petaloid, open distally, slit-pored, anterior pair longer than posterior; apical system posterior, with 4 gonopores; peristome subpentagonal. [A diverse genus which requires subdivision.] *Cret.(Berrias.-Ceno-man.),* S.Eu.(Medit.)-S.Am.(Colombia), ?U.Cret. (Senon.), N.Am.——Fig. 433,*2*. **T. retusus* (Lamarck), L.Cret., France; *2a-c,* aboral, oral, lat., ×1; *2d,* apical region, enlarged (136h).

**Adytaster** Lambert, 1895, p. 162 [**Cyclaster lucentinus* Cotteau, 1890, p. 48; OD]. Test elongate, posteriorly rostrate and truncate, with anteriorly eccentric apical system; only paired ambulacra petaloid, with conjugate pores. [Poorly known; provisionally referred to Toxasteridae.] *Eoc.,* Eu.(Spain.).——Fig. 433,*3*. **A. lucentinus* (Cotteau); *3a-d,* aboral, oral, lat., post., ×1 (136h). [=*Adetaster* Delage & Hérouard, 1904, p. 268.]

**Aphelaster** Lambert, 1920, p. 83 [**A. integer,* p. 83; OD]. Test subconical; ambulacra flush, petaloid, alike, with pores transversely elongate. *L. Cret.(Hauteriv.),* Eu.(Fr.-Mallorca).——Fig. 433, *1*. **A. integer* (Gauthier), France; *1a,b,* aboral, post., ×1 (136h).

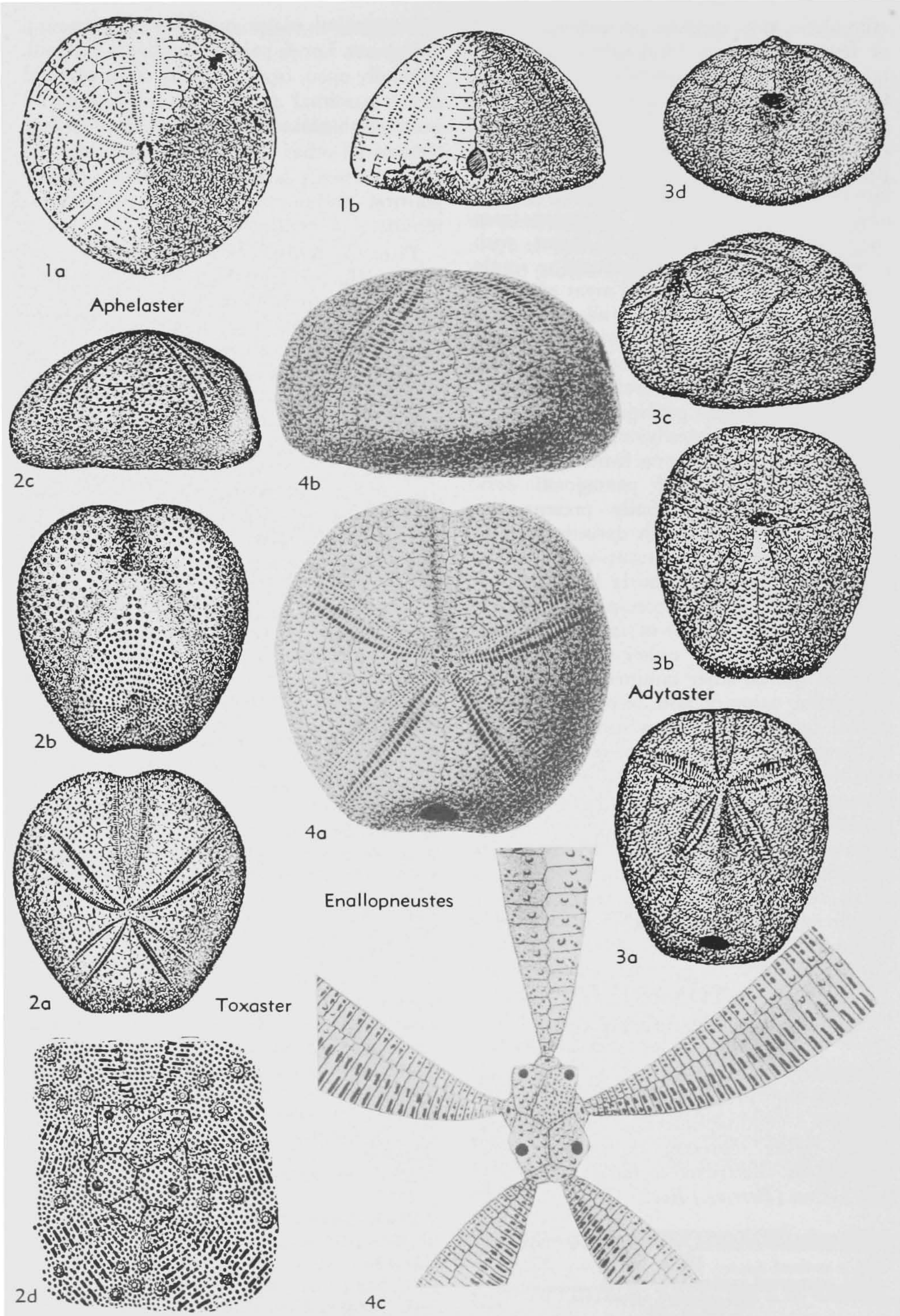



FIG. 433. Toxasteridae (p. U551, U553).

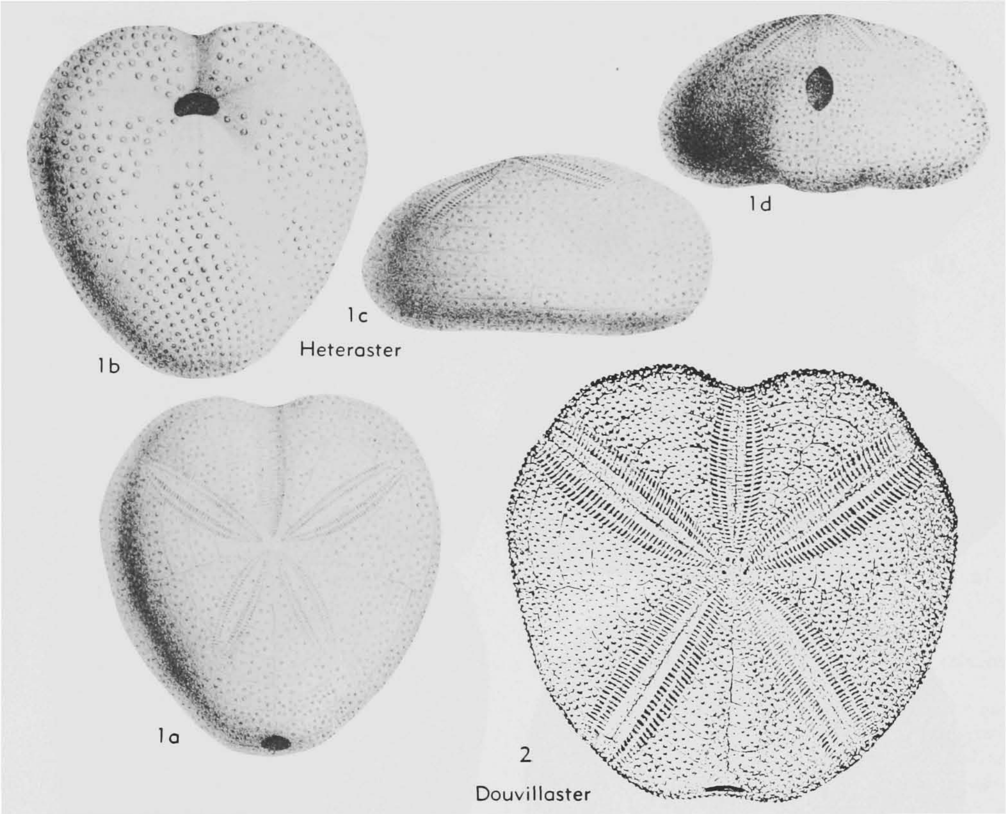



FIG. 434. Toxasteridae (p. *U*553).

**Douvillaster** LAMBERT, 1917, p. 18 [*nom. nov. pro Hypsaster* POMEL, 1883 (*non* POMEL, 1869, p. 16)] [**Epiaster vatonnei* COQUAND, 1878, p. 92; OD]. Test broad and rather low, with anterior sinus; apical system ethmophract, with 4 gonopores; all ambulacra having very large, somewhat depressed petals with transversely slitted pores; some specimens showing traces of peripetalous fasciole, serving to place this genus on borderline between Toxasteridae and Hemiasteridae. *Cret.(Apt.-Turon.),* Medit.——FIG. 434,*2*. **D. vatonnei* (COQUAND), N.Afr.(Alg.); aboral, ×1 (136h).

**Enallopneustes** POMEL, 1883, p. 44 [**Holaster jullieni* PERON & GAUTHIER, 1881, p. 53; OD]. Resembling *Toxaster* but with petaloid frontal ambulacrum, slightly anterior apex, and (unlike typical toxasterids) marginal fasciole; pores in petals of anterior plate series round, but in posterior plate series elongate. [MORTENSEN's (1950, pt. I, p. 411) opinion that this genus represents a toxasterid offshoot parallel to the Hemiasteridae but not properly classifiable with hemiasterids is accepted.] *U.Cret.(Santon.),* N.Afr.——FIG. 433, *4*. **E. jullieni* (PERON & GAUTHIER); *4a,b,* aboral, lat., ×1.5; *4c,* apical disc, enlarged (214).

**Heteraster** D'ORBIGNY, 1853, p. 175 [**Spatangus oblongus* BRONGNIART, 1821, p. 555; SD LAMBERT & THIÉRY, 1924, p. 438] [=*Enallaster* D'ORBIGNY, 1853, p. 181 (type, *Hemipneustes grenovii* FORBES, 1852, pl. 5); *Epiaster* D'ORBIGNY, 1854, p. 186 (type, *Micraster trigonalis* DESOR, 1847, p. 189, SD POMEL, 1883, p. 43); *Pseudoepiaster* SEUNES, 1888, p. 803; *Taeniaster* LAMBERT, 1895 (*non* BILLINGS, 1858)]. Resembling *Toxaster* but frontal ambulacrum semipetaloid, with pores alternating regularly or irregularly between round pores and slits, or short and long slits; anterior poriferous zones of paired petals in some species much narrower than posterior zones. [Specimens from Texas (Alb.) show traces of multiple fascioles.] *L.Cret.(Barrem.)-U.Cret.(Cenoman.),* Arabia-Medit.-N. Am.-S. Am. ——FIG. 434,*1*. *H. trigonalis* DESOR, Cret., (Alb.), Eu.; *1a-d,* aboral, oral, lat., post., ×1 (142).——FIG. 435,*1a-e*. **H. oblongus* (BRONGNIART), L. Cret.(Barrem.-Apt.), Medit.; *1a-d,* aboral, oral, lat., post., ×1.5; *1e,* apical disc, enlarged (142). ——FIG. 435,*1f*. *H. grenovii* (FORBES), Alb., Eng.; pore-pattern in frontal ambulacrum, enl. (136h).

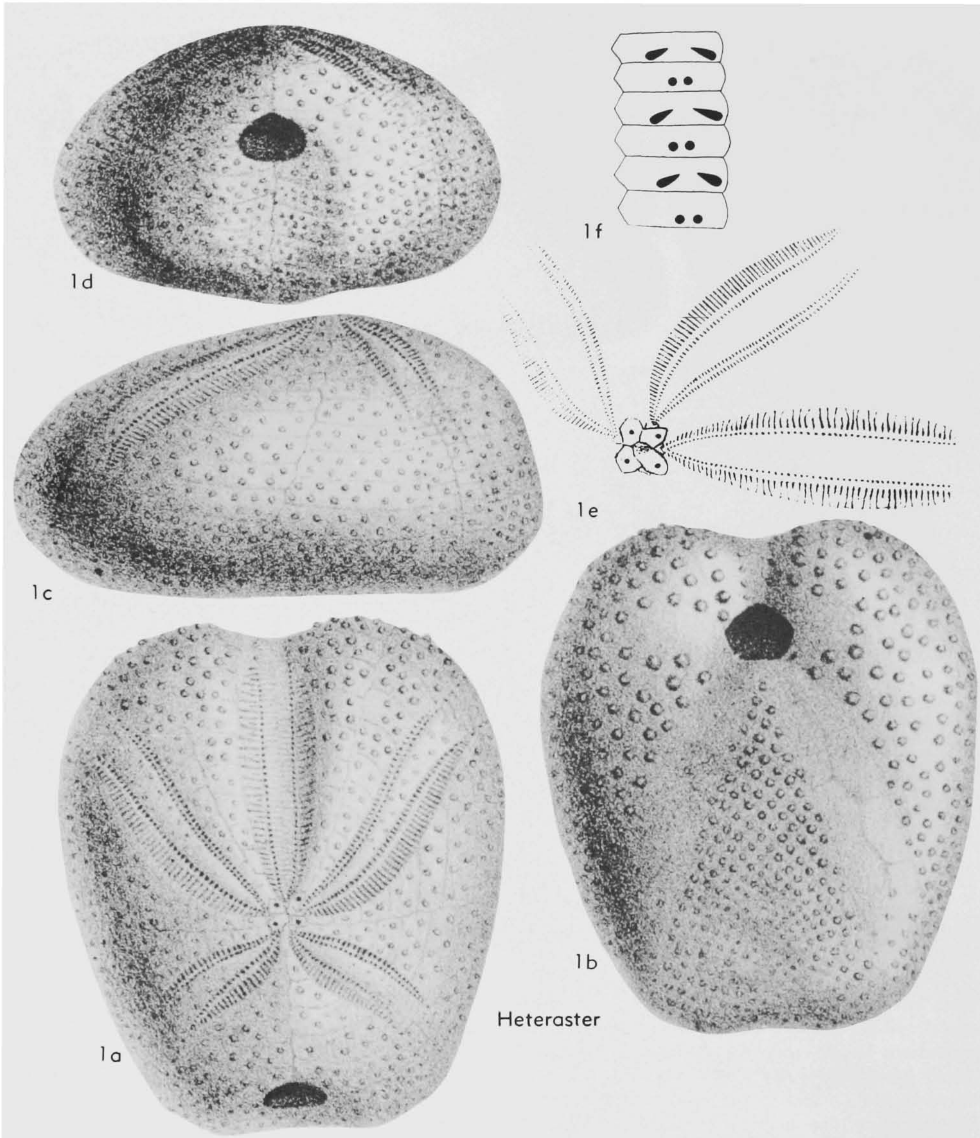



FIG. 435. Toxasteridae (p. U553).

**Isaster** DESOR, 1858, p. 359 [**Spatangus aquitanicus* GRATELOUP, 1836, p. 74; OD]. Orally flattened ovoid; 3 gonopores; ambulacra somewhat petaloid, slightly depressed, open, lacking pores beyond ends of petals; peristome labiate. *Paleoc.(Dan.)*, Eu. (Fr.).——FIG. 438,*1*. **I. aquitanicus* (GRATELOUP); *1a-d*, aboral, oral, lat., post., ×1; *1e*, amb. III, enlarged (all 142).

**Isomicraster** LAMBERT, 1901, p. 959 [**I. stolleyi*; OD]. High, conical form with deep anterior sinus and distinctly heart-shaped outline; closely resembling *Micraster* (Micrasteridae) but differing in absence of fascioles. *U.Cret.(Turon.-Senon.)*, Eu.-N.Afr.-Madag., Mex.——FIG. 436,*1*. **I. stolleyi*, Ger.; *1a-c*, aboral, oral, lat., ×1 (136h).

**Isopatagus** MORTENSEN, 1948, p. 113 [**I. obovatus*; OD]. Resembling *Isaster* but more inflated, and with pores beyond ends of petals; 3 gonopores. [This genus appears to be the only living spatangoid in which circumoral tube feet have double pores and is interpreted as the most primitive living spatangoid known. Bathyal.] *Rec.*, Indonesia. ——FIG. 439,*1*. **I. obovatus*; *1a-c*, aboral, oral, lat., ×0.75; *1d*, apical disc, ×0.6 (all 136h).

**Macraster** ROEMER, 1888, p. 191 [**M. texanus*; OD]. Like *Toxaster* but with paired petals of nearly equal length; anterior ambulacrum with long slit-pores arranged in chevrons; traces of peripetalous fasciole present, suggesting relation with *Hemiaster*, thus linking Toxasteridae with Hemiasteridae. *Cret.(Apt.-Cenoman.)*, Medit.-N. Am.-S.Am.——FIG. 438,*2*. **M. texanus*, L.Cret. (Alb.), USA(Tex.); *2a,b*, aboral, lat., ×0.8 (Roemer, 1888); *2c*, detail of apex, enlarged (136h).

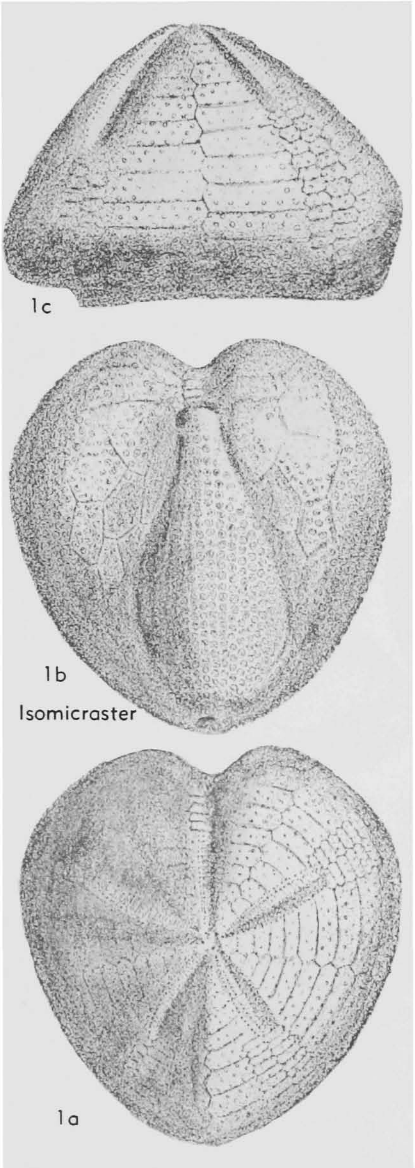



FIG. 436. Toxasteridae (p. *U*554).

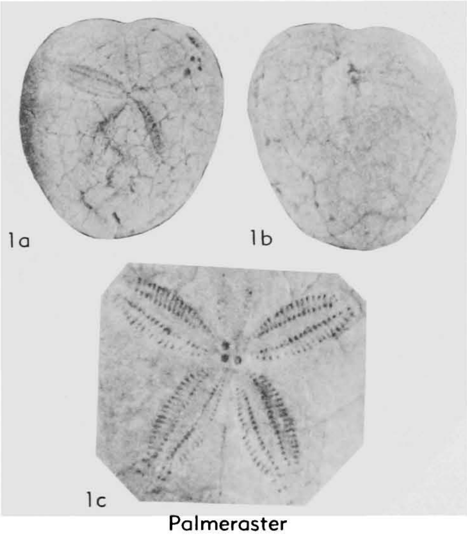



FIG. 437. Toxasteridae (p. *U*555).

**Mokotibaster** LAMBERT, 1933, p. 17 [**M. hourcqui*; OD]. Broadly rounded in outline; apical system with madreporite adjoining posterior ocular plates, gonopores 4; ambulacra petaloid, pores conjugate and outer ones transversely elongate; peristome semilunar; periproct round; tuberculation uniform. *U.Cret.(Maastricht.)*, Madagascar.——FIG. 440,*2*. **M. hourcqui*; *2a-c*, aboral, oral, lat., ×1 (136h).

**Palmeraster** SÁNCHEZ ROIG, 1949, p. 268 [**P. palmeri*; OD]. Test distinctly heart-shaped with frontal sinus extending to anteriorly located peristome; apical system ?ethmophract, with 3 or 4 gonopores; paired ambulacra having closed petals with round pores, outer pore of each pair much larger than inner; frontal ambulacrum nonpetaloid, with small, distant pores; periproct transversely oval, on truncated rear rear of test. *U.Eoc.*, Cuba. ——FIG. 437,*1a,b*. *P. herrerai* SÁNCHEZ ROIG; *1a,b*, aboral, adoral, ×0.7 (216d).——FIG. 439,*1c*. **P. palmeri*; enlarged apical area (216d).

**Polydesmaster** LAMBERT, 1920, p. 16 [**P. fourtaui*; OD]. Robust heart urchin with deep frontal sinus and truncate posterior end; apical system with 4 gonopores, but structure otherwise unknown. Paired petals well developed, frontal pair longer than posterior, and closed; marginal fasciole present, in some double or multiple on sides, other fascioles lacking. [*Polydesmaster* may be allied with *Enallopneustes*, as a branch of the toxasterids which developed a marginal fasciole, and which never flourished.] *U.Cret.(Cenoman.)*, Eu.(Fr.). ——FIG. 440,*1*. **P. fourtaui*; *1a-c*, aboral, lat., lat., ×1 (136i).

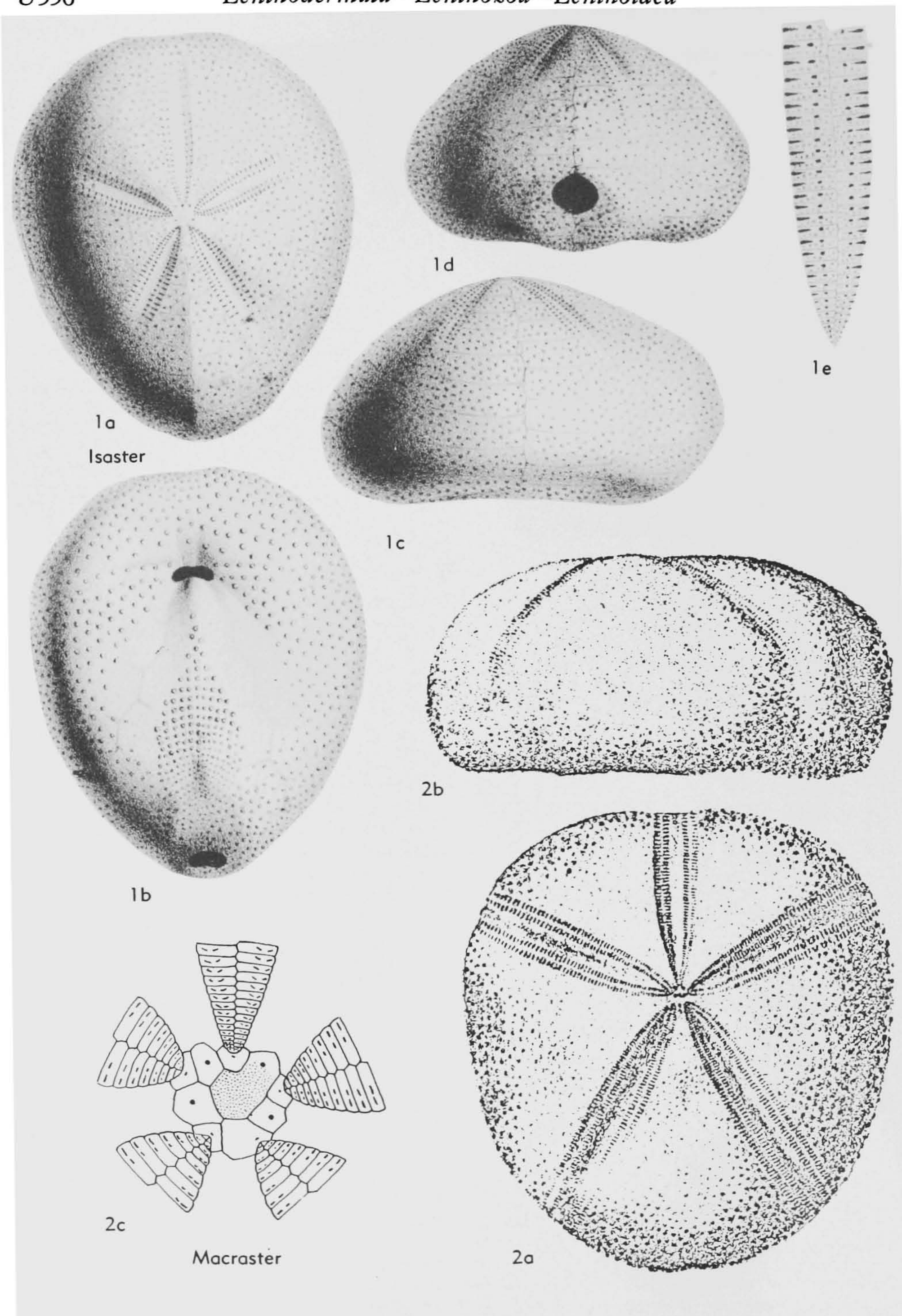



FIG. 438. Toxasteridae (p. U554-U555).

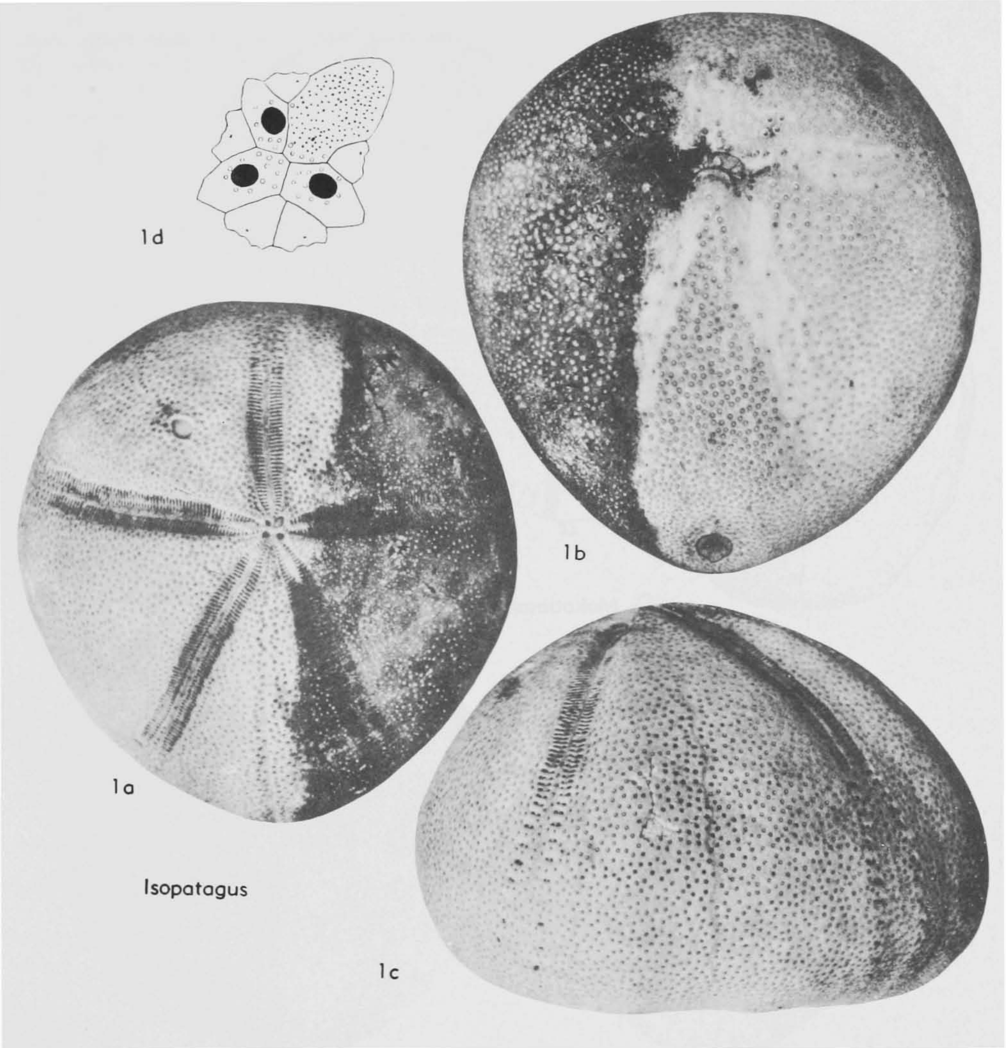



FIG. 439. Toxasteridae (p. *U*554).

## Suborder HEMIASTERINA A. G. Fischer, new suborder

[=Prymnadetes DUNCAN, 1889, *partim*]

Petaloid spatangoids having peripetalous fasciole, in some families combined with lateroanal or marginal fasciole, but none with subanal fasciole. Apical system ethmophract to ethmolytic. Primary spines developed in few members of Schizasteridae. *L.Cret.(Apt.)-Rec.*

### Family HEMIASTERIDAE Clark, 1917

[Hemiasteridae CLARK, 1917, p. 159]

Heart urchins with ethmophract or ethmolytic apical systems, bearing 2 to 4 gonopores; peristome labiate; paired ambulacra generally petaloid, tending to be more closed than those of toxasterids; peripetalous fasciole present (Fig. 441). Primary spines absent. Plastron ranging from protamphisternous to mesamphisternous. [Modern forms are mud-dwellers ranging from the lower neritic zone to bathyal zone.] *L.Cret.(Apt.)-Rec.*

The Hemiasteridae were derived from the Toxasteridae by acquisition of a peripetalous fasciole. *Macraster, Douvillaster,* and *Palhemiaster* are intermediate forms.

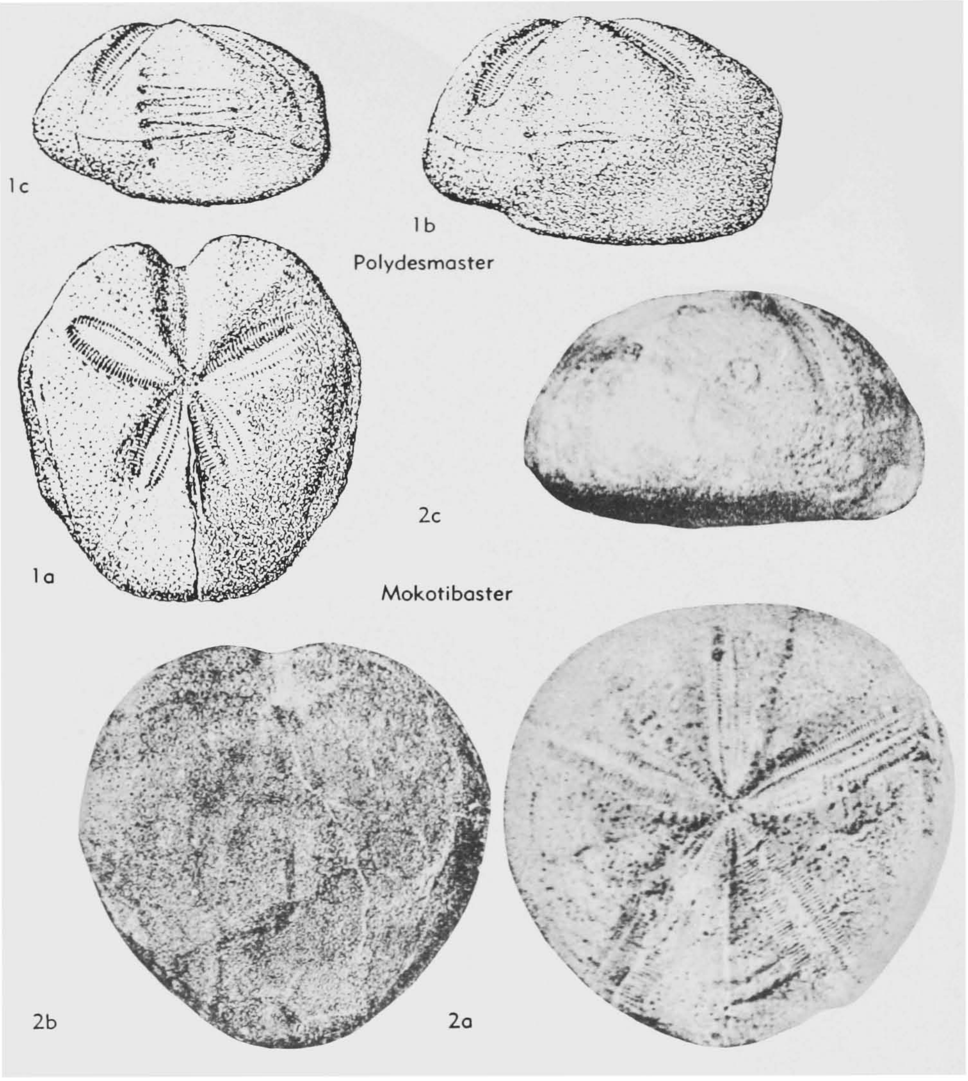



FIG. 440. Toxasteridae (p. U555).

**Hemiaster** AGASSIZ, 1847, p. 16 [**Spatangus bufo* BRONGNIART, 1822, p. 84; SD SAVIN, 1903, p. 22] [=*Leucaster* GAUTHIER in PERON, 1887, p. 386 (type, *L. remensis* GAUTHIER, 1887, p. 387); *Peroniaster* GAUTHIER, 1887, p. 246 (type, *P. cotteaui*), probably juvenile *Hemiaster*]. Test broad, high relative to length, abruptly truncated in rear, showing slight frontal sinus; apical system ethmophract, with 4 gonopores; frontal ambulacrum nonpetaloid or semipetaloid, with small round pores; paired ambulacra having relatively short petals, frontal pair longest. *L.Cret.(Apt.)-Rec.*, cosmop. [=*Perionaster* GAUTHIER, 1887, p. 245 *(nom. null.)*.]

**H. (Hemiaster)** [=*H. (Integraster)* LAMBERT & THIÉRY, 1924, p. 504 (type, *Hemiaster ligeriensis* D'ORBIGNY, 1853, p. 255)]. Test inflated, frontal sinus moderately deep; paired petals slightly flexed, posterior pair somewhat shorter than anterior pair; in some species pores of anterior plate row of each petal smaller than those of posterior plate row. *L.Cret.(Apt.)-Eoc.*, Eu.——FIG. 442,*1*. **H. bufo* (BRONGNIART), U.Cret. (Cenoman.), Fr.; *1a-d*, aboral, oral, lat., post., ×1.5 (142).

**H. (Bolbaster)** POMEL, 1869, p. 15 [**Spatangus prunella* LAMARCK, 1816, p. 33; OD]. Test subglobular, with only faint traces of anterior sinus; petals small. *U.Cret.(Maastricht.)-Paleoc.,* Eu.——Fig. 442,*2*. **H. (B.) prunella* (Lamarck); *2a-c,* aboral, oral, lat., ×1 (136h).

**H. (Gregoryaster)** Lambert, 1907, p. 59 [**Pericosmus coranguinum* Gregory, 1892, p. 615; OD]. Test high, abruptly truncated in rear; petals long and straight, subequal; frontal sinus faint. *U.Cret.(Senon.),* Eu.——Fig. 442,*3*. **H. (G.) coranguinum* (Gregory), Malta; *3a,b,* aboral, lat., ×1 (136h).

**H. (Holanthus)** Lambert & Thiéry, 1924, p. 505 [**H. hickmanni* Koehler, 1914, p. 142; OD]. Test inflated, lacking frontal sinus; petals very large. *U.Cret.(Cenoman.)-Rec.,* Eu.-Ind.O.

**H. (Leymeriaster)** Lambert & Thiéry, 1924, p. 500 [**H. leymeriei* Agassiz, 1847, p. 122; OD]. Moderately inflated, frontal sinus shallow, anterior petals very much longer than posterior ones. *U.Cret.(Cenoman.)-Mio.,* Eu.——Fig. 443, *2*. **H. (L.) leymeriei* (Agassiz), *U.Cret.* (Turon.); *2a-c,* aboral, oral, lat., ×1 (136i).

**H. (Mecaster)** Pomel, 1883, p. 42 [**H. fourneli* Agassiz in Agassiz & Desor, 1847, p. 16; OD]. Relatively low, subhexagonal, with marked frontal sinus; petals subequal in length, distinctly flexed. *U. Cret.(Cenoman.-Senon.),* Eu.-S. Am. ——Fig. 443,*1*. **H. (M.) fourneli* (Deshayes), *1a-c,* aboral, oral, lat., ×1 (136h).

**H. (Trachyaster)** Pomel, 1869, p. 473 [**T. globosus*; SD Pomel, 1883, p. 38]. Resembling *H. (Hemiaster)* but ethmolytic, subgenera grading into each other. *Paleoc.(Dan.)-Plio.,* Medit.-India. ——Fig. 448,*1*. **H. (T.) globosus,* Alg.; *1a-d,* aboral, oral, lat., post., ×1; *1e,* apical disc, ×6 (136h).

**Cheopsia** Fourtau, 1908, p. 149 [**C. mortenseni*; OD]. Small, outline oval, with frontal sinus, oral side flat, aboral side depressed in front and rostrate in rear; structure of apical system unknown; aboral ambulacra sunken, paired ones petaloid; interporiferous zones and posterior interambulacrum lacking tubercles; presence of peripetalous fasciole suggests that this form may belong to hemiasterids. *Eoc.,* Egypt.——Fig. 443,*3*. **C. mortenseni*; *3a,b,* aboral, lat., ×1 (136i).

**Crucibrissus** Lambert, 1920, p. 27 [**Macropneustes integer* de Loriol, 1891, p. 15; OD]. Large ovoid, lacking frontal sinus, sloping from anterior vertex to sharp edge overhanging submarginal periproct; frontal ambulacrum nonpetaloid; petals narrow, depressed; peripetalous fasciole near edge of test. [Tentatively assigned to hemiasterids.] *Eoc.,* Italy-Armenia-Cuba.——Fig. 443,*5*. **C. integer* (de Loriol), Italy; *5a,b,* aboral, lat., ×0.8 (136h).

**Distefanaster** Checchia-Rispoli, 1902, p. 72 [**D. garganicus*; OD]. High, subcircular, with deep frontal sinus; apical system ethmophract, with 2 gonopores, lacking genital plate 3; petals sunken, peristome slit-shaped. *Eoc.,* Italy-Madagascar.——Fig. 444,*2*. **D. garganicus,* Italy; *2a,b,* aboral, oral, ×1; *2c,* apical system, enlarged (136h).

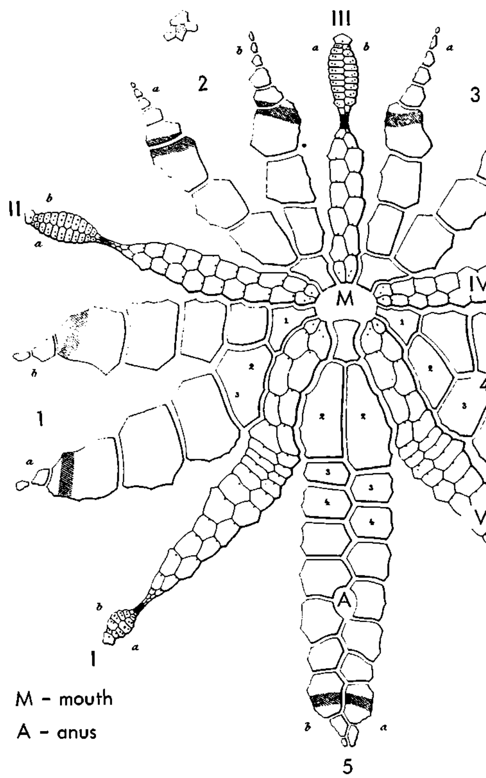



Fig. 441. Plate diagram of *Hemiaster* (Lovén).

**Ditremaster** Munier-Chalmas, 1885, p. 1076 [**Hemiaster nux* Desor, 1853, p. 278; SD Cotteau, 1887, p. 422]. Subglobular, with faint frontal sinus; 2 gonopores; paired ambulacra petaloid, posterior pair very short, about 0.3 length of anterior ones. [May be schizasterid, but lateral fasciole not ascertained.] *Eoc.-Plio.,* cosmop.——Fig. 443,*4*. **D. nux* (Desor), Eoc., Fr.; *4a-c,* aboral, oral, post., ×1.5 (27e).

**Hernandezaster** Sánchez Roig, 1949, p. 211 [**H. hernandezi*; OD]. Test lacking frontal depression, pointed at rear, with inframarginal periproct, and anterior lunate peristome; petals depressed; apical system ethmophract, with 4 gonopores; pores of frontal ambulacrum microscopic. *Oligo.,* Cuba.——Fig. 444,*1*. **H. hernandezi*; *1a-c,* aboral, adoral, lat., ×1 (136h).

**Heterolampas** Cotteau, 1862, p. 198 [**H. maresi*; OD]. Comparatively low and rounded, lacking frontal sinus; distinct from other hemiasterids in having all ambulacra equally petaloid; apical system ethmophract, with 4 gonopores. *U.Cret. (Senon.),* N.Afr.——Fig. 444,*3*. **H. maresi*; *3a-c,* aboral, oral, lat., ×1.5; *3d,* apical disc, enl. (214).

**Holcopneustes** Cotteau, 1889, p. 33 [**Trachyaster*

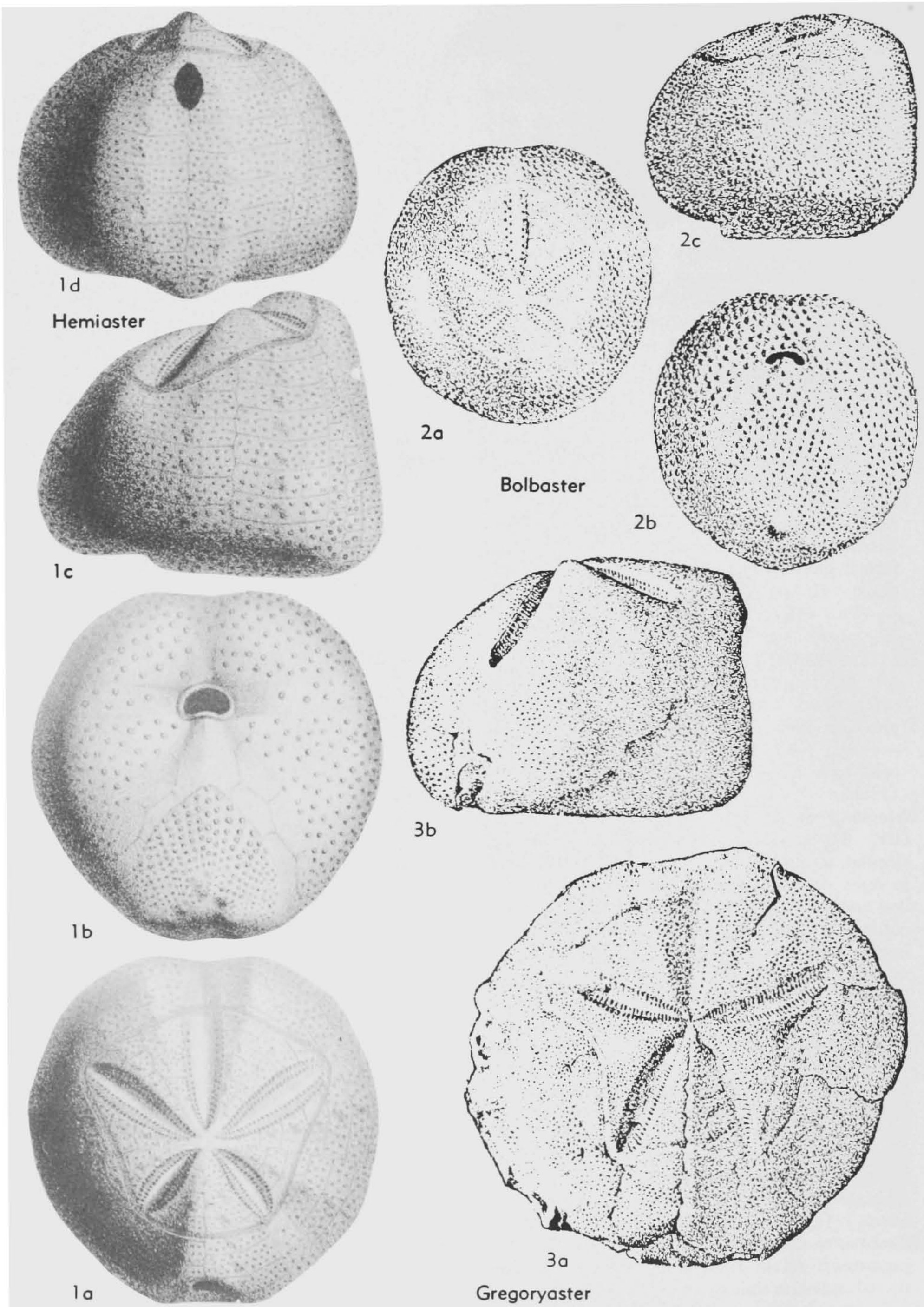



FIG. 442. Hemiasteridae (p. U558-U559).

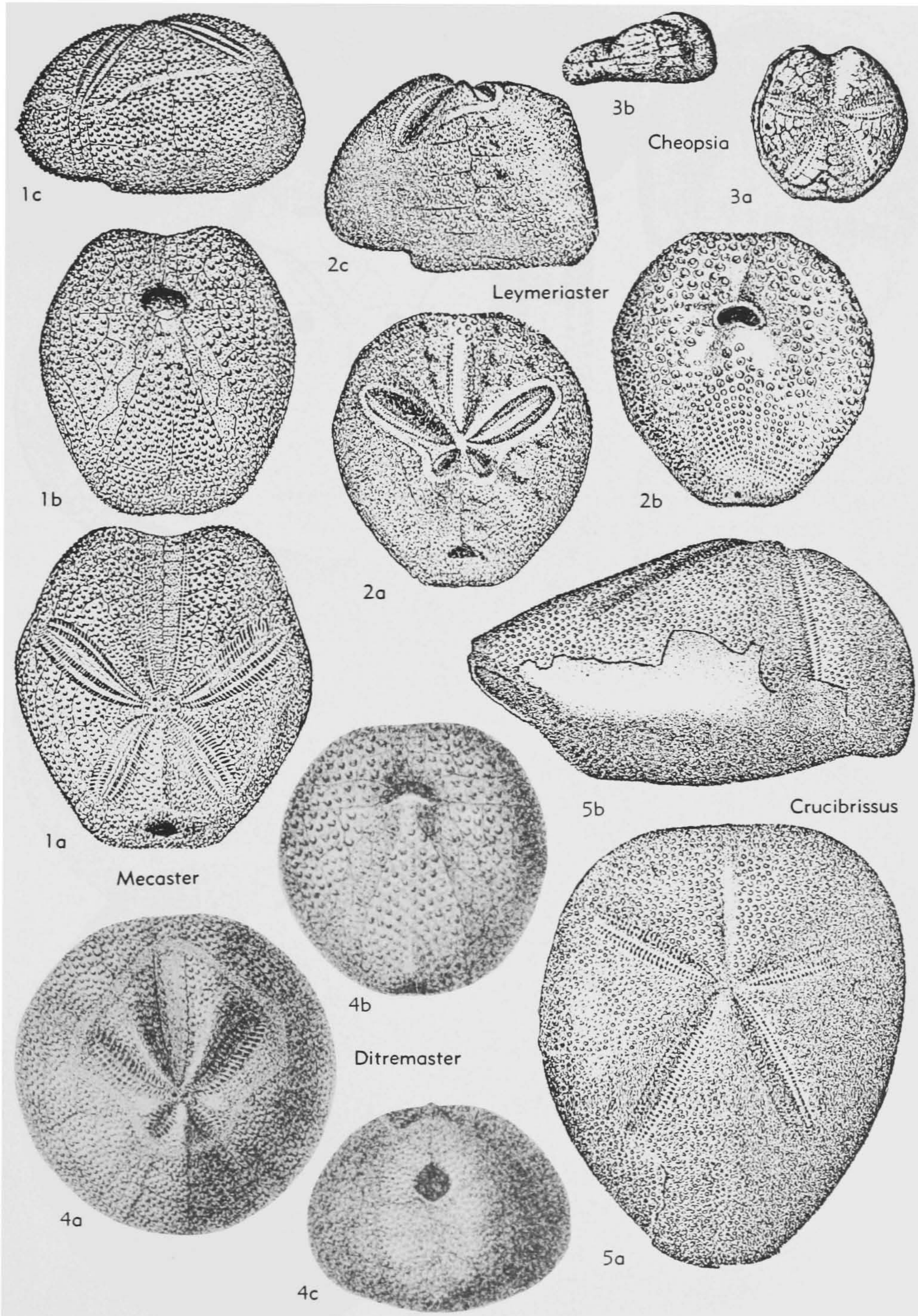



FIG. 443. Hemiasteridae (p. U559).

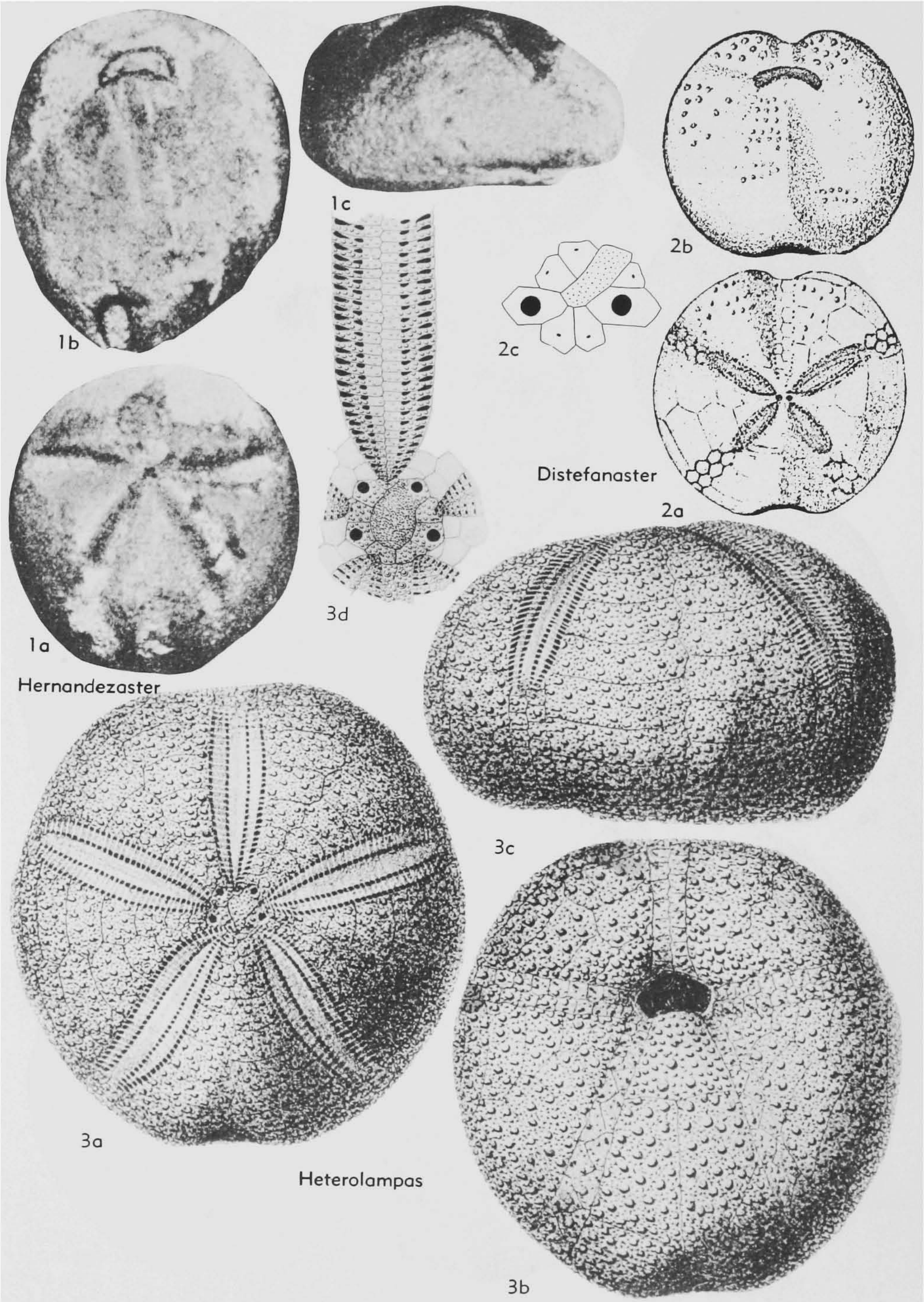



FIG. 444. Hemiasteridae (p. U559, U564).

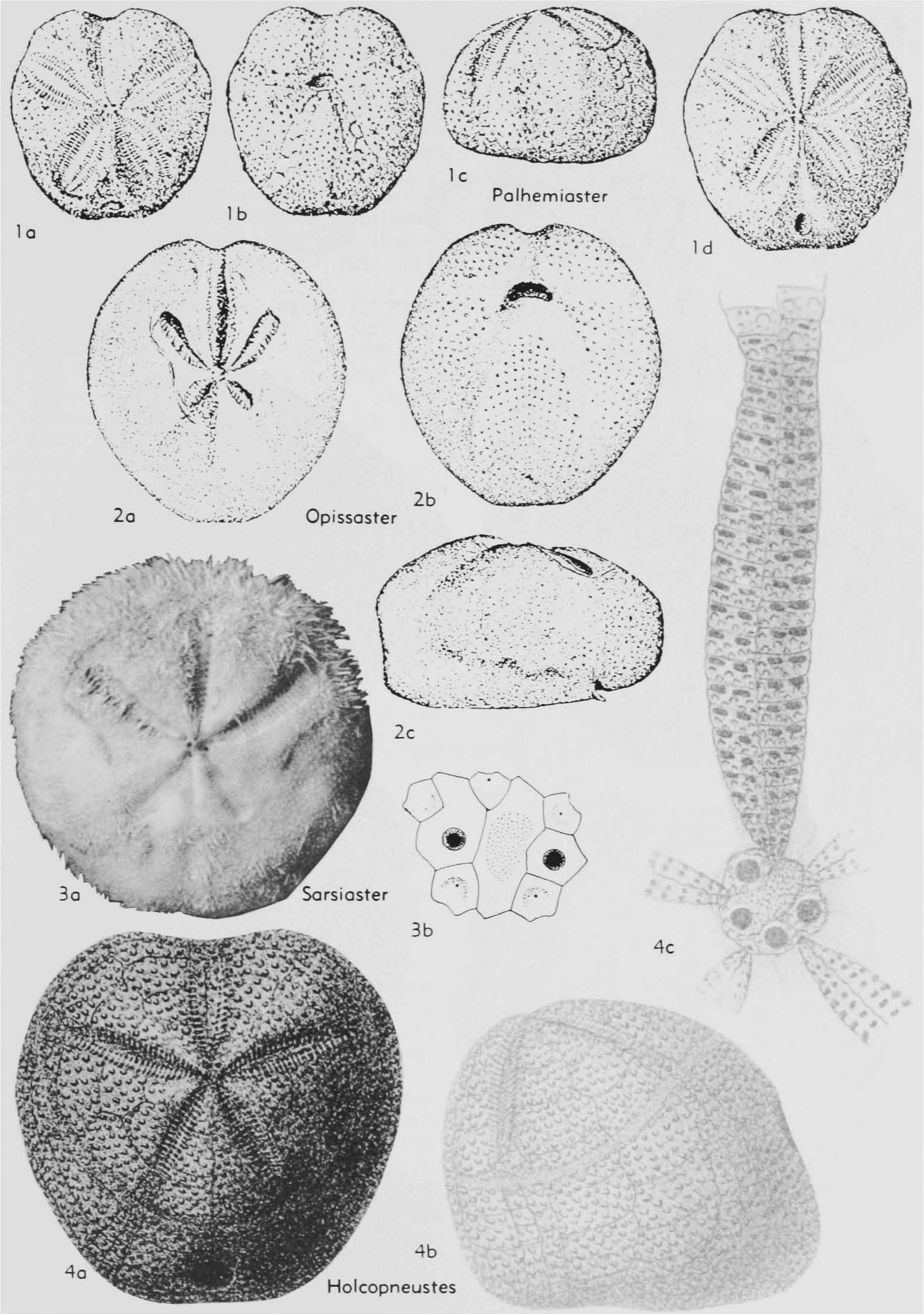



FIG. 445. Hemiasteridae (p. *U*564-*U*565).

*gourdoni* Cotteau, 1887, p. 34; OD]. Resembling *Hemiaster* but highest in front, with very obliquely truncated rear, ethmolytic apical system, and fasciole which intersects ambulacra well beyond ends of petals. *Paleoc.(Dan.)-Oligo.*; Medit.-Madag.——Fig. 445,*4*. **H. gourdoni* (Cotteau), Eoc., Spain; *4a,b,* aboral, lat., ×1.5; *4c,* apical disc, ×4.3 (27f).

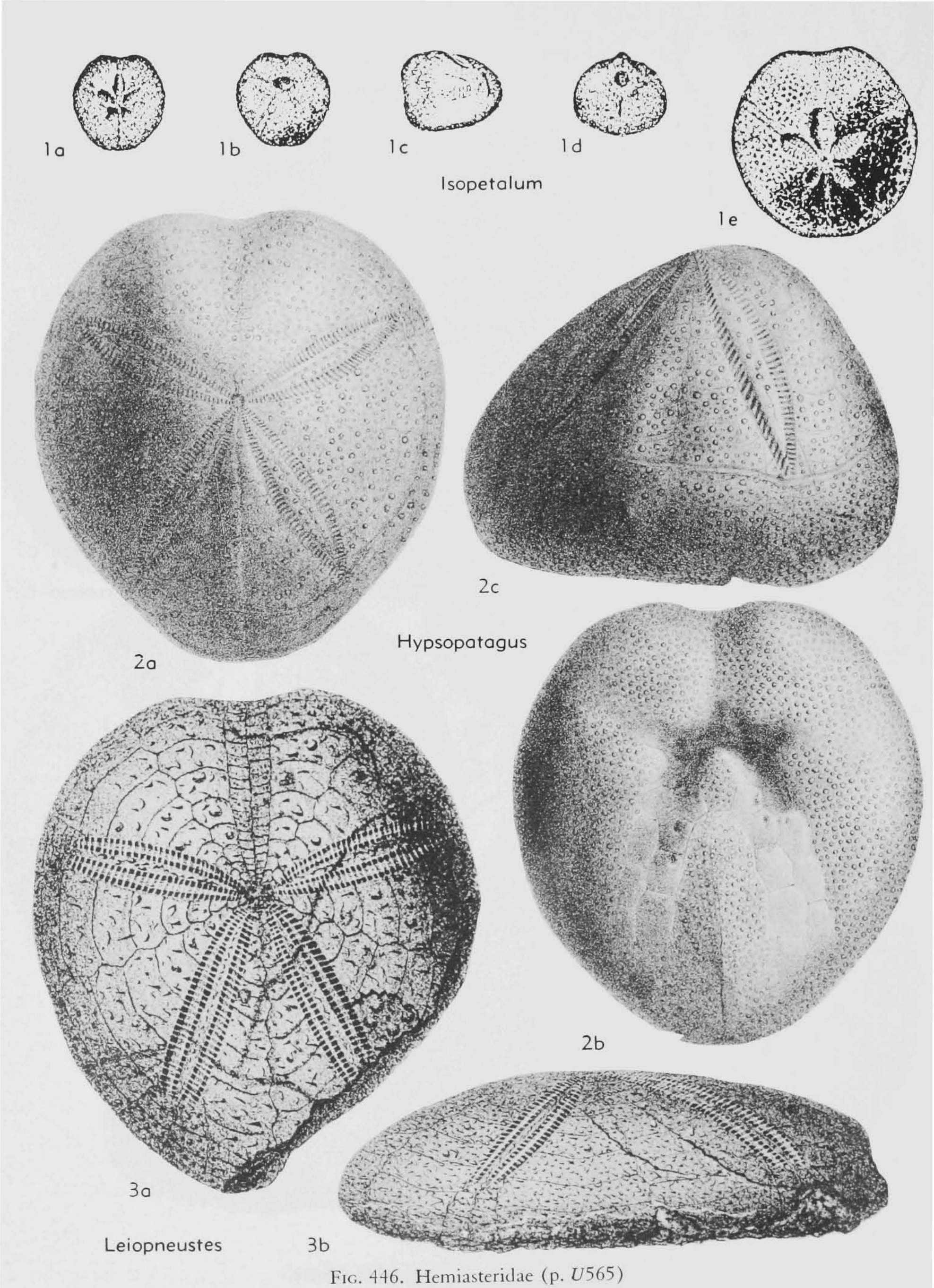



Fig. 446. Hemiasteridae (p. U565)

**Hypsopatagus** POMEL, 1869, p. xii [**Macropneustes meneghini* DESOR, 1858, p. 411; OD] [=*Hypsospatangus* COTTEAU, 1890, p. 13 *(nom. van.)*; *Trachypneustes* MUNIER-CHALMAS, 1891, p. 265]. Outline ovoid, frontal sinus gentle; apical system ethmolytic, with 4 gonopores; frontal ambulacrum nonpetaloid, bearing small, distant pores; petals narrow, closed. *Eoc.-Oligo.*, Eu.-Asia-N.Am.

**H. (Hypsopatagus).** Test conical, its vertex in front of apical system. *Eoc.-Oligo.*; Eu.-Asia(India).——FIG. 446,*2*. **H. (H.) meneghini* (DESOR), Oligo., Italy; *2a-c*, aboral, oral, lat., ×0.75 (204a).

**H. (Leiopneustes)** COTTEAU, 1885, p. 123 [**Brissus antiquus* AGASSIZ, 1847, p. 120; OD] [=*Stenopatagus* LAMBERT, 1911, p. 37 (type, ?)]. Test very much flattened. *Eoc.-Oligo.*, Eu.-N.Am.——FIG. 446,*3*. **H. (L.) antiquus* (AGASSIZ), Eoc., Fr.; 3a,b, aboral, lat., ×1.5 (27e).

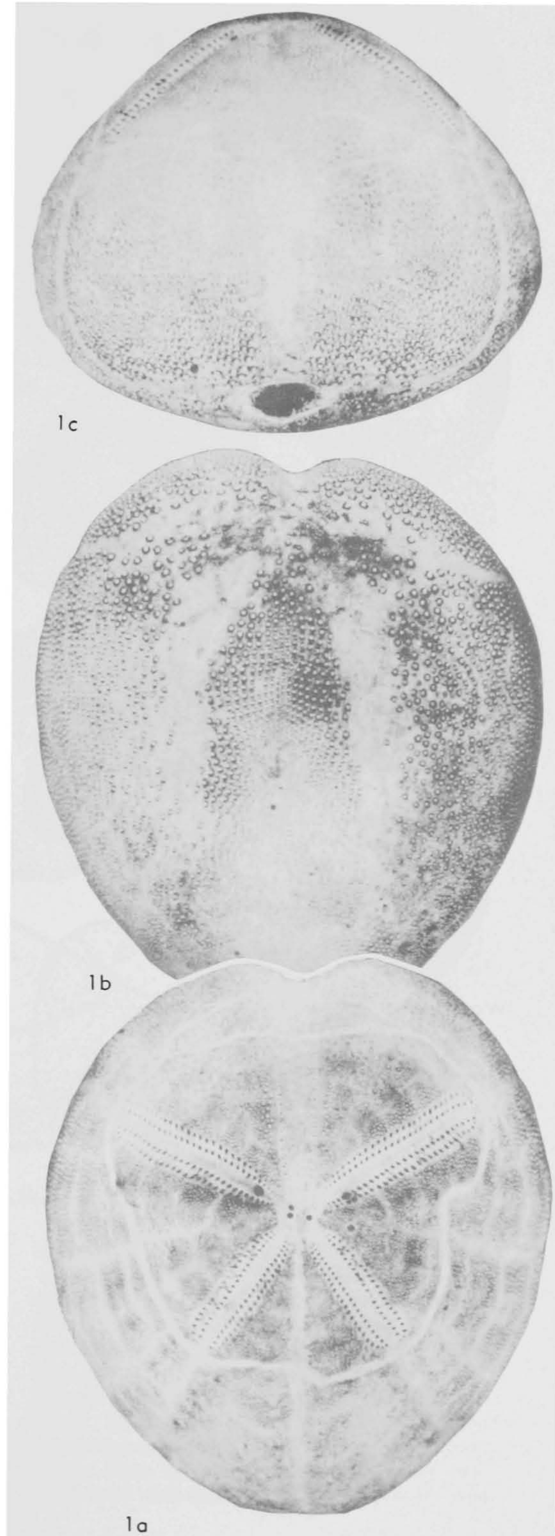
**Isopetalum** LAMBERT, 1911, p. 188 [**Linthia pseudoverticale* OPPENHEIM, 1900, p. 107; OD] [=*Homoianthoides* LAMBERT, 1920, p. 162]. Small, globose test with truncated rear; apical system unknown; 5 small petals, posterior pair shortest; peripetalous fasciole present; probably a hemiasterid. *Oligo.*, Italy.——FIG. 446,*1*. **I. pseudoverticale* (OPPENHEIM); *1a-d*, aboral, oral, lat., post., ×1; *1e*, aboral side, ×2 (136h).

**Opissaster** POMEL, 1883, p. 37 [**O. polygonalis*; OD]. Outline ovoid, deep frontal sinus; deeply depressed petals; apical system ethmolytic, with 2 to 4 gonopores. *Eoc.-Plio.*, Medit.-India-Carib.——FIG. 445,*2*. **O. polygonalis*, Mio., N.Afr. (Alg.), *2a-c*, aboral, oral, lat., ×1 (136h).

**Palhemiaster** LAMBERT, 1916, p. 90 [**P. peroni*; OD]. Intermediate between *Hemiaster* and *Macraster* (Toxasteridae) in having incomplete peripetalous fasciole, developed only in rear part of test. *Cret.(Apt.-Cenoman.)*, N.Afr.(Alg.)-N.Am.——FIG. 445,*1*. **P. peroni*, Alg.; *1a-d*, aboral, oral, lat., aboral, ×1 (136h).

**Sarsiaster** MORTENSEN, 1950, p. 155 [**S. griegii*; OD]. Differs from *Ditremaster* in having lower test and greater length of posterior petals (about half length of anterior ones). [Abyssal.] *Rec.*, Mid.Atl.——FIG. 445,*3*. **S. griegii*; *3a*, aboral, ×1; *3b*, apical system, ×5 (both 136h).

**Vomeraster** LAMBERT, 1920, p. 27 [**Hemiaster verrucosus* COQUAND, 1862, p. 327; OD]. Small, posterior beaklike, high; apical system in front of vertex, ethmophract, with 4 gonopores; frontal ambulacrum nonpetaloid; petals small, especially posterior ones; plates showing unusually coarse tuberculation and depressed sutures, which distinguish this genus from all other known hemiasterids. *U.Cret.(Senon.)*, N.Afr.(Alg.)-Antarctica.——FIG. 448,*2*. **V. verrucosus* (COQUAND), Alg., *2a,b*, aboral, lat., ×1.2 (136h).




Faorina

FIG. 447. Schizasteridae (p. *U576*).

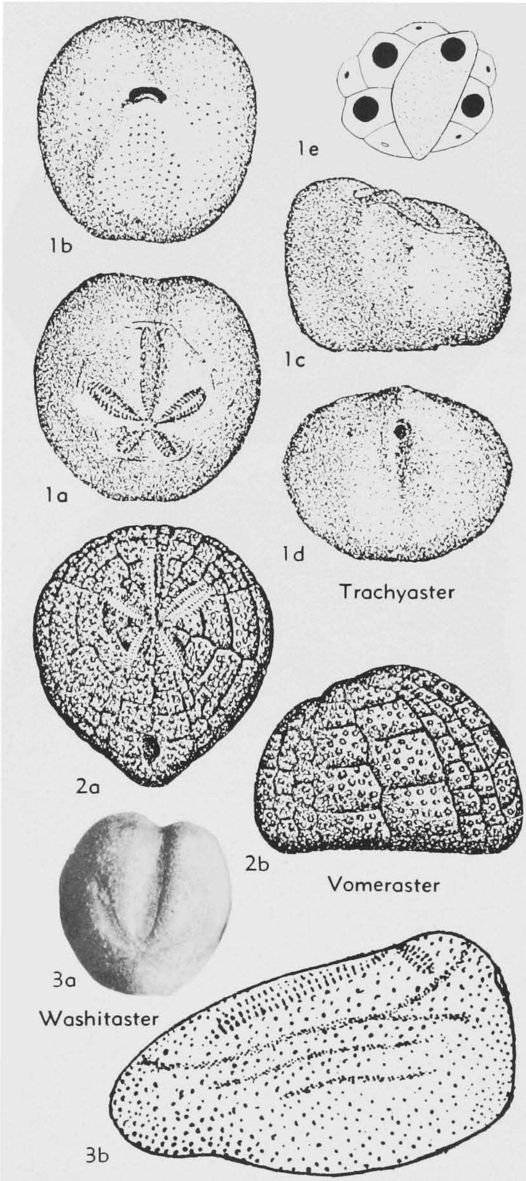



FIG. 448. Hemiasteridae (p. U559, U565, U566).

**Washitaster** LAMBERT, 1927, p. 271 [*Hemiaster riovistae* ADKINS, 1920, p. 115; OD]. Outline ovoid, with marked frontal sinus, apical system and vertex near posterior end; ethmophract, with 4 gonopores; frontal ambulacrum deeply sunken, nonpetaloid; paired ambulacra petaloid, frontal petals much longer than posterior ones; anterior plate row in anterior petals having much smaller pores than posterior row, which has outer pores developed as transverse slits; peristome anterior, subpentagonal; periproct round, high on extended posterior end; peripetalous fasciole multiply developed along sides, may have branches leading toward periproct, which suggest beginnings of latero-anal fasciole. [This genus points in the direction of the Schizasteridae.] *L.Cret.(Alb.)*, USA(Tex.).——FIG. 448,*3*. **W. riovistae* (ADKINS); *3a*, aboral, ×1 (174); *3b*, lat., ×1 (136h).

## Family PALAEOSTOMATIDAE Lovén, 1867

[*nom. correct.* MEISSNER, 1904, p. 1402 (*pro* Palaeostomata LOVÉN, 1867, p. 2)] [=Leskiidae GRAY, 1855, p. 63]

Differs from Hemiasteridae in possessing pentagonal, rather than labiate, peristome, and (among Recent members, at least), 5 triangular peristomial plates; ethmophract to fused apical system, with 2 to 4 gonopores; peripetalous fasciole (Fig. 449). Plastron protamphisternous to mesamphisternous. [Recent forms neritic.] *U.Cret.-Rec.*

This family appears to represent a minor offshoot of the Hemiasteridae.

**Palaeostoma** LOVÉN in A. AGASSIZ, 1872, p. 147 [*pro Leskia* GRAY, 1851, p. 184 (*non* ROBINEAU DESVOIDY, 1830)] [**Leskia mirabilis* GRAY, 1851, p. 184] [=*Skouraster* LAMBERT, 1937, p. 89 (type, *S. rochi*)]. Small, ovoid, inflated; apical system anterior, plates fused, 2 gonopores; paired ambulacra broadly petaloid; frontal ambulacrum nonpetaloid, pores arranged in single radial row, distal one of each pair comma-shaped. *Eoc.*, N.

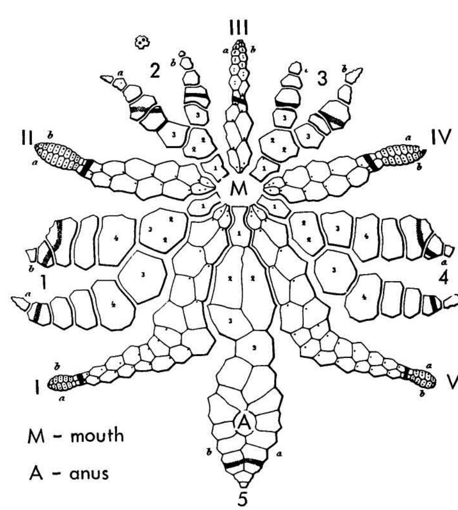



FIG. 449. Plate diagram of *Palaeostoma* (Lovén).

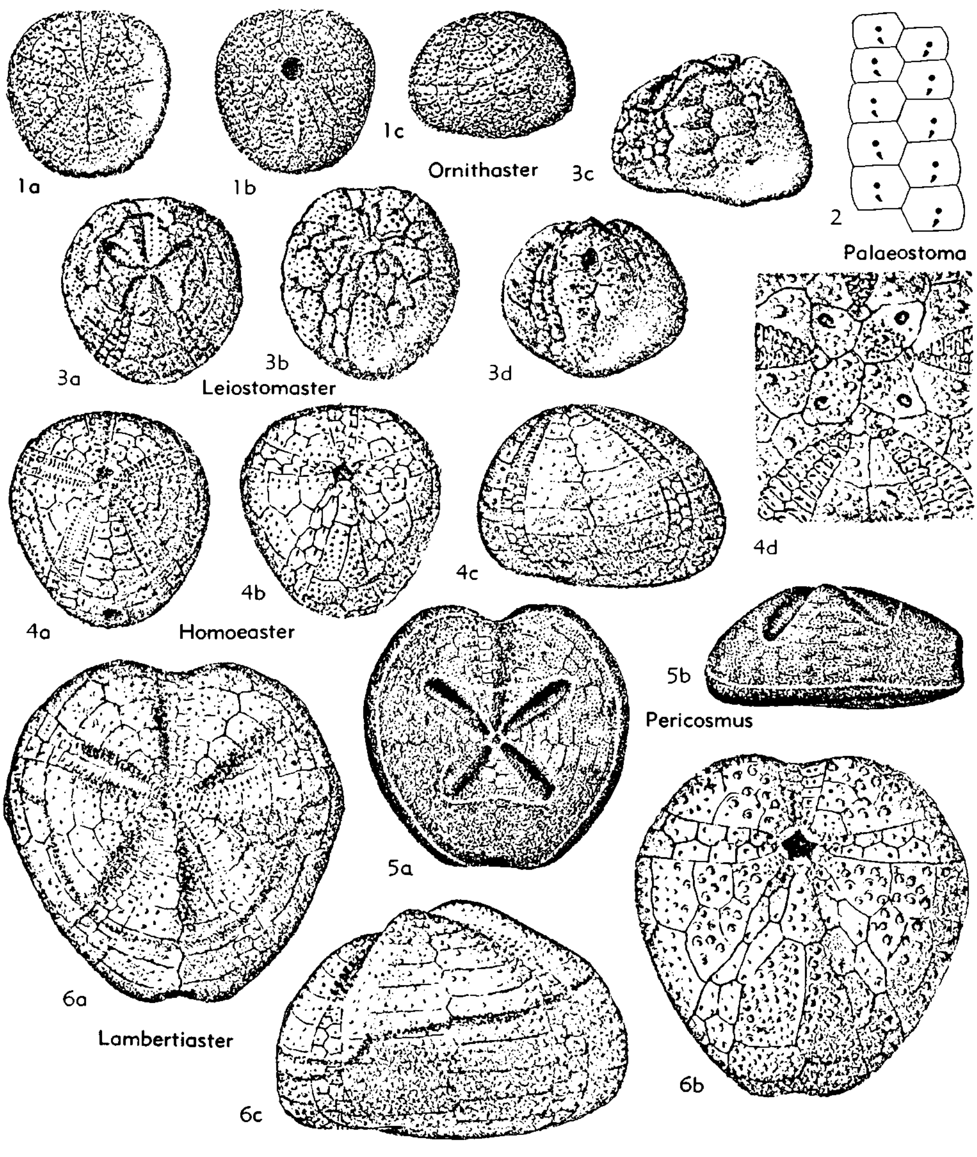



FIG. 450. Palaeostomatidae *(1-4,6)*; Pericosmidae *(5)* (p. U566-U568).

Afr.; *Rec.,* IndoPac.-Red Sea.——FIG. 450,*2*; 451, *1*. **P. mirabile* (GRAY), Rec.; 450,*2*, part of amb. III, ×10 (136h); 451,*1*, aboral, ×1 (136h).

**Homoeaster** POMEL, 1883, p. 44 [**H. tunetanus*; OD]. Small, ovoid; apical system ethmophract, with 4 gonopores; ambulacra nearly flush, paired ones subpetaloid; pores in petals elongate, especially in outer rows. *U.Cret.,* N.Afr.——FIG. 450,*4*. **H. tunetanus*; *4a-c,* aboral, adoral, lat., ×1; *4d,* apical region, enlarged (136h).

**Lambertiaster** GAUTHIER, 1892, p. 28 [**L. douvillei*; OD]. Heart-shaped, posterior low; apical system ethmophract; paired ambulacra with sunken petals, anterior ambulacrum nonpetaloid, depressed. *U. Cret.(Senon.),* N.Afr.(Tunisia)-N.Am.(Tex.).——FIG. 450,*6*. **L. douvillei,* Tunisia; *6a-c,* aboral, oral, lat., ×1 (136h).

**Leiostomaster** LAMBERT, 1920, p. 162 [**L. gentili*; OD]. Small, inflated test with beaked posterior and bulging plates; apical system anterior, ethmophract, with 4 gonopores; paired ambulacra developed into short petals, frontal ambulacrum non-

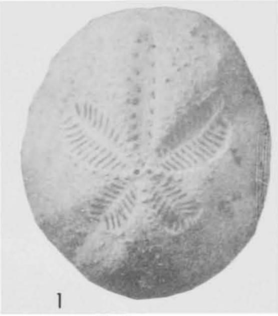



FIG. 451. Palaeostomatidae (p. *U566-U567*).

petaloid, depressed. *U.Cret.(Senon.)*, N.Afr.(Alg.)-N.Am.(Tex.).——FIG. 450,*3*. **L. gentili*, Alg.; *3a-d*, aboral, oral, lat., post., ×1 (136h).

**Ornithaster** COTTEAU, 1886, p. 710 [**O. evaristei*; OD]. Differing from *Homoeaster* chiefly in having round, rather than elongate, pores in petals. *U.Cret.*, Medit.-Iran-Madagascar.——FIG. 450,*1*. **O. evaristei*; *1a-c*, aboral, oral, lat., ×1 (136h).

## Family PERICOSMIDAE Lambert, 1905

[Pericosmidae LAMBERT, 1905, p. 153]

Peripetalous fasciole passing above periproct and entirely separate marginal fasciole passing below periproct, peripetalous fasciole may branch anteriorly, and one or other fasciole may disappear anteriorly; apical system ethmolytic, with 3 or 4 gonopores; paired ambulacra having depressed petals which tend to have distal plates occluded; radioles lacking. [Neritic to upper bathyal.] *Eoc.-Rec.*

The Pericosmidae are probably derived from the Hemiasteridae, by acquisition of a marginal fasciole.

**Pericosmus** L. AGASSIZ, 1847, p. 19 [**Micraster (Pericosmus) latus*; SD DE LORIOL, 1875, p. 115] [=*Megalaster* DUNCAN, 1877, p. 61 (type, *M. compressus*, OD)]. Characters of family. *Eoc.-Rec.*, IndoPac.-Medit.-Carib.

**P. (Pericosmus)**. Apex subcentral to somewhat anterior; petals moderately broad, straight, subequal; anterior sinus moderately deep; marginal fasciole generally complete. *Eoc.-Rec.*, cosmop. ——FIG. 450,*5*. **P. (P.) latus* (AGASSIZ); *5a,b*, aboral, lat., ×1 (136i).

**P. (Lambertona)** SÁNCHEZ ROIG, 1952, p. 257 [**Victoriaster lamberti* SÁNCHEZ ROIG, 1924, p. 127; OD]. Large, anterior groove even deeper than in *P. (Victoriaster)*, forming marginal notch extending back to peristome, petals narrow and deeply sunken, anterior pair much longer than posterior, curved; marginal fasciole narrow and incomplete. *Eoc.*, Cuba.——FIG. 452, *1*. **P. (L.) lamberti* SÁNCHEZ ROIG; *1a,b*, oral, aboral, ×0.5 (216e).

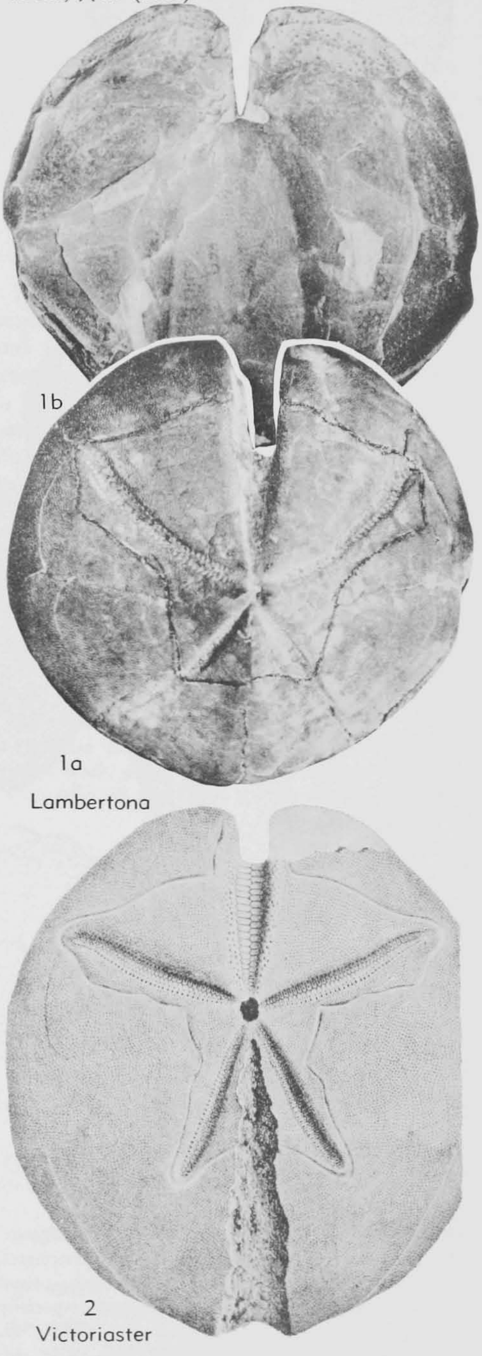



FIG. 452. Pericosmidae (p. *U568-U569*).

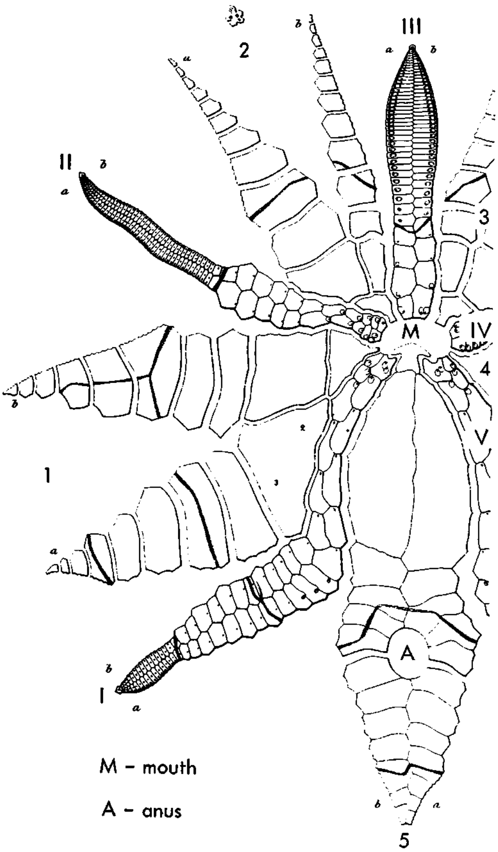



FIG. 453. Plate diagram of *Schizaster* (Lovén).

**P. (Victoriaster)** LAMBERT, 1920, p. 27 [**Pericosmus gigas* M'COY, 1882, p. 15; OD]. Large; apex anteriorly excentric; anterior ambulacrum in deep furrow; petals narrow, deeply sunken, gently flexed; marginal fasciole incomplete. *Mio.*, Australia.——FIG. 452,*2*. **P. (V.) gigas* (M'COY), aboral, ×0.5 (136h).

## Family SCHIZASTERIDAE Lambert, 1905

[*nom. transl.* MORTENSEN, 1951, p. 204 *ex* Schizasterinae LAMBERT in DONCIEUX, 1905]

Heart urchins generally characterized by having both peripetalous and latero-anal fasciole (exceptions, *Amphipneustes, Proraster*); apical system ethmophract to ethmolytic, bearing 2 to 4 gonopores; spines generally uniformly coarse, but some genera showing tuft of longer spines at rear (for maintenance of sanitary canal), and a few show definite differentiation of primary tubercles and spines. Plastron, mesamphisternous to holamphisternous (Fig. 453). [Neritic to abyssal.] *U.Cret.(Cenoman.)-Rec.*

The Schizasteridae most probably were derived from the Hemiasteridae by added development of a lateroanal fasciole. Some specimens of the hemiasterid *Washitaster* (L.Cret.) show lateroanal branches extending from the peripetalous fasciole (Fig. 448,*3b*), providing a morphological link between the two families. Of special interest are the sexually dimorphous, marsupial genera *Tripylus, Abatus,* and *Amphipneustes.*

**Schizaster** L. AGASSIZ, 1836, p. 185 [**S. studeri*; SD ICZN Op. 209, 1948] [=*Brachybrissus* POMEL, 1883, p. 37 (type, *Spatangus ambulacrum* DESHAYES, 1831, p. 255; OD); *Aplospatangus* LAMBERT, 1907, p. 113 (type, *Schizaster eurynotus* AGASSIZ, 1836, p. 67)]. Test high, sloping anteriorly from posterior vertex, beaked over periproct; ambulacra sunken, frontal one deeply depressed; posterior petals 0.3 to 0.5 as long as anterior pair; apical system ethmolytic with 2 to 4 gonopores. *Eoc.-Rec.*, cosmop.

**S. (Schizaster).** Apical system posterior; pores in frontal ambulacrum arranged in single row; gonopores 2. *Eoc.-Rec.*, cosmop.——FIG. 454,*2*. **S. (S.) studeri*, Eoc., Fr.; *2a-e*, aboral, oral, lat., ×1.5 (27e).

**S. (Hypselaster)** CLARK, 1917, p. 185 [**Schizaster (Periaster) limicola* A. AGASSIZ, 1878, p. 193; OD]. Distinguished from *S. (Schizaster)* by its incomplete latero-anal fasciole; gonopores 2. *Rec.*, cosmop. —— FIG. 454,*1*. **S. (H.) limicola* (AGASSIZ); *1a-d*, aboral, adoral, lat., post., ×1 (2); *1e*, apical system, enlarged (136i).

**S. (Ova)** GRAY, 1825, p. 431 [**Spatangus canaliferus* LAMARCK, 1816; SD ICZN Op. 209, 1948 [*non Ova* POMEL, 1887, p. 701] [=*Nina* GRAY, 1855, p. 60]. Apical system posterior; pores in anterior ambulacrum arranged in irregularly crowded double series; gonopores 2. *Rec.*, Medit. ——FIG. 455,*1*. **S. (Ova) canaliferus* (LAMARCK); *1a-c*, aboral, oral, lat., ×1.5 (1).

**S. (Paraster)** POMEL, 1869, p. 14 [**Schizaster gibberulus* L. AGASSIZ, 1847, p. 128; OD] [=*Prymnaster* KOEHLER, 1914, p. 187 (type, *P. angulatus*); *Rotundaster* LAMBERT & THIÉRY, 1925, p. 526 (type, *Schizaster foveatus* AGASSIZ, 1889, p. 350)]. Resembling *Periaster* but having ethmolytic apical system with 4 gonopores. [Tropics.] *Eoc.-Rec.*, cosmop.——FIG. 456,*2*. **P. gibberulus* (AGASSIZ), Rec.; *2a*, aboral, ×1.5 (136i); *2b*, apical system, ×10 (136i).

**S. (Tripylaster)** MORTENSEN, 1907, p. 122 [**Tripylus philippii* GRAY, 1851, p. 132; OD]. Apical system subcentral, ambulacral pores as in *S. (Schizaster)*. *Rec.*, S.S.Am.——FIG. 455,*2*. **S.*

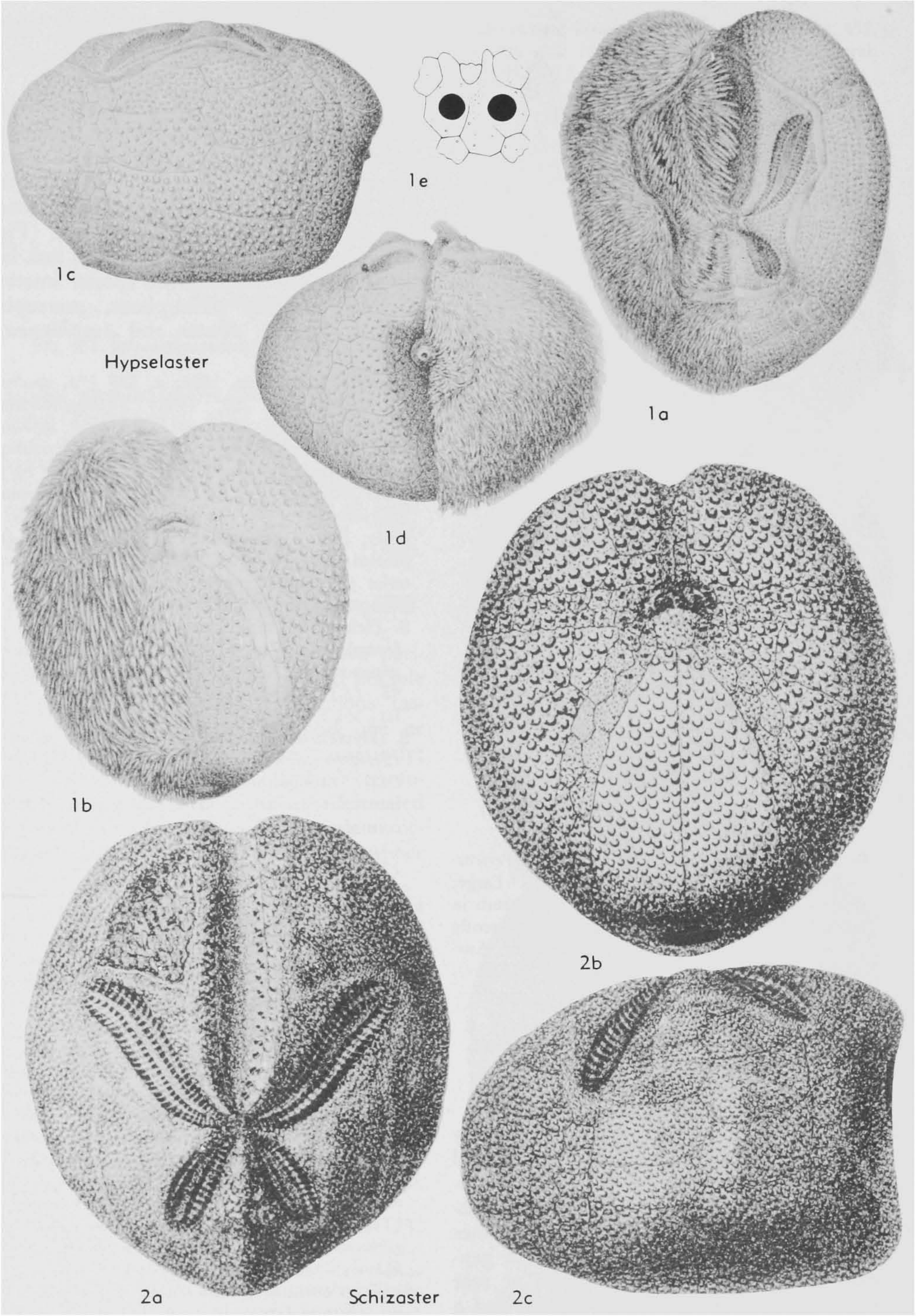



FIG. 454. Schizasteridae (p. U569).

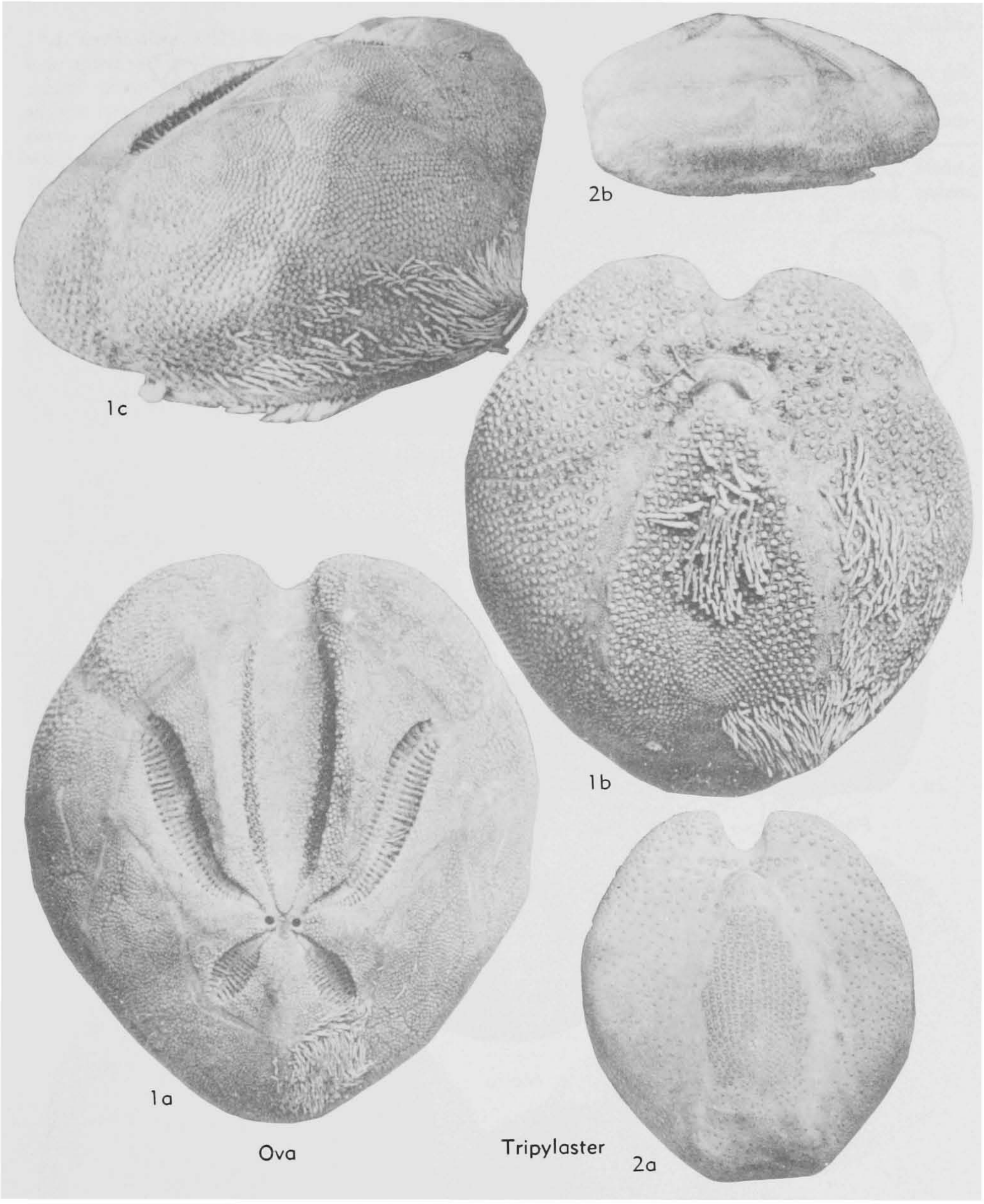



FIG. 455. Schizasteridae (p. *U*569).

*(T.) philippii* (GRAY); *2a,b,* oral, lat., ×1 (136i).

**Abatus** TROSCHEL, 1851, p. 72 [**Spatangus (Tripylus) cavernosus* PHILIPPI, 1845, p. 435; OD] [=*Spatagodesma* AGASSIZ, 1898, p. 83 (type, *S. diomedae*); *Pseudabatus* KOEHLER, 1911, p. 60 (type, *P. nimrodi*); *Parabatus* KOEHLER, 1912 *(nom. null.)*]. Marsupial echinoid, much like *Tripylus,* distinguished by anterolateral petals which reach peripetalous fasciole and by loss of lateroanal fasciole in adults. *?Paleoc.(Dan.),* Madag.; *Rec.,* Antarctic.——FIG. 457,2. **A. cavernosus* (PHILIPPI), Rec., Antarctic; *2a,b,* aboral with spines, ♀ with young; *2b,* ♂ without spines; *2c,* oral; all ×1.5 (2).

**Agassizia** AGASSIZ & DESOR, 1847, p. 20 [*nom. correct. pro Agassisia* VALENCIENNES in DU PETIT-THOUARS, 1846, pl. 1 (incorrect orig. spelling)]

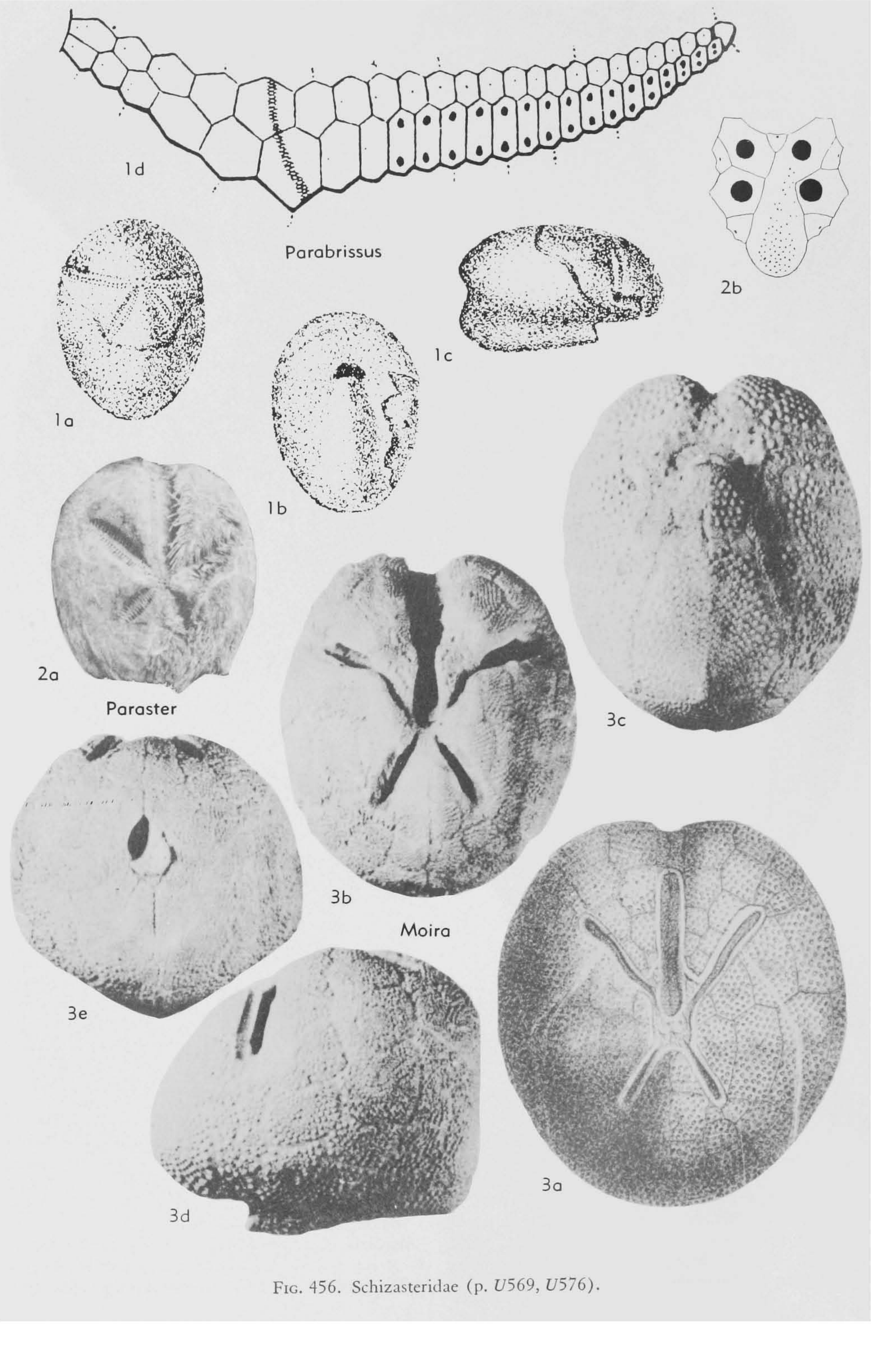



FIG. 456. Schizasteridae (p. *U*569, *U*576).

[**A. scrobiculata*; OD]. Egg-shaped, with ethmolytic apical system showing 4 gonopores and fused genital plates; frontal ambulacrum flush, petals slightly sunken and curiously modified; in anterior petals anterior plate row bearing tiny tube feet which emerge through microscopic pores, whereas pores of posterior plate row are normally developed; posterior petals much shorter and may be normal or similarly modified. *Eoc.-Rec.*, N.Am.-Eu.(Medit.)-Asia(Persian Gulf).

**A. (Agassizia).** Anterior plates of anterolateral petals reduced in size, their pores microscopic throughout; posterior petals normal or similarly modified. *Eoc.-Rec.*, N.Am.-Medit.-Persian Gulf.——FIG. 457,*1*. **A. (A.) scrobiculata*, Rec., Medit.; *1a,b*, aboral, lat., ×1 (1); *1c*, apical system,

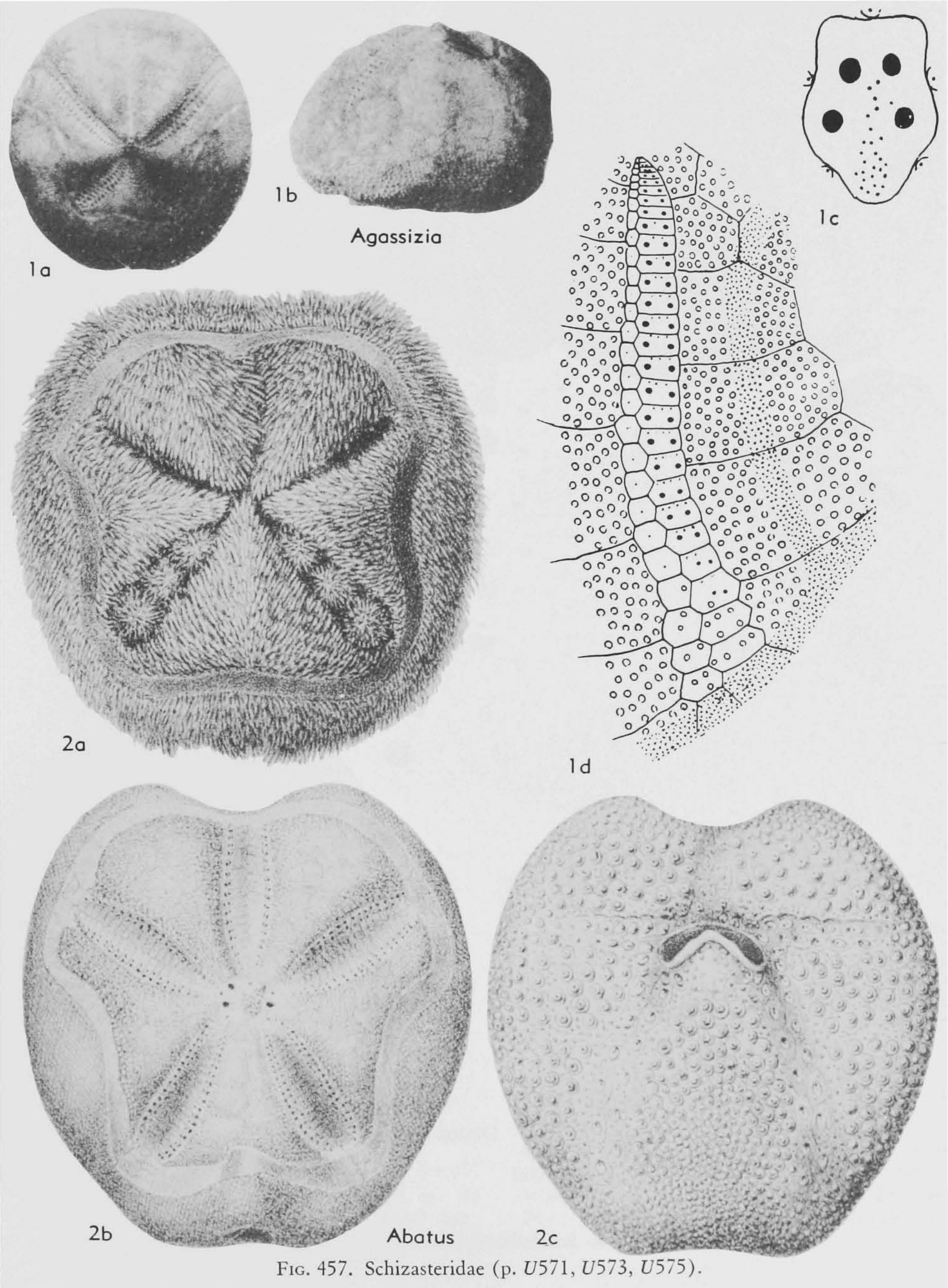



FIG. 457. Schizasteridae (p. *U*571, *U*573, *U*575).

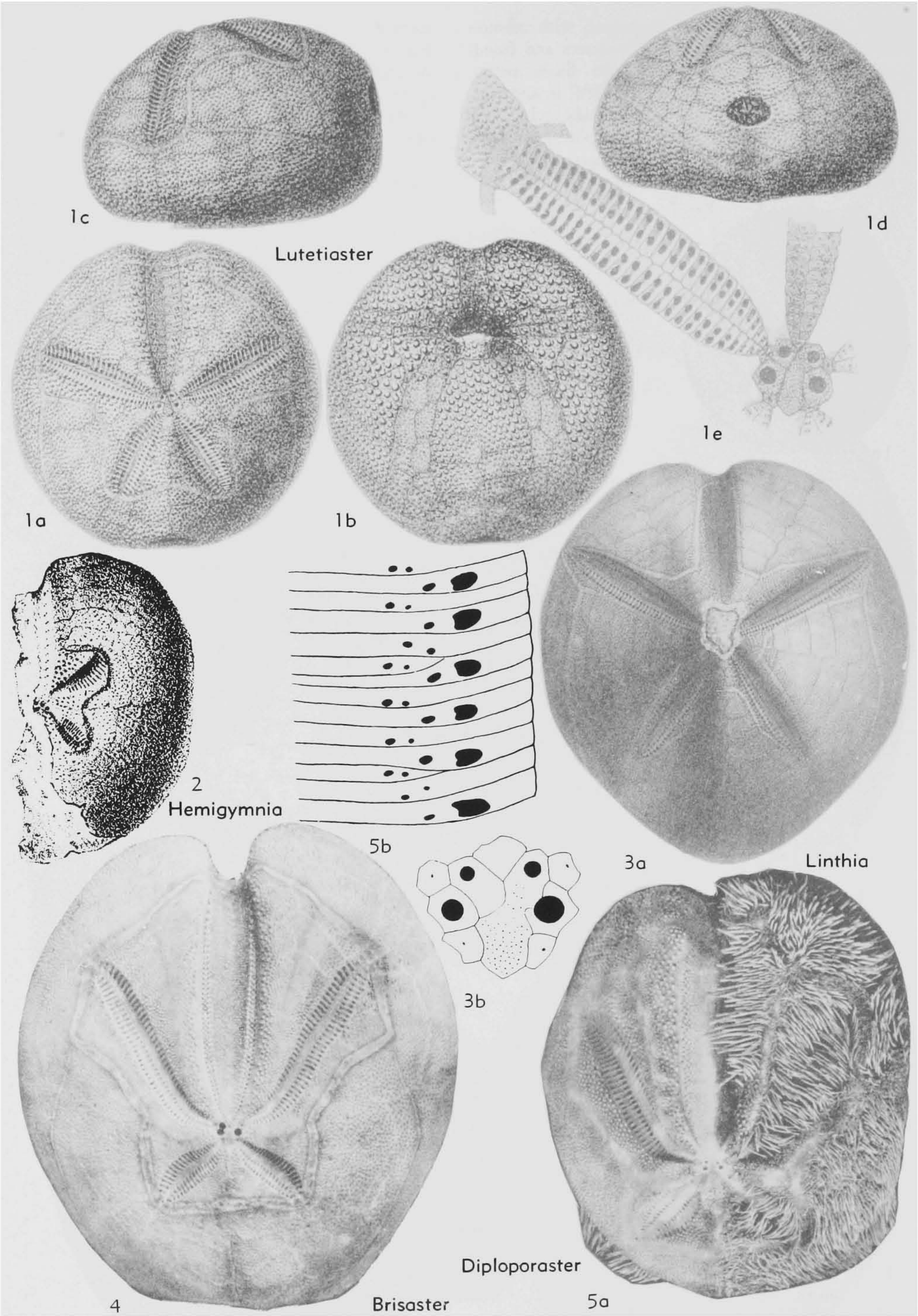



FIG. 458. Schizasteridae (p. U575-U576).

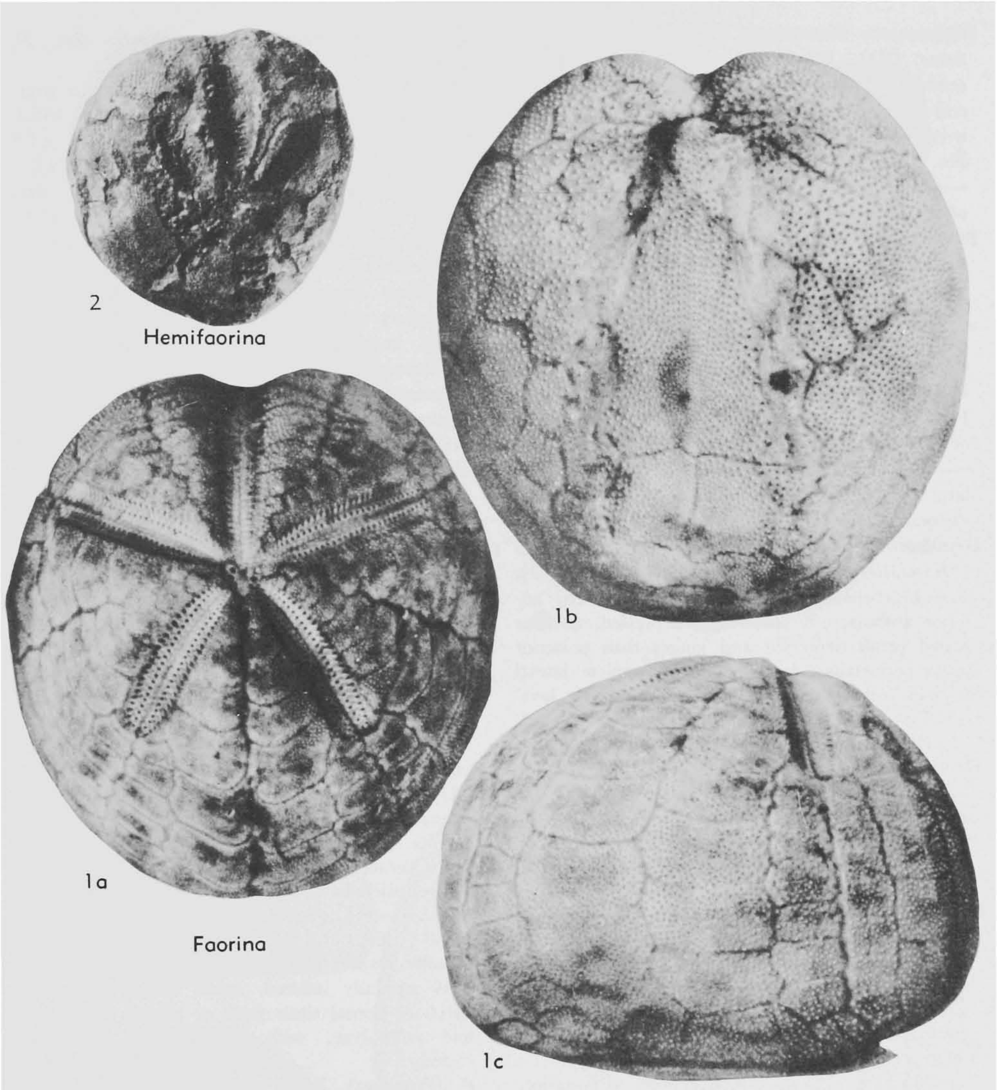



Fig. 459. Schizasteridae (p. *U*576).

×10; *1d*, detail of anterolateral petal, ×10 (*1c,d*, 136i).

**A. (Anisaster)** Pomel, 1886, p. 610 [**Agassizia gibberula* Cotteau, 1876, p. 193; SD Cotteau, 1887, p. 381] [=*Eoagassizia* Grant & Hertlein, 1938, p. 115 (type, *E. alta*)]. Anterior plates of anterolateral petals only slightly reduced in size or not at all, pores in this plate row partly normal, partly microscopic. *Eoc.-Oligo.*, N.Am.-Medit.

**Amphipneustes** Koehler, 1900, p. 815 [**A. lorioli*; OD] [=*Antipneustes* Koehler, 1926, p. 69 (*nom. van.*)]. Sexually dimorphous and marsupial, like *Abatus* and *Tripylus*; differs by having paired pores in anterior ambulacrum, and in lacking all fascioles. *Rec.*, Antarctic.

**Brisaster** Gray, 1855, p. 61 [**Brissus fragilis* Düben & Koren, 1844, p. 280; OD] [=*Lymanaster* Lambert, 1920, p. 162 (type, *Schizaster townsendi* A. Agassiz, 1898, p. 82; OD] [=*Indiaster* Lambert, 1920, p. 27 (type, *Brisaster indicus* Koehler, 1914, p. 201)]. Resembling *Schizaster* but with only 3 gonopores, lower test, and deep anterior sinus which continues into sunken peristomial region; lateroanal fasciole may be reduced or lost in adults. *Oligo.-Rec.*, cosmop.——Fig. 458,*4*. **B. fragilis* (Düben & Koren), Rec.; aboral, ×1 (136i).

**Diploporaster** MORTENSEN, 1950, p. 160 [*D. *barbatus*; OD]. Ethmolytic, with 4 gonopores; resembling *Paraster* but with more rounded posterior end and pores of frontal ambulacrum arranged in irregular double series. *Rec.*, Red Sea-Ind.O.——FIG. 458,*5a*. **D. barbatus*; aboral, ×1 (136i). ——FIG. 458,*5b*. *D. savignyi* (FOURTAU); detail of ant. amb, enl. (136i).

**Faorina** GRAY, 1851, p. 132 [**F. chinensis*; OD] [=*Atrapus* TROSCHEL, 1851, p. 72; *Sinaechinus* HAYASAKA, 1948, p. 93 (type, *S. kawaguchii*)]. Test spheroidal, with deeply sunken ambulacra; apical system ethmolytic, with 3 gonopores; peripetalous fasciole well developed, double in front, with lateroanal branches. *Rec.*, W.Pac.-IndO.——FIG. 447,*1*. *F. kawaguchii* HAYASAKA, Rec., Bay of Tonkin; *2a-c*, aboral, oral, post., ×1 (197). ——FIG. 459,*1*. **F. chinensis*; *1a-c*, aboral, oral, lat., ×1 (136i). [=*Favorina* GRAY, 1885, p. 57 (*nom. null.*).]

**Hemifaorina** JEANNET & MARTIN, 1937, p. 289 [**Hemiaster tuber* HERKLOTS, 1854, p. 15; OD]. Test heart-shaped, with faint frontal notch; anterior ambulacrum broad and depressed, anterior paired petals depressed and longer than posterior ones; peripetalous fasciole and incomplete lateral fasciole; otherwise poorly known. *U.Mio.*, Java. ——FIG. 459,*2*. **H. tuber* (HERKLOTS); aboral, ×1 (91).

**Hemigymnia** ARNAUD, 1898, p. 118 [**H. aturica*; OD]. Ovoid, with deep frontal sinus; apical system central, ethmophract, with 3 gonopores; petals very short, sunken, with slit-shaped pores. *Paleoc. (Dan.)*, Fr.——FIG. 458,*2*. **H. aturica*; aboral, ×1.5 (136i).

**Linthia** DESOR, 1853, p. 278 [**L. insignis*; OD] [=*Escheria* DESOR, 1853, p. 143, *non Escheria* HEER, 1847]. Rounded to broadly heart-shaped, with depressed frontal ambulacrum forming frontal sinus; apical system ethmolytic, with 4 gonopores; peripetalous fasciole deeply embayed between petals. *U.Cret.(Senon.)-Plio.*, cosmop.

**L. (Linthia).** Apical system central to anterior, periproct vertically elongate. *U.Cret.(Senon.)-Plio.*, cosmop.——FIG. 458,*3a*. **L. (L.) insignis*, Eoc., Switz.; aboral, ×0.7 (44).——FIG. 458,*3b*. *L. (L.) sudanensis* (BATHER), Eoc., Afr.; apical system, enl. (136i).

**L. (Lutetiaster)** LAMBERT, 1920, p. 27 [**Spatangus subglobosus* LAMARCK, 1816, p. 33; OD]. Periproct transversely elongate, apical system central to slightly posterior. *Eoc.-Mio.*, Medit.——FIG. 458,*1*. **L. (L.) subglobosa* (LAMARCK), Eoc., Fr.; *1a-d*, aboral, oral, lat., post., ×1; *1e*, apical system, enl. (27e).

**Moira** A. AGASSIZ, 1872, p. 146 [*pro Moera* MICHELIN, 1855, p. 246 (*non* LEACH, 1814; *nec* HÜBNER, 1918; *nec* ADAMS, 1851)] [**Spatangus atropos* LAMARCK, 1816, p. 32; SD *nom. conserv.* ICZN Op. 209, 1948]. Distinguished from *Schizaster* by deeply sunken nature of its petals. *Eoc.-Rec.*, N. Am.-Pac.

**M. (Moira).** Petals almost closed by their overhanging sides. *Eoc.-Rec.*, N.Am.——FIG. 456,*3*. **M. atropos* (LAMARCK), Rec.; *3a*, aboral, ×1.5 (44); *3b-e*, aboral, oral, lat., post., ×1.5 (24).

**M. (Moiropsis)** A. AGASSIZ, 1881, p. 205 [**Schizaster claudicans* A. AGASSIZ, 1879, p. 21; OD]. Petals more open, not so overhung by their sides. *Mio.-Rec.*, W.Pac.

**Parabrissus** BITTNER, 1880, p. 59 [**P. pseudoprenaster*; OD]. Resembling *Prenaster* in oval shape, anterior position of apical system, which is ethmolytic, with 4 gonopores, and in transverse orientation of anterolateral petals; resembling *Agassizia* in having anterior plates of anterolateral petals reduced in size, and their pores almost eliminated. Latero-anal fasciole not reported. *Eoc.*, Alps.——FIG. 456,*1*. **P. pseudoprenaster*; *1a-c*, aboral, oral, lat., ×1.5; *1d*, detail of anterolateral petal (all 136i).

**Periaster** D'ORBIGNY, 1853, p. 269 [**Spatangus elatus* DESMOULINS, 1837, p. 406; SD LAMBERT, 1918, p. 8]. High-crowned test; petals sunken, posterior pair short; apical system ethmophract, with 4 gonopores. *U.Cret. (Cenoman.)-Eoc.*, Medit.——FIG. 460,*2*. **P. elatus* (DESMOULINS), Senon., Fr.; *2a-d*, aboral, oral, lat., post., ×1.5 (142); *2e*, apical system, ×10 (136i).

**Peribrissus** POMEL, 1869, p. xiii [**P. saheliensis*; OD]. Resembling *Prenaster* in ovoid outline and anterior, ethmolytic, 4-pored apical system; differing in flatter shape and deep frontal sinus; anterior petals distinctly longer than posterior ones; coarse tubercles along edges of frontal sinus. *Mio.*, Medit.——FIG. 460,*3*. **P. saheliensis*; aboral, ×0.8 (136i).

**Prenaster** DESOR, 1853, p. 279 [**P. alpinus*; OD]. Test ovoidally inflated, apical system central to anterior, frontal sinus faint or absent; apical system ethmolytic, with 4 gonopores. *Eoc.-Rec.*, cosmop.

**P. (Prenaster).** Apical system far forward; petals depressed, posterior paired petals longer than anterior ones; peripetalous fasciole extending onto oral side in anterior part of test. *Eoc.*, cosmop. ——FIG. 461,*1*. **P. (P.) alpinus*, Eoc., Alps; *1a-c*, aboral, lat., post., ×1.5 (44).

**P. (Protenaster)** POMEL, 1883, p. 36 [*pro Desoria* GRAY, 1851, p. 132 (*non* NICOLLET, 1942)] [**Desoria australis* GRAY, 1851, p. 133; OD]. Apical system central or anterior; petals nearly equal in length, or posterior pair shorter than anterior; peripetalous fasciole not drawn down onto oral side of test. *Rec.*, S.Pac.——FIG. 461,*2*. **P. (P.) australis* (GRAY); *2a-c*, aboral, oral, lat., ×1 (1).

**P. (Saviniaster)** LAMBERT, 1911, p. 33 [**S. migueli*; OD]. Resembling *P. (Prenaster)*, but petals narrower and flush. *Eoc.*, Eu.(Fr.).

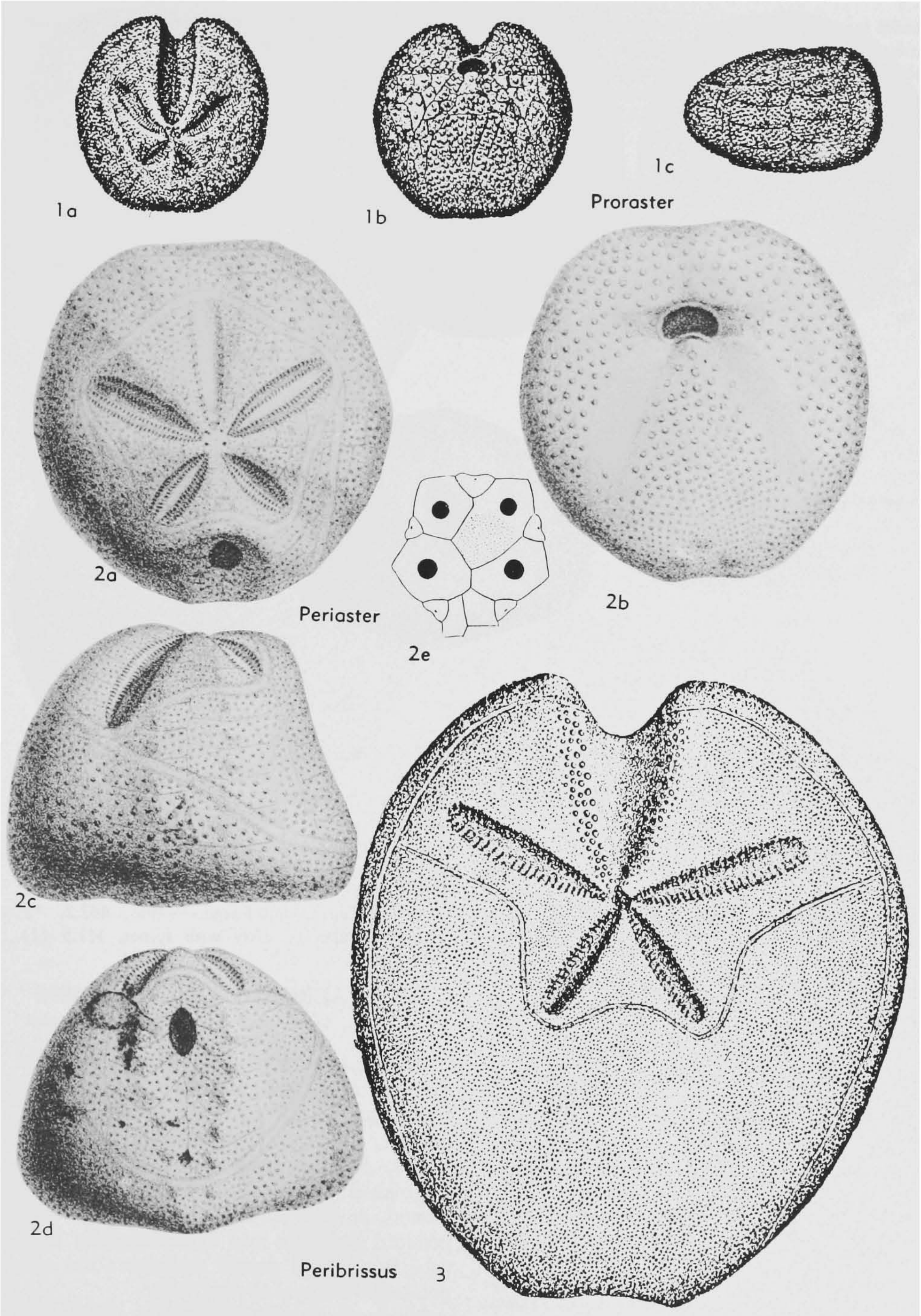



FIG. 460. Schizasteridae (p. *U*576, *U*578).

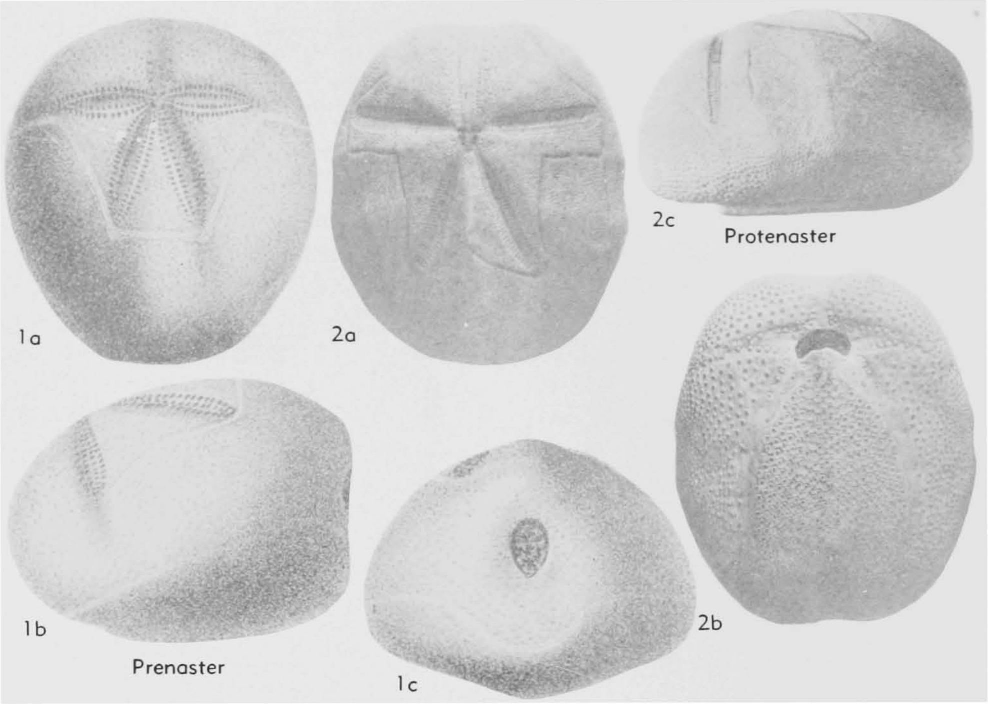



FIG. 461. Schizasteridae (p. U576).

**Proraster** LAMBERT, 1895, p. 256 [**Schizaster atavus* ARNAUD in COTTEAU, 1883, p. 13] [=*Sanfilippaster* CHECCHIA-RISPOLI, 1932, p. 313 (type, *Proraster geayi* COTTEAU, 1908, p. 26)]. Much like *Paraster,* with 4-pored ethmolytic apical system, distinguished by very deeply sunken anterior ambulacrum and by lacking lateroanal fasciole. *U.Cret.(Cenoman.-Senon.),* cosmop.——FIG. 460, *1.* **P. atavus* (ARNAUD); *1a-c,* aboral, oral, lat., ×1 (136i).

**Pseudobrissus** LAMBERT, 1905, p. 155 [**Brissus corsicus* COTTEAU, 1877, p. 325; OD]. Large, ovoid, with slight frontal sinus; petals very long and narrow, deeply depressed, anterolateral ones oriented transversely; apical system undescribed. *Mio.,* Corsica.——FIG. 462,*3.* **P. corsicus* (COTTEAU); oral, ×0.75 (21c).

**Schizopneustes** THIÉRY, 1907, p. 64 [*pro Dipneustes* ARNAUD, 1891, p. 152 (*non* HOERNES, 1866)] [**Dipneustes aturicus* ARNAUD in COTTEAU, 1891, 1893, p. 152; OD]. Broadly heart-shaped, with deeply depressed frontal ambulacrum and sinus, and overhanging rear; anterior petals well developed, posterior ones small and rudimentary; structure of apical system uncertain. *Paleoc.(Dan.),* SW.Fr.——FIG. 462,*1.* **S. aturicus* (ARNAUD); *1a,b,* aboral, lat., ×0.8 (136i).

**Tripylus** PHILIPPI, 1845, p. 344 [**T. excavatus*; OD] [=*Hamaxitus* TROSCHEL, 1851, p. 72 (obj.); *Parapneustes* KOEHLER, 1912, p. 161 (type, *P. cordatus*)]. Marsupial and sexually dimorphous; ethmolytic, with 2 or 3 gonopores; paired ambulacra petaloid, sunken, anterior pair or both pairs deeply depressed in females to form marsupia; frontal ambulacrum subpetaloid; anterolateral petals not reaching peripetalous fasciole. *Rec.,* Antarctic-Tierra del Fuego.——FIG. 462,*2.* **T. excavatus*; aboral, partly with spines, ×1.5 (1).

## Family AEROPSIDAE Lambert, 1896

[*nom. correct.* Aeropsidae CLARK, 1917, p. 133 (*pro* Aeropidae LAMBERT, 1896)]

Aberrant spatangoids, convergent toward *Pourtalesia* in tendency to vase or bottle shape; apical system ethmophract to ethmolytic, gonopores 2 to 4; lacking primary spines, having peripetalous fasciole; distinguished above all by specialization of frontal ambulacrum for respiration, with petaloid structure and extraordinarily large tube feet, while paired ambulacra are subpetaloid. [Bathyal-abyssal.] *Rec.*

No fossils can be referred to this family with any degree of certainty. Derivation of the aeropsids remains in doubt, but may be from the Hemiasteridae.

**Aeropsis** Mortensen, 1907, p. 90 [*pro Aerope* Jeffreys, 1876, p. 212, 380 (*non* Leach, 1813; *nec* Albers, 1860)] [**Aerope rostrata* Wyville Thomson, 1877, p. 380; OD]. Shape cylindroid; apical system ethmophract, somewhat anterior, with 2 to 4 gonopores; anterior ambulacrum broad, with large, obliquely placed pore-pairs; paired ambulacra nonpetaloid; peripetalous fasciole developed in frontal part of test. *Rec.*, cosmop.——Fig. 463,*1*. **A. rostrata* (Wyville Thomson);

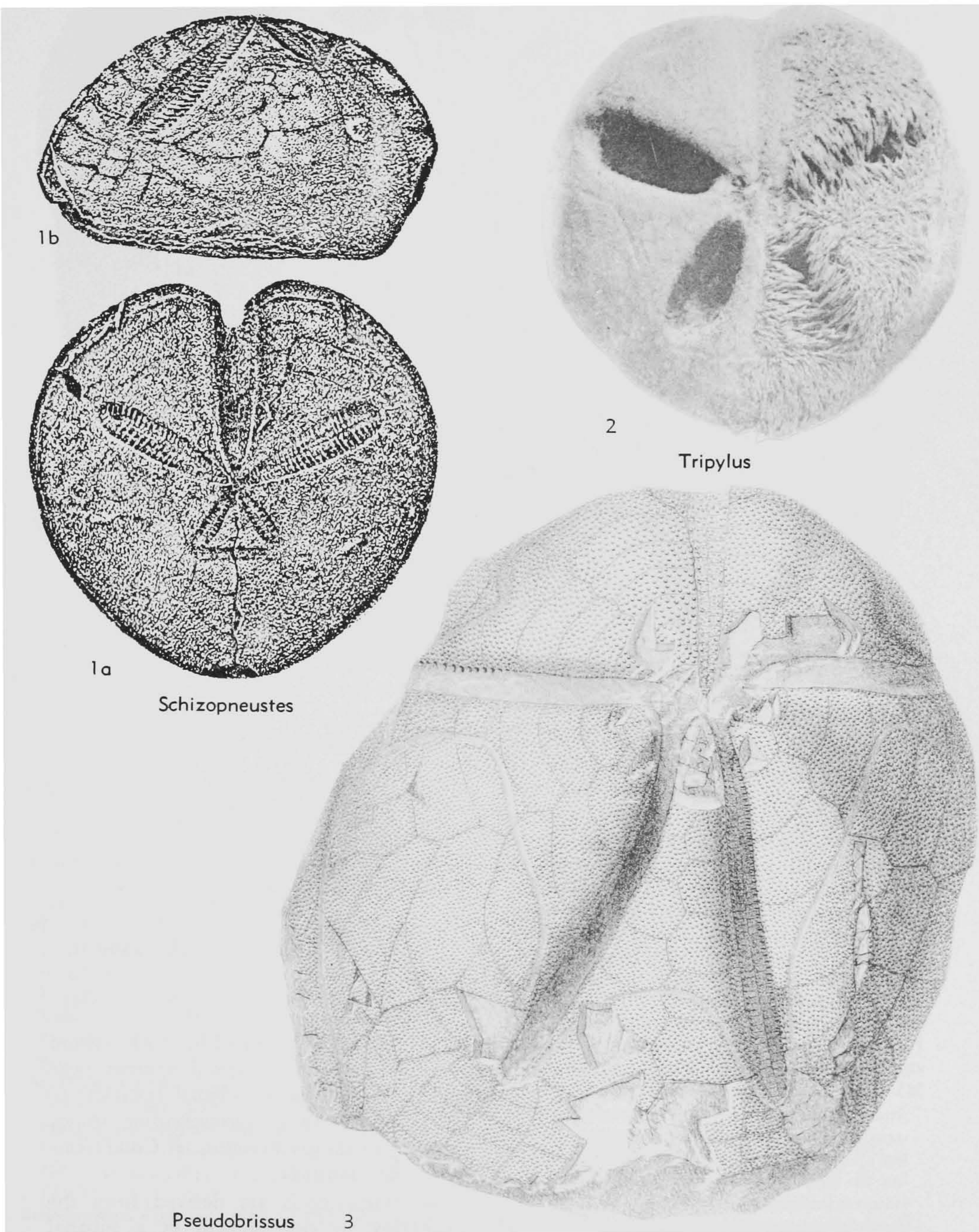



Fig. 462. Schizasteridae (p. U578).

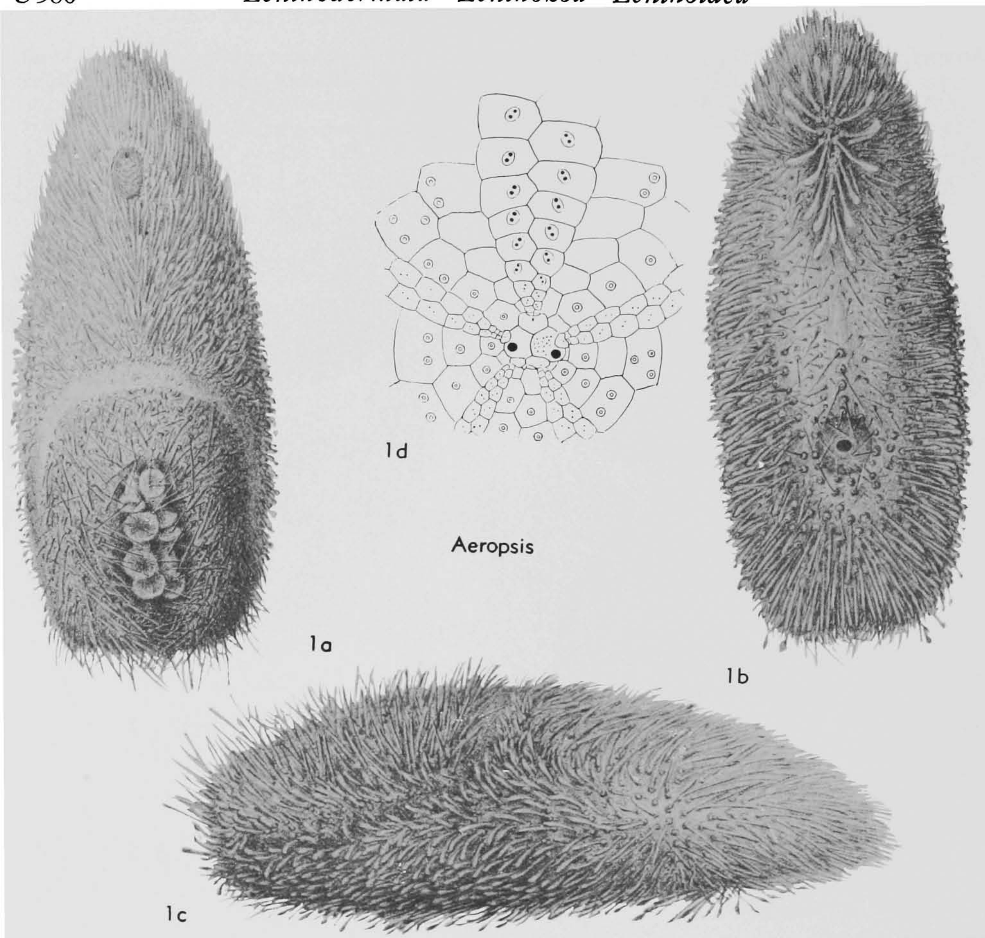



FIG. 463. Aeropsidae (p. U578-U579).

*1a-c,* aboral, oral, lat., ×1 (2); *1d,* detail of apical region (136h).

**Aceste** WYVILLE THOMSON, 1877, p. 376 [**A. bellidifera*; OD] [=*Acestina* LAMBERT & THIÉRY, 1924, p. 432 (*nom. van.*)]. Shape oval, with deep frontal sinus; apical system posterior, ethmolytic, with 2 gonopores; frontal ambulacrum very large, deeply sunken on oral and apical sides, bearing large pores for giant, flower-like tube feet; paired ambulacra nonpetaloid, bearing small pores which are paired only in anterior rows of anterolateral ambulacra. [Bathyal.] *Rec.,* cosmop.——FIG. 464, *1.* **A. bellidifera,* ×1.3; *1a,* aboral with spines and tube feet, ×2; *1b-e,* aboral, oral, lat., post., ×1 (2); *1f,* apical system, ×27 (136h).

## Suborder MICRASTERINA A. G. Fischer, new suborder

[=Prymnodesmia DUNCAN, 1889]

Petaloid spatangoids with subanal fasciole (absent in some members of Loveniidae), which may be combined with peripetalous or internal fasciole. Primary spines developed except in Micrasteridae. *Cret.(Cenoman.)-Rec.*

### Family MICRASTERIDAE Lambert, 1920

[*nom. transl.* MORTENSEN, 1950, p. 362 (*ex* Micrasterinae LAMBERT, 1920, p. 16)]

Heart-shaped spatangoids, with ethmophract to transitional apical systems bearing 3 or 4 gonopores; subanal fascioles; no primary tubercles or corresponding spines. Plastron mesamphisternous. *U.Cret.(Cenoman.)-Eoc.,* cosmop.

The micrasterids are derived from the toxasterids, by development of a subanal

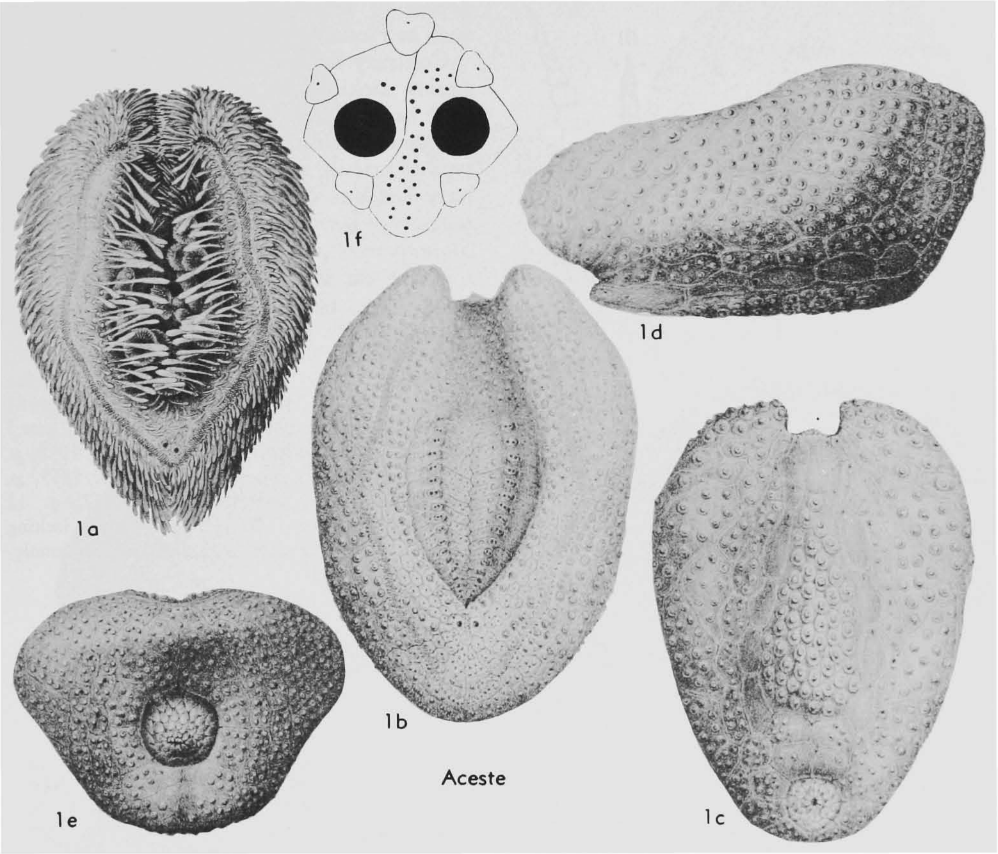



FIG. 464. Aeropsidae (p. U580).

fasciole (Fig. 465). *Isomicraster* may be a connecting link.

**Micraster** L. AGASSIZ, 1836, p. 184 [**Spatangus coranguinum* LESKE, 1778, p. 221] [=*Pycnaster* POMEL, 1883, p. 42 (obj.)]. Test heart-shaped, rostrate; 4 gonopores; paired petals broad, with round or elongate conjugate pores. *U.Cret.(Cenoman.)-Paleoc.(Dan.)*, Eu.-Madag.-Cuba.

**M. (Micraster).** Anterior ambulacrum narrow, pores round and not conjugate; paired petals broad, with round to elongate, conjugate pores. *U. Cret. (Cenoman.-Senon.)*, Eu.-Medit.-Madag.-Cuba.——FIG. 467,*2*. **M. (M.) coranguinum* (LESKE), Santon., Eng.; *2a-d*, aboral, oral, lat., post., ×1; *2e*, apical system, enlarged (173).

**M. (Gibbaster)** GAUTHIER, 1887, p. 381 [**M. (G.) fastigatus*; OD]. Anterior ambulacrum like paired ones, which resemble those of *M. (Micraster)*. *U. Cret.(Santon.)-Paleoc.(Dan.)*, Eu.——FIG. 467,*1*. **M. (G.) fastigatus*; *1a-c*, aboral, oral, lat., ×1 (136h).

**Brissopneustes** COTTEAU, 1887, p. 712 [**B. vilanovae*; OD]. Distinguished from *Micraster* by its 3 gonopores and weak frontal sinus; pores in frontal ambulacrum small. [At least one species (*B. danicus*, Danian, Denmark) shows the sexual dimorphism (depressed ambulacral areas in females) distinctive of marsupial spatangoids.] *U.Cret. (Maastricht.)-Eoc.*, Eu.-India-Madag.——FIG. 468, *1*. **B. vilanovae*; U.Cret., Eu.; *1a-c*, aboral, oral, lat., ×1 (136h).

**Isopneustes** POMEL, 1883, p. 43 [**Cyclaster bourgeoisi* COTTEAU, 1869, p. 328; OD]. Differs from *Micraster* in slight anterior sinus, which does not extend to margin; presence of subanal fasciole not established in type-species, hence assignment to Micrasteridae tentative. *U.Cret.(Turon.)-Eoc.*, Eu. ——FIG. 468,*3*. *I. subquadratus* (DESOR), Eoc., Italy; *3a,b*, aboral, oral, ×1 (136h).

**Ovulaster** COTTEAU, 1884, p. 328 [**O. gauthieri*; OD]. Text ovoid, with frontal sinus; apical system ethmophract, with 4 gonopores; ambulacra not distinctly petaloid, pores small, especially in anterior ambulacrum; subanal fasciole; periproct placed high on truncate rear. Sternum symmetrical. *U.Cret.*, Medit.——FIG. 468,*2a-c*. **O. gauthieri*;

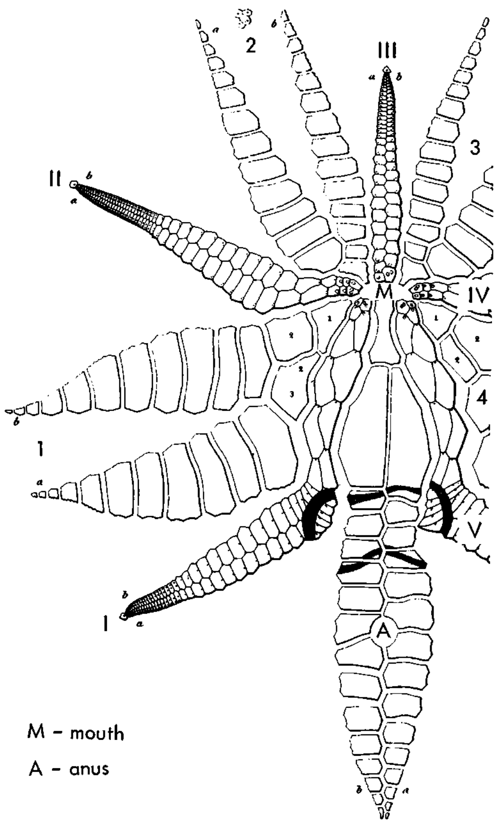



FIG. 465. Plate diagram of *Micraster* (Lovén).

*2a-c,* aboral, oral, lat., ×1 (136i).——FIG. 467, *2d. O. auberti,* apical system, enl. (136h).

## Family BRISSIDAE Gray, 1855

[*nom. transl.* LAMBERT, 1901, p. 969 (*ex* Brissina GRAY, 1855, p. 49)] [incl. Unifasciidae COOKE, 1959, p. 79; Cyclasteridae POSLAVSKAYA, 1965]

Heart urchins typically provided with both peripetalous and subanal fascioles, latter with anal branches in some; apical system ethmophract to ethmolytic, with 2 to 4 gonopores; spine cover normally including large radioles, generally located within fasciole-enclosed areas. Plastron ultramphisternous. [Neritic to bathyal.] *U.Cret.(Santon.)-Rec.*

The brissids seem to have been derived from the Micrasteridae by addition of a peripetalous fasciole, development of primary tubercles, and eventually of an ethmolytic apical system (Fig. 466). This is suggested in particular by the *Micraster*-like nature of some of the primitive brissids, such as *Plesiaster.*

Contrary to common usage a number of genera lacking the typical brissid fascioles have been included here, because their other characters indicate close relationship to typical brissid genera. These forms, which have lost one or both fascioles, are *Mauritanaster, Unifascia, Macropneustes,* and *Stomaporus,* and these form a bridge to some of the asterostomatids.

**Brissus** GRAY, 1825, p. 431 [*nom. conserv.* ICZN, 1948 (Op. 209, p. 369) (*non* MÜLLER, 1781, *nec* MODEER, 1793, *nec* LINK, 1807, *nec* OKEN, 1815, *nec* DAHL, 1823)] [**Spatangus brissus unicolor* LESKE, 1778, p. 248; SD ICZN, Op. 209, 1948] [=*Bryssus* MARTENS, 1869, p. 128 *(nom. van.)* (obj.); *Brissus (Allobrissus)* MORTENSEN, 1950, p. 162 (type, *Brissus agassizii* DÖDERLEIN, 1855, p. 36; *Sandiegoaster* SÁNCHEZ ROIG, 1952, p. 12 (type, *S. durhami*; OD)]. Test ovoid, lacking frontal sinus; apex anterior, apical system ethmoly-

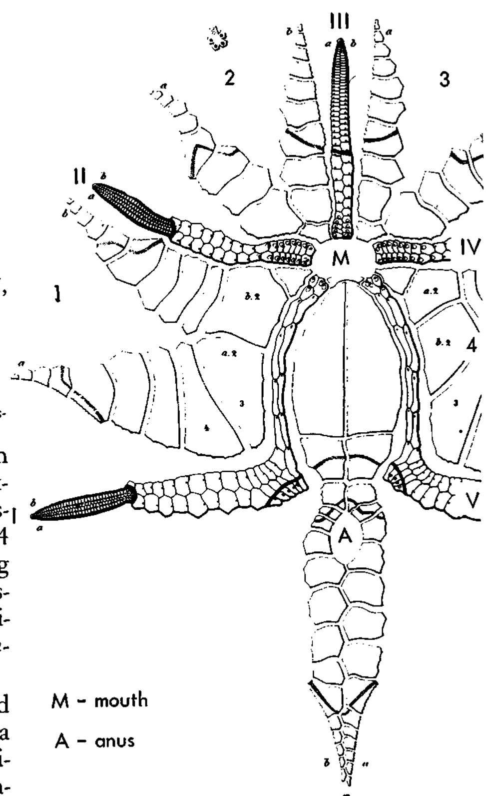



FIG. 466. Plate diagram of *Brissus* (Lovén).

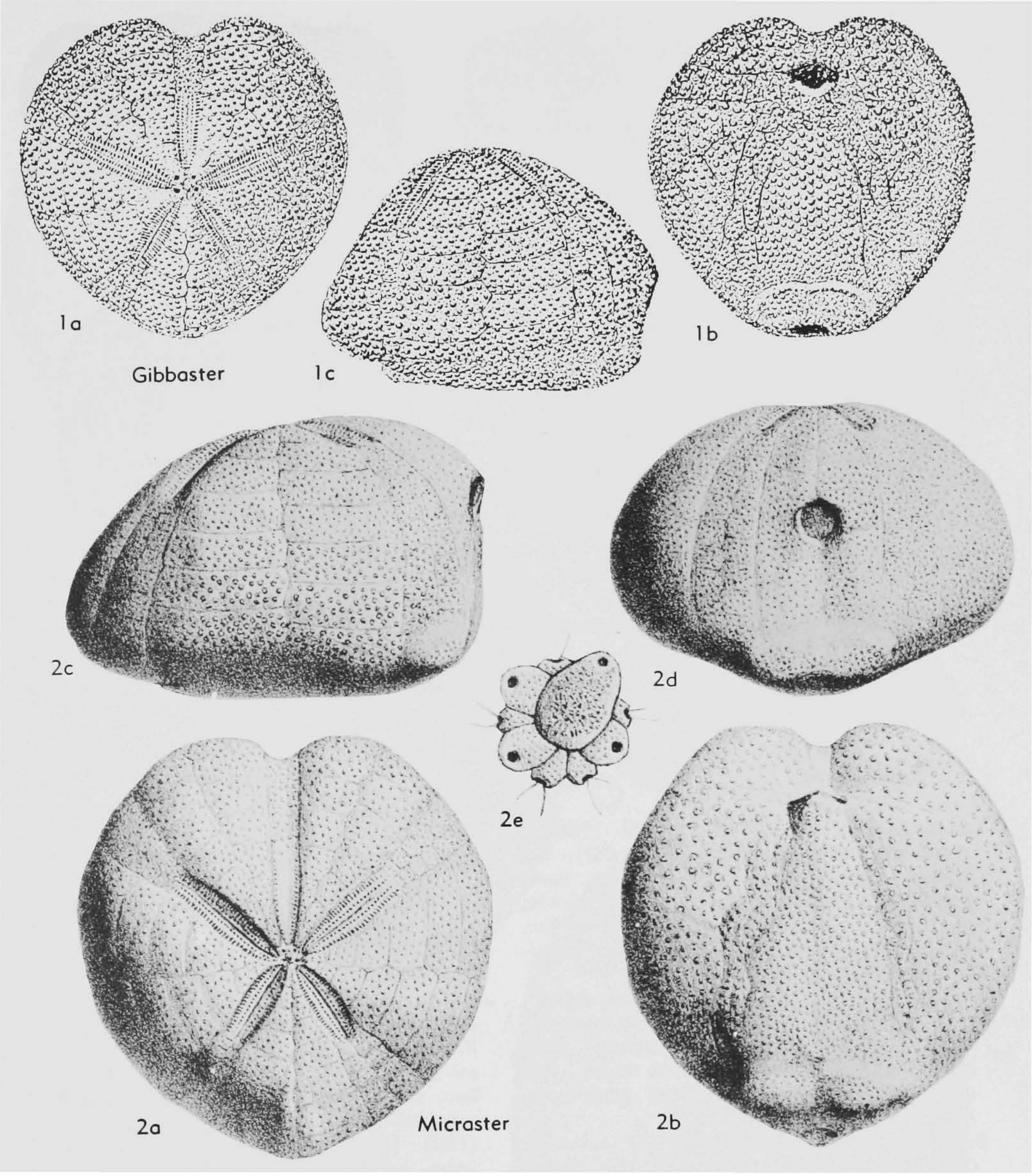



FIG. 467. Micrasteridae (p. *U*581).

tic, with 4 gonopores; petals sunken, anterior pair transversely oriented; subanal fasciole broad, with lateral lobes. *Eoc.-Rec.*, cosmop.——FIG. 469,*1*. **B. unicolor* (LESKE), Rec., Cuba; *1a-d*, aboral, oral, lat., post., ×3 (24).

**Aguayoaster** SÁNCHEZ ROIG, 1952, p. 10 [**A. aguayoi*; OD]. Small, inflated, forwardly inclined; gentle anterior sinus; apical system far anterior, ethmolytic, gonopores 4; differs from *Cionobrissus* in having depressed petals, and a raised, rostrate posterior ambulacrum, and in lacking an anal snout and a deeply depressed anterior ambulacrum on oral side. *Eoc.*, Cuba.——FIG. 470,*3*. **A. aguayoi*, *3a-c*, aboral, oral, lat., ×0.5 (216d).

**Anabrissus** MORTENSEN, 1950, p. 161 [**Brissus damesi* A. AGASSIZ, 1881, p. 197; OD]. Small, oval, lacking frontal sinus; ambulacra flush, paired ones petaloid; apical system ethmolytic, with 3 gonopores; peripetalous fasciole rudimentary. *Rec.*,

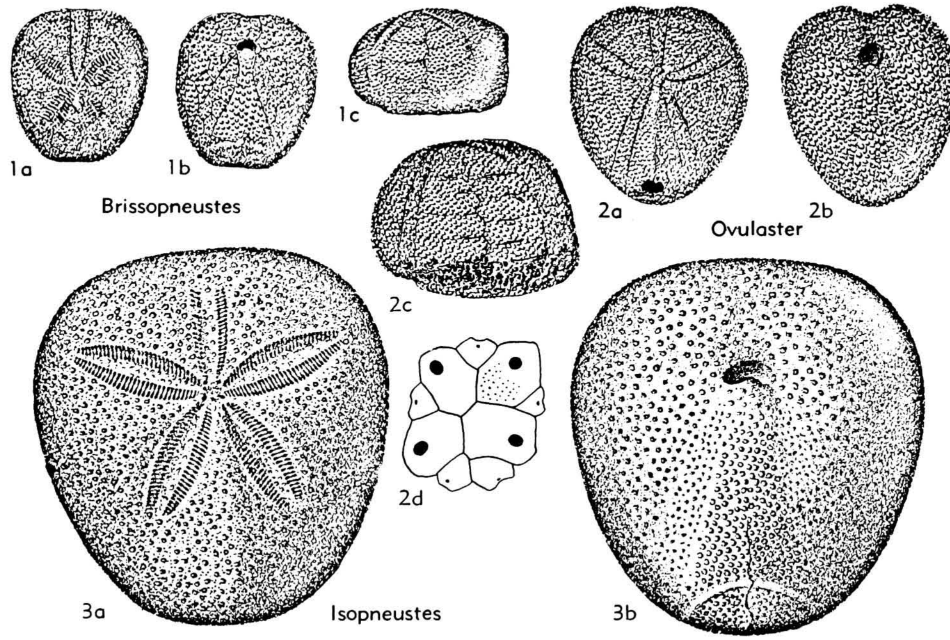



FIG. 468. Micrasteridae (p. U581).

trop. Atl.——FIG. 471,*2*. **A. damesi* (AGASSIZ); *2a-c,* aboral, oral, lat., ×3; *2d,* apical system, enlarged (136i).

**Anametalia** MORTENSEN, 1950, p. 161 [**Brissus sternaloides* BOLAU, 1874, p. 177; OD]. Resembling *Cionobrissus* but frontal sinus weak, slight depression running from this to peristome; anal fasciole rudimentary. *Rec.,* Indonesia.——FIG. 469,*2*. **A. sternaloides* (BOLAU); *2a-c,* aboral, oral, lat., ×1.5 (136i).

**Arcaechinus** KIER, 1957, p. 891 [**A. auraduensis*; OD]. Differs from *Brissus* mainly in having 3 gonopores (genital 2 being imperforate), long labrum and long, narrow sternum. *L.Eoc.,* Afr. (Somaliland).——FIG. 470,*1*. **A. auraduensis*; *1a,b,* aboral, post., ×1 (94).

**Brissopatagus** COTTEAU, 1863, p. 143 [**B. caumonti*; OD] [=*Brissospatangus* COTTEAU, 1886 *(nom. van.)*]. Differs from *Eupatagus* in having large depressions in front of anterior petals or in front of all petals. *Eoc.,* cosmop.——FIG. 470,*2*. **B. caumonti,* Fr.; *2a-c,* aboral, oral, lat., ×1 (27e). [=*Brissospatagus* AGASSIZ, 1874, p. 174 *(nom. van.)*.]

**Brissopsis** L. AGASSIZ in AGASSIZ & DESOR, 1847, p. 14 [**Brissus lyrifer* FORBES, 1841, p. 187; SD DESOR, 1858, p. 378] [=*Brissopsis* AGASSIZ, 1840, p. 13 *(nom. nud.)*; *Kleinia* GRAY, 1851, p. 133 (type, *K. luzonica*); *Toxobrissus* DESOR, 1858, p. 399 (type, *Brissopsis elegans* AGASSIZ, 1847, p. 184); *Brissoma* POMEL, 1888, p. 41 (type, *Brissopsis cluciei* WRIGHT, 1855, p. 37); *Zeugaster* LAMBERT, 1907, p. 106 (type, *Brissopsis lamberti* GAUTHIER, 1900, p. 42)]. Ovate, somewhat depressed, with slight frontal sinus; ethmolytic, gonopores 2 to 4; ambulacra slightly depressed; paired ones petaloid, may have rudimentary pores in proximal plates; petals confluent in some species *("Kleinia")*; subanal fasciole may be lost in adults. *Eoc.-Rec.,* cosmop.——FIG. 471,*1a-c*. **B. lyrifera* (FORBES), Rec., Gulf Mex., *1a,b,* aboral, lat., ×1; *1c,* oral (part, showing periproct and subanal fasciole), enl. (175b).——FIG. 471,*1d*. *B. luzonica,* GRAY, Rec., Red Sea; detail of petals, enl. (136i).——FIG. 472,*1a-d*. *B. pacifica* AGASSIZ, Rec., Pac.; *1a-d,* apical system showing gradual reduction of genital pore in interamb 3, ×7.5 (136i). [=*Bryssopsis* MEISSNER, 1903, p. 1343 *(nom. van.)* (obj.); *Toxobryssus* MEISSNER, 1903, p. 1395 *(nom. van.)*; *Brissospatagus* AGASSIZ, 1874 *(nom. van.)*.]

**Cionobrissus** A. AGASSIZ, 1879, p. 206 [**C. revinctus*; OD]. Ovally elongate, inflated, with deep frontal sinus; periproct above posterior snout; apical system anterior, ethmolytic, with 4 gonopores; anterior ambulacrum flush on apical side, slightly depressed at ambitus, deeply depressed on oral side; petals depressed. *Eoc.-Rec.,* Iran-SW. Pac.——FIG. 472,*2*. **C. revinctus,* Rec., SW.Pac.; *2a,b,* frontal amb., apical system, ×5 (136i); *2c-e,* oral, lat., post., ×1 (2). [=*Cionobryssus* MEISSNER, 1903, p. 1343 *(nom. van.)* (obj.).]

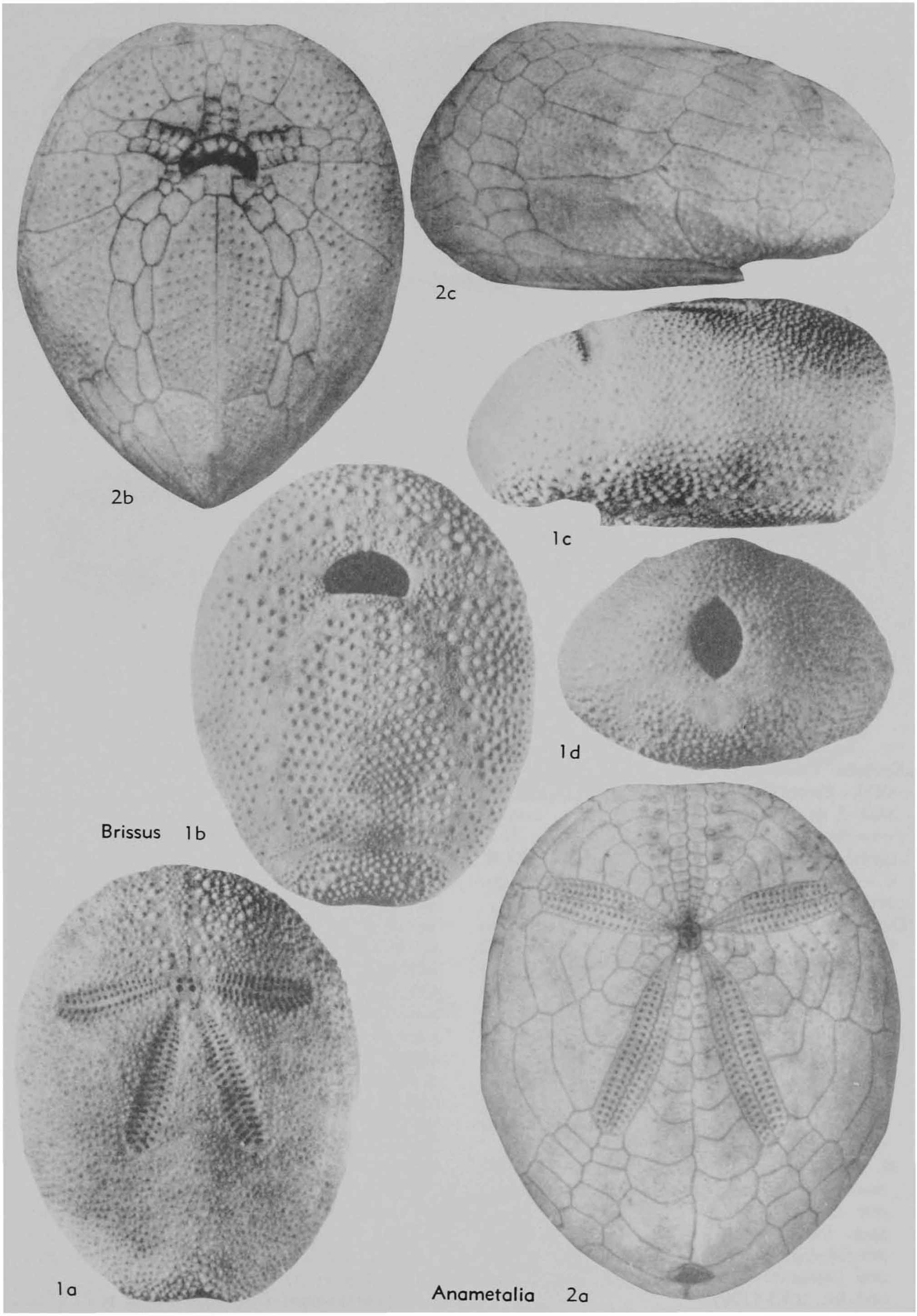



FIG. 469. Brissidae (p. *U*582-*U*584).

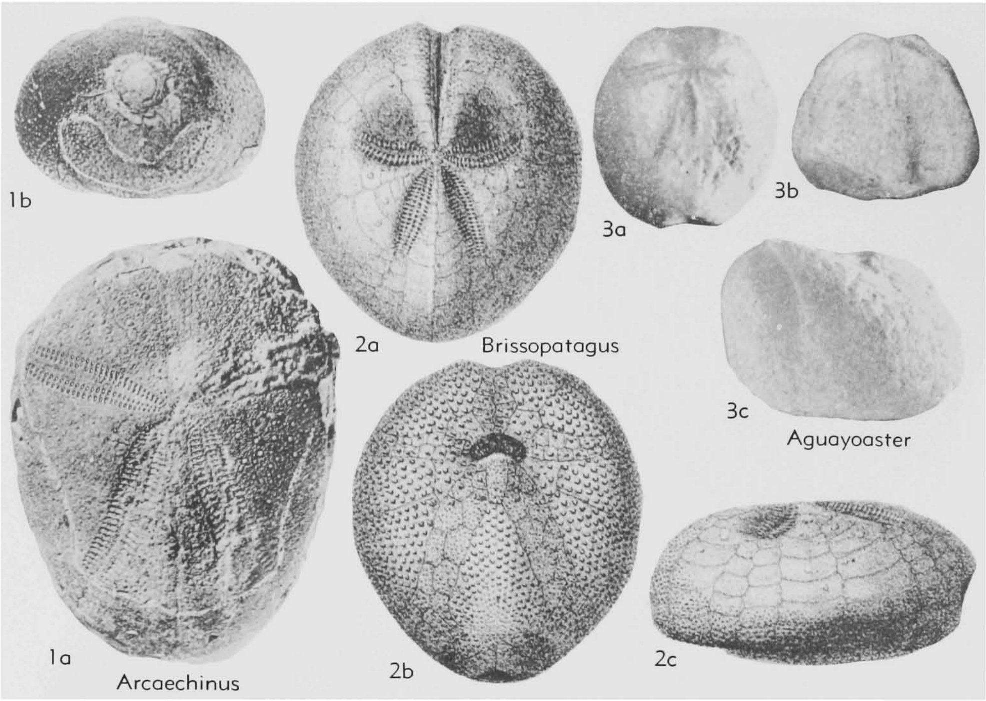



FIG. 470. Brissidae (p. U583-U584).

**Cyclaster** COTTEAU, 1856, p. 345 [**C. declivus*; OD]. Resembling *Brissopsis,* but ethmophract, with 3 gonopores. *U.Cret.(Senon.)-Rec.,* cosmop. ——FIG. 473,*1a-d*. **C. declivus,* Eoc., Fr.; *1a-d,* aboral, oral, lat., post., ×1 (27e).——FIG. 473,*1e*. *C. recens* MORTENSEN, Rec., Indochina; apical system, ×6 (136i).

**Diplodetus** SCHLÜTER, 1900, p. 364 [**D. brevistella*; OD]. Similar to *Plesiaster* but frontal sinus weak and frontal ambulacrum with obliquely placed pores; ethmophract, with 4 gonopores; petals small. *U.Cret.(Santon.)-Eoc.,* Eu.-Afr.(Madag.).

**D. (Diplodetus).** Apical system near center; anterior petals longest; rear of test rostrate; subanal fasciole not ascertained. *U.Cret.(Santon.)-Eoc.,* Eu.-Afr.(Madag.).——FIG. 473,*3*. **D. (D.) brevistella,* U.Cret.(Santon.), Eu.; *3a-c,* aboral, oral, lat., ×0.7 (218).

**D. (Protobrissus)** LAMBERT, 1907, p. 719 [**P. mortenseni*; OD]. Small, petals subequal, anterior pair diverging laterally from anteriorly placed apex. *U. Cret.(Senon.)-Paleoc.(Dan.),* Eu. (Fr.)-Afr.(Madag.).——FIG. 473,*2*. **D. (P.) mortenseni* LAMBERT, Paleoc.(Dan.), Fr.; *2a-c,* aboral, oral, lat., ×1.5 (106).

**Eupatagus** L. AGASSIZ, 1847, p. 9 [**E. valenciennesi*; SD POMEL, 1883, p. 28] [=*Pseudopatagus* POMEL, 1885, p. 18 (type, *P. cruciatus*; OD); *Melitia* FOURTAU, 1913, p. 68 (type, *Metalia melitensis* GREGORY, 1891, p. 621); *Heterospatangus* FOURTAU, 1905, p. 606 (type, *Macropneustes lefebvrei* DELORIOL, 1881, p. 50); *Euspatangus* COTTEAU, 1869, p. 257 *(nom. van.)*; *Perispatangus* FOURTAU, 1905, p. 605 (type, *Euspatangus libyeus* DE LORIOL, 1881, p. 52); *Koilospatangus* LAMBERT, 1906, p. 185 (obj.); *Zanolettiaster* SÁNCHEZ ROIG, 1952, p. 14 (type, *Z. herrerae*; OD); *Megapatagus* SÁNCHEZ ROIG, 1953, p. 58 (type, *M. franciscanus*; OD)]. Test ovoid in outline, low, oral side flat; apical system anterior, ethmolytic, with 4 gonopores; paired ambulacra with closed petals; frontal ambulacrum nonpetaloid, pores in single series, phyllodes weak; primary tubercles on aboral side only within peripetalous fasciole. *Eoc.-Rec.,* cosmop.

**E. (Eupatagus).** Ambitus rounded, frontal sinus weak or absent. *Eoc.-Rec.,* cosmop.——FIG. 474, *4*; 475,*1*. **E. valenciennesi,* Rec., Australia; 474,*4a,b,* aboral, oral views of specimen with spines, ×1.5 (2); 474,*4c,* apical system, ×3 (136i); 475,*1a-c,* aboral, oral, lat., bare test, ×0.9 (Fischer, n).

**E. (Gymnopatagus)** DÖDERLEIN, 1901, p. 23 [**G. valdiviae*; OD]. Differing from *Eupatagus* in its deeper frontal sinus (heart-shaped outline) and sharper ambitus; many species are intermediate.

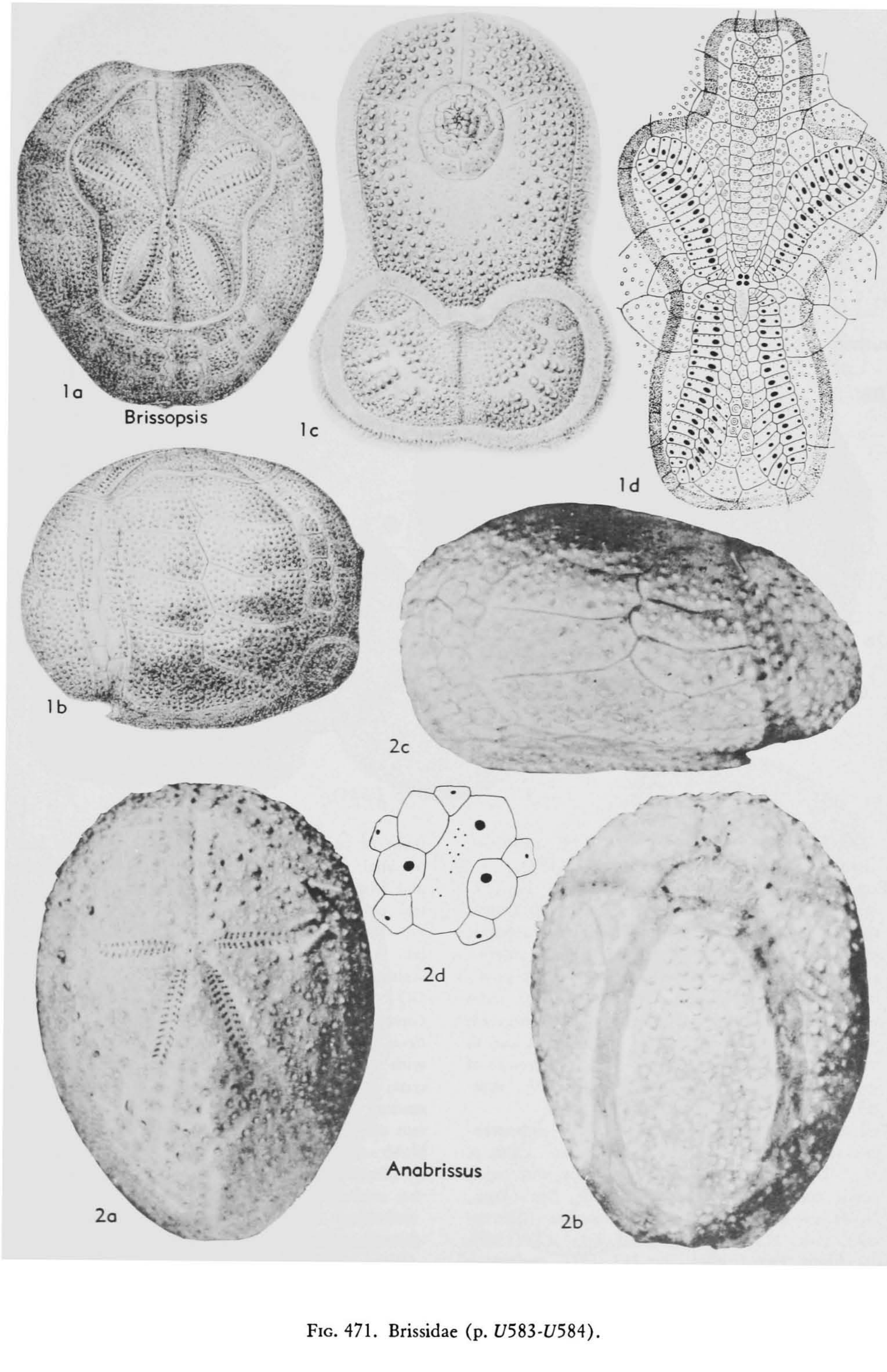



FIG. 471. Brissidae (p. U583-U584).

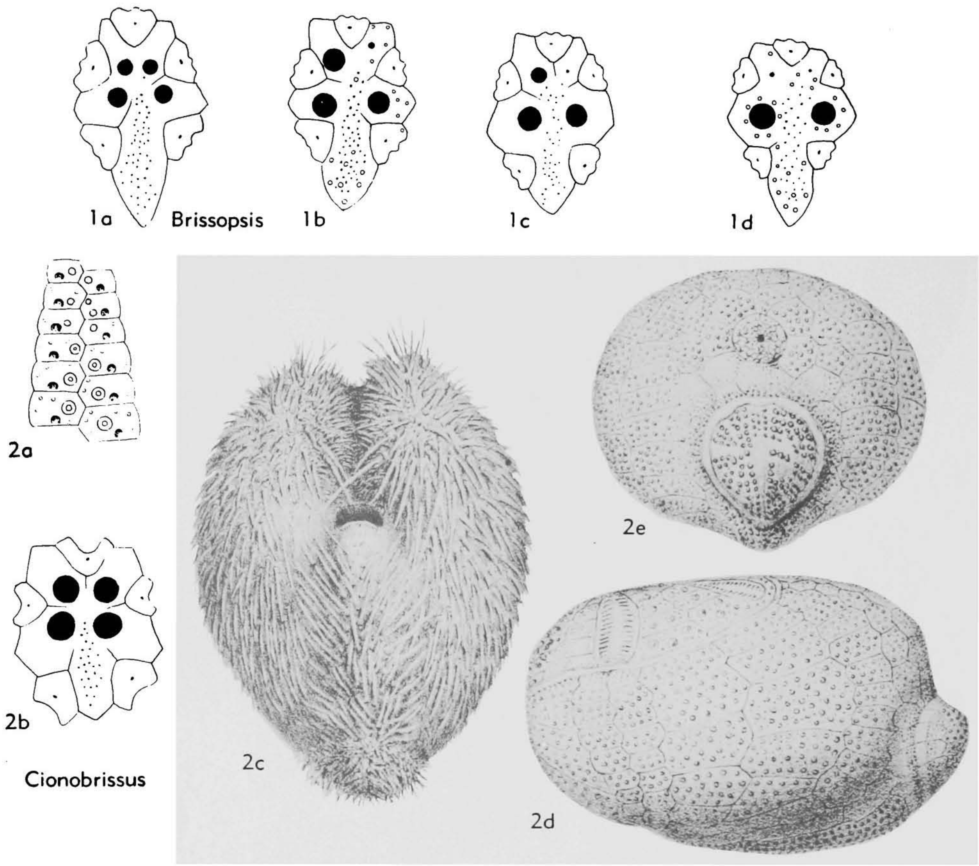



FIG. 472. Brissidae (p. *U*584).

*Eoc.-Rec.,* cosmop.——FIG. 477,*2*. **G. valdiviae,* Rec., Afr.; *2a,b,* aboral, oral, ×1.5 (187).

**Fernandezaster** SÁNCHEZ ROIG, 1952, p. 17 [**F. mortenseni*; OD]. Outline hexagonal with frontal sinus; vaulted aboral side divided into 5 separate lobes by sunken petals and less depressed anterior ambulacrum; posterolateral petals confluent proximally, occupying single median groove, from which distal parts of petals diverge at 45 degrees; with peripetalous and subanal fascioles. [Close to the *Brissopsis luzonica* or *"Kleinia"* group of species.]. *Eoc.,* Cuba.——FIG. 476,*2*. **F. mortenseni*; aboral, ×0.5 (216d).

**Fourtaunia** LAMBERT, 1902, p. 53 [**Hypsospatangus santamariae* GAUTHIER in FOURTAU, 1900, p. 56; OD]. Resembling *Eupatagus* but with open petals and reniform subanal fasciole. *Eoc.-Oligo.,* N.Afr.——FIG. 473,*4*. **F. santamariae* (GAUTHIER), Eoc., N.Afr.; *4a,b,* aboral, lat., ×1 (136i).

**Gillechinus** FELL, 1964, p. 213 [**G. cudmorei*; OD]. Resembling *Eupatagus* and *Plagiobrissus,* differing from *Eupatagus* in its rather open petals and restriction of large tubercles to areas in front of paired petals, from *Plagiobrissus* in lack of anal fasciole and reniform subanal fasciole, and from both in nearly circular outline and central position of apical system. *U.Eoc.,* Australia. ——FIG. 476,*1*. **G. cudmorei*; *1a-c,* aboral, oral, lat., ×1 (59).

**Gualtieria** AGASSIZ, 1847, p. 10 [**G. orbignyana*; OD] [=*Gualteria* AGASSIZ, 1872 *(nom. null.)*; *Gualtiera* QUENSTEDT, 1874 *(nom. null.)*; *Gaultieria* GREGORY, 1900 *(nom. null.)*]. Outline ovoid, with only trace of frontal sinus; frontal ambulacrum apetaloid, paired ambulacra with petals extending beyond peripetalous fasciole; apical system ethmolytic, with 4 gonopores. *Eoc.-Mio.,* Eu.-N.Afr.-Australia.

**G. (Gualtieria).** Oral side bearing ridges and nodes on ambulacra, near peristome on frontal interambulacra and on posterior interambulacrum; frontal ambulacrum slightly depressed. *Eoc.-Oligo.,* Eu.-N.Afr.——FIG. 474,*1*. **G. (G.) orbignyana,* Eoc., Fr.; *1a-c,* aboral, oral, post., ×1.5 (44).

**G. (Blaviaster)** LAMBERT, 1920, p. 26 [*pro Tem-*

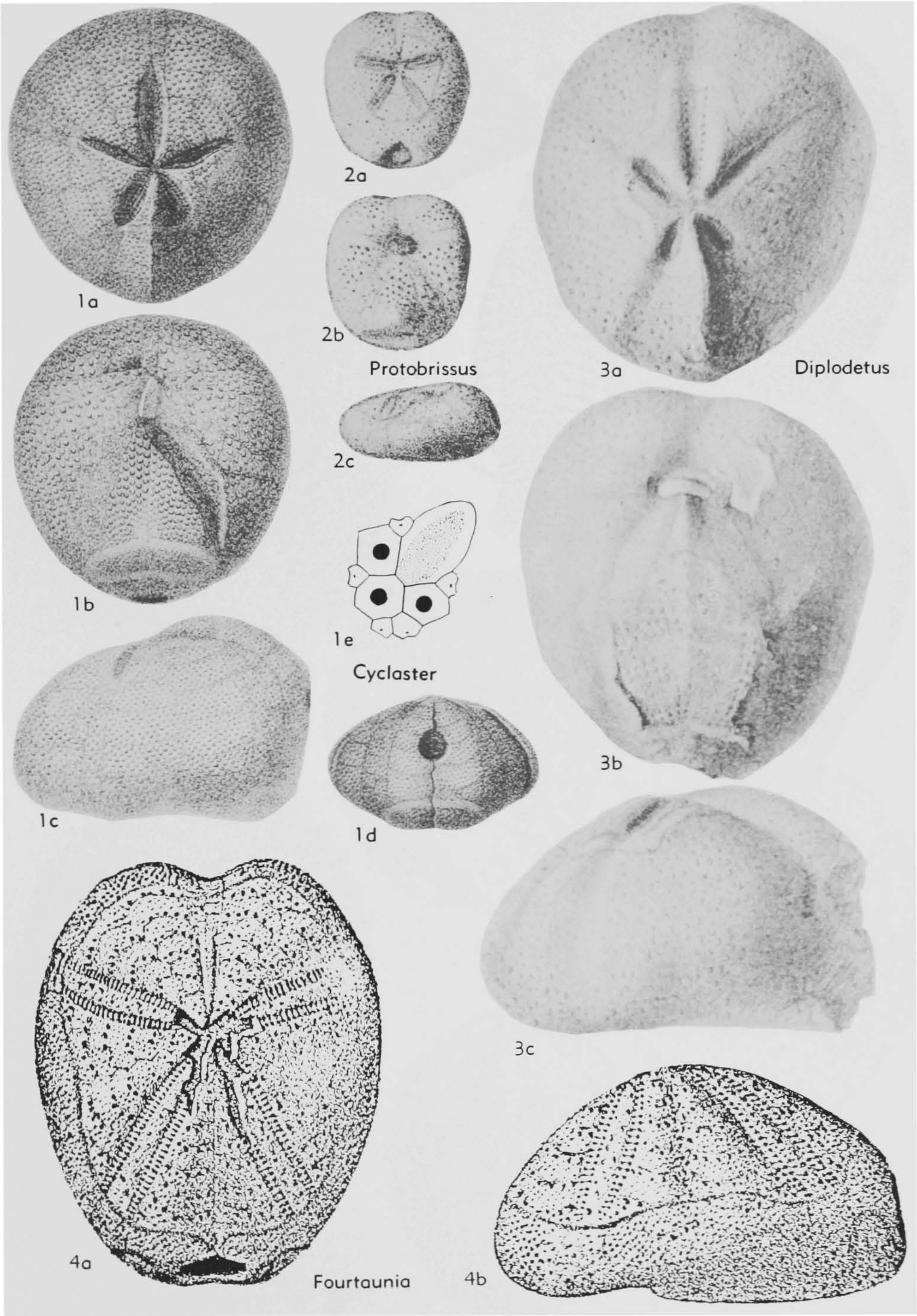



FIG. 473. Brissidae (p. *U*586, *U*588).

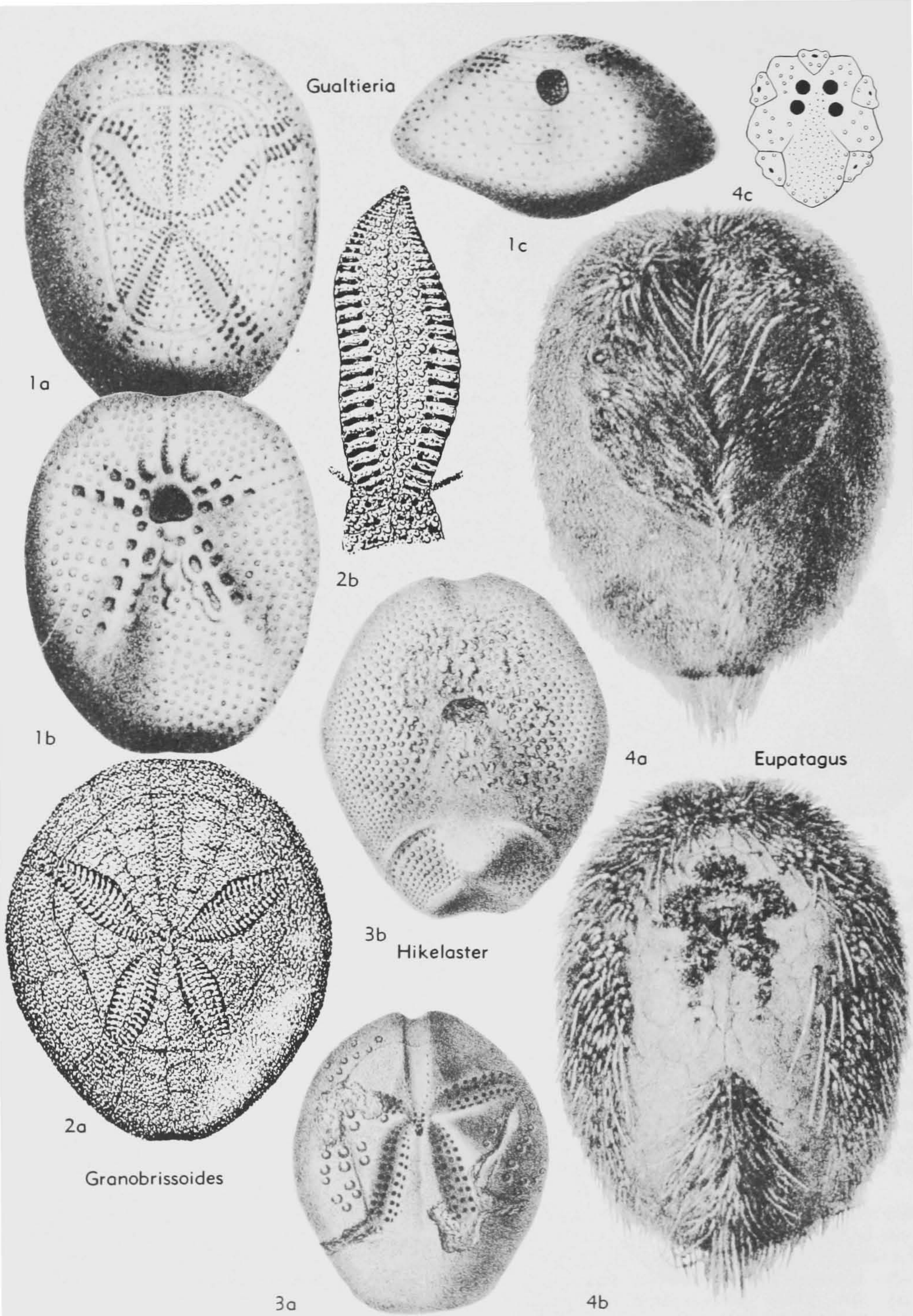



FIG. 474. Brissidae (p. U586, U588, U591).

*naster* LAMBERT, 1912, p. 105 (*non* VERRILL, 1894)] [**Temnaster grossouvrei* LAMBERT, 1912, p. 63; OD]. Lacking nodes and ridges on oral side. *Eoc.*, Fr.

**G. (Granobrissoides)** LAMBERT, 1920, p. 26 [**Gaultieria australiae* COTTEAU, 1889; OD]. Frontal ambulacrum flush; tips of petals crossing peripetalous fasciole only slightly; oral side unknown. *Mio.*, Australia.——FIG. 474,*2*. **G. (G.) australiae* COTTEAU; *2a*, aboral, ×1; *2b*, petal, enl. (136i).

**Herreraster** SÁNCHEZ ROIG, 1951, p. 52 [**H. herrerae*; OD]. Resembles *Fourtaunia* in heart shape and long, open petals, but differs in having broader petals, lacking anterior sinus, and having small submarginal periproct. [Obscure fascioles and open petals suggest that this genus forms bridge to certain asterostomatids such as *Antillaster*.] *Oligo.*, Cuba.——FIG. 478,*1*. **H. herrerae*; *1a,b*, oral, aboral, ×0.3 (216c).

**Hikelaster** LAMBERT & THIÉRY, 1920, p. 27 [*pro Troschelia* DUNCAN & SLADEN, 1883, p. 27 (*non* MOERCH, 1876)] [**Troschelia tuberculata* DUNCAN & SLADEN, 1883, p. 27; OD]. Differing from *Eupatagus* in its sharply defined, depressed frontal ambulacrum, sunken petals with tiny pores in apical plates but large round pores distally, and presence of large primary tubercles outside of (as well as within) peripetalous fasciole. *Mio.*, India. ——FIG. 474,*3*. **H. tuberculatus* (DUNCAN & SLADEN); *3a,b*, aboral, oral, ×1 (47).

**Idiobryssus** CLARK, 1939, p. 173 [**I. coelus*; OD]. Test ovate, with oral side convex and apical side saddle-shaped; no frontal sinus; paired ambulacra weakly petaloid; peristome central, periproct on apical side; peripetalous and subanal fascioles present; adults unknown. [Juveniles, possibly malformed.] *Rec.*, Pac.O.——FIG. 477,*1*. **I. coelus*; *1a,b*, aboral, lat., ×3 (181).

**Lajanaster** SÁNCHEZ ROIG, 1926, p. 100 [**L. jacksoni*; OD] [=*Lajanaster* LAMBERT & SÁNCHEZ ROIG, 1924 *(nom. nud.)*]. *Eupatagus*-like, rather flat, with narrow slightly depressed petals and narrow sternum; primary aboral tubercles occur in narrow zones at anterior margin of paired petals. *Oligo.-Mio.*, Cuba.——FIG. 478,*3*. **L. jacksoni*, Oligo.; *3a,b*, aboral, oral, ×0.5 (216b).

**Lissospatangus** MORTENSEN, 1950, p. 162 [**L. hirsutus*; OD]. Differing from *Eupatagus* in absence of primary tubercles on apical side. *Rec.*, Australia.——FIG. 477,*3*. **L. hirsutus*; *3a,b*, aboral, oral, ×1 (136i).

**Macropneustes** L. AGASSIZ, 1847, p. 8 [**M. deshayesi*; SD JACKSON, 1922, p. 4]. Differs from *Eupatagus* chiefly in having depressed petals, and broad test; frontal sinus distinct. *Eoc.-Rec.*, cosmop. [=*Plagiopneustes* FOURTAU, 1905, p. 609 (type, *M. crassus* AGASSIZ).]

**M. (Macropneustes).** Petals large, ambitus rounded; peripetalous fasciole not forming embayments between petals. *Eoc.-Rec.*, Medit.-Carib.——FIG. 479,*1*. **M. (M.) deshayesi*, Eoc., Fr.; *1a-d*, aboral, oral, lat., post., ×1 (27e).

**M. (Deakia)** PAVAY, 1875, p. 304 [**Deakia rotundata*; OD]. Test depressed, ambitus sharp, petals small, fasciole embayed. *Eoc.*, Eu.-India. ——FIG. 480,*1*. **M. (D.) rotundata* (PAVAY), Hungary; *1a,b*, aboral, oral, ×1 (136i).

**Mariania** AIRAGHI, 1901, p. 211 [**Macropneustes marmorae* AGASSIZ, 1847, p. 326; OD] [=*Air-*

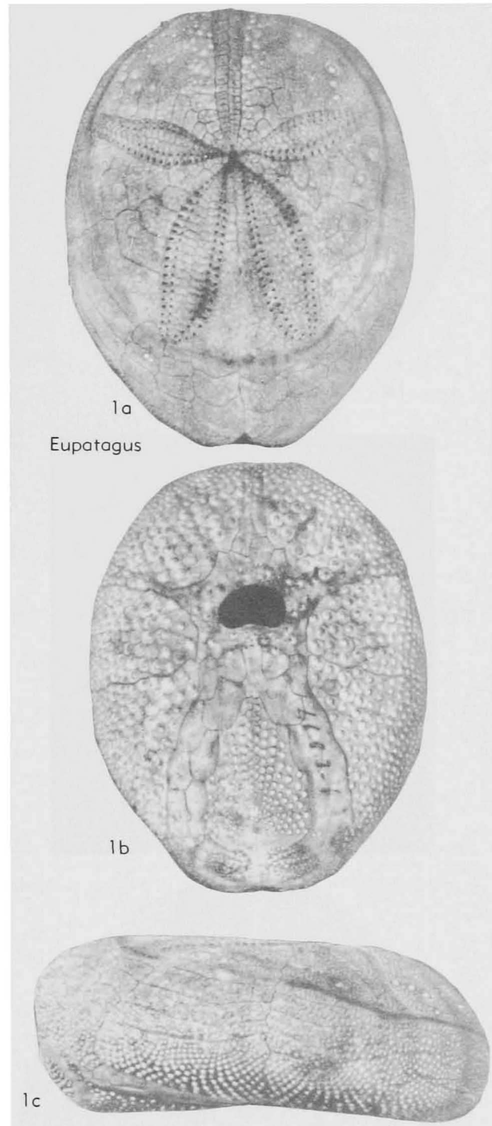



FIG. 475. Brissidae (p. U586).

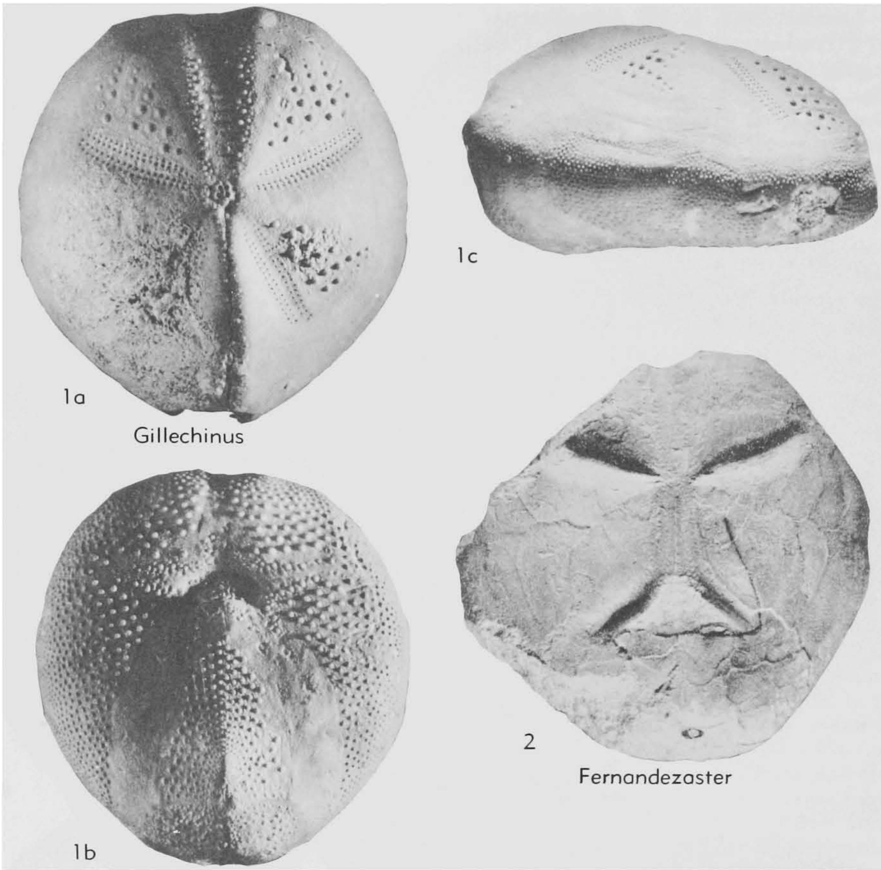



FIG. 476. Brissidae (p. *U*588).

*aghia* LAMBERT, 1910, p. 3 *(nom. van.)*]. Test broad, heart-shaped, with frontal sinus; apical system ethmolytic, with 4 gonopores; paired ambulacra forming broad petals; frontal ambulacrum nonpetaloid, with pore-pairs placed obliquely; no fascioles. *Oligo.-Mio.*, S.Eu.——FIG. 480,*2*. **M. marmorae* (AGASSIZ), Mio., Corsica; *2a,b,* aboral, lat., ×1 (21c).

**Mauritanaster** LAMBERT, 1920, p. 22 [**M. gentili*; OD]. Essentially a small *Macropneustes* lacking both fascioles. *Tert.*, Morocco.——FIG. 481,*1*. **M. gentili,* Tert., N.Afr.; *1a,b,* aboral, lat., ×1 (136i).

**Megapneustes** GAUTHIER, 1898, p. 678 [**M. grandis*; OD]. Essentially a *Fourtaunia* lacking subanal fasciole. *Eoc.*, Egypt.——FIG. 483,*1*. **M. grandis*; *1a,b,* aboral, lat., ×1 (136i).

**Meoma** GRAY, 1851, p. 131 [**M. grandis*; OD]. Resembles *Macropneustes,* but has deeply sunken, narrow petals and a peripetalous fasciole which is deeply re-entrant between them; test high, ambitus rounded; primary tubercles small and episternal pre-anal area not as differentiated as in the more highly developed brissids such as *Eupatagus*. *Eoc.-Rec.*, tropics.

**M. (Meoma)** [=*Rhyssobrissus* AGASSIZ, 1863, p. 27; *Hemibrissus* POMEL, 1869, p. 13 (type, *Spatangus ventricosus* LAMARCK, 1816)]. Frontal sinus moderate, subanal fasciole incomplete, reniform. *Rec.*, Caribbean and Panamanian faunas. ——FIG. 479,*2*. *M. (M.) ventricosa* (LAMARCK), Carib.; *2a,b,* aboral, oral, ×0.6 (1).

**M. (Plethotaenia)** H. L. CLARK, 1917, p. 233 [**Macropneustes spatangoides* AGASSIZ, 1883, p. 64; OD]. Resembling *M. (Deakia)* in general form but with very deep frontal sinus, petals in which only poriferous zones are depressed, periproct located on apical side, and heart-shaped, rather than reniform, subanal fasciole; peripetalous fasciole double or multiple. *Rec.*,

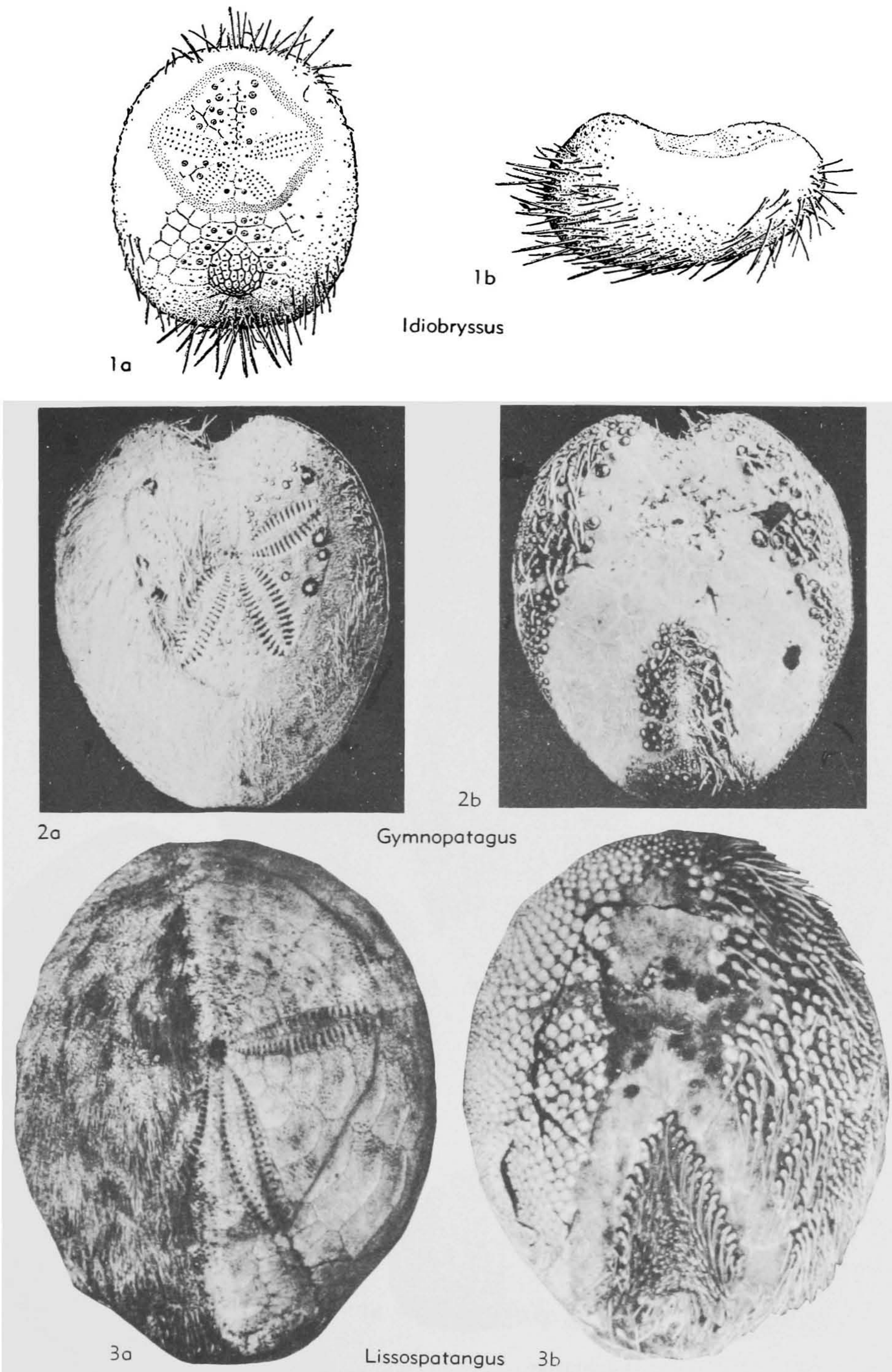



FIG. 477. Brissidae (p. *U*586, *U*588, *U*591).

Atl.O.——FIG. 480,3. *M. (P.) spatangoides (AGASSIZ); 3a,b, aboral (part), lat., ×0.75 (175b).

**M. (Schizobrissus)** POMEL, 1869, p. 13 [**Brissus cruciatus* AGASSIZ, 1847, p. 91] [=*Peripneustes* COTTEAU, 1875, p. 38 (type, *P. antillarum*; OD].

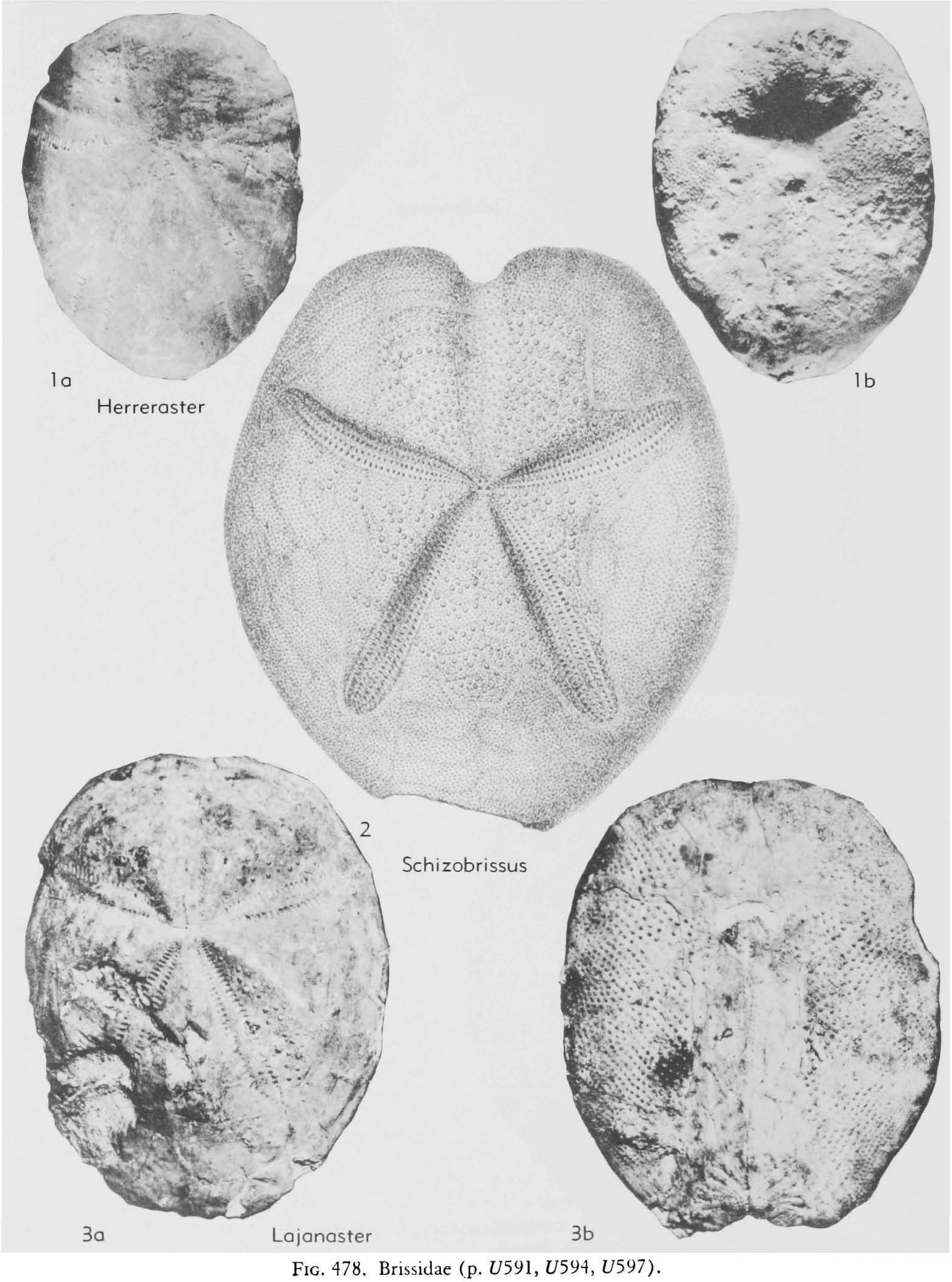



FIG. 478. Brissidae (p. U591, U594, U597).

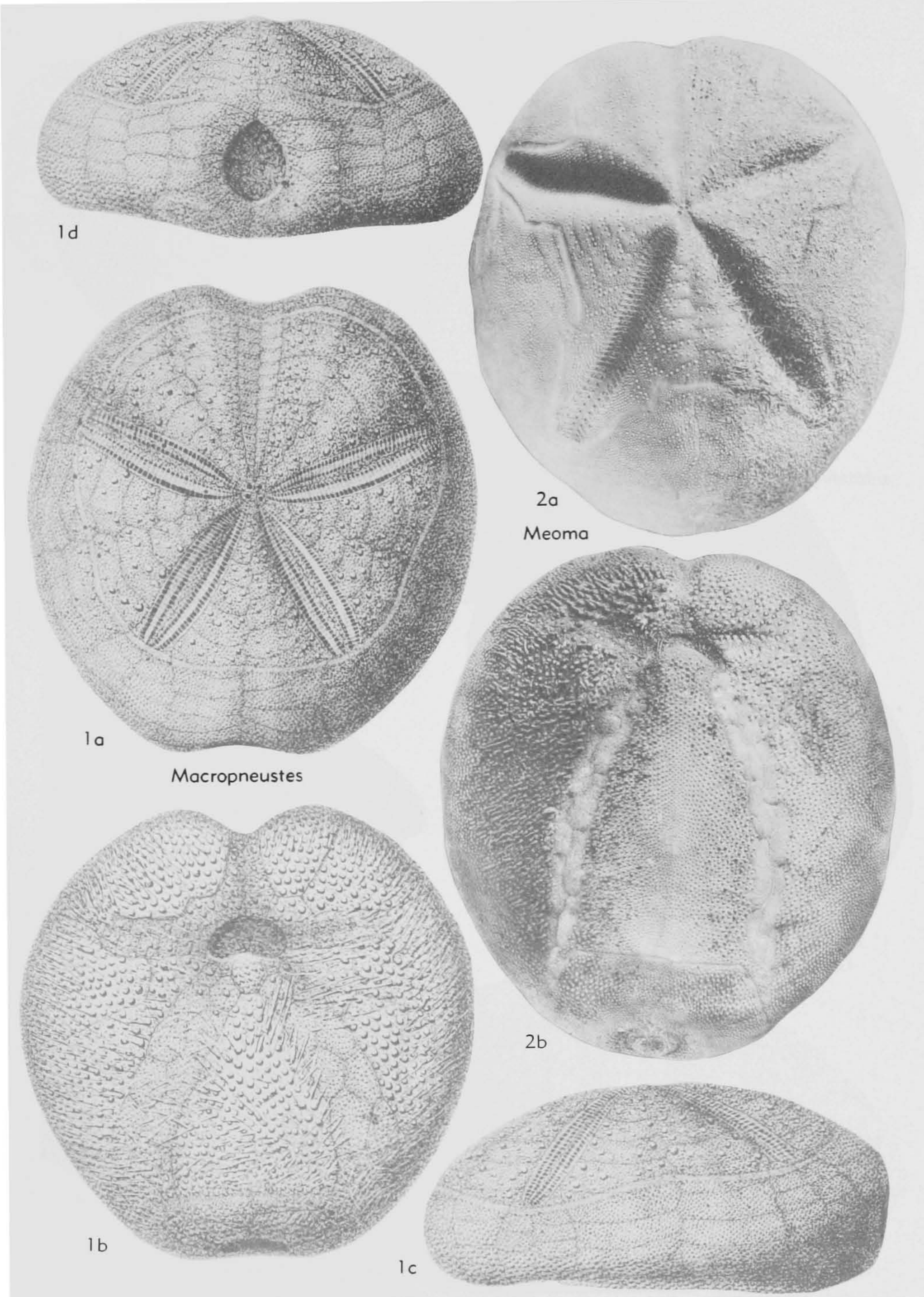



FIG. 479. Brissidae (p. *U*591-*U*592).

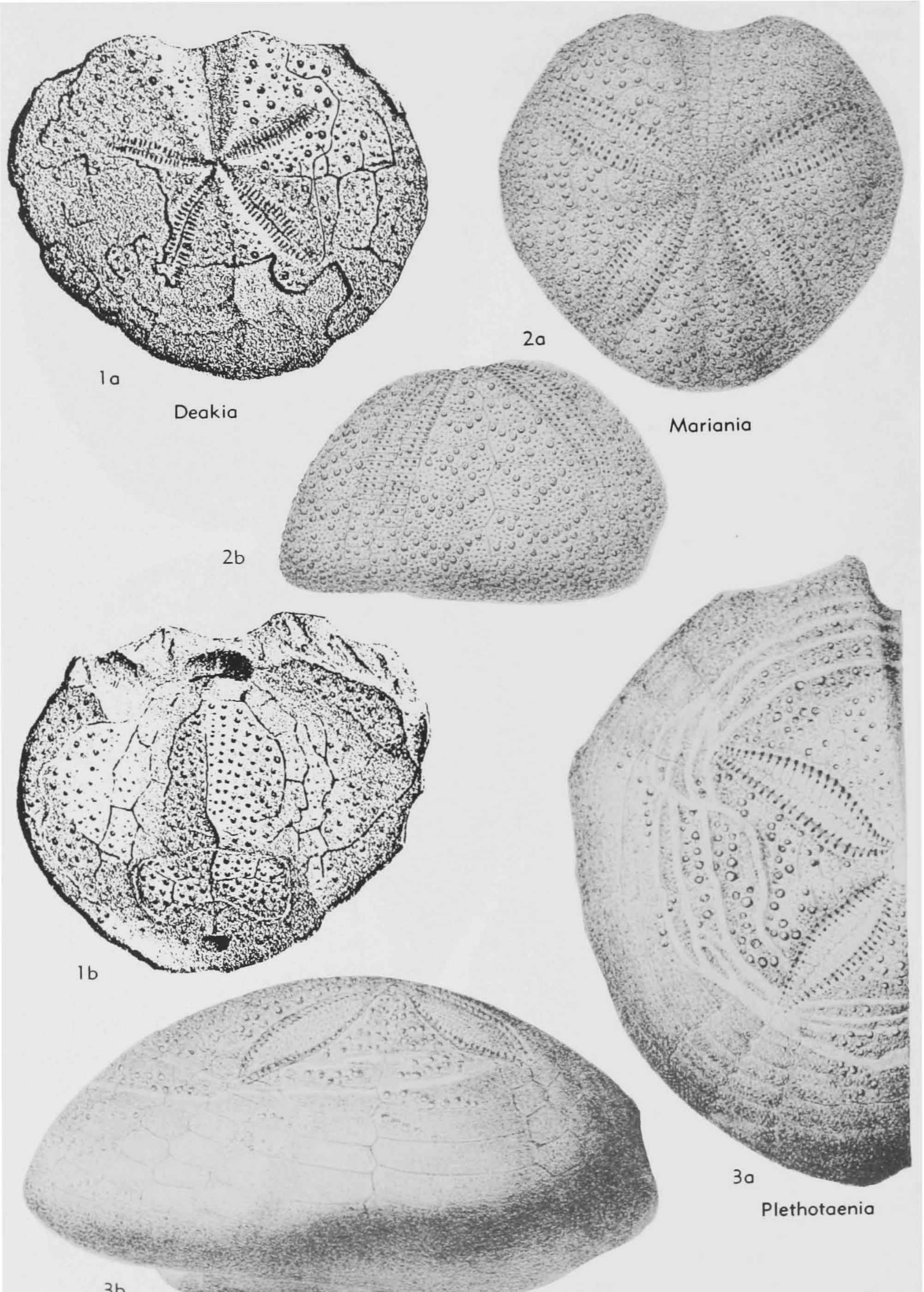



FIG. 480. Brissidae (p. U591-U592, U594).

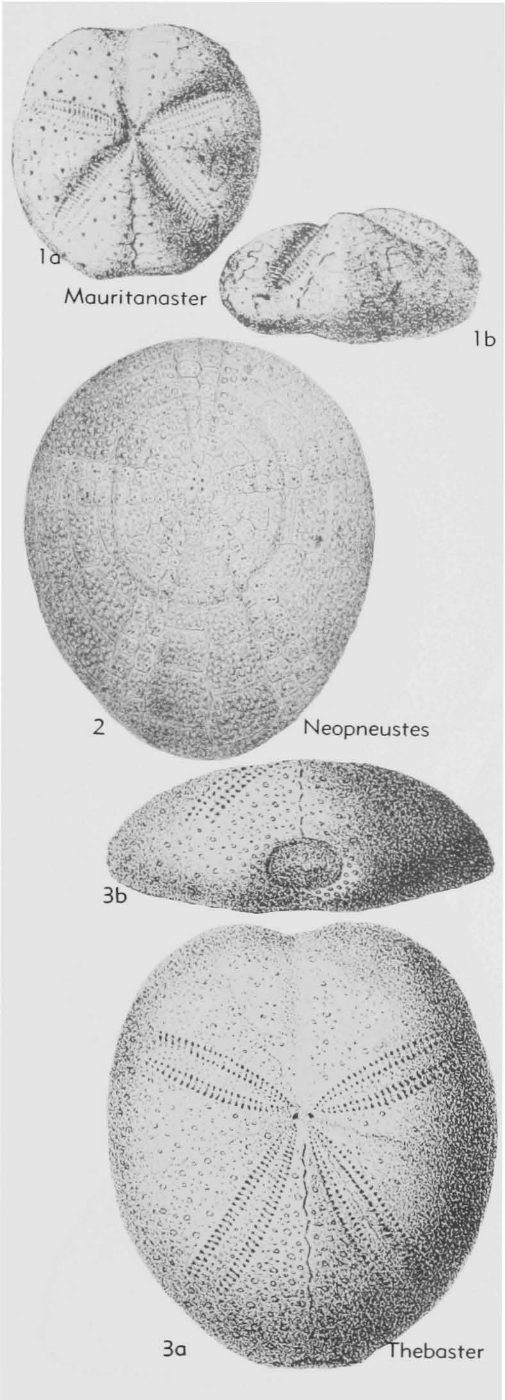



FIG. 481. Brissidae (p. U592, U600-U602).

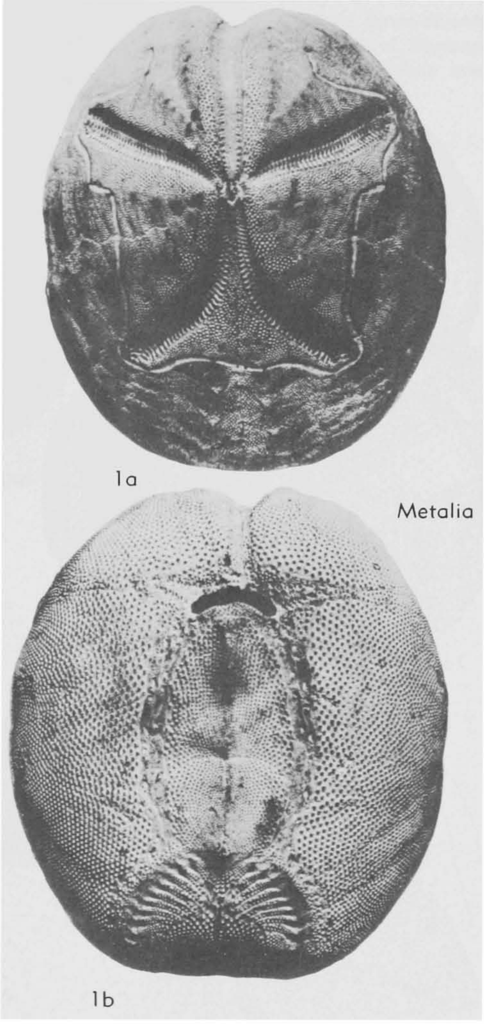



FIG. 482. Brissidae (p. U597, U599).

Frontal sinus deep, subanal fasciole annular. *Eoc.-Mio.*, tropic.——FIG. 478,2. *M. (Schizobrissus) antillarum* (COTTEAU), Eoc., Cuba, aboral, ×0.7 (136i).

**Metalia** GRAY, 1855, p. 51 [**Spatangus sternalis* LAMARCK, 1816, p. 326; OD] [=*Xanthobrissus* AGASSIZ, 1863, p. 28 (type, *X. garreti*); *Prometalia* POMEL, 1883, p. 34 (type, *Brissus robillardi* DE LORIOL, 1876, p. 9); *Eobrissus* BELL, 1904, p. 236 (type, *E. townsendi*); *Metaliopsis* FOURTAU, 1913, p. 68 (type, *Echinus maculosus* GMELIN, 1788, p. 3199)]. Differs from *Brissus* mainly in having narrow, nonlobate subanal fasciole with anal branches; large tubercles lacking within peripetalous fasciole. *?Eoc., Rec.,* IndoPac.——FIG.

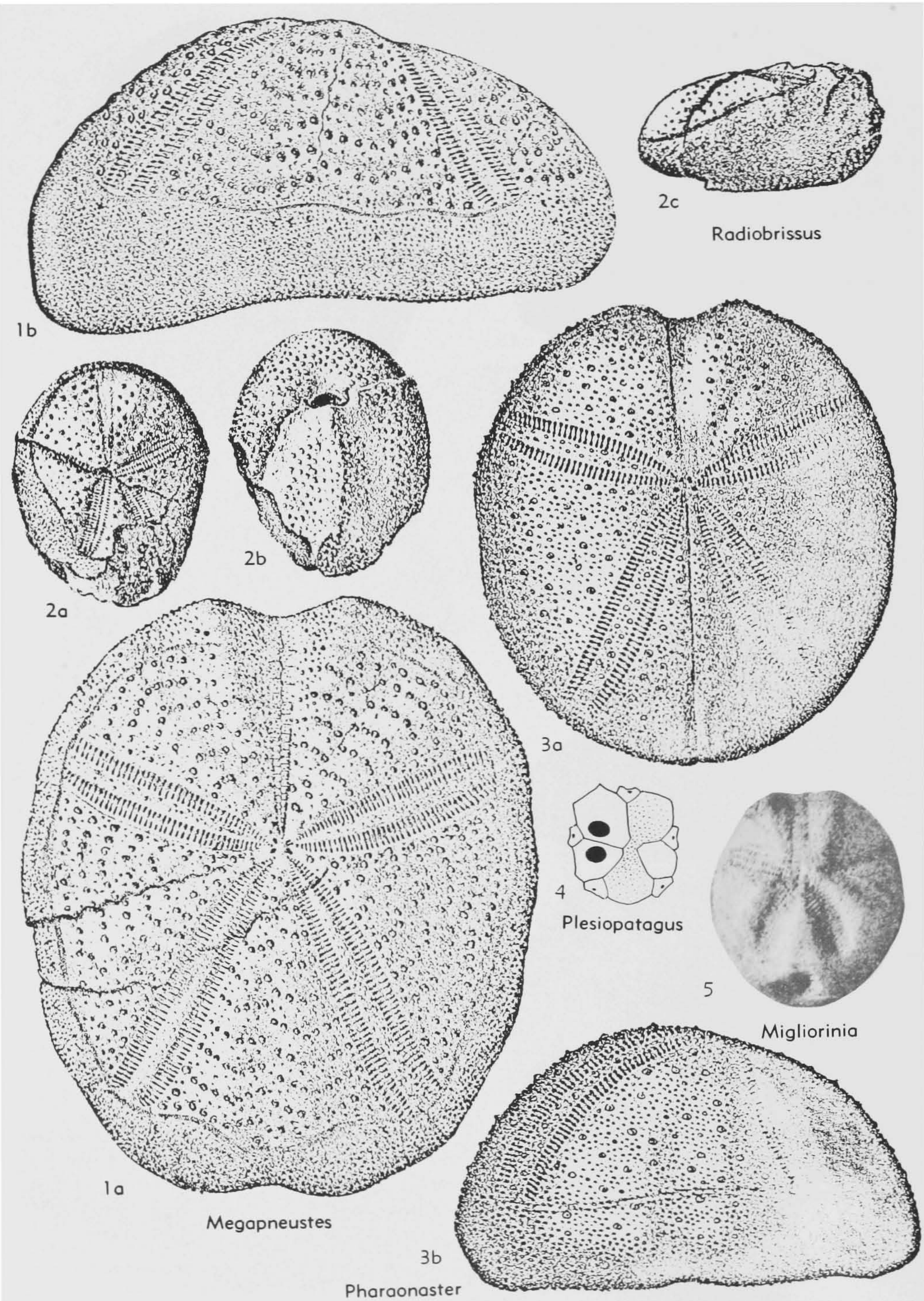



Fig. 483. Brissidae (p. U592, U599-U601, U603).

482,*1*. **M. sternalis* (LAMARCK), Rec.; *1a,b*, aboral, oral, ×0.5 (1).

**Migliorinia** CHECCHIA-RISPOLI, 1942, p. 305 [**M. migiurtina*; OD]. Small, depressed forms of ovoid outline, differing from small species of *Eupatagus* only in having narrower interporiferous zones

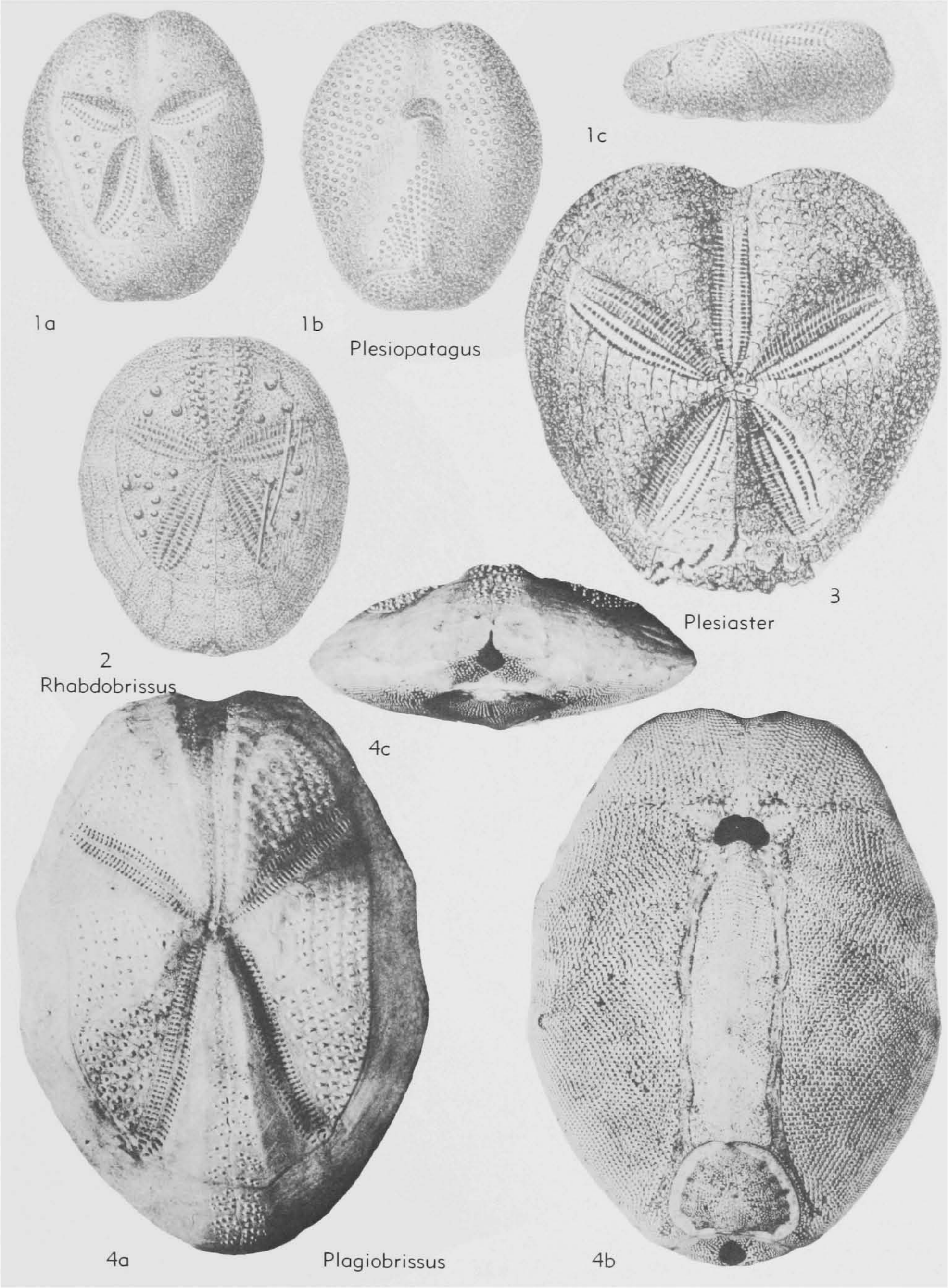



FIG. 484. Brissidae (p. *U*602-*U*603).

in petals, and by lacking large tubercles inside the area circumscribed by the peripetalous fasciole. *Eoc.*, Somaliland.——FIG. 483,5. **M. migiurtina*; aboral, ×1 (136i).

**Neopneustes** DUNCAN, 1889, p. 258 [**Rhynobrissus micrasteroides* AGASSIZ, 1878, p. 192; OD]. Small, ovoid, with somewhat anterior 4-pore apical system; ambulacra flush, not distinctly petaloid. *Rec.*,

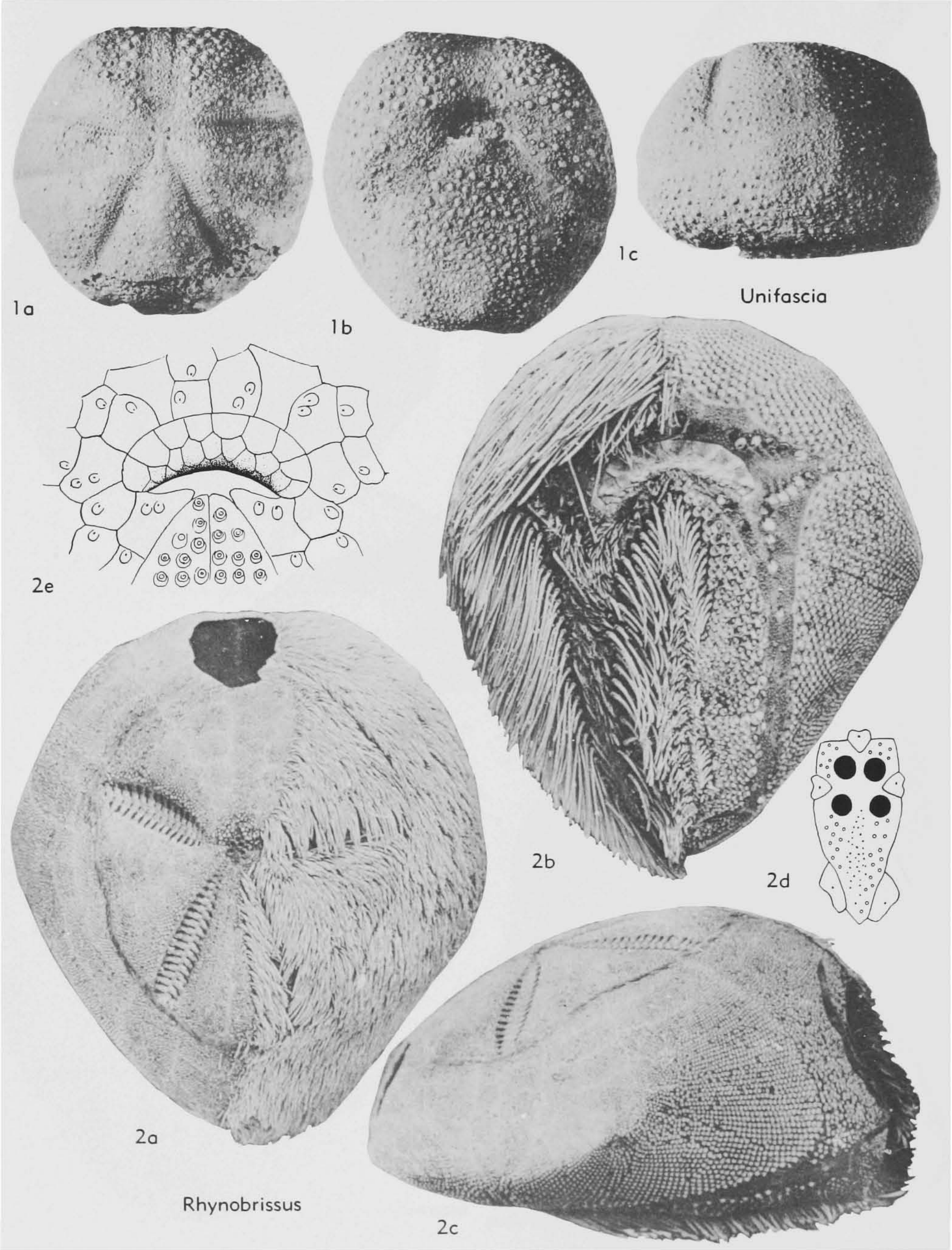



FIG. 485. Brissidae (p. *U*604-*U*605).

W.Atl.——Fig. 481,*2*. **N. micrasteroides* (Agassiz); aboral, ×1.5 (175b).

**Pharaonaster** Lambert, 1920, p. 26 [**Macropneu-*

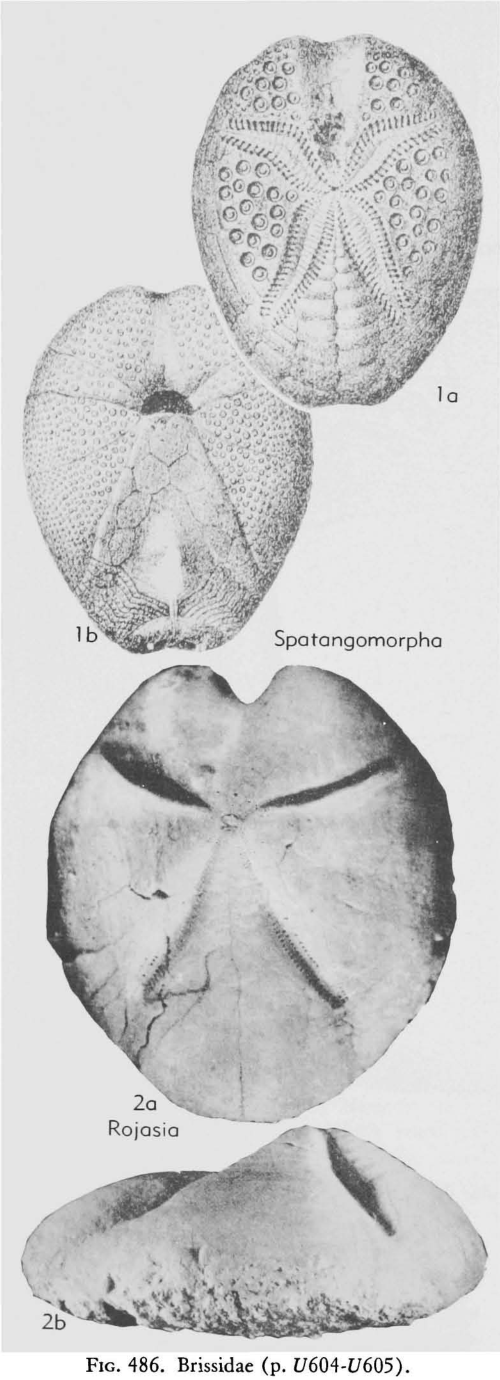



Fig. 486. Brissidae (p. *U*604-*U*605).

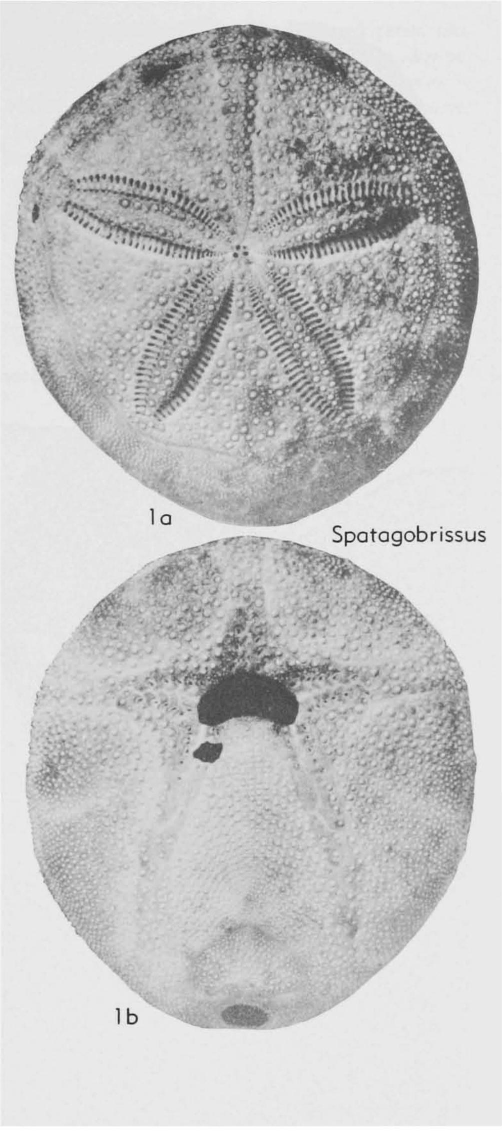



Fig. 487. Brissidae (p. *U*605).

*stes ammon* Agassiz, 1847, p. 115; OD]. Closely resembling *Megapneustes* and *Fourtaunia* but with flush petals and rounded rather than truncate posterior end, and having peripetalous and subanal fascioles. Differs from *Stomaporus* in having broader interporiferous areas and fascioles. *Eoc.*, N.Afr.-?N.Am.

**P. (Pharaonaster).** Test almost hemispherical. *Eoc.*, N.Afr.-?N.Am.——Fig. 483,*3*. **P. (P.) ammon* (Agassiz), Egypt; *3a,b*, aboral, lat., ×0.8 (136h).

**P. (Thebaster)** Checchia-Rispoli, 1941, p. 6 [**Macropneustes fischeri* de Loriol, 1881, p. 74; OD]. Depressed, with broadly transverse

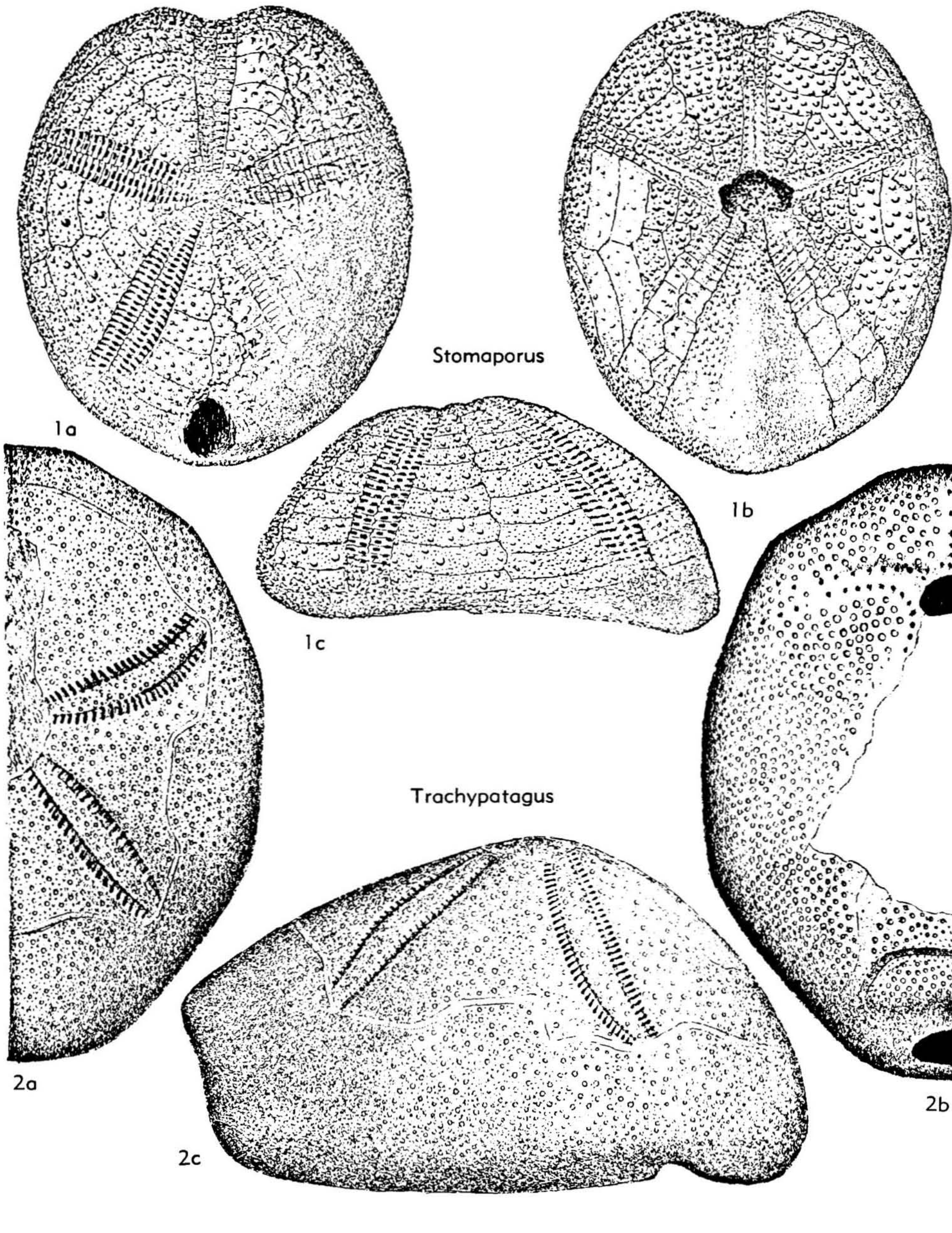



FIG. 488. Brissidae (p. U605).

periproct. *Eoc.,* Egypt.——FIG. 481,*3.* **P. (T.) fischeri* (DE LORIOL); *3a,b,* aboral, lat., ×1 (136h).

**Plagiobrissus** POMEL, 1883, p. 29 [*pro Plagionotus* AGASSIZ & DESOR, 1847, p. 119 (*non* MULSANT, 1842); *pro Plagiostomus* D'ORBIGNY, 1854, p. 151 (*non Plagiostoma* SOWERBY, 1812; *nec Plagiostomus* HERMANSEN, 1847)] [**Echinus grandis* GMELIN, 1788, p. 320; OD]. Differs from *Eupatagus* chiefly in having anal branches on subanal fasciole, long plastron, short labrum, and long, narrow, flexed petals. *Eoc.-Rec.,* cosmop.

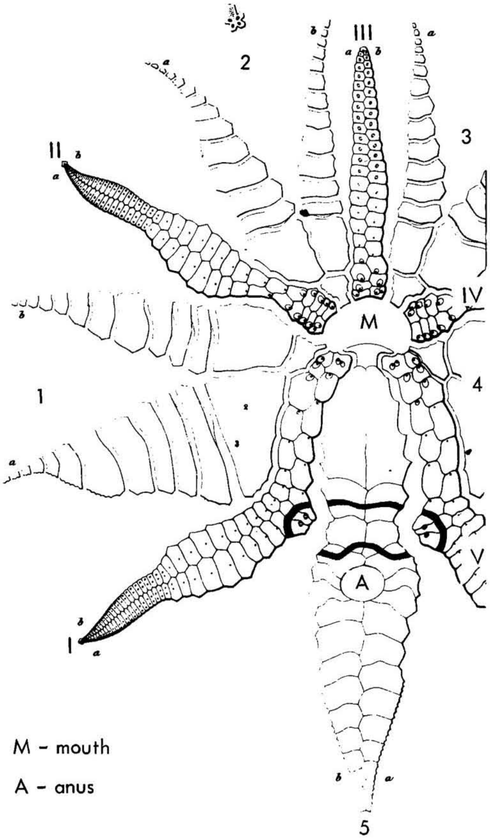



FIG. 489. Plate diagram of *Spatangus* (Lovén).

**P. (Plagiobrissus).** Frontal sinus well defined. *Eoc.-Rec.,* cosmop.——FIG. 484,*4*. **P. (P.) grandis* (GMELIN), Rec., W.Indies; *4a-c,* aboral, oral, post., ×0.3 (24).

**P. (Rhabdobrissus)** COTTEAU, 1889, p. 281 [**R. jullieni*; OD] [=*Mortensenaster* LAMBERT, 1922, p. 44 (type, *Metalia costae* GASCO, 1876, p. 4)]. Lacking frontal sinus. *Rec.,* tropic seas.——FIG. 484,*2*. **P. (R.) jullieni,* Liberia; aboral, ×1 (27e). [=*Rhabdobryssus* MEISSNER, 1903, p. 1343 *(nom. van.)* (obj.).]

**Plesiaster** POMEL, 1883, p. 42 [**Micraster peini* COQUAND, 1862, p. 245; OD]. Closely resembles *Micraster,* but having peripetalous fasciole; pores in frontal ambulacrum resembling those of paired petals, outer one elongate; ethmophract, 4 gonopores. *U. Cret.(Santon.-Campan.),* Eu.-N. Afr.-N. Am.——FIG. 484,*3*. **P. peini* (COQUAND), U.Cret. (Santon.), N.Afr.; aboral, ×1 (136i).

**Plesiopatagus** POMEL, 1883, p. 32 [**Eupatagus cotteaui* DE LORIOL, 1880, p. 611; OD] [=*Plesiospatangus* COTTEAU, 1886 *(nom. van.)*]. Resembles *Eupatagus* but with depressed petals like *Macropneustes,* and only 2 gonopores. *Eoc.,* Egypt. ——FIG. 483,*4*; 484,*1*. **P. cotteaui* (DE LORIOL); 483,*4*, apical system, enl. (136i); 484,*1a-c,* aboral, oral, lat., ×1 (136i).

**Radiobrissus** FOURTAU, 1913, p. 66 [**R. gneffensis*; OD]. Small, ovoid test lacking frontal sinus; ethmolytic, 4 gonopores; frontal ambulacrum flush, paired ambulacra petaloid, with round, conjugate pores; adapical plates in anterior plate row of anterolateral petals with rudimentary pores. *Mio.,* Egypt.——FIG. 483,*2*. **R. gneffensis*; *2a-c,* aboral, oral, lat., ×1 (136i).

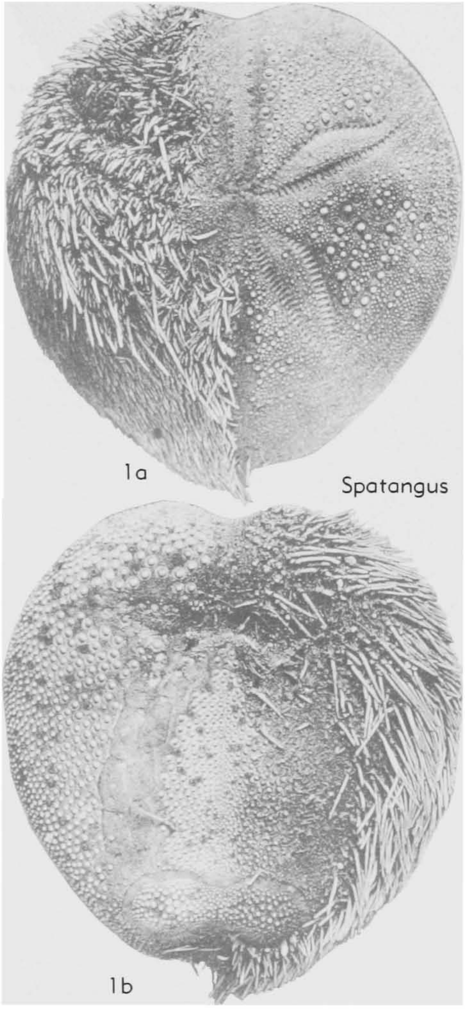



FIG. 490. Spatangidae (p. *U*605, *U*608).

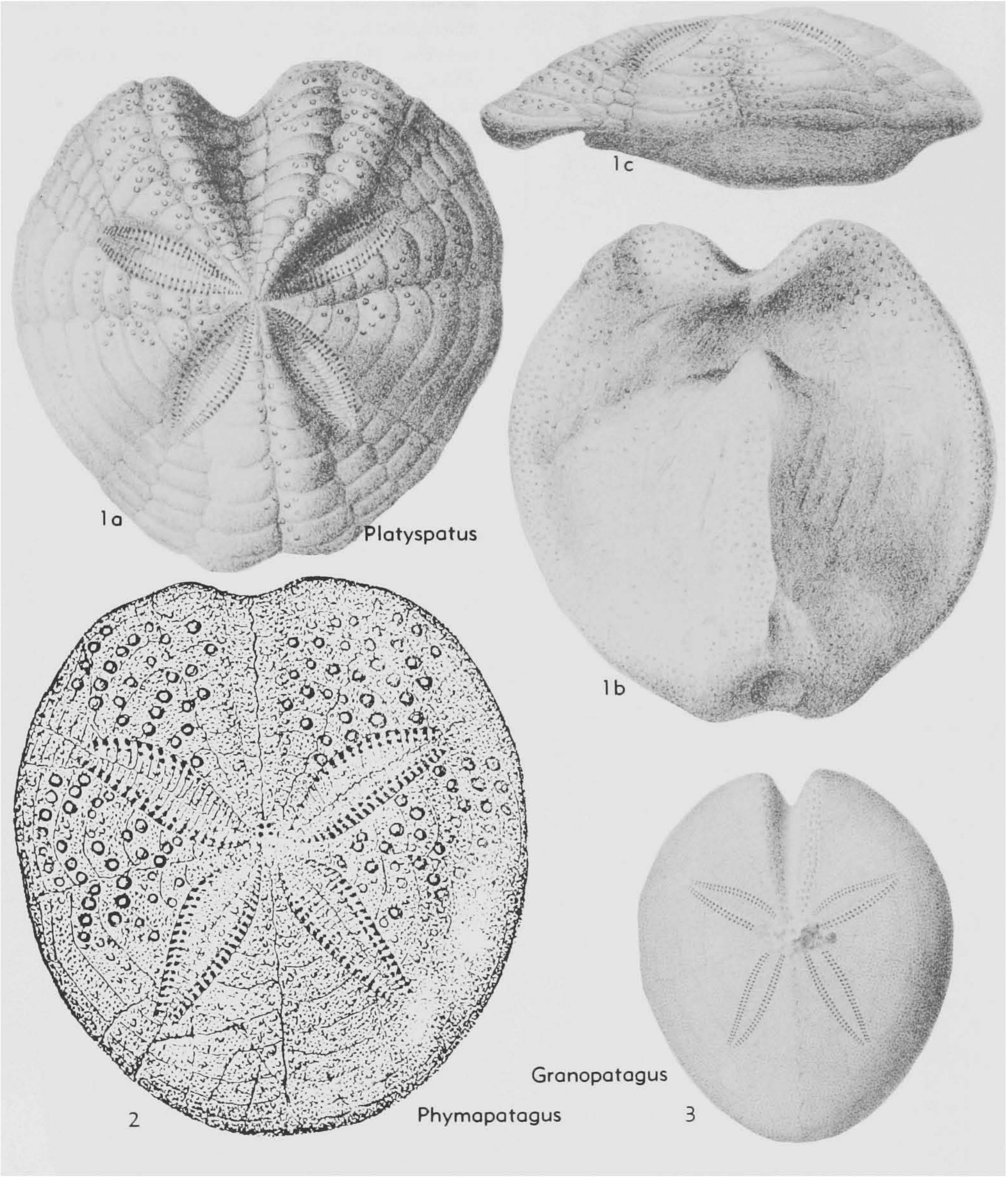



FIG. 491. Spatangidae (p. U608).

**Rhynobrissus** A. AGASSIZ, 1872, p. 58 [**R. pyramidalis*; OD] [=*Rhinobrissus* QUENSTEDT, 1874, *nom. van.*]. Ovoid test with flattened oral side and sharp ambitus, lacking frontal sinus; ethmolytic, with 4 gonopores; frontal ambulacrum flush, petals depressed; posterior paired interambulacra not extending to peristome; anal fasciole well developed. *Rec.*, Pac.-W.Australia.——FIG. 485,2. **R. pyramidalis*; *2a-c*, aboral, oral, lat., ×1.5 (1); *2d,e*, apical system and peristome, ×13, ×6 (136i). [=*Rhinobryssus* MEISSNER, 1903, p. 1343 (*nom. van.*) (obj.).]

**Rojasia** SÁNCHEZ ROIG, 1951, p. 57 [**R. rojasi*; OD]. Resembling *Schizobrissus* but distinctive in form, anteriorly excentric apex rising as pyramid over flat posterior part of test; deep frontal sinus; gonopores 4; petals long, narrow, open, slightly flexed, deeply depressed; peripetalous

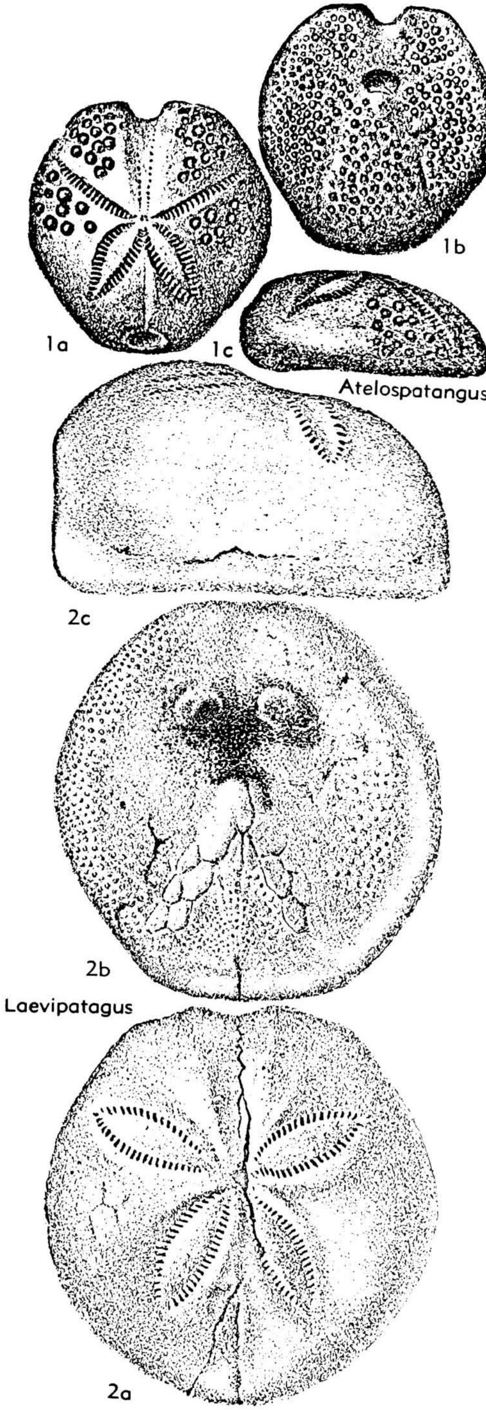



FIG. 492. Spatangidae (p. *U*608-*U*609).

fasciole embayed, subanal fasciole not ascertained, oral side not known; one of largest fossil echinoids. *Eoc.*, Cuba.——FIG. 486,*2*. **R. rojasi*, *2a,b*, oral, lat., ×0.3 (216c).

**Spatagobrissus** CLARK, 1923, p. 402 [**S. mirabilis*; OD]. Resembles *Eupatagus* but lacking frontal sinus; oral side slightly convex; petals relatively far open; primary tubercles inside and outside peripetalous fasciole. *Rec.*, S.Afr.——FIG. 487,*1*. **S. mirabilis*; *1a,b*, aboral, oral, ×0.86 (136i).

**Spatangomorpha** BOEHM, 1882, p. 237 [**S. eximia*; OD]. Like *Eupatagus*, but more (about 8) ambulacral plates included in subanal fasciole, and posterior ambulacra meet to separate labrum from sternum. Anterior ambulacrum somewhat depressed. *Mio.-Plio.*, India-Java.——FIG. 486,*1*. **S. eximia*, Mio., Indonesia; *1a,b*, aboral, oral, ×1 (136i).

**Stomaporus** COTTEAU, 1888, p. 977 [**S. hispanicus*; OD]. Resembling *Fourtaunia* and *Megapneustes* but with narrower interporiferous zones in petals and appearing to lack fascioles altogether. *Eoc.*, Spain.——FIG. 488,*1*. **S. hispanicus*; *1a-c*, aboral, oral, lat., ×0.8 (33).

**Trachypatagus** POMEL, 1869, p. xi [**T. oranensis*; OD ][=*Leiopatagus* POMEL, 1869, p. xii *(nom. nud.)*]. Differs from *Eupatagus* in being uniformly tuberculate; no frontal sinus; peristome far forward. *Eoc.-Mio.*, Medit.——FIG. 488,*2*. **T. oranensis*, Mio., Alg.; *2a-c*, aboral, oral, lat., ×0.25 (33). [=*Liopatagus* POMEL *(nom. null.)*.]

**Unifascia** COOKE, 1959, p. 79 [**Macropneustes carolinensis* CLARK, 1915; OD]. Closely resembles *Macropneustes* but lacking anal and peripetalous fascioles, and having marginal fasciole; primary tubercles on nearly whole test. [Type genus (monotypic) of Unifasciidae COOKE, 1959.] *Eoc.*, SE.N.Am.——FIG. 485,*1*. **U. carolinensis* (CLARK); *1a-c*, aboral, oral, lat., ×1.5 (24).

## Family SPATANGIDAE Gray, 1825

[Spatangidae GRAY, 1825, p. 430 ] [=Prospatangidae LAMBERT, 1905, p. 34, Maretiidae LAMBERT, 1905, p. 47]

Heart urchins having subanal fasciole only; apical system ethmolytic; gonopores 3 or 4; anterior ambulacrum with only small pores arranged in single series; paired ambulacra petaloid, with petals nearly flush or flush; primary spines differentiated, in some forms recessed into camellae. Plastron holamphisternous to ultramphisternous (Fig. 489). [Littoral to bathyal.] *Eoc.-Rec.*

**Spatangus** GRAY, 1825, p. 430 (*non* LESKE, 1778, *nom. nud.*) [**Spatagus purpureus* MÜLLER, 1776, p. 236; SD ICZN, Op. 209, 1948] [=*Prospatangus* LAMBERT, 1902, p. 55]. Heart-shaped, right side normally projecting slightly beyond left; 4 gonopores; ambulacra of normal structure or nearly so. *Eoc.-Rec.*, cosmop.

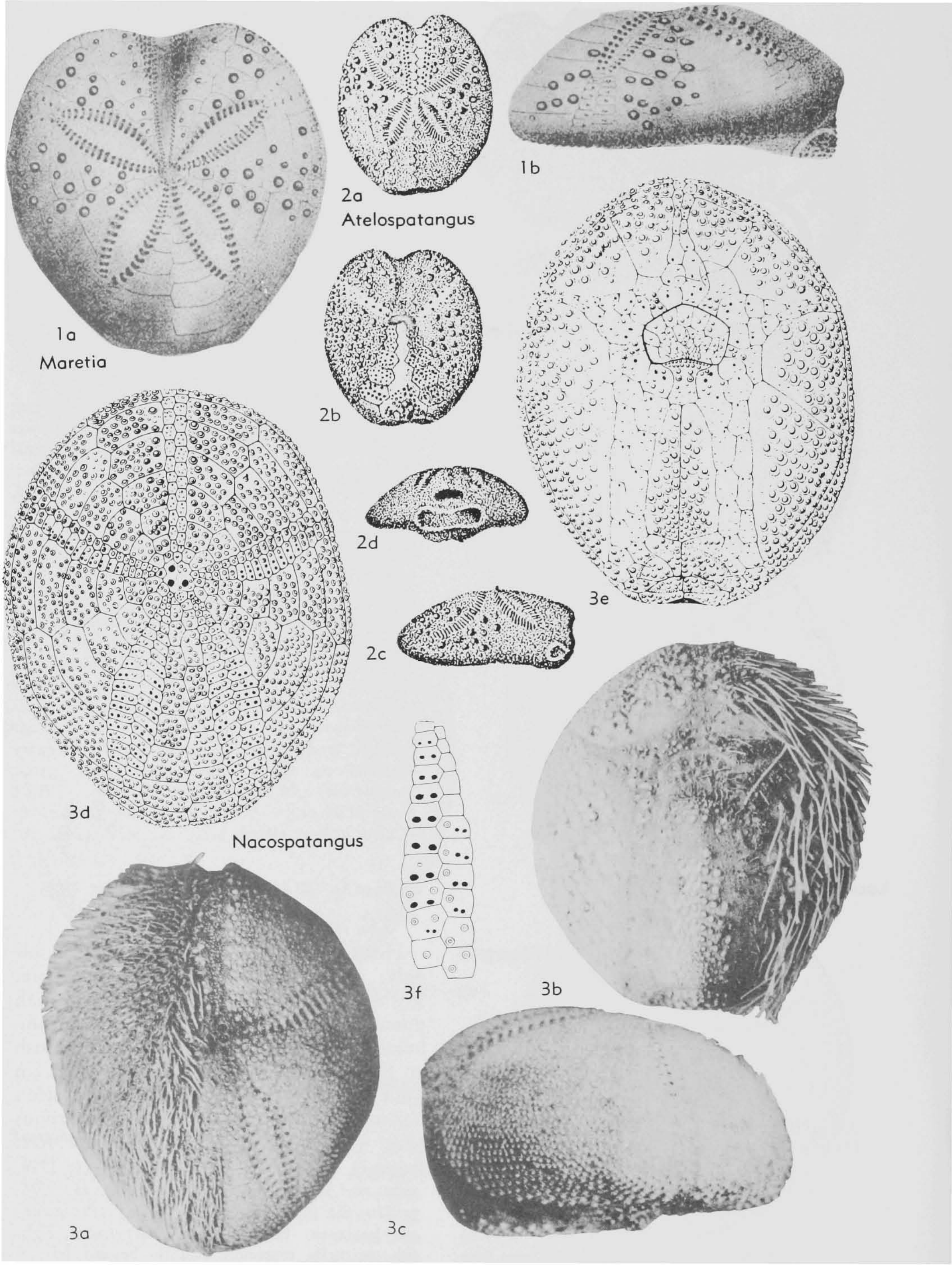



FIG. 493. Spatangidae (p. U608-U609).

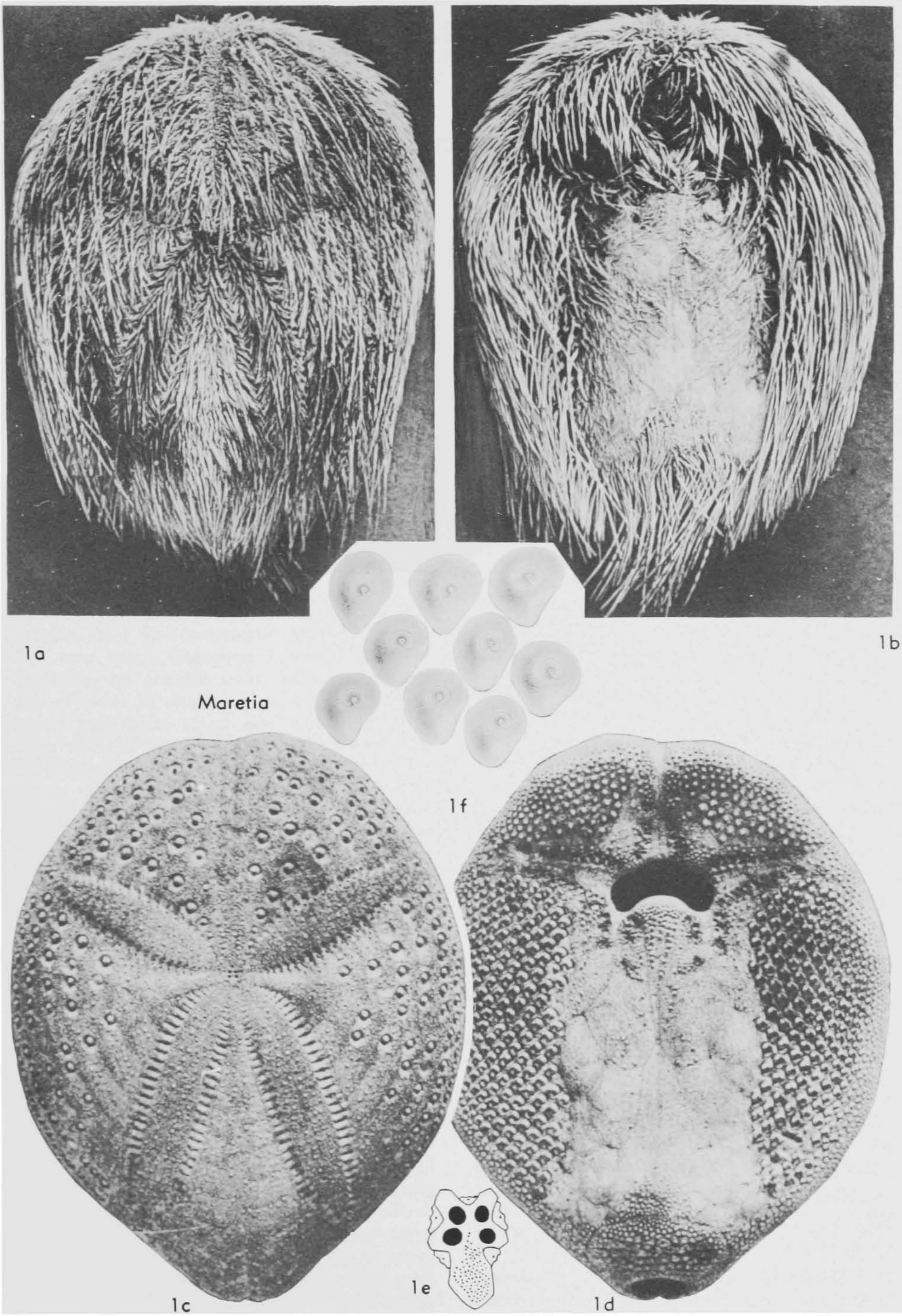



FIG. 494. Spatangidae (p. U609).

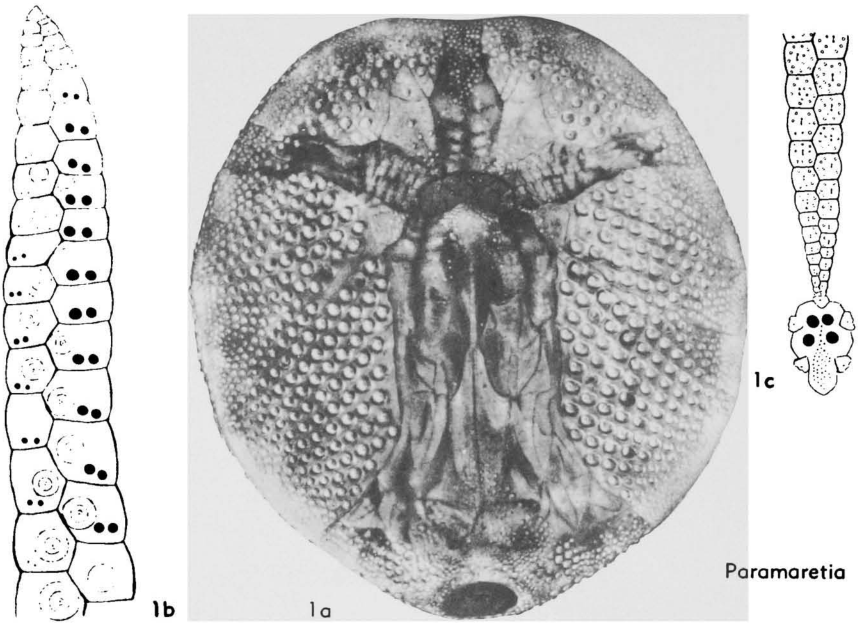



FIG. 495. Spatangidae (p. U609).

**S. (Spatangus).** Primary tubercles scattered over interambulacra. *Eoc.-Rec.,* cosmop.——FIG. 490, *1.* **S. (S.) purpureus* (MÜLLER), Rec., Eu.; *1a,b,* aboral, oral, ×0.7 (1).

**S. (Granopatagus)** LAMBERT, 1914, p. 193 [**Spatangus lonchophorus* MENEGHINI in DESOR, 1858, p. 422; OD]. Primary tubercles only along edge of frontal sinus and in posterior interambulacrum. *Eoc.-Rec.,* Medit.-Ind.O.-W.Pac.——FIG. 491,*3.* **S. (G.) lonchophorus* MENEGHINI, Eoc., Italy; aboral, ×0.6 (41). [=*Concophorus* LAUBE, 1869, p. 36; *Conchophorus* DUNCAN, 1889, p. 252 (*non* GRAY, 1821) *(laps. cal.)*; *Lonchophorus* POMEL, 1883, p. 29 (*non* GERMAR, 1824, *nec* ESCHSCHOLTZ, 1825, *nec* SCHOENHERR, 1838, *nec* LUND, 1839.]

**S. (Phymapatagus)** LAMBERT, 1910, p. 3 [**Spatangus britannus* TOURNOUER; SD COTTEAU, 1897, p. 12]. Primary tubercles lacking in posterior interambulacrum; anterior petals with only rudimentary pores in uppermost plates of anterior series. *Eoc.-Mio.,* Eu.——FIG. 491,*2.* **S. (P.) britannus* TOURNOUER, Mio., Fr.; aboral, ×0.75 (136i).

**S. (Platyspatus)** POMEL, 1883, p. 29 [**Spatangus chitinosus* SISMONDA, 1841, p. 31; OD]. Petals small, slightly depressed; frontal sinus large; primary tubercles distributed over all interambulacral plates. *Eoc.-Mio.,* Medit.——FIG. 491,*1.* **S. (P.) chitinosus* SISMONDA, Mio., Italy; *1a-c,* aboral, oral, lat., ×1 (206a).

**Atelospatangus** KOCH, 1885, p. 115 [**A. transilvanicus*; OD] [=*Oppenheimia* COSSMANN, 1900, p. 186, *pro Lambertia* OPPENHEIM, *non* DESVOIDY, 1863, *nec* SOWERBY, 1869, *nec* PERUGIA, 1894 (type, *Lambertia giardinalei* OPPENHEIM, 1899, p. 28)]. Small flattened test with frontal sinus and 4 gonopores, distinguished by having anterior plate series of anterolateral petals reduced to small plates with pores small or absent. *Eoc.-Mio.,* S.Eu.——FIG. 492,*1. A. giardinalei* (OPPENHEIM), U.Eoc., Italy; *1a-c,* type-species of *Oppenheimia,* aboral, oral, lat., ×1 (136i).——FIG. 493, *2.* **A. transilvanicus,* Romania; *2a-d,* aboral, oral, lat., post., ×1 (136i).

**Hemimaretia** MORTENSEN, 1950, p. 160 [**Maretia elevata* DÖDERLEIN, 1907, p. 263; OD]. Resembling *Maretia (Hemipatagus)* with some primary tubercles housed in camellae, but has only weakly developed phyllodes, and only 3 gonopores; anterior paired petals incomplete, having reduced pores in proximal plates of anterior plate row. *Rec.,* E.Afr.

**Laevipatagus** NOETLING, 1885, p. 211 [**Spatangus (Micraster) bigibbus* VON BEYRICH, 1848, p. 100; OD] [=*Leiospatangus* MAYER, 1861, p. 119

*(nom. nud.)*]. Intermediate between *Spatangus* and *Maretia* in having frontal half of plastron bare; gonopores 4, no large aboral tubercles, 2 peculiar interambulacral bulges in front of peristome. *Eoc.*, Baltic region.——FIG. 492,*2*. **L. bigibbus* (VON BEYRICH); *2a-c,* aboral, oral, lat., ×1 (136i).

**Maretia** GRAY, 1855, p. 48 [**Spatangus planulatus* LAMARCK, 1816, p. 326; OD] [=*Hemipatagus* DESOR, 1858, p. 416 (type, *Spatangus hoffmanni* GOLDFUSS, 1826, p. 152); *Tuberaster* PERON & GAUTHIER, 1885, p. 46 (type, *T. tuberculatus* PERON & GAUTHIER; *Thrichoproctus* A. AGASSIZ (M.S., *nom. nud.*); *Plagiopatagus* LÜTKEN (in *litteris, nom. nud.)*]. Test oval to heart-shaped; large tubercles on apical side except in posterior interambulacrum; 4 genital pores. Primary tubercles may be recessed in camellae. *Eoc.*(cosmop.)-*Rec.*(IndoPac.).——FIG. 493,*1*. *M. hoffmanni* (GOLDFUSS), Oligo., Ger.; *1a,b,* aboral, lat., ×1 (44).——FIG. 494,*1*. **M. planulata* (LAMARCK), Rec.; *1a-d,* aboral and oral, with and without spines, ×1.5 (1); *1e,* apical system, ×6; *1f,* detail showing ear-shaped tubercles on oral side, ×6 (136i). [=*Thrichoproctus* AGASSIZ, 1872, p. 139 *(nom. nud.)*.]

**Nacospatangus** A. AGASSIZ, 1873, p. 189 [**N. gracilis*; OD] [=*Nacopatagus* AGASSIZ, 1881, p. 219, *nom. van.*]. Gonopores 3, weakly developed phyllodes, no anterior sinus, reduction or total loss of pores in anterior plate series of anterior paired ambulacra; apical side with few or no large tubercles and ampullae. *Rec.*, IndoPac.

**N. (Nacospatangus).** Periproct not sunken; no primary spines. *Rec.*, Pac.O.-Ind.O.——FIG. 493,*3*. **N. (N.) gracilis* AGASSIZ, *3a-c,* adoral, aboral, lat., ×3 (175a); *3d,e,* aboral, oral, ×3 (3); *3f,* detail of anterolateral petal, enl. (136i).

**N. (Pseudomaretia)** KOEHLER, 1914, p. 107 [**Maretia alta* A. AGASSIZ, 1863, p. 3601; OD] [=*Lonchophorus* STUDER, 1880, p. 879 (type, *L. interruptus*), *non* GERMAR, 1837, *nec* POMEL, 1883; *Gonimaretia* CLARK, 1917, p. 240 (type, *G. tylota*)]. Periproct sunken; a few primary spines. *Rec.*, Japan-Ind.O.

**Paramaretia** MORTENSEN, 1950, p. 160 [**P. multituberculata*; OD]. Differs from *Maretia* in having narrow, open petals and in rudimentary nature of pores in anterior plate series of anterior petals; distinct from *Nacospatangus* and *Hemimaretia* in having 4 gonopores and deep phyllodes. *Rec.*, Australia.——FIG. 495,*1*. **P. multituberculata*; *1a,* oral, ×0.7; *1b,* sketch of petal, ×2; *1c,* apical system, ×3.75 (136i).

**Semipetalion** SZÖRÉNYI, 1963, p. 194 [**Atelospatangus (Semipetalion) anomon* SZÖRÉNYI; OD]. Resembles *Hemimaretia, Nacospatangus* and *Paramaretia* in incomplete nature of anterior paired petals, which lack normal pores in proximal part of anterior plate row. Gonopores 4; deep anterior sinus; anterior petals long, open, somewhat depressed, posterior petals short, broad, closed, flush; phyllodes not well developed. *U.Eoc.*, Hung.

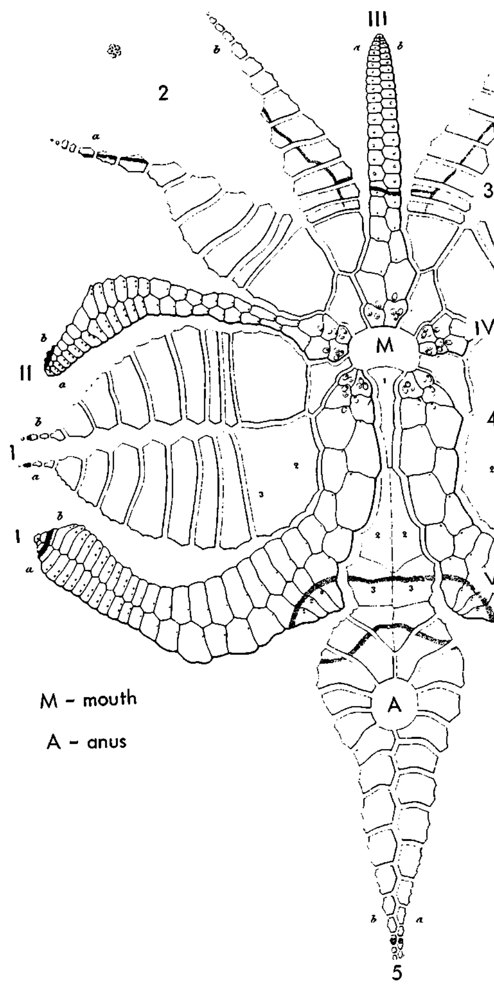



FIG. 496. Plate diagram of *Lovenia* (Lovén).

## Family LOVENIIDAE Lambert, 1905

[Loveniidae LAMBERT, 1905, p. 34]

Distinguished from all other echinoids by possession of internal fasciole, surrounding apical system and parts of anterior ambulacrum (exception: *Homolampas*). Subanal fasciole generally present and peripetalous fasciole as well in *Breynia* and *Homolampas*; apical system ethmolytic, with 3 or 4 gonopores; paired ambulacra petaloid, with anterior pair commonly fused into trans-

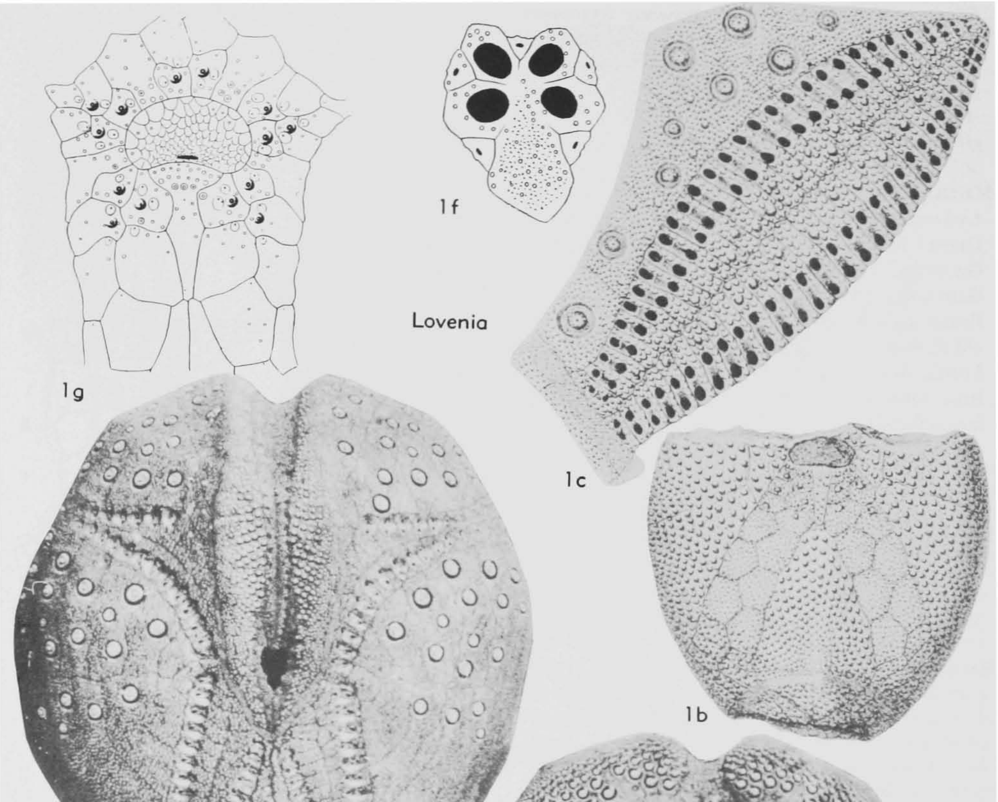



FIG. 497. Loveniidae (p. U613).

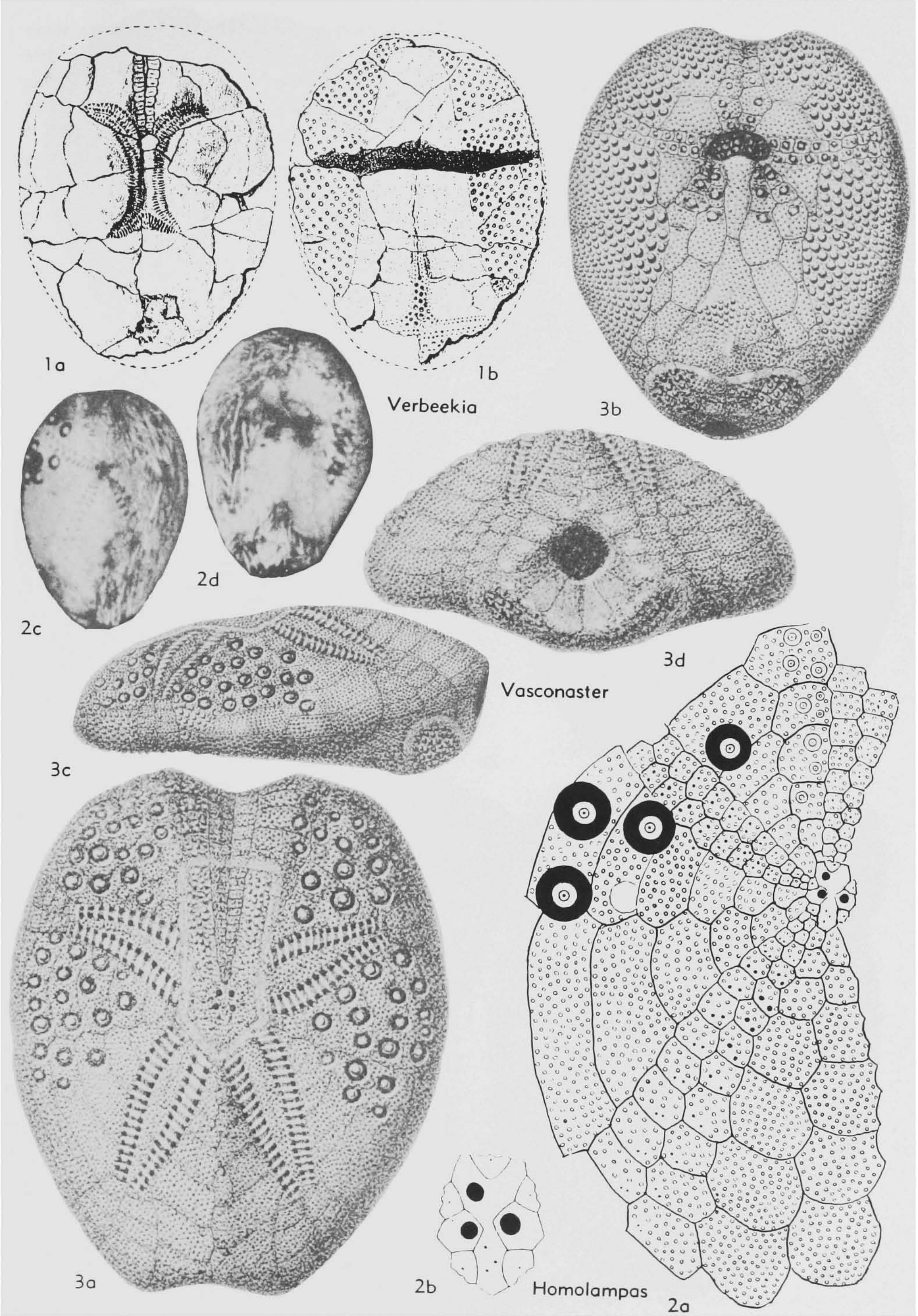



FIG. 498. Loveniidae (p. U613-U614).

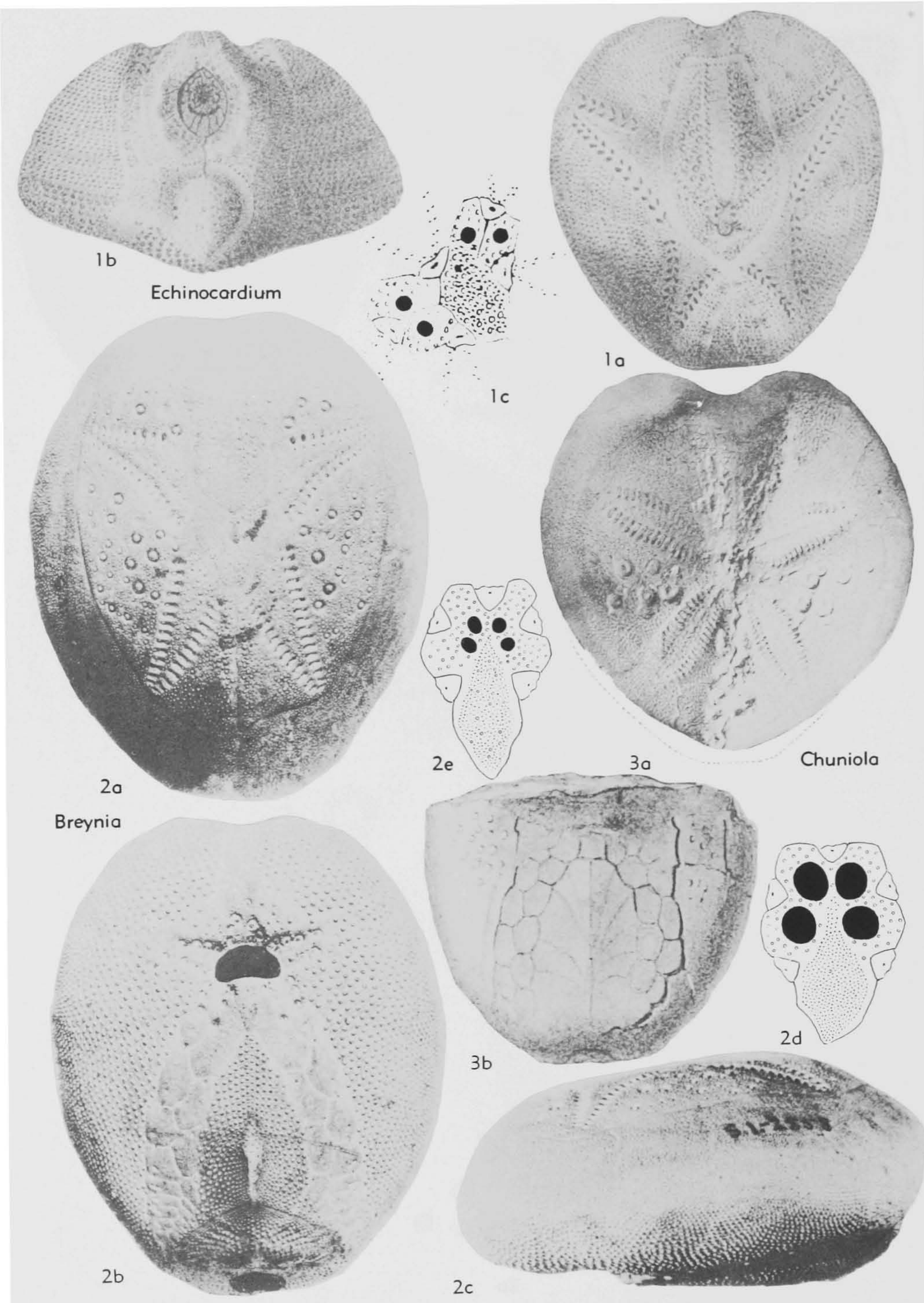



Fig. 499. Loveniidae (p. U613).

verse crescent; anterior ambulacrum apetaloid. Primary spines may be recessed in camellae. Plastron ultramphisternous (Fig. 496). [Neritic to bathyal.] *Eoc.-Rec.*

The loveniids, as a whole, appear to be derived from the Spatangidae, by acquisition of an internal fasciole. The occurrence of a peripetalous fasciole in *Breynia* suggests the possibility that this genus may have been derived from the Brissidae, and that the family Loveniidae, as now constituted, is polyphyletic.

**Lovenia** DESOR, 1847, p. 10 [**Spatangus elongatus* GRAY, 1845, p. 436; OD]. Test low, oval to heart-shaped, with subanal and internal fascioles; gonopores 3 or 4; spheridia housed in cysts surrounding peristome; in some species primary tubercles of paired ambulacral areas recessed into camellae. *Eoc.-Rec.*, cosmop.

**L. (Lovenia)**. Anterior margins of anterolateral petals forming crescentic line; primary tubercles of ambulacra noncrenulate, recessed in ampullae. *Oligo.-Rec.*, cosmop.——FIG. 497,*1*. **L. (L.) elongata* (GRAY), Rec., *1a,b,* aboral, oral, ×1 (27f); *1c,* amb., enl. (Cotteau, 1889); *1d,e,* aboral, oral, ×1.5 (1); *1f,* apical system, ×6; *1g,* spheridial cysts, ×4.5 (136i).

**L. (Vasconaster)** LAMBERT, 1915, p. 191 [*pro Sarsella* POMEL, 1883, p. 28 (*non* HAECKEL, 1879)] [**Breynia sulcata* HAIME, 1853, p. 216; OD]. Petals not forming transverse crescent; primary tubercles not recessed in ampullae. *Eoc.-Rec.*, cosmop.——FIG. 498,*3*. **L. (V.) sulcatus* (HAIME), Oligo., Fr.; *3a,* aboral, ×1.5; *3b-d,* oral, lat., post., ×1 (all 27e).

**Breynia** DESOR, 1847, p. 12 [**Spatangus australasiae* LEACH, 1815]. Resembles *Lovenia* but with peripetalous fasciole in addition to subanal and internal ones, large generally noncrenulate tubercles of paired interambulacral areas located in camellae. *Oligo.-Rec.*, Medit.-India-W. Pac.——FIG. 499,*2*. **B. australasiae* (LEACH), Rec.; *2a-c,* aboral, oral, lat., ×1 (1); *2d,e,* apical systems of male and female, both ×5 (136i).

**Chuniola** GAGEL, 1903, p. 531 [**C. carolinae*; OD]. No fascioles known in this heart-shaped urchin, described from internal molds, but presence of ampullate primary tubercels in 3 posterior interambulacra, combined with bare plastron and short, broad labrum suggest relationship to *Lovenia. Mio.*, Ger.——FIG. 499,*3*. **C. carolinae*; *3a,b,* aboral, oral, ×1.5 (194).

**Echinocardium** GRAY, 1825, p. 430 [**Echinus cordatus* PENNANT, 1777, p. 58; SD ICZN, Op. 209, 1948] [=*Amphidetus* AGASSIZ, 1836, p. 184 (obj.)]. Differs from typical loveniids in scarcity of large spines and tubercles, and absence of deep areoles or camellae; subanal fasciole with pair of

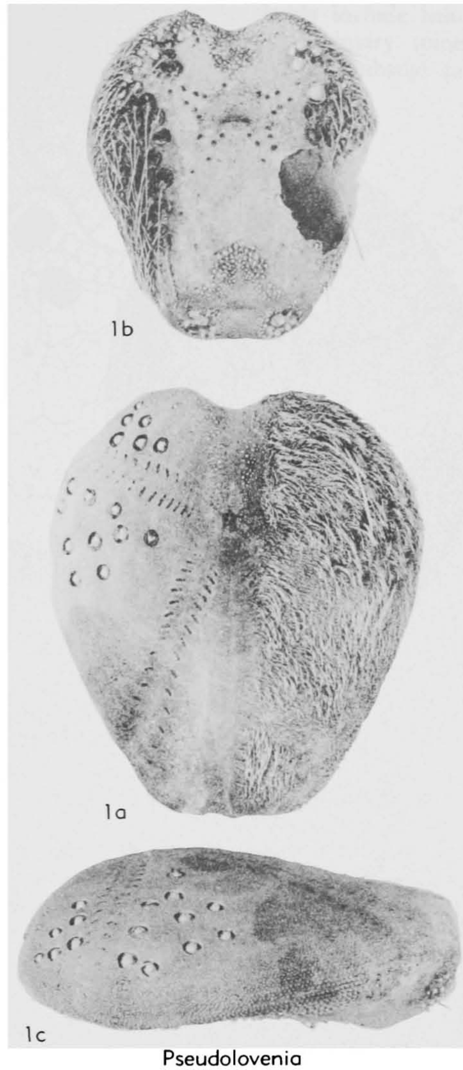



FIG. 500. Loveniidae (p. U614).

anal branches. *Oligo.-Rec.*, cosmop.——FIG. 499,*1*. **E. cordatum* (PENNANT), Rec., English Channel; *1a,b,* aboral, post., ×1.5; *1c,* apical system, enl. (185).

**Homolampas** A. AGASSIZ, 1874, p. 137 [*pro Lissonotus* AGASSIZ, 1869, p. 273 (*non* GISTL, 1848; *nec* BLYTH, 1853; *nec* SCHÖNHERR, 1917)] [**Lissonotus fragilis* AGASSIZ, 1869, p. 273; OD]. Test fragile ovoid, with frontal sinus; 3 gonopores; ambulacra flush, nonpetaloid; subanal and peripetalous fascioles present; resembling loveniids in having noncrenulate primary tubercles sunk in camellae, and therefore placed in this family de-

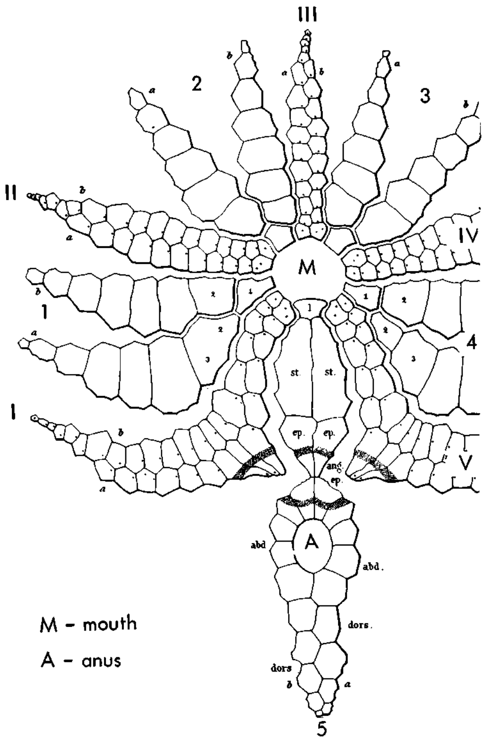



FIG. 501. Plate diagram of *Palaeotropus* (Lovén).

spite absence of internal fasciole. *Rec.*, IndoPac. ——FIG. 498,*2*. **H. fragilis* (AGASSIZ); *2a*, aboral, ×6; *2b*, apical system, ×12; *2c,d*, aboral, oral, ×1.5 (136i).

**Pseudolovenia** AGASSIZ & CLARK, 1907, p. 255 [**P. hirsuta*; OD]. Differs from *Lovenia* in having subpetaloid, distally diverging ambulacra. *Rec.*, Hawaii.——FIG. 500,*1*. **P. hirsuta*; *1a-c*, aboral, oral, lat., ×1 (21).

**Verbeekia** FRITSCH, 1877, p. 90 [**V. dubia*; OD] [*non Verbeekia* PENECKE, 1908, p. 657; *nec* SILVESTRI, 1908, p. 137] [=*Verbeckia* POMEL, 1883, p. 35 *(nom. van.)*]. Poorly known spatangoid of oval outline, with peculiarly confluent petals and small sternum, which suggests placement in Loveniidae. *Eoc.*, Borneo.——FIG. 498,*1*. **V. dubia*; *1a,b*, aboral, oral, ×1 (193).

## Suborder ASTEROSTOMATINA A. G. Fischer, new suborder

Petals weakly developed or absent, fascioles of various types or absent, primary spines present or absent, apical system ethmolytic, plastron mesamphisternous to ultramphisternous. Restricted to family Asterostomatidae. [Probably a polyphyletic grouping of aberrant members of the Hemiasterina and Micrasterina, which have reduced petals or fascioles or both and have in some cases returned to a nearly radial symmetry, in adaptation to other habitats. This suborder is to be regarded as a taxonomic convenience or necessity rather than as a biologically meaningful unit.]*Eoc.-Rec.*

### Family ASTEROSTOMATIDAE Pictet, 1857

[Asterostomatidae PICTET, 1857, p. 205] [=Paleopneustidae AGASSIZ, 1904, p. 150; Antillasterinae LAMBERT & THIÉRY, 1924, p. 439; Palaeopneustidae MORTENSEN, 1950, p. 181]

Heterogeneous, polyphyletic grouping of ethmolytic spatangoids showing tendencies to lose petaloid structure and fascioles, and, in some forms, to re-establish superficial radial symmetry (Fig. 501). Peristome labiate, phyllodes well developed, test generally fragile; most possess radioles. Plastron mesamphisternous, holamphisternous or ultramphisternous. *Eoc.-Rec.*

The Recent forms live on mud bottoms of the bathyal and abyssal zone, and are mud-feeders. The abyssal forms are notable for loss of petals, and reduction of pores in the frontal ambulacrum.

Older workers, including MORTENSEN, considered the asterostomatids or palaeopneustids as primitive. MORTENSEN suggested that they represent a root group of the Spatangoida, collateral with the toxasterids, and derived from the collyritids; he considered them ancestral to the loveniids and pericosmids, and possibly to the palaeostomatids and aeropsids as well. However, their apical system, plastron, spination, and fascioles are not primitive, and their time distribution does not support this ancestral role. It seems more reasonable to ascribe their loss of petals and other spatangoid characters to secondary adaptation to a mode of life not typically spatangoid. If we accept this view—that they are somewhat aberrant end forms—then their diversity of fascioles takes on meaning. It becomes evidence of a polyphyletic origin of the group, of convergent adaptation to the asterostomatid mode of life by hemiasterids, brissids, spatangoids, and loveniids.

The majority of asterostomatid genera show the presence of the peripetalous fasciole, at least in early stages of their ontogeny. These forms probably include hemiasterids which developed primary spines, and brissids which lost their subanal fas-

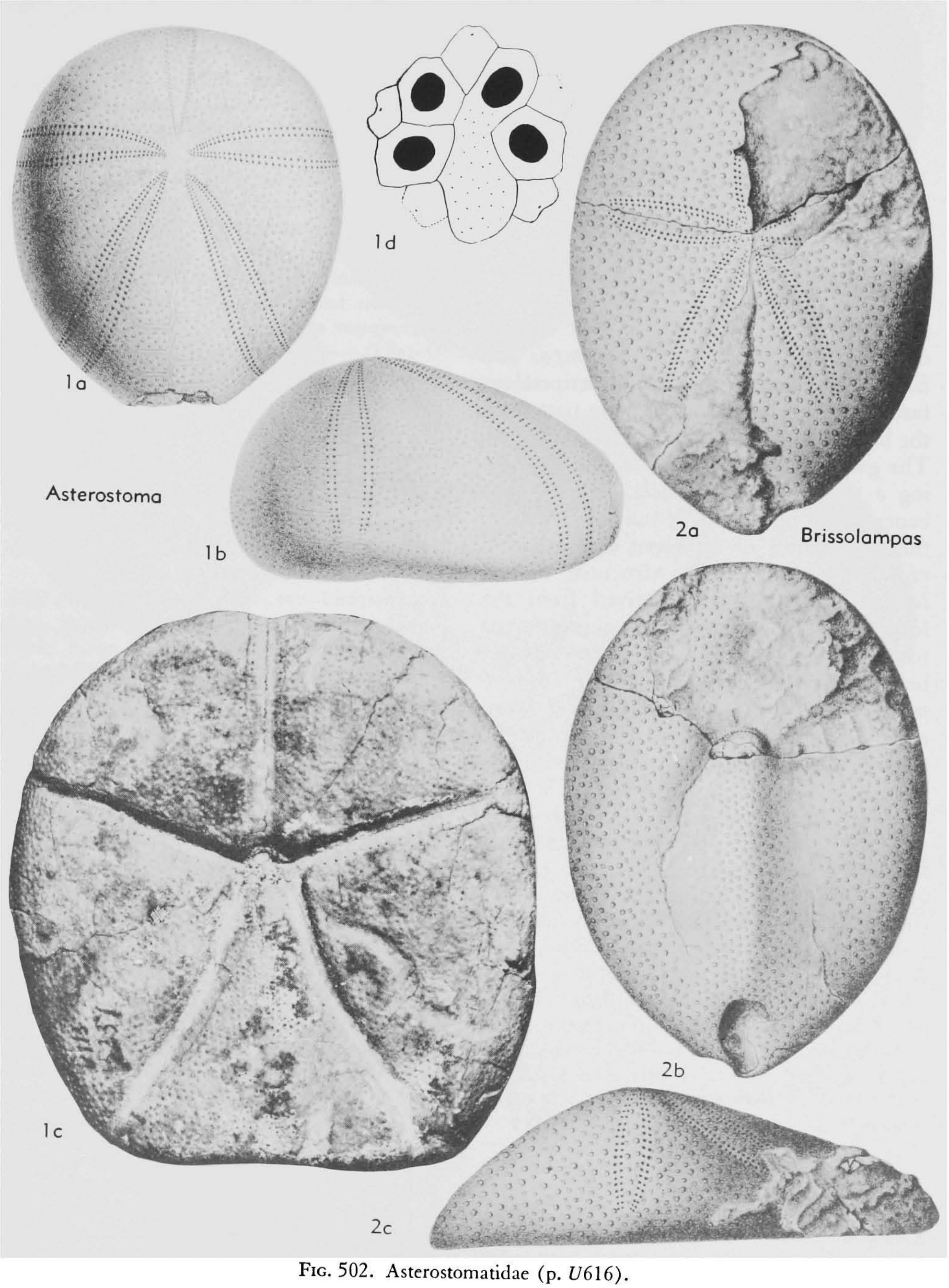



FIG. 502. Asterostomatidae (p. *U*616).


FIG. 503. Asterostomatidae (p. U616).

ciole. Other genera retain at least vestiges of a subanal fasciole, in *Pycnolampas* and *Elipneustes* combined with a peripetalous fasciole. These may be derived in part from the brissids and in part from the spatangids. The genus *Peripatagus* stands alone in having a true marginal fasciole, which passes beneath the periproct. It may derive from the pericosmids or represent an independent development of this structure. *Homolampas* is so obviously derived from the loveniids that it has here been transferred to that family, just as the more obvious brissid derivatives *Megapneustes, Stomaporus, Pharaonaster, Thebaster,* and *Mariania,* placed by MORTENSEN in the asterostomatid group, are here grouped with the brissids.

The reduction of petals and ambulacral pores, the loss of fascioles, and, in some forms, the development of circular outlines are changes which run directly counter to the evolutionary adaptation of spatangoids to a burrowing mode of life. Perhaps the asterostomatids represent a return to life on or at the surface of the sea floor.

**Asterostoma** AGASSIZ, 1847, p. 168 [**A. excentricum*; OD]. Test ovoid, flattened on oral side; apical system with 4 gonopores; paired ambulacra subpetaloid, open at ambitus; central zones of ambulacra form furrows which extend from peristome to ambitus; no fascioles. *Eoc.*, Antilles.——FIG. 502,*1*. **A. excentricum*; *1a,b,* aboral, lat., ×0.5 (142); *1c,* oral side, showing grooves, ×0.75 (216b); *1d,* apical system, ×6 (136h).

**Antillaster** LAMBERT, 1909, p. 103 [**Asterostoma cubensis* COTTEAU, 1871, p. 5; OD] [=*Pseudasterostoma* SÁNCHEZ ROIG, 1952, p. 5 (obj.) (*nom.* DUNCAN, 1889, p. 203)]. Differs from *Asterostoma* in lacking furrows on oral side, or having such furrows incompletely developed (only in anterolateral pair, and extending only part way from peristome toward margin). *Eoc.-Mio.*, Antilles.——FIG. 503,*1*; 504,*4*. **A. cubensis* (COTTEAU), Cuba; 503,*1*, oral, ×0.3 (216b); 504,*4a,b,* aboral, lat., ×0.6 (21b).

**Argopatagus** A. AGASSIZ, 1879, p. 209 [**A. vitreus*; OD] [=*Meijeria* DÖDERLEIN, 1906, p. 242 (type, *Phrissocystis humilis* DE MEIJÈRE, 1902, p. 14); *Phrissocystis* A. AGASSIZ, 1898, p. 80 (type, *P. aculeata* A. AGASSIZ, 1904, p. 187)]. Test flat, delicate; ambulacra not petaloid, and only apical 4 or 5 plates of each showing paired pores; genital plates fused, gonopores 4; phyllodes well developed; subanal fasciole present though *Phrissocystis* lacks this fasciole and may represent a gerontic *Argopatagus vitreus* or a distinct form. *Rec.*, Pac. O.-Ind.O.——FIG. 504,*3*. **A. vitreus,* Pac.O.; *3a-c,* aboral, oral, lat., ×1 (2).

**Brissolampas** POMEL, 1883, p. 31 [**Paleopneustes conicus* DAMES, 1877, p. 47; OD]. Outline ovoid, with pointed posterior; oral side flat; periproct inframarginal; all ambulacra similarly petaloid, with round pores, thus distinguished from *Pygospatangus*; fascioles lacking. *Mio.*, Italy-Cuba.——FIG. 502,*2*. **B. conicus* (DAMES), Italy; *2a-c,* aboral, oral, lat., ×0.6 (41).

**Brissomorpha** LAUBE, 1871, p. 72 [**B. fuchsi*; OD]. Distinctively shaped test, with posterior beak bearing periproct on its underside; apical system anteriorly eccentric, with 4 gonopores; petals narrow, open, with round pores; peripetalous fasciole present, others not ascertained. *Mio.*, Austria - Algeria - Indonesia.——FIG. 504,*2*. **B. fuchsi*, Austria; *2a,b,* aboral, oral, ×0.75 (204b).

**Cleistechinus** DE LORIOL, 1882, p. 27 [**C. canaverii*; OD]. Appears to differ from *Palaeobrissus* mainly in having pores in frontal ambulacrum reduced to simple unpaired condition; gonopores 2; ambulacra not petaloid, their pores microscopic; subanal fasciole present. *Mio.*, Italy.——FIG. 504, *1*. **C. canaverii*; *1a-c,* aboral, oral, lat., ×1 (136h).

**Delopatagus** KOEHLER, 1907, p. 147 [**D. brucei*; OD]. High, with nearly circular outline and posteriorly eccentric apex; gonopores 3; paired ambulacra slightly petaloid, slightly depressed, anterior pair longer than posterior; frontal ambulacrum apetaloid, bearing pores only in uppermost plates; no fascioles. [Abyssal.] *Rec.*, Antarctic.

**Elipneustes** KOEHLER, 1914, p. 213 [**Eurypneustes denudatus* KOEHLER, 1914, p. 71; OD] [=*Eurypneustes* KOEHLER, 1914a, p. 71 (*non* DUNCAN & SLADEN, 1882)]. Close to *Linopneustes* but distinguished by having only faint frontal sinus and pores in anterior ambulacrum placed in obliquely arranged pairs. *Rec.*, Ind.O.

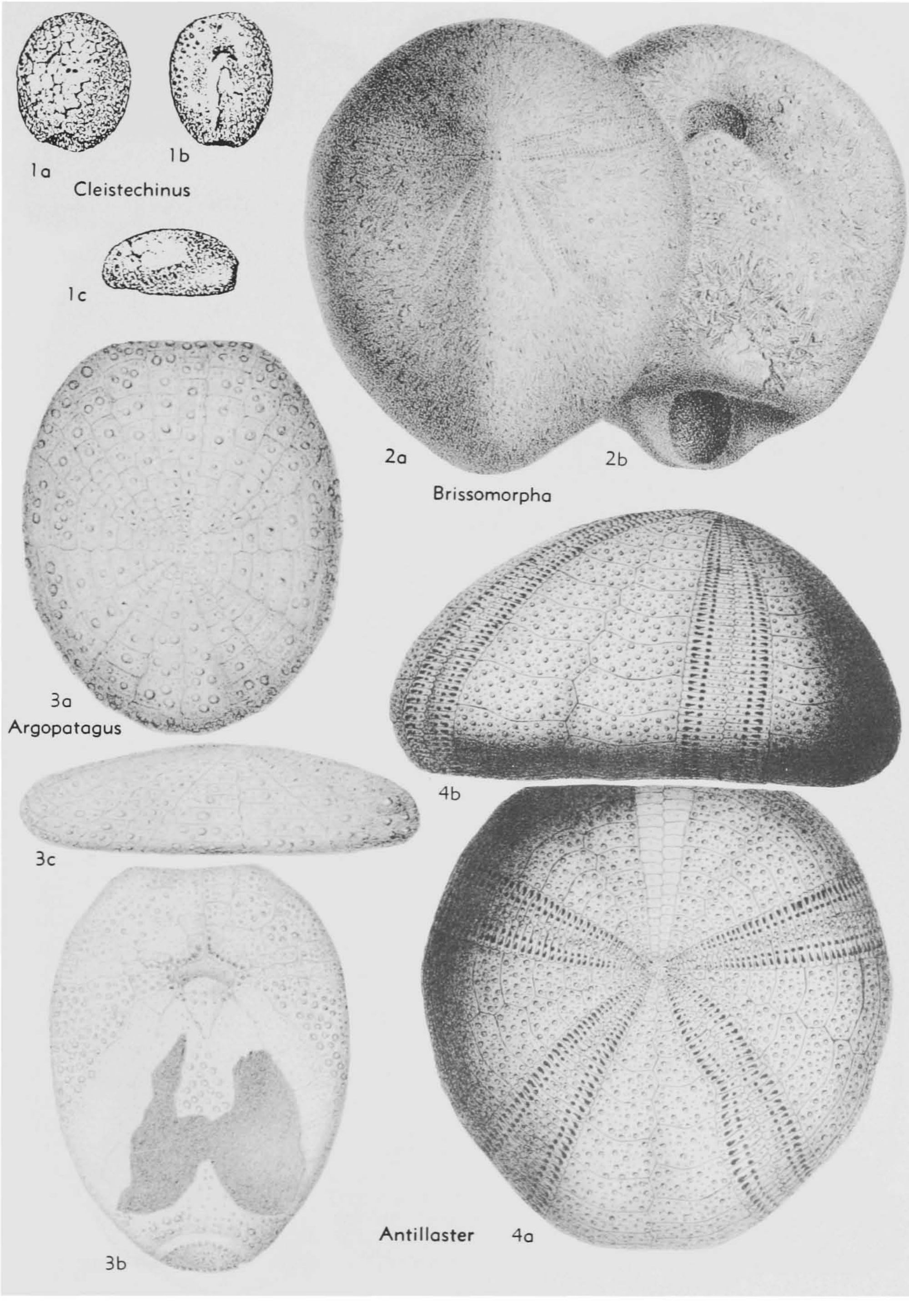



FIG. 504. Asterostomatidae (p. *U*616).

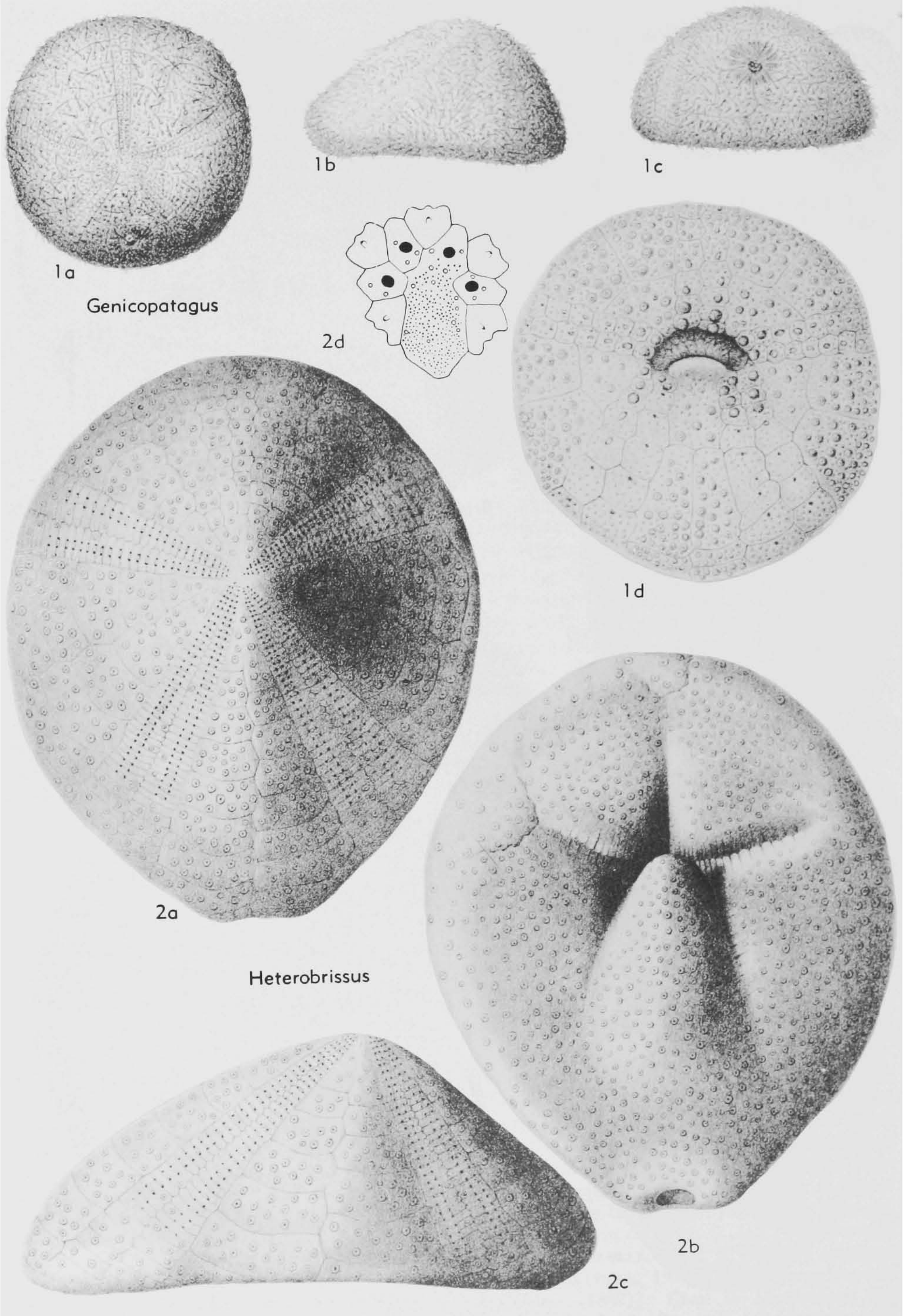



FIG. 505. Asterostomatidae (p. *U*622).

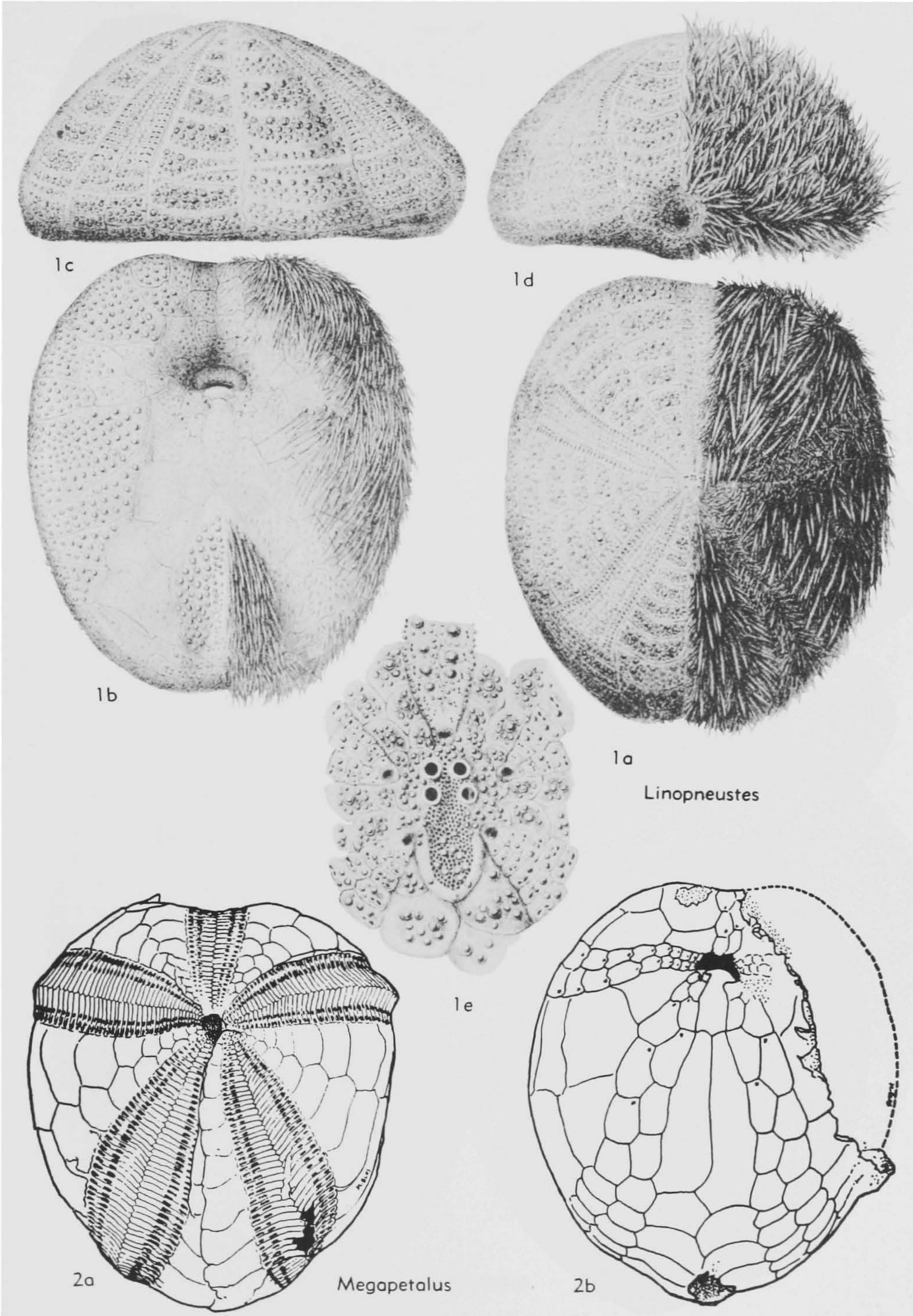



Fig. 506. Asterostomatidae (p. *U*622).

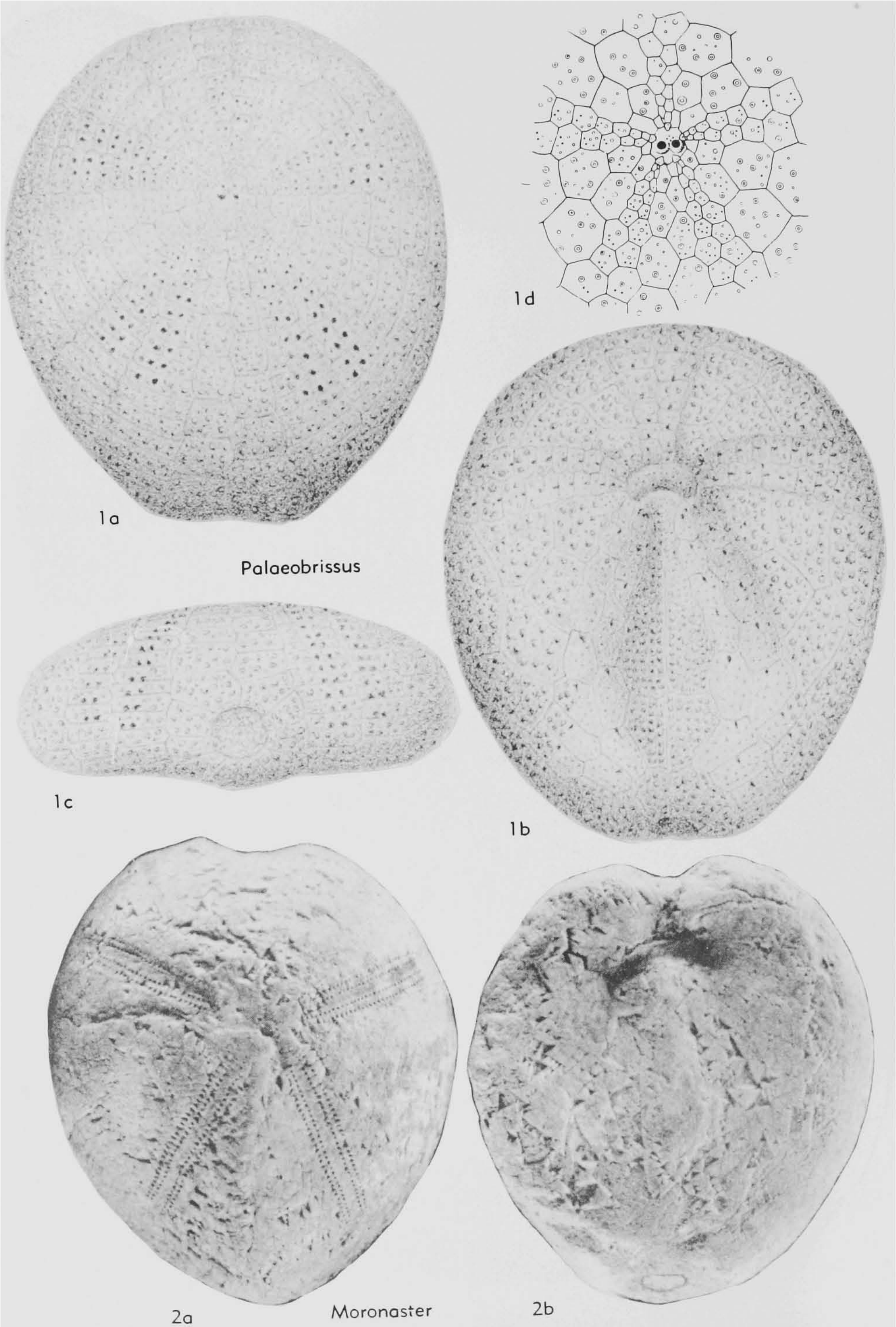



FIG. 507. Asterostomatidae (p. U622).

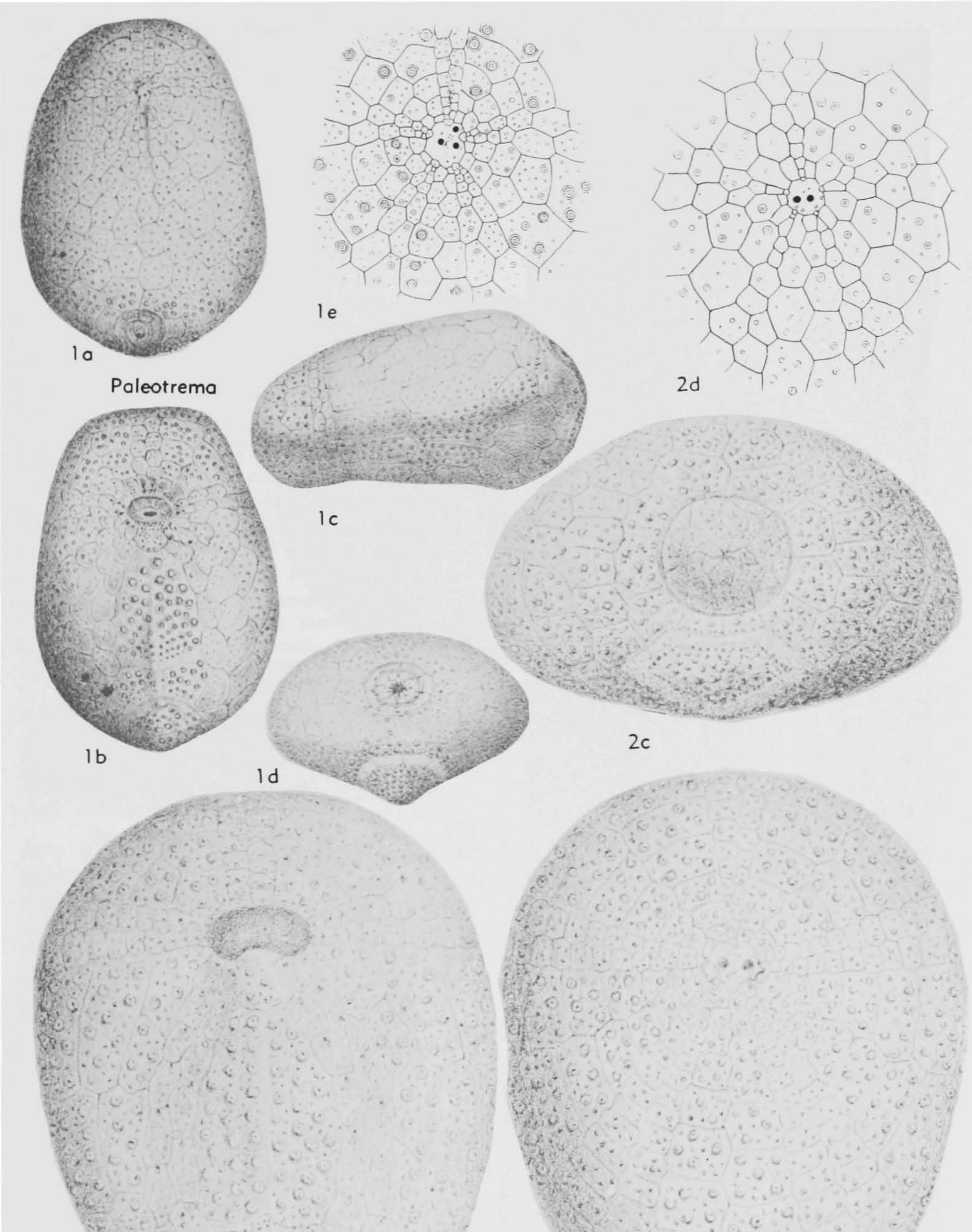



FIG. 508. Asterostomatidae (p. *U*622, *U*624).

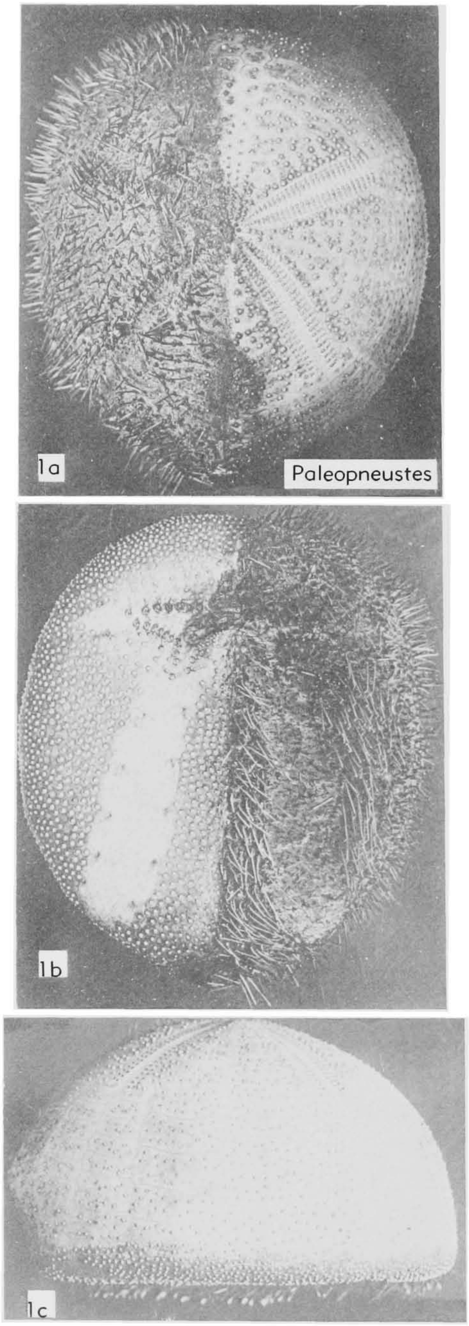



FIG. 509. Asterostomatidae (p. U624).

**Genicopatagus** A. AGASSIZ, 1879, p. 210 [*G. affinis; OD]. Test low arched, ovoid in outline, with faint frontal sinus; ambulacra flush, nonpetaloid, but having double pores; apical system ethmolytic, with 3 gonopores; no apical primary spines, no fascioles. [Abyssal.] *Rec.*, Antarctic.——FIG. 505,*1*. **G. affinis*; *1a-c*, aboral, lat., post., ×1.5; *1d*, oral, ×1 (all 2).

**Heterobrissus** MANZONI & MAZZETTI, 1877, p. 354 [*H. montesi; OD] [=*Archaeopneustes* GREGORY, 1892, p. 163 (type, *Palaeopneustes hystrix* AGASSIZ, 1880, p. 60)]. Like *Palaeopneustes* in outline and ambulacral characters but with deep phyllodes, 4 gonopores, and larger primary tubercles; fascioles lacking. *Mio.-Rec.*, trop. seas.——FIG. 505, *2a-c*. **H. montesi*, Mio., Italy; *2a-c*, aboral, oral, lat., ×0.75 (206b).——FIG. 505,*2d*. *H. niasicus*, Rec., Ind.O.; *2d*, apical system, ×4 (136h).

**Linopneustes** A. AGASSIZ, 1881, p. 167 [*Paleopneustes murrayi A. AGASSIZ, 1873, p. 168; OD]. Resembles *Paleopneustes* in shape and radial arrangement of pores in frontal ambulacrum, but differs in having 4 gonopores and frontal sinus; juveniles with marginal and subanal fasciole, adults may retain former. *Rec.*, trop. seas.——FIG. 506,*1*. **L. murrayi* (AGASSIZ); *1a-d*, aboral, oral, lat., post., ×0.75; *1e*, apical system, enl. (2).

**Megapetalus** CLARK, 1929, p. 259 [*M. lovenioides; OD]. Differs from all known asterostomatids in having 5 equal, very large, flush, open petals; gonopores 4; fascioles lacking. *Mio.*, N.Am. (Calif.).——FIG. 506,*2*. **M. lovenioides*; *2a,b*, aboral, oral, ×0.75 (226).

**Moronaster** SÁNCHEZ ROIG, 1952, p. 13 [*M. moronensis; OD]. Heart-shaped, with distinct frontal sinus; frontal ambulacrum nonpetaloid; petals long, open, with subequal pores, slightly depressed; periproct inframarginal; peristome labiate; apical structure and nature of plastron unknown; fascioles appear absent. [Clearly a spatangoid, but surface preservation of known specimens is too poor to be certain of absence of fascioles; hence family assignment remains uncertain.] *Eoc.*, Cuba.——FIG. 507,*2*. **M. moronensis*; *2a,b*, aboral, oral, ×0.75 (216d).

**Palaeobrissus** A. AGASSIZ, 1883, p. 56 [*P. hilgardi; OD]. Test oval, depressed, lacking frontal sinus; gonopores 2 (posterior) in young specimens, 1 or 2 additional (anterior) rudimentary pores in adults, ambulacra flush, nonpetaloid to slightly petaloid (in paired ambulacra of large specimens); no large tubercles or spines; subanal fasciole present in young, obliterated in adults; no peripetalous fasciole. *Rec.*, Antilles.——FIG. 507,*1*. **P. hilgardi*; *1a-c*, aboral, oral, post., ×1.5; *1d*, apical region, ×4 (136i). [=*Palaeobryssus* MEISSNER, 1903, p. 1343 *(nom. van.)* (obj.).]

**Palaeotropus** LOVÉN, 1872, p. 1085 [*P. josephinae; OD]. Differs from *Palaeobrissus* in having uni-

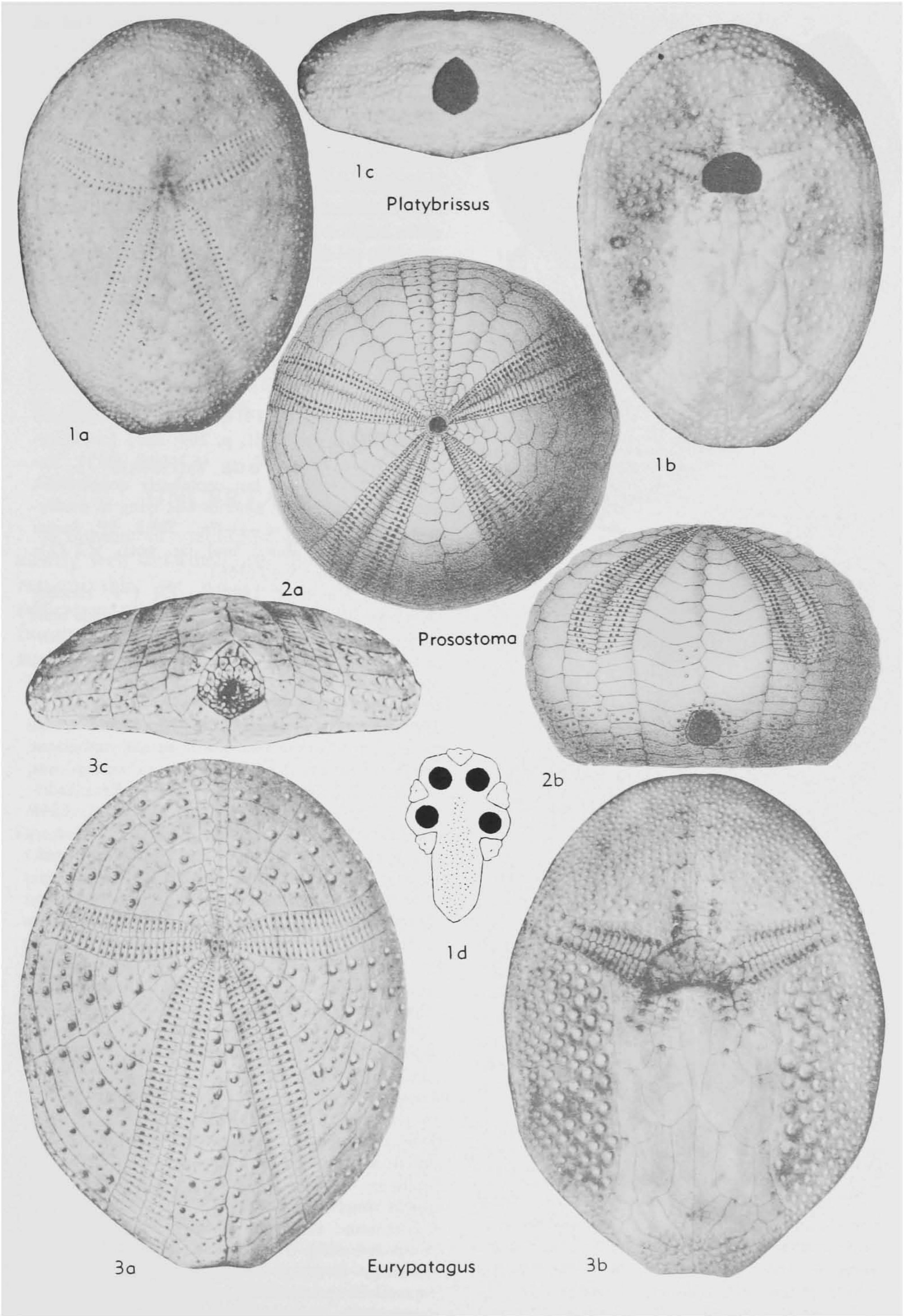



FIG. 510. Asterostomatidae (p. *U*624-*U*625).

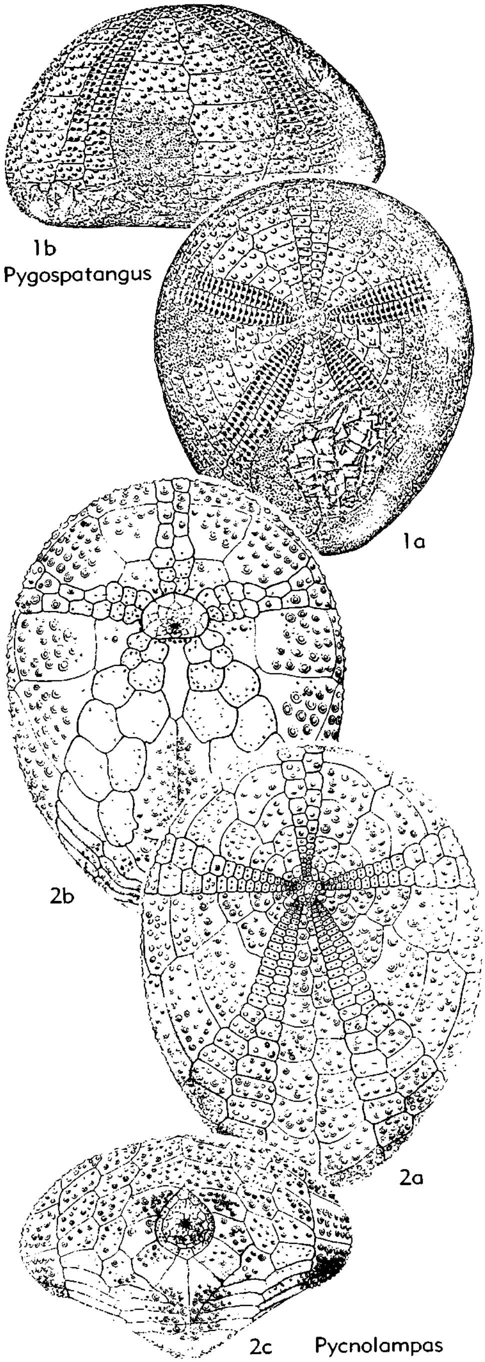



FIG. 511. Asterostomatidae (p. U625).

serial ambulacral plates in apical area, and in being completely nonpetaloid. *Rec.*, trop. Atl.——FIG. 508,*2*. **P. josephinae*; *2a-c,* aboral, oral, post., ×1.5 (175c); *2d,* apical region, enl. (136i).

**Paleopneustes** A. AGASSIZ, 1873, p. 223 [**P. cristatus*; OD ][=*Palaeopneustes* DUNCAN, 1889, p. 223 *(nom. van.)*]. Test high, roundly conical, lacking frontal sinus; apical system central, with 3 gonopores; paired ambulacra petaloid, flush, open; anterior ambulacrum with double pores but arranged in single row; phyllodes weakly developed, tubercles small; young specimens showing wide peripetalous fasciole, which resembles marginal fasciole but excludes periproct. *?Tert.*, N. Am.; *Rec.*, Gulf Mexico-Carib.——FIG. 509,*1*. **P. cristatus,* Rec., Gulf Mexico; *1a-c,* aboral, oral, lat., ×0.5 (175a).

**Paleotrema** KOEHLER, 1914, p. 45 [**Palaeotropus loveni* A. AGASSIZ, 1881, p. 204; OD] [=*Palaeotrema* KOEHLER, 1914, p. 45 *(laps. cal.)*]. Resembles *Palaeobrissus* but completely nonpetaloid, and has 3 gonopores, anterior one lying in madreporite. *Rec.*, IndoPac.——FIG. 508,*1*. **P. loveni* (AGASSIZ); *1a-d,* aboral, oral, lat., post., ×2 (2); *1e,* apical region, ×4 (136h).

**Peripatagus** KOEHLER, 1895, p. 231 [**P. cinctus*; OD]. Small, nearly circular in outline, with faint frontal sinus; gonopores 3 or 4; ambulacra completely nonpetaloid, having only few, simple pores; marginal fasciole present. *Rec.*, Azores.

**Platybrissus** GRUBE, 1865, p. 61 [**P. roemeri*; OD]. Test elliptical, depressed, lacking frontal sinus; gonopores 4; ambulacra flush, paired ambulacra petaloid; subanal fasciole present in young, but tending to disappear in adults. *Mio.-Rec.*, IndoPac. [=*Platybryssus* MEISSNER, 1903, p. 1343 *(nom. van.)* (obj.).]

**P. (Platybrissus).** Test relatively narrow, peristome narrow, tubercles small, phyllodes moderately developed. *Mio.-Rec.*, IndoPac.——FIG. 510,*1*. **P. (P.) roemeri,* Rec.; *1a-c,* aboral, oral, post., ×1; *1d,* apical system, ×6 (136h).

**P. (Eurypatagus)** MORTENSEN, 1948, p. 133 [**E. ovalis*; OD]. Test and peristome broader, tubercles larger, and phyllodes deeper than in *P. (Platybrissus)*. *Tert.*, Java; *Rec.*, IndoPac.——FIG. 510,*3*. **P. (E.) ovalis,* Rec.; *3a-c,* aboral, oral, post., ×1 (136h).

**Plesiozonus** DE MEIJERE, 1902, p. 12 [**Plesiozonus hirsutus*; OD]. Resembles *Prosostoma* in being large and rounded, with paired petals which are closed and have their last plates occluded; its petals are narrower, and test may show shallow frontal sinus and peripetalous fascioles; gonopores 3; peristome elliptical, anterior, depressed. *Rec.*, Philip.-Indonesia.

**Prosostoma** POMEL, 1883, p. 55 [**Asterostoma jimenoi* COTTEAU, 1870, p. 40; OD] [=*Pseudasterostoma* DUNCAN, 1889, p. 203 (obj.)]. Very large, hemispherical test with 4 large closed flush petals in which some terminal plates are occluded; fascioles not ascertained; oral side unknown. *Mio.*, Cuba.——FIG. 510,*2*. **P. jimenoi* (COTTEAU); *2a,b,* aboral, post., ×0.6 (184a).

**Pycnolampas** AGASSIZ & CLARK, 1907, p. 252 [**P. oviformis*; OD]. Test elliptical, lacking frontal sinus; paired ambulacra subpetaloid, flush; frontal ambulacrum with only simple pores; delicate peripetalous fasciole and well-developed subanal fasciole present. *Rec.*, Hawaii.——FIG. 511,*2*. **P. oviformis*; *2a-c,* aboral, oral, post., ×2.7 (21).

**Pygospatangus** COTTEAU, 1888, p. 977 [**P. salvae*; OD]. Differs from *Brissolampas* in having higher test and nonpetaloid frontal ambulacrum; differs from *Antillaster* and *Asterostoma* in petals not reaching ambitus, round conjugate pores, and inframarginal periproct. *Eoc.*, Spain.——FIG. 511,*1*. **P. salvae*; *1a,b,* aboral, lat., ×0.6 (136h).

## Suborder and Family UNCERTAIN

A number of spatangoid genera are sufficiently well described and illustrated to be recognizable, yet we lack knowledge of critical parts necessary for even tentative family assignment within the order.

**Barnumia** COOKE, 1953, p. 29 [**B. browni*; OD]. Shape bulbous but not accurately known; all ambulacra petaloid, flush, petals open; apical system ethmophract, gonopores 4; marginal fasciole, passing beyond end of petals; plastron unknown. [Assignment to spatangoids uncertain.] *Cret.* (*?Campan.*), Guatemala.——FIG. 512,*2*. **B. browni*; *2a,b,* aboral, oral, ×1 (183).

**Cestobrissus** LAMBERT, 1912, p. 100 [**C. lorioli*; OD]. Ovoid test with apical system far anterior, posterior end truncated; structure of apical system unknown; peristome anterior; fasciole described as marginal, but MORTENSEN has suggested that it may represent peripetalous and lateroanal fascioles with rear part of former obliterated, in which case this form belongs to the Schizasteridae. *Eoc.*, SW.Fr.——FIG. 513,*1*. **C. lorioli*; *1a,b,* aboral, lat., ×1 (136i).

**Cottreaucorys** LAMBERT, 1920, p. 26 [**Homoeaster blayaci* COTTEAU, 1909, p. 248; OD]. Test ovoid, with rear extended into subanal tail; apical system anterior, with 4 gonopores; ambulacra subpetaloid, short, simple, evidently not differentiated; peripetalous fasciole present. [May be ancestral to *Aeropsis*.]. *U. Cret.* (*Maastricht.*), N. Afr. (Alg.).——FIG. 513,*3*. **C. blayaci* (COTTEAU); *3a,b,* aboral, lat., ×1.5 (184b).

**Enichaster** DE LORIOL, 1882, p. 30 [**E. oblongus*; OD]. Shape flattened and elongate, with parallel sides; gonopores 4; paired ambulacra petaloid; appears to lack fascioles; oral surface not known, classification uncertain, possibly not a spatangoid. *Oligo.*, Italy.——FIG. 514,*1*. **E. oblongus*; *1a,b,* aboral, lat., ×1.5 (205a).

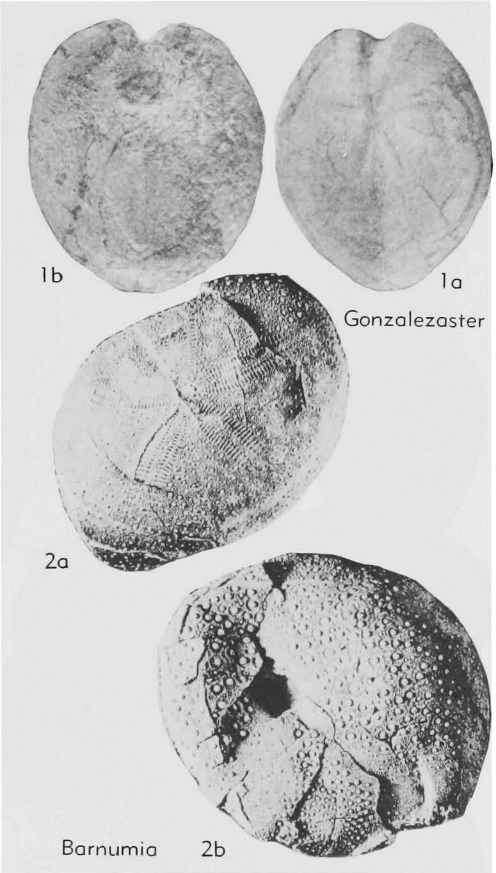



FIG. 512. Spatangoida, Suborder and Family Uncertain (p. *U625*).

**Gonzalezaster** SÁNCHEZ ROIG, 1952, p. 14 [**Nudobrissus lamberti* SÁNCHEZ ROIG, 1949, p. 222]. Heart-shaped in outline, highest in rear; apical system anteriorly excentric, probably ethmophract; gonopores 2(?); anterior ambulacrum apetaloid, deeply sunken; paired petals slightly depressed, very narrow, open, the frontal pair transverse; fascioles appear to be lacking. *Upper Eoc.*, Cuba.——FIG. 512,*1*. **G. lamberti* (SÁNCHEZ ROIG), *1a,b,* aboral, oral, ×0.5 (216d).

**Homoeopetalus** ARNOLD & H. L. CLARK, 1934, p. 146 [**H. axiologus*; OD]. Discoidal form of subcircular outline, with posterior apex and somewhat sunken petals; nature of apical system and oral surface unknown; fascioles not observed; shape and narrowness of interporiferous zones in petals make this echinoid very distinctive, but its family relations are unclear. *Tert.*, Jamaica.——FIG. 514, *3*. **H. axiologus*; *3a,b,* aboral side, ×1 (177).

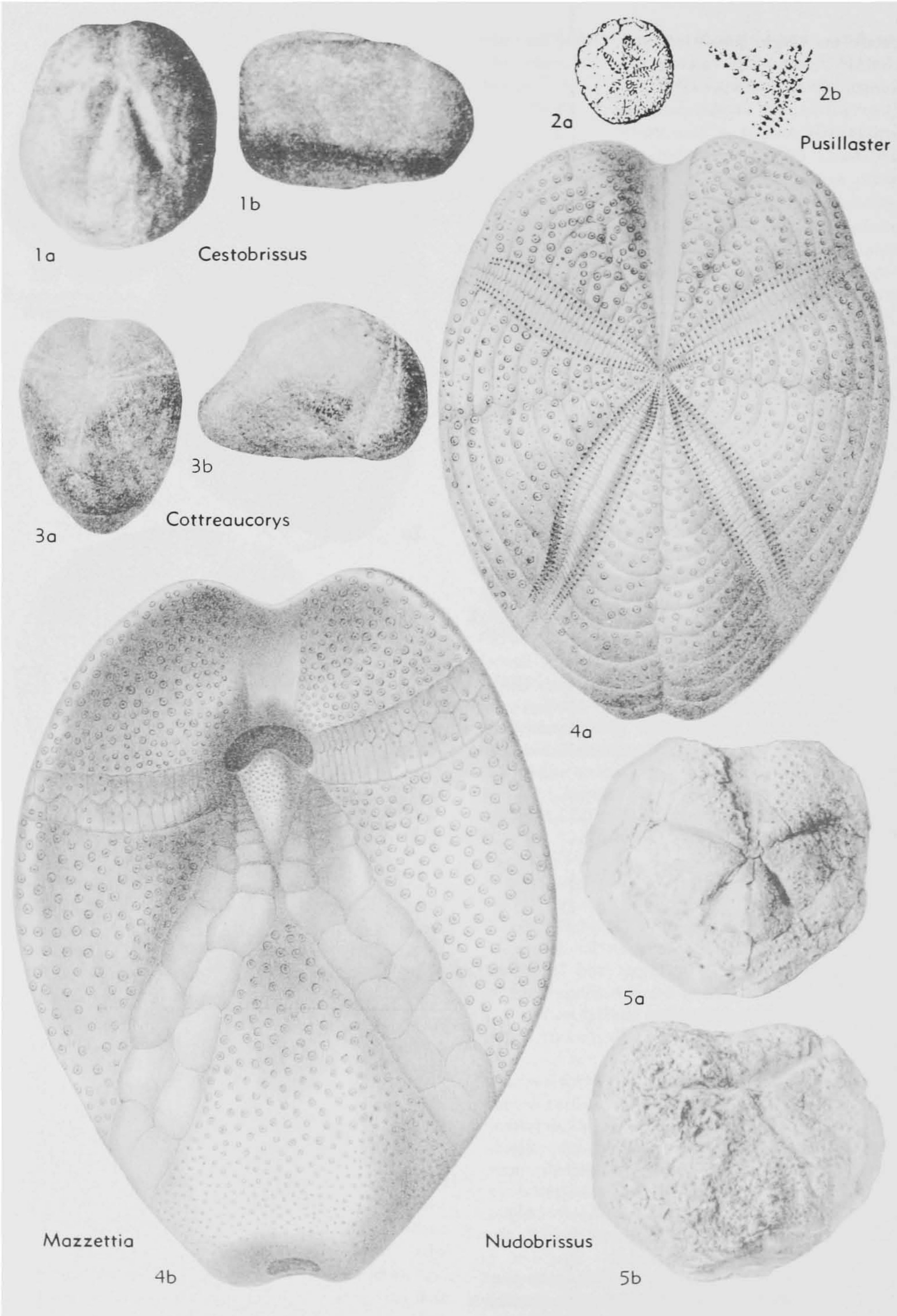



FIG. 513. Spatangoida, Suborder and Family Uncertain (p. U625, U627).

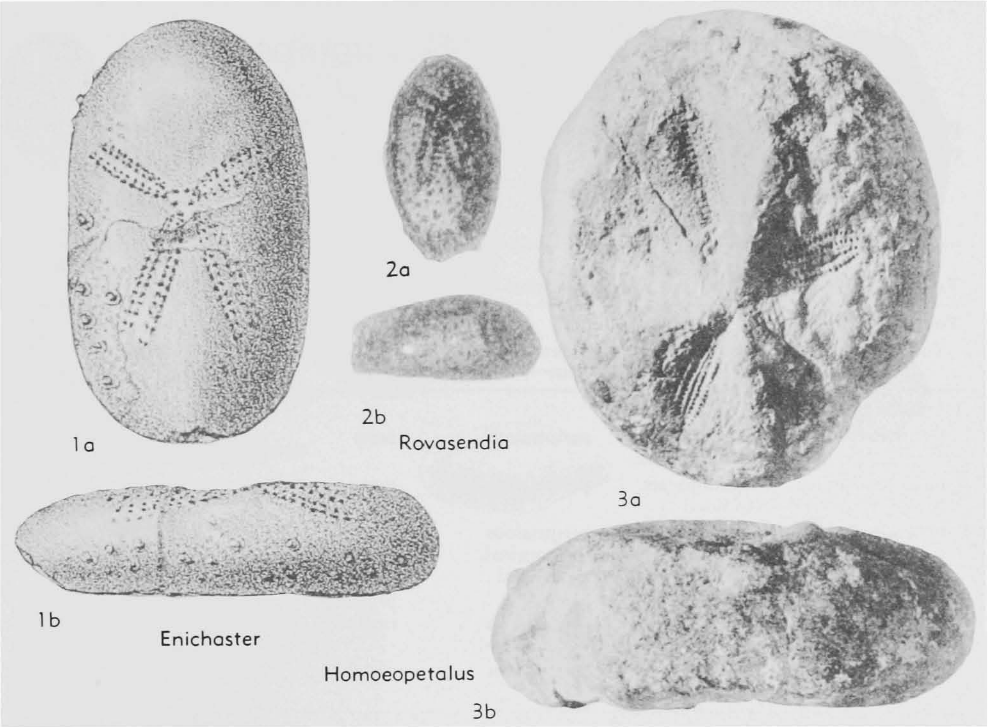



FIG. 514. Spatangoida, Suborder and Family Uncertain (p. *U625*, *U627*).

**Mazzettia** LAMBERT & THIÉRY, 1915, p. 192 [*pro Manzonia* POMEL, 1883, p. 29 (*non* BRUSINA, 1870)] [**Maretia pareti* MANZONI, 1878, p. 158; OD]. Test low, heart-shaped, with deep frontal sinus; gonopores 4; only paired ambulacra petaloid, bearing conjugate pores; petals nearly closed in some species; anterolateral ambulacra with distinct phyllodes; tubercles large, fascioles lacking. [From its general appearance one would tend to classify this genus as a spatangid or a brissid, but typical fascioles of these groups are lacking and the narrow ambulacra in the rear of the test show that *Mazzettia* is not closely related to any echinoid with subanal fascioles. If its structure has been correctly described it stands apart from other spatangoids.] *Mio.*, Italy-Sardinia.——FIG. 513,*4*. **M. pareti* (MANZONI); *4a,b,* aboral, oral, ×0.75 (206a).

**Niponaster** LAMBERT, 1920, p. 45 [**N. hokkaidensis*; OD]. Adorally flat, aborally arched; apical system ethmophract, gonopores 4; petals long, open, undifferentiated, flush; fasciole described as marginal but may be peripetalous. Amphisternous plastron places genus among spatangoids, but family uncertain. *U.Cret.*, Japan.

**Nudobrissus** LAMBERT, 1920, p. 27 [*pro Dictyaster* STEFANINI, 1908, p. 472 (*non* ALCOCK & WOOD-MASON, 1896)] [**Pericosmus malatinus* MAZZETTI, 1885, p. 13; OD]. Resembles *Spatangus (Platyspatangus)*, but with pore pairs of frontal ambulacrum placed obliquely, and bearing more numerous large tubercles; nature of fascioles uncertain. *Mio.*, Italy.——FIG. 513,*5*. **N. malatinus* (MAZZETTI); *5a,b,* aboral, oral, ×1 (220).

**Pusillaster** LAMBERT, 1920, p. 17 [**P. dallonii*; OD]. Depressed, oval form, with small, flush petals, anterior pair much longer than posterior and curiously pointed; nature of apical system and fascioles not known. [Probably a juvenile, of uncertain family affinities.] *U.Cret.(Maastricht.)*, N. Afr.(Alg.).——FIG. 513,*2*. **P. dallonii*; *2a,* aboral, ×1; *2b,* part of petals, enl. (136h).

**Royasendia** AIRAGHI, 1901, p. 213 [**R. canavarii*; OD]. Elongate ovate test with flattened oral side, very small; apical system anterior, with 4 gonopores; ambulacra flush, paired ones petaloid; tuberculation fine, uniform; fascioles not reported; structure of apical system and plastron unknown. [May be a juvenile.] *U.Eoc.*, Italy.——FIG. 514,*2*. **R. canavarii*; *2a,b,* aboral, lat., ×2 (176a).

## SUMMARY OF SPATANGOIDS

The following Table 1 provides a comparative survey of main morphological features of spatangoid echinoids which have been described and illustrated and it shows their relation to the suborders and families recognized in the *Treatise.*

TABLE 1. *Taxonomic Divisions and Morphological Features of Spatangoids*

| TAXA | APICAL SYSTEM | FASCIOLES | PRIMARY SPINES | SPECIAL FEATURES |
|---|---|---|---|---|
| TOXASTERINA | | | | |
| Toxasteridae | ethmophract | generally none | none | protamphisternous to mesamphisternous |
| HEMIASTERINA | | | | |
| Hemiasteridae | ethmophract to ethmolytic | peripetalous | none | protamphisternous to mesamphisternous |
| Palaeostomatidae | ethmophract to fused | peripetalous | none | protamphisternous, pentagonal peristome with 5 buccal plates |
| Pericosmidae | ethmolytic | peripetalous + marginal, no subanal | none | |
| Schizasteridae | ethmophract to ethmolytic | generally peripetalous + lateroanal | present in few | mesamphisternous |
| Aeropsidae | ethmophract to ethmolytic | peripetalous | none | anterior ambulacrum petaloid, paired ambulacra nonpetaloid |
| MICRASTERINA | | | | |
| Micrasteridae | ethmophract to transitional | subanal | none | mesamphisternous |
| Brissidae | ethmophract to ethmolytic | peripetalous + subanal | present | ultramphisternous |
| Spatangidae | ethmolytic | subanal | present | holamphisternous, ant. ambulacrum nonpetaloid |
| Loveniidae | ethmolytic | internal, peripetalous (some), subanal (mostly) | present | ultramphisternous, ant. ambulacrum nonpetaloid |
| ASTEROSTOMATINA | | | | |
| Asterostomatidae | ethmolytic | various or none | present (mostly) | ultramphisternous, reduced petals, spines, fascioles |

## NEOLAMPADOIDS

By J. WYATT DURHAM and CAROL D. WAGNER

### Order NEOLAMPADOIDA Philip, 1963

[*nom. transl. et correct.* DURHAM & WAGNER, herein (*ex* suborder Neolampadina PHILIP, 1963, p. 725] [Materials for this order prepared by J. WYATT DURHAM and CAROL D. WAGNER]

Ambulacra nonpetaloid, with pores simple or lacking adapically; incipient floscelle may be present; apical system tetrabasal or monobasal; 2 to 4 genital pores. *U.Eoc.-Rec.*

The seven genera referred to this order are mostly poorly known and understood. Seemingly only two of the living species (*Neolampas rostellata* and *Tropholampas loveni*) are known from more than one or two described specimens. Until recently (PHILIP, 1963) the group had not been reported in the fossil record. The two genera (*Pisolampus* PHILIP and *Notolampas*

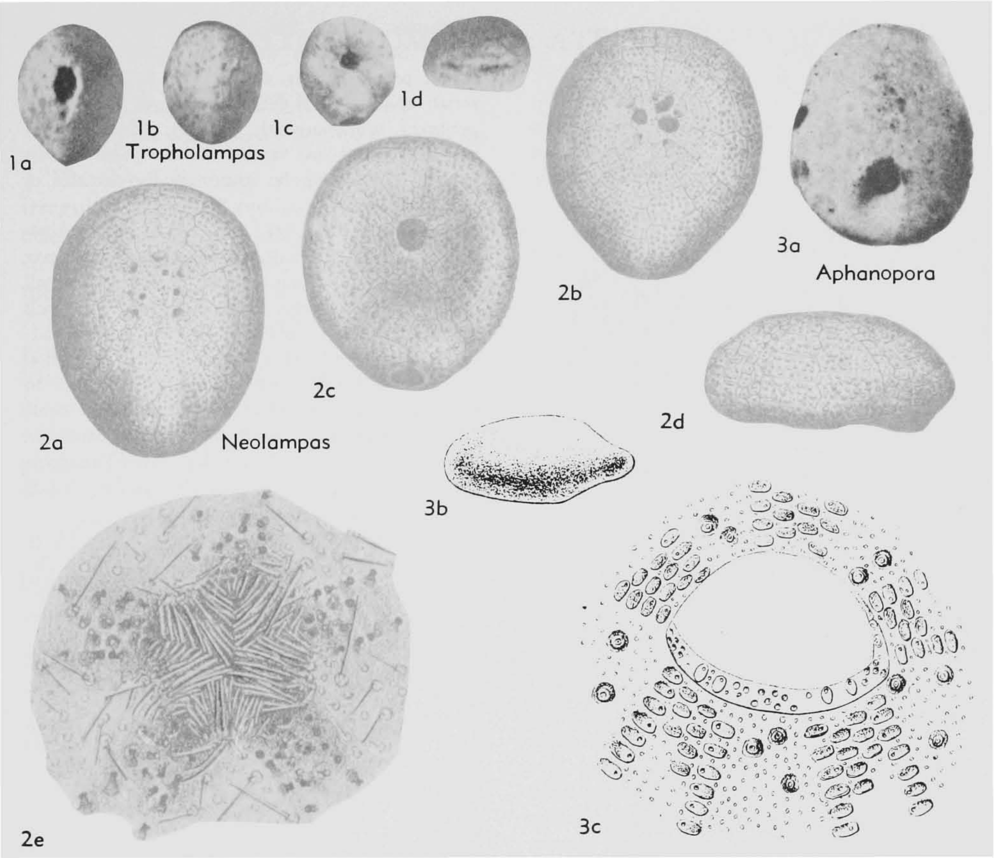



FIG. 515. Neolampadidae (p. *U*630).

PHILIP) occurring as fossils are each represented by several specimens and thus are better described than some of the living species. The affinities of the group were considered by MORTENSEN to be with the Cassiduloida and the two fossil genera support this conclusion, having moderately developed phyllodes and traces of bourrelets. The lack of petals adapically and nature of the ambulacral pores suggest that the group is secondarily specialized from a cassiduloid ancestry or that it was derived from an ancestor with poorly developed bourrelets and petals. The Eocene *Pisolampas* has a monobasal apical system and thus presumably cannot be ancestral to such younger genera as *Nannolampas* with a tetrabasal apical system.

The living neolampadoids are known from depths as great as 1,260 m. *(Neolampas),* although most specimens seem to have been taken between 135 and 400 m. The apical system of females in *Tropholampas* and *Anochanus* is sunken to form a marsupium and it has been suggested that the two specimens on which the genus *Aphanopora* is based are actually males of the species on which the genus *Anochanus* is based (known only from females). The test is generally small (less than 15 mm. in length) and commonly is less than 10 mm. The primary spines are short and sparsely distributed. Tridentate, ophicephalous, and triphyllous pedicellariae are known. The spheridia are perradially located, either singly or in groups.

## Family NEOLAMPADIDAE Lambert, 1918

[Neolampadidae LAMBERT, 1918, p. 12 (34), 40 (62)]

Characters of order. *U.Eoc.-Rec.*

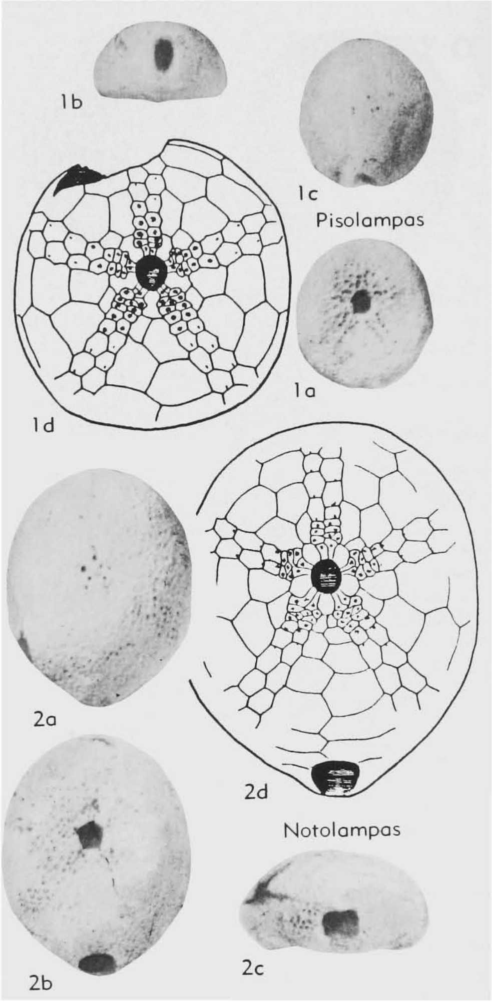



FIG. 516. Neolampadidae (p. U630).

**Neolampas** A. AGASSIZ, 1869, p. 271 [*N. rostellata*; OD]. Small, ovoid, oral side sunken toward peristome: ambulacra nonpetaloid, pores small aborally, larger orally, incipient phyllode; apical system monobasal, 3 genital pores; periproct on truncated posterior end, may have long anal tube; peristome round or elongate along anteroposterior axis, buccal membrane with small calcareous rods; tubercles perforate and crenulate; bourrelets present; tridentate, ophicephalous and triphyllous pedicellariae; spheridia in groups. *Rec.*, Atl.-Medit.——FIG. 515,*2*. *N. rostellata*, Florida Straits; *2a*, aboral view, male, ×4; *2b*, aboral view, female, ×3; *2c*, oral view, ×3; *2d*, profile view, ×3; *2e*, peristomial area, ×8 (Kier, n).

**Anochanus** GRUBE, 1868, p. 178 [*A. sinensis*; OD]. Small, oval; ambulacra apparently with simple primaries only, nonpetaloid, pore pairs uniserial; apical system deeply sunken in the female; periproct supramarginal; primary spines of embryos arranged in vertical rows. [This poorly known genus may be based on the females of *Aphanophora*.] *Rec.*, China Sea.

**Aphanopora** DE MEIJERE, 1902, p. 8 [*A. echinobrissoides*; OD]. Small, ovoid, somewhat concave orally; ambulacra nonpetaloid, pores very small aborally, 2 transverse oval depressions in each ambulacral plate adorally with pore pair in adradial depression; apical system central, 2 genital pores, 1 hydropore; periproct supramarginal, in groove; peristome anterior, transversely oval; ophicephalous and tridentate pedicellariae. *Rec.*, Timor-S.Sulu Sea.——FIG. 515,*3*. *A. echinobrissoides*; *3a*, aboral view, ×2; *3b*, profile, ×1.3; *3c*, peristomial area, enlarged (208).

**Nannolampas** MORTENSEN, 1948, p. 339 [*Neolampas tenera* DE MEIJERE, 1902, p. 8; OD]. Like *Neolampas* except apical system with separate genital plates, 2 genital pores; no occluded plates in ambulacra adorally. *Rec.*, Timor.

**Notolampas** PHILIP, 1963, p. 719 [*N. flosculus*; OD]. Test elongate posteriorly; apical system monobasal, 3 genital pores; ambulacra with single pores adapically; periproct inframarginal; floscelle developed, included plates in phyllodes. *L.Mio.*, Australia.——FIG. 516,*2*. *N. flosculus*; *2a-c*, aboral, oral, post. view, ×2; *2d*, adoral plate arrangement, ×3.5 (142a).

**Pisolampas** PHILIP, 1963, p. 718 [*P. concinna*; OD]. Test subhemispherical; apical system monobasal, 3 genital pores, ocular plates may be without ocular pores, may not be in contact with apical disc; ambulacral pores rudimentary or lacking adapically; periproct supramarginal, at adapical end of shallow groove; bourrelets faint, phyllodes present, included plate in 2 posterior phyllodes. *U.Eoc.*, Australia.——FIG. 516,*1*. *P. concinna*; *1a-c*, oral, post. and aboral views, ×2; *1d*, adoral plate arrangement, ×3.5 (142a).

**Tropholampas** H. L. CLARK, 1923, p. 395 [*Catopygus loveni* STUDER, 1880, p. 878; OD]. Very small, subconical aborally, flattened orally; ambulacra nonpetaloid, pores uniserial adorally, absent aborally, ambulacra somewhat discontinuous with apical system which is deeply sunken in female, slightly concave in male, with 4 genital pores, 1 hydropore; peristome round, subpentagonal or elongate oval; periproct on truncated posterior end; primary spines form hood over marsupium in females; tridentate, triphyllous, and ophicephalous pedicellariae; one spheridium in each ambulacrum. *Rec.*, S.Afr.——FIG. 515,*1*. *T. loveni* (STUDER); *1a,b*, aboral views of female and male, ×2.5; *1c,d*, oral and profile views, ×2.5 (136f).

# GNATHOSTOMATA or ATELOSTOMATA

## Order UNCERTAIN

[Materials for this section prepared by CAROL D. WAGNER and J. WYATT DURHAM, University of California at Berkeley]

The five following inadequately known irregular genera have usually been associated with the Cassiduloida, but in the restricted definition of this group adopted in the *Treatise,* they cannot be assigned to it. All genera have ambulacra built of simple primary plates with small pores, lack phyllodes and at most have feebly developed bourrelets, have tetrabasal apical system (or unknown), in some with complementary plates. There are faint indications of gill slits in *Loriolella,* but none in others. All lack good indication of lantern, and have a small peristome.

**Desorella** COTTEAU, 1855, p. 713 [**Hyboclypus elatus* DESOR in AGASSIZ IN DESOR, 1847, p. 152; SD COTTEAU, 1873, p. 333] [=*Desoria* COTTEAU, 1855, p. 221, (obj.) (*non* NICOLET, 1842; *nec* GRAY, 1851)]; *Pachyclypus* DESOR, 1858, p. 195 (type, *Dysaster semiglobosus* DESOR, 1842, p. 18); *Pachyclypeus* COTTEAU, 1873, p. 389 *(nom. null.)*]. Medium-sized to large, low-arched aborally, pulvinate orally; trivium somewhat separated from bivium; ambulacral plates all simple primaries, pores not conjugate, pairs oblique; apical system central, elongate, 4 genital plates, complemental plates present; periproct posterior, in groove, may have series of narrow catenal plates between apical system and periproct; peristome central, sunken, slightly oblique, no bourrelets or phyllodes; primary tubercles perforate, noncrenulate, scrobiculate, not in vertical series. [Apical system suggestive of some Holasteroida.] *Jur.(Oxford.-Kimmeridg.),* Eu.——FIG. 517,*2*. **D. elata* (DESOR), Oxford., Eng.; *2a,b*, aboral, end views, ×0.7; *2c*, apical system, ×1.5 (224).

**Galeroclypeus** COTTEAU, 1873, p. 360 [**G. peroni*; OD]. Medium-sized, inflated, subconical aborally, pulvinate orally, outline circular; ambulacra subpetaloid, plates all primaries, outer pore slightly elongate, pores apparently not conjugate; apical system subcentral, complemental plates separating posterior ocular plates, 4 genital plates; periproct supramarginal, in slight groove; peristome slightly anterior, sunken, subdecagonal, no bourrelets; tubercles perforate, crenulate, indistinctly scrobiculate. *M.Jur.(Bathon.),* Fr.——FIG. 517,*3*. **G. peroni*; *3a*, aboral, ×0.7; *3b,* adoral portion of ambulacrum, enlarged; *3c,* apical system, ×10 (Kier, n; 27b).

**Infraclypeus** GAUTHIER, 1875, p. 23 [**I. thalebensis*; OD]. Large, aboral side low-arched, oral side nearly flat, outline round; ambulacra of simple primaries throughout, pores small, in oblique pairs, not conjugate; apical system central, somewhat elongate, no genital 5; periproct inframarginal, apparently connected with apical system by series of small, elongate plates in slight furrow; peristome central, slightly oblique, no branchial slits, no bourrelets; tubercles small, not in vertical series. [Apical system suggestive of some Holasteroida.] *M.Jur.(Bathon.)-U.Jur.(Tithon.),* Algeria.——FIG. 517,*4*. **I. thalebensis*; *4a-c*, aboral, oral, profile, ×0.75; *4d*, adoral portion of ambulacram I, ×10 (Kier, n; 35).

**Loriolella** FUCINI, 1904, p. 1 [**Cidaris ludovici* MENEGHINI, 1867, p. 17; OD] [=*Pseudopygaster* HAWKINS, 1922, p. 213 (type, *P. eos*)]. Corona large, low arched, oral side flattened; ambulacral plates all simple primaries, pores small, pairs uniserial; apical system unknown; periproct large, oval, on posterior margin; peristome small, circular, central, branchial slits indistinct; interambulacral plates each with large single primary tubercle situated close to adradial margin; miliary tubercles numerous. *L.Jur.(U.Pliensbach.),* Italy-Iran.——FIG. 517,*5a,b*. **L. ludovici* (MENEGHINI), Italy; *5a,b*, oral, post. views, ×1 (136f).——FIG. 517,*5c*. *L. eos* (HAWKINS), Iran; part of ambulacrum I, enlarged (196c).

**Menopygus** POMEL, 1883, p. 52 [**Galeropygus nodoti* COTTEAU, 1859, p. 52; OD] [=*Pyrinodia* POMEL, 1883, p. 53 (type, *Desorella guerangeri* COTTEAU, 1862, p. 67; *Pyrenodia* POMEL, 1883, p. 130 *(nom. null.)*]. Small to medium-sized, outline round or slightly ovoid; ambulacra of simple primary plates, pore zones simple, pores larger adapically; apical system central, four genital plates, complemental plates; periproct contiguous with apical system, in deep furrow; peristome central, somewhat oblique, without branchial slits; tubercles perforate, crenulate, numerous, not in vertical series. *Jur.(Bajoc.-Raurac.),* Eu.——FIG. 517,*1*. **M. nodoti* (COTTEAU), *Raurac*., Fr.; *1a-c*, aboral, oral, lat. views, ×1 (36).

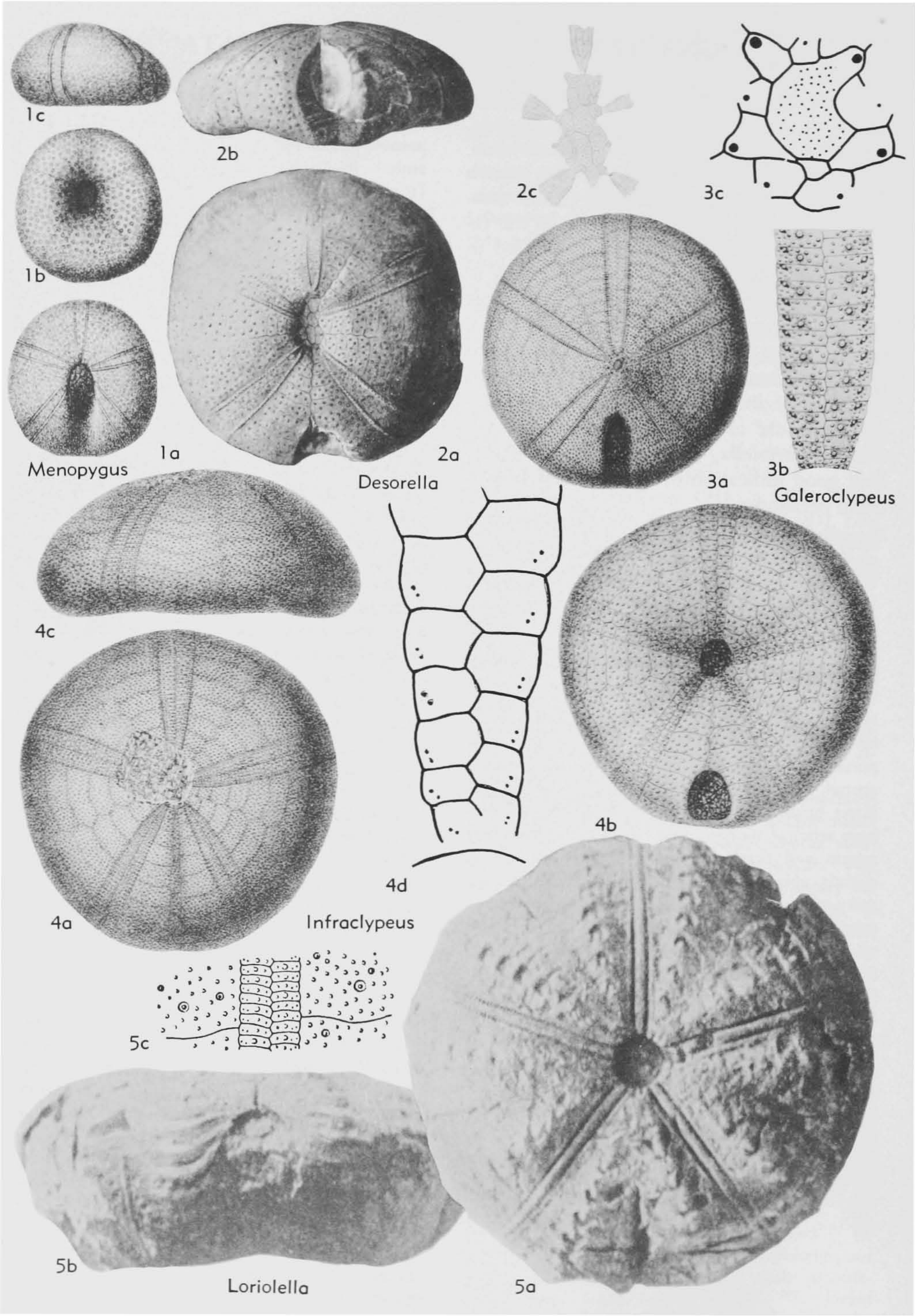



FIG. 517. Gnathostomata or Atelostomata, Order Uncertain (p. U631).

## DOUBTFUL NOMINAL GENERA OF ECHINOIDS

**Amygdala** Gray, 1825, p. 431. [Unrecognizable spatangoid.]
**Bathyspatus** Pomel, 1883, p. 39. [Unrecognizable juvenile schizasterid.]
**Brissoides** Leske, 1778, p. 29. [?Spatangoida.]
**Cardiopatagus** Pomel, 1883, p. 32. [?Spatangoida.]
**Cassis** Parkinson, 1811 (*non* Scopoli, 1877), p. 21 (see Quenstedt, 1874, p. 586). [?Spatangoida.]
**Cataproctus** Lambert, 1931, p. 147.
**Coenocentrotus** Clark, 1912, p. 348.
**Conoclypeus** Gray, 1840 *(nom. nud.)*, p. 64. [?Cassiduloida, Family Galeritidae.]
**Corystus** Pomel, 1883. [?Cassiduloida.]
**Diegocorys** Lambert & Thiéry, 1925.
**Discogalerus** Quenstedt, 1873 *(nom. nud.)*, p. 411. [Cassiduloida, ?Family Galeritidae.]
**Echinobrissus** Breynius in Pomel, 1883, p. 58.
**Echinonaus** de la Beche, 1822, p. 42 *(nom. van. pro Echinopygus* d'Orbigny, 1856).
**Insuflaster** Borchard in d'Orbigny, 1854, p. 124 [=*Insufulaster* Agassiz, 1872, p. 65 *(nom. null.)*].
**Mecostobrissus** Lambert, 1912, p. 30 [=?*Nucleolus* von Martens, 1866].
**Melobosis** Girard, 1851, p. 364 [=*Melebosis* Girard, 1851, p. 365 *(nom. null.)*].
**Mengaudia** Lambert, 1917, p. 105.
**Neopatagus** Sánchez-Roig, 1953, p. 258. [?Spatangoida.]
**Nucleolus** von Martens, 1866, p. 179.
**Oligopodia** Duncan, 1889, p. 176.
**Ova** Gray, 1825, p. 431 [=*Ovum* de Blainville, 1830, p. 184 *(nom. van.)*]. [?Spatangoida.]
**Pleraster** Quenstedt, 1874, p. 666. [?Spatangoida.]
**Proechinus** Cuénot, 1891, p. 644. [Paleozoic non-cidaroid.]
**Spatangus** Leske, 1778, p. 230 [=*Spatangites* Leske, 1778, p. 244 *(nom. van.)*]. [?Spatangoida.]
**Tingitanaster** Lambert & Thiéry, 1925, p. 603.
**Trichaelina** Barrois, 1887, p. 1. [?Echinacea.]
**Trichodiadema** Agassiz, 1863, p. 354. [?Diadematacea.]

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# HOLOTHURIANS

By Don L. Frizzell, Harriet Exline, and David L. Pawson

CONTENTS



## DEFINITION

### Class HOLOTHUROIDEA de Blainville, 1834

[*nom. transl.* Orton, 1876, p. 253 (*ex* ?order—rank unstated —Holothuroidea E. P. Wright, 1868, p. 652, *nom. correct. pro* order Holothuridea de Blainville, p. 188)] [=Fistulides Lamarck, 1801; order Cylindroïdes de Blainville, 1822; order Fistulidae Fleming, 1822; Holothurina Brandt, 1835; Scytodermata Burmeister, 1837; order Holothuriadae Forbes, 1840; order Cirrhis Vermigrada Forbes, 1841; Ascidiastella Austin & Austin, 1842; order Holothuriae Müller & Troschel, 1842; order Holothuridae Gervais in d'Orbigny, 1845; order Holothuriacea Düben & Koren, 1846; order Holothurioidea von Siebold, 1848; Holothurida Gray, 1848; Scytactinata Bronn, 1860] [Diagnosis prepared by Don L. Frizzell, Harriet Exline, & D. L. Pawson. Research on authorship and synonymy of class by H. B. Fell and J. W. Durham.]

Armless, mostly unattached echinoderms, tough leathery body wall containing strongly developed radial and longitudinal muscles, lacking articulated test; body typically cylindroid, elongated orally-aborally, mouth located at or near extremity defined as oral and encircled by ring of tentacles, which are altered podia in Recent orders but of uncertain homology in Arthrochirotida, anus at or near opposite end; ambulacral grooves represented by closed canals; podia variously disposed along ambulacra, in interambulacral areas, or lacking; single gonad, with or without external madreporite; symmetry pentameral, modified by secondary bilateral symmetry in dorsoventral plane, with bivium on dorsal side formed by *C* and *D* rays and trivium on ventral side formed by *E, A,* and *B* rays. Skeletal elements usually reduced to microscopic sclerites of varied shape and very great number, coalesced in some to form test of imbricating plates; pharynx surrounded by calcareous ring (peripharyngeal crown) composed typically of 5 radial and 5 interradial pieces, but in Apodida and Arthrochirotida commonly more than 10; articulated axial skeleton in tentacles of Arthrochirotida. [Holothurians are marine, generally benthonic invertebrates that crawl over the substrate or vegetation or burrow in sea-bottom mud; rarely they are sluggish swimmers and may be pelagic. They are found living at all depths but are most abundant in warm shallow waters. The class possibly is polyphyletic.] *?Ord., L.Dev.-Rec.*

## PHYLOGENY AND EVOLUTION OF HOLOTHUROIDS

By David L. Pawson

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### INTRODUCTION

Most echinoderms are well known as fossils, for their calcareous exoskeletons are readily preserved, but the holothuroids are poorly known in the fossil record. Very few entire holothurian fossils are known (5), and according to Madsen (1956, 1957) several Cambrian fossils discovered and described by Walcott (1911, 1918) as holothuroids should now be interpreted as coelenterates and annelids. However, more recently Lehmann (1958) and Seilacher

(1961) have described some unequivocal holothurians from Lower Devonian shales. The calcareous deposits of the body wall (sclerites) of holothuroids have been studied by micropaleontologists for at least 80 years. These skeletal elements are known to range from the Devonian (and possibly Ordovician) to the present day.

The most thorough work to date on fossil holothurian sclerites is that of Deflandre-Rigaud (1953, 1962) and Frizzell & Exline (1955). Until recently (2), no serious attempt has been made to incorporate the groups of fossil holothurian sclerites into the classification of present-day forms, despite the fact that several families and even perhaps genera appear to have become differentiated as far back as the Upper Paleozoic. At least, some Paleozoic and later sclerites so closely resemble sclerites of some extant forms that there is no reason why they cannot be classified together. For example, certain Carboniferous wheels may be interpreted as belonging to either the order Elasipodida or the order Apodida (family Chiridotidae). Lattice plates of the Middle Ordovician genus *Thuroholia* and the Devonian and later genus *Eocaudina* greatly resemble those of some extant dendrochirotacean genera. These sclerites are plates composed of a single layer of calcite, freely perforated; very similar plates form a test in certain extant holothuroids.

Morphological and other evidence points to a close relationship between holothuroids and echinoids. The primitive Ordovician echinoids *Aulechinus, Ectinechinus,* and *Eothuria* had a test composed of irregularly arranged imbricating plates, and it also seems likely that a similar test of imbricating plates occurred in early holothuroids. The discovery of the Helicoplacoidea (3) in Lower Cambrian deposits is of special importance, for these earliest known echinozoans had a fusiform body and a plated test. Unlike echinoids and holothurians, *Helicoplacus* had no regularly arranged meridional ambulacra.

Early holothurians are believed to have been plated forms. However, with the passage of time, the skeletal plates of most holothuroids have tended to become reduced, and in only a few genera is a test retained. Remarkably, all of the plated genera now extant are found in a single subclass, the Dendrochirotacea (12).

Fell (4) inferred that the ambulacral plate system of edrioasteroids is possibly homologous with the calcareous ring of holothuroids. This suggested homology is very striking in the case of the complex calcareous ring, such as is found in the genera *Placothuria, Pentadactyla,* and others (Fig. 95, *2,3,4*). Fell (4) believes that the calcareous ring has arisen as a consequence of the development of an introvert (a structure found only in the subclass Dendrochirotacea). If the holothurian calcareous ring does, in fact, represent what was once a series of ambulacral plates, this would serve to explain the absence of any evidence of external ambulacral plates in holothuroids, despite the persistence of well-developed radial water vessels and tube feet in most groups, and the origin of the complex calcareous ring. The complex type of calcareous ring, with long posterior projections, is found in only a small number of genera, and again all of these genera are members of the Dendrochirotacea. The simple type of calcareous ring, which has short posterior projections or lacks them completely, has probably undergone secondary reduction. This will be discussed below.

It is possible, then, that primitive holothuroids may have possessed both a complex calcareous ring and plates in the body wall.

## PLACOTHURIIDAE

If the assumptions made previously are correct, then the family Placothuriidae (comprising the single presently known genus *Placothuria*) includes the most primitive holothuroids living today (Fig. 92,*1*). Members of this family have a plated body and a very complex calcareous ring (11, pl. 7; 12).

## SHAPE OF TENTACLES

Throughout the class Holothuroidea the shape of the tentacles surrounding the mouth is a character employed in separating major taxa (at the subclass or order level). In the subclass Dendrochirotacea, with which we are primarily concerned here, two distinct tentacle types are recognizable. One, the dendrochirote type, is tree-shaped, usually richly branched (Fig. 518,2). The other is dactylochirote (12), that is, simple finger-shaped or digitate (Fig. 518,*1*).

So complex a structure as the dendrochirote tentacle could scarcely have arisen *de novo* without previous simpler stages. Such stages would probably be tentacles resembling relatively unmodified tube feet. Thus it seems reasonable to regard the genera with finger-like tentacles as representing an earlier grade of differentiation than those with richly branched tentacles. However, the finger-like tentacles of extant genera may well have been secondarily derived from a dendrochirote type, and it would be unwise to interpret the extant dactylochirotes as exactly matching the ancestors of the dendrochirotes.

The Placothuriidae, here regarded as the most primitive extant holothuroids, have well-branched tentacles, but it is concluded that the skeletal morphology supplies evidence in favor of the view that the placothuriids, despite their dendritic tentacles, are more archaic than any known dactylochirote family. In a revised classification of the holothuroids (12) the dendrochirotes are placed before the dactylochirotes, the tentacles of the latter group being regarded as secondarily simplified. The tentacles of molpadid and apodid holothuroids may be similarly interpreted as secondarily simplified, although no known evidence is available to support this.

## DACTYLOCHIROTE HOLOTHUROIDS

The order Dactylochirotida includes three families, Ypsilothuriidae, Vaneyellidae, and Rhopalodinidae, which share some interesting and important features. The body of all genera is invested in a test of overlapping or contiguous skeletal plates approximately 1 mm. in diameter; it is usually U-shaped, with mouth and anus directed dorsally; the calcareous ring is always simple, lacking complex posterior processes. In the Vaneyellidae, the body is relatively flexible and fusiform, but usually assumes a U-shape, whereas in the Ypsilothuriidae and Rhopalodinidae the body is rigid. In the Ypsilothuriidae the mouth and anus are placed at the ends of short "siphons," while in Rhopalodinidae the body is flask-shaped, with mouth and anus close together, at the top of the "neck."

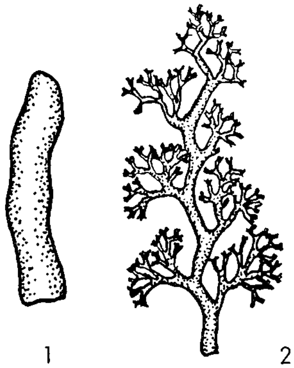

FIG. 518. Holothuroid tentacles (diagram.) (PAWSON & FELL, n).——*1.* Simple finger-like tentacle of dactylochirote.——*2.* Complexly branched tentacle of dendrochirote.

## DENDROCHIROTE HOLOTHUROIDS

The presence of large plates in the body wall is not a character restricted to the dactylochirotes; several dendrochirote taxa are also characterized by possessing large plates which form a more or less rigid test over all or part of the body. Three families, the Paracucumidae, Placothuriidae, and Psolidae, have such a test. The Paracucumidae are based on the single Antarctic genus *Paracucumis,* which has a U-shaped plated body, possesses a simple calcareous ring, and apparently lacks tube feet. The placothuriids also have a U-shaped body, and as mentioned above, have a complex calcareous ring. The Psolidae comprise specialized forms, as noted subsequently.

Apart from the taxa discussed above, the remainder of the dendrochirotes (except for some little-known species) have small, nonimbricating skeletal deposits in the body wall, although some genera (e.g., *Pseudocnus*) have a rather rigid body, owing to the presence of great numbers of these deposits.

## CALCAREOUS RING

All members of the order Dactylochirotida have a simple calcareous ring, but within the order Dendrochirotida the ring displays an extraordinary diversity in shape and size (Fig. 95,*2-8*). The work of HEDING & PANNING (1954) on the Phyllophoridae, as the family formerly was known, demonstrates admirably the variation in the calcareous ring. The subfamilies proposed by these workers are based chiefly on the structure of the ring, as also are the subfamilies proposed by PANNING (1949) in his revision of the Cucumariidae, as then known. In a revised classification of the Holothuroidea proposed elsewhere (12), the taxa employed by PANNING (1949) and HEDING & PANNING (1954) remain substantially unaltered. If tentacle numbers are disregarded, the dendrochirote subfamilies may be arranged as follows (excluding Paracucumidae, Placothuriidae, and Psolidae, discussed elsewhere in this chapter):

1. Calcareous ring complex, with paired or unpaired posterior processes composed of a mosaic of minute pieces—Thyoninae, Phyllophorinae, Semperiellinae.
2. Posterior processes entire—Sclerodactylinae, Cladolabinae.
3. Posterior processes rudimentary or lacking—Cucumariinae, Colochirinae, Thyonidiinae.

The boundary between the second and third groups is not clearly defined, and suggests a gradual evolutionary sequence.

## PSOLID HOLOTHUROIDS

Members of the peculiar family Psolidae have a body which is partly invested by plates, with a soft thin ventral sole sharply defined from the plated dorsal side of the body (Fig. 94,*1*). The body commonly is flattened and limpet-like, and psolids live firmly attached to a solid substrate by the tube feet surrounding the sole. In the genus *Psolus* no tube feet occur on the dorsal side of the body, but they are present, though rudimentary, in the related genus *Psolidium*. No psolid is known to possess a complex calcareous ring. Psolids exhibit strong bilateral symmetry, which is manifest even in young stages. Internal anatomy, however, reflects a former radial symmetry, and it is probable that the ancestor of the psolids was a radially symmetrical holothuroid. The sole has probably developed as a result of reduction of the calcareous deposits on the ventral side of the body, in response to adoption of a sedentary way of life. The psolids may be regarded as pelmatozoan holothuroids; many other dendrochirotes exhibit this tendency toward a pelmatozoan habit.

## OTHER HOLOTHURIAN GROUPS

No special attention has been directed here to other holothurian assemblages, respectively grouped in the subclass Aspidochirotacea (orders Aspidochirotida, Elasipodida) and the subclass Apodacea (orders Apodida, Molpadiida). Tentacles of the Aspidochirotacea terminate in an approximately circular disc. The body is bilaterally symmetrical, with dorsal tube feet modified into papillae or warts (Aspidochirotida) or elongate sensory processes (Elasipodida). THÉEL (1882) has conjectured on the possible antiquity of elasipod holothuroids, but concluded that they do not comprise an ancestral stock, being secondarily adapted to deep-sea life. The presence of a madreporite with external opening, not hanging free in the body cavity, is interpreted as a logical consequence of the absence of respiratory trees, rather than as a primitive feature.

Molpadiids and apodids have simple digitate or pinnate tentacles. Both usually lack tube feet entirely. It is probable that their common characters denote parallel evolution and convergence, rather than close relationship. A remarkable feature of some Apodida and Molpadiida is the presence of anchors and anchor plates in the body wall, those in one order differing morphologically from those in the other. In both groups the anchors project through the body wall, and they doubtless serve in the same way as accessory locomotor organs.

## CLASSIFICATION OF HOLOTHUROIDS

A revised classification of holothuroids is given briefly below. A formal proposal of this classification is made elsewhere (12). An attempt is made here to incorporate into the classification the fossil families diagnosed by FRIZZELL & EXLINE (5) and DEFLANDRE-RIGAUD (2). The scheme below does not differ greatly from that proposed by DEFLANDRE-RIGAUD (2). As can be seen, the two classifications can be united only when some of the fossil families are subdivided. It is hoped that in the future a classification satisfactory to both paleontologists and neontologists will emerge.

*Subclasses and Orders of Holothuroids*

Class HOLOTHUROIDEA

Subclass DENDROCHIROTACEA

Order **Dendrochirotida**: includes fossil families Calclamnidae, Priscopedatidae (part), Stichopitidae *(Binoculites)*, Schlumbergeritidae; and extant families Placothuriidae, Paracucumidae, Psolidae, Phyllophoridae, Sclerodactylidae, Cucumariidae.

Order **Dactylochirotida**: includes extant families Ypsilothuriidae, Vaneyellidae, Rhopalodinidae.

Subclass ASPIDOCHIROTACEA

Order **Aspidochirotida**: includes fossil families Stichopitidae, (except *Binoculites* and *Calcligula*), Priscopedatidae (part); and extant families Holothuriidae, Stichopodidae, Synallactidae.

Order **Elasipodida**: includes fossil families Protocaudinidae, Theeliidae *(Palaeochiridota primaeva)*; and extant families Deimatidae, Laetmogonidae, Elpidiidae, Psychropotidae, Pelagothuriidae.

Subclass APODACEA

Order **Apodida**: includes fossil families Achistridae, Synaptitidae, Calcancoridae, Theeliidae (except *Palaeochiridota primaeva*); and extant families Synaptidae, Chiridotidae, Myriotrochidae.

Order **Molpadiida:** includes fossil families Stichopitidae *(Calcligula)*, Exlinellidae; and extant families Molpadiidae, Caudinidae, Gephyrothuriidae.

Subclass and order UNCERTAIN

Fossil families Etheridgellidae, Calclyridae.

## SUMMARY

Morphological evidence offered by extant holothuroids, in conjunction with certain data on fossil forms, indicates that primitive extant forms were provided with a test made up of imbricating calcite plates, and their general structure may have approximated that of the present-day Dendrochirotacea. The initial body shape may have been cylindrical, with mouth and anus at opposite poles, but independent pelmatozoan and eleutherozoan lines probably evolved on several occasions. Internal skeletal morphology suggests that the earliest holothuroids were related in some way to edrioasteroids.

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# HOLOTHUROIDEA—FOSSIL RECORD

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## INTRODUCTION

### HISTORICAL RÉSUMÉ

Complete holothurians are known as fossils from three authenticated occurrences, two in the famous lithographic limestone of Solnhofen (Jurassic) and the other in Lower Devonian beds of Germany. Otherwise, the paleontological record of the class Holothuroidea consists of isolated sclerites, the calcareous elements of the body wall. Many workers have contributed data on fossil holothurian sclerites, but only a few contributions stand as mileposts in the advancement of knowledge of the group.

The first sclerite species was named by Münster in 1843 (32; *Synapta sieboldii*). Curiously, this specimen is the only synaptid-type anchor ever to be recorded from the Jurassic.

Critical study of fossil holothurian sclerites began with an account of British Carboniferous forms by Etheridge in 1881 (12), and of French Eocene specimens by Schlumberger in 1888 (39) and 1890 (40). Both authors described subjective assemblages, attempting to relate their taxa to the Linnean classification of Recent Holothuroidea. Schlumberger, however, at the suggestion of Théel, proposed the radical innovation of a purely artificial genus.

Attention was again focused on holothurian remains a half century later by the work of Croneis & McCormack (6). In a study of American Carboniferous sclerites, they presented a summary review and critique of classification that has strongly influenced the trends of modern micropaleontological research. Croneis later proposed the *"ordo militaris,"* a parataxonomic and non-

Linnean classificatory arrangement intended for use outside the conventional rules of zoological nomenclature, that currently is accepted by some European specialists.

FRIZZELL & EXLINE (14) published a monographic review of fossil holothurian sclerites in 1956, including a classification intended for use in the *Treatise*. Briefly, they proposed a dual arrangement: (1) a series of parataxonomic families, without ordinal implication, based on isolated sclerites; and (2) the Linnean arrangement of Recent holothurians and complete fossils. The binomina of the sclerite classification are subject to the International Code of Zoological Nomenclature. This system has been generally accepted, although with some modification and occasional rejection of its nomenclatural requirements.

The latest comprehensive taxonomic treatment of holothurian sclerites, summarizing researches carried on in France for about two decades, was published in 1961 by DEFLANDRE-RIGAUD (10). Her monograph follows the pattern of FRIZZELL & EXLINE, but within the framework of CRONEIS' "*ordo militaris*," so that marked differences in nomenclature have resulted. Moreover, some different interpretations of the morphology of sclerites have resulted in modifications of the classification.

A major advance was made by RIOULT in 1961 (37), with his detailed zonation of selected sclerite species of the Jurassic (Lias). RIOULT demonstrated that some holothurian species had remarkably short stratigraphic ranges, and that their sclerites may be used in practical biostratigraphy.

The latest development in taxonomy of sclerites is the advent of quantification. Statistical studies by HAMPTON (22,23) and CARINI (3) indicate an approach that should lead to a better understanding of holothurian microfossils and to significant improvement in the taxonomy of the group.

Currently (1965), KRISTAN-TOLLMANN is studying fossil holothurian remains in Austria, having contributed notably to knowledge of the sclerite faunas of both Triassic (30a, 30d) and Miocene (30b) age.

## STATUS OF CURRENT KNOWLEDGE

Sclerite assemblages are very incompletely known, even though the number of nominal species has doubled during the decade of 1956-65 (compare FRIZZELL & EXLINE, 14, p. 35-42). Moreover, emphasis has been given to an exceedingly limited part of the geologic column.

The fauna of the Jurassic has been relatively well described. A number of its components are large and have attracted the attention of paleontologists for a century and a quarter. Many more, especially the minute forms requiring special techniques in handling, have been described in the admirable contributions of DEFLANDRE-RIGAUD. Similarly, the conspicuous species of the Carboniferous have interested enough workers for the fauna to be moderately well recorded. Unfortunately, little has been published on the critical pre-Carboniferous occurrences, although holothurians are known to have existed during Devonian time, questionable sclerites have been reported from Ordovician strata, and assemblages of the Permotriassic have been neglected.

Post-Jurassic holothurian remains, which generally are very minute and fragile, have received scant notice. Virtually no work has been done on Cretaceous faunas and very little on those of the Cenozoic, although these assemblages are critical in relation to an overall understanding of the development of the Holothuroidea.

## NEEDED RESEARCH

Tremendous opportunities exist for basic research on fossil holothurian remains. As with most work on esoteric groups, application to the more practical aspects of biostratigraphy is contingent upon the results of purely scientific investigation. Classification and nomenclature are essential prerequisites to the recording of stratigraphic and paleoecological data, and much more information must be compiled before satisfactory conclusions may be formulated.

Probably the most rewarding investigation, in terms of new genera and species, would be research on the sclerite assemblages of Cretaceous and Cenozoic strata. A wealth of material, for example, although of inconspicuous microscopic size, may be found in the post-Paleozoic shallower-water deposits of the American Gulf and Atlantic coastal plains and coasts. No doubt the

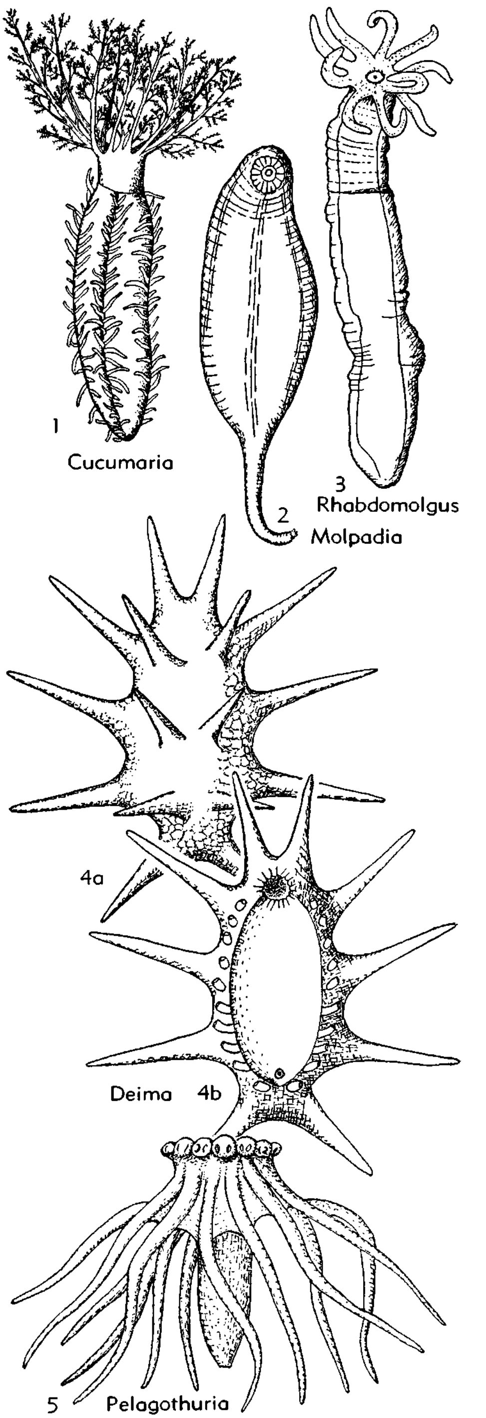


Fig. 519. Representative Recent holothurians (14, fig. 1-5).——*1. "Cucumaria" planci* (Brandt).——*2. Molpadia musculus* (Risso).——3. *Rhabdomolgus ruber* Keferstein.——*4a,b. Deima atlanticum* Hérouard.——*5. Pelagothuria natatrix* Ludwig.

same situation is to be found in marginal marine deposits of other areas.

Of even more importance in relation to problems of evolution of the Holothuroidea would be a search for unequivocal sclerites in Silurian and Ordovician strata. Specimens might be sparse or nonexistent, and their separation from embryonic spicules of other echinoderms difficult, but evidence from that part of the stratigraphic column could be critically important. Of only slightly less worth, relative to taxonomic problems, and with abundant material known to be available, would be an investigation of assemblages of the Permian.

Refinement of the sclerite classification is greatly to be desired, but it will become possible only as the gaps in knowledge of assemblages from critical stratigraphic intervals are lessened. Each new discovery, however, must have a direct bearing on the taxonomic arrangement, whether to diminish apparent discontinuities, to emphasize the separation of recognized units, or to introduce new sclerite types into the classification.

## MORPHOLOGY

### GENERAL FEATURES

In external appearance, holothurian echinoderms are elongate and typically cylindrical, reaching an adult length of 3 mm. to 5 m. (Fig. 519,*1*). The larger end of the body, containing the mouth, usually is armed with buccal tentacles, and at the other extremity is the anus. The basic symmetry is pentameral, with five longitudinal ambulacral lines extending along the body. A secondary bilateral symmetry is marked by the bivium (two ambulacra) above and the trivium (three ambulacra) below. The ambulacra typically are marked by double rows of podia, that may comprise tube feet below and tentacles above. Podia may be partly or entirely absent, however, and in some forms are distributed in the interrays. When relaxed, the body is somewhat soft, but it is hard and rigid when contracted. External plates are lacking, except in the pseudotest of certain groups, the supporting structures of the body normally consisting of the extremely numerous, microscopic, calcareous sclerites of the body wall.

Departure from the basic pattern of the

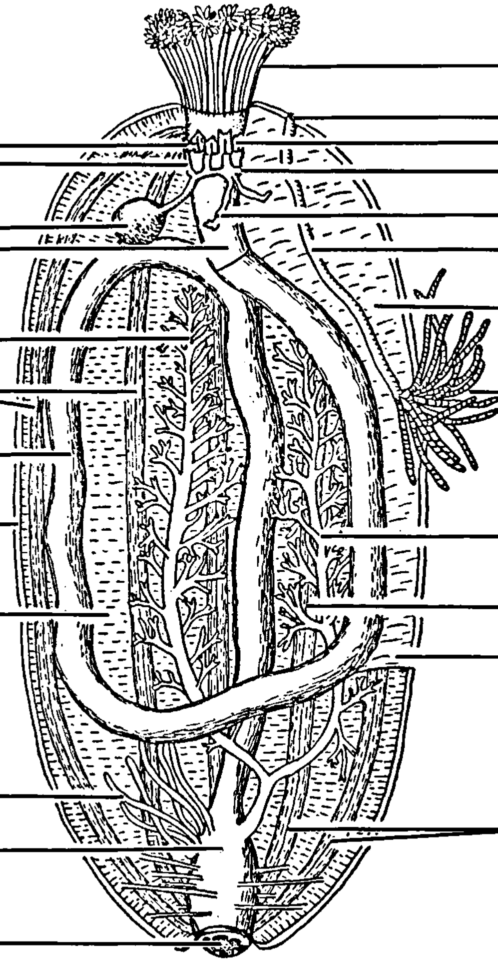


FIG. 520. Morphology of a typical holothurian (14, fig. 6, modified from Parker & Haswell, after Leuckart).

class, in various groups, is marked. Tube feet are absent in the apodous holothurians (Fig. 519,*2,3*), some of which are produced posteriorly into a tail-like appendage. Dorsoventral flattening has occurred in the elasopodidans (Fig. 519, *4a,b*) and an octopus-like tentacular development in the aberrant genus *Pelagothuria* (Fig. 519,*5*). Another developmental trend is toward curvature of the body, resulting from a habit of burrowing or of semipermanent fixation to the substratum. In the psolids, this has resulted in migration of the mouth and anus to the upper surfaces of the body. Curvature in *Rhopalodina* reached an extreme, the mouth and anus being contiguous at the end of a long neck.

Anatomical structures are illustrated in Figure 520, except for omission of the ampullae, retractor muscles, and hemal system. Of major interest to paleontologists is the body wall, in which the sclerites are embedded, and the peripharyngeal crown or calcareous ring (radial and interradial plates indicated in the diagram). The body wall consists of three elements: a leathery external cuticle or epidermis; a layer of connective tissue; and an internal muscle layer, beneath which is a thin epithelium of platy cells with vibratile cilia. The connective tissue is firm beneath the epidermis, becoming softer and more gelatinous toward the muscle layer. It contains most of the calcareous sclerites of the skeletal system.

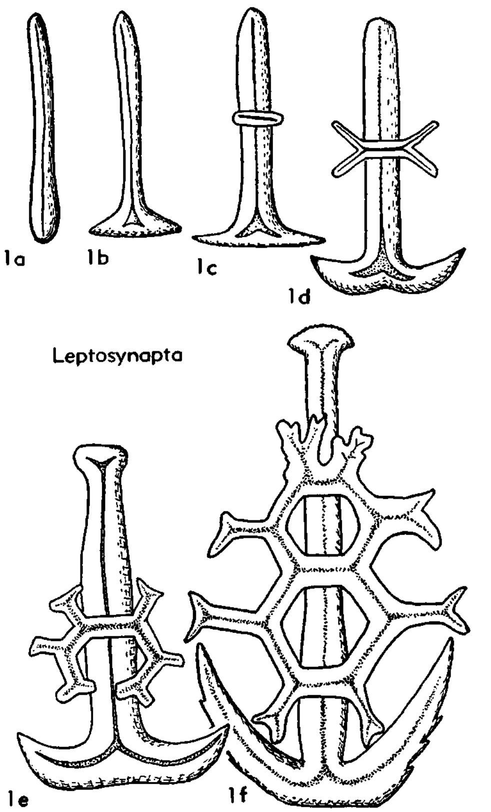


FIG. 521. Successive stages in development of anchor and anchor plate of *Leptosynapta inhaerens* (O. F. MÜLLER) (14, fig. 7a-f).

## SKELETAL ELEMENTS

The calcareous ring (peripharyngeal crown), surrounding the pharynx, typically is composed of five radial and five or more interradial plates, the number ordinarily corresponding to the number of buccal tentacles. In some forms, the cloacal opening is armed with five toothlike anal plates composed of calcium carbonate. A madreporite, also calcareous, is internal and greatly reduced in size. By far the greatest number of skeletal elements, however, is that of the sclerites; HAMPTON (20) has estimated a recovery of 20,600,000 from a single specimen of *Holothuria impatiens* (FORSKÄL).

Sclerites are calcareous bodies of diverse shape and form. They are highly modified paedomorphic structures, comparable in the adult holothurian to the larval spicules of its presumably fully plated ancestors. Nevertheless, they are of functional as well as phyletic importance. Some sclerites serve to reinforce the body wall, preventing its collapse, in extreme development even forming a protective armor. Curved rods surround the podia, overlapping to construct a flexible but semirigid appendage, and a sieve plate at the end of each tube foot supports its suction disk. In apodous forms, anchors evolved independently in the Apodida and Molpadiida. Anchors and wheels, found in other forms without tube feet, presumably function as tractional devices both for burrowing and for clinging to weeds and other surfaces of the sea bottom. A holothurian may have a single kind of sclerite or none, but an association of several types is usual.

Formation of the sclerite, except for simple rods and the minute grains known as miliary granules, typically follow a conventional pattern like that of the larval spicules of crinoids, asteroids, echinoids, and ophiuroids (HYMAN, 1955, 26). A rod is secreted, at each end of which are formed two branches at 120 degrees, the rods and arms constituting the primary cross. With additional branching and thickening, the form of a net, plate, or rosette is assumed (Fig. 521). Other sclerites, especially of the podia, are modified into simple or curved rods, or otherwise depart from the prototypical lattice-plate pattern, and growth may proceed in a plane other than that of the primary cross. Some wheels preserve the primary cross as the internal boundary of four central perforations. Others (Fig. 522) begin as a disc, continue to form a multirayed star, and later develop transverse bars that unite to make the rim of the wheel.

Each holothurian sclerite behaves optically as a single crystal of calcite, as do the plates of other echinoderms. The position of the optic axis of this crystal, as determined with a polarizing microscope, has been considered to be of taxonomic importance (SCHMIDT, 41). Typically, it is perpendicular to the plane of the primary cross (SCHMIDT's "lattice-plate rule"). Continuing growth in the initial plane leaves the optic axis normal to the plane of the sclerite, whereas departure from the initial plane results in an optic axis that is inclined to or parallel with the ultimate plane of the sclerite. Isomorphism in sclerites of relatively unrelated holothurians therefore might be shown by study with polarized light. Two exceptions to the "lattice-plate rule" have been recognized. (1) All radially symmetrical sclerites have the optic axis coincident with the main morphological axis. (2) In some sclerites, such as the "buckles" of *Holothuria,* the optic axis lies in the plane of

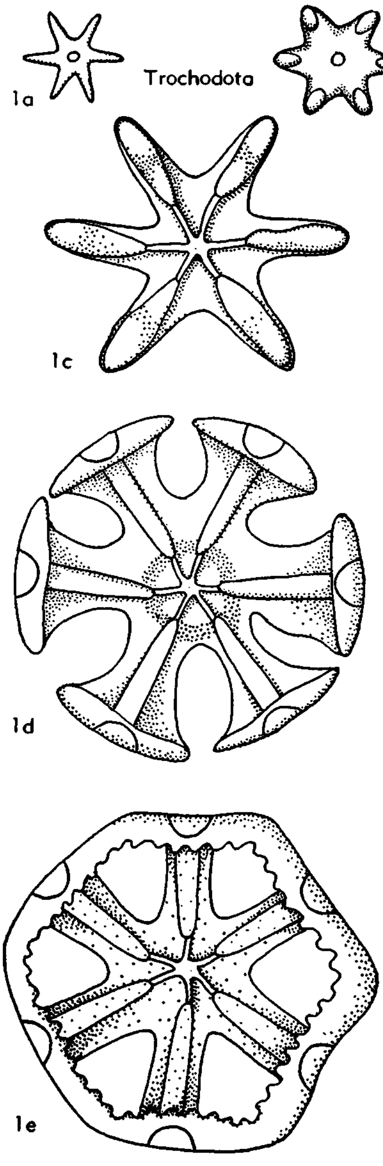


FIG. 522. Successive stages in development of *Chiridota*-type wheel, illustrated by *Trochodota venusta* (SEMON) (14, fig. 8a-e).

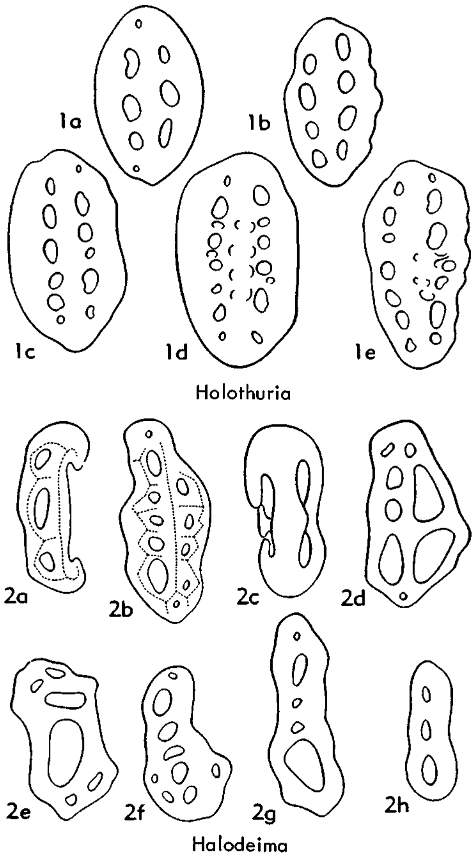


FIG. 523. Intraspecific variability of sclerites in *(1a-e) Holothuria umbrina* RÜPPELL & LEUCKART and *(2a-h) Halodeima insignis* (LUDWIG) (14, fig. 9a-e, 10a-h).

the primary cross, rather than perpendicular to it.

HAMPTON (20) analyzed chemically the sclerites of *Holothuria impatiens,* a circumtropical littoral species, finding an appreciable amount (3.36 percent) of magnesium. Earlier workers had demonstrated, in asteroid ossicles, a progressive increase in magnesium carbonate content with rise in water temperature. HAMPTON therefore suggested that among holothurians (1) the position of the optic axis may be related to concentration of magnesium in the calcite of the sclerite, and (2) the crystallographic relationship might be of ecological rather than taxonomic importance.

Variation in form follows several patterns. Differences are evident among sclerites of a single type in one individual (Fig. 523,*1,2*) and in different individuals from the same population. Similarly, differences may exist in forms from more or less widely separated geographic areas. Sclerites vary, too, with the ontogenetic development of the individual, those of dissimilar types and in various parts of the body appearing at different times. They may increase in number and size, or become scarcer and smaller.

Current trends toward quantification have resulted inevitably in statistical treatment of holothurian sclerites. HAMPTON (21) initiated statistical studies with an analysis of discoidal sclerites from the Jurassic of England. In a second paper (22), a mathematical separation was given for assemblages of plates of the Recent *Holothuria impatiens* and *Cucumaria saxicola* BRADY & ROBERTSON. Still later, HAMPTON (23) analyzed statistically a series of fossil rods from the English Jurassic, with a resultant reduction of five nominal "species" to a single specific-level taxon. CARINI (3) presented an analysis of wheels from the Middle Pennsylvanian of Oklahoma, demonstrating at once a wide range in variation of number of spokes (6-10) and a very marked consistency in occurrence of the modal number (8). These studies, although of unquestioned importance, offer some reassurance to workers of nonmathematical bent. Quantification gives the apparent objectivity of numerical expression of variability, but the systematic results differ very little from those of conventional taxonomy.

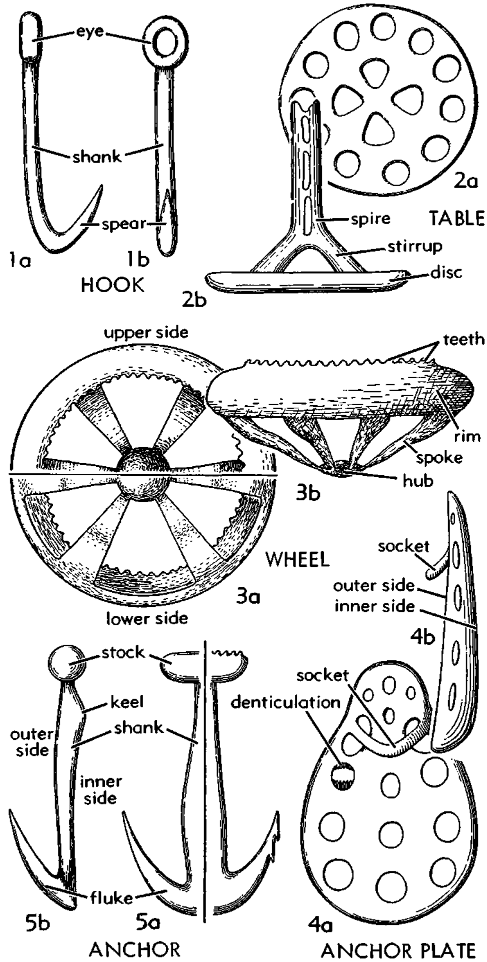


FIG. 524. Terminology of holothurian sclerites (14, fig. 17-21).

## TERMINOLOGY OF SCLERITES

Conventionally and for sake of simplicity, holothurian sclerites are designated by the names of common objects which they resemble (e.g., hooks, anchors, wheels, tables, baskets, spectacles, rods, racquets, ladles, discs, plates, rosettes). In general, morphological terms are either self-explanatory or defined in the following glossary. Illustrations are considered necessary only for hooks (Fig. 524,*1a,b*), tables (Fig. 524,*2a,b*), wheels (Fig. 524,*3a,b*), anchor plates (Fig. 524,*4a, b*), and anchors (Fig. 524,*5a,b*).

### *Glossary of Morphological Terms Applied to Holothurians*

**anchor.** Sclerite in shape of anchor; synaptid-type with stock, shank, and 2 or 3 flukes; molpadiid-type lacking stock.

**anchor plate.** Perforate plate, oval, concavo-convex or flat, typically with socket at narrow end; socket may be single or double, extending across plate or restricted to one or both lateral margins; holes typically denticulate.

**bilaminar.** Composed of 2 recognizable layers.

**C-rod.** Curved rod, usually not branching.

**crossbar.** Bar crossing eye of hook; also +-shaped division at center of disc in table.

**disc.** Tabular component of table; also discoidal sclerite (typically imperforate).

**eye.** Ringlike part of hook, in some partly closed by one or more crossbars; also may occur at end of rod.

**fluke.** Recurved component of anchor; 2 or 3 in synaptid-type, only 2 in molapadiid-type; may be denticulate.

**hook.** Sclerite in form of common hook used in angling; with eye, shank, and spear.

**hub.** Cylindrical or hemispherical projection on central portion of wheel; usually on lower surface of sclerite, but may be on upper surface or both.

*ladle. See* racquet.

**lyre.** Sclerite consisting of central shaft, short neck, and 2 marginal arms that join shaft at base and below neck.

**molpadiid type.** Referring to sclerites of Recent family Molpadiidae; specifically, racquets and stockless anchors.

**pillars.** Tiny rodlike structures, making up spire or connecting discrete layers; larger and straighter than trabeculae.

**plate.** Tabular to concave perforate sclerite of variable shape; usually single layer, although bilaminar and multilayered plates occur; socket and stirrup absent, and holes never denticulate.

**pseudospire.** Spinelike projection from center of discoidal sclerite.

**racquet.** Straight or slightly arched rod with discoidal or elliptical flattened expansion (usually perforate) at one end (alternatively spoon or ladle).

**rim.** Outer component of wheel; may be recurved; usually flangelike, but may be circular in cross section; inclined to plane of wheel or within it; inner margin of upper side typically denticulate or dentate.

**rod.** Elongate sclerite, circular in cross section, with one or more axes.

**shank.** In hook, part connecting eye and spear; in anchor, connection between flukes and (where present) stock.

**sieve plate.** Circular, subcircular, or polygonal perforate plate, unilaminar.

**socket.** Straplike bar or complex structure at small end of anchor plate.

**spear.** Recurved part of hook.

**spire.** Rodlike component of table (alternatively turret).

**spoke.** Radial component of wheel, connecting central portion and rim.

*spoon. See* racquet.

**stirrup.** Stirrup-shaped component of table; usually connecting disc and spire; attached to disc by 2, 3, or 4 feet.

**stock.** Terminal bar of synaptid-type anchor, at 90 degrees to shank; of varying shape, may be finely denticulate.

**synaptid type.** Referring to sclerites of Recent family Synaptidae; specifically, anchor plates and stocked anchors.

**table.** Sclerite consisting of disc with central spire at 90 degrees to plane of disc; spire and disc usually connected by stirrup with 2, 3, or 4 feet; spire may be reduced or obsolete.

**tetraradiate rod.** Rod with 4 branches in one plane; some with 5th branch at 90 degrees to major plane.

**trabeculae.** Tiny rodlike connections between layers of sclerite; smaller and less regular than pillars.

*turret. See* spire.

**turriform.** Tower-like; specifically referring to spire and disc of table.

**wheel.** Sclerite in form of vehicular wheel, with hub (usually on lower surface), spokes (typically flat), and rim; rim usually recurved, commonly denticulate on inner margin of upper side; central portion perforate, with indented markings, or solid and smooth.

## COMPLETE FOSSILS

Entire individual holothurians are among the rarest of fossil invertebrates, only three species being known: *Palaeocucumaria hunsrueckiana* LEHMANN, from the Lower Devonian of Germany; and *Protholothuria armata* GIEBEL and *Pseudocaudina brachyura* BROILI, both from the Jurassic Solnhofen Limestone of Germany. Numerous other fossils have been incorrectly referred to the Holothurioidea (FRIZZELL & EXLINE, 14, p. 30-35; SEILACHER, 42).

Because of their actual or potential bearing on the over-all taxonomy of the class, illustrations and diagnoses of these taxa are included here.

## Order ARTHROCHIROTIDA Seilacher, 1961

[*nom. correct.* FRIZZELL & EXLINE, herein (*pro* Arthrochirota SEILACHER, 1961)]

Holothurians with articulated axial skeleton in their tentacles; sclerites stout and imperforate. *L.Dev.*

The order is known with certainty only in the Devonian, although the evidence of isolated sclerites indicates that it may have ranged as high as the Jurassic. The articulated axial skeleton of the tentacles is unlike any structure known in Recent holothurians.

### Family PALAEOCUCUMARIIDAE Frizzell & Exline, new family

Characters at present coextensive with those of order, genus, and species. *L.Dev.*

**Palaeocucumaria** LEHMANN, 1958, p. 85 [**P. hunsrueckiana*; OD]. Characters coextensive with those of type-species, consisting of small holothurians (body length, without tentacles, *ca.* 20-50 mm.;

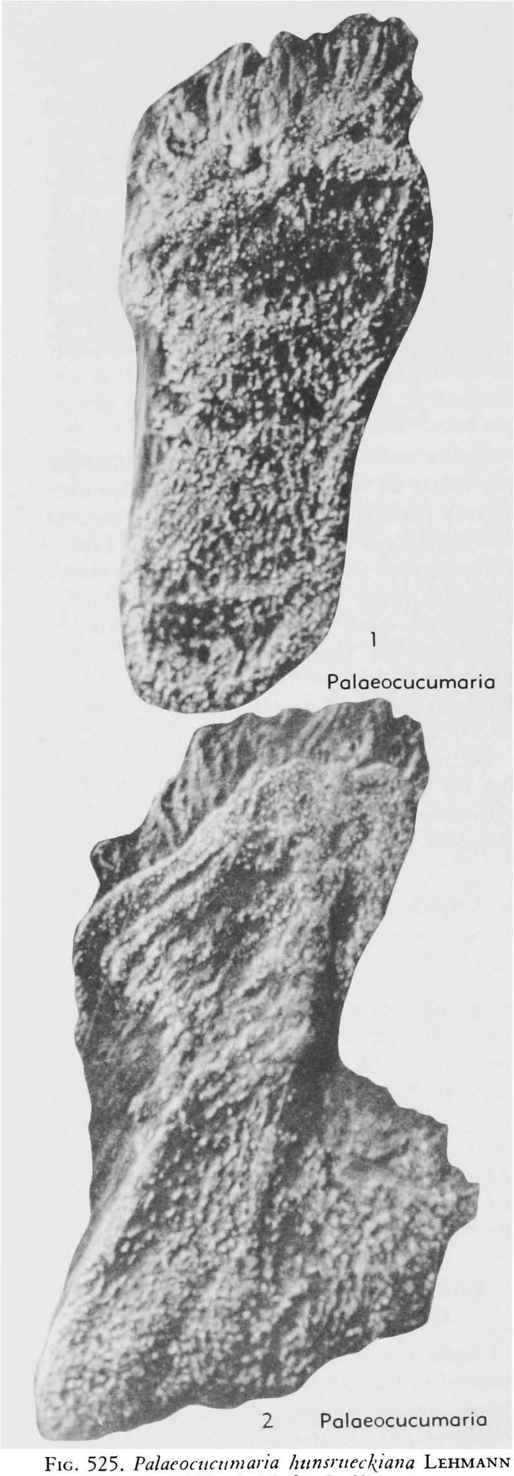


FIG. 525. *Palaeocucumaria hunsrueckiana* LEHMANN (42, pl. 10, fig. 2a,3).

width, 6-18 mm.) without distinctly set-off ambulacral areas; sclerites of body wall to 0.3 mm. diameter, imperforate, in posterior half of body produced into short spines; widened anterior end bearing numerous (*ca.* 20) unbranched tentacles, each with calcareous articulated axial skeleton; calcareous ring of 5 radials and 10 (or more?) interradials (42, p. 67). *L.Dev.,* Eu.(Ger.).——FIG. 525,*1,2*. **P. hunsrueckiana*; *1,2,* flattened specimens showing spinose sclerites of body wall and unbranched tentacles, ×2.5, ×4 (42). [*non Palaeocucumaria* FRENTZEN, 1964.]

## ?Order ASPIDOCHIROTIDA Brandt, 1835

Body bilaterally symmetrical, dorsal tube feet modified into papillae or warts. *Carb.-Rec.* (sclerites); *Jur.-Rec.* (complete remains).

### Family HOLOTHURIIDAE Ludwig, 1894

Represented by complete and dissociated remains. *Jur.-Rec.*

**Protholothuria** GIEBEL, 1857, p. 388 [**P. armata*; SD FRIZZELL & EXLINE, herein]. Characters coextensive with those of type-species, described as "cylindrical, moderately thick, tapering near ends, dimensions not given; exterior set with tiny (0.5 mm. and less in length) calcareous bodies; calcareous bodies of exterior cylindrical and 4-sided prisms, occasionally with one end strongly thickened, unlike all sclerites described from Jurassic; body lacking tentacles and without trace of longitudinal muscles" (14, p. 31). [The peculiar calcareous bodies of the exterior (sclerites?) suggest that the species might belong to the Arthrochirotida, but owing to lack of the tentacles of GIEBEL's specimen, it is impossible to confirm or reject this conclusion. *Protholothuria annulata* GIEBEL is eliminated from the genus because it is considered to be a sipunculoid worm.] *Jur.,* Eu.(Ger.).——FIG. 526,*1*. **P. armata;* whole specimen, ×1 (47).

## Order DENDROCHIROTIDA Brandt, 1835

Represented by dissociated sclerites of several families but not by complete fossil remains of any species. *Ord.-Rec.*

## Order APODIDA Brandt, 1835

Represented by dissociated sclerites of several families but by complete fossils only by *Pseudocaudina*. *Carb.-Rec.*

## Family SYNAPTIDAE Burmeister, 1837

**Pseudocaudina** Broili, 1926, p. 348 [**P. brachyura*; OD] [*non* Heding, 1932]. Characters coextensive with those of type-species. "Body in shape of a short club, widest near anterior end, posterior one-third attenuated; length, *ca.* 13.0 cm., maximum diameter 5.2 cm., diameter at anterior end, 2.6 cm., diameter of posterior portion, 2.0 cm.; tentacles absent and viscera not preserved; skin without sclerites (presumably not preserved)" (14, p. 32). *Jur.*, Eu.(Ger.).——Fig. 526,2. **P. brachyura*; entire specimen, ×1 (45).

# PALEONTOLOGY OF HOLOTHURIAN SCLERITES

## CLASSIFICATION

The philosophy and practice of taxonomy, as applied to holothurian remains, have been discussed at length in recent publications (Frizzell & Exline, 14; Deflandre-Rigaud, 10). Frizzell & Exline proposed a dual classification of fossil Holothuroidea for use in the *Treatise,* namely, (1) entire specimens placed within the Linnean hierarchy, and (2) isolated sclerites arranged within an objective, but almost completely artificial familial arrangement that is independent of ordinal categories. Both series were accepted as subject to the *International Code of Zoological Nomenclature.* Deflandre-Rigaud accepted the sclerite families of Frizzell & Exline, adding several others and numerous genera and species. Her multiple classification, however, exceeds the duality of earlier arrangements, including (1) the arrangement of discrete sclerites, specifically excluded from the requirements of the *Code;* (2) a set of "taxa," composed of subjective assemblages of dissimilar sclerites, subject to the *International Code;* and (3) inclusion of both "taxa" and "parataxa" within the orders of the zoological classification (complete fossil holothurians being ignored). Current workers are divided between adherence to the Frizzell & Exline scheme and that of Deflandre-Rigaud.

The present classification of sclerites is that of Frizzell & Exline, with some additions and inclusion of modifications by De-


Fig. 526. Holothurians.——*1. Protholothuria armata* Giebel, Jur., Ger. (47, pl. 6, fig. 2).——*2. Pseudocaudina brachyura* Broili, Jur., Ger. (45).

FLANDRE-RIGAUD. Subjective assemblages ("taxa" of DEFLANDRE-RIGAUD) are ignored as being over-speculative. Some differences in interpretation of sclerite morphology are to be found in our arrangement, as opposed to that of DEFLANDRE-RIGAUD. In general, however, the divergence is a matter of nomenclature rather than basic taxonomy.

## NOMENCLATURE

Stability and uniformity are the objectives of zoological nomenclature. To realize them, we treat all binomina of the holothurian classification according to the *International Code of Zoological Nomenclature,* regardless of the intention of the authors of those names. The classificatory arrangement of sclerite types obviously is parataxonomic. To understand it, however, demands the consistent application of names under a generally accepted set of rules.

We adopt the following nomenclatural principles in dealing with all taxa based wholly or in part on fossil sclerites. That confusion is inherent in deviation from these principles is indicated in the synonymic entries of the section on Systematic Descriptions, below.

(1) All binominal names that have been validly proposed are accepted, *subject to the principle of priority,* whether considered by their authors to be taxa or parataxa.

(2) Familial names must be based upon type-genera and formulated in the conventional manner.

(3) Type-specimens and type-species are inviolate. They may not be changed because of revised concepts for the taxa based upon them.

(4) Names applied to subjective assemblages are nomenclaturally coequal with those used for isolated sclerites. The rules for homonymy, synonymy, and priority apply to both schemes of classification, and a taxon cannot be recognized simultaneously as a single sclerite type and as a component of an assemblage.

## EVOLUTIONARY TRENDS

Development of holothurians involved structures of the anatomy to a much greater extent than the calcareous elements of the integument. Because of the extreme rarity of complete holothurian fossils, the trends of evolution remain largely a matter for speculation. Limited conclusions, however, may be drawn from the morphological and developmental features of the sclerites.

Except for the miliary granules, the least complex sclerites are the rod, from which the primary cross is formed, and the disc that precedes certain wheels. The primary cross develops into various buckles, plates, and quadriperforate wheels. Plates, in turn, precede tables and buttons, and are modified by straps and sockets into such complex sclerites as the synaptid-type anchor plate. From unilaminar plates arise those that are multilaminar. The structural development of complicated sclerites from the basic cross is inherent in ontogenetic development and presumably is of phylogenetic significance as well.

Some progressive evolutionary trends are evident within restricted lineages. In the wheels of the Protocaudinidae, the central perforations of *Protocaudina* (Fig. 527,*1*) of the Devonian to Pennsylvanian are open. Those of its Permian to Triassic descendent *Microantyx* (Fig. 527,*2*) are closed. Hooks of the Achistridae show two developmental sequences: the eye of *Achistrum* (Fig. 527,*3*) is predominantly simple in earlier species (Mississippian), becoming progressively crossbarred or irregular in later forms (Jur.-Cret.). *Aduncrum* (Fig. 527,*4*), known from Triassic and Jurassic strata, shows an apparently discontinuous change of the position of the eye, that structure lying in the plane of the spear rather than at 90 degrees to it.

Convergence must have played a major role in evolution of the sclerite, but in general it cannot be evaluated from the evidence of fossils. Plates, rods, tables, and other types owe their similarity to an essential developmental feature in common, origin from the primary cross. In some examples, however, convergence can be recognized. The molpadiid-type anchor (Fig. 527,*5*), lacking a stock and supported by a group of ladles rather than a plate (as visible, of course, only in Recent individuals), is an obvious analogue of the synaptid-type anchor (Fig. 527,*6,7*) that is complete with stock and is supported by an anchor plate (plates of the Synaptitidae). In another example of convergence, the quadriperforate wheel of the

*Protocaudina-Microantyx* lineage (Fig. 527, *1,2*) is superficially like the generically unnamed wheel of *"Protocaudina" mortenseni* (Fig. 527,*1d*). The latter, however, lacks the expanded rim of *Protocaudina* and has, in addition, a stirrup that has not been found in sclerites of that genus. Convergence, again, resulted from modification of the primary cross in different lineages.

Evolutionary progression, in another important instance, is shown by the ontogeny of living holothurians: In the Synaptidae of the Apodida, *Chiridota*-like wheels are formed during the auricularia larval stage, later being replaced by the typical anchors and anchor plates of the adult. The phylogenetic importance of this sequence is supported by the data of chronogenesis: chiridotid-type wheels are known from the Pennsylvanian (genus *Thallatocanthus*), whereas the earliest record of synaptid-type sclerites is from the Jurassic. Similarly, the fully-plated larva of *Cucumaria chronhjelmi* Théel (Fig 528,*1,2*) may be taken as evidence for the existence of an as yet unsubstantiated ancestral plated holothurian, probably pre-Devonian and perhaps as early as the Ordovician.

## PALEOECOLOGY

Holothurians live in all seas and at all depths, only seldom entering water of lowered salinity, and it may be inferred that ancient forms had a similar distribution. They are most abundant in shallow tropical waters, becoming much rarer in polar seas. Their ubiquity, however, did not result in preservation of holothurian remains at all depths, and in deeper water were immediately dissolved upon disintegration of their containing tissues.

Geologically, the major importance of the class may have been in working over the sediments of the sea floor, with the resultant destruction of initial stratification. As an example, it has been estimated that aspidochirotidan holothurians, in an area of 1.7 square miles in a sound in the Bermuda region, pass from 500 to 1,000 tons of sand through their bodies each year (Crozier, 1918, according to Hyman, 26, p. 212).

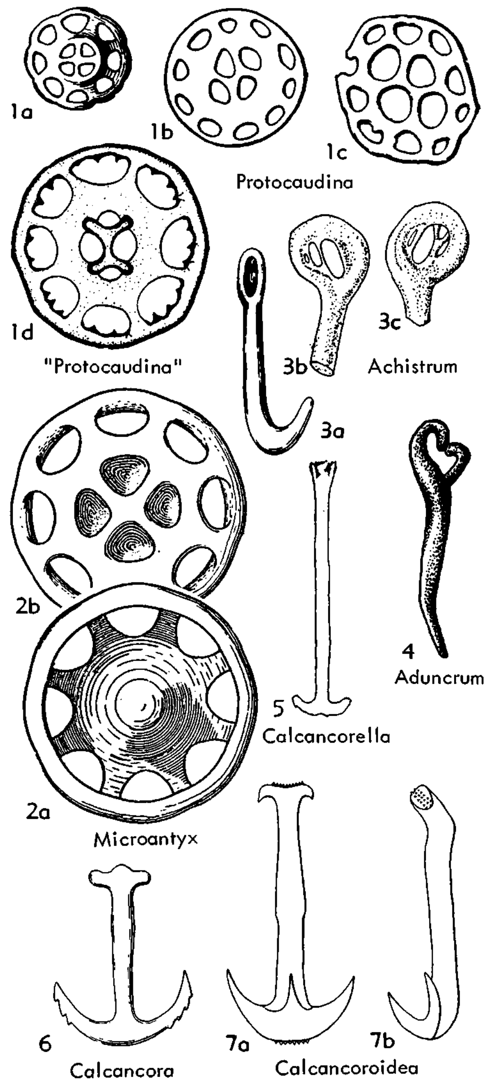


Fig. 527. Morphological features of holothurian sclerites (various sources).

Brief accounts of the paleoecology of holothurians have been published by Frizzell & Exline (15) and of their ecology by Deichmann (11) and incidentally by Bruun (2) and Dales (7). Frizzell and Exline have given an extended account of holothurian paleoecology (14, p. 42-45) and ecology (14, p. 22-30), and Hyman (26, especially p. 207-218) has included a great deal of important ecological data.

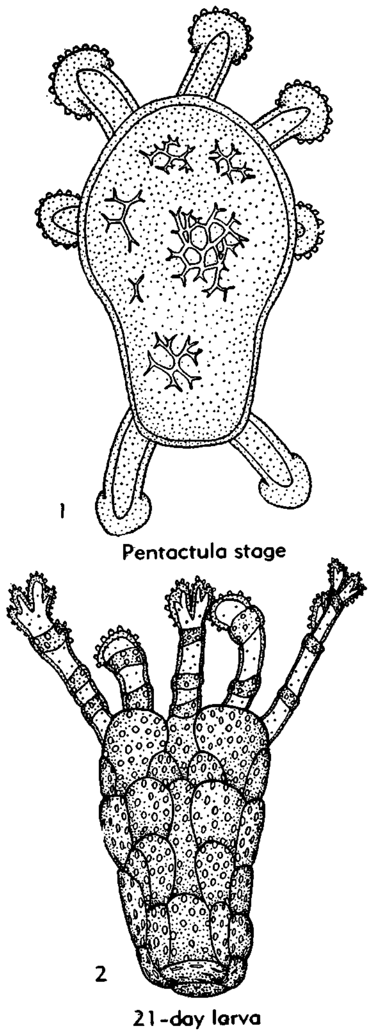


FIG. 528. Larval stages (*Cucumaria chronhjelmi* THÉEL) (14, fig. 15-16).——*1. Pentactula.*——*2.* 21-day larva.

## STRATIGRAPHIC DISTRIBUTION

The presence of holothurian remains in Ordovician rocks is not yet certain, although additional evidence has recently been recorded (RESO & WEGNER, 34). Unequivocal holothurian sclerites first occur in the Devonian, but few of that age have received taxonomic treatment. Rapid evolution seems to have occurred during the Carboniferous and Jurassic Periods. That conclusion, however, may reflect only the greater amount of research that has been applied to the sclerites of those times.

In general, these microfossils are less suited to the needs of the biostratigrapher than to those of the paleozoologist. Their typical minuteness, fragility, and ecological restriction limit considerably their usefulness. RIOULT (37), however, found that the larger sclerites of the Jurassic have practical correlative value, and he zoned the Upper Triassic-Lias (Rhaetian to Toarcian stages) on the basis of 28 holothurian species.

The geographic ranges of extinct holothurians are largely a matter for speculation, as sufficient evidence for their establishment has not yet become available. Restriction to broad paleozoogeographic provinces may be postulated, however, with varying lateral extent and ecological tolerance. Known examples of trans-Atlantic distribution are: *Protocaudina traquairii* (ETHERIDGE), in the Lower and Upper Carboniferous of Scotland and Mississippian to Permian of the central United States; *Eocaudina gutschicki* FRIZZELL & EXLINE and *E. mccormacki* FRIZZELL & EXLINE, in the Lower Carboniferous of Scotland and Pennsylvanian of Texas; and *Rigaudites cuvillieri* (DEFLANDRE-RIGAUD), in the Paleocene of the southern United States and Eocene (Cuisian) of France.

The nominal taxa of sclerites, in stratigraphic order, are summarized below.

### *Stratigraphic Occurrence of Holothurian Sclerites*

PALEOZOIC
- ORDOVICIAN
  - Calclamnidae
    - *Thuroholia cribriformis* GUTSCHICK
    - *T. crinerensis* RESO & WEGNER
    - *T. croneisi* GUTSCHICK
    - *T. overbrookensis* RESO & WEGNER
    - Other sclerites of possibly holothurian origin, reported by RESO & WEGNER (34), have been compared with those of *Mortensenites* and *Binoculites*. Their occurrence reinforces interpretation of the sieve plates of *Thuroholia* as holothurian remains.
- DEVONIAN
  - Calclamnidae
    - *Eocaudina bohemica* (PRANTL)
    - *E. septaforaminalis* MARTIN
  - Etheridgellidae
    - *Palaeocucumaria hunsrueckiana* LEHMANN
    - *Palaeocucumaria hunsrueckiana*, based upon a complete fossil, is included in this list because

its sclerites if found alone would be referred without question to the Etheridgellidae. More typical sclerites, as yet undescribed (1), include ". . . sieve plates, wheels, needles, and a multiradiate sclerite."

Protocaudinidae
*Protocaudina hexagonaria* MARTIN

CARBONIFEROUS (undifferentiated)
Stichopitidae
*Tetravirga etheridgei* FRIZZELL & EXLINE
*T. fordelensis* FRIZZELL & EXLINE
Calclamnidae
*Eocaudina gutschicki* FRIZZELL & EXLINE
*E. mccormacki* FRIZZELL & EXLINE
*E. scotica* FRIZZELL & EXLINE
Achistridae
*Achistrum nicholsoni* ETHERIDGE
Protocaudinidae
*Protocaudina traquairii* (ETHERIDGE)
Paleochiridotidae
*Paleochiridota primaeva* (ETHERIDGE)
*P. robertsoni* (ETHERIDGE)

MISSISSIPPIAN
Stichopitidae
*Parvispina spinosa* (FRIZZELL & EXLINE)
*Tetravirga curta* FRIZZELL & EXLINE
*Uncinulina angulata* FRIZZELL & EXLINE
*U. arcuata* (DEFLANDRE-RIGAUD)
Calclamnidae
*Eocaudina cribellum* FRIZZELL & EXLINE
*E. cribrum* FRIZZELL & EXLINE
*E. elongata* FRIZZELL & EXLINE
*E. marginata* (LANGENHEIM & EPIS)
*E. mccormacki* FRIZZELL & EXLINE
*E. spicata* (GUTSCHICK)
Achistridae
*Achistrum breve* GUTSCHICK
*A. frizzelli* LANGENHEIM & EPIS
*A. ludwigi* CRONEIS
*A. nicholsoni* ETHERIDGE
Protocaudinidae
*Microantyx botoni* GUTSCHICK
*Protocaudina hannai* CRONEIS
*P. traquairii* (ETHERIDGE)
Paleochiridotidae
*Paleochiridota plummerae* CRONEIS
*Rota campbelli* GUTSCHICK
*R. martini* LANGENHEIM & EPIS

PENNSYLVANIAN
Stichopitidae
*Tetravirga imperforata* FRIZZELL & EXLINE
Calclamnidae
*Eocaudina floydensis* SUMMERSON & CAMPBELL
*E. gutschicki* FRIZZELL & EXLINE
*E. irregularis* SUMMERSON & CAMPBELL
*E. mccormacki* FRIZZELL & EXLINE
*E. wanlessi* SUMMERSON & CAMPBELL
*Petropegia radiata* SUMMERSON & CAMPBELL
*P. spinosa* SUMMERSON & CAMPBELL
Etheridgellidae
*Etheridgella biconvexa* SUMMERSON & CAMPBELL
*E. porosa* CRONEIS
Achistridae
*Achistrum brownwoodense* CRONEIS
*A. ludwigi* CRONEIS
Theeliidae
*Thallatocanthus consonus* CARINI
*Theelia? hexaneme* SUMMERSON & CAMPBELL
Protocaudinidae
*Protocaudina kansasensis* (HANNA)
*P. traquairii* (ETHERIDGE)
Paleochiridotidae
*Paleochiridota plummerae* CRONEIS

PERMIAN
Stichopitidae
*Parvispina harpago* KORNICKER & IMBRIE
*Uncinulina lunata* KORNICKER & IMBRIE
Achistridae
*Achistrum brownwoodense* CRONEIS
*A. permianum* (SPANDEL)
Theeliidae
*Protheelia geinitziana* (SPANDEL)
Protocaudinidae
*Microantyx permiana* KORNICKER & IMBRIE
*Protocaudina kansasensis* (HANNA)
*P. traquairii* (ETHERIDGE)

MESOZOIC

TRIASSIC
Stichopitidae
*Rhabdotites rectus* FRIZZELL & EXLINE
Calclamnidae
*Calclamnoidea canalifera* KRISTAN-TOLLMANN
*Eocaudina cassianensis* FRIZZELL & EXLINE
*E.? circumvallata* KRISTAN-TOLLMANN
*E. eurymarginata* KRISTAN-TOLLMANN
*E. grandis* KRISTAN-TOLLMANN
*E. guembeli* FRIZZELL & EXLINE
*E. hexagona* KRISTAN-TOLLMANN
*E. trema* KRISTAN-TOLLMANN
*Fissobractites subsymmetricus* KRISTAN-TOLLMANN
*Mortensenites insolitus* KRISTAN-TOLLMANN
Achistridae
*Aduncrum triassicum* (FRIZZELL & EXLINE)
Theeliidae
*Acanthotheelia rhaetica* KRISTAN-TOLLMANN
*A. spinosa* FRIZZELL & EXLINE
*Theelia agariciformis* KRISTAN-TOLLMANN
*T. guembeli* KRISTAN-TOLLMANN
*T. petasiformis* KRISTAN-TOLLMANN
*T. pralongiae* KRISTAN-TOLLMANN
*T. rosetta* KRISTAN-TOLLMANN
*T. tubercula* KRISTAN-TOLLMANN
Protocaudinidae
*Microantyx antyx* (KRISTAN-TOLLMANN)
Kaliobullitidae
*Kaliobullites umbo* KRISTAN-TOLLMANN

JURASSIC
Stichopitidae

*Binoculites irregularis* FRIZZELL & EXLINE
*B. jurassicus* (SAID & BARAKAT)
*B. perforatus* FRIZZELL & EXLINE
*B. terquemi* FRIZZELL & EXLINE
*Calcligula? ficta* DEFLANDRE-RIGAUD
*C.? jurassica* FRIZZELL & EXLINE
*C. perforata* FRIZZELL & EXLINE
*Cucumarites feifeli* (MORTENSEN)
*Cu. solidus* (DEFLANDRE-RIGAUD)
*Ornaticannula bonheurei* DEFLANDRE-RIGAUD
*O. micralcyonarites* DEFLANDRE-RIGAUD
*O. tesseyrei* DEFLANDRE-RIGAUD
*Rhabdotites dorsetensis* HODSON, HARRIS & LAWSON
*R. mortenseni* DEFLANDRE-RIGAUD
*Stichopites mortenseni* DEFLANDRE-RIGAUD
*Uncinulina polymorpha* TERQUEM
*U. subrecta* FRIZZELL & EXLINE
*U. terquemi* FRIZZELL & EXLINE

Calclamnidae
*Calclamna germanica* FRIZZELL & EXLINE
*Calclamnella elliptica* (DEFLANDRE-RIGAUD)
*C. fragosa* DEFLANDRE-RIGAUD
*C. jurassica* FRIZZELL & EXLINE
*C. robusta* DEFLANDRE-RIGAUD
*C. transversa* DEFLANDRE-RIGAUD
*Calclamnoidea angulata* (DEFLANDRE-RIGAUD)
*C. collaris* (DEFLANDRE-RIGAUD)
*C. irregularis* FRIZZELL & EXLINE
*C. perforata* (FRENTZEN)
*C. proteus* (MORTENSEN)
*Costigerites piveteaui* DEFLANDRE-RIGAUD
*Eocaudina ambigua* (DEFLANDRE-RIGAUD)
*E. compacta* (DEFLANDRE-RIGAUD)
*E. dentata* (DEFLANDRE-RIGAUD)
*E. dentigera* (DEFLANDRE-RIGAUD)
*E. diplococcus* (DEFLANDRE-RIGAUD)
*E. diversimeata* (DEFLANDRE-RIGAUD)
*E. heteropora* (DEFLANDRE-RIGAUD)
*E. inflata* (DEFLANDRE-RIGAUD)
*E. micropora* (DEFLANDRE-RIGAUD)
*E. mortenseni* FRIZZELL & EXLINE
*E. nigrivaccae* (DEFLANDRE-RIGAUD)
*E. pauciperforata* (DEFLANDRE-RIGAUD)
*E. punctifera* (DEFLANDRE-RIGAUD)
*E. radiata* (DEFLANDRE-RIGAUD)
*E. robusta* (DEFLANDRE-RIGAUD)
*E. sparsispinosa* (DEFLANDRE-RIGAUD)
*E. squamma* (DEFLANDRE-RIGAUD)
*E. undata* (DEFLANDRE-RIGAUD)
*Mortensenites circularis* FRIZZELL & EXLINE
*M. cuneus* FRIZZELL & EXLINE
*M.? elongatus* DEFLANDRE-RIGAUD
*M. liasicus* (TERQUEM)
*Paracucumarites? anceps* DEFLANDRE-RIGAUD
*P. hamptoni* DEFLANDRE-RIGAUD
*P. porosa* DEFLANDRE-RIGAUD
*Parvioctoidus spinosus* DEFLANDRE-RIGAUD

Etheridgellidae
*Frizzellus irregularis* HAMPTON

Achistridae
*Achistrum bartensteini* FRIZZELL & EXLINE
*A. bathonianum* FRIZZELL & EXLINE
*A. bichordatum* FLETCHER
*A. gamma* HODSON, HARRIS & LAWSON
*A. issleri* CRONEIS
*A. monochordatum* HODSON, HARRIS & LAWSON
*A. trichordatum* FLETCHER
*Aduncrum cordatum* (HAMPTON)
*Ad.? pilgrimi* (FLETCHER)

Priscopedatidae
*Priscopedatus aegyptiacus* SAID & BARAKAT
*P. affinis* DEFLANDRE-RIGAUD
*P. apertus* DEFLANDRE-RIGAUD
*P. asymmetricus* DEFLANDRE-RIGAUD
*P. crux* DEFLANDRE-RIGAUD
*"P." exlineae* SAID & BARAKAT
*P.? frizzelli* SAID & BARAKAT
*P. guyaderi* RIOULT
*P. heteroporus* DEFLANDRE-RIGAUD
*P. hystrix* DEFLANDRE-RIGAUD
*P. normannus* DEFLANDRE-RIGAUD
*P. plenus* DEFLANDRE-RIGAUD
*P. pseudaffinis* DEFLANDRE-RIGAUD
*P. spectabilis* DEFLANDRE-RIGAUD
*P. spinifer* DEFLANDRE-RIGAUD
*Prisculatrites deflandreae* (FRIZZELL & EXLINE)
*Pr. schlumbergeri* (DEFLANDRE-RIGAUD)
*Pr. triceratium* DEFLANDRE-RIGAUD
*Pr. tricostatus* DEFLANDRE-RIGAUD
*Staurocumites bartensteini* DEFLANDRE-RIGAUD

Exlinellidae
*Exlinella frizzelli* DEFLANDRE-RIGAUD
*Pedatopriscus pinguis* (DEFLANDRE-RIGAUD)

Schlumbergeritidae
*Schlumbergerites sievertsae* DEFLANDRE-RIGAUD

Theeliidae
*Auricularites arcuatus* DEFLANDRE-RIGAUD
*A. parviradiatus* DEFLANDRE-RIGAUD
*Hemisphaeranthos costifera* TERQUEM & BERTHELIN
*H. sieboldi* (SCHWAGER)
*H. terquemi* (DEFLANDRE-RIGAUD)
*Micradites incertus* DEFLANDRE-RIGAUD
*Stueria bajocica* (KAPTARENKO-CHERNOUSOVA)
*S. carpenteri* (MOORE)
*S. helvetica* (ZWINGLI & KÜBLER)
*S. malmensis* (FRIZZELL & EXLINE)
*S. novosundgarica* (KAPTARENKO-CHERNOUSOVA)
*S. oreli* (KAPTARENKO-CHERNOUSOVA)
*S. samarica* (KAPTARENKO-CHERNOUSOVA)
*Theelia angulata* (DEFLANDRE-RIGAUD)
*T. atava* (WAAGEN)
*T. clavata* (DEFLANDRE-RIGAUD)
*T. convexa* (WHIDBORNE)
*T. crassidentata* (DEFLANDRE-RIGAUD)
*T. florealis* (FRENTZEN)
*T. florida* (TERQUEM & BERTHELIN)
*T. heptalampra* (BARTENSTEIN)
*T. mortenseni* (DEFLANDRE-RIGAUD)
*T.? quinquelobata* (TERQUEM)

*T. rigaudae* (RIOULT)
*T. sinaiensis* SAID & BARAKAT
*T. speciosa* (DEFLANDRE-RIGAUD)
*T. vetusta* (SCHWAGER)
*T. wessexensis* HODSON, HARRIS & LAWSON
Protocaudinidae?
*"Protocaudina" mortenseni* DEFLANDRE-RIGAUD
*"P." paucispinosa* DEFLANDRE-RIGAUD
Synaptitidae
*Amphitriodites insignis* DEFLANDRE-RIGAUD
*Sclerothurites clypeus* DEFLANDRE-RIGAUD
*Spandelites arcuatus* DEFLANDRE-RIGAUD
*S. irregularis* (DEFLANDRE-RIGAUD)
*S. lehmanni* DEFLANDRE-RIGAUD
Calcancoridae
*Calcancora sieboldii* (MÜNSTER)
CRETACEOUS
Calclamnidae
*Eocaudina inaequipora* (A. H. MÜLLER)
*E. lobata* (A. H. MÜLLER)
*E. multipora* (A. H. MÜLLER)
Achistridae
*Achistrum huckei* (FRIZZELL & EXLINE)
Theeliidae
*Hemisphaeranthos simplex* A. H. MÜLLER
*Stueria frankei* (O. MÜLLER)
*Theelia rara* (A. H. MÜLLER)
*T. rotula* (EGGER)
*T. venusta* (A. H. MÜLLER)
Synaptitidae
*Rigaudites plummerae* FRIZZELL & EXLINE
*R. spinosus* FRIZZELL & EXLINE
*R. tallali* FRIZZELL & EXLINE
CENOZOIC
PALEOCENE
Synaptitidae
*Rigaudites cuvillieri* (DEFLANDRE-RIGAUD)
Calcancoridae
*Calcancora beurleni* TINOCO
EOCENE
Calclamnidae
*Calclamnella irregularis* (SCHLUMBERGER)
*C. margaritata* (SCHLUMBERGER)
*Calclamnoidea inaequalis* (SCHLUMBERGER)
*Eocaudina? schlumbergeri* (DEFLANDRE-RIGAUD)
Priscopedatidae
*Priscopedatus anceps* SCHLUMBERGER
*P. aspergillum* SCHLUMBERGER
*P. corolla* SCHLUMBERGER
*P. crassus* SCHLUMBERGER
*P. cribellum* SCHLUMBERGER
*P. echinatus* SCHLUMBERGER
*P. eiffeli* SCHLUMBERGER
*P. multiforis* SCHLUMBERGER
*P. normani* SCHLUMBERGER
*P. propinquus* SCHLUMBERGER
*P. pyramidalis* SCHLUMBERGER
Theeliidae
*Theelia curriculum* (SCHLUMBERGER)
*T. deflandreae* FRIZZELL & EXLINE
*T. ingens* (JOSHUA)
*T. lanceolata* (SCHLUMBERGER)
*T. undulata* (SCHLUMBERGER)
*Stueria elegans* SCHLUMBERGER
*S. operculum* (SCHLUMBERGER)
Synaptitidae
*Croneisites laevigatus* (SCHLUMBERGER)
*Rigaudites bastropanus* FRIZZELL & EXLINE
*R. cuvillieri* (DEFLANDRE-RIGAUD)
*Synaptites circularis* (SCHLUMBERGER)
*S. eocoenus* (SCHLUMBERGER)
*S. renifer* (SCHLUMBERGER)
*S. stueri* (SCHLUMBERGER)
*S. truncatus* (SCHLUMBERGER)
Calcancoridae
*Calcancora chaussiensis* FRIZZELL & EXLINE
*C. cuvillieri* DEFLANDRE-RIGAUD
*C. gallica* FRIZZELL & EXLINE
OLIGOCENE
Stichopitidae
*Calcligula elgeri* DEFLANDRE-RIGAUD
Calclamnidae
*Calclamna fusiformis* DEFLANDRE-RIGAUD
*Elgerius innienensis* DEFLANDRE-RIGAUD
*E. ostrea* DEFLANDRE-RIGAUD
*Eocaudina holsatica* (DEFLANDRE-RIGAUD)
*E. scabra* (DEFLANDRE-RIGAUD)
*E. speciosa* (DEFLANDRE-RIGAUD)
Priscopedatidae
*Dictyothurites corbisema* DEFLANDRE-RIGAUD
*D. spatuliger* DEFLANDRE-RIGAUD
*Priscopedatus conspicuus* DEFLANDRE-RIGAUD
Theeliidae
*Stueria intercessa* (DEFLANDRE-RIGAUD)
*S. mirabilis* (DEFLANDRE-RIGAUD)
*S. undosa* (DEFLANDRE-RIGAUD)
Synaptitidae
*Croneisites oligocaenicus* (SPANDEL)
*Rigaudites cunninghami* (DEFLANDRE-RIGAUD)
Calcancoridae
*Calcancora mississippiensis* FRIZZELL & EXLINE
*Calcancoroidea spandeli* FRIZZELL & EXLINE
*C. trifida* FRIZZELL & EXLINE
Calcancorellidae
*Calcancorella spectabilis* (DEFLANDRE-RIGAUD)
MIOCENE
Stichopitidae
*Parvispina subsymmetrica* (KRISTAN-TOLLMANN)
Calclamnidae
*Calclamnoidea goniaia* KRISTAN-TOLLMANN
*C. medioangusta* KRISTAN-TOLLMANN
*C. ocellata* KRISTAN-TOLLMANN
*C. spania* KRISTAN-TOLLMANN
*Eocaudina kuepperi* (DEFLANDRE-RIGAUD)
*E. subtrigonalis* KRISTAN-TOLLMANN
*E. tortoniensis* (DEFLANDRE-RIGAUD)
*Mortensenites hemisphaericus* KRISTAN-TOLLMANN
*M. reticulatus* KRISTAN-TOLLMANN
*Pachopsites annulatus* KRISTAN-TOLLMANN
Alexandritidae

*Alexandrites alexandri* KRISTAN-TOLLMANN
Theeliidae
*Theelia eisenstadtensis* KRISTAN-TOLLMANN
*T. muellendorfensis* KRISTAN-TOLLMANN
Synaptitidae
*Croneisites incrassatus* KRISTAN-TOLLMANN
*C. insignis* KRISTAN-TOLLMANN
*Synaptites aspis* KRISTAN-TOLLMANN
*Synaptites austriacus* (DEFLANDRE-RIGAUD)
*S. pappi* (DEFLANDRE-RIGAUD)
Calcancoridae
*Calcancora arduohamata* KRISTAN-TOLLMANN

## SYSTEMATIC DESCRIPTIONS

### Family STICHOPITIDAE Frizzell & Exline, 1956

[=Rhabdorotiformidae DEFLANDRE-RIGAUD, 1961]

Rods (including spoons, ladles, and racquets), single or multiradiate, solid or perforate, simple or with one or both ends modified. *Carb.-Pleist.*

**Stichopites** DEFLANDRE-RIGAUD, 1953, p. 6 [**S. mortenseni*; OD]. Simple, straight or slightly angular rods, without terminal discs or knobs, not spinose. *Jur.-Pleist.*, Eu.-Egypt.——FIG. 529,*2*. **S. mortenseni*, Jur., Ger.; *2a-c*, all ×20 (14). [=*Prostichopus* FRENTZEN, 1964.]

**Binoculites** DEFLANDRE-RIGAUD, 1952, p. 5 [**B. terquemi*; OD]. Simple, straight or slightly arched rods, eye or flattened perforate disc at each end. *Jur.*, Eu.-Egypt.——FIG. 529,*3a*. **B. terquemi*, Ger.; ×40 (14).——FIG. 529,*3b,c*. *B. issleri* DEFLANDRE-RIGAUD, Ger.; ×40 (14). [=*Cucumariopsis* FRENTZEN, 1964.]

**Calcligula** FRIZZELL & EXLINE, 1956, p. 70 [**C. perforata*; OD] [=*Molpadioites* DEFLANDRE-RIGAUD, 1961 *(partim)*]. Racquets, spoons, and ladles (molpadiid type); simple rods with single terminal disc, which is variously perforate. *Jur.-Pleist.*, Eu.-Egypt.——FIG. 529,*6a*. *C. elgeri* DEFLANDRE-RIGAUD, Oligo., Ger.; ×40 (9).——FIG. 529,*6b*. **C. perforata*, Jur., Ger.; ×50 (14).

**Cucumarites** DEFLANDRE-RIGAUD, 1952, p. 5 [**Cucumaria feifeli* MORTENSEN, 1937, p. 5; OD] [*non* DEFLANDRE-RIGAUD, 1949 *(nom. nud.)*; DEFLANDRE-RIGAUD (1948), 1961, p. 55 (type, *Eocaudina mortenseni* FRIZZELL & EXLINE, 1956, p. 88)] [=*Ornaticannula* DEFLANDRE-RIGAUD, 1961, p. 44 *(partim)*]. Tri- and multiradiate rods. *Jur.-Pleist.*, Eu.——FIG. 529,*8a*. **C. feifeli* (MORTENSEN), Jur., Ger.; ×50 (14).——FIG. 529,*8b*. *C. solidus* (DEFLANDRE-RIGAUD), Jur., Fr.; ×400 (14). [=*Procucumaria* FRENTZEN, 1964.]

**Ornaticannula** DEFLANDRE-RIGAUD, 1961, p. 44 [**O. bonheurei*; OD]. Angular C-rods with spines and branches. *Jur.-Pleist.*, Eu.——FIG. 529,*7*. **O. bonheurei*, Jur., Fr.; ×170 (10).

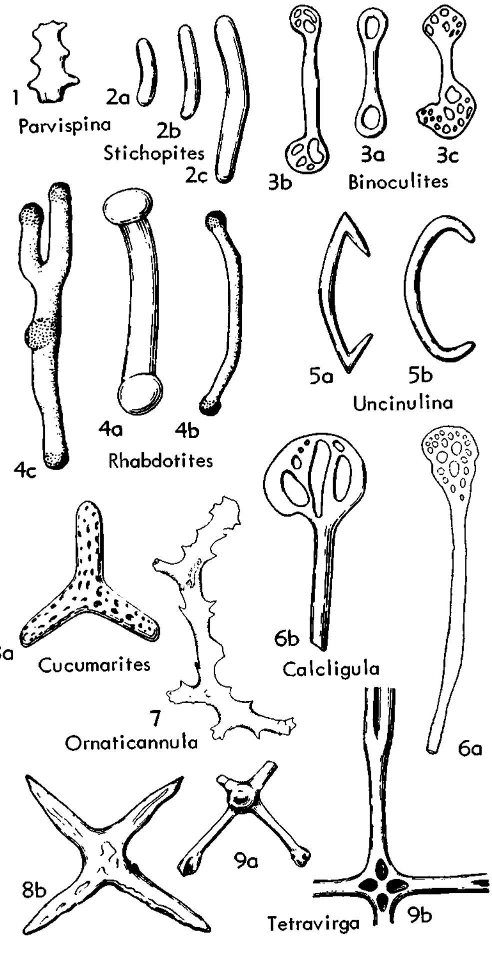


FIG. 529. Stichopitidae (p. *U662-U664*).

**Parvispina** KORNICKER & IMBRIE, 1958, p. 94 [**Stichopites spinosus* FRIZZELL & EXLINE, 1956, p. 61; OD]. Straight, tapering, spinose rods. *Miss.-Mio.*, N.Am.-Eu.——FIG. 529,*1*. **P. spinosa* (FRIZZELL & EXLINE), Miss., USA(Ill.); ×25 (14).

**Rhabdotites** DEFLANDRE-RIGAUD, 1952, p. 9 [**R. mortenseni*; OD] [=*Chiridotella* DEFLANDRE-RIGAUD, 1961, p. 36 *(partim)*]. Simple or branching, straight or slightly arched rods; ends knobbed. *Trias.-Pleist.*, Eu.——FIG. 529,*4a*. **R. mortenseni*, Jur., Ger.; ×25 (14).——FIG. 529,*4b*. *R. dorsetensis* HODSON, HARRIS & LAWSON, Jur., Eng.; ×30 (25).——FIG. 529,*4c*. *R. bifidus* HODSON, HARRIS & LAWSON, Jur., Eng.; ×30 (25). [=*Chirobaculus* FRENTZEN, 1964.]

**Tetravirga** Frizzell & Exline, 1956, p. 73 [**T. imperforata*; OD]. Rods with 4 arms in single plane at 90 degrees. *L.Carb.-Penn.*, N.Am.-Eu.——Fig. 529,*9a*. **T. imperforata*, Penn., USA (Tex.); ×25 (14).——Fig. 529,*9b*. *T. etheridgei* Frizzell & Exline, L.Carb., Scot.; ×? (14).

**Uncinulina** Terquem, 1862, p. 433 [**U. polymorpha*; OD] [=*Ambulacrites* Rioult, 1960].

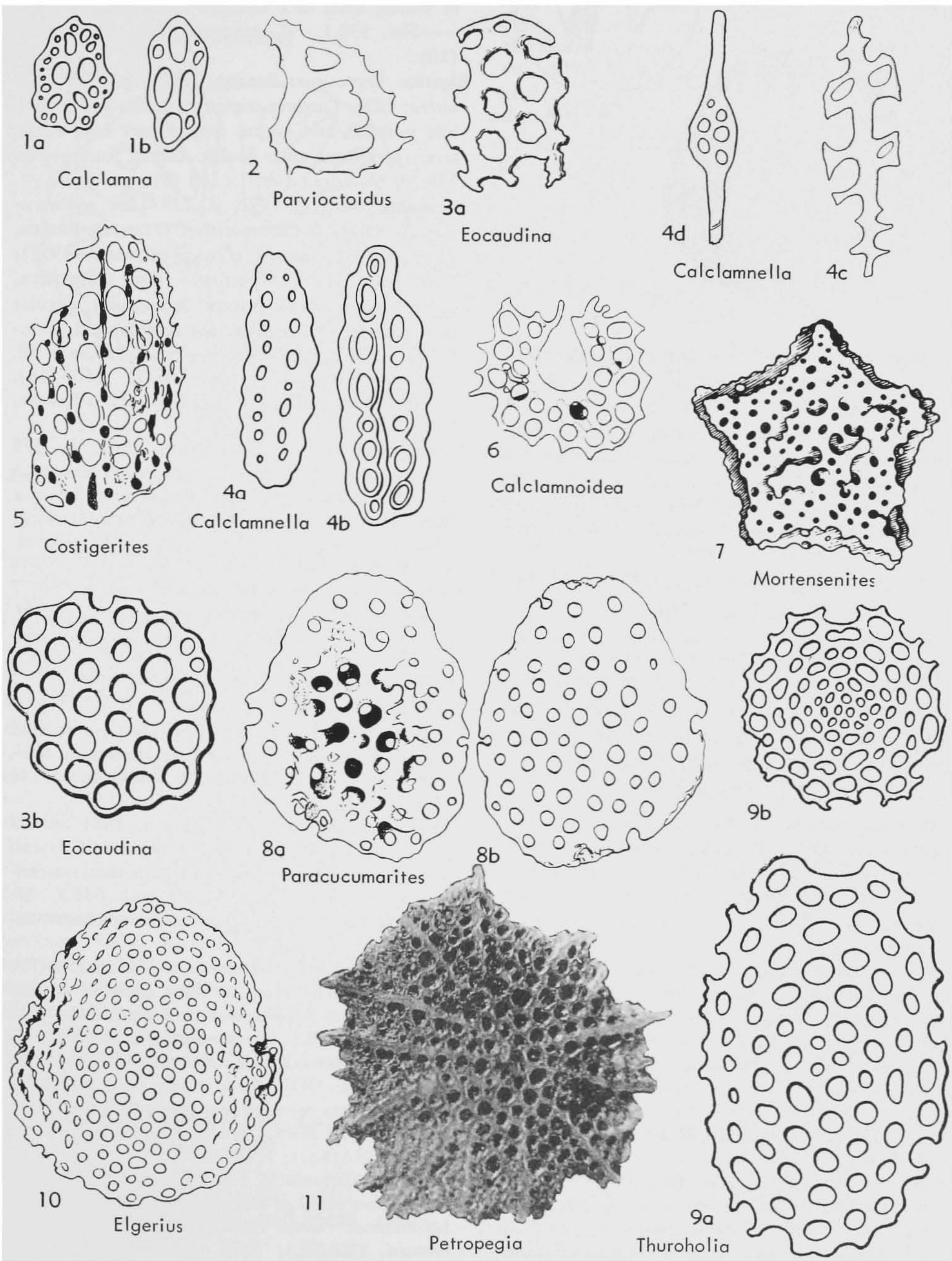


Fig. 530. Calclamnidae (p. *U664-U665*).

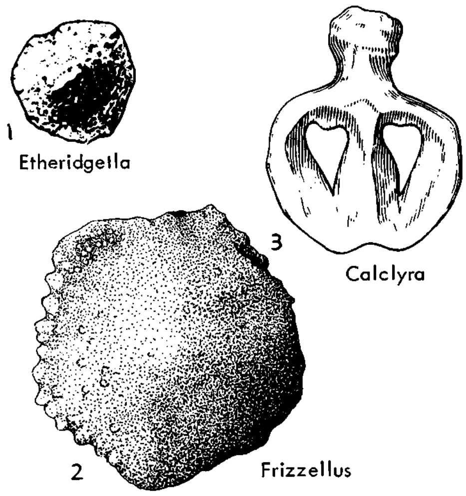


FIG. 531. Etheridgellidae *(1,2)*; Calclyridae *(3)* (p. *U665-U666*).

C-rods unornamented, consistently arched or bent; ends simple and tapering. *Carb.-Pleist.*, N.Am.-Eu.——FIG. 529,*5a*. **U. polymorpha*, Jur., Fr.; ×25 (14).——FIG. 529,*5b*. *U. terquemi* FRIZZELL & EXLINE, Jur., Fr.; ×25 (14).

## Family CALCLAMNIDAE Frizzell & Exline, 1956

[=Platanchoriformidae DEFLANDRE-RIGAUD, 1952 *(partim)*; Pachopsitidae KRISTAN-TOLLMANN]

Perforate plates, usually thin, rarely multilayered, flat or concavo-convex, shape variable, outline commonly indefinite; perforations not denticulate; lacking socket, strap or spire. *?Ord., Dev.-Pleist.*

**Calclamna** FRIZZELL & EXLINE, 1956, p. 76 [**C. germanica*; OD]. Bilaterally symmetrical broad plates; hole pattern cruciform of more than 2 holes. *Jur.*, Eu.-Egypt.——FIG. 530,*1*. **C. germanica*, Jur., Ger.; *1a,b*, ×40 (14). [=*Cibrum* FRENTZEN, 1964.]

**Calclamnella** FRIZZELL & EXLINE, 1956, p. 77 [**Priscopedatus irregularis* SCHLUMBERGER, 1890, p. 199; OD]. Elongate perforate plates with holes in 2 rows. *Jur.-Pleist.*, Eu.——FIG. 530,*4a,b*,. **C. irregularis* (SCHLUMBERGER), Eoc., Fr.; ×200 (14).——FIG. 530,*4c*. *C. transversa* DEFLANDRE-RIGAUD, Jur., Fr.; ×265 (10).——FIG. 530,*4d*. *C. fusiformis* DEFLANDRE-RIGAUD, Oligo., Ger.; ×105 (9).

**Calclamnoidea** FRIZZELL & EXLINE, 1956, p. 79 (*emend.* DEFLANDRE-RIGAUD, 1961, p. 50) [**Priscopedatus collaris* DEFLANDRE-RIGAUD, 1946, p. 514; OD]. Perforate plates in form of collar, with broad central space susceptible to closure. *Trias.-Pleist.*, Eu.——FIG. 530,*6*. **C. collaris* (DEFLANDRE-RIGAUD), Jur., Fr.; ×400 (10). [=*Palaeocucumaria* FRENTZEN, 1964.]

**Costigerites** DEFLANDRE-RIGAUD, 1961, p. 54 [**C. piveteaui*; OD]. Elongate perforate plates with sides essentially parallel, ornamented with pustules or bosses; holes in 2 or more rows. *Jur.-Eoc.*, Eu.——FIG. 530,*5*. **C. piveteaui*, Jur., Fr.; ×400 (10).

**Elgerius** DEFLANDRE-RIGAUD, 1959, p. 192 [**E. ostrea*; OD]. Concavo-convex perforate plates, outline rounded and entire, central part with single layer, peripheral zone double. *Oligo.*, Eu.——FIG. 530,*10*. **E. ostrea*, Ger.; ×160 (9).

**Eocaudina** MARTIN, 1952, p. 729 [**E. septaforaminalis*; OD] [=*Cucumarites* DEFLANDRE-RIGAUD, (1948), 1961 (*non* DEFLANDRE-RIGAUD, 1952); *Thuroholia* AUCTT. *(partim)* (*non* GUTSCHICK, 1954)]. Sieve plates (except Ordovician), circular to hexagonal or irregular, not multilayered. *Dev.-Pleist.*, Eu.-Egypt-N.Am.——FIG. 530,*3a*. **E. septaforaminalis*, Dev., USA(Iowa); ×60 (14).——FIG. 530,*3b*. *E. gutschicki* FRIZZELL & EXLINE, Penn., USA(Tex.); ×45 (14).

**Fissobractites** KRISTAN-TOLLMANN, 1963, p. 375 [**F. subsymmetricus*; OD]. Subcircular disc with numerous radially elongate perforations; 4 major holes at 90° position; stirrup and spire lacking. *Trias.*, Eu.(Aus.).——FIG. 531A,*2*. **F. subsymmetricus*; ×82.5 (30c).

**Mortensenites** DEFLANDRE-RIGAUD, 1952, p. 7 [**Gromia liasica* TERQUEM, 1866, p. 402 (=*M. sievertsi*); OD]. Multilayered perforate plates with variable outline. *Trias.-Mio.*, Eu.——FIG. 530,*7*. **M. liasicus* (TERQUEM), Ger.; ×95 (14).

**Pachopsites** KRISTAN-TOLLMANN, 1964, p. 94 [**P. annulatus*; OD]. Subelliptical perforate plates, with large eccentric hole; rim of hole thickened. *Mio.*, Eu.(Aus.).——FIG. 531B,*1*. **P. annulatus*; ×130 (30b).

**Paracucumarites** DEFLANDRE-RIGAUD, 1961, p. 67 [**P. hamptoni*; OD]. Perforate plates of 2 layers; 2nd layer occupying central part, in some extending to periphery. *Jur.*, Eu.——FIG. 530,*8*. **P. hamptoni*, Fr.; *8a,b*, views of same specimen; ×400 (10).

**Parvioctoidus** DEFLANDRE-RIGAUD, 1961, p. 54 [**P. spinosus*; OD]. Flat lamellar sclerites, outline irregular; with 2 holes of very different size. *Jur.*, Eu.——FIG. 530,*2*. **P. spinosus*, Fr.; ×265 (10).

**Petropegia** SUMMERSON & CAMPBELL, 1958, p. 966 [**P. radiata*; OD]. Sieve plates with peripheral spines, in some forms spines terminate radial ridges across sclerite. *Penn.*, N.Am.——FIG. 530,*11*. **P. radiata*, USA(Ky.); ×16 (43).

**Thuroholia** GUTSCHICK, 1954, p. 827 [**T. croneisi*; OD]. Sieve plates of Ordovician only; questionably holothurian. *Ord.*, N.Am.——FIG. 530,*9a*. **T. croneisi*, USA(Ill.); ×40 (14).——FIG. 533,*9b*. *T. cribriformis* GUTSCHICK, USA(Ill.); ×80 (14).

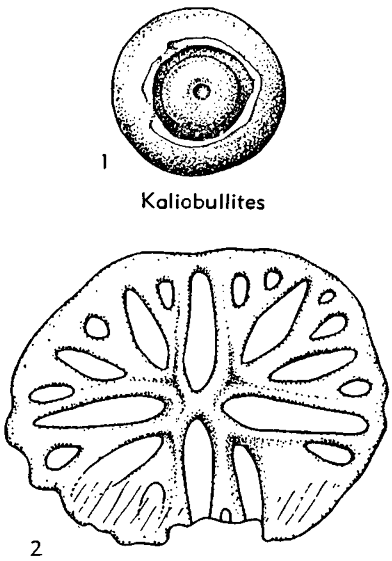


FIG. 531A. Calclamnidae *(2)*; Kaliobullitidae *(1)* (p. *U*664, *U*670).

## Family ETHERIDGELLIDAE Frizzell & Exline, 1956

Thickened, imperforate discs, angular to subcircular, with low to very high central pseudospire in some forms; surface granular. *Dev.-Jur.*

**Etheridgella** CRONEIS, 1932, p. 144 [**E. porosa*; OD]. Biconvex; pseudospire low or absent; margin smooth. *Penn.,* N.Am.——FIG. 531,*1*. **E. porosa,* USA(Tex.); ×25 (14).

**Frizzellus** HAMPTON, 1958, p. 309 [**E. irregularis*; OD]. Flat to concavo-convex, margin denticulate. *Trias.-Jur.,* Eu.——FIG. 531,*2*. **F. irregularis,* Eng.; ×85 (21).

**Palaeocucumaria** LEHMANN, 1958, p. 85 [**P. hunsrueckiana,* OD]. Sclerites strongly dimorphic: in anterior part of animal circular to subcircular, strongly inflated, without pseudospire; posterior sclerites with very long spinelike pseudospire; isolated sclerites probably should be described as individual species of *Etheridgella. L.Dev.,* Eu.

## Family ACHISTRIDAE Frizzell & Exline, 1956

[=Platanchoriformidae DEFLANDRE-RIGAUD, 1952 *(partim)*; Achistrulidae DEFLANDRE-RIGAUD, 1961]

Hooks with eye, shank, and spear. *Carb.-Cret.*

**Achistrum** ETHERIDGE, 1881, p. 194 [**A. nicholsoni*; OD] [=*Ancistrum* BATHER, 1900 *(non* MAUPAS, 1883); *Cancellrum* HAMPTON, 1958; *Spinrum* HAMPTON, 1958; *Achistrulum* DEFLANDRE-RIGAUD, 1961]. Eye at 90 degrees to plane of spear, rim entire; eye open or crossed by simple or bifurcating crossbars. *Carb.-Cret.,* Eu.-Egypt-N.Am.——FIG. 527,*3a*. **A. nicholsoni,* L. Carb., Scot.; ×? (14).——FIG. 527,*3b*. *A. bichordatum* FLETCHER, Jur., Eng.; ×30 (13).——FIG. 527,*3c*. *A. trichordatum* FLETCHER, Jur., Eng.; ×30 (13).

**Aduncrum** HAMPTON, 1958, p. 76 [**Achistrum cordatum* HAMPTON, 1957, p. 509; OD]. Eye in plane of spear; rim of eye not entire, in some composed of 2 small, recurved, hooklike processes. *Trias.-Jur.,* Eu.——FIG. 527,*4*. **A. cordatum* (HAMPTON), Jur., Eng.; ×35 (19).

## Family CALCLYRIDAE Frizzell & Exline, 1956

Lyres comprising sclerites with central shaft and neck, 2 marginal arms joining neck and base of shaft; questionably holothurian. *Penn.-Perm.*

**Calclyra** FRIZZELL & EXLINE, 1956, p. 99 [**Prosynapta eiseliana* SPANDEL, 1898, p. 44; OD] [=*Prosynapta* SPANDEL, 1898 *(non* CUÉNOT, 1891)]. Diagnosis as for family. *Penn.-Perm.,* N.Am.-Eu. ——FIG. 531,*3*. **C. eiseliana* (SPANDEL), Perm., Ger.; ×195 (14).

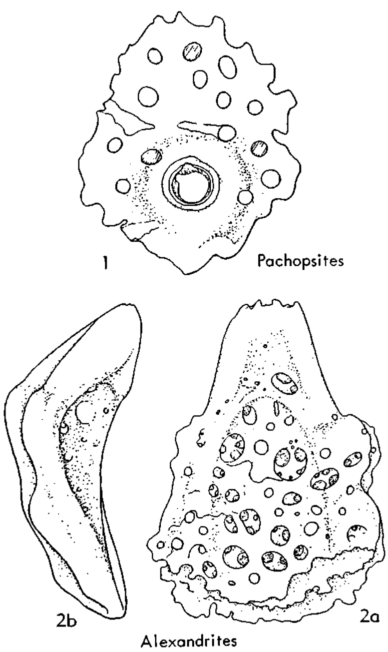


FIG. 531B. Calclamnidae *(1)*; Alexandritidae *(2)* (p. *U*664, *U*668).

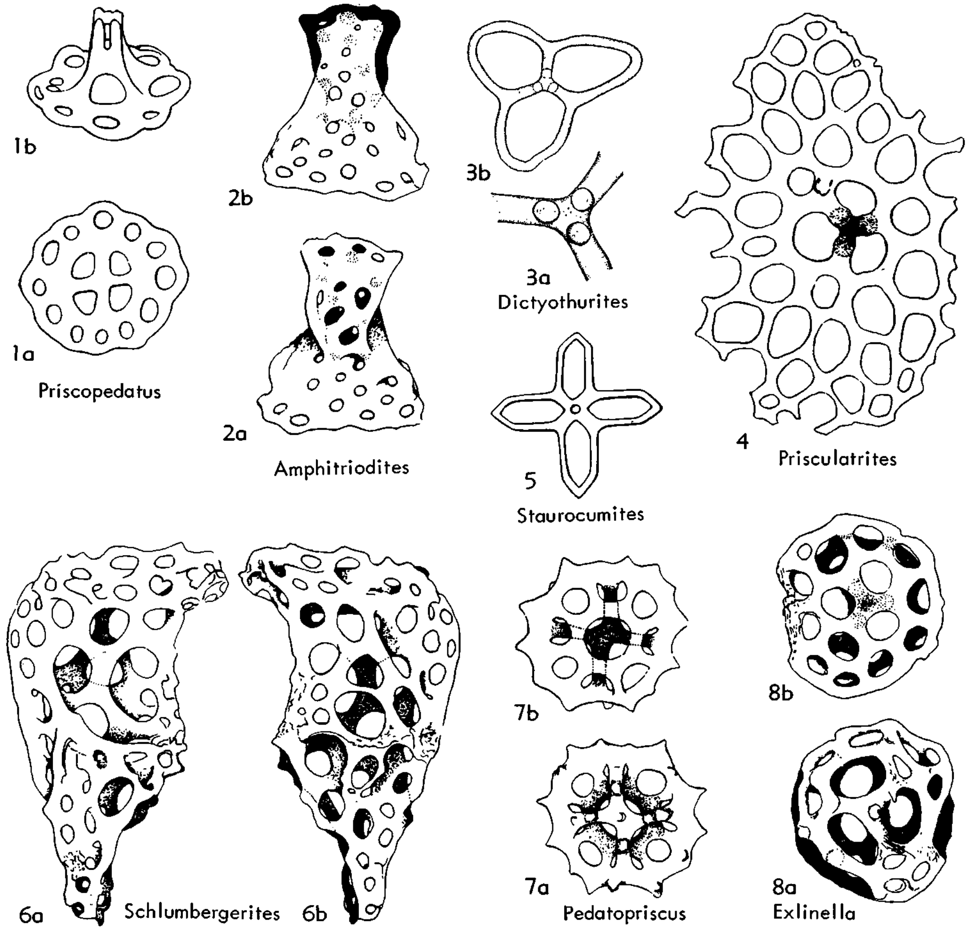


FIG. 532. Priscopedatidae *(1,3-5)*; Exlinellidae *(7-8)*; Schlumbergeritidae *(2,6)* (p. *U666-U667*).

## Family PRISCOPEDATIDAE Frizzell & Exline, 1956

[=Turriformidae DEFLANDRE-RIGAUD, 1952]

Tables with perforate disc and central spire or stirrup or both; holes not denticulate. *Jur.-Pleist.*

**Priscopedatus** SCHLUMBERGER, 1890, p. 192 [**P. pyramidalis* SCHLUMBERGER; SD FRIZZELL & EXLINE, 1956, p. 101]. Tables or turriform sclerites, with crossbar or stirrup of 4 branches mounted above large opening or making 4 perforations; with or without spire or turret with 4 pillars rising from disc; spire smooth, spiny, or with costae; outline of disc circular, subcircular, or polygonal, border smooth, undulating or of inverted scallops; holes circular, elliptical, or polygonal. *Jur.-Pleist.*, Eu.-Egypt-N.Am.——FIG. 532, *1*. **P. pyramidalis*, Eoc., Fr.; *1a,b*, basal and oblique views; ×180 (14).

**Dictyothurites** DEFLANDRE-RIGAUD, 1959, p. 193 [**D. corbisema*; OD]. Disc an open trefoil, 3 bosses at center representing spire. *Oligo.-Pleist.*, Eu.——FIG. 532,*3*. **D. corbisema,* Oligo., Ger.; *3a*, ×105; *3b*, ×265 (9).

**Prisculatrites** DEFLANDRE-RIGAUD, 1961, p. 80 [**Priscopedatus schlumbergeri* DEFLANDRE-RIGAUD, 1946, p. 514; OD]. Tables or turriform sclerites with stirrup of 3 branches arising between 3 central perforations of disc, spire present in some; outline of disc subcircular, elliptical, or polygonal; margin smooth, undulating, or irregular; single-layered except in *P. triceratium* DEFLANDRE-RIGAUD. *Jur.-Pleist.*, Eu.——FIG. 532,*4*. **P. schlumbergeri* (DEFLANDRE-RIGAUD), Jur., Fr.; ×400 (10).

**Staurocumites** DEFLANDRE-RIGAUD, 1952, p. 6 [**S. bartensteini*; OD]. Disc an open quatrefoil; spire short, with 4-footed stirrup. *Jur.*, Eu.——FIG. 532,

5. **S. bartensteini,* Ger.; ×50 (14). [=*Crux* FRENTZEN, 1964.]

### Family EXLINELLIDAE Deflandre-Rigaud, 1961

Sclerite lenticular, bilaminar; discrepantly perforate upper and lower surfaces fused at periphery, joined within by trabeculae or pillars. [The family includes 2 monotypic genera. Generic definitions therefore may be subject to revision with discovery of other species.] *Jur.-Pleist.*

**Exlinella** DEFLANDRE-RIGAUD, 1961, p. 84 [**E. frizzelli*; OD]. Periphery smooth; 3 central holes on one surface and 4 on other surface. *Jur.-Pleist.,* Eu.——FIG. 532,*8*. **E. frizzelli,* Jur., Fr.; *8a,b,* both sides of holotype; ×400 (10).

**Pedatopriscus** DEFLANDRE-RIGAUD, 1961, p. 85 [**Priscopedatus pinguis* DEFLANDRE-RIGAUD, 1946; OD]. Outline irregular; single central hole on one surface and 4 on other surface. *Jur.-Pleist.,* Eu. ——FIG. 532,*7*. **P. pinguis* (DEFLANDRE-RIGAUD), Jur., Fr.; *7a,b,* views of paratype; ×400 (10).

### Family SCHLUMBERGERITIDAE Deflandre-Rigaud, 1961

Bilaminar or very irregularly multilaminar perforate sclerites. [The family includes 2 monotypic genera, and may be composite.] *Jur.*

**Schlumbergerites** DEFLANDRE-RIGAUD, 1961, p. 87 [**S. sievertsae*; OD]. Very irregularly perforate, with double or triple layer at least in part; perforations numerous, large in central part, smaller toward edges, but irregular. *Jur.,* Eu.——FIG. 532, *6*. **S. sievertsae,* Fr.; *6a,b,* views of holotype; ×400 (10).

**Amphitriodites** DEFLANDRE-RIGAUD, 1961, p. 93 [**A. insignis*; OD]. Regularly perforate; 2 layers united by short trabeculae, opposingly triangular; margins not entirely connected. *Jur.,* Eu.——FIG. 532,*2*. **A. insignis,* Fr.; *2a,b,* views of holotype; ×400 (10).

### Family ALEXANDRITIDAE Kristan-Tollmann, 1964

Multilayered concavo-convex perforate plates, angularly pyriform, strongly curved; small end thickened, thickening continuing as raised ridge across concave side of plate. *Mio.*

**Alexandrites** KRISTAN-TOLLMANN, 1964, p. 95 [**A. alexandri*; OD]. Diagnosis as for family. *Mio.,* Eu.(Aus.).——FIG. 531B,*2*. **A. alexandri*; *2a,b,* convex surface and lateral view; ×130 (30b).

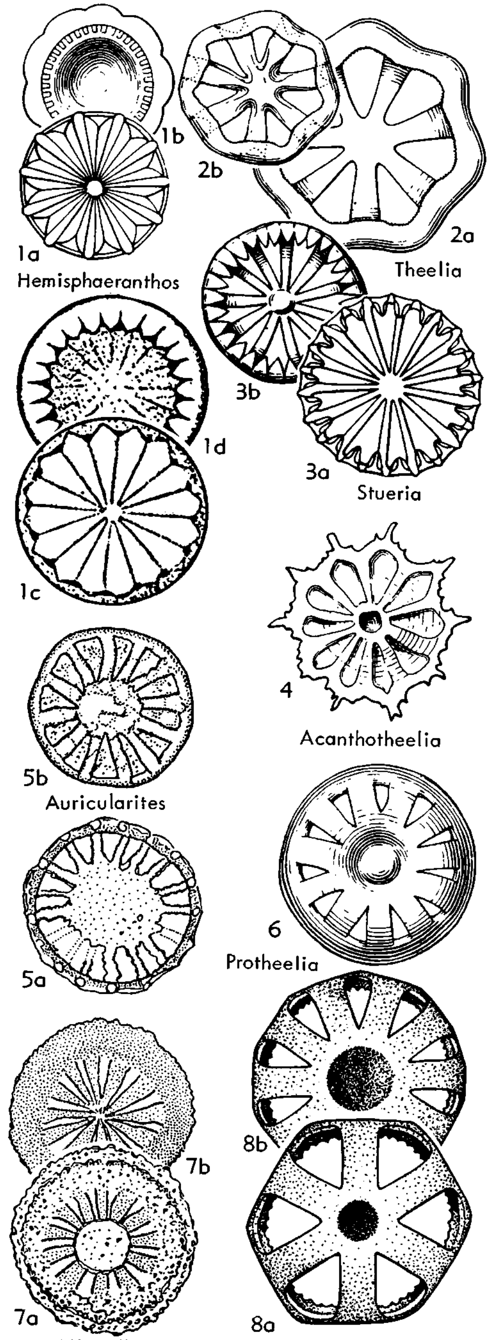


FIG. 533. Theeliidae (p. *U668*).

## Family THEELIIDAE Frizzell & Exline, 1956

[=Rotiformidae DEFLANDRE-RIGAUD, 1952; Chiridotitidae DEFLANDRE-RIGAUD, 1957 (*nom. correct.* DEFLANDRE-RIGAUD, 1961, *pro* Chiridotitesidae); Rhabdorotiformidae DEFLANDRE-RIGAUD, 1961 (*partim*)]

Concavo-convex wheels, with outer rim and inner central portion, spokes connecting rim and central portion, interspoke spaces present except in *Hemisphaeranthos;* central part small, nonquadripartite; spokes long, tapering very slightly if at all. *Penn.-Pleist.*

**Theelia** SCHLUMBERGER, 1891, p. 197 [**Chirodota undulata* SCHLUMBERGER, 1888; OD] [*non Theelia* LUDWIG, 1889, (*nom. nud.*); *Theelia* LUDWIG, 1891] [=*Chiridotites* DEFLANDRE-RIGAUD, 1949; *Chiridotella* DEFLANDRE-RIGAUD, 1961 (*partim*)]. Spokes 6-10; rim inclined to plane of wheel, curving upward and inward, denticulate on inner margin, teeth not extending to periphery as seen from above; center imperforate, typically with hemispherical or conical tubercle or button. *?Penn., Trias.-Pleist.,* Eu.-Egypt-? N. Am.-Australia.——FIG. 533,*2*. **T. undulata* (SCHLUMBERGER), Eoc., Fr.; *2a,* lectotype, ×205; *2b,* ×100 (14).

**Acanthotheelia** FRIZZELL & EXLINE, 1956, p. 112 [**A. spinosa*; OD]. Spokes numerous (10 in type-species); rim in plane of wheel, not denticulate; periphery scalloped and spinose; central portion perforate. *Trias.,* Eu.——FIG. 533,*4*. **A. spinosa,* Italy; ×50 (14).

**Auricularites** DEFLANDRE-RIGAUD, 1950, p. 42 [**A. parviradiatus*; OD]. Tiny wheels resembling those of *Theelia,* but with many more spokes (12-28); differing from *Stueria* in having smooth or extremely finely dentate rim. *Jur.,* Eu.——FIG. 533, *5a*. **A. parviradiatus,* Fr.; ×425.——FIG. 533,*5b*. *A. arcuatus* DEFLANDRE-RIGAUD, Fr.; ×425 (46).

**Hemisphaeranthos** TERQUEM & BERTHELIN, 1875, p. 109 [**H. costifera*; SD FRIZZELL & EXLINE, 1956, p. 128] [=*Myriotrochites* DEFLANDRE-RIGAUD, 1949 (*nom. nud.*); *Myriotrochites* DEFLANDRE-RIGAUD, 1951, p. 35 (*partim*) (type, *Chirodota sieboldi* SCHWAGER, 1865; SD DEFLANDRE-RIGAUD, 1961, p. 100]. Spokes 10-16, contiguous, flat on upper side, raised and petal-like on lower side, forming hemispherical surface of upper side of sclerite; rim inclined to plane of wheel, finely to coarsely denticulate. *Jur.-U.Cret.,* Eu.——FIG. 533,*1a,b*. **H. costifera,* Jur., Fr.; *1a,b,* lower and upper views; ×100 (14).——FIG. 533,*1c,d*. *H. simplex* A. H. MÜLLER, U.Cret., Ger.; *1c,d,* lower and upper sides, ×100 (31).

**Micradites** DEFLANDRE-RIGAUD, 1950, p. 43 [**M. incertus*; OD]. Minute wheels of unestablished affinities. *Jur.,* Eu.——FIG. 533,*7*. **M. incertus,* Fr.; *7a,b,* opposite sides, ×425 (46).

**Protheelia** FRIZZELL & EXLINE, 1956, p. 111 [**Chirodota geinitziana* SPANDEL, 1898, p. 44; OD]. Spokes numerous (11-13 in type-species), flat; rim flat, thick, lying in plane of wheel, not denticulate; with central hub. *Perm.,* Eu.——FIG. 533,*6*. **P. geinitziana* (SPANDEL), Ger.; ×185 (14).

**Stueria** SCHLUMBERGER, 1888, p. 440 [**S. elegans*; OD] [=*Actinoclava* O. MÜLLER, 1911 (proposed as diatom); *Myriotrochites* DEFLANDRE-RIGAUD, 1951, p. 35 (*partim*)]. Spokes 11-17; rim inclined to plane of wheel, curving upward and inward, coarsely dentate, teeth extending to periphery as seen from above; hub typically simple. *Jur.-Pleist.,* Eu.-Egypt.——FIG. 533,*3a*. **S. elegans,* Eoc., Eu.(Fr.); ×135 (14).——FIG. 533,*3b*. *S. malmensis* FRIZZELL & EXLINE, Jur., Eu.(Ger.); ×100 (14).

**Thallatocanthus** CARINI, 1962, p. 391 [**T. consonus*; OD]. Spokes 6-10; rim denticulate, curving upw[illegible] inward; hub cylindrical, extending below [illegible]ane of opposite sides of wheel. *M. Penn.,* N.Am.——FIG. 533,*8*. **T. consonus,* USA (Okla.); *8a,b,* ×125 (3).

## Family PROTOCAUDINIDAE Deflandre-Rigaud, 1961

[=Disciformidae DEFLANDRE-RIGAUD, 1952 (*partim*); Theeliidae FRIZZELL & EXLINE, 1956 (*partim*)]

Wheels with quadripartite center; central divisions perforate or impressed; spokes very short; Mesozoic forms with central stirrup on ?lower side. *Dev.-Jur.*

**Protocaudina** CRONEIS, 1932, p. 137 [**Cheirodota? traquairii* ETHERIDGE, 1881, p. 196; OD]. Spokes 8-10; rim inclined to plane of wheel, dentate; central part large, with 4 central perforations. *Dev.-Perm.,* Eu.-N.Am.——FIG. 527,*1a*. **P. traquairii* (ETHERIDGE), Carb., Scot., ×? (14).——FIG. 527,*1b*. *P. kansasensis* (HANNA), Penn., USA (Tex.); ×70 (14).——FIG. 527,*1c*. *P. hexagonaria* MARTIN, Dev., USA(Iowa); ×65 (14).

**Microantyx** KORNICKER & IMBRIE, 1958, p. 93 [**M. permiana*; OD]. Central divisions impressed on lower surface; boss on upper surface of central portion. *L.Miss.-Perm., ?Trias.,* N.Am.-Eu.——FIG. 527,*2*. *M. botoni* GUTSCHICK, L.Miss., USA (Ind.); *2a,b,* upper and lower views; ×90 (17).

**Unnamed genus "Protocaudina"** ("*P.*" *mortenseni* DEFLANDRE-RIGAUD, 1946, p. 514; "*P.*" *paucispinosa* DEFLANDRE-RIGAUD, 1961, p. 106). Wheels with quadripartite central perforations, spokes very short, central portion wide; rim in plane of wheel, circular to elliptical in cross section, coarsely denticulate between spokes; ?lower surface with 4-footed stirrup rising above central perforations, attachment between laterally adjacent holes. *Jur.,* Eu.——FIG. 527,*1d*. "*P.*" *mortenseni* DEFLANDRE-RIGAUD, Fr.; ×400 (10).

**Family PALEOCHIRIDOTIDAE Frizzell & Exline, new family**

[=Disciformidae DEFLANDRE-RIGAUD, 1952 *(partim)*; Theeliidae FRIZZELL & EXLINE, 1956 *(partim)*; Protocaudinidae DEFLANDRE-RIGAUD, 1961 *(partim)*]

Wheels with large nonquadripartite center; spokes short, rapidly tapering; rim inclined to plane of wheel. *Carb.*

**Paleochiridota** CRONEIS, 1932, p. 139 [**P. plummerae*; OD]. Central part solid, with raised hub on lower surface, sometimes with pattern of deeply excavated depressions on lower side. *Carb.*, Eu.-N.Am.——FIG. 534,*3*. **P. plummerae*, Penn., USA(Tex.); *3a-c*, lower, upper, and lat. views; ×90 (14).

**Rota** LANGENHEIM & EPIS, 1957, p. 170 (*sensu*

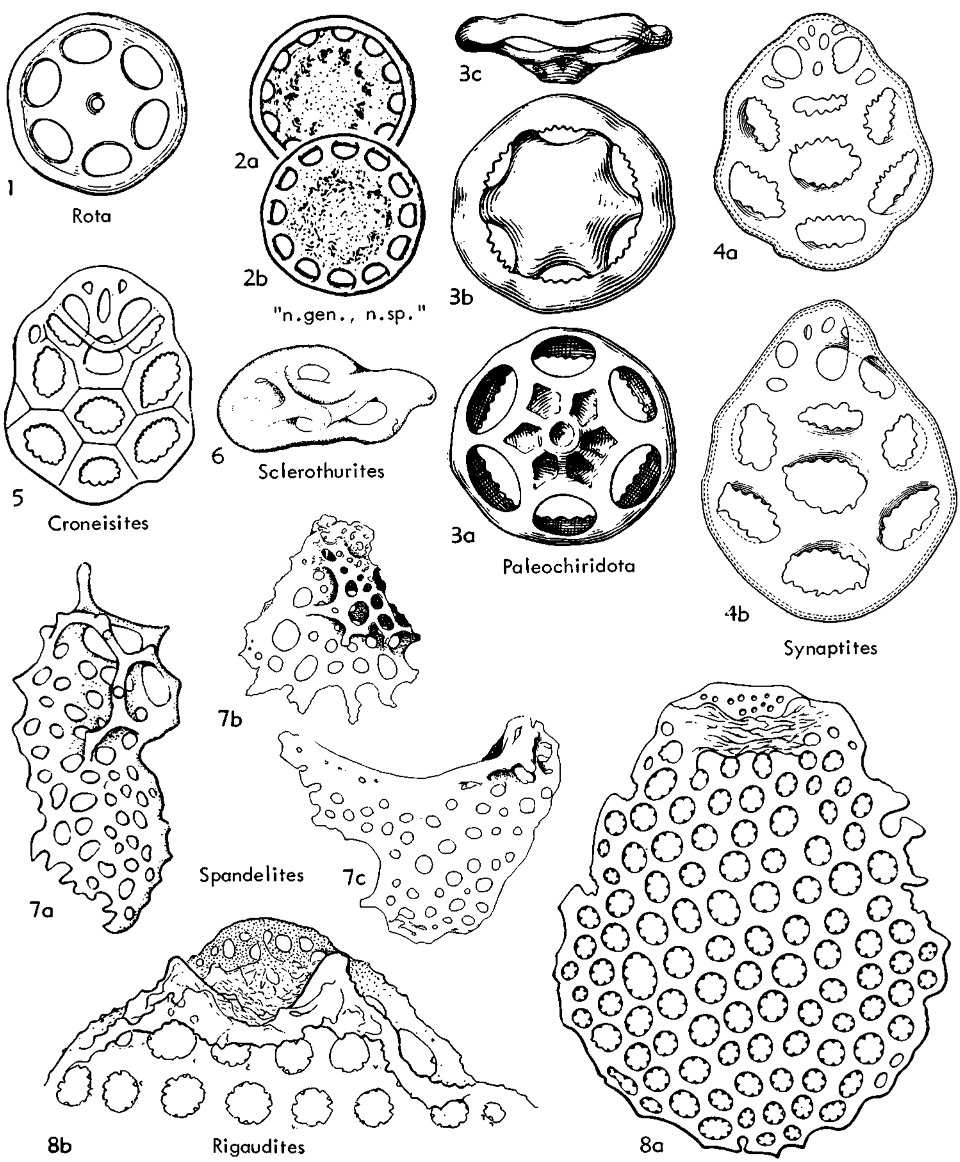


FIG. 534. Paleochiridotidae *(1-3)*; Synaptitidae *(4-5, 7-8)*; Family Uncertain *(6)* (p. *U*670-*U*671).

GUTSCHICK, 1959, p. 135) [**R. martini*; OD]. Central portion with tiny hole, rim finely to coarsely denticulate on inner margin [secondary perforations of rim not confirmed]. *Miss.*, N.Am. ——FIG. 534,*1*. *R. campbelli* GUTSCHICK, L.Miss., USA(Ind.); ×70 (17).

**Unnamed genus** ("n.gen., n.sp.," GUTSCHICK, 1959, p. 136). Spokes extremely short; central portion imperforate; rim inclined to plane of wheel; each interspoke area on outer side marked by circular depression about half distance from center to margin. *Miss.*, N.Am.——FIG. 534,*2*. "N. gen., n.sp.," *L.Miss.*, USA(Ind.); upper and lower views; ×75 (17).

## Family KALIOBULLITIDAE Kristan-Tollmann, 1963

Concavo-convex, compact wheels; with hub on lower surface and broad rim at 90° to plane of wheel; spokes lacking, central portion connected with rim by solid septum. *Trias.*

**Kaliobullites** KRISTAN-TOLLMANN, 1963, p. 377 [**K. umbo*; OD]. Diagnosis as for family. *Trias.*, Eu.(Aus.).——FIG. 531A,*1*. **K. umbo*; ×55 (30c).

## Family SYNAPTITIDAE Frizzell & Exline, 1956

[=Platanchoriformidae DEFLANDRE-RIGAUD, 1952 *(partim)*; Synaptellidae DEFLANDRE-RIGAUD, 1961]

Elongate unilaminar perforate plates, upper end narrower than lower, typically concave on outer surface and convex on inner surface, typically with socket at small end on outer surface; socket single, double, complex, or absent; perforations variable in number, usually denticulate, with fine teeth on margins. *Jur.-Pleist.*

**Synaptites** DEFLANDRE-RIGAUD, 1949, p. 1 [**Synapta eocoena* SCHLUMBERGER, 1888, p. 437; SD DEFLANDRE-RIGAUD, 1952, p. 8] [=*Synaptellus* DEFLANDRE-RIGAUD, 1961, p. 89 (obj.)]. Oval to elliptical, small, flat or concavo-convex; socket single or double, greatly reduced or absent, at one or both margins but not crossing sclerite; perforations 10-20, denticulate. *Eoc.-Pleist.*, Eu.-N. Am. —— FIG. 534,*4*. **S. eocoenus* (SCHLUMBERGER), Eoc., Fr.; topotypes; ×225 (14).

**Croneisites** FRIZZELL & EXLINE, 1957, p. 113 [**Synapta oligocaenica* SPANDEL, 1900, p. 50; OD]. Oval to elliptical, very small, concavo-convex; socket narrow, straplike, arcuate, connecting margins of sclerite; perforations 10-20, smooth or finely denticulate. *Eoc.-Mio.*, Eu.——FIG. 534,*5*. **C. oligocaenicus* (SPANDEL), Oligo., Ger.: ×195 (14).

**Rigaudites** FRIZZELL & EXLINE, 1957, p. 102 [**Synaptites cuvillieri* DEFLANDRE-RIGAUD, 1949, p. 3; OD]. Oval to broadly elliptical, large, concavo-convex, with socket and protruding lip at small end; socket M-shaped (rarely U-shaped); perforations 20-150, finely denticulate. *L.Cret.-Oligo.*, Eu.-N.Am.——FIG. 534,*8*. **R. cuvillieri* (DEFLANDRE-RIGAUD); *8a*, Eoc., Fr., ×90 (14); *8b*, Paleoc., USA(Tex.), detail of socket, ×165 (16).

**Spandelites** FRIZZELL & EXLINE, 1957, p. 101 [**Synaptites? irregularis* DEFLANDRE-RIGAUD, 1949, p. 10; OD]. Irregular, with simple and primitive socket composed of connecting trabeculae; perforations numerous, unequal in size, elliptical to subcircular, smooth. *Jur.*, Eu.(Fr.).——FIG. 534, *7a*. **S. irregularis* (DEFLANDRE-RIGAUD); ×400 (10).——FIG. 534,*7b*. *S. lehmanni* DEFLANDRE-RIGAUD; ×265 (10).——FIG. 534,*7c*. *S. arcuatus* DEFLANDRE-RIGAUD; ×265 (10).

## Family CALCANCORIDAE Frizzell & Exline, 1956

[=Platanchoriformidae DEFLANDRE-RIGAUD, 1952 *(partim)*]

Synaptid-type anchors, with shank, stock, and flukes; stock smooth or denticulate; flukes double or triple, smooth or with teeth on lower margins. *?Jur., Cret.-Pleist.*

**Calcancora** FRIZZELL & EXLINE, 1956, p. 150 [**C. mississippiensis*; OD]. Flukes double. [Unpublished record from L.Cret., Del Rio Clay, Austin, Texas; FRIZZELL & EXLINE.] *?Jur., Cret.-Pleist.*, Eu.-N.Am.-S.Am.——FIG. 527,*6*. **C. mississippiensis*, Oligo., USA(Miss.); ×90 (14).

**Calcancoroidea** FRIZZELL & EXLINE, 1956, p. 154 [**C. spandeli*; OD]. Flukes triple. *Oligo.*, Eu.——FIG. 527,*7*. **C. spandeli*, Ger.; *7a,b*, outer and lat. views; ×130 (14).

## Family CALCANCORELLIDAE Frizzell & Exline, new family

[=Calcancoridae FRIZZELL & EXLINE *(partim)*]

Molpadiid-type anchors, with shank and flukes, stock replaced by a terminal thickening. *Oligo.-Pleist.*

**Calcancorella** DEFLANDRE-RIGAUD, 1961, p. 95 [**Synaptites (Calcancora) spectabilis* DEFLANDRE-RIGAUD, 1959, p. 198; OD] [=*Molpadioites* DEFLANDRE-RIGAUD, 1961, p. 36 *(partim)*]. Diagnosis as for family. *Oligo.-Pleist.*, Eu.——FIG. 527,*5*. **C. spectabilis* (DEFLANDRE-RIGAUD), Oligo., Ger.; ×40 (9).

## POSITION UNCERTAIN

**Sclerothurites** DEFLANDRE-RIGAUD, 1961, p. 111 [**S. clypeus*; OD]. Small plates with few holes and very simple socket or stirrup. *Jur.*, Eu.——FIG. 534,*6*. **S. clypeus*, Fr.; ×265 (10).