TREATISE ON INVERTEBRATE PALEONTOLOGY

Prepared under Sponsorship of
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Directed and Edited by
RAYMOND C. MOORE

Part U
ECHINODERMATA 3

By J. WYATT DURHAM, K. E. CASTER, HARRIET EXLINE, H. B. FELL, A. G. FISCHER, D. L. FRIZZELL, R. V. KESLING, P. M. KIER, R. V. MELVILLE, R. C. MOORE, D. L. PAWSON, GERHARD REGNÉLL, W. K. SPENCER, GEORGES UBAGHS, CAROL D. WAGNER, and C. W. WRIGHT

VOLUME 2

THE GEOLOGICAL SOCIETY OF AMERICA, INC.
and
THE UNIVERSITY OF KANSAS PRESS

1966

Second Printing 1986
Third Printing 1992
Fourth Printing 1998*

Library of Congress Catalogue Card Number 53-12913
ISBN 0-8137-3022-8

*Distributed by the Geological Society of America, Inc., P.O. Box 9140, Boulder, Colorado 80301, from which current price lists of parts in print may be obtained and to which all orders and related correspondence should be directed. Editorial office for the *Treatise*: Paleontological Institute, 121 Lindley Hall, The University of Kansas, Lawrence, Kansas 66045.

PART U
ECHINODERMATA 3
ASTEROZOA—ECHINOZOA

By J. Wyatt Durham, K. E. Caster, Harriet Exline, H. B. Fell, A. G. Fischer, D. L. Frizzell, R. V. Kesling, P. M. Kier, R. V. Melville, R. C. Moore, D. L. Pawson, Gerhard Regnéll, W. K. Spencer, Georges Ubaghs, Carol D. Wagner, and C. W. Wright

VOLUME 2

ECHINACEA

By H. Barraclough Fell and David L. Pawson
[Victoria University of Wellington, New Zealand (transferred to Harvard University and Smithsonian Institution)]

INTRODUCTION

By H. Barraclough Fell

The Echinacea comprise endocyclic Euechinoidea in which the lantern is of stirodont or camarodont type. The assemblage is here divided into six orders embracing 15 families. As in the Diadematacea, so also in the Echinacea, the older and more primitive genera exhibit ambulacra with the simple structure seen in cidaroids. The great majority of genera, however, develop compound ambulacral (amb) plates, following several patterns, as described below. The primary tubercles, initially perforate and crenulate, tend in derived groups to become imperforate and noncrenulate. The spines (radioles), initially massive cylindrical rods of cidaroid facies, tend to lose the cortex and collar in later groups; unlike the Diadematacea, the spines are invariably solid.

The oldest Echinacea so far recognized are of Late Triassic age, and thus the superorder seems to have been differentiated at about the same time as the Diadematacea, and presumably both groups are derived from cidaroids. The surviving orders of Echinacea are predominantly shallow-water and littoral forms of cosmopolitan distribution, though the few survivors of the oldest echinacean families are for the most part found only in deep water. All six orders still have Recent representatives, though five of the 15 families are extinct. The youngest order (Echinoida) is not known earlier than the Cretaceous, and its four included families seem to be at their maximum development at the present time. Among these are some of the largest extant echinoids. Venomous species are seldom encountered, with exception of some Toxopneustidae, which have large aboral globiferous pedicellariae equipped with poison glands. The families Echinidae, Echinometridae, and northern Pacific Strongylocentrotidae are today the most numerous and conspicuous echinoids of the littoral zone. As fossils in the Tertiary they are less conspicuous than some members of the endocyclic orders, but this is a reflection not so much of their lesser importance in Tertiary seas, as rather of their lesser opportunity for preservation as fossils, since wave action and the absence of mud in reef areas frequented by most Echinoida would tend to destroy their tests or to reduce them to unidentifiable fragments. The Temnopleuroida prefer quieter, deeper offshore waters, often tolerating soft bottom. Probably for this reason the families of Temnopleuroida are much more conspicuous as fossils in Tertiary sediments than are the Echinoida. Of the older groups of Echinacea, only the Tiarechinidae seem to have been adapted to reef habitats, though it is not improbable that other reef-dwelling forms may have evolved during the Mesozoic, and have left only remains so fragmentary that they have not yet been recognized.

As in the Diadematacea, the test and spines have fundamentally the same structure as has been described above (p. *U*315) for Cidaroida. The following features, however, require special mention.

MORPHOLOGY

By H. Barraclough Fell

TEST

The body shape is essentially subspherical (e.g., *Echinus,* see Fig. 322,*2c*), but is subject to great variation in the relative values of vertical and horizontal diameters, leading to tall subcylindrical or conical forms on the one hand (e.g., *Diplotagma,* Fig. 301,*2b*), or flattened, almost discoidal tests on the other hand (e.g., *Coelopleurus,* Fig. 305,*1b*; *Plistophyma,* Fig. 301,*1a*; *Actinophyma,* Fig. 295,*2c*). The majority of genera have a more or less hemispherical test, somewhat flattened below. Among the Echinoida, unequal development of the horizontal diameters leads to ellipsoidal forms in the families Echinometridae and Parasaleniidae. Such elongation along one or other of the horizontal axes is not always related to the anteroposterior axis of symmetry, and is not induced by exocyclic migration of the periproct, as in pygasteroids or other so-called irregular groups of echinoids. In general, the symmetry is consistently radial, with no evidence of truncation on the posterior side (interamb 5), nor any corresponding truncation or elongation on the anterior side (amb III). Evidence of the existence of an anteroposterior axis is nonetheless easy to find, if the apical system be taken into account. The size of the body ranges from minute forms, such as the Pliocene temnopleurid *Pseudodicoptella,* with a test less than 3 mm. in diameter, to massive echinometrids such as *Evechinus,* in which the test may measure 150 mm. in diameter, and the echinoid *Echinus esculentus,* some specimens of which are 200 mm. in diameter. The test may be very delicate, but the sutures between the plates remain rigid, so that the flexibility seen in Diadematacea is here lacking. Among tropical genera of Echinometridae the plates may become greatly thickened and the test correspondingly robust and heavy. In the Arbacioida and Temnopleuroida a minute doweling or ball-and-socket interlocking of adjacent plates, which adds to rigidity of the test, is demonstrable.

APICAL SYSTEM

The apical system is initially dicyclic in the Mesozoic Echinacea (e.g., *Pseudosalenia,* see Fig. 274,*2a*) and this fundamental pattern is retained throughout the group, including Tertiary and Recent representatives (e.g., *Echinus,* see Fig. 322,*2b*). However, as in the Cidaroida and Diadematacea, the anus shows a persistent tendency to move toward the rear along the anteroposterior axis passing through amb III and interamb 5; this leads to the insertion of ocular I (e.g., *Acrosalenia,* Fig. 273,*3b*), or more commonly to the insertion of both ocular I and ocular V (e.g., *Pseudocentrotus,* see Fig. 321,*3a*). Somewhat rarely ocular IV may also become insert (e.g., *Sterechinus,* see Fig. 322,*3*), or the whole apical system may return to its archaic pre-echinacean monocyclic condition (e.g., *Hemidiadema,* see Fig. 311,*1f*). The anus may tend to move posterolaterally, so that some genera consistently exhibit a posterodextral anus, and a consequential adapical displacement of oculars I and II (e.g., *Heterosalenia,* see Fig. 274,*1f*); these features may be of systematic value in defining genera, but only occasionally are of higher significance. A notable example is the Saleniinae, where posterodextral displacement of the anus is consistent, and constitutes the main subfamilial character. Although such deviations in position of the anus occur repeatedly in various families, the great majority of genera exhibit a simple backward movement of the anus, in the direction of interamb 5, with only individual variants among species where slight dislocation to one side or the other can be detected. Thus, even in such genera of Echinometridae as have acquired an ellipsoidal test, through elongation along one or other of the horizontal axes, the major axis of morphological symmetry (anteroposterior axis) remains unaffected, as proved by the consistent insertion of oculars I and V, through resorption of the adproctal borders of the adjacent genital plates. This axis of symmetry corresponds to the Lovénian plane, and is the same as can be observed even in some of the Cidaroida. It is also the same as that which becomes the major plane of bilateral symmetry in the various exocyclic orders. A peculiarity of the Salenioida is the development of a single family polygonal suranal plate (see Fig. 274,*2a*), or several such plates. This characteristic gives the apical system of that order a calyx-like appearance. The Arbacioida have four or five triangular suranal plates which simulate the anal pyramid of some pelmatozoans and provide one of the ordinal characters of arbacioids (though usually lost in fossil specimens).

LANTERN AND PERISTOME

The major morphological distinction between the Diadematacea and Echinacea rests in the structure of the lantern. All orders of Diadematacea retain an aulodont lantern, essentially like that of the Cidaroida, having unkeeled teeth and an open foramen magnum in the jaw. The four stirodont orders of Echinacea (Salenioida, Hemicidaroida, Phymosomatoida, Arbacioida) have acquired a keel on the inner surface of each of the five teeth. The camarodont Echinacea probably arose from the stirodont stock (retaining the keeled dental apparatus), but differ in having the foramen magnum of the jaw closed by overgrowth of the epiphyses, which meet in the interradial mid-line of each jaw. As noted below (p. *U*437), a similar condition evidently arose independently in the Orthopsida, but since these latter betray through other evidence an origin from aulodont, rather than stirodont, ancestors, they cannot be classified with the camarodont Echinacea, and must stand as an isolated group.

Buccal plates (paired ambulacral elements imbedded in the peristomial membrane) have already been noted in the Diadematacea, and these structures occur also in the Echinacea.

The peristome itself varies considerably in size and outline. The peristome is large in all stirodont orders, but may be relatively small in the camarodonts. Its outline is more or less pentagonal or decagonal in the stirodont orders, where the gill slits are generally rather distinct (e.g., *Hemicidaris,* see Fig. 280,*1b*); this is also true of the Toxopneustidae among the camarodont orders (e.g., *Schizechinus,* see Fig. 320,*3a*). The other camarodont families have rather indistinct gill slits, and consequently a more rounded peristome. Gill slits are not apparent in the Tiarechinidae (see Fig. 325,*1b, 2d*), a family of uncertain affinity, here provisionally associated with the stirodonts (on account of arbacioid features).

The development of accessory (secondary) plates in the peristomial membrane varies with the family and seems to have little relationship to the ordinal category. Thus, among camarodont orders, both temnopleuroid and echinoid genera are known where the peristomial membrane is almost naked, with only scattered plates, whereas other genera may have very strongly plated membranes (notably the family Echinidae). The nature of the peristomial membrane is unknown in most of the fossil stirodont families, though it is rather densely plated in the extant representatives, especially in the Saleniidae (e.g., *Salenocidaris,* see Fig. 276,*4b*).

AMBULACRA

The ambulacral plates of Echinacea are nearly always compounded and are invariably so in the camarodont orders, as also in one stirodont order (Arbacioida). However, simple amb plates persist in some members of the older, more primitive stirodont orders (Salenioida, Hemicidaroida, Phymosomatoida), all of which originated in the Late Triassic and Early Jurassic. Among the Saleniidae, simple amb plates are known only in the Salenioida, though we may infer that primitive Acrosaleniidae will eventually be discovered with the same character. In Acrosaleniidae so far known, the plates are compounded in trigeminate groups, according to the diadematoid pattern (p. *U*231), the larger element being the median one of each triad (e.g., *Heterosalenia,* see Fig. 274, *1b*). The pore pairs form a single series, disposed meridionally in each column, though a partial triserial arrangement may develop adorally. In the Saleniidae, simple bigeminate or trigeminate plates occur (e.g., *Hyposalenia,* see Fig. 277,*1d*); with exceptionally (in the one genus *Polysalenia,* see Fig. 275,*1a-c*) a polyporous condition. The compounding is always diadematoid.

In Hemicidaroida the plates invariably are compounded in diadematoid groups, with polyporous plates the general rule in the Pseudodiadematidae (see Figs. 286, 288-291). In the Hemicidaridae the plates are compounded adorally, but above the ambitus the ambulacrum contracts abruptly, so that on the aboral surface the plates are simple primaries, carrying only small tubercles (e.g., *Plesiocidaris,* see Fig. 281,*1a*).

Primary plates occur in some genera of

Phymosomatidae, among Phymosomatoida, and also in the Tiarechinidae (here assigned to the order Plesiocidaroida). In more specialized Phymosomatidae the plates are compounded, some in polyporous and even in diplopodous plates (i.e., with the tube feet arranged in two vertical series on each plate). Trigeminate and polyporous plates occur in the Stomechinidae. As in the preceding orders, the compounding in Phymosomatoida is invariably of the diadematoid type. Examples of these are illustrated in Figures 293-304.

The Arbacioida (see Figs. 305-309) exhibit compound plates, usually trigeminate but polyporous in some, though some instances of simple plates without compounding are known (but never involving the entire ambulacrum). In all Arbacioida the compounding is of the **arbacioid type** (p. *U*231), in which the larger median element is flanked on either side by demiplates, a condition evidently derived from the diadematoid pattern. Where the plates remain simple, the triads exhibit an incipient arbacioid arrangement.

Among the camarodont Echinacea, where compounding of plates is invariable, the oldest known family of Temnopleuroida (Glyphocyphidae, see Fig. 310-312, appearing in the Early Jurassic) has trigeminate or polyporous plates developed according to the **diadematoid pattern.** The pore pairs are arranged monoserially and are not widened at the peristome. The Glyphocyphidae are not known to have survived beyond the late Eocene and they are the only camarodont group of Echinacea in which diadematoid compounding occurs.

In all other camarodont Echinacea the compounding follows a pattern not previously encountered, known as the **echinoid type;** in this pattern the largest element in the compound plate is not the median, but the lowermost member (e.g., *Gracilechinus,* see Fig. 322,*1b*). If polyporous plates develop, the additional demiplates therefore are always located above the major element (e.g., *Echinometra,* see Fig. 324,*6*). Compound ambs of the echinoid types are not known earlier than the Middle Cretaceous, and they are the only type of amb found in all families which have originated since that time.

Among the Temnopleuroida, trigeminate echinoid plates occur in the family Temnopleuridae, where the pore zones may be monoserial, biserial, or pluriserial, but are not widened adorally. Trigeminate or polyporous plates of echinoid type occur in the Toxopneustidae, where the pore zones are greatly widened in some forms toward the peristome.

Trigeminate echinoid plates characterize the Parasaleniidae, among the Echinoida; some Echinidae and some Echinometridae have similar plates. In all Strongylocentrotidae, most Echinometridae, and some Echinidae, polyporous echinoid plates are developed. The pore zones are commonly petaloid or widened adorally in the Echinometridae. In this family compounding reaches an extreme, with as many as 16 separate amb plates uniting together and sharing in production of a relatively enormous primary tubercle (e.g., *Heterocentrotus,* see Fig. 324,*7a-c*).

It is apparent that similar, though independent, evolution has occurred in each of the groups of Echinacea, always along the same general lines—i.e., simple amb plates tending to form bigeminate or trigeminate compounds, yielding in turn 4-geminate, 5-geminate, or higher multiples of polyporous compounding; initially the compounding followed diadematoid patterns, but (assuming the Glyphocyphidae to be ancestral to other Temnopleuroida) this was transformed into echinoid compounding in mid-Cretaceous times.

INTERAMBULACRA

In oldest stirodont Echinacea, notably the Salenioida, Hemicidaroida, and some Phymosomatoida (groups which can be traced back to the Late Triassic and Early Jurassic), the interambulacra present a cidaroid aspect (e.g., *Heterosalenia,* see Fig. 274,*1a*; *Hemicidaris,* see Fig. 280,*1f*). This is on account of the massive development of a single primary tubercle on each interamb plate. In the Salenioida and Hemicidaridae (Hemicidaroida), the areole is correspondingly enlarged to carry musculature of the large spine supported on the tubercle. The areoles may be confluent, as in many cidaroids, and the secondary tubercles very reduced and restricted to admedian and adradial borders of each plate. The massive primary tubercles form a single, very conspicuous and prominent series in each interamb column. These features seem to point to a cidaroid, rather than diadematoid, derivation of the early stirodont Echinacea. In some Pseudodiadematidae, and still more in later families, the secondary tubercles may become enlarged, and even equal the primaries, so as to form several series in each area, arranged vertically and horizontally (e.g., *Tetragramma,* see Fig. 291,*1h*). In later groups, especially the camarodonts, the primary tubercles suffer considerable reduction in size, with corresponding reduction in the radioles, and simultaneous development of additional secondary or tertiary and miliary tubercles on the residual area of each plate. These developments result in a more uniform and more nearly spherical surface of the test as a whole, the interambs presenting less contrast to the ambs. However, the primary tubercles may become very conspicuous and enlarged as a secondary development in some camarodonts, and this is especially true of the Echinometridae. When this occurs, it is usually accompanied by a corresponding enlargement of primaries on the ambulacral plates, made possible by very advanced compounding of the amb plates, as noted under that heading.

In Arbacioida the interamb is characterized by persistence into the adult state of the initial primordial unpaired interamb plates adjoining the peristome, some carrying an unpaired median tubercle near its distal angle. A still more remarkable condition occurs in the Upper Triassic Tiarechinidae, where the primordial interamb plate supports a median (i.e., third) column of interamb plates, situated between the two columns normally present in Euechinoidea. Whether this should be interpreted as persistence of pluriserial structure, presumably inherited from a Paleozoic ancestor, is very uncertain. It does suggest, however, that the Arbacioida may be related to the Tiarechinidae or derived from them.

TUBERCLES

The evolution of tubercles in all groups of Echinacea presents an orderly sequence in which an initially perforate and crenulate condition (see Fig. 280,*1f*) is supplanted by later evolved imperforate and noncrenulate conditions (see Fig. 306,*3b*). The two transients (perforate passing to imperforate, and crenulate passing to noncrenulate) evolved more or less independently at different rates in different families, with the result that sometimes "mosaic" phases are seen, in which a relatively advanced condition of one variable may be combined with a relatively primitive condition of another.

Taking first the four stirodont orders, the oldest known family of Salenioida (Acrosaleniidae) appeared first in the Early Jurassic, with perforate crenulate tubercles, these forms surviving only to the Late Cretaceous; in Late Jurassic time the Saleniidae arose, with imperforate tubercles, though still retaining the crenulate condition, even in the present-day representatives of the family. Of the Hemicidaroida, both families (Hemicidaridae, Pseudodiadematidae) appeared first with perforate crenulate tubercles (in Late Triassic and Early Jurassic times, respectively), and both families retained these characters until their final extinction in the Late Cretaceous. Of the Phymosomatoida, the family Phymosomatidae appeared in the Early Jurassic, already with imperforate tubercles, though retaining the crenulation (see Fig. 297,*2c*). Since other characters suggest a relationship with Hemicidaroida, we may guess that the Phymosomatidae are imperforate derivatives of that order, the first such derivatives to arise, and still retaining the original crenulation. The Stomechinidae differ from the Phymosomatidae in having lost the crenulation (see Fig. 304, *3d*), and must therefore represent a further derivative of the same line, and they too are known from the Early Jurassic. Both these phymosomatoid families have persisted to the present time, each represented by a single known surviving genus. The Arbacioida, comprising the single known family Arbaciidae, appeared first in the Middle Jurassic, at which time they had already acquired the imperforate noncrenulate tubercles which they retained throughout their subsequent history; their origin is possibly to be sought among the Tiarechinidae, which had developed tubercles of the same type in Late Triassic time, though the derivation of the Tiarechinidae themselves is at present obscure.

Taking now the two camarodont orders of Echinacea, the Temnopleuroida first appeared in the fossil record in the early Jurassic, and as would be expected, have perforate crenulate tubercles. The imperforate condition first appeared in the family Temnopleuridae (in the Middle Cretaceous), combined with crenulation, though in a few genera (mainly of the later Tertiary) the crenulation is vestigial or lost. The third temnopleuroid family (Toxopneustidae) is not known prior to the early Oligocene, when they already had imperforate, noncrenulate tubercles, a condition retained to the present time. Of the four families of Echinoida, none is known with certainty before the Paleocene (Echinometridae), though some doubtful members of the family Echinidae occur in Early Cretaceous sediments. These families (also Strongylocentrotidae and Parasaleniidae) all present imperforate noncrenulate tubercles and retain this feature to the present time.

Summarizing, then, the dominant modern groups of Echinacea (Temnopleuroida, Echinoida) were the last to become differentiated, and all six surviving families of these two orders have imperforate tubercles; five of the six have also lost the crenulation. Of the more ancient groups which still have surviving members, the Arbacioida, like Echinoida and Temnopleuroida, have imperforate noncrenulate tubercles; and the relict groups of Late Triassic and Early Jurassic derivation, are each represented in Recent faunas only by imperforate members. The only crenulate Echinacea which still have surviving members are the families Saleniidae and Phymosomatidae, and these survivors are clearly relicts of early Mesozoic faunas, retaining an archaic aspect.

EPISTROMA

A characteristic feature of the Arbacioida and some Temnopleuroida (Glyphocyphidae, Temnopleuridae) is the development of sculpture on the surface of the test. This consists of substance (epistroma) in the form of raised ridges or prominences, associated in some genera with indentations or pits, producing more or less complex patterns in relief. In the Arbacioida the epistroma, if present, tends to assume the form of globules or warts of calcite on the surface of the plates. In denuded tests (e.g., *Glypticus,* see Fig 309,*1d*), the epistroma may simulate tubercles, though of course no spines are carried on the warts. In Temnopleuroida the epistroma may appear as ridges which unite chains of secondary tubercles, commonly in more or less radiating or zigzag patterns about or between the primary tubercles (see Fig. 313,315,321). In the temnopleurid *Pseudechinus,* such epistroma may be present only in very young stages and may constitute almost the only evidence of the temnopleurid affinity of species of the genus (see Fig. 317,*1b*). In some Temnopleuroida well-defined pits or sunken areas may occur, usually along the sutures or at the angles of the plates (e.g. *Temnotrema,* see Fig. 317,*4*). Many echinaceans exhibit sculpture on the apical system and epistroma here is especially characteristic of some Salenioida (e.g., *Hyposalenia,* see Fig. 277,*1f, h-j*).

SPINES

As noted above (p. U343), the primary spines (radioles) in the Diadematacea are usually hollow and delicate. The Echinacea differ markedly, and in this respect approach the Cidaroida in having solid (commonly rather massive) spines. In addition, other cidaroid features may be present, notably development of an external cortex layer on the spine, and consequent presence of a transitional collar zone at the base of the shaft, where the cortex is lacking. It is significant that spines of more or less cidaroid character, including a cortex and collar, occur in the oldest and most primitive orders of Echinacea, the Salenioida (see Figs. 273,*1a*; 274,*2e*), Hemicidaroida (see Fig. 280-285), some Phymosomatoida (see Fig. 293) and Arbacioida (see Fig. 306). These point to a cidaroid, rather than diadematoid, ancestry of the stirodont groups. In some Phymosomatoida the cortex and collar are lacking and such features are unknown in any of the camarodont Echinacea. The data suggest that the spines of Echinacea developed initially from a cidaroid pattern and gradually lost the cidaroid character, the temnopleuroid and echinoid types representing late divergent phases.

CLASSIFICATION AND EVOLUTIONARY TRENDS

By H. Barraclough Fell

The foregoing review of morphological features discloses some striking similarities to Cidaroida in the earlier stirodont orders, and we may conclude that the origin of the stirodont Echinacea must lie among Cidaroida, an opinion already expressed by Mortensen (136i). The characters of the spines especially exclude Diadematacea as possible ancestral forms, save only the Pedinoida—and these latter are excluded since pedinoids had already lost crenulation of the tubercles. The widespread occurrence of diadematoid compounding in both Diadematacea and stirodont Echinacea seemingly points to a common origin for both groups, though it is not yet possible to suggest any particular cidaroid group which might be ancestral. Recently Durham & Melville (52) have proposed a possible diadematoid ancestry for the stirodont Echinacea, on the basis of occurrence in the English Lower Jurassic of echinoids with perforate crenulate tubercles, hollow spines, and keeled teeth. The material is stated, however, to be insufficiently known for description. While it is impossible to discuss this view at length without further details, the criticism must be made that hollow spines seem most unlikely to have given rise to the characteristic massive cidaroid spines of early families of stirodont echinoids, whereas it is no more difficult to envisage the independent development of keeled teeth in diadematoids than the double origin of camarodont dentition, and the latter is now generally accepted. The fact that most Diadematacea share with Echinacea paired buccal plates in the peristomal membrane might be cited as evidence of affinity, since known cidaroids do not share this feature. However, a multiplated peristome is known in the Salenioida, and the general weight of other evidence (reviewed by Mortensen, 136b) seems to exclude the Diadematidae from ancestry of Salenioida. Therefore, a cidaroid origin of the stirodont Echinacea is here preferred as being open to fewer objections. The Salenioida and Hemicidaroida probably share a common early Triassic ancestry. In the former order the Acrosaleniidae would be the earlier stock, giving rise to Saleniidae in mid-Jurassic times, some members of the latter still surviving. Among the Hemicidaroida, the Pseudodiadematidae were differentiated by Late Triassic time and evidently represent the older of the two familial lines involved, having relatively generalized ambulacral structure. From them the Hemicidaridae arose at the beginning of the Jurassic, and from these in turn the Phymosomatoida developed by assuming imperforate tubercles. Subsequent loss of crenulation would lead to differentiation of the Stomechinidae, presumably from Phymosomatidae.

The origin of the Arbacioida seems to lie among the Tiarechinidae, but the source from which the Tiarechinidae arose is not clear.

The camarodont Echinacea were thought by Mortensen (136i) to have arisen as two distinct lines derived from stirodont Echinacea. The Temnopleuroida may have evolved from Pseudodiadematidae, if we accept the Glyphocyphidae as the earliest members of that order. Alternatively, if the Glyphocyphidae be regarded as a separate line, then it would be feasible to seek a phymosomatid ancestry for the Temnopleuridae and Toxopneustidae, since these families share imperforate tubercles, and the older Temnopleuridae also share crenulation with the Phymosomatidae.

The Echinoida were thought by Mortensen (136i) to represent another camarodont development from a stirodont ancestry, which he sought among the Stomechinidae, presumably because imperforate noncrenulate tubercles appeared first in Stomechinidae.

Durham & Melville (52), citing an earlier opinion of Mortensen (136b), have suggested an origin for the Arbacioida among the Hemicidaroida, but this view is difficult to relate to the known history of the evolution of the tubercles. It seems that the Tiarechinidae are a more promising source, though little is known of this Triassic family.

Durham & Melville (52) recognized five orders of Echinacea (Hemicidaroida, Phymosomatoida, Arbacioida, Temnopleuroida, Echinoida), the last three here treated as proposed by them. The Hemicidaroida were considered by Durham & Melville to

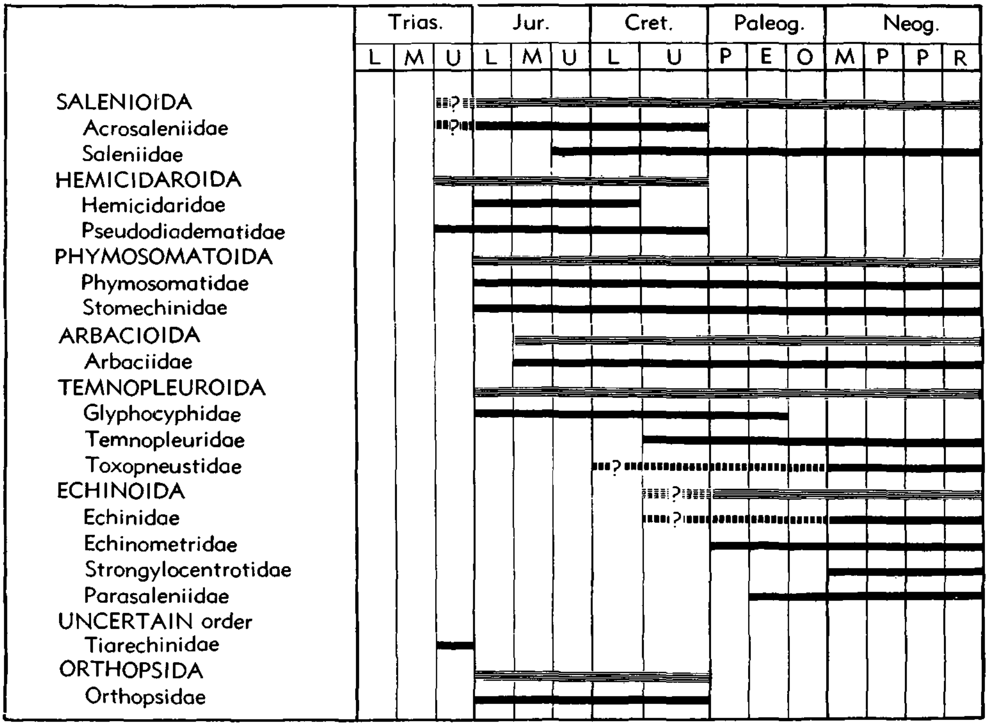

FIG. 272. Time ranges of families and orders of Echinacea and of Orthopsida (Echinacea or Diadematacea).

comprise the Acrosaleniidae, Saleniidae, and Hemicidaridae. Such an assemblage is exceedingly difficult to define, because the same authors refer the Pseudodiadematidae to the Phymosomatoida. As already indicated by MORTENSEN (136i), the Hemicidaroida must represent the initial stock of a line which included the Pseudodiadematidae, and although MORTENSEN did not then give reasons for his opinion, the foregoing review of morphological features suggests that it is well founded. Consequently, the ordinal arrangement here adopted places the Pseudodiadematidae and Hemicidaridae together in the Hemicidaroida, defined primarily as stirodont Echinacea, sharing perforate crenulate tubercles, as well as other features already indicated. The Saleniidae and Acrosaleniidae stand alone, as MORTENSEN has maintained, characterized by the peculiar features of the apical system. Accordingly, a separate order Salenioida (=Calycina) is here preferred to encompass these two families, the more so since their near relationship to the other stirodont Echinacea is rather doubtful.

As inferred by MORTENSEN (136i), the Orthopsidae, although camarodont, cannot be derived from stirodont Echinacea, and must represent a separate line, perhaps of aulodont origin. DURHAM & MELVILLE (52) excluded the family from the camarodont orders of Echinacea and associated it with the Hemicidaroida. However, other reasons can be advanced for excluding Orthopsidae from the Hemicidaroida, and since insufficient evidence at present warrants erecting a separate superorder for their reception, the Orthopsidae are here regarded as a distinct order, Orthopsida, of uncertain superordinal affiliation.

STRATIGRAPHICAL DISTRIBUTION

By H. BARRACLOUGH FELL

The recorded time ranges of the orders and families of Echinacea are indicated in

Figure 272. Owing to lack of information on the buccal plating and pedicellariae in most fossil genera, it is impracticable to represent peak development of genera by variation in the thickness of the lines, for sampling on the basis of fossils is not directly comparable with that of extant forms, and such comparison would give misleading emphasis to Recent genera.

SYSTEMATIC DESCRIPTIONS

By H. BARRACLOUGH FELL and DAVID L. PAWSON

Superorder ECHINACEA Claus, 1876

[*nom. correct.* DURHAM & MELVILLE, 1957 (*pro* Echinideae CLAUS, 1876)] [Diagnosis prepared by J. W. DURHAM and R. V. MELVILLE]

Corona rigid; periproct within apical system; branchial slits present in adult; perignathic girdle complete in adult; lantern present in adult, teeth keeled. *U.Trias.-Rec.*

Order SALENIOIDA Delage & Hérouard, 1903

[*nom. transl.* FELL & PAWSON, herein (*ex* Salenina DELAGE & HÉROUARD, 1903, p. 235] [=Calycina GREGORY, 1900 (name not based on any included taxon)]

Lantern stirodont. Test of cidaroid facies (each interamb plate with single large primary tubercle and number of much smaller secondary tubercles). Ambs simple or compounded in diadematoid manner. Apical system with one or several large, polygonal suranal plates, closely connected with the oculogenital ring, simulating a calyx. Inner border of oculogenital ring angular, not circular or oval. Periproct posterior (toward genital 5) or posterodextral (toward ocular I), encroaching on posterior edge of suranal plate, or plates, which become emarginated. Primary tubercles usually crenulate. Primary spines of cidaroid facies, with collar and cortex layer. *?U.Trias., L.Jur.-Rec.*

Family ACROSALENIIDAE Gregory, 1900

[Acrosaleniidae GREGORY, 1900, p. 306]

Primary tubercles perforate, crenulate (exceptionally some aboral amb tubercles noncrenulate). Apical system large, usually dicyclic, but oculars I and V insert in some. Gill slits distinctly developed on peristome. Primary spines large, cylindrical, tapering or clavate, with solid medulla and outer cortex. Tridentate and ophicephalous pedicellariae known in some species. Amb plates simple, or arranged in diadematoid triads, or fused into diadematoid compound plates (in some polyporous at ambitus). Test small to moderate (up to 40 mm. horizontal diameter), low, hemispherical to pentagonal. *?U.Trias., L.Jur.-U.Cret.*

Acrosalenia L. AGASSIZ, 1840, p. 38 [**A. spinosa*; OD] [=*Milnia* HAIME, 1849, p. 217 (type, *Hemicidaris angularis* AGASSIZ, 1846, p. 337); *Thylosalenia* POMEL, 1883, p. 102 (type, *Hemicidaris patella* AGASSIZ); *Plesiosalenia* VALETTE, 1906, p. 5 (type, *Acrosalenia pentagona* COTTEAU)]. Low, hemispherical. Periproct displaced toward genital 5, or ocular I, or exceptionally penetrating into interamb 5. Ambs trigeminate throughout; or simple aborally with alternately large and small tubercles. Pore pairs in linear series, or in arcs of 3 near peristome. Primary spines elongate, cylindrical, smooth or granulated. *?U.Trias. (Rhaet.); L. Cret.(Hettang.),* Eu.-E. Afr.-Madag.——FIG. 273,*1*. *A. hemicidaroides* WRIGHT, Bathon., Eng.; *1a,b*, test, aboral (with spines), oral, ×0.7 (172).——FIG. 273,*2*. *A. marcoui* COTTEAU, U.Jur.(Kimmeridg.), Fr.; *2a*, amb plates near peristome, ×3.3; *2b*, interamb, ×2 (27d).——FIG. 273,*3*. **A. spinosa*; *3a*, amb column, ×2 (50); *3b*, apical system, ×1.3 (27d).——FIG. 273,*4*. *A. patella* (AGASSIZ), L.Cret.(Neocom.), Fr.; interamb, ×2 (27d).

Heterosalenia COTTEAU, 1861, p. 96 [**H. martini*; OD] [=*Metacrosalenia* CURRIE, 1925, p. 55 (type, *M. pseudocidaroides*; OD)]. Like *Pseudosalenia*, but periproct displaced to right towards ocular I. Radioles unknown. *U.Jur.(Oxford.),* Eu.-E.Afr. (Somalia); *U.Cret.(Senon.),* Eu.-Jamaica.——FIG. 274,*1*. **H. martini*, U.Cret.(Senon.), Fr.; *1a,b*, interamb, amb, ×2.7; *1c-e*, test lat., aboral, oral, ×1.3; *1f*, apical system, ×2.7 (27a).

Monodiadema DE LORIOL, 1890, p. 58 [**M. cotteaui*; OD]. Like *Acrosalenia*, but all amb plates simple primaries. Apical system caducous; with conspicuous posterior elongation (as in some species of *Acrosalenia*). *U.Jur.,* Eu., N.Afr.——FIG. 275, 2. **M. cotteaui*, U.Jur.(Oxford.), Port.; *2a,b*, test, lat., aboral, ×1.3 (105); *2c,d*, test, oral, and amb, ×1.3, ×2 (124); *2e*, secondary spine, ×? (105); *2f*, amb plates, detail, ×10 (136c).

Polysalenia MORTENSEN, 1932, p. 490 [**P. notabilis*; OD]. Like *Pseudosalenia*, but tubercles almost all imperforate (some perforate examples indicating, however, affinity with Acrosaleniidae rather than Saleniidae). Primary amb plates polyporous at ambitus, and enlarged, their tubercles almost as large as interamb tubercles. Amb plates trigeminate aborally. *U.Cret.(Senon.),* Sweden.——FIG. 275,

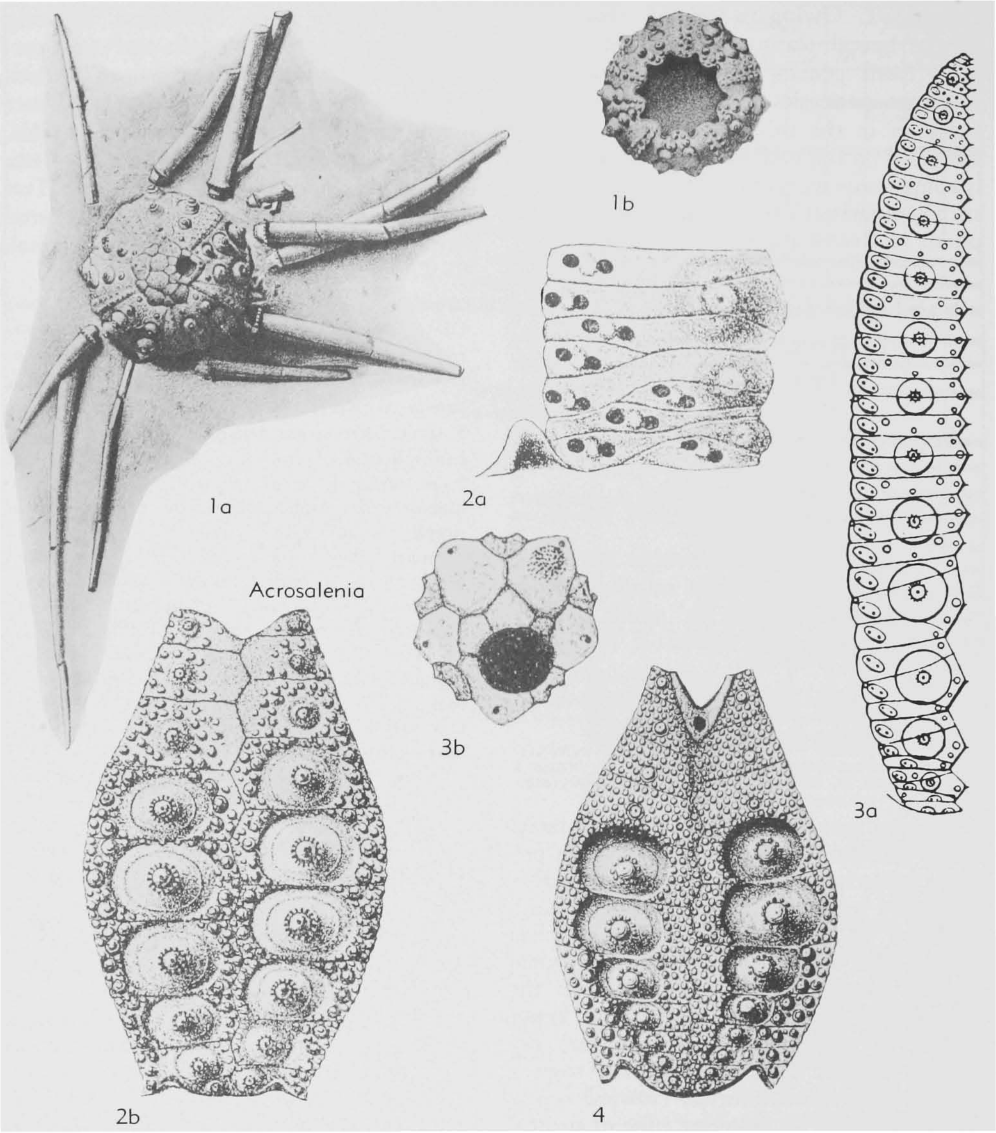

FIG. 273. Acrosaleniidae (p. U375).

*1. *P. notabilis; 1a-c,* test, aboral, lateral, oral, ×0.73 (136c).

Pseudosalenia COTTEAU, 1859, p. 22 [**P. flexuosa;* OD (=*Acrosalenia aspera* L. AGASSIZ, 1838)] [=*Amphisalenia* POMEL, 1883, p. 95 (?type); *Perisalenia* VALETTE, 1906, p. 6 (type, *Acrosalenia gauthieri* COTTEAU)]. Like *Acrosalenia,* but ambs sinuate, trigeminate below ambitus, with simple amb plates aborally, where tubercles are imperforate noncrenulate. Periproct on mid-line, displaced towards genital 5. Primary spines cylindrical (?or ovoid-clavate). *U.Jur.,* Eu., *M.Cret.,* Eu.-Asia Minor(Lebanon)-C.Am.(Honduras). ——FIG. 274,*2a-d. *P. aspera,* U.Jur., Fr.; *2a,* apical system, ×3.3; *2b-d,* test, aboral, oral, lat., ×1.3 (27d).——FIG. 274,*2e.* (?) *P. zumoffeni* DE LORIOL, Cenoman., Lebanon; primary spine (possibly of this species), ×3.3 (125).

Recrosalenia CURRIE, 1925, p. 47 [**R. somaliensis;* OD]. Like *Monodiadema,* but amb plates near peristome arranged in diads or triads. *U.Jur. (Bathon.* or *Callov.),* N. Afr. (Somalia).——FIG.

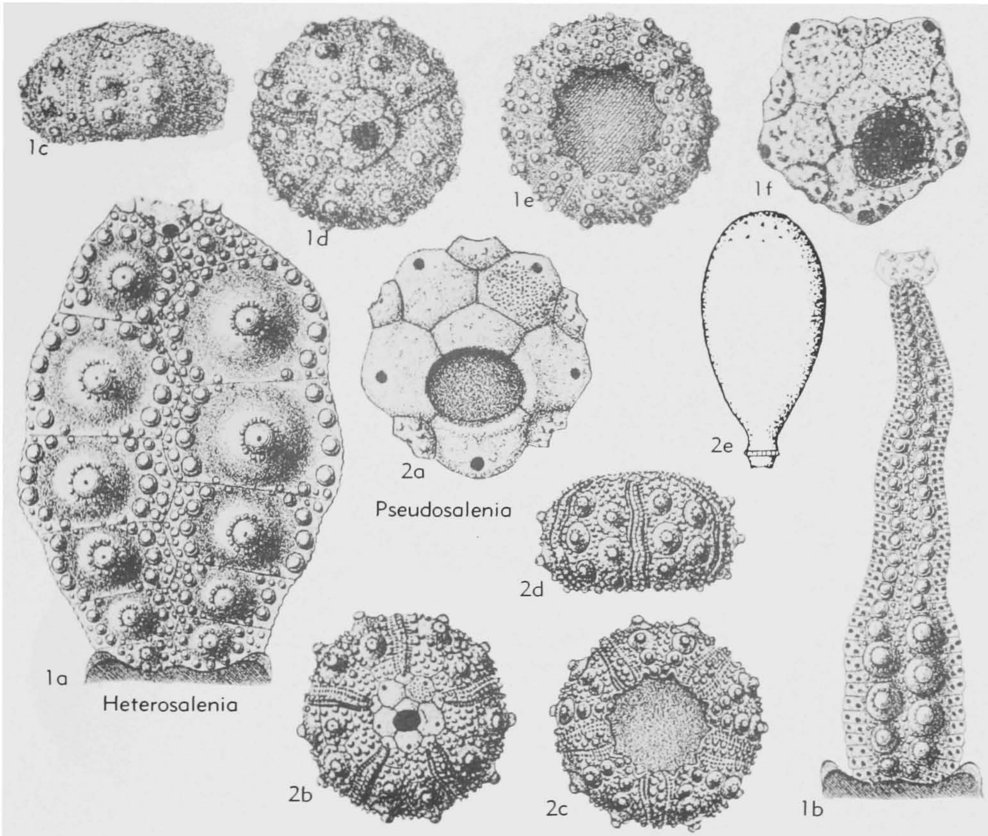

FIG. 274. Acrosaleniidae (p. *U375-U376*).

275,*3*. **R. somaliensis*; *3a*, interamb, ×3.3; *3b*, III amb triad, ×12; *3c*, test, lat. ×,1.7 (39).

Family SALENIIDAE L. Agassiz, 1838

[*nom. correct.* HAIME, 1849, p. 218 (*pro* des Salenies AGASSIZ, 1838, p. 5)]

Primary tubercles imperforate. Primary amb tubercles noncrenulate; primary interamb tubercles usually crenulate. Apical system large, usually dicyclic, but oculars I and V insert in some. Gill slits usually developed on peristome. Primary spines long and slender, with more or less spinulose cortical layer on shaft. Amb plates simple, bigeminate, or trigeminate (apparently of diadematoid type, but outlines difficult to distinguish); pore zones usually straight (exceptionally widened at peristome). Spheridia present, on amb mid-line near peristome, near pores at ambitus, free, or exceptionally in pits. Pedicellariae of tridentate, ophicephalous and triphyllous types; globiferous type unknown. Tests mostly small (up to 15 mm. horizontal diameter, but exceptionally reaching 45 mm.). *U.Jur.-Rec.*

Subfamily SALENIINAE L. Agassiz, 1838

[*nom. correct.* HAIME, 1849, p. 218 (*pro* des Salenies AGASSIZ, 1838, p. 5)]

Periproct displaced posterodextrally, toward ocular I, hence lying to right of anteroposterior axis amb III-interamb 5. *L. Cret.-Rec.*

Salenia GRAY, 1835, p. 58 [**Cidarites scutigera* MÜNSTER (in GOLDFUSS), 1826, p. 121; OD] [=*Cidarelle* DESMOULINS, 1835, p. 200 (type, *Echinus petaliferus* DEFRANCE); *Bathysalenia* POMEL, 1838, p. 94 (?type)]. Test hemispherical, usually small (5-15 mm. horiz. diam.), some up to 25 mm. horiz. diam. Ambs bigeminate throughout, each compound plate carrying 2 pore pairs and 1 primary tubercle. Pore zones straight, not con-

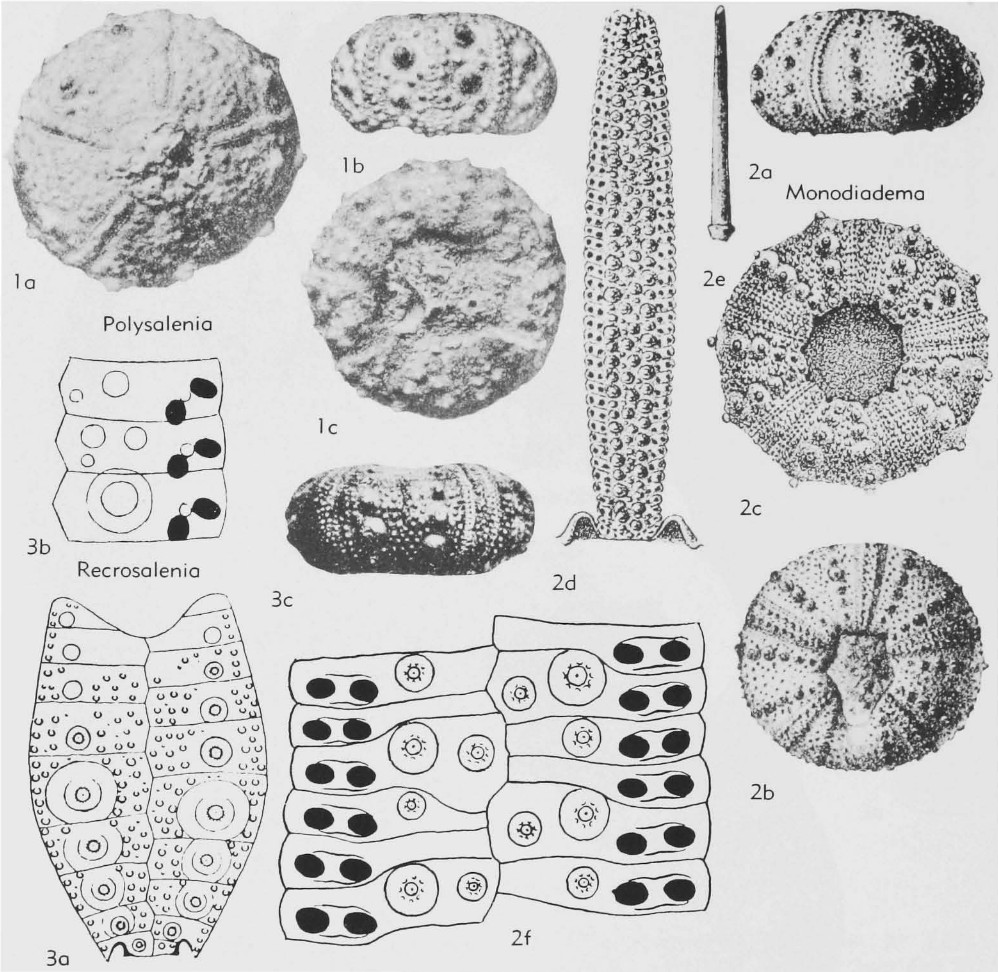

FIG. 275. Acrosaleniidae (p. U375-U377).

spicuously widened at peristome. Primary spines usually slender and curved, thorny and verticillate, some expanded distally; in living species usually banded with red. *L.Cret.(Neocom.)-U.Cret.*, Eu.-Afr.-Asia-N. Am.-Australia; *Eoc.*, Eu.-Afr.-N.Am.; *L.Oligo.*, N.Am.(Ore.); *Mio.*, N.Afr.; *Rec.*, Indo-Pac.-Carib. (tropic-subtropic), archibenthal.——FIG. 276,*2a*. *S. goesiana* LOVÉN, Rec., Carib. (90-540 m.); detail of interamb and adjacent pore zones, ×7 (1).——FIG. 276,*2b,c*. *S. neocomensis* COTTEAU, L.Cret., Fr.; amb adoral, ×0.3, ×7 (27a). —— FIG. 277,*3*. *S. rejaudryi* ARNAUD, Senon., Eu.; interamb, ×3.3 (8).——FIG. 278,*2*. *S. tumidula* CLARK, Paleoc., N.Am.(N.J.); *2a-c*, test aboral, lat., oral, ×2 (24).

Salenocidaris A. AGASSIZ, 1869, p. 254 [**S. varispina*; OD]. Test small (less than 20 mm. horiz. diam.). As for *Salenia*, but amb plates bigeminate only at peristomial region, elsewhere simple, each plate carrying one pore pair and one tubercle. Primary spines long, slender, thorny, verticillate; in living species unicolored, not banded with red. *Rec.*, IndoPac.-Atl. (200-300 m.).——FIG. 276,*4a*. **S. varispina*, Carib. (567 m.); test of juvenile, oral, ×13.3 (3).——FIG. 276,*4b,c*. *S. miliaris* A. AGASSIZ, Pac. (1,200-3,000 m.); *4b*, peristome and adoral region, ×7 (27a); *4c*, amb, ×0.7 (20).

Salenidia POMEL, 1883, p. 94 [**Salenia gibba* AGASSIZ; SD LAMBERT & THIÉRY, 1910, p. 212] [=*Pleurosalenia* POMEL, 1883, p. 94 (*teste* MORTENSEN, 1935, p. 347)]. Like *Salenocidaris*, but ambs consisting throughout of primary plates, each with tubercle and pore pair. *M.Cret.-U.Cret. (Alb.-Senon.)*, Eu.; *Eoc.*, Pak.; *U.Eoc.(Aldingan.)*, Australia.——FIG. 276,*3*. *S. blandfordi* DUNCAN & SLADEN, Eoc., Pak.; amb plates, ×13.3 (47).——

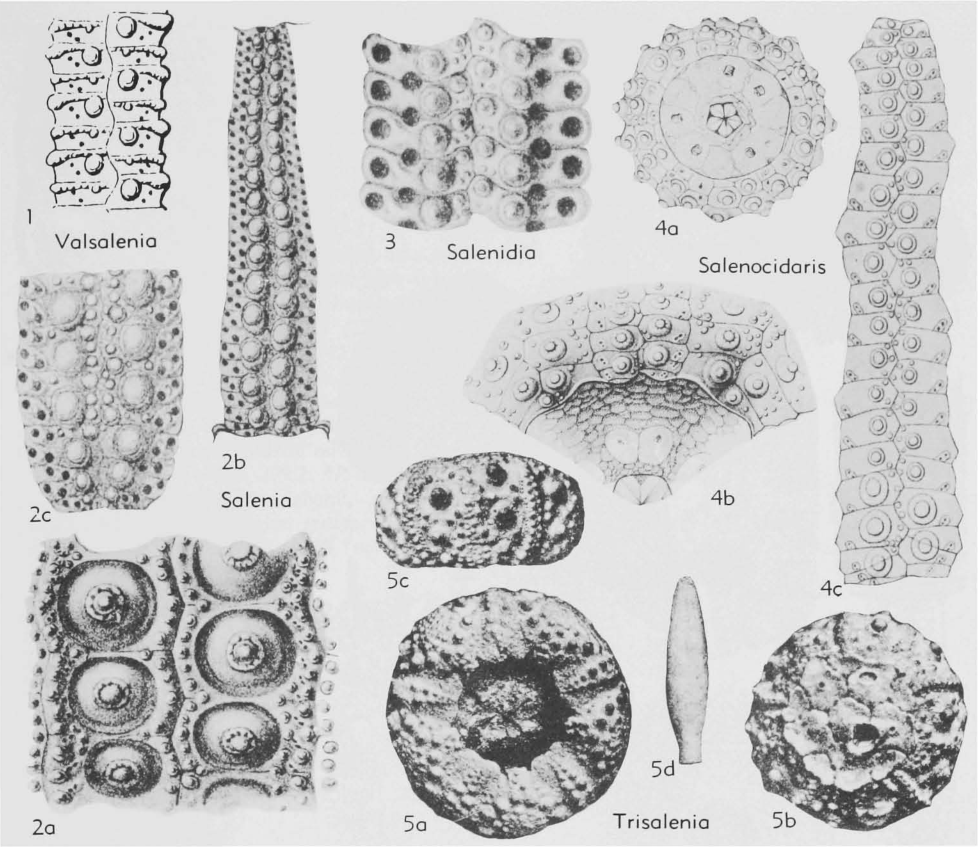

FIG. 276. Saleniidae (Saleniinae) (p. *U377-U379*).

FIG. 277,*2*. *S. heberti* (COTTEAU), Senon., Fr.; *2a,b*, amb, interamb, ×3.3 (27a).

Trisalenia LAMBERT, 1895, p. 262 [**Salenia loveni* COTTEAU, 1859; OD]. Test relatively large (up to 45 mm. horiz. diam.). Ambs trigeminate at ambitus, bigeminate adapically; pore zones much widened at peristome. Apical system smooth. Spines claviform. *U.Cret.(Senon.)*, Eu.——FIG. 276,*5*. **T. loveni* (COTTEAU), Sweden; *5a-d*, test, oral, aboral, lat., primary spine, ×0.7 (137).

Valsalenia MORTENSEN, 1934, p. 165 [**Salenia garumnensis* VALETTE, 1905; OD]. Like *Salenidia* but successive amb tubercles alternately large and small, and conspicuous transverse ridge defining adapical margin of each plate. *Paleoc.(Dan.)*, Eu. ——FIG. 276,*1*. **S. garumnensis* (VALETTE), Fr.; amb detail, ×4 (165).

Subfamily HYPOSALENIINAE Mortensen, 1934

[Hyposaleniinae MORTENSEN, 1934, p. 165]

Periproct displaced posteriorly toward genital 5, hence lying in anterioposterior axis amb III-interamb 5. *U.Jur.-U.Cret.*

Hyposalenia DESOR, 1856, p. 147 [**Echinus acanthoides* DESMOULINS; SD MORTENSEN, 1935, p. 344] [=*Peltastes* L. AGASSIZ, 1838, p. 27 (obj.) (*non* ROSSI, 1807); *Peltosalenia* QUENSTEDT, 1874, p. 36 (obj.)]. Test small (10-15 mm. horiz. diam.). Ambs bigeminate, with 1 tubercle and 2 pore pairs on each plate; pore zones uniserial. Interamb tubercles large, crenulate. Apical system with conspicuous striations, or sutural depressions; apical plates commonly elaborately sculptured. *U.Jur.(Kimmeridg.)-U.Cret.(Senon.)*, Eu.——FIG. 277,*1a-e*. **H. acanthoides* (DESMOULINS), Cenoman., Fr.; *1a-c*, test, aboral, lat., oral, ×1.3; *1d,e*, amb, interamb, ×7 (27a).——FIG. 277,*1f,g*. *H.* bunburyi (FORBES), Cenoman., Eng.; *1f,g*, apical system, test lat., ×2.7 (173).——FIG. 277,*1h*. *H. clathrata* (AGASSIZ), Cenoman., Eng.; apical system, ×2.7 (27a).——FIG. 277,*1i*. *H. wrighti* DESOR, Cenoman., Eng.; apical system, ×2.7 (27a).——FIG. 277,*1j*. *H. heliophora* (AGASSIZ & DESOR), Senon., Eu.; apical system, ×2.7 (27a). [=*Peltaris* QUENSTEDT, 1873, p. 236.]

Idiocidaris DE LORIOL, 1909, p. 228 [**I. lamberti*;

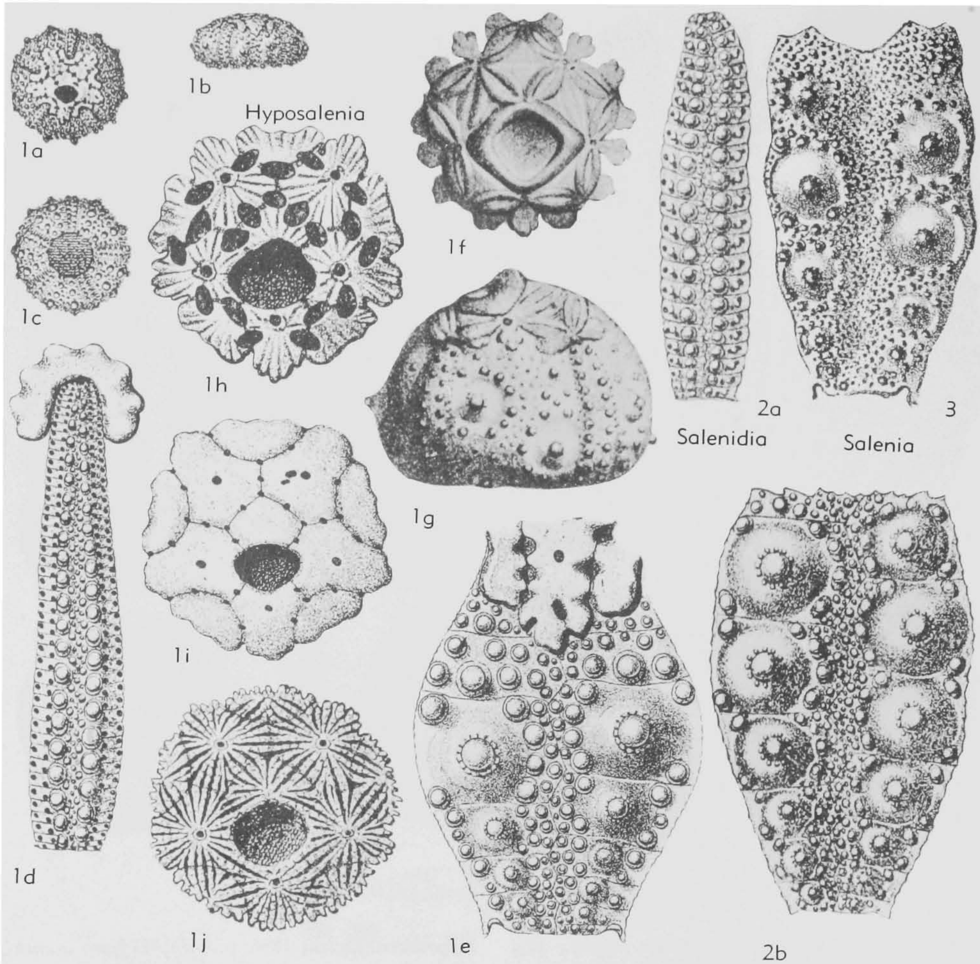

FIG. 277. Saleniidae (Saleniinae) *(2-3)*, (Hyposaleniinae) *(1)* (p. *U*377-*U*379).

OD]. Test small (8 mm. horiz. diam.). Apical system bearing sculptured, elevated pentagonal figure with each angle on ocular plate. Ambs simple, one tubercle and one pore pair on each plate; pore zones uniserial. One large crenulate tubercle on each interamb plate. *M.Cret.(Cenoman.)*, Asia Minor.——FIG. 279,*3*. **I. lamberti*, Syria; *3a*, test, aboral, ×1.3; *3b,c*, apical system, amb detail, ×5.3; *3d*, interamb, ×5.3 (126).

Glyphopneustes POMEL, 1869, p. xl [**Goniophorus problematicus* COTTEAU, 1880, p. 121; OD] [=*Coptophyma* PERON & GAUTHIER, 1879, p. 209 (obj.)]. Test small (10-12 mm. horiz. diam.), spherical. Ambs simple, plates grouped in triads, with primary tubercle on every 3rd plate. Spheridial pit (like that of *Goniophorus*) on amb plates adoral to tubercle-bearing place of each triad. Interamb plates each bearing one very large crenulate tubercle, suture between adjacent areoles depressed. Apical system dicyclic; no suranal plate. *M.Cret.*, N.Afr.——FIG. 278,*1*. **G. problematicus* (COTTEAU), Cenoman., Alg.; *1a*, interamb, ×5.3 (26); *1b*, amb adoral, ×8 (26); *1c*, amb adoral, ×10 (35, modified); *1d*, apical system, ×8 (26); *1e*, amb plates, detail, ×30 (136d); *1f*, interamb plates, detail, ×13.3 (136d).

[The systematic position of this genus is uncertain, the dicyclic apical system and transverse depressed suture on the interamb plates pointing to a temnopleurid affinity; on the other hand, the spheridial pits parallel those of *Goniophorus*, and the simple amb plates have nearer parallels among Saleniidae than in the Temnopleuridae. The balance of evidence favors a saleniid relationship in the opinion of MORTENSEN (136d), who has clarified some details of its structure.]

Goniophorus L. AGASSIZ, 1838, p. 30 [**G. lunulatus*; SD LAMBERT & THIÉRY, 1910, p. 209] [=*Gonosalenia* QUENSTEDT, 1872, p. 36 (?type)]. Test small (15 mm. horiz. diam.). Apical system with sculptured elevated ridges forming geometrical figures (rhombs and triangles); no sutural pits. Ambs bigeminate (possibly trigeminate adorally); pore zones uniserial. Amb plates each adorally bearing spheridial pit between adjacent primary tubercles. Interamb plates each with one large crenulate primary tubercle. Spines finely striated, cortex possibly lacking. *M.Cret.(Alb.-Cenoman.)*, Eu.-N.Am.——FIG. 279,*1*. **G. lunulatus*, Cenoman., Fr.; *1a-c*, test, aboral, lat., oral, ×1.7 (173); *1d*, adoral part of amb, with spheridial pits, ×7 (27a, modified); *1e*, interamb, ×3.3 (173); *1f,g*, interamb, amb, ×3.3 (27a).

Poropeltaris QUENSTEDT, 1875, p. 242 [**P. sculptopunctata*; OD]. Test small (9 mm. horiz. diam.). Apical system smooth, with depressed sutural pits. Ambs bigeminate, 1 tubercle for each 2 pore pairs. One large noncrenulate tubercle on each interamb plate. *U.Jur.*, Eu.——FIG. 279,*2*. **P. sculptopunctata*, Oxford., Ger.; *2a*, test, aboral, ×1.3; *2b,c*, amb, interamb, ×7; *2d*, apical system, ×4 (125). [=*Poropeltis* DUNCAN, 1889, p. 46 *(nom. null.)*.]

Order HEMICIDAROIDA Beurlen, 1937

[*nom. transl.* DURHAM & MELVILLE, 1957, p. 254 (*ex* suborder Hemicidarina BEURLEN, 1937, p. 65) (herein restricted to Hemicidaridae+Pseudodiadematidae)]

Lantern stirodont. Apical system lacking large polygonal suranal plates, not simulating calyx. Primary tubercles perforate, usually also crenulate (noncrenulate in *Cidaropsis*). *U.Trias.-U.Cret.*

Family HEMICIDARIDAE Wright, 1857

[Hemicidaridae WRIGHT, 1857, p. 68]

Test of moderate size, usually flattened adorally, commonly rather high. Ambs narrowing abruptly above ambitus, aboral ambulacral tubercles abruptly decreasing in size; amb plates compounded in diadematoid manner on adoral side, but usually simple primaries above ambitus. Peristome large, with conspicuous gill slits. Primary spines of cidaroid type, with distinct collar and cortex; secondary spines flattened. Pedicellariae and spheridia unknown. *L.Jur.-U.Cret.(Cenoman.)*.

Hemicidaris L. AGASSIZ, 1838, p. 3 [**Cidarites crenularis* LAMARCK, 1816, p. 59 (=*H. intermedia* COTTEAU, 1880, p. 41); SD GOLDFUSS, 1836, p. 122] [=*Hemipygus* ETALLON, 1859, p. 221 (juvenile stage, *fide* SEGUIN, 1906, p. 1167)]. Aboral amb plates not all simple primaries, usually bigeminate plates alternating with simple plates; ambital and adoral amb plates trigeminate or polyporous. All primary tubercles perforate, crenulate; large amb tubercles on each column; interamb plates with well-developed tubercles throughout, no naked space or reduced tubercles aborally. Primary spines elongate, cylindrical, tapering. *M.Jur.(Bajoc.)-U.Cret.(Cenoman.)*, Eu.-Asia Minor-N. Afr.-Madag.-N.Am.——FIG. 280,*1a-e*; 281,*2a,b*.

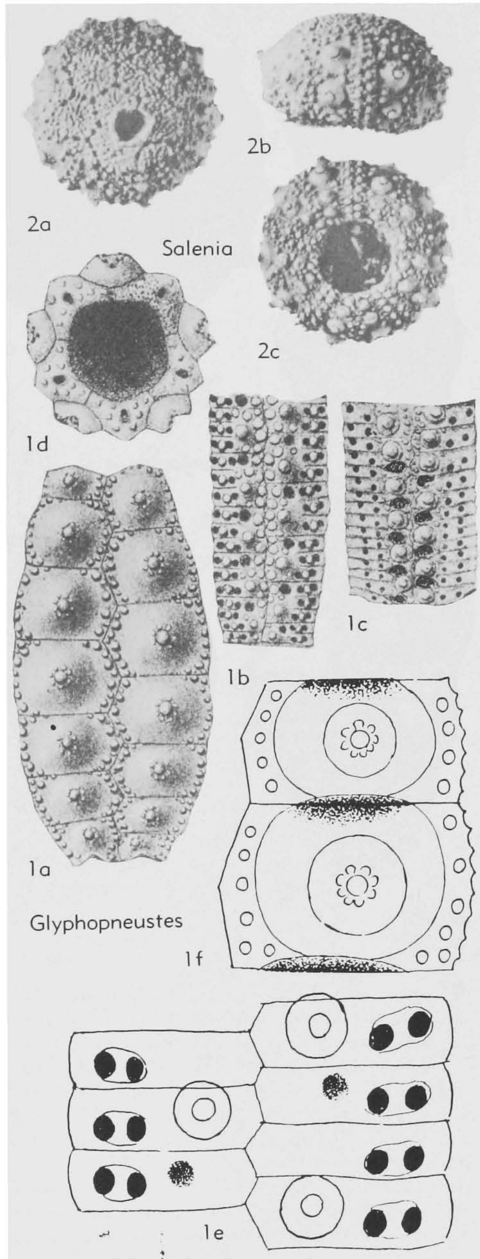

FIG. 278. Saleniidae (Saleniinae) *(2)*, (Hyposaleniinae) *(1)* (p. U377-U378, U380).

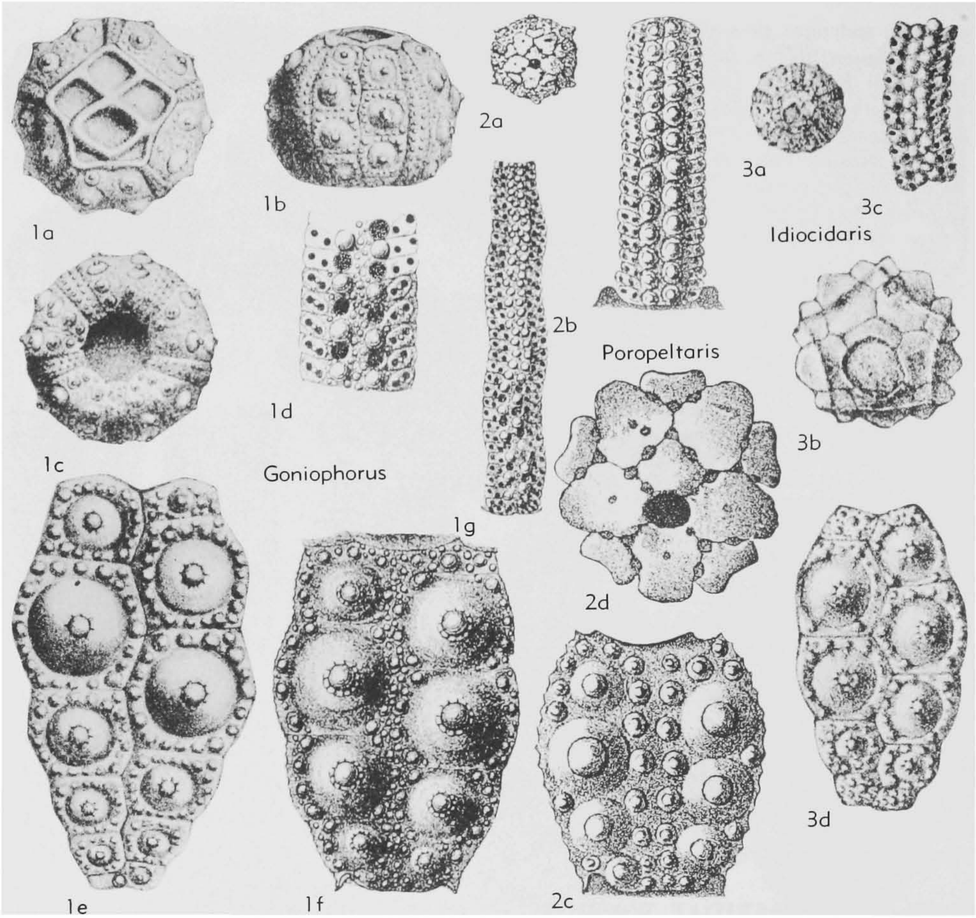

FIG. 279. Saleniidae (Hyposaleniinae) (p. U379-U381).

*H. crenularis (LAMARCK), U.Jur.(Oxford.), Fr.; 280,1a-c, test aboral, oral, lat., ×1.1 (27c); 280, 1d, test with spines, ×0.7 (172); 280,1e, amb, ×2 (27c); 281,2a,b, details of amb compounding, ×2 (46).——FIG. 280,1f. H. glasvillei COTTEAU, U.Jur.(Portland.), Fr.; interamb, ×2 (27c).——FIG. 281,2c. H. mondegoensis (DE LORIOL), Jur., Port.; structure of amb plate, ×2 (124).

Asterocidaris COTTEAU, 1859, p. 14 [*A. notodi; SD LAMBERT & THIÉRY, 1910, p. 169]. Like *Gymnocidaris,* but upper interamb plates devoid of primary and secondary tubercles, hence 5 interambulacral naked areas form star-shaped pattern about apex. *Jur.(Bathon.-Oxford.),* Eu.——FIG. 282,2a-c. *A. notodi, Oxford., Fr.; 2a,b, test, aboral, lat., ×1.2; 2c, interamb, ×3.3 (27c).——FIG. 282,2d,e. A. minor COTTEAU, Bathon., Fr.; 2d, apical system, ×2.3; 2e, amb adoral, ×5.3 (27c).

Cidaropsis COTTEAU, 1863, p. 374 [**Hemicidaris minor* AGASSIZ, 1840, p. 9; OD]. Primary tubercles noncrenulate (some with weak crenulation); otherwise as *Pseudocidaris. M.Jur.(Bathon.),* Fr. ——FIG. 283,1. *C. minor (AGASSIZ); 1a,b, test, aboral, lat., ×1.3; 1c, spine, ×1.2; 1d-g, apical system, amb, interamb, detail of aboral part of amb in large specimen, all ×3.3 (27c).

Gymnocidaris L. AGASSIZ, 1838, p. 3 [**Hemicidaris diademata* AGASSIZ, 1838, p. 49; SD LAMBERT & THIÉRY, 1910, p. 168] [=*Prodiadema* POMEL, 1869, p. 38 (type, *Cidarites agassizi* ROEMER, 1839, p. 70)] [*non Gymnocidaris* A. AGASSIZ, 1863 (=*Eucidaris* POMEL, 1883)]. Like *Hemicidaris* but upper interambulacral primary tubercles reduced. *M.Jur.(Bathon.),* Eu.——FIG. 284,1. *G. diademata (AGASSIZ), Fr.; 1a-c, test, aboral, oral, lat., ×1.1; 1d, amb, ×2.3 (27c); 1e,f, primary spine, ×1.1, ×3.2 (27c).

Hemitiaris POMEL, 1883, p. 96 [**Hemicidaris stramonium* L. AGASSIZ, 1840, p. 47; SD LAMBERT & THIÉRY, 1910, p. 170]. Like *Gymnocidaris,* but primary amb tubercles arranged in unpaired median series at ambitus, and in some species also

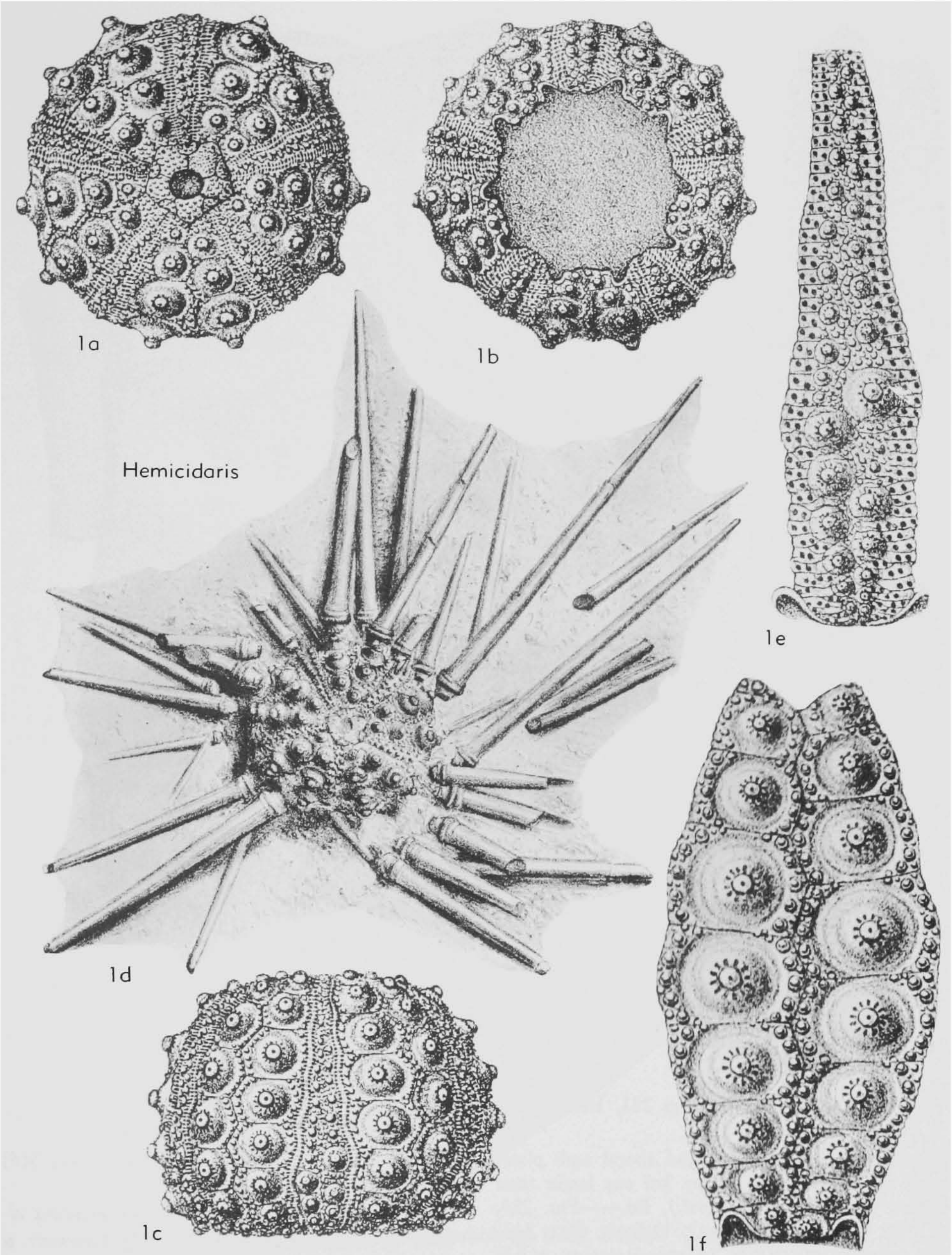

FIG. 280. Hemicidaridae (p. *U*381-*U*382).

aborally. *U.Jur.*, Eu.——FIG. 285,*1*. **H. stramonium* (AGASSIZ), Kimmeridg., Fr.; *1a,b*, test with spines, aboral, oral, ×0.7; *1c*, amb, ×2.7 (27c). ——FIG. 285,*2*. *H. purbeckensis* (FORBES), Portland., Fr.; amb detail, ×4 (27c).——FIG. 285,*3*. *H. morinica* (SAUVAGE & RIGAUX), Portland., Fr.; amb, ×2 (27c).

Hessotiara POMEL, 1883, p. 97 [**Diadema florescens* AGASSIZ, 1840, p. 17; OD]. Like *Hemicidaris*, but no polyporous amb plates, ambital plates

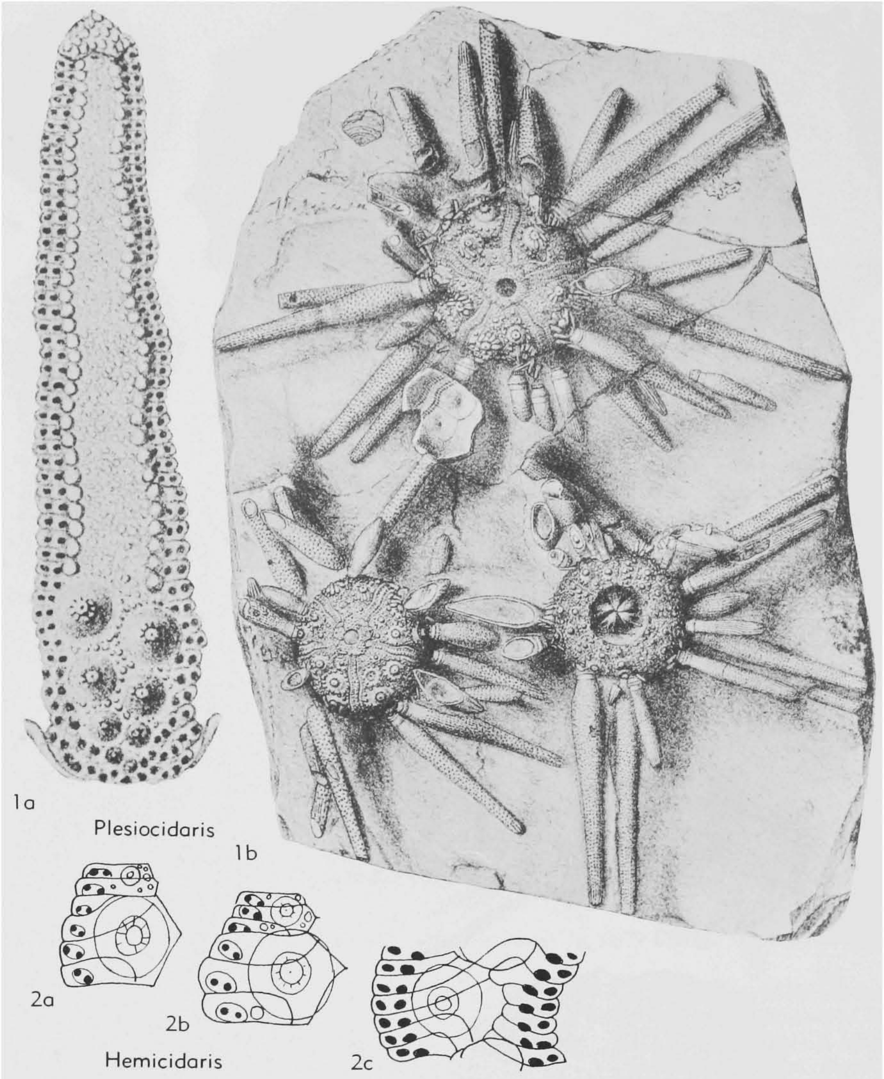

FIG. 281. Hemicidaridae (p. *U*381-*U*382, *U*384).

trigeminate or bigeminate, and aboral amb plates with reduced tubercles, every 3rd one larger than others. *Jur.(Hettang.-Oxford.)*, Eu.——FIG. 284, 2. **H. florescens* (AGASSIZ), Oxford., Fr.; *2a,b,* test, aboral, lat., ×1.3; *2c,* apical system, ×3.3; *2d,e,* interamb, amb, ×3.3 (27c).

Heterodiadema COTTEAU, 1864, p. 75 [**Hemicidaris libyca* DESOR, 1846, p. 338; SD LAMBERT & THIÉRY, 1910, p. 180]. Test low, hemispherical, or higher; apical system caducous, produced posteriorly; ambs with trigeminate plates. Spines small, but with distinct collar. *U.Cret.(Cenoman.-Turon.)*, S.Eu.-N.Afr.-Tex.——FIG. 286,*1*. **H. libycum* (DESOR), Turon., N.Afr.; *1a-c,* test aboral, lat., oral, ×1; *1d,e,* amb, amb detail, ×2, ×4; *1f-h,* spines, ×4 (27a).

Plesiocidaris POMEL, 1883, p. 95 [**Hemicidaris alpina* L. AGASSIZ, 1840, p. 52; SD LAMBERT & THIÉRY, 1910, p. 168]. Like *Gymnocidaris,* but all aboral amb plates simple primaries, all equally developed, each with noncrenulate imperforate tubercle, compounding restricted to subambital region. *L.Jur.-U.Jur.,* Eu.-N.Afr.——FIG. 281,*1a*. **P. alpina* (AGASSIZ), Kimmeridg., Switz.; amb, ×5.3 (5).——FIG. 281,*1b*. *P. durandi* (PERON & GAUTHIER), Kimmeridg., Fr.; tests with spines, ×0.7 (35).

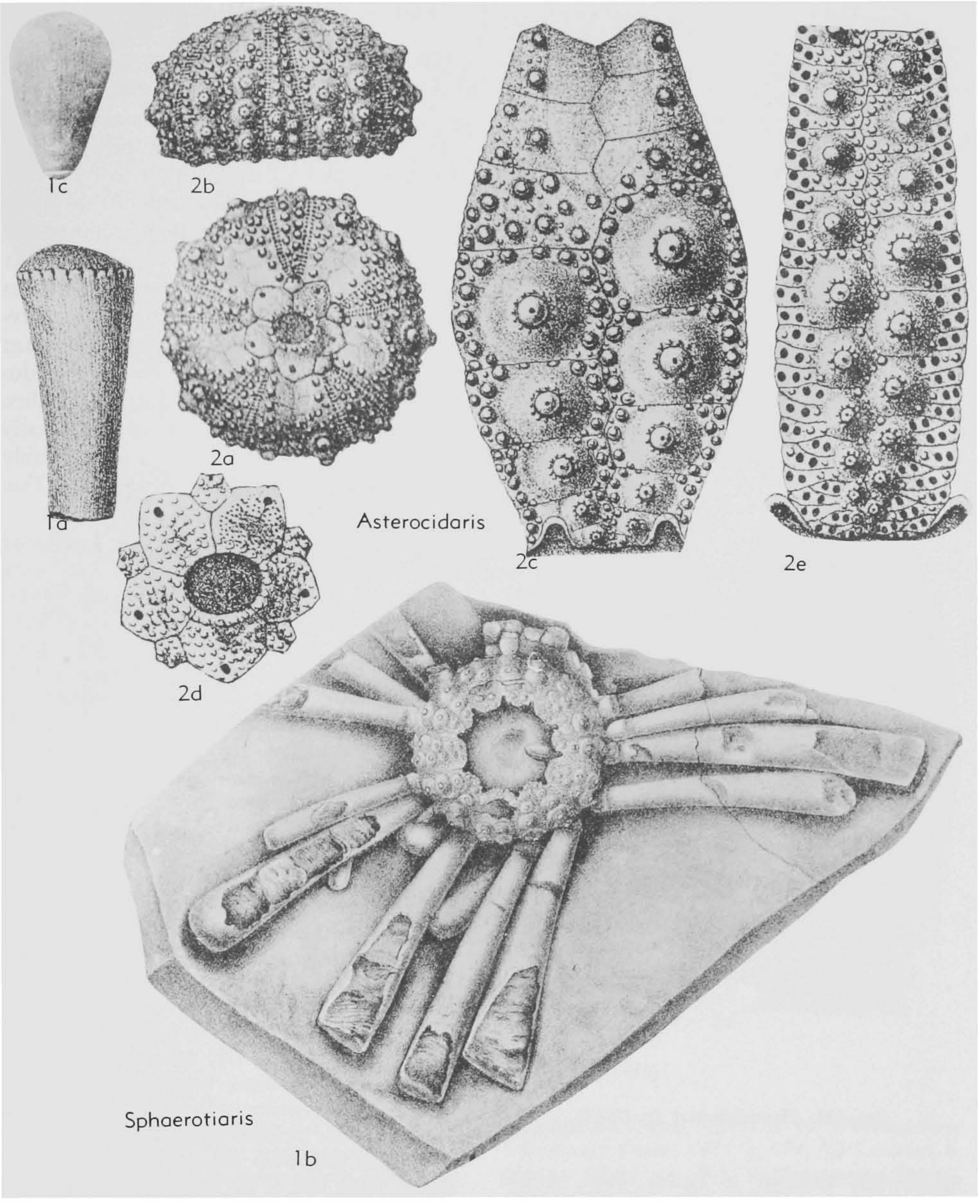

FIG. 282. Hemicidaridae (p. U382, U386).

Pseudocidaris ÉTALLON, 1859, p. 5 [*Hemicidaris thurmanni L. AGASSIZ, 1840, p. 50; SD LAMBERT & THIÉRY, 1910, p. 167]. Ambs as in *Plesiocidaris,* interambs as in *Hemicidaris.* Primary spines massive ovoid-clavate. *M.Jur.(Bathon.)-M.Cret.(Cenoman.),* Eu.-C.Asia-India-N.Afr. ——FIG. 287,*1. P. mammosa* (AGASSIZ), U.Jur.(Oxford.), Fr.; *1a,* test with spines, ×1.1; *1b,* amb, ×4; *1c,d,* spines, ×1.7 (27c).——FIG. 287,*2. P. clunifera* (AGASSIZ), L.Cret.(Neocom.), Fr.; test, aboral, ×1.1 (27a).——FIG. 287,*3. P. lusitanica* DE LORIOL, U.Jur.(Kimmeridg.), Port.; *3a,* base of spine showing collar and cortex on shaft, ×7; *3b,* interamb, ×3.3 (124).——FIG. 287,*4. P. subcrenularis* GAUTHIER, U.Jur.(Kimmeridg.), N.Afr.; terminal crown of spine, ×2.7 (27c). ——FIG. 287,*5. P. rupellensis* (COTTEAU), U.Jur.(Kimmeridg.), Fr.; primary spine, ×1.1 (27c).

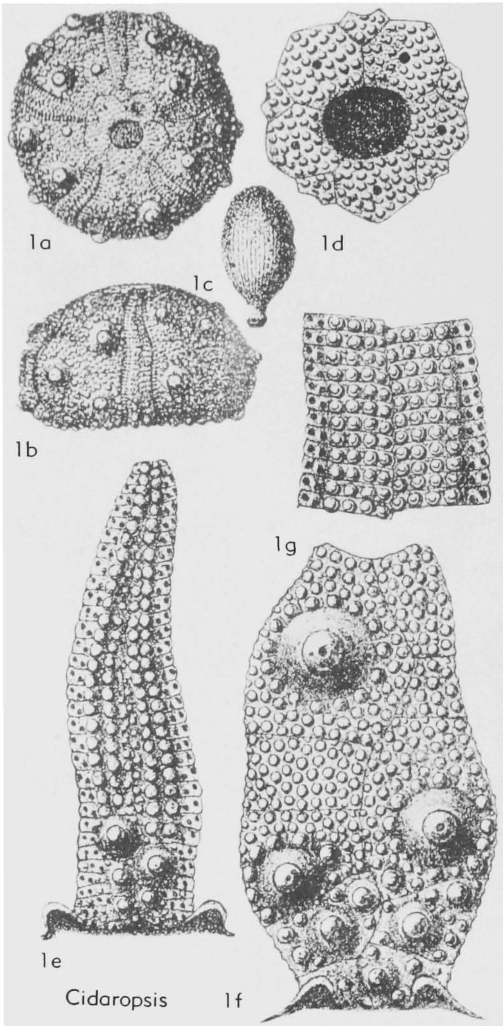

FIG. 283. Hemicidaridae (p. U382).

Sphaerotiaris LAMBERT & THIÉRY, 1914, p. 274 [**Hemicidaris quenstedti* MERIAN in DESOR, 1858, p. 56; OD] [=*Tiaris* QUENSTEDT, 1873, p. 258 (obj.) (preocc.); *Dorytiaris* BEURLIN, 1937, p. 65 (type, *Hemicidaris intermedia* FLEMING, 1828, p. 178)]. Like *Gymnocidaris*, but primary spines clavate, greatly enlarged. *U.Jur.*, Eu.-N.Afr.——FIG. 282,*1a,b*. **S. quenstedti* (MERIAN), Oxford., Fr.; *1a*, terminal crown of primary spine, ×1.2 (27a); *1b*, test with spines, oral, ×0.7 (5).——FIG. 282,*1c*. *S. koechlini* (COTTEAU), N.Afr.; primary spine, ×0.7 (112).

Family PSEUDODIADEMATIDAE Pomel, 1883

[Pseudodiadematidae POMEL, 1883, p. 100]

Ambs continuing uniformly throughout, not abruptly narrowed above ambitus, and with primary tubercles not abruptly reduced in size aborally. Test of small to moderate size, commonly very flattened. Amb plates compounded in diadematoid manner, in some species polyporous or with diplopodous arrangement adapically. Interamb plates may carry either one large tubercle or several large tubercles, in which case they form vertical series. Apical system usually caducous. Peristome large, with distinct gill slits. Primary spines slender, striated, usually without collar. Tridentate and probably ophicephalous pedicellariae known in *Trochotiara*, also spheridia. *U.Trias.-U.Cret.*

Pseudodiadema DESOR, 1855, p. 63 [**Cidarites pseudodiadema* LAMARCK, 1816, p. 59; OD] [=*Stereopyga* POMEL, 1883, p. 102 (type, *Pseudodiadema moorei* WRIGHT, 1857, p. 108; SD MORTENSEN, 1935, p. 432); *Aplodiadema* DE LORIOL, 1902, p. 49 (type, *Pseudodiadema langi* DESOR, 1868, p. 180)]. Pore zones not diplopodous adapically; compound amb plates trigeminate adapically, primary tubercle covering main part of 3 components. No conspicuous naked median space adapically in interambs. Apical system compact, not caducous. Each interamb plate with one large primary tubercle. *L.Jur.(Hettang.)-L.Cret.(Apt.)*, Eu.-N.Afr.-India.——FIG. 288,*3a,b*. *P. moorei* WRIGHT, *L.Jur.(Toarc.)*, Eng.; *3a,b*, test, aboral, oral, ×1 (172).——FIG. 288,*3c,d*. **P. pseudodiadema* (LAMARCK), U.Jur., Fr.; *3c*, amb, ×2 (27d); *3d*, test and spines, oral, ×1 (5).

Acrocidaris L. AGASSIZ, 1840, p. 9, 18 [**A. nobilis*; OD] [=*Acrotiaris* QUENSTEDT, 1872, p. 279 (*fide* MORTENSEN, 1935, p. 452, type undetermined)]. Test moderate to large, hemispherical, flattened below. Apical system not produced posteriorly. Pore zones not diplopodous adapically, compound amb plates polyporous adapically. Primary tubercles on upper side of test noncrenulate. Large primary tubercle on each genital plate. *M.Jur.(Bathon.)-U.Cret.(Cenoman.)*, Eu.-Crimea-Mex.——FIG. 289,*2a,b*. **A. nobilis* L. AGASSIZ, U.Jur. (Kimmeridg.), Switz.; *2a*, apical system, ×2.7; *2b*, test, oral, ×1 (27d).——FIG. 289,*2c*. *A. formosa* L. AGASSIZ, U.Jur.(Oxford.), Switz.; test, aboral, ×1 (27d).——FIG. 289,*2d*. *A. minor*, L. AGASSIZ, L.Cret.(Valangin.), Switz.; amb detail, ×2 (27a).

Diplopodia M'COY, 1848, p. 412 [**D. pentagona*; OD] [=?*Pseudoplopodia* VALETTE, 1906, p. 24

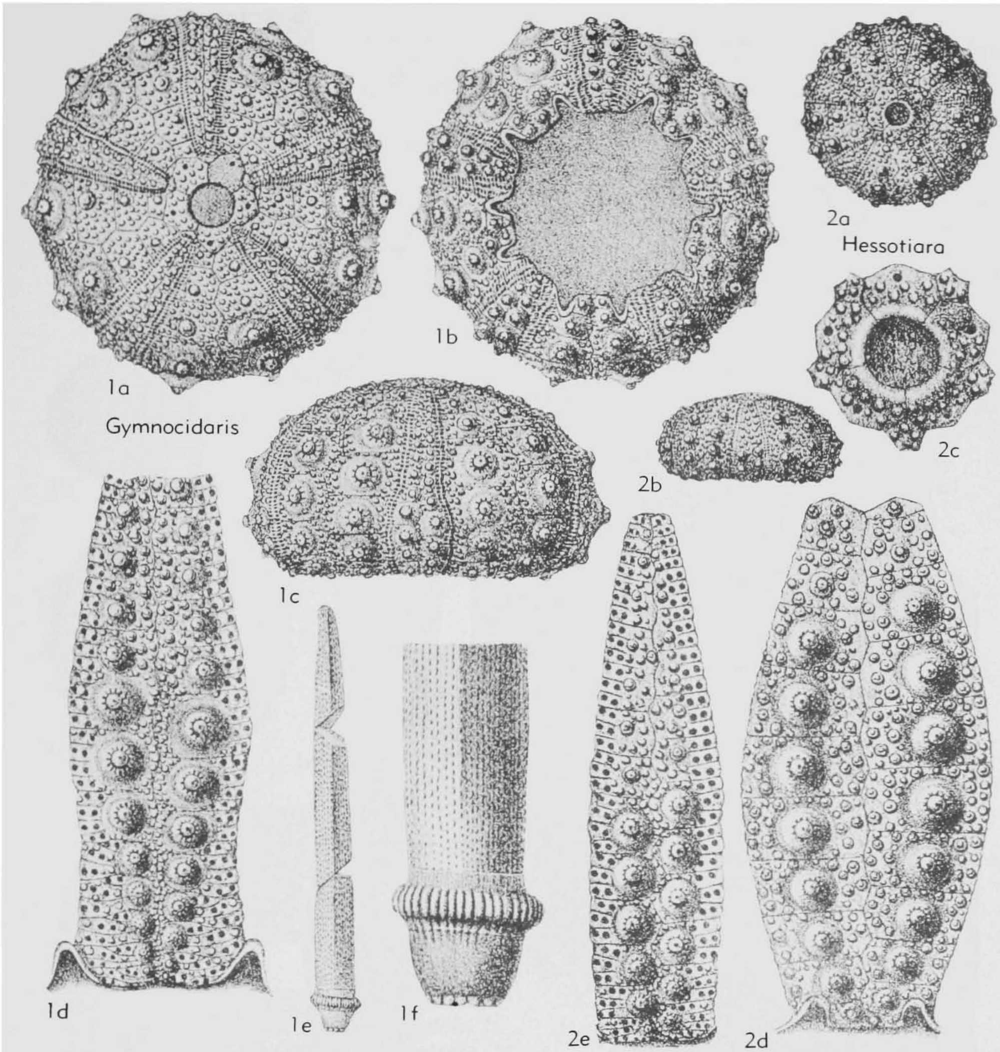

FIG. 284. Hemicidaridae (p. *U382-U384*).

(no type desig.); ?*Polyplodia* VALETTE, 1907, p. 61 (no type desig.)]. Test wheel-shaped, of moderate size. Apical system not produced posteriorly. Pore zones diplopodous adapically. Only one large tubercle on each interamb plate. *U.Trias.(Rhaet.)-U.Cret.(Cenoman.)*, Eu.-N.Afr.-Asia.——FIG. 290, *2. D. morieri* (COTTEAU), *M.Jur.(Bathon.)*, Fr.; *2a-c*, test, lat., aboral, oral, ×1; *2d*, amb detail, ×3.3 (27d).

Dumblea CRAGIN, 1893, p. 149 [**D. symmetrica*; OD]. Like *Pedinopsis*, but amb plates trigeminate; minutely crenulate (*fide* COOKE, 1955, p. 90). *L. Cret.(Washitan.)*, USA(Tex.)-Mex.——FIG. 286,*3*. **D. symmetrica*, Tex.; *3a,b*, amb, interamb, plates, ×8 (22); *3c*, test, oral, ×1.3 (23).

Hypodiadema DESOR, 1858, p. 61 [**Hemicidaris saleniformis* DESOR, 1853, p. 179; SD LAMBERT & THIÉRY, 1910, p. 171] [=*Gymnotiara* POMEL, 1883, p. 101 (type, *Pseudodiadema varusense* COTTEAU, 1880, p. 231)]. Adapical amb plates not pronouncedly compound, primary tubercle small, not covering much more than median component plate. Apical system compact, not caducous. Each interamb plate with one large primary tubercle. *L. Jur. (Pliensbach.)-L. Cret. (Valangin.)*, Eu.-?N. Am.——FIG. 288,*1. H. desoriana* (COTTEAU), U. Jur.(Kimmeridg.), Fr.; amb, ×2.7 (27d).

Loriolia NEUMAYR, 1881, p. 105 [**Diadema foucardi* COTTEAU, 1851, p. 286; OD] [=*Heterotiara* POMEL, 1883, p. 105 (obj.)]. Amb plates trigemin-

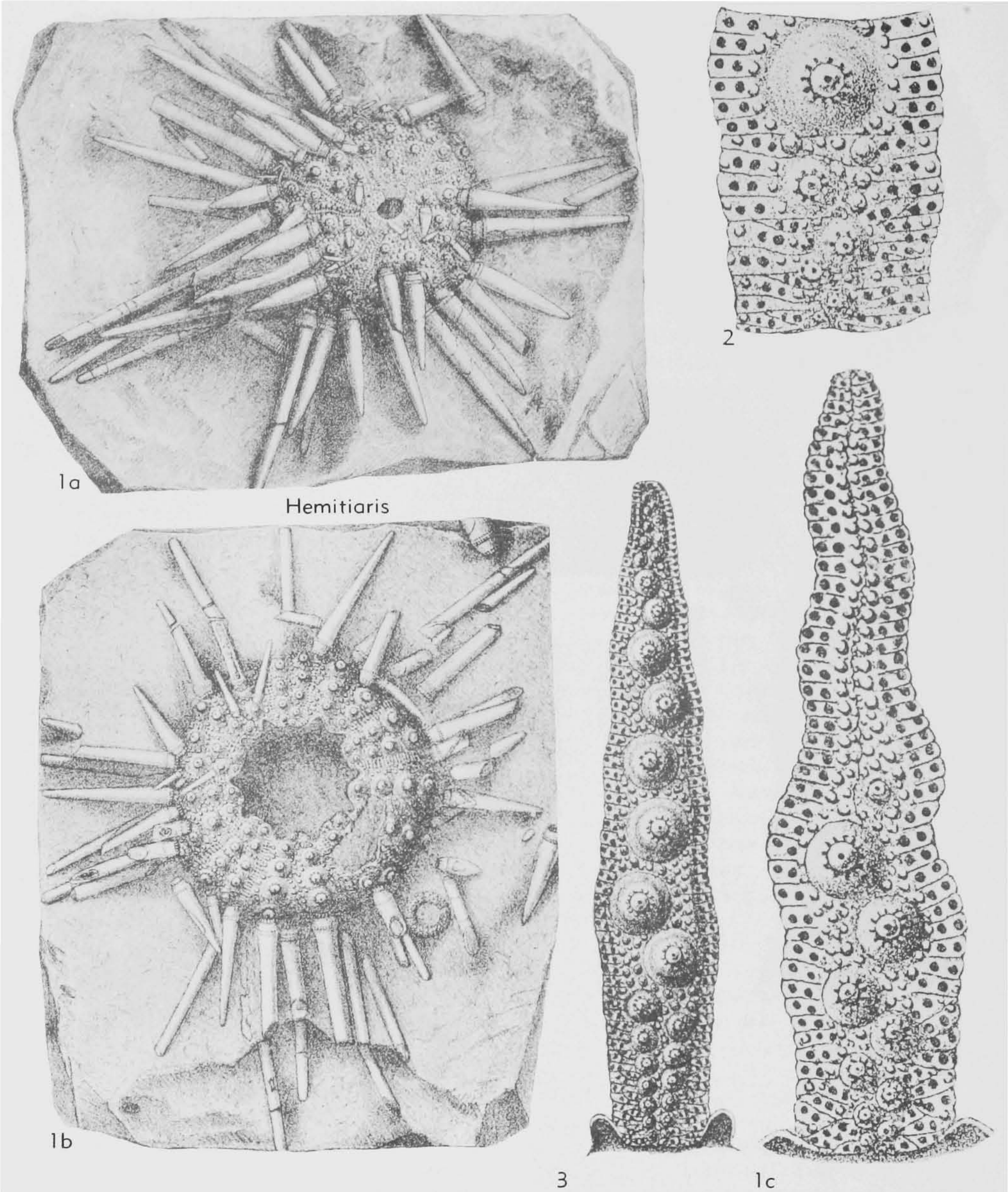

FIG. 285. Hemicidaridae (p. U382-U383).

ate, pore zones widened at peristome, pores in indistinct arcs of 3. Primary amb tubercles diminishing very gradually in size aborally. Apical system caducous, produced posteriorly. *L.Cret.* *(Neocom.)*, Fr.; ?*Apt.*, USA(Tex.).——FIG. 286, 2. **L. foucardi* (COTTEAU), Neocom., Fr.; *2a,* test, lat., ×1.3; *2b,c,* amb, interamb, ×4 (27a).

Microdiadema COTTEAU, 1863, p. 77 [**Arbacia richeriana* COTTEAU, 1869, p. 397; OD, M]. Test hemispherical, very small (7 mm. diam.). Amb plates compound, trigeminate. Interamb plates each with 3 more prominent tubercles. Apical system small, dicyclic. *L.Jur.(Pliensbach.)*, Fr.

Pedinopsis COTTEAU, 1863, p. 176 [**P. meridanensis*; OD]. Test medium-sized to large, subhemispherical or subconical. Ambs with pore pairs biserial throughout, or at least to below ambitus where they may be monoserial. Amb tubercles

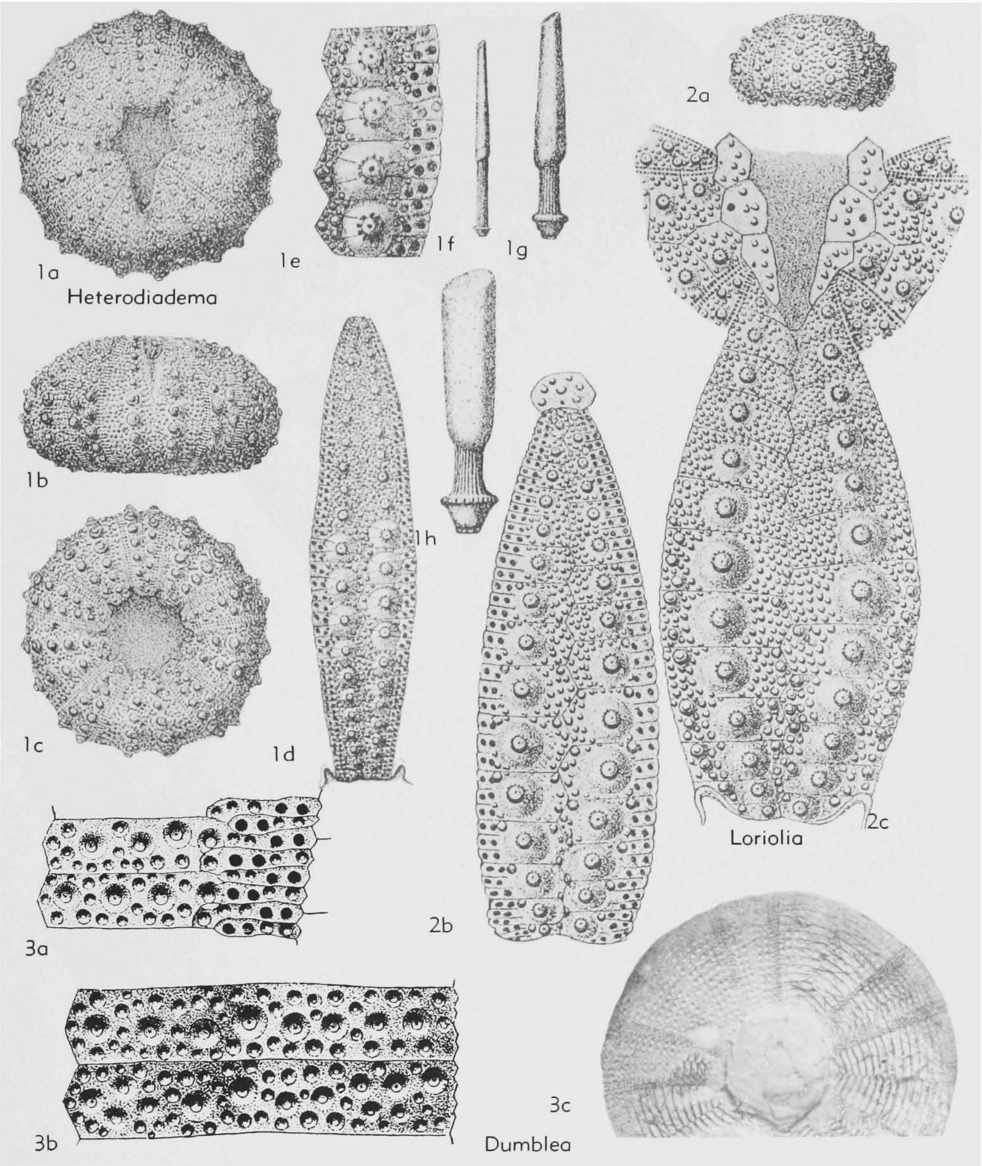

FIG. 286. Hemicidaridae *(1)*; Pseudodiadematidae *(2-3)* (p. *U*384, *U*387-*U*388).

small, weakly crenulate, similar to interamb primary tubercles. Interambs wtih numerous equal-sized tubercles, forming vertical and horizontal series. *U.Cret.(Cenoman.),* Eu.; *U.Cret.(Austin.),* USA(Tex.).——FIG. 291,*2*. **P. meridanensis* COTTEAU, Cenoman., Fr.; amb detail, ×4 (27a).

Polydiadema LAMBERT, 1888, p. 14 [**Cidaris mamillanum* ROEMER, 1836, p. 26 (=*Pseudodiadema davidsoni* WRIGHT, 1857, p. 108; OD] [=*Plesiodiadema* DUNCAN, 1885, p. 31 (*non* POMEL, 1883) (obj.); *Placodiadema* DUNCAN, 1889, p. 64; *Leptarbacia* CLARK & TWITCHELL, 1915, p. 53 (type, *L. argutus*); *Polypedina* LAMBERT, 1933, p. 46 (type, *P. tounatensis*)]. Test of moderate size, flattened. Ambs polyporous, at least aborally, some to peristome; pore pairs not in double series, pore zones more or less undulating. Primary amb tubercles same size as interamb primaries. Median area of interambs usually naked adapically. Apical system large, caducous. *L.Jur.(Domer.)-U.Cret.*

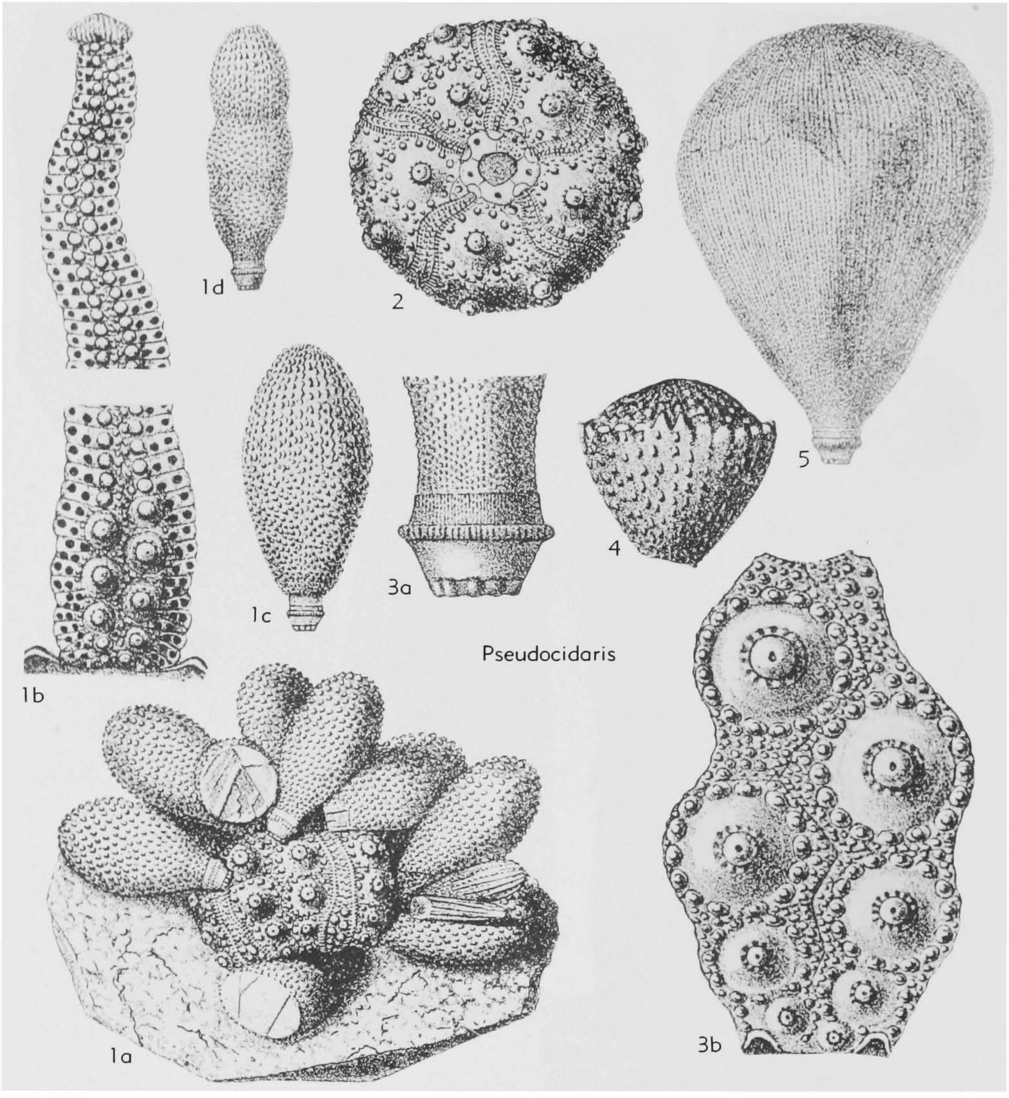

FIG. 287. Hemicidaridae (p. U385).

(Cenoman.), Eu.-N.Afr.-USA(Tex.).——FIG. 290, *1a-c*. *P. tenue* (DESOR), Cenoman., Fr.; *1a,b*, amb, interamb, ×2.7; *1c*, interamb plate, ×5.3 (27a). ——FIG. 290,*1d-g*. **P. davidsoni* (WRIGHT), U. Jur.(Oxford.), Eng.; *1d-f*, test, aboral, oral, lat., ×1; *1g*, test detail, ×2.7 (172).

Tetragramma L. AGASSIZ, 1840, p. 24 [**Cidarites variolare* BRONGNIART, 1821, pl. M, fig. 9; SD LAMBERT & THIÉRY, 1910, p. 187] [=*Hexagramma* POMEL, 1883, p. 104 (?type); *Acanthechinopsis* GREGORY, 1906, p. 219 (obj.); *Orthodiadema* LAMBERT & THIÉRY, 1908, p. 20 (type, *Pseudodiadema subangulatum* STOLICZKA, 1873, p. 44); *Strictotiara* LAMBERT & THIÉRY, 1925, p. 564 (type, *Tetragramma argonnensis* LAMBERT, 1925, pl. 2, fig. 14-16; OD]. Like *Diplopodia*, but with 2 large tubercles on each interamb plate. Diplopodous arrangement confined to adapical part. Primary tubercles conspicuous. *U.Jur.(Kimmeridg.)-U. Cret. (Cenoman.)*, S. Eu.-N. Afr.-Asia Minor-India-N.Am.——FIG. 291,*1a-c*. **T. variolare* (BRONGNIART), U.Cret.(Cenoman.), Fr.; *1a-c*, test, aboral, oral, lat., ×1 (27a).——FIG. 291, *1d,e*. *T. raulini* (DESOR), L.Cret.(Neocom.), Fr.;

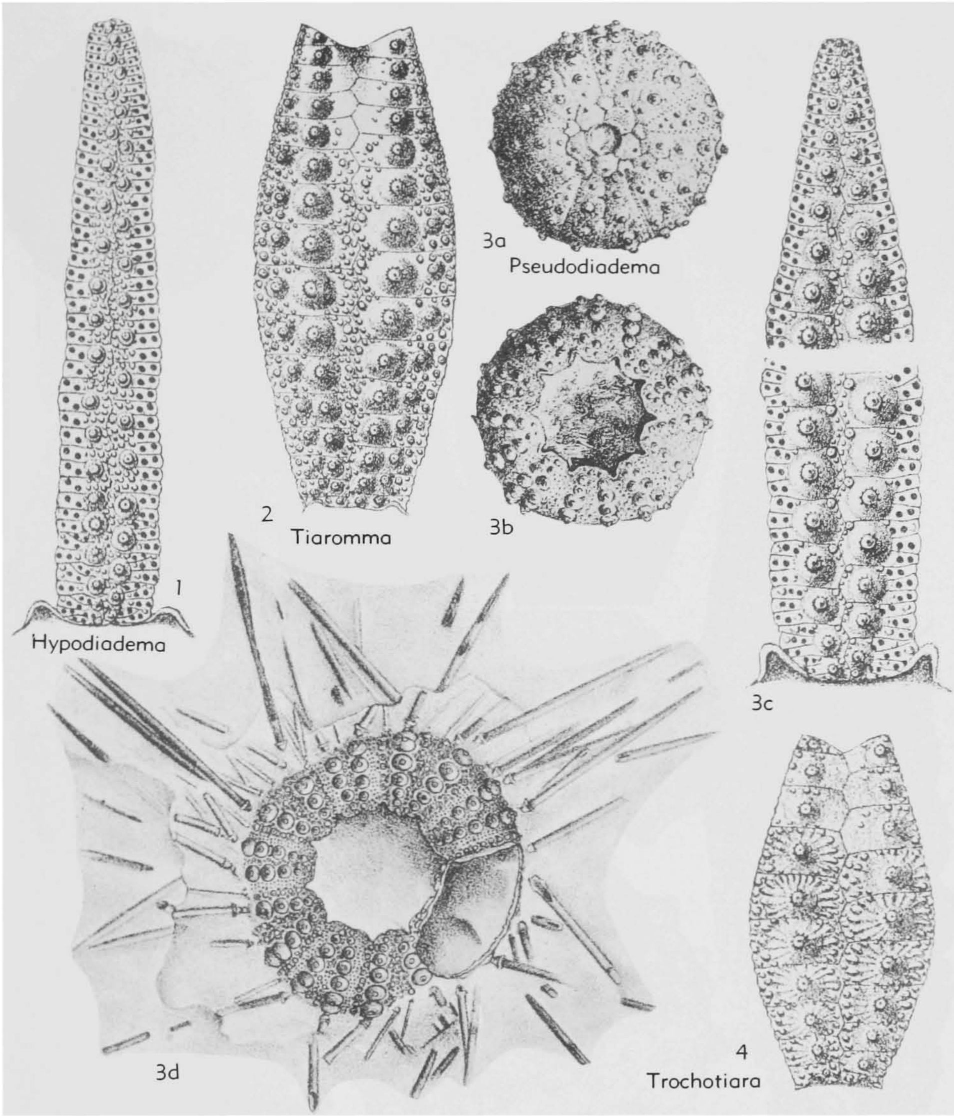

FIG. 288. Pseudodiadematidae (p. *U*386-*U*387, *U*391).

1d,e, amb, part of interamb, ×2 (27a).——FIG. 291,*1f*. *T. renevieri* (COTTEAU), L.Cret.(Apt.), Fr.; interamb plates, ×2.7 (27a).——FIG. 291, *1g,h*. *T. malbosi* (AGASSIZ), L.Cret.(Apt.), Fr.; aboral part of amb and interamb, ×4 (27a).

Tiaromma POMEL, 1883, p. 105 [**Pseudodiadema schlüteri* DE LORIOL, 1887, p. 22; SD LAMBERT & THIÉRY, 1910, p. 189]. Like *Acrocidaris* but with primary tubercles on upper side of test crenulate and with no large primary tubercle on each genital plate. Conspicuous sunken naked median space adapically in interambs. *U.Cret.(Cenoman.)*, Fr.-Port.——FIG. 288,*2*. **T. schlüteri* (DE LORIOL), Fr.; interamb, ×2 (27a).

Trochotiara LAMBERT, 1901, p. 236 [**Diadema priscum* L. AGASSIZ, 1840; OD] [=*Tiarella* POMEL, 1883, p. 104 (type?) (*fide* LAMBERT & THIÉRY, 1910, p. 181) (*non Tiarella* SWAINSON, 1840, *nec* SCHULTZE, 1876)]. Test small, flattened, wheel-shaped. Amb plates compound, trigeminate, some quadrigeminate at ambitus; pores in straight series, widened at peristome. Primary amb tubercles of same size as primary interamb tubercles. Median interamb space naked, more or less sunken adapically. *L.Jur.(Pleinsbach.)-U.Cret.(Cenoman.)*, Eu.-N.Afr.-Asia Minor.——FIG. 288,*4*. *T. gauthieri* COTTEAU, L.Jur.(Pliensbach.), Fr.; interamb, ×1.3 (species with radiating epistroma) (27d).

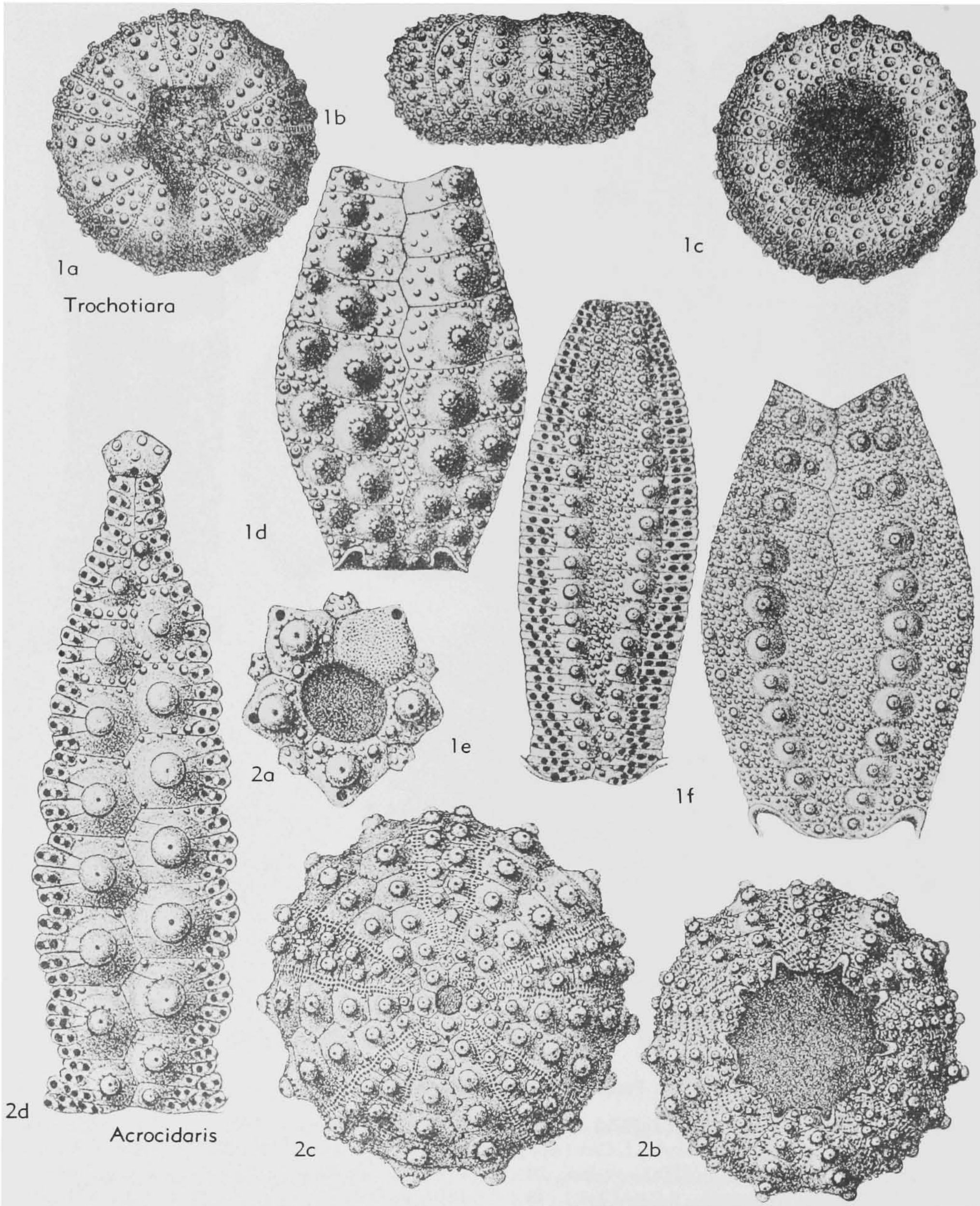

FIG. 289. Pseudodiadematidae (p. U386, U391).

——FIG. 289,*1a-c*. **T. prisca* (L. AGASSIZ), U. Jur.(Oxford.), Switz.; *1a-c*, test, aboral, lat., oral, ×1.3 (27d).——FIG. 289,*1d*. *T. thiriai* (ÉTALLON), U.Jur.(Portland.), Fr.; interamb, ×2.7 (27d).——FIG. 289,*1e,f*. *T.? bourgeti* (DESOR), Cret., Fr.; *1e,f*, amb, interamb, ×2.7 (species apparently transitional to *Pseudodiadema*) (27d).

Family UNCERTAIN

Allomma POMEL, 1883, p. 105 [**Pseudodiadema normanniae* COTTEAU, 1863; OD]. Like *Gymnocidaris*, but transverse row of tubercles replacing single large primary tubercle on subambital interamb plates. *U.Cret.*, Eu.——FIG. 292,*2*. **A. normanniae* (COTTEAU), Cenoman., Fr.; *2a-c*, test,

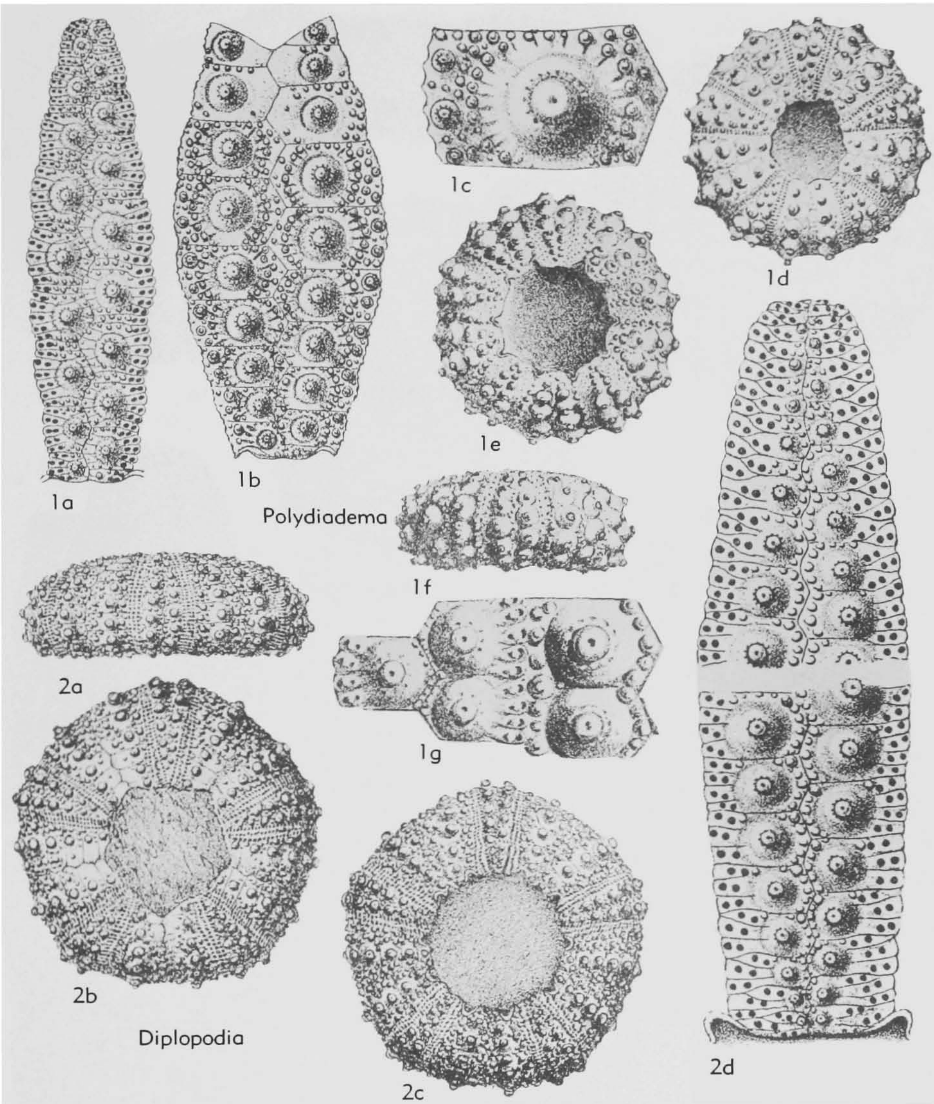

FIG. 290. Pseudodiadematidae (p. *U386-U387, U389-U390*).

lat., aboral, oral, ×1.3; *2d*, amb, ×5.3 (27a); *2e*, partially reconstructed apical system (which, if correct, may indicate some affinity with Acrosaleniidae), ×5.3 (115).

Colpotiara POMEL, 1883, p. 105 [**Heterodiadema matheyi* DE LORIOL, 1870, p. 83; OD]. Like *Asterocidaris*, but primary tubercles persisting on otherwise naked upper interamb plates. Enlarged primary tubercles irregularly developed on some amb plates and lacking from some ambital plates. Test small (*ca.* 10 mm. horiz. diam.), flattened above and below. Apical system caducous. *U. Jur.*, Eu.——FIG. 292,*1*. **C. matheyi* (DE LORIOL), Oxford., Switz.; *1a,b*, amb, interamb, ×4.7; *1c*, test, oral, ×1.3 (122).

Trochodiadema DE LORIOL, 1900, p. 70 [**T. abramense*; OD]. Like *Gymnocidaris*, but amb plates trigeminate, and amb tubercles reduced above ambitus; pore zones straight. Apical system caducous. Radioles unknown. Test flattened above and below (less than 20 mm. horiz. diam.). *U.Cret. (Turon.)*, Eu.——FIG. 292,*3*. **T. abramense*,

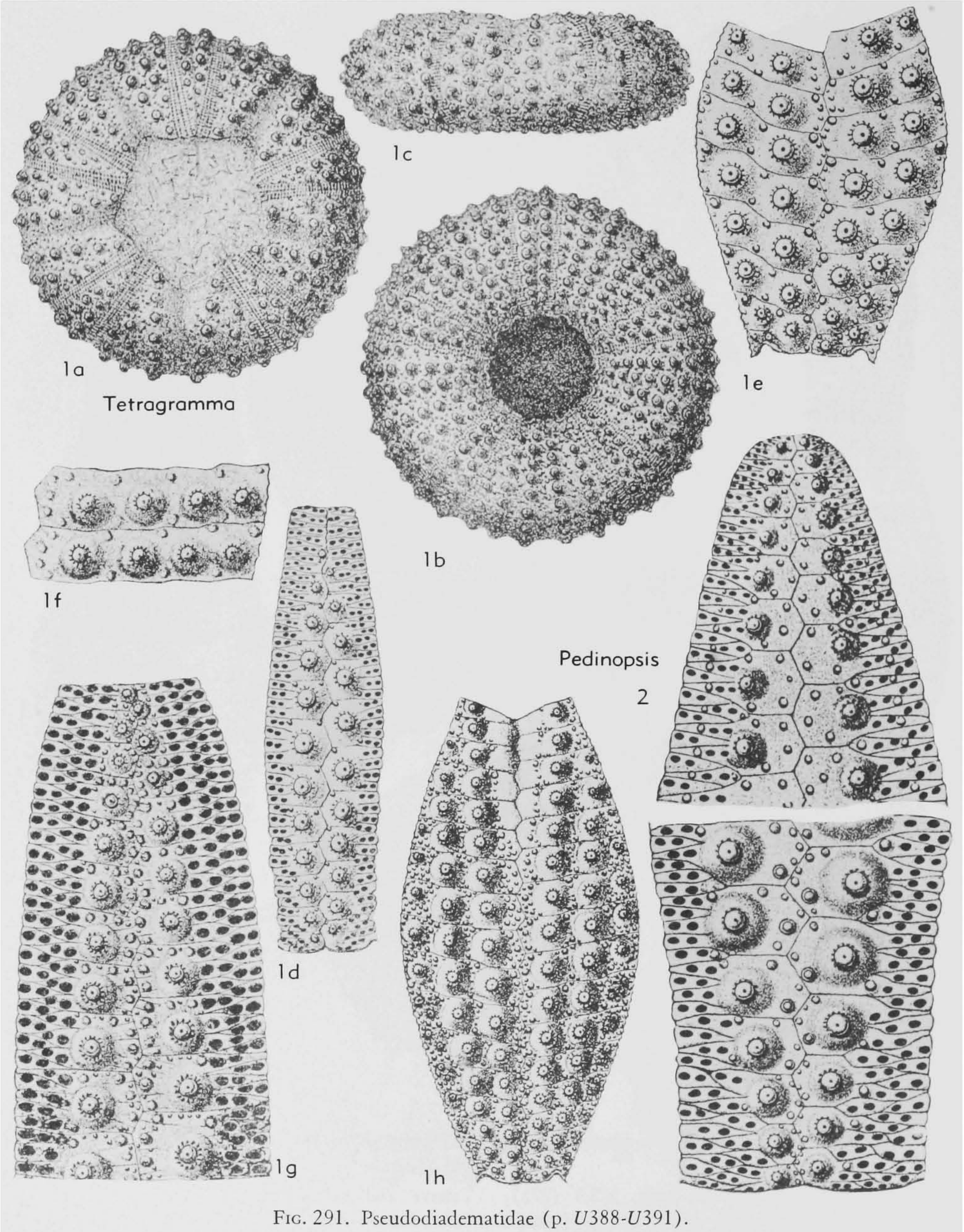

FIG. 291. Pseudodiadematidae (p. U388-U391).

Port.; *3a-c,* test aboral, oral, lat., ×1.3; *3d,e,* amb, interamb, ×3.3 (125).

Order PHYMOSOMATOIDA Mortensen, 1904

[*nom. transl.* DURHAM & MELVILLE, 1957, p. 254 (*ex* suborder Phymosomina MORTENSEN, 1904, p. 56)] [=Phymosomatoida DURHAM & MELVILLE, 1957, *minus* Pseudodiadematidae (herein referred to Hemicidaroida)]

Lantern stirodont. Apical system lacking large polygonal suranal plates, not simulating calyx. Primary tubercles imperforate. Amb plates simple throughout, or (more usually) compounded in diadematoid manner, trigeminate or polyporous. *L.Jur.-Rec.*

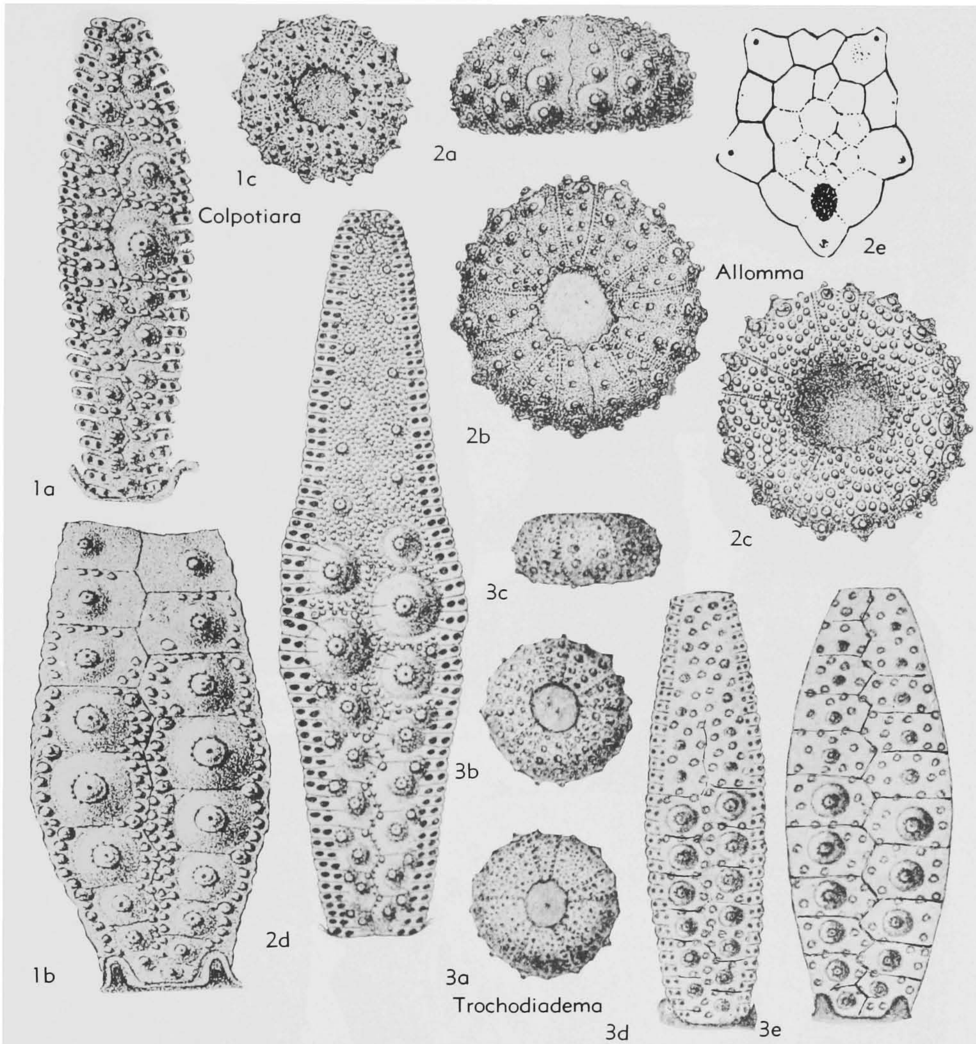

FIG. 292. Family Uncertain (p. U392-U393).

Family PHYMOSOMATIDAE Pomel, 1883

[*nom. correct.* MEISSNER, 1904, p. 1359 (*pro* les Phymosomiens POMEL, 1883, p. 90)] [=Cyphosominae LAMBERT, 1897, p. 498]

Primary tubercles crenulate, amb tubercles usually as large as interamb tubercles. Amb plates simple or compound; polyporous and diplopodous in more specialized genera. Apical system dicyclic or monocyclic, commonly prolonged posteriorly into interamb 5, usually caducous. Exceptionally (e.g., *Acrocidaris*) polygonal suranal plates resembling those of Salenioida occurring in periproct. Peristome large, with distinct gill slits. Primary spines with thin cortex and distinct collar. Pedicellariae (known in *Glyptocidaris*) ophicephalous, tridentate, triphyllous, and globiferous. Spheridia placed beside tube feet, not in pits. *L.Jur.-Rec.*

Phymosoma HAIME, 1853, p. 197 [**Cidaris koenigi* MANTELL, 1822; SD LAMBERT & THIÉRY, 1910, p. 223] [=*Cyphosoma* L. AGASSIZ, 1838, p. 4 (*non* MANTELL, 1822; SD LAMBERT & THIÉRY, 1910, p. 90 (?type); *Pliocyphosoma* POMEL, 1883, p. 90 (?type); *Phymatosoma* LAMBERT & THIÉRY, 1910,

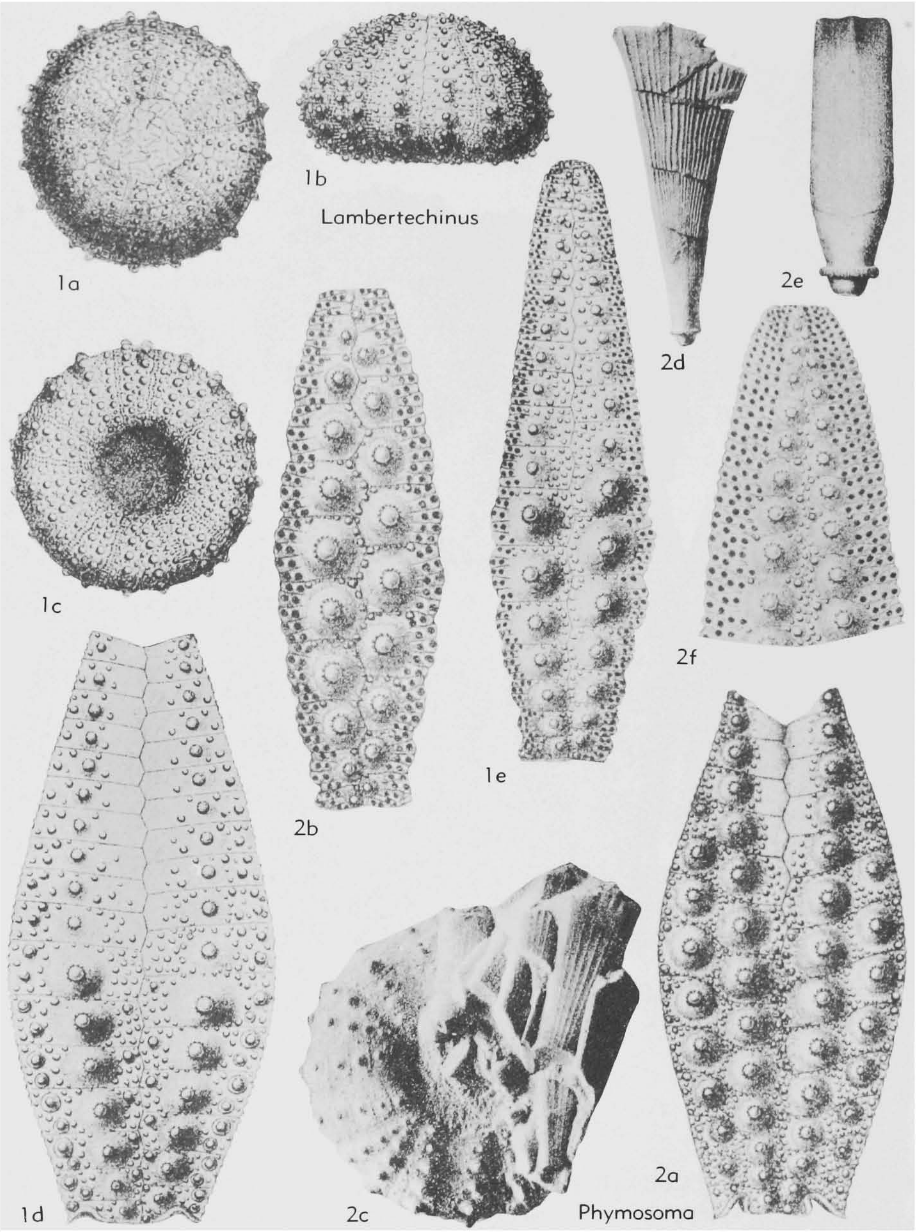

FIG. 293. Phymosomatidae (p. U395-U396, U400).

p. 223 (obj.) *(nom. van.)*; *Cosmocyphus* POMEL, 1883, p. 91 (type, *Cyphosoma salmanni* COQUAND)]. Test low, flattened above, medium-sized. Amb plates compound, polyporous, pore pairs in double series adapically. Primary tubercles without conspicuous radiating striae, tubercles forming regular series. *U.Jur.(Oxford.)-Eoc.,* Eu.-N.Afr.-Madag.-India-N. Am.-S. Am.——FIG. 293,*2a*. *P. major* (COQUAND), Cret., Fr.; interamb, ×1.3 (27a).——FIG. 293,*2b*. *P. regulare* (AGASSIZ), U. Cret.(Turon.), Switz.; amb, ×1.3 (27a).——FIG. 293,*2c,d*. *P. taeniatum* VON HAGENOW, U.Cret. (Senon.), Denm.; *2c,d,* test and spine, ×1 (147). ——FIG. 293,*2e*. *P. subnudum* (COTTEAU), U.Cret. (Senon.), Fr.; spine, ×2 (27a).——FIG. 293,*2f*. *P. girumnense* (DESOR), U.Cret.(Senon.), Fr.; amb, ×1.3 (27a). [=*Dixieus* COOKE, 1948, p. 606.]

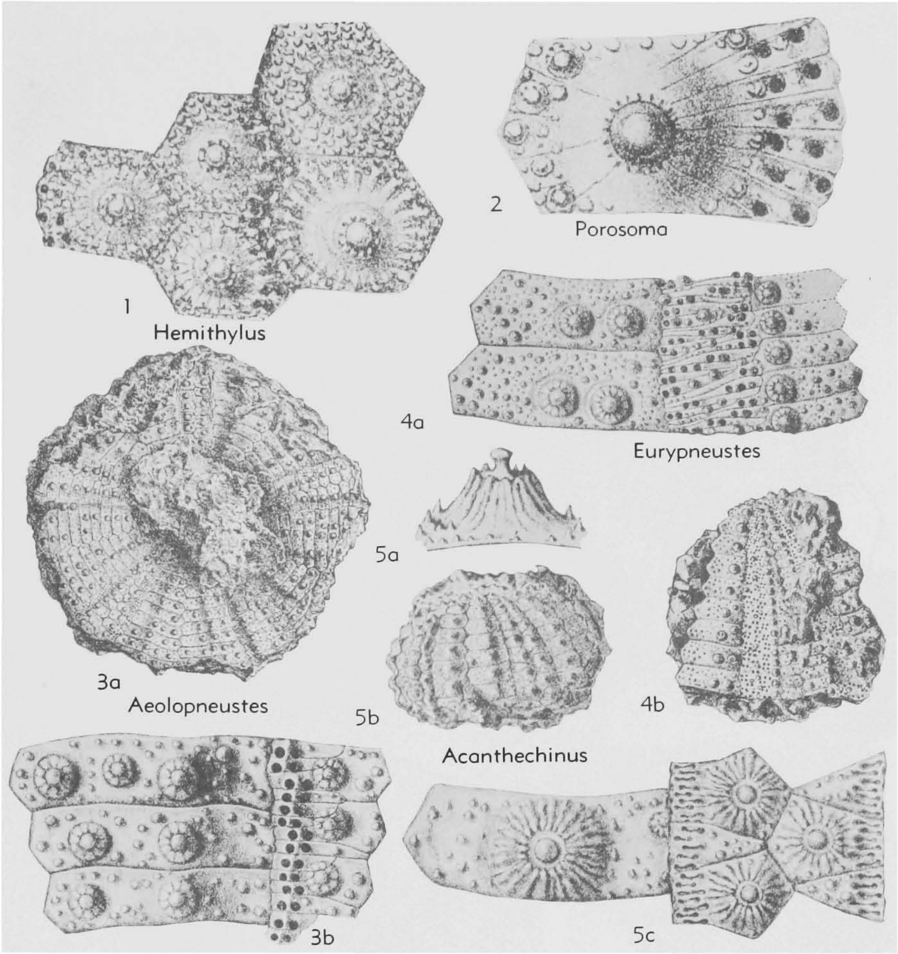

FIG. 294. Phymosomatidae (p. *U*397-*U*400, *U*402).

Acanthechinus DUNCAN & SLADEN, 1882, p. 34 [**A. nodulosus*; OD, M]. Test small, hemispherical, flattened adorally. Ambs polyporous; pore pairs in double series adapically, in single series adorally. Primary tubercles in regular double series in both areas, sharply crenulate, with ridged flanks. *L.Eoc.(Ranikot.)*, W.Pak.——FIG. 294,*5*. **A. nodulosus*, W.Sind.; *5a*, tubercle, profile, ×10; *5b*, test, lat., ×0.87; *5c*, amb and interamb plates, ×4.7 (47).

Actinophyma COTTEAU & GAUTHIER, 1895, p. 96 [**A. spectabile*; OD, M]. Like *Acanthechinus*, but with secondary and miliary tubercles not sharply pointed and spiny; impression at admedian end of horizontal interamb sutures. *U.Cret.*, Asia Minor-Iran.——FIG. 295,*2*. **A. spectabile*, Senon, Iran; *2a,b*, amb plates (aboral); interamb plates, ×1.3; *2c,d*, test, lat., aboral, ×0.7 (34).

Aeolopneustes DUNCAN & SLADEN, 1882, p. 47 [**A. delorioli*; OD, M]. Test large, subconical. Ambs polyporous, with pores adapically almost horizontal arcs of 5 or 6, adorally narrowing to form straight vertical series. Primary tubercles small, in regular series; secondaries same size as primaries, also forming vertical series. *L.Eoc.*, W.Pak.——FIG. 294,*3*. **A. delorioli*, Ranikot., W.Sind; *3a*, test, oral, ×0.7; *3b*, amb and interamb plates, ×2.7 (47).

Eurypneustes DUNCAN & SLADEN, 1882, p. 45 [**E. grandis*; OD, M]. Test large, probably subconical. Ambs as broad as interambs, amb plates polyporous; pore zones very wide, pore pairs arranged in 3 vertical series. Primary tubercles in regular double series in each area, but secondary interamb tubercles almost reaching size of primaries and forming series outside of primary series. *L.Eoc.*,

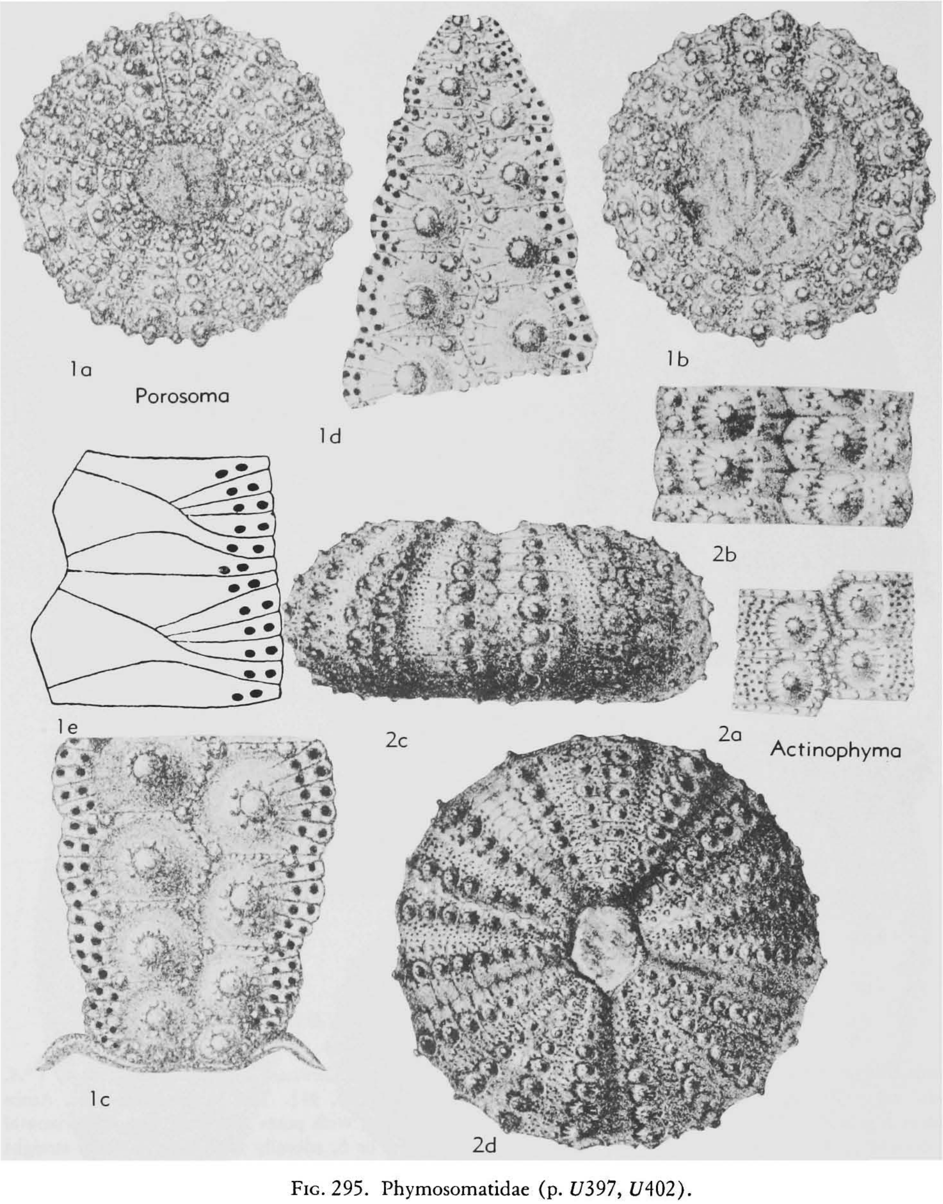

FIG. 295. Phymosomatidae (p. U397, U402).

W.Pak.——FIG. 294,4. *E. *grandis*, Ranikot, W. Sind; *4a*, amb and interamb plates, ×2; *4b*, part of test, ×0.7 (47).

Gauthieria LAMBERT, 1888, p. 7 [**Cyphosoma radiata* SORIGNET; OD] [=*Cosmocyphus* POMEL, 1883, p. 91 (type *Cyphosoma saemanni* COQUAND)]. Test low, flattened. Amb plates polyporous throughout; pore zones simple, undulating. Primary tubercles large, in only 2 series in each area. Apical system large, monocyclic, pentagonal, extending into posterior interamb. *U.Cret.(Turon.-Senon.)*, Eu.-N.Afr.-Madag.; *Paleoc.*, N.Am.——FIG. 296,*1a-e*. **G. radiata* (SORIGNET), U.Cret. (Senon.), Fr.; *1a-c*, test, aboral, oral, lat., ×1.3; *1d*, amb, ×3.3; *1e*, interamb, ×3.3 (27a).——FIG. 296,*1f,g*. *G. speciosa* (W. B. CLARK), Paleoc., USA(N.J.); *1f,g*, test, aboral, oral (holotype), ×2 (24).

Glyptocidaris A. AGASSIZ, 1853, p. 356 [**G. crenularis*; OD] [=*Heteractechinus* LAMBERT & THIÉRY, 1910, p. 274 (type, *H. heteroporus* LAMBERT, 1897, p. 499); *Heteractis* LAMBERT, 1897 (type,

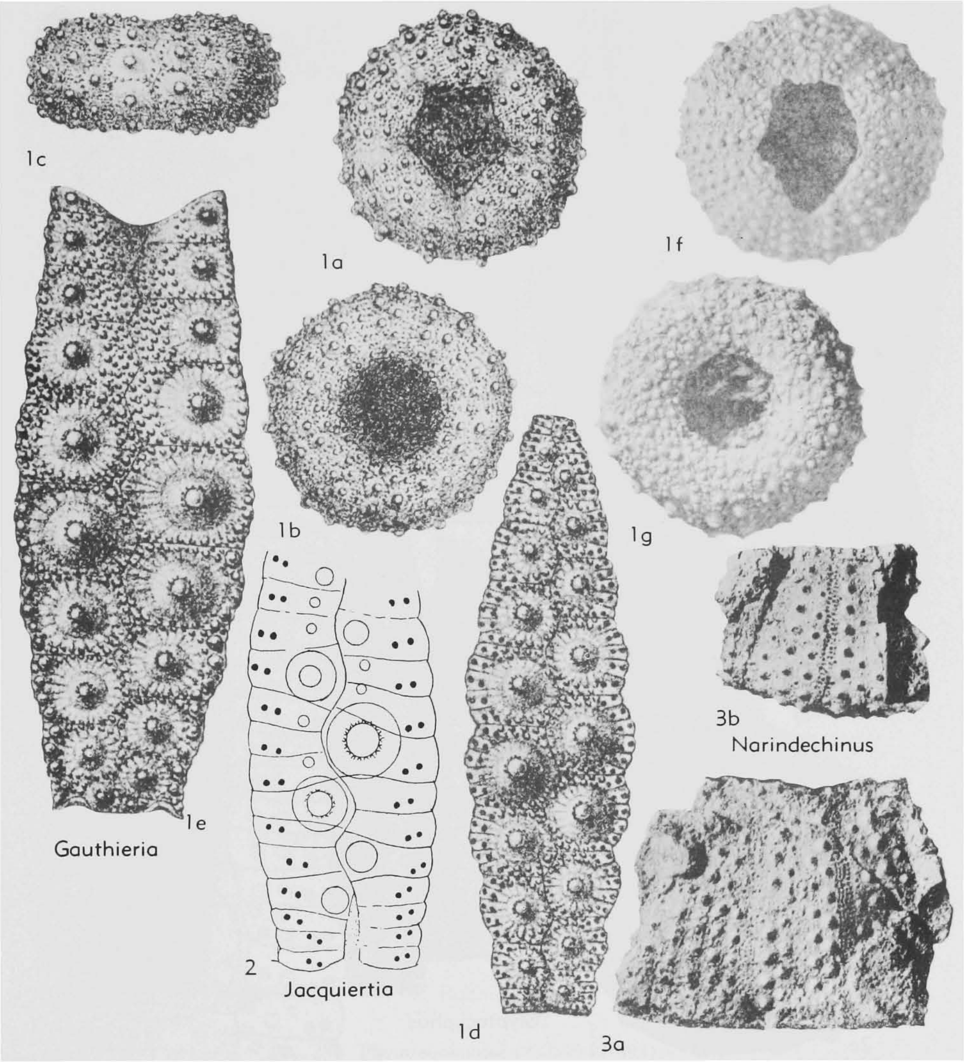

FIG. 296. Phymosomatidae (p. *U*398, *U*400-*U*401).

H. heteroporus) (*non Heteractis* MILNE-EDWARDS & HAIME, 1853)]. Test low, hemispherical, large. Amb plates compound, polyporous, pore pairs in double series only at ambitus, in single series adapically. Apical system with ocular I insert. [The type-species is the only known Recent phymosomatid.] *Eoc.*, Fr.; *Plio.*, N.Am.(Ore.)-S.Japan; *Rec.*, N.Japan.

Glyptocyphus POMEL, 1883, p. 87 [**Cyphosoma difficilis* L. AGASSIZ; OD, M]. Test small, low, wheel-shaped. Amb plates polyporous, with primary tubercles reduced to single or alternating series. Apical system with oculars exsert. *U.Cret.*, Eu.——FIG. 297,*1*. **G. difficilis* (AGASSIZ), Cenoman., Fr.; *1a,b*, interamb, amb, ×3.3; *1c-e*, test, lat., aboral, oral, ×1 (27a).——FIG. 297,*2*. *G. rotatus* (FORBES), Cenoman., Fr. *(2a)*, Eng. *(2b-e)*; *2a*, amb, ×?(3); *2b*, amb plates, ×16.7 (136d); *2c*, test plates, ×7 (173); *2d,e*, test, lat., aboral, ×3.3 (173).

Hemithylus ARNAUD, 1895, p. 236 [**Thylechinus rejaudryi* COTTEAU, 1894; OD]. Test small, low hemispherical. Amb plates polyporous, 4 or 5 geminate adorally, trigeminate adapically; pore zones simple. Primary tubercles large, wtih radiating striae; plates otherwise covered by close granu-

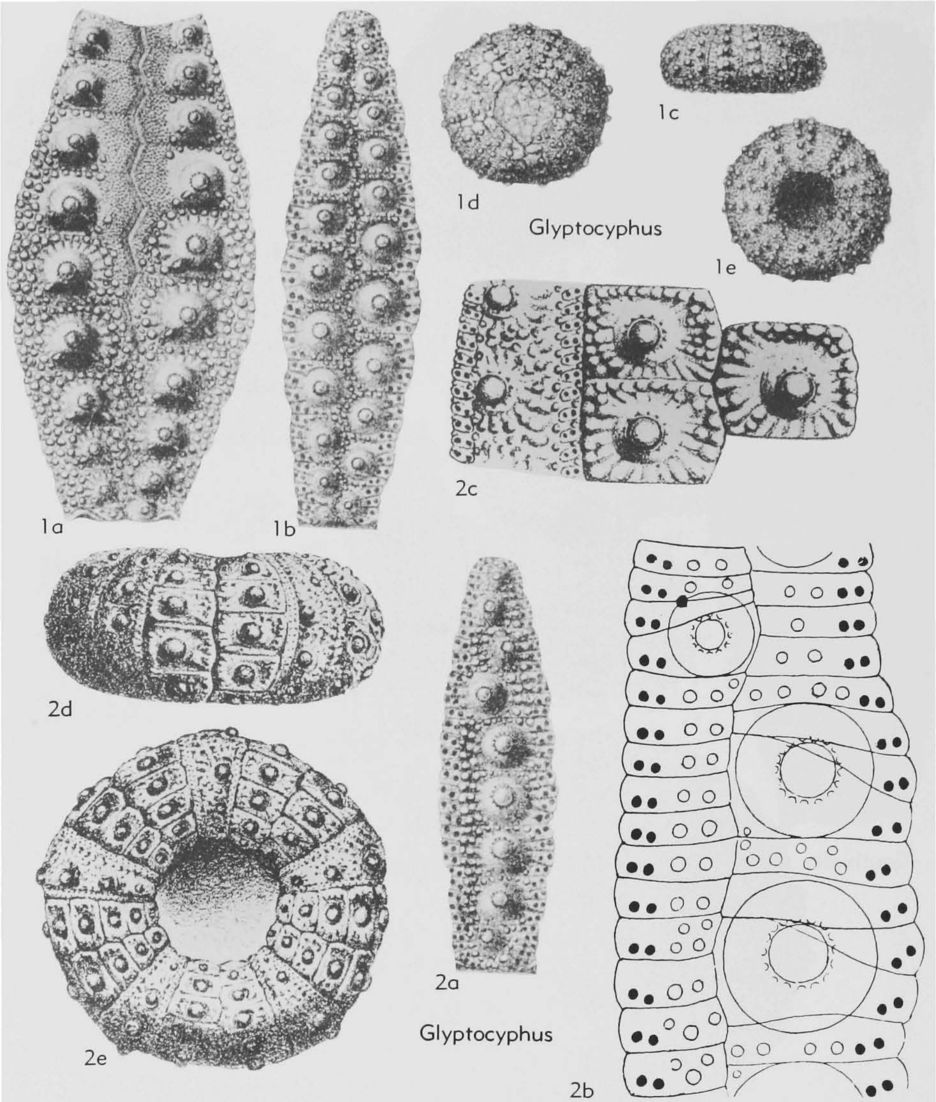

FIG. 297. Phymosomatidae (p. U399).

lation. *U.Cret.*, Eu.——FIG. 294,*1*. **H. rejaudryi* (COTTEAU), Senon., Fr.; detail of test plates, ×5.3 (26).

Jacquiertia MERCIER, 1936, p. 419 [**J. minuta* MORTENSEN & MERCIER, 1939, p. 58; OD]. Test small, depressed. Amb plates simple aborally, trigeminate, diadematoid, adorally; pore pairs in straight series throughout. Primary tubercles distinct only at ambitus. Interamb plates each with primary tubercle, diminishing in size adapically and adorally. *L.Jur.*, N.Fr.——FIG. 296,*2*. *J. minuta* MORTENSEN & MERCIER, Toarc., Calvados; amb detail, ×14.7 (136c).

Lambertechinus COSSMAN, 1899, p. 45 [**Asteropsis lapparenti* COTTEAU, 1883, p. 21; OD] [=*Asteropsis* COTTEAU, 1883, p. 21 (obj.) *(preocc.)*; *Actinopsis* LAMBERT, 1897, p. 500 (obj.) *(preocc.)*; *Psilosoma* POMEL, 1883, p. 91 *(preocc.)*]. Like *Phymosoma*, but with primary tubercles diminishing abruptly in size above ambitus. *U.Cret.*, Eu. ——FIG. 293,*1*. *L. arnaudi* (COTTEAU), Senon., Fr.; *1a-c*, test, aboral, lat., oral, ×1.3; *1d,e*, interamb, amb, ×3.3 (27a).

Leptechinus GAUTHIER, 1889, p. 107 [**Cyphosoma heinzi* PERON & GAUTHIER, 1884, p. 96; OD] [=*Peronia* DUNCAN, 1889, p. 82 (obj.); *Proto-*

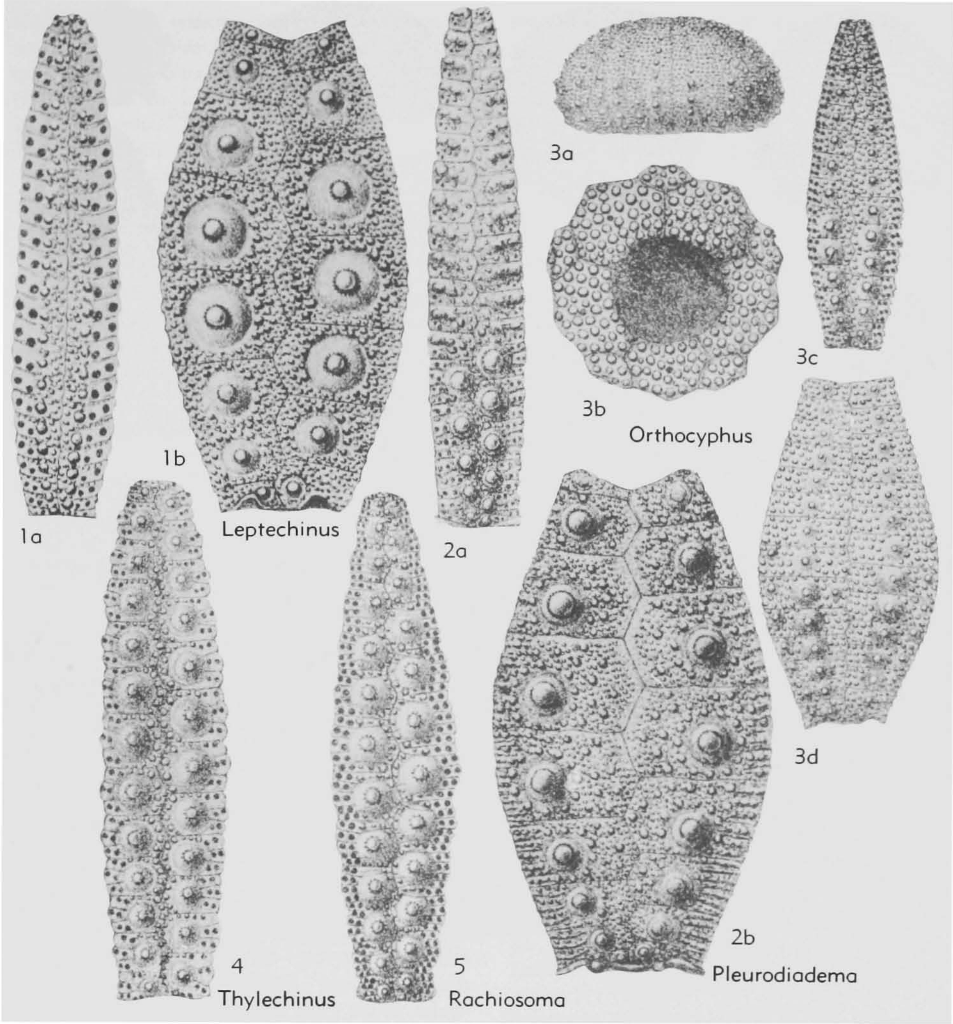

FIG. 298. Phymosomatidae (p. U400-U403).

tiara LAMBERT, 1900, p. 34 (type, *Pleurodiadema jutieri* COTTEAU, 18??)] [*non Leptechinus* TORNQUIST, 1897 (=*Tornquistellus* BERG, 1899)]. Test small, low hemispherical. Ambs with simple primaries; pores in regular simple series. No distinct primary amb tubercles. Interamb primaries forming regular series, widely separated from each other. Apical system with oculars all broadly insert. *L.Jur.(Pliensbach.)-L.Cret.(Neocom.),* Eu.-N.Afr.——FIG. 298,*1*. **L. heinzi* (PERON & GAUTHIER), Neocom., Algeria; *1a,b,* amb, interamb, ×4 (35).

Micropsis COTTEAU, 1856, p. 8 [**M. desori*; OD] [=*Micropsidia* POMEL, 1869, p. XLI (?type)]. Test medium-sized, subhemispherical. Amb plates may be trigeminate near peristome, elsewhere polyporous; pore zones simple, undulating. Primary tubercels small, secondaries commonly of same size, forming vertical and horizontal series. *L.Jur.(Toarc.),* Fr.

Narindechinus LAMBERT, 1933 [**N. checchiai*; OD]. Like *Phymosoma,* but with up to 10 series of large interamb tubercles, and 4 series of amb tubercles. *Eoc.,* Madag.——FIG. 296,*3*. **N. checchiai,* M. Eoc. (Lutet.); *3a,b,* test fragments (± enl.?) (113).

Pleurodiadema DE LORIOL, 1870, p. 196 [**P. stutzi*; OD] [=*Phalacrechinus* LAMBERT, 1900, p. 37 (type, *Pleurodiadema gauthieri* COTTEAU, 1883, p. 408)]. Like *Leptechinus* but with amb plates simple adapically, trigeminate adorally, primary tubercles developed on oral side not continuing

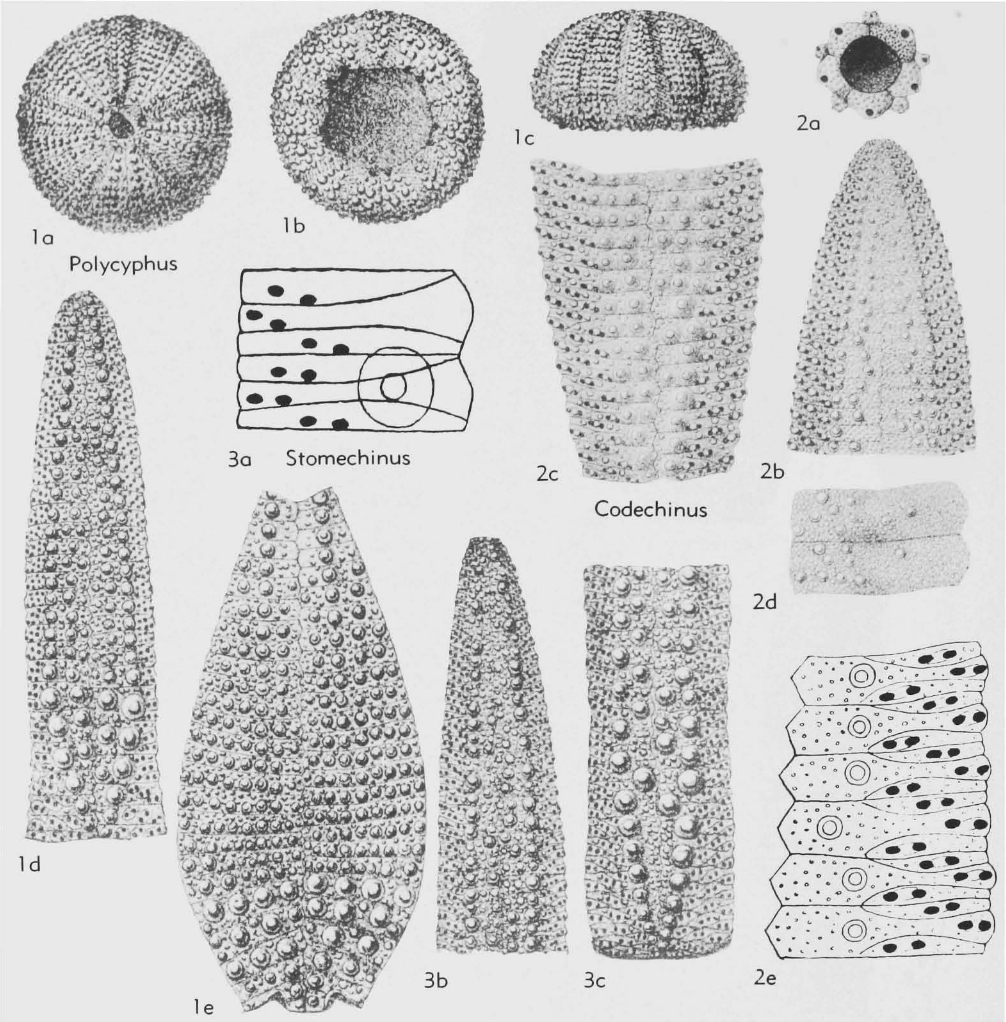

FIG. 299. Stomechinidae (p. U403, U406).

above ambitus. Oculars broadly exsert. *Jur. (Bathon.-Oxford.),* Eu.-N.Afr.——FIG. 298,2. **P. stutzi,* U.Jur.(Argov.), Switz.; *2a,b,* amb, interamb, mag. unknown (27d).

Porosoma COTTEAU, 1856, p. 648 [**Cyphosoma cribrum* L. AGASSIZ; SD MORTENSEN, 1935, p. 474] [=*Coptosoma* DESOR, 1855 (obj.) (*non* LAPORTE, 1833); *Microsoma* COTTEAU, 1886, p. 76 (?type); *Euporophyma* GAUTHIER, 1901, p. 31 (type, *Coptosoma lefebvrei* GAUTHIER, 1901, p. 31; SD BATHER, 1902, p. 76)]. Amb plates compound, polyporous, pores in single series only. Apical system small, only ocular I insert. Test of moderate size, low hemispherical. *L. Cret. (Neocom.)-Oligo.,* Eu.-N. Afr.-S.Afr.-N.Am.——FIG. 295,*1a-c.* **P. cribrum* (AGASSIZ), Eoc., Fr.; *1a,b,* test, aboral, oral, ×1 (27e); *1c,* adoral part of amb, ×2.7 (27e).——FIG. 294,*2*; 295,*1d. P. rousseli* (COTTEAU), Eoc., Fr.; 294,*2,* amb plate, ×8 (27e); 295,*1d,e,* aboral part of amb, ×2, amb enl., ×2.7 (27e).

Rachiosoma POMEL, 1883, p. 91 [**Cyphosoma delamarrei* DESHAYES, 1831; SD LAMBERT & THIÉRY, 1911, p. 221] [=*Miocyphosoma* POMEL, 1883, p. 90 (?type)]. Like *Gauthieria* but with periproctal plates not polygonal, not of acrosaleniid type. *L.Cret.-U.Cret.,* Eu.-N.Afr.-N.Am.——FIG. 298,*5.* **R. delamarrei* (DESHAYES), U.Cret.(Senon.), Fr.; amb, ×2 (27a).

Thylechinus POMEL, 1883, p. 91 [**Cyphosoma said* PERON & GAUTHIER, 1881, p. 172; SD LAMBERT & THIÉRY, 1911, p. 214] [=*Psilosoma* POMEL, 1883, p. 91 (*fide* LAMBERT & THIÉRY, 1911, p. 214); *Cenchritechinus* LAMBERT, 1911, p. 11]. Test hemispherical, of moderate size. Amb plates trigeminate. Apical system dicyclic, oculars usually widely exsert. Female (of type-species) with sunken aboral marsupia in interambs. *U.Cret.-Oligo.*, Eu.-N.Afr.-India-Peru. [=?*Terina* AGASSIZ, 1838 *(nom. nud.)*.]

T. (Thylechinus). Ambs and interambs with single regular series of primary tubercles in each column. No large secondary tubercles. *U.Cret. (Senon.)-Oligo.*, Eu.-N.Afr.-India-Peru.——FIG. 298,*4*. *T. aublini* (COTTEAU), Senon., Fr.; amb, mag. unknown (27a).

T. (Orthocyphus) ARNAUD, 1896, p. 234 [**Cyphosoma pulchellus* COTTEAU; SD MORTENSEN, 1935, p. 476] [=*Psilosoma* POMEL, 1883, p. 91]. Primary tubercles much reduced in size adapically. *U.Cret.*, Fr.——FIG. 298,*3*. **T. (O.) pulchellus* (COTTEAU), Senon; *3a*, test, lat., ×5.3; *3b*, apical system, ×16.7; *3c,d*, amb, interamb, ×10 (27a).

T. (Mistechinus) DE LORIOL, 1897, p. 8 [**M. mayeri*; OD, M] [=*Egyptechinus* LAMBERT, 1936, p. 41 (type, *E. cuvillieri*; OD)]. Primary amb tubercles reduced adapically and adorally. *Eoc.*, Egypt.

T. (Orthechinus) GAUTHIER, 1889, p. 105 [**O. tunetanus*; OD]. Secondary tubercles well developed, forming vertical series beside primary series. Apical system with some oculars insert. *U. Cret. (Senon.)-Eoc.*, Eu.-N. Afr.-Asia Minor-Iran-N.Am.

Family STOMECHINIDAE Pomel, 1883

[*nom. correct.* DURHAM & MELVILLE, 1957, p. 254 (*pro* les Stomechiens POMEL, 1883, p. 81)] [=Stomopneustidae MORTENSEN, 1903, p. 133]

Primary tubercles noncrenulate. Amb tubercles usually as large as interamb tubercles. Ambs compounded in diadematoid manner, trigeminate or polyporous (in *Echinotiara* some adapical plates remain simple); diplopodous ambs may occur adapically or throughout. Apical system dicyclic or monocyclic, usually small, seldom extending backward. Peristome large, with usually distinct gill slits. Primary spines without cortex or collar. Pedicellariae (known in *Stomopneustes*) of ophicephalous, tridentate, triphyllous and globiferous types. Spheridia placed beside tube feet, not in pits. *L.Jur.-Rec.*

Stomechinus DESOR, 1856, p. 124 [**Echinus bigranularis* LAMARCK, 1816; SD LAMBERT, 1901, p. 237] [=*Sporotaxis* POMEL, 1883, p. 84 (*nom. nud.*, based on erroneous figure); *Cretacechinus* LAMBERT & THIÉRY, 1911, p. 253 (type, *Stomechinus camarensis* DE LORIOL, 1887, p. 65)]. Test hemispherical or depressed, medium-sized to large (80 mm. diam.). Amb plates trigeminate, pores arranged in arcs of 3; primary tubercle on every 2nd amb plate, pore zones broad, widened adorally. *L. Jur.(Domer.)-L. Cret.(Neocom.)*, Eu.-SW. USSR(Turkmenia)-N. Afr.-NE. Afr.——FIG. 299,*3a*. *S. choffati* DE LORIOL, Bajoc., Port.; amb plates, *ca.* ×3.3 (123).——FIG. 299,*3b,c*. *S. perlatus* (DESMAREST), U.Jur.(Oxford.), Fr.; *3b,c*, amb aboral, adoral, ×1.3 (27d).

Circopeltis POMEL, 1883, p. 89 [**Leiosoma meridanensis* COTTEAU, 1867, p. 765; SD LAMBERT & THIÉRY, 1914, p. 254] [=*Strictechinus* COTTEAU, 1893, p. 169 (type, *S. pouechi*); *Micropsina* COTTEAU, 1893, p. 630 (type, *M. baudoni*); *Circopeltaris* VALETTE, 1907, p. 109 (type, *C. baicheri*)]. Test of medium size, low hemispherical. Ambs polyporous, pore pairs in single undulating line. Primary tubercles large, in 2 regular series in each area. Secondary tubercles may form vertical series along sides of primaries. *U.Cret.-Eoc.*, Eu.——FIG. 304,*2*. **C. meridanensis* (COTTEAU), U.Cret.(Turon.), Fr.; amb, ×7 (27a).

Codechinus DESOR, 1856, p. 111 [**Echinus rotundus* GRAS, 1848; OD, M]. Test subglobular, of moderate size. Amb plates trigeminate, pore pairs in oblique arcs of 3, with tendency to form 3 vertical series. Tubercles of both areas small, imperforate, noncrenulate, not forming regular series; larger and more numerous adorally. *L. Cret.(Apt.)*, Eu-N.Afr.——FIG. 299,*2*. **C. rotundus* (GRAS), Fr.; *2a*, apical system, ×3.3; *2b,c*, details of amb, ×5.3; *2d*, interamb plates, ×5.3 (*2a-d*, 27a); *2e*, amb plates, ×10 (136c).

Diplechinus LAMBERT, 1931, p. 15 [**D. hebbriensis*; OD, M]. Test moderate in size, subhemispherical. Ambs with pore pairs in simple line at ambitus, in double series adapically and in arcs of 3 at peristome. Primary amb tubercles not regular on all plates. Adorally, secondary tubercles form longitudinal series along with primary series. *L. Jur.*, N.Afr.——FIG. 300,*4*. **D. hebbriensis*, Domer., Morocco; *4a,b*, adapical and ambital amb plates, ×? (136b).

Diplotagma SCHLÜTER, 1870, p. 63 [**D. altum*; OD, M]. Test very high, of medium size. Pore zones diplopodous throughout. Primary tubercles very small, in 2 regular series in both areas. Secondary tubercles numerous, but not in series. *U.Cret.*, Eu.——FIG. 301,*2*. **D. altum*, Senon., Ger.; *2a*, amb detail, ×2; *2b-d*, test, lat., aboral, oral, ×1 (151).

Echinotiara POMEL, 1883, p. 83 [**Echinodiadema bruni* COTTEAU, 1885; OD, M] [=*Echinodiadema* COTTEAU, 1869, p. 141 (obj.) (*non* VERRILL, 1867)]. Test subhemispherical, small to moderate-sized. Ambs adorally of trigeminate plates, pore pairs in arcs; adapically plates simple primaries or incipiently compound pore pairs forming approximately straight line. *M.Jur.(Bathon.)-U.Cret. (Maastricht.)*, Eu.-N.Afr.-NE.Afr.——FIG. 300,*1*; 302,*2a,b*. **E. bruni* (COTTEAU), Bathon., Fr.; 300,*1*, amb, ×8; 302,*2a*, interamb, ×5.3 (27d).——FIG. 302,*2b*. *E. neocomiensis* (DE LORIOL),

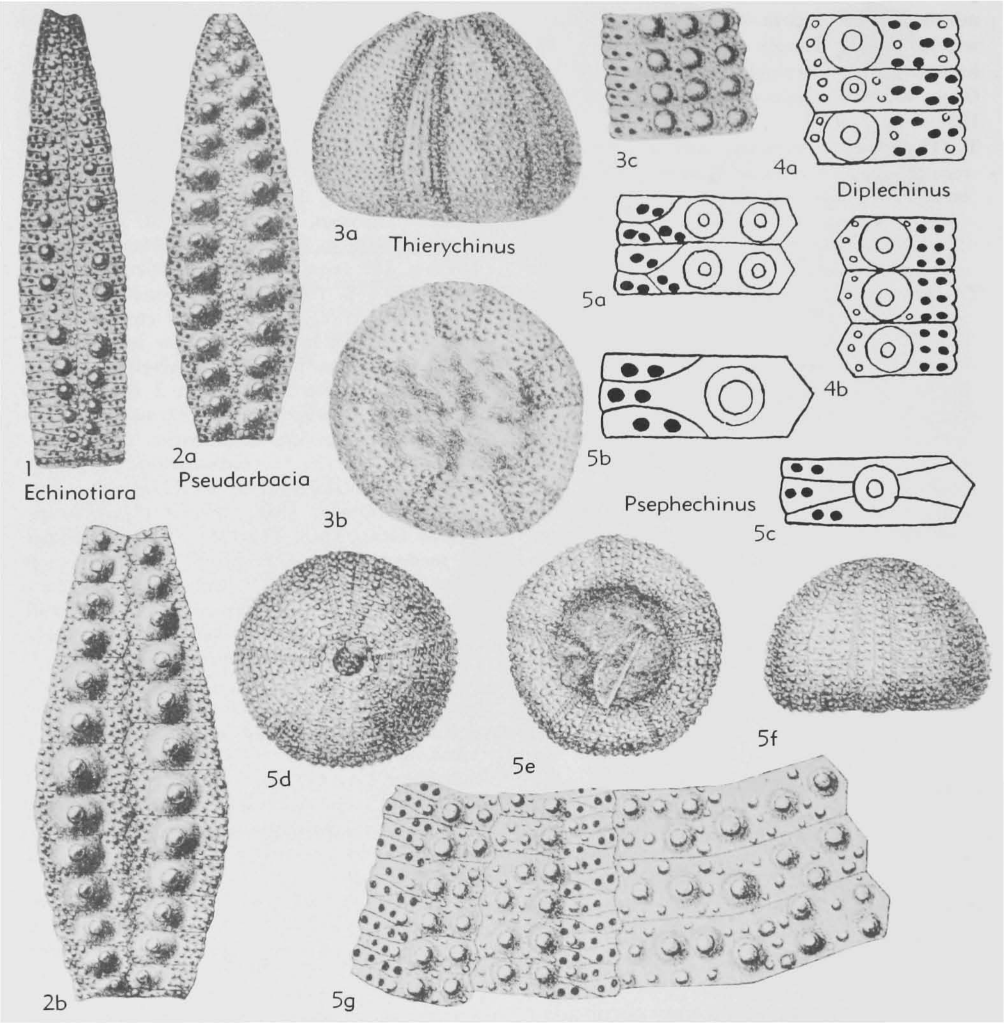

FIG. 300. Stomechinidae (p. U403-U404, U406-U407).

Neocom., Port.; amb, ×5.3 (123).——FIG. 302, *2c. E. somaliensis* CURRIE, Jur., Somaliland; amb plates, *ca.* ×8 (151).

Gomphechinus POMEL, 1883, p. 90 [**Leiosoma selim* PERON & GAUTHIER; OD]. Test flattened, wheel-shaped, of medium size. Ambs polyporous, diplopodous. Primary tubercles in regular series; secondary tubercles as large as primaries, forming vertical series. Apical system large, pentagonal, caducous, scarcely smaller than peristome. *U.Cret.,* N.Afr.-Madag.——FIG. 303,*1*. **G. selim* (PERON & GAUTHIER), Senon., Alg.; *1a-c,* test, aboral, oral, lat., ×1.2; *1d,* amb, ×1.7 (35).

Jeannetia MERCIER, 1936, p. 421 [**J. mortenseni*; OD, M]. Test small, hemispherical. Amb plates compound trigeminate adorally, simple primaries adapically; pore pairs in single series. Interamb primary tubercles in regular series. Aboral side almost wholly naked, especially in median areas of ambs and interambs. *L.Jur.-M.Jur.(Bajoc.-Callov.),* Fr.-USA(Wyo.).——FIG. 302,*1*. **J. mortenseni,* Hettang.; *1a,b,* amb, interamb, ×? (136c). [=*Parastomechinus* PHILIP, 1963, p. 1111 (type, *P. brightoni*; OD).]

Noetlingaster VREDENBURG, 1911, p. 46 [**Protechinus paucituberculatus* NOETLING, 1897, p. 14; OD] [=*Protechinus* NOETLING, 1897, p. 14 (preocc.) (obj.); *Noetlingia* LAMBERT, 1898, p. 126 (preocc.) (obj.)] [*non Noetlingia* HALL & CLARK, 1894, *nec* BEURLEN, 1928]. Test medium-sized to very large, hemispherical or subconical. Amb plates trigeminate. Pore pairs characteristic,

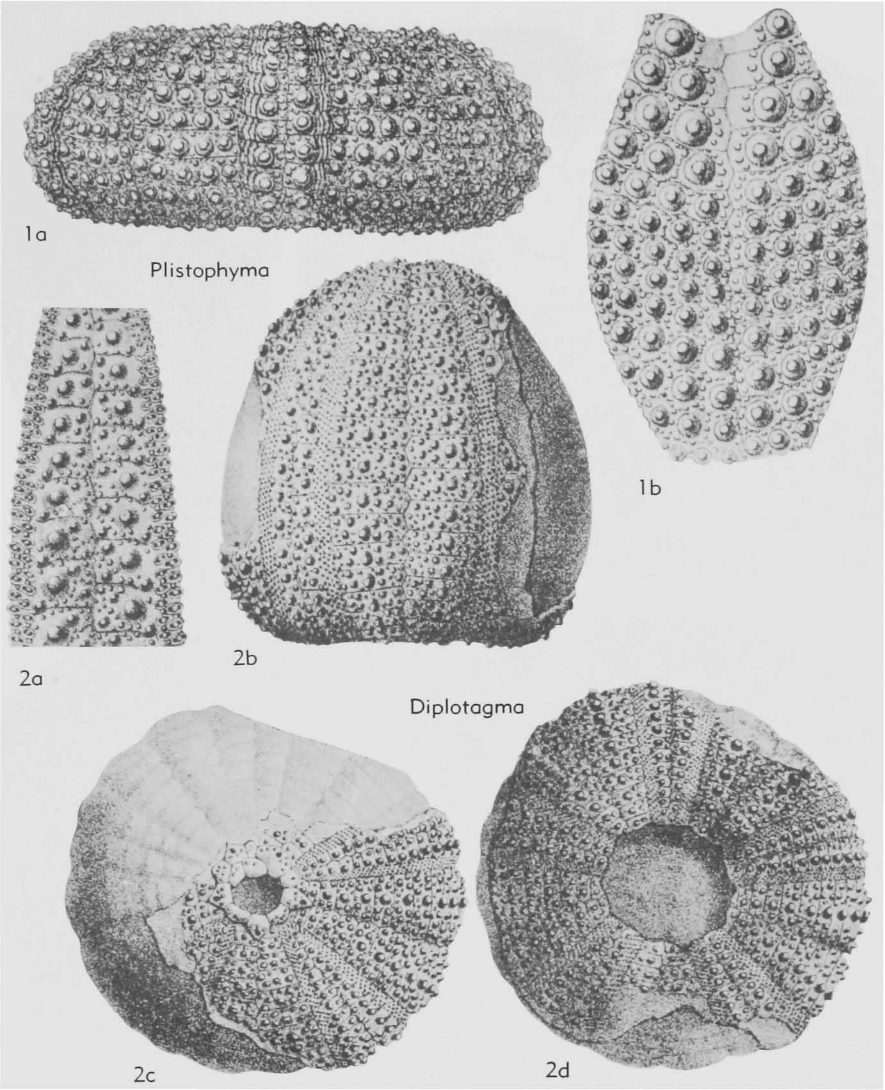

FIG. 301. Stomechinidae (p. U403, U408).

2 large pairs close to edge of area, one small pair farther inward occupying small separate plate. *U.Cret.(Maastricht.)*, N.Afr.-Madag.-Pak.——FIG. 302,*3*. *N. sanfilippoi* CHECCHIA-RISPOLI, Tripolitania; *3a*, test, lat., ×0.8 (19); *3b*, amb, adapical part, ×4.7 (136c).

Phymechinus DESOR, 1856, p. 133 [**Echinus mirabilis* L. AGASSIZ; OD] [=*Alternechinus* SCHLÜTER, 1870, p. 62 (type, *A. cretaceus*)]. Test large, subhemispherical. Ambs polyporous, pore pairs in double series throughout. Primary tubercles large, in 2 regular series in each area; secondaries scarcely reaching size of primaries. Apical system small (0.2 horiz. diam.). Peristome very large (0.5 horiz. diam.). *M.Jur.(Bajoc.)-U.Cret.*, Eu.——FIG. 303,*2*. **P. mirabilis* (AGASSIZ), U.Jur.(Oxford.), Fr.; *2a*, detail of amb, ×5.3; *2b-d*, test, aboral, oral, lat., ×1.2 (27d).

Phymotaxis LAMBERT & THIÉRY, 1914, p. 253 [**Leiosoma tournoueri* COTTEAU, 1867, p. 768; OD] [=*Micropeltis* POMEL, 1883, p. 89 (obj.) *non* REDTENBACHER, 1867; *nec* KRAATZ, 1880)]. Test low hemispherical, medium-sized. Ambs polyporous, pore pairs in double series adorally, in single undulating line adapically. Primary tubercles in 2 regular series in each area. *U.Cret.-*

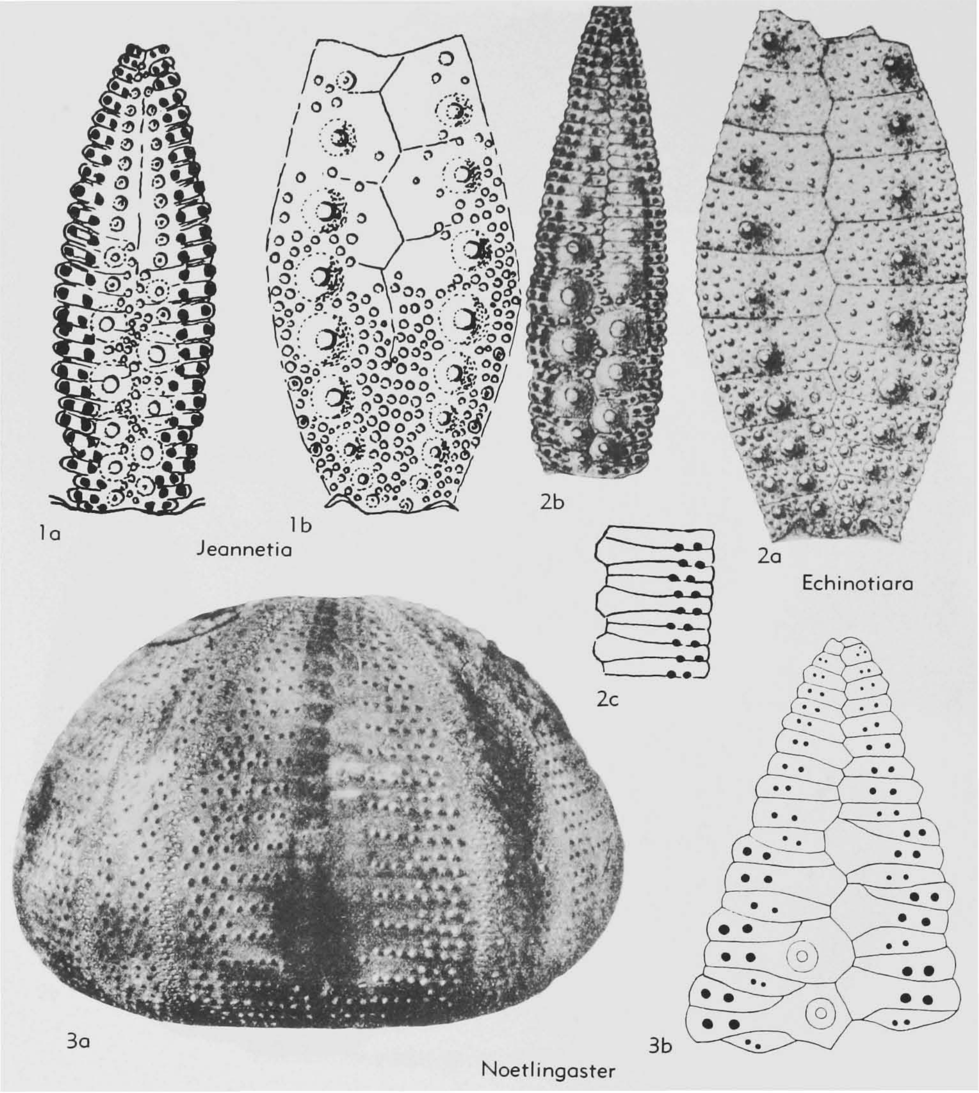

FIG. 302. Stomechinidae (p. U403-U405).

Eoc., Eu.——FIG. 304,*1.* **P. tournoueri* (COTTEAU), U.Cret.(Senon.), Fr.; *1a-c,* test, aboral, oral, lat., ×1.2 (27a).

Polycyphus L. AGASSIZ & DESOR, 1846, p. 361 [**P. normannus*; OD, M] [=*Sporadocyphus* POMEL, 1883, p. 81 (?type)]. Test small, hemispherical. Amb plates trigeminate, pores in arcs of 3. Primary tubercles small, indistinguishable from numerous secondaries. Tubercles abruptly larger adorally. *M. Jur.-U. Jur.,* Eu.-C. Asia(Tibet)-Madag. ——FIG. 299,*1.* **P. normannus,* Bathon., Fr.; *1a-c,* test, aboral, oral, lat., ×1.3; *1d,e,* amb, interamb, ×3.3 (27d).

Psephechinus POMEL, 1883, p. 81 [**Stomechinus michelini* COTTEAU, 1884; OD] [=*Tiarotropus* POMEL, 1883, p. 82 (?type)]. Like *Polycyphus* but of moderate size, with distinguishable primary tubercles; tubercles not abruptly larger adorally. *L.Jur.-L.Cret.,* Eu.-N.Afr., S.Am.-?N.Am.——FIG. 300,*5a.* *?P. hyatti* (W. B. CLARK), Jur., ?N.Am.; amb plates, ×? (136b).——FIG. 300,*5b-g.* *P. morierei* (COTTEAU), M.Jur.(Bathon.), Fr.; *5b,c,* amb plates, ×8; *5d-f,* test, aboral, oral, lat., ×1.2; *5g,* test plates, detail, ×7 (27d).

Pseudarbacia LAMBERT, 1897, p. 515 [**Leiosoma archiaci* COTTEAU, 1866; OD, M]. Test of mod-

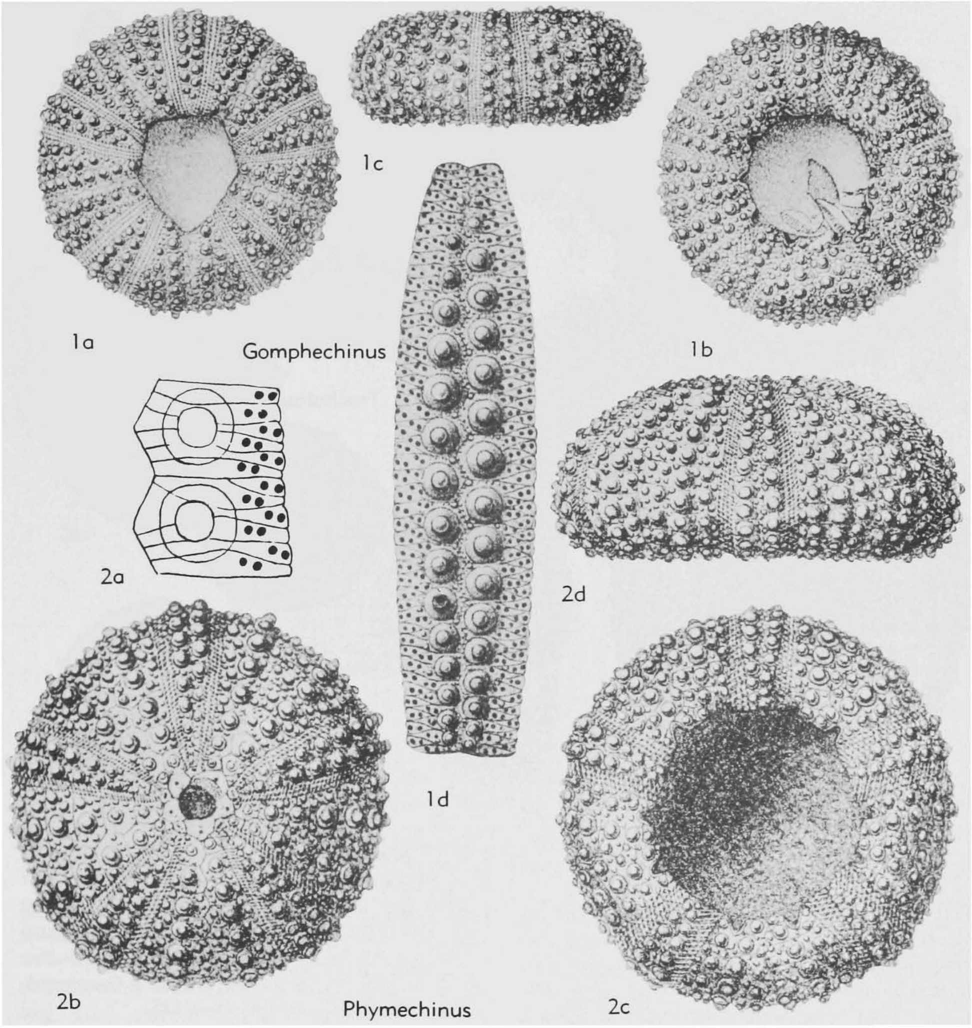

FIG. 303. Stomechinidae (p. U404-U405).

erate size, low hemispherical. Ambs trigeminate, pore pairs in single undulating line, not distinctly in arcs of 3. *U.Cret.*, Eu.——FIG. 300,*2*. **P. archiaci* (COTTEAU), Turon., Fr.; *2a,b*, amb, interamb, ×3.3 (27a).

Stomopneustes L. AGASSIZ, 1841, p. 7 [**Echinus variolaris* LAMARCK, 1816, p. 47; OD, M]. Test large, hemispherical. Amb plates compound, each consisting of 4-6 trigeminate plates covered by very large primary tubercle. Pore zones broad, somewhat petaloid adorally. Primary tubercles forming regular series. Conspicuous undulating median furrow in each interamb. [The type-species is the only known Recent stomechinid.] *Mio.*, Java; *Rec.*, tropical W.IndoPacific.

Thierychinus LAMBERT, 1910, p. 5 [**T. delaunayi*; OD, M]. Test of moderate size, high, subconical. Amb plates trigeminate, pore pairs arranged in double series. Tubercles numerous, imperforate, noncrenulate; secondary tubercles reaching same size as primaries, forming regular horizontal series on each plate in both areas. *Jur.(Vesul.)*, Fr.——FIG. 300,*3*. **T. delaunayi*, St. Gaultier; *3a,b*, test, lat., oral, ×0.93; *3c*, amb plates, ×5.3 (115).

Tiarechinopsis LAMBERT, 1936, p. 15 [**T. besairiei*; OD, M]. Test small, subconical, flattened below. Amb plates compound, trigeminate; pore zones simple adorally, adapically "pseudotrigeminate." Tubercles well developed adorally, 2 series in ambs, 4 in interambs. Primary tubercles scarcely distinguishable among small granules adapically. *M.Jur.(Bajoc.)*, Madag.

Triadechinus ARNOLD & H. L. CLARK, 1927, p. 20 [**T. multiporus*; OD]. Test large, hemispherical.

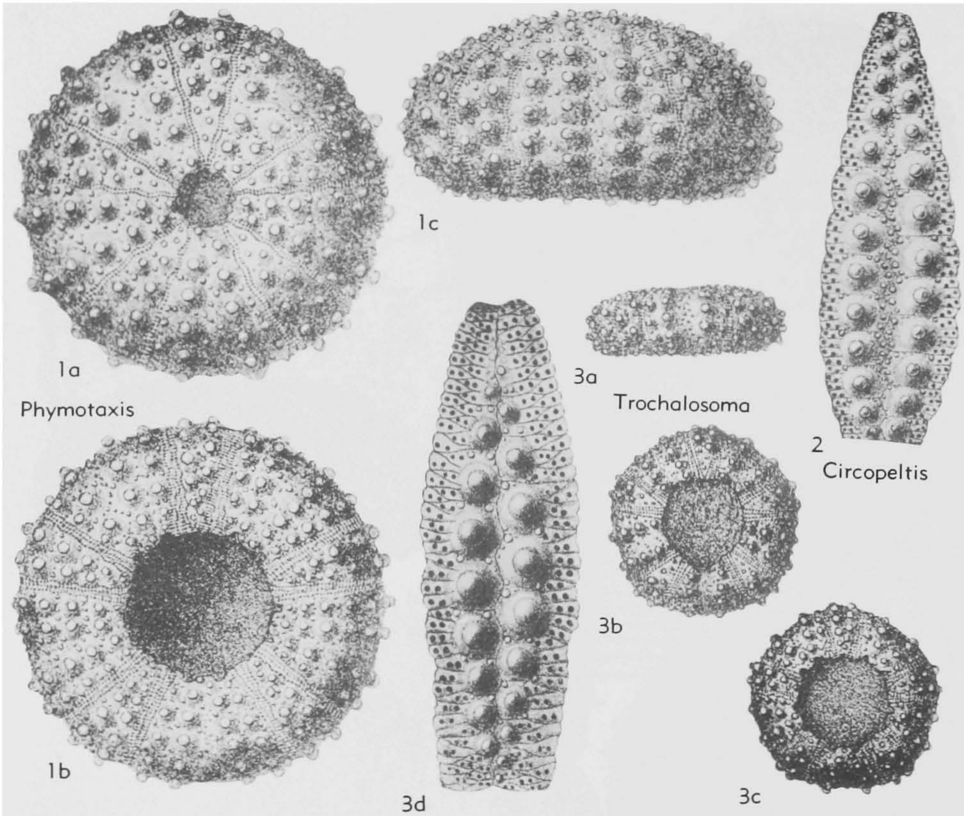

FIG. 304. Stomechinidae (p. U403, U405-U406, U408).

Pore pairs crowded, in 3 vertical series. Primary tubercles large, not in regular double series in ambs adapically; tubercles regularly alternating in interambs but wide apart, plates being very high. Interamb mid-line conspicuous depressed groove. *?Cret.*, Jamaica.

Trochalosoma LAMBERT, 1897, p. 515 [**Leiosoma rugosum* COTTEAU, 1860, p. 271; OD] [=*Leiosoma* COTTEAU, 1860, p. 271 (obj.) (*non* STEPHENS, 1831, *nec* CHEVROLAT, 1837); *Plesiopeltis* LAMBERT, 1897, p. 517 (type, *Circopeltis gourdoni* COTTEAU, 1889)]. Test flattened, wheel-shaped, of medium size. Ambs trigeminate orally, polyporous from ambitus, pore pairs in double series, adapically. Apical system large, caducous. *U.Cret.*, Fr.-Jamaica.

T. (Trochalosoma). Secondary tubercles not as large as primaries, not forming horizontal and vertical series. *U.Cret.-Senon.*, Fr.——FIG. 304,*3*. **T. (T.) rugosum* (COTTEAU); *3a-c*, test, lat., aboral, oral, ×1.3; *3d*, amb, ×4 (27a).

T. (Plistophyma) PERON & GAUTHIER, 1881, p. 176 [**P. africanum*; OD]. Secondary tubercles as large as primaries forming horizontal and vertical series. *U.Cret.(Senon.)*, Eu.-N.Afr.-Iran. ——FIG. 301,*1a*. *T. (P.) vidali* (COTTEAU), Spain(Catalonia); test, lat., ×1.2 (26).——FIG. 301,*1b*. **T. (P.) africanum* (PERON & GAUTHIER), Alg.; interamb, mag. unknown (35).

Family UNCERTAIN

Boletechinus COOKE, 1955, p. 93 [**B. macglameryae*; OD] [=*Boletechinus* COOKE, 1953, p. 4 *(nom. nud.)*]. Like *Orthocyphus*, but with depressed sutures, and oculars I and V broadly insert. *U.Cret.(Maastricht.)* USA(Ala.).

Order ARBACIOIDA Gregory, 1900

[*nom. transl.* DURHAM & MELVILLE, 1957, p. 255 (*ex* Arbacina GREGORY, 1900, p. 307)]

Lantern stirodont. Ambs invariably including some compounded plates of arbacioid type; simple plates, if present, restricted to adapical or adoral extremities. Primary tubercles imperforate, noncrenulate, usually

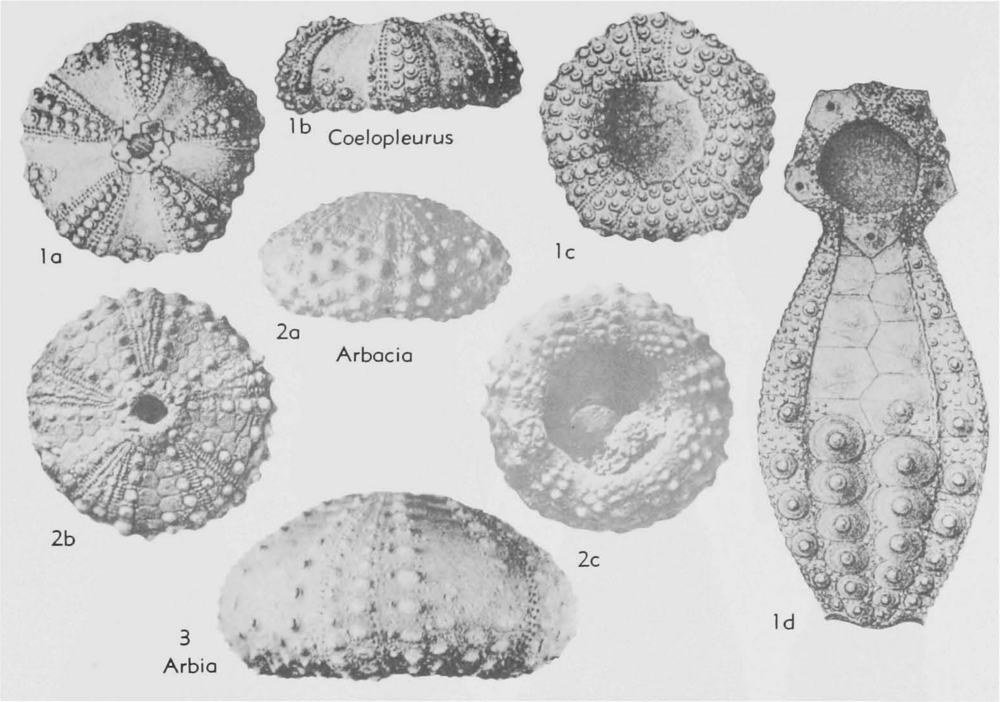

FIG. 305. Arbaciidae (p. *U*409-*U*410, *U*412).

rather inconspicuous, those of interamb being larger. Epistroma commonly present, simulating tubercles, but not carrying spines. Primordial interamb plates persisting, commonly prolonged on distal margin, where unpaired tubercle may occur. Apical system usually dicyclic, periproct covered by 4 or 5 conspicuous triangular anal valves, simulating anal pyramid. Primary spines with more or less development of cortex, usually smooth; secondary spines poorly developed or lacking. Pedicellariae triphyllous, tridentate, and ophicephalous. Spheridia typically placed in deep pits along amb mid-line. *M.Jur. (Bathon.)-Rec.*

Family ARBACIIDAE Gray, 1855

[*nom. correct.* GREGORY, 1900, p. 307 (*pro* Arbaciadae GRAY, 1855, p. 36)] [=Echinocidaridae TROSCHEL, 1872, p. 293]

Characters of order. Test small to moderate-sized; exceptionally (e.g., *Arbacia, Tetrapygus*) reaching 50-75 mm. horiz. diam., usually subconical, flattened below, some spherical, plates soldered together by ball-and-socket processes between them. *M.Jur.-Rec.*

Arbacia GRAY, 1835 (July), p. 58 [**Cidaris pustulosa* LESKE, 1778, p. 150 (=*Echinus lixula* LINNÉ, 1758, p. 664; OD)] [=*Echinocidaris* DESMOULINS, 1835 (Aug.), p. 200 (obj.); *Agarites* L. AGASSIZ, 1841, p. 7 (type, *Echinus punctulatus* LAMARCK, 1816, p. 363); *Anapesus* HOLMES, 1860 (type, *A. carolinus*, =*Echinus punctulatus*); *Pygomma* TROSCHEL, 1872, p. 309 (type, *Echinus spatuliger* VALETTE]. Test low hemispherical or subconical, flattened adorally, of medium size. Ambs with trigeminate plates, pore zones straight, narrow above ambitus, conspicuously widened adorally. Primary amb tubercles in regular series. Interambs with numerous primary tubercles in horizontal and vertical series. No secondary tubercles. Adapically interambs have conspicuous naked spaces. *?U. Mio., Plio.,* USA(S.Car.); *Pleist.,* USA(S.Car.)-Italy; *Rec.,* E.N.Am.-W.N.Am.-Falkland Is.-Eu.-W.Afr.-Medit. (probable origin on W.Am. coasts, with Plio. and post-Plio. extension across Atlantic).——FIG. 305,*2*. *A. waccamaw* COOKE, ?U.Mio., USA(S.Car.); *2a-c,* test, lat., aboral, oral, ×1 (24).

Acropeltis L. AGASSIZ, 1840, p. 11, 19 [**A. aequituberculata*; OD]. Test small, hemispherical, flattened below. Amb plates compound, trigeminate, pore zones straight. Primary amb tubercles well developed, continuing to apical system. Interamb tubercles also well developed, in single regular

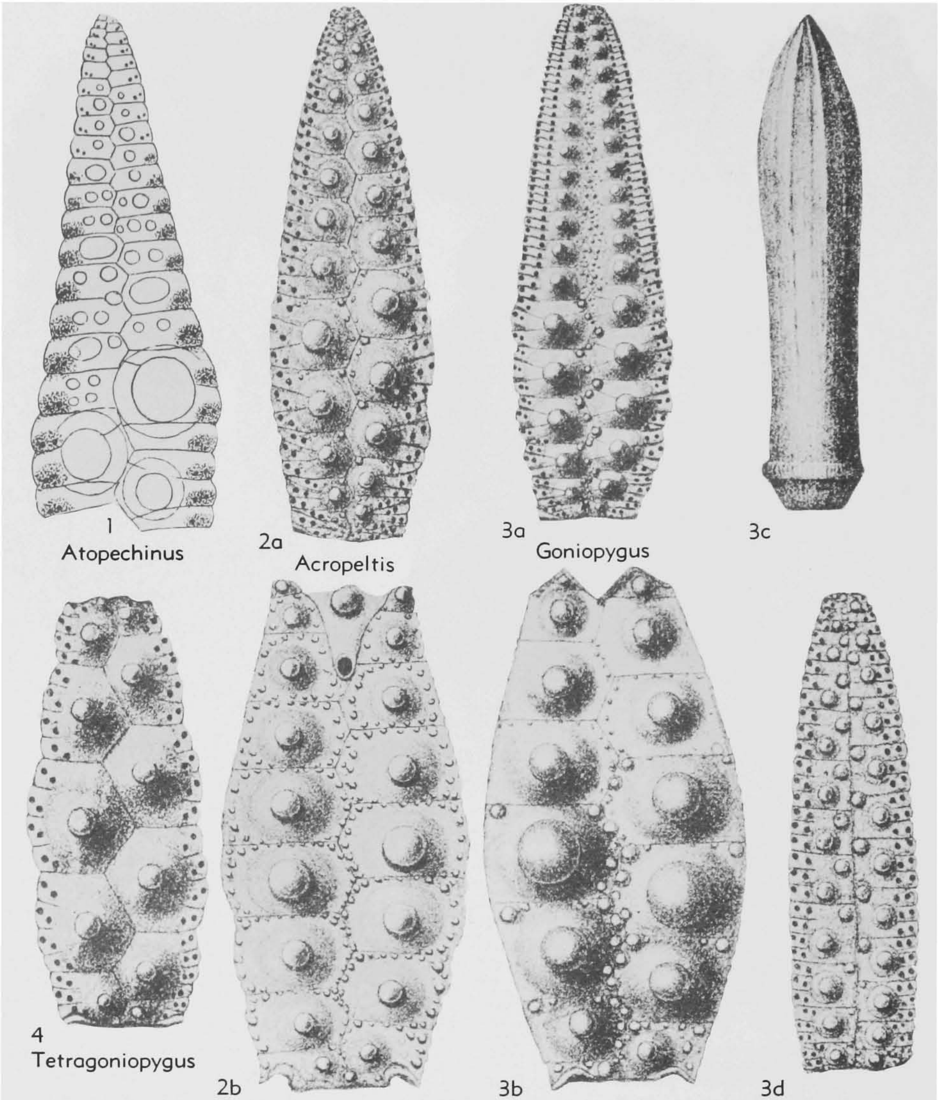

FIG. 306. Arbaciidae (p. U409-U412).

series. Apical system characteristic, with single large tubercle on each genital plate. *U.Jur.*, Eu.-N. Afr.——FIG. 306,*2*. **A. aequituberculata,* Oxford., Fr.; *2a,b,* amb, interamb, ×5.3 (27d).

Acrosaster LAMBERT, 1910, p. 30 [**A. michaleti*; OD, M]. Test small, hemispherical. Ambs with simple primary plates adapically, compound trigeminate plates adorally. Amb plates each with granule or tubercle adapically, and with larger primary tubercle adorally. Interambs with large primary tubercles adorally, tubercles small adapically, wtih deep areole. [Apical system sexually dimorphic.] *M.Jur.(Bathon.)*, Fr.

Arbaciella MORTENSEN, 1910, p. 327 [**A. elegans*; OD, M]. Like *Arbacia,* but small forms, with pore zones but slightly widened adorally. Tubercles confined to adoral side. *Rec.,* W.Afr.

Arbia COOKE, 1948, p. 606 [**Coelopleurus aldrichi* W. B. CLARK, 1915, p. 158; OD]. Like *Arbacia,* but having simple amb plates adapically, and spheridial pits. *U.Oligo.,* USA(Ala.); *L.Mio.,* USA (Miss.).——FIG. 305,*3*. **A. aldrichi* (W. B.

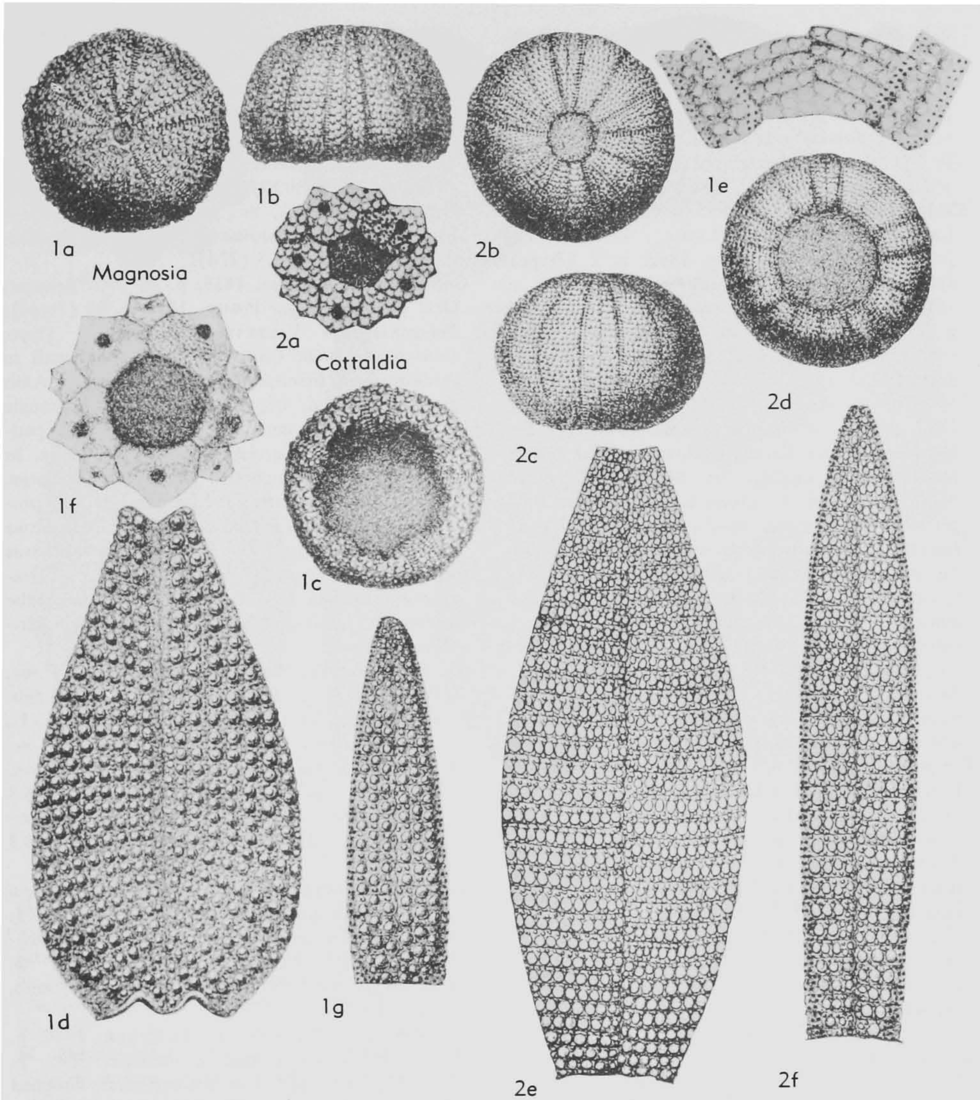

FIG. 307. Arbaciidae (p. U412-U413).

CLARK), *U.Oligo.*, USA(Ala.), test, lat. (syntype), ×1 (24).

Atopechinus THIÉRY, 1928, p. 100 [**A. cellensis*; OD, M]. Test small, subhemispherical. Amb plates compound trigeminate adorally, simple primaries adapically; pore zones simple, straight, undulating adorally. Amb plates with large primary tubercles adorally, which are reduced to small granules adapically. Interamb primary tubercles large throughout. *M.Jur.(Bathon.)*, Eu.——FIG. 306,*1*. **A. cellensis*, Fr.; amb, adapical, ×8 (136b).

Baueria NOETLING, 1885, p. 184 [**B. geometrica*; OD]. Test small to moderate-sized, low hemispherical, rounded. Amb plates compound, trigeminate. Primary tubercles in both areas and abruptly at ambitus. Adapical side with striae, granules of which are partly developed into spine-like knobs. Apical system also decorated with granular striae. *Eoc.*, Ger.-Fr.

Codiopsis L. AGASSIZ, 1840, p. 13, 19 [**Echinus doma* DESMAREST, 1825; SD LAMBERT & THIÉRY, 1914, p. 263] [=*Pseudocodiopsis* VALETTE, 1906, p. 19 (type, *Codiopsis alpina* GRAS); *Hemicodiopsis* POMEL, 1883, p. 82 (?type); *Piliscus* POMEL, 1883, p. 82 (?type)]. Test hemispherical or almost spherical, flattened below, of moderate size. Ambs with compound trigeminate plates. Amb and interamb tubercles confined to adoral side. Small stalked granules present adapically and adorally. *U.Jur.-Eoc.*, Eu.-N. Afr.-Asia Minor-N. Am.-Carib. ——FIG. 308,*1a*. *C. regalis* ARNAUD, U.Cret. (Senon.), Fr.; interamb, ×1.7 (26).——FIG. 308, *1b-g*. **C. doma* (DESMAREST), U.Cret.(Cenoman.), Fr.; *1b,c*, amb, interamb, ×2; *1d*, apical system, ×3.3; *1e-g*, test, aboral, lat., oral, ×1.1 (27a).

Coelopleurus L. AGASSIZ, 1840, p. 12, 19 [**C. equis* (=**Cidaris coronalis* LESKE, 1778); OD] [=*Keraiophorus* MICHELIN, 1862, p. 2 (?type); *Spileccia* HEBERT & MUNIER-CHALMAS, 1878, p. 1313 *(nom. nud.)*; *Phrissopleurus* POMEL, 1883, p. 88 (?type); *Delbosia* POMEL, 1883, p. 88 (?type); *Sykesia* POMEL, 1883, p. 88 (type, *C. pratti* D'ARCHIAC & HAIME); *Murravechinus* TATE, 1894, p. 191 *(nom. nud.)*; *Coeloclypeus* WALTHER, 1893, p. 321 *(nom. nud., ?lapsus calami)*]. Test low hemispherical flattened below, rounded or subpentagonal in outline (up to 50 mm. horiz. diam.). Amb plates compound, trigeminate, with primary tubercles in regular series throughout. Interambs with primary tubercles adorally, becoming reduced or lacking adapically. Ambs usually raised above level of interambs. Interambs adapically with naked median space. *Eoc.-Rec.*, cosmop.; *Rec.*, species mainly deep-water.——FIG. 305,*1*. **C. coronalis* (LESKE), Eoc.(Lutet.), Fr.; *1a-c*, test, aboral, lat., oral, ×1.2 (44); *1d*, interamb and apical system, ×3.3 (27e). [=*Koeraiaphorus* COTTEAU, 1863, p. 377 *(nom. null.)*.]

Cottaldia DESOR, 1856, p. 113 [**Echinus benettiae* KÖNIG, 1820, p. 2; OD, M] [=*Cotteaudia* LAMBERT & THIÉRY, 1910, p. 229 (obj.) *(nom. van.)*]. Test small to moderate-sized, almost spherical. Ambs compound, trigeminate, but with pores in single straight series. Tubercles numerous, small, uniform, arranged in transverse series. *U.Cret. (Cenoman.)*, Eu.-N.Afr.-?W.Afr.——FIG. 307,*2*. **C. benettiae* (KÖNIG), Fr.; *2a*, apical system, ×3.3; *2b-d*, test, aboral, lat., oral, ×1.2; *2e,f*, interamb, amb, ×3.3 (27a). [=*Heterocosmus* POMEL, 1883, p. 83.]

Dialithocidaris A. AGASSIZ, 1898, p. 75 [**D. gemmifera*; OD, M]. Test small, subconical, flattened adorally. Amb plates trigeminate, pore zones widened adorally. Primary tubercles adorally, continuing halfway to the apical system. Numerous papillae adapically, arranged in horizontal series in interambs. Test not sculptured. Apical system large, with 4 anal valves. *Rec.*, Panama (3,200 m.).

Glypticus L. AGASSIZ, 1840, p. 13, 19 [**Echinus hieroglyphicus* GOLDFUSS, 1826; OD] [=*Hologlyptus* POMEL, 1883, p. 88 (preocc.); *Panglyptus* LAMBERT & THIÉRY, 1914, p. 262 (type, *Glypticus kaufmanni* COTTEAU)]. Test low, hemispherical flattened adorally, of moderate size. Amb plates compound, trigeminate, with pores in straight series adapically, in arcs adorally. Amb and interamb primary tubercles well developed adorally, smaller adapically, where they are barely distinguishable in coarse epistroma. *Jur.(Callov.-Tithon.)*, Eu.-N.Afr.-AsiaMinor.——FIG. 309,*1a-d*. **G. hieroglyphicus* (GOLDFUSS), U.Jur.(Oxford.), Fr.; *1a,b*, test, aboral, lat., ×1.2; *1c,d*, amb, interamb, ×2.3 (27d).——FIG. 309,*1e*. *G. integer* DESOR, U.Jur.(Kimmeridg.), Fr.; amb, ×2.3 (27d).——FIG. 309,*1f*. *G. sulcatus* (GOLDFUSS), U.Jur.(Kimmeridg.), Fr.; amb, ×2.3 (27d).——FIG. 309,*1g*. *G. kaufmanni* COTTEAU, Jur.(Oxford.), Fr.; amb, ×2.3 (27d).

Goniopygus L. AGASSIZ, 1838, p. 19 [**G. peltatus*; OD] [=*Cyphopygus* POMEL, 1883, p. 89 (?type); *Polygoniopygus* VALETTE, 1906, p. 11 (type, *Goniopygus pillati* COTTEAU; OD)] Test small to medium-sized, hemispherical, flattened below. Amb plates compound, trigeminate, or quadrigeminate at ambitus; pore zones simple, widened at peristome. Primary tubercles of both areas large, in regular series throughout. Apical system large, genital plates elongate. [*Polygoniopygus* was proposed as a subgenus intended to include polyporous species of *Goniopygus*, but a trigeminate form was selected as the type by VALETTE (1906). *Tetragoniopygus* FELL & PAWSON now embraces the polyporous species.] *U.Jur.-Eoc.*, Eu.-Asia-N.Afr.-N.Am.-S.Am.

G. (Goniopygus). Amb plates trigeminate. *U.Jur. (Portland.)-Eoc.*, Eu.-Asia-N. Afr.-N.Am.-S.Am. ——FIG. 306,*3a*. *G. (G.) major* L. AGASSIZ, U. Cret.(Cenoman.), Fr.; amb, *ca.* ×3.3 (27a).——FIG. 306,*3b,c*. *G. (G.) noguesi* COTTEAU, L.Cret. (Neocom.), Spain; interamb, spine, *ca.* ×3.3 (27a).——FIG. 306,*3d*. *G. (G.) arnaudi* COTTEAU, U.Cret.(Turon.), SW.Fr.; amb, *ca.* ×3.3 (32).

G. (Tetragoniopygus) FELL & PAWSON, 1965, herein [**Goniopygus supremus* HAWKINS, 1924, p. 313; OD]. Amb plates partly quadrigeminate. *Cret.-Paleoc.*, Eu.-N. Am.-Carib.——FIG. 306,*4*. *G. (P.) minor* SORIGNET, Paleoc.(Mont.), Fr.; amb, *ca.* ×3.3 (27a).

Habrocidaris A. AGASSIZ & H. L. CLARK, 1906, p. 234 [**Podocidaris scutata* A. AGASSIZ, 1880, p. 72; OD]. Test small, low hemispherical, flattened adorally. Proximal 4 or 5 amb plates simple, remainder trigeminate. Tubercles confined to adoral surface and ambitus; only small papillae adapically. Apical system large, with 5 anal valves. *Rec.*, Hawaii-Carib.

Heteropodia DE LORIOL in WHITE, 1887, p. 254 [**H. whitei*; OD, M]. Test small, very low, flat adorally, slightly convex adapically. Pore zones simple, straight, pores large, widely separated adapically, becoming smaller and close together adorally, disappearing altogether near peristome. Primary amb and interamb tubercles developed only at ambitus. *Cret.*, Brazil.

Magnosia MICHELIN, 1858, p. 34 [**Echinus nodulosus* GOLDFUSS, 1826; OD] [=*Tuberculina* EBRAY, 1858, p. 52 (obj.)]. Test small to moderate-sized, hemispherical, with oral side flattened. Amb

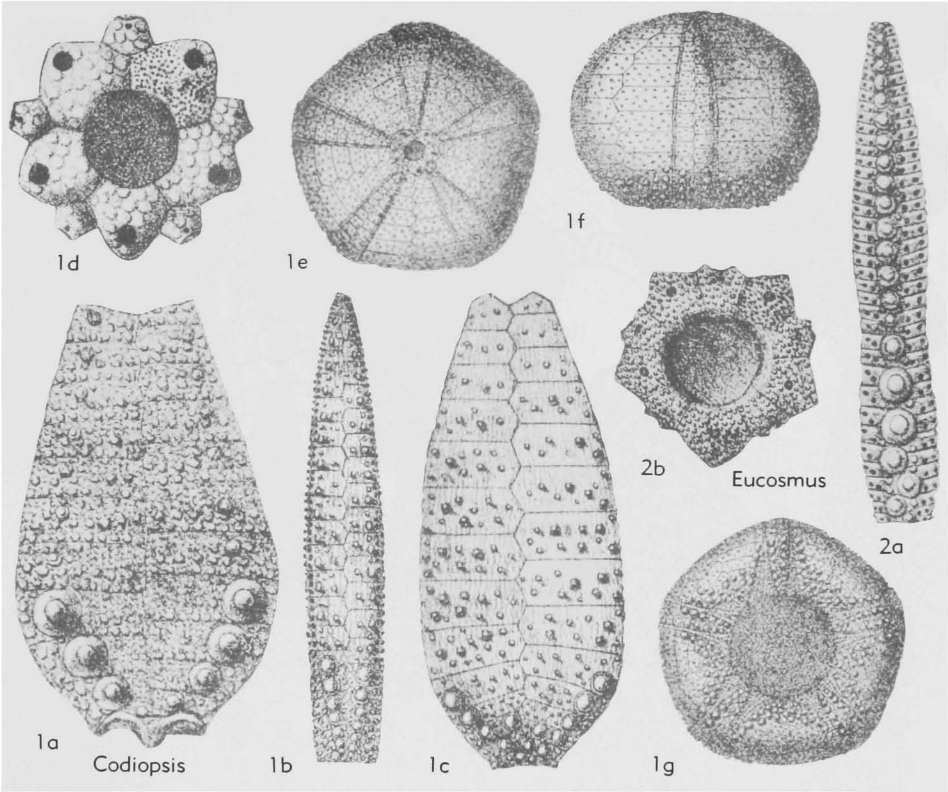

FIG. 308. Arbaciidae (p. *U*411-*U*413).

plates compound, trigeminate, pores in straight line adapically, forming arcs of 3 near peristome. Interamb tubercles in vertical and horizontal series, primary tubercles indistinguishable. *M.Jur. (Bathon.) - U. Cret. (Cenoman.),* Eu.-N. Afr.-Asia Minor.

M. (Magnosia). Amb tubercles forming at least double series. Apical system dicyclic. *M.Jur. (Bathon.)-U. Cret. (Cenoman.),* Eu.-N. Afr.-Asia Minor.——FIG. 307,*1a-d. *M. (M.) nodulosa* (GOLDFUSS), U.Jur.(Oxford.), Fr.; *1a-c,* test, aboral, lat., oral, ×1.1; *1d,* interamb, ×3.3 (27d).——FIG. 307,*1e,f. M. (M.) peroni* COTTEAU, M.Jur.(Bathon.), Fr.; *1e,* interamb, adoral, with primordial plate, ×3.3 (91); *1f,* apical system, ×3.3 (27d).——FIG. 307,*1g. M. (M.) pilos* (L. AGASSIZ), *L.Cret.(Valangin.),* Fr.; amb, ×2 (27a).

M. (Eucosmus) L.AGASSIZ, 1846, p. 356 [**E. decoratus*; OD] [=*Eucosmechinus* LAMBERT & THIÉRY, 1914, p. 270 (obj.) *(nom. van.)* (to replace *Eucosmus,* supposedly preocc. by *Eucosma* HUBNER, 1826)]. Amb tubercles reduced to single median series. Apical system of some monocyclic. *U.Jur.-L.Cret.,* Eu.-N.Afr.——FIG. 308,*2. M. (E.) meslei* (GAUTHIER), L.Cret.(Neocom.), Algeria; *2a,* amb, ×2.3; *2b,* apical system, ×3.3 (35).

Pleiocyphus POMEL, 1883, p. 82 [**Glypticus regularis* ÉTALLON, 1862; OD, M]. Like *Glypticus* but with adapical surface of test provided with true tubercles in regular transverse series. Epistroma lacking. *M.Jur.,* Eu.-AsiaMinor.——FIG. 309,*2. P. burgundiacus* (MICHELIN), Callov., Fr.; *2a-c,* test, aboral, oral, lat., ×1.2 (27d).

Podocidaris A. AGASSIZ, 1869, p. 258 [**P. sculpta*; OD]. Test very small, low hemispherical, flattened below. Amb plates trigeminate, pore zones simple. Tubercles confined to adoral side. Numerous slender papillae adapically, arranged in longitudinal series, connected by vertical and horizontal elevated ridges, giving sculptured appearance [250-800 m.]. *Rec.,* Malaya-Hawaii-Carib.

Pygmaeocidaris DÖDERLEIN, 1905, p. 621 [**Podocidaris prionigera* A. AGASSIZ, 1879, p. 199; OD, M]. Like *Dialithocidaris,* but with no tubercles adapically, only papillae. Pore zones scarcely widened adorally. Only 4 anal valves. [600-3,000 m.] *Rec.,* Ind.O.

Tetrapygus L. AGASSIZ, 1841, p. 7 [**Echinus niger*

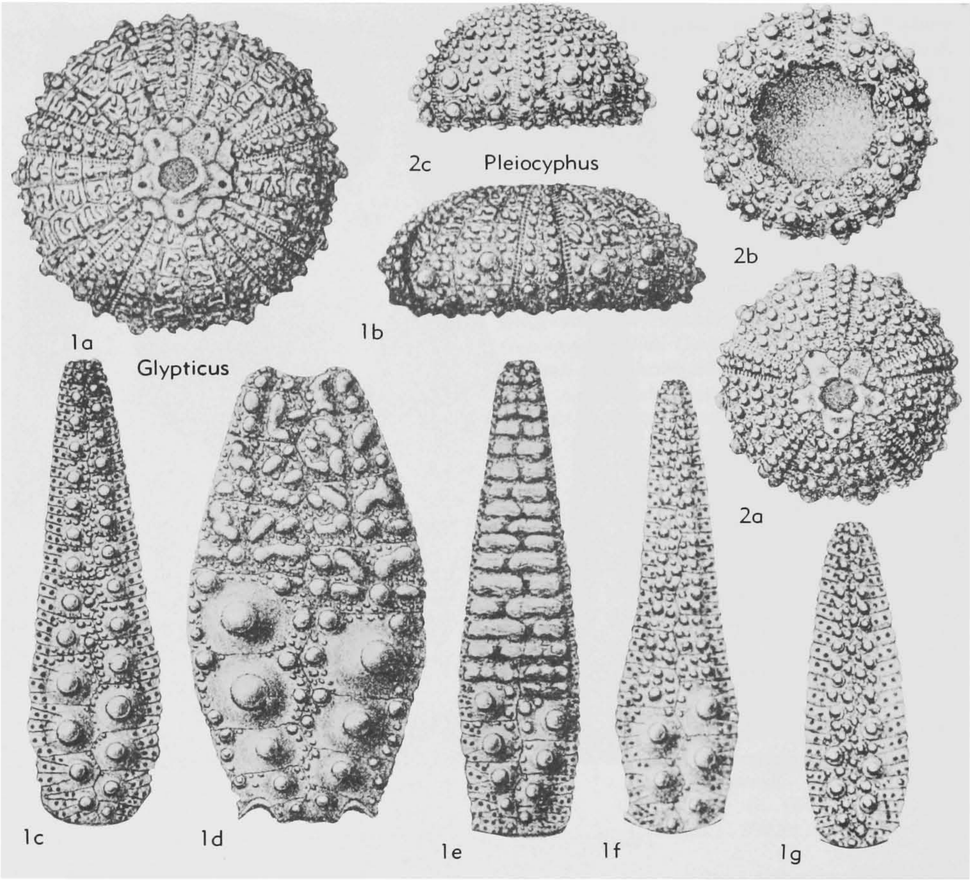

FIG. 309. Arbaciidae (p. *U*412-*U*413).

MOLINA, 1782, p. 175; OD, M] [=*Echinocidaris* DUNCAN, 1889, p. 94 (*non* DESMOULINS, 1835)]. Test low, hemispherical, flattened below. Ambs polyporous, pore zones widened toward peristome. Primary interamb tubercles in regular vertical and horizontal series; secondary tubercles present. [Littoral.] *Rec.* Peru-Chile.

Order TEMNOPLEUROIDA Mortensen, 1942

[*nom. transl.* DURHAM & MELVILLE, 1957, p. 255 (*ex* suborder Temnopleurina MORTENSEN, 1942, p. 225)]

Lantern camarodont (unknown in Glyphocyphidae). Test usually sculptured with ridges (epistroma) or sutural depressions or both, at least in immature stages; if test not sculptured, then gill slits very deep and conspicuous. Radioles solid. *L.Jur.-Rec.*

Family GLYPHOCYPHIDAE Duncan, 1889

[*nom. transl. et emend.* MORTENSEN, 1942, p. 225 (*ex* Glyphocyphinae DUNCAN, 1889, p. 96)]

Tubercles perforate, crenulate. Test sculptured. Ambs compounded in diadematoid manner, trigeminate or polyporous. *L.Jur.-Eoc.*

Glyphocyphus HAIME, 1853, p. 202 [**Echinus radiatus* HOENINGHAUS, 1826; SD LAMBERT & THIÉRY, 1911, p. 193]. Small, hemispherical. Amb plates trigeminate, in 2 regular series, with primary tubercles also forming 2 regular series. Interambs each with 2 regular series of primary tubercles. Depressions in horizontal sutures in both ambs and interambs. *U.Cret.(Cenoman.)*, Eu.-N.Afr.; *Eoc.*, Eu.

G. (Glyphocyphus). Apical system monocyclic, elongate. *U. Cret. (Cenoman.)*, W. Eu.-N. Afr.

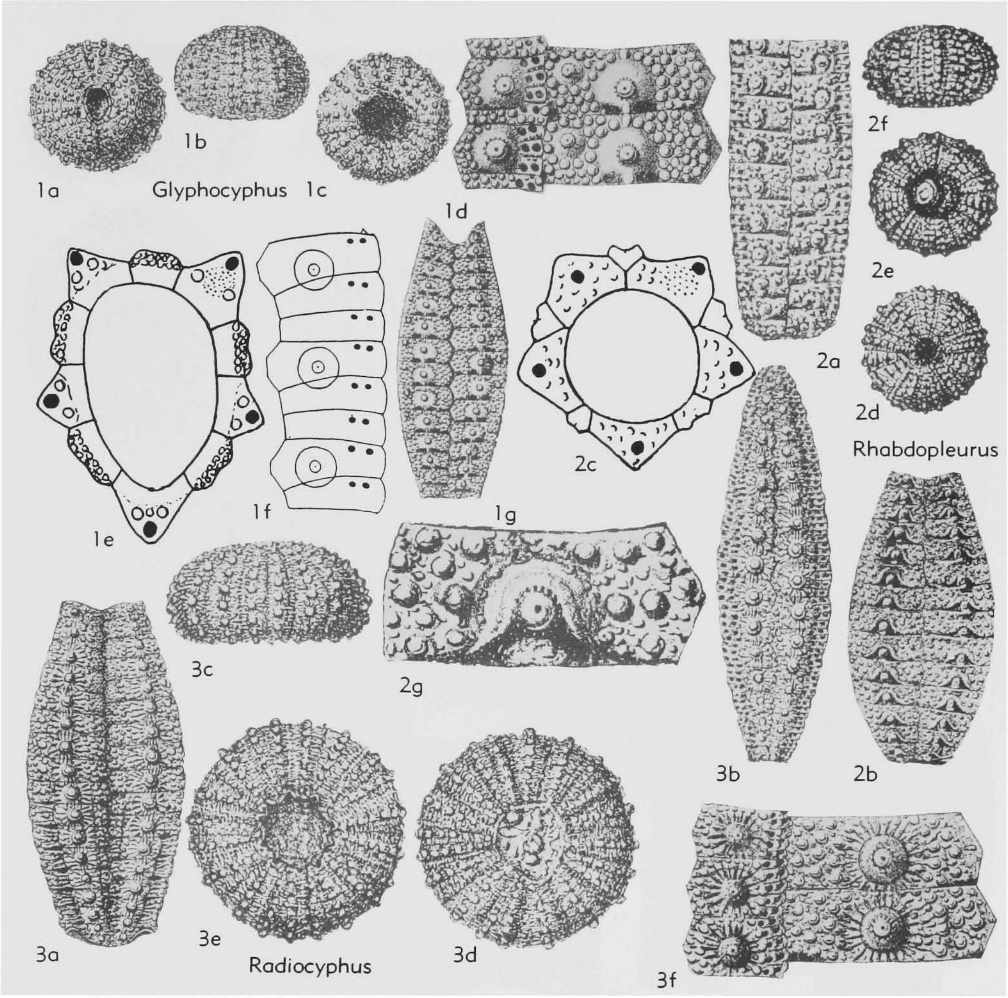

FIG. 310. Glyphocyphidae (p. *U*414-*U*415, *U*417-*U*418).

(Alg.).——FIG. 310,*1*. **G. (G.) radiatus* (HOENINGHAUS), Fr.; *1a-c*, test, aboral, lat., oral, ×1 (27a); *1d,e*, test plates, apical system, ×8 (27a); *1f*, amb, ×10 (112); *1g*, interamb, ×3.3 (27a).

G. (Rhabdopleurus) COTTEAU, 1893, p. 594 [**Glyphocyphus ataxensis* COTTEAU, 1886, p. 725; OD] [=*Cryptocyphus* LAMBERT & THIÉRY, 1914, p. 274 (obj.)] [*non Rhabdopleura* ALLMAN, 1869; *nec* DAWSON, 1870; *nec* DE KONINCK, 1881]. Apical system with oculars I and V only insert. Periproct not elongate. *Eoc.*, Eu.——FIG. 310,*2*. **G. (R.) ataxensis* (COTTEAU), M.Eoc., Fr.; *2a*, amb, ×7; *2b*, interamb, ×3.3; *2c*, apical system, ×8; *2d-f*, test, aboral, oral, lat., ×1.2; *2g*, interamb plate, ×13.3 (27a).

Ambipleurus LAMBERT, 1932, p. 198 [**Dictyopleurus douvillei* LAMBERT, 1824; OD] [=*Medochechinus* JEANNET, 1935, p. 559 (type, *M. fabrei*)]. Small, hemispherical. Amb plates trigeminate; primary tubercles in regular series in each column in ambs and interambs. Horizontal sutures with well-developed pits. Apical system dicyclic, with ocular I insert. *Eoc.*, Eu.-Egypt-W. Pak.——FIG. 311,*3a*. **A. douvillei* (LAMBERT), Egypt; test detail, ×3.3 (112).——FIG. 311,*3b,c*. *A. darchiaci* DUNCAN & SLADEN, W.Pak.(W.Sind); *3b,c*, test detail (*3c* weathered), ×? (47).——FIG. 311,*3d-f*. *A. darguini* (JEANNET), Fr.; *3d-f*, test, lat., aboral, oral, ×1.3 (90).

Arachniopleurus DUNCAN & SLADEN, 1882, p. 42 [**A. reticulatus*; OD]. Small, low hemispherical. Plates polyporous, pores in slight arcs; tubercles of both areas on raised scrobicules with radiating costae. Elaborate network of costae on plates. No sutural pits. *Eoc.*, Asia(W.Pak.)-Eu.(Italy-Spain).

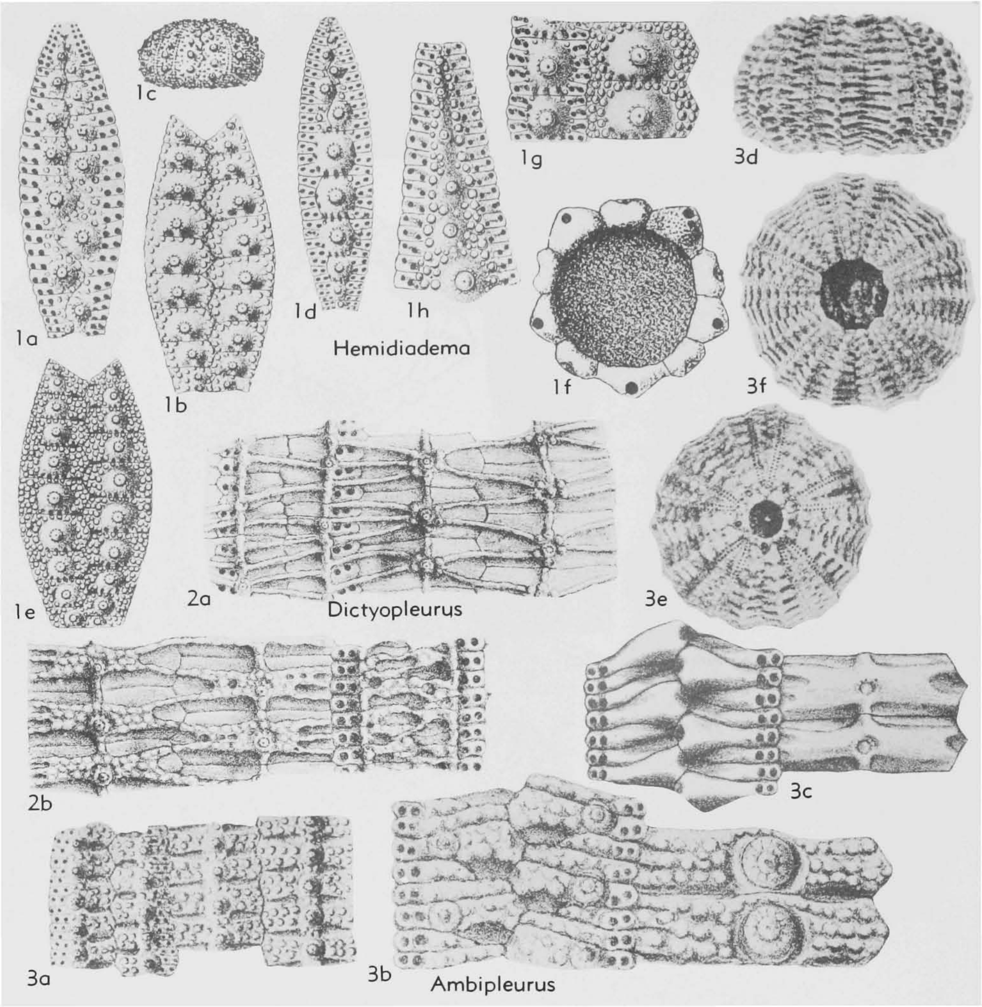

FIG. 311. Glyphocyphidae (p. U415-U417).

——FIG. 312,*1*. **A. reticulatus*, W.Pak.(W.Sind); test detail, mag. unknown (47).

Dictyopleurus DUNCAN & SLADEN, 1882, p. 38 [**D. ziczac*; OD]. Small, hemispherical. Amb plates trigeminate, amb and interamb tubercles small, united by raised costae, forming complicated network on plates; no depressions in horizontal sutures. Apical system dicyclic, with ocular I insert. *Eoc.*, Asia(W.Pak.).——FIG. 311,*2a*. **D. ziczac*, W.Sind; test detail, ?mag. (47).——FIG. 311,*2b*. *D. haimei* DUNCAN & SLADEN, W.Sind; test detail, mag. unknown (47).

Echinopsis L. AGASSIZ, 1840, p. 9, 18 [**Echinus elegans* DESMOULINS, 1837; OD] [=*Hebertia* MICHELIN, 1859, p. 147 (type, *H. parisiensis*)]. Hemispherical, of moderate size. Amb plates trigeminate, pores in single series; primary amb tubercles small, in regular series, close to pores. Median space with small secondaries. Interambs with 2 regular series of small primary tubercles and irregularly arranged secondaries. *Eoc.*, Eu.-W. Afr.——FIG. 312,*4a-c*. **E. elegans* (DESMOULINS), Fr.; *4a*, apical system, ×4.7; *4b,c*, test, aboral, lat., ×1.2 (27e).——FIG. 312,*4d-f*. *E. parisiensis* (MICHELIN), Fr.; *4d*, primary spine, ×8; *4e*, amb detail, ×5.3; *4f*, interamb detail, ×3.3 (27e).

Glyptodiadema POMEL, 1883, p. 102 [**Pseudodiadema cayluxense* COTTEAU, 1880; OD, M]. Amb plates trigeminate, pores in single line, except near peristome, where they form arcs of 3. Primary amb tubercles on every 3rd plate. Interamb tubercles in regular series. Plates otherwise covered by small tubercles of uniform size. Horizontal

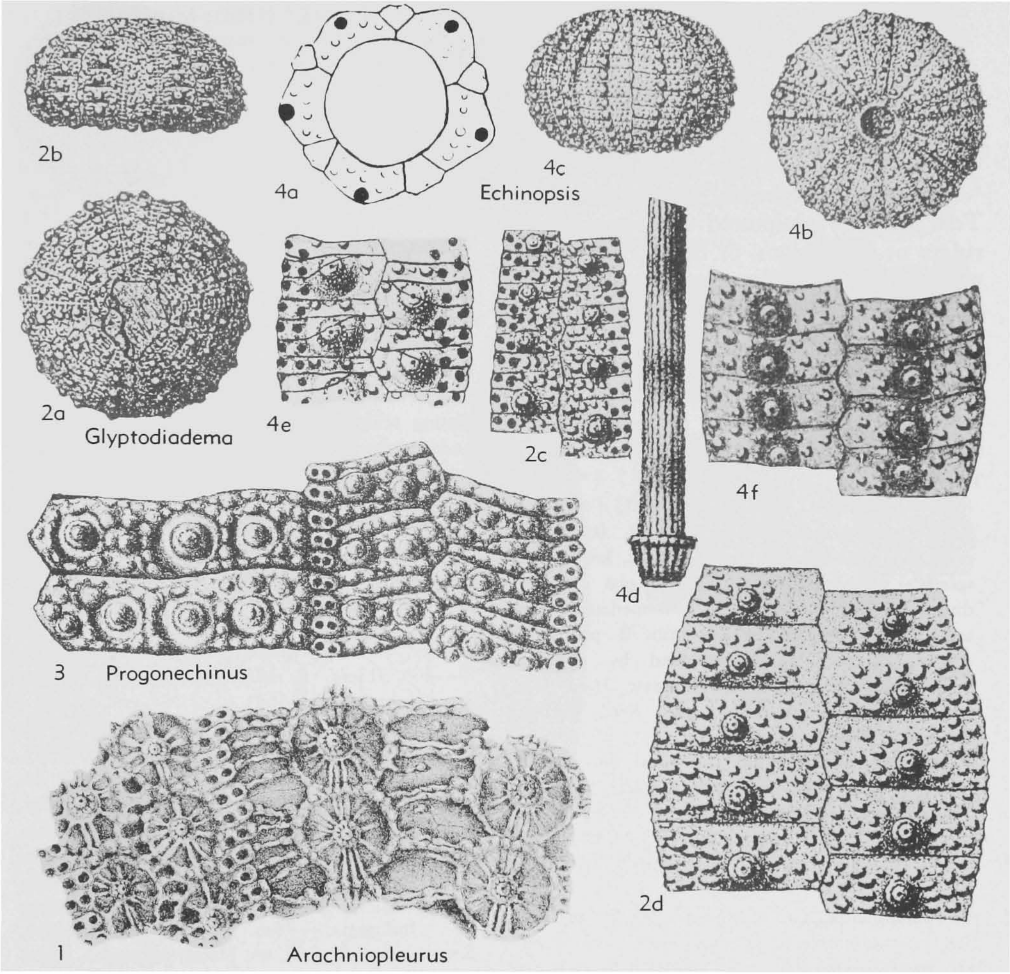

FIG. 312. Glyphocyphidae (p. *U*415-*U*417).

sutures with distinct depressions. *L.Jur.*, W.Eu.——FIG. 312,*2*. **G. cayluxense* (COTTEAU), Pleinsbach., Fr.; *2a,b*, test, aboral, lat., ×1.7; *2c,d*, amb, interamb, detail, ×5.3 (27d).

Hemidiadema L. AGASSIZ, 1846, p. 351 [**H. rugosum*; OD]. Small, low hemispherical. Amb plates trigeminate, alternating with small primary plates; thus primary tubercles arranged in single series; interambs with regular series of primary tubercles in each column. Amb and interamb horizontal sutures with small round depressions. *L.Cret. (Neocom.)-U. Cret. (Cenoman.)*, W. Eu. —— FIG. 311,*1a-c*. *H. intermedium* COTTEAU, Cenoman., Fr.; *1a,b*, amb, interamb, ×3.3; *1c*, test, lat., ×1.3 (27a).——FIG. 311,*1d-g*. **H. rugosum*, Apt., Fr.; *1d,e*, amb, interamb, ×3.3; *1f*, apical system, ×7; *1g*, test detail, ×5.3 (27a).——FIG. 311,*1h*. *H. neocomiense* COTTEAU, Neocom., Fr.; amb detail, ×7 (31).

Progonechinus DUNCAN & SLADEN, 1882, p. 43 [**P. eocenicus*; OD, M]. Small, hemispherical, flattened, concave below. Ambs and interambs tumid, marginal outline of test dented; pore zones simple, pore pairs in single line; interporiferous zone broad, with 4 series of larger tubercles. Interamb plates with up to 4 large tubercles at ambitus. *Eoc.*, Asia(W.Pak.).——FIG. 312,*3*. **P. eocenicus*, W.Sind; detail of test plates, ×13.3 (47).

Radiocyphus COTTEAU, 1890, p. 98 [**R. vilanovae*; OD]. Hemispherical, of moderate size. Amb plates polyporous; primary tubercles of both series with radiating depressions in areoles. Interamb horizontal sutures have depressions adorally. *Eoc.*, W. Eu.——FIG. 310,*3*. **R. vilanovae*, Spain; *3a,b*, interamb, amb, ×2; *3c-e,* test, lat., aboral, oral, ×1.2; *3f,* test detail, ×5.3 (33).

Family TEMNOPLEURIDAE A. Agassiz, 1872

[Temnopleuridae AGASSIZ, 1872, p. 285; *emend.* DUNCAN, 1889, p. 96, MORTENSEN, 1942, p. 225]

Tubercles imperforate, usually crenulate. Test generally sculptured conspicuously by ridges or depressions, or both. Ambs compounded in echinoid manner, invariably trigeminate; pores arranged monoserially or in several vertical series; pore zones not expanded adorally. Gill slits shallow. Pedicellariae of globiferous, triphyllous, ophicephalous and (usually also) tridentate types. *U.Cret.(Cenoman.)-Rec.*

Temnopleurus L. AGASSIZ, 1841, p. 7 [**Cidaris toreumatica* LESKE, 1778, p. 155; OD] [=*Prymnechinus* KOEHLER, 1927, p. 109 (type, *P. proctalis*)]. Moderate in size or small, low hemispherical or subconical. Angular pits present, distinct; ambs with one pit, from median suture to primary tubercle; in interambs 2 pits, one medial, other adradial, separated by primary tubercle. Tubercles distinctly crenulate. *Mio.,* Asia (India-Indonesia-Iran); *Plio.,* Iran; *Rec.,* W.Pac.-IndoPac.

T. (Temnopleurus). Anus subcentral; no distinct suranal plate. Pits small or obsolete adorally. *Mio.,* Asia (India-Indonesia-Iran); *Plio.,* Iran; *Rec.,* W.Pac.-IndoPac.——FIG. 313,*2.* **T. (T.) toreumatica* (LESKE), Mozambique; amb plates, ×5.3 (136d).

T. (Toreumatica) GRAY, 1855, p. 39 [**T. reevesi*; OD] [=*Coptopleura* IKEDA, 1940, p. 92 (type, *C. sema*)]. Anus excentric, suranal plate distinct. Pits remain distinct adorally. *Rec.,* W.Pac.-IndoPac.

Amblypneustes L. AGASSIZ, 1841, p. 7 [**Echinus ovum* LAMARCK, 1816, p. 48; OD]. Moderate in size, ovate or hemispherical. Angular pores present, usually indistinct. Tubercles smooth or at most indistinctly crenulate. Buccal plates small, lacking pedicellariae. Apical system small, reguarly dicyclic. *Rec.,* Australia-Tasmania-?N.Z.——FIG. 313,*4. A. pachistus* H. L. CLARK, S.Australia; amb plates, ×5.3 (136d).

Arbacina POMEL, 1869, p. xli [**Echinus monilis* DESMAREST, 1816; OD]. Small, hemispherical or subconical. Angular pores or pits lacking. Tubercles circular, not indented. Test lacking sculpture, but with depressions in horizontal sutures. Dense secondary tuberculation; tubercles near primaries may be elongate. *L.Mio.-Plio.,* Eu.-W.Afr.——FIG. 313, *1a-e.* **A. monilis* (DESMAREST), Helvet., Fr.; *1a,b,* test, aboral, lat., ×1.2; *1c,* test, detail, ×8 (109); *1d,* interamb, ×13.3 (136d); *1e,* amb, ×10 (12).——FIG. 313,*1f. A. romana* (MERIAN), Plio., Sicily; interamb, ×13.3 (136d).

Asterechinus MORTENSEN, 1942, p. 288 [**A. elegans*; OD, M]. Small, hemispherical. Angular pores or pits lacking; sculpture visible but inconspicuous; tubercles crenulate and indented. Buccal membrane naked outside buccal plates. Spines faintly serrate. *Rec.,* Indonesia.——FIG. 313,*5.* **A. elegans,* Admiralty Is.; *5a,* interamb, ambital region, ×8 (136d); *5b,c,* amb, aboral, oral, ×8 (136d).

Brochopleurus FOURTAU, 1920, p. 25 [**Temnechinus stellulatus* DUNCAN & SLADEN, 1886, p. 304; OD]. Small, hemispherical. Angular pores and pits lacking. Primary tubercles noncrenulate. Distinct radiating sculpture around primary and some secondary tubercles. Apical system dicyclic, Gill slits small, indistinct. *Eoc.,* N. Am.(Ala.)-?N. Afr. (Egypt); *M.Oligo.(Landon.),* N.Z.; *U.Oligo-L.Mio. (Janjuk.),* Australia-N.Z.; *M.Mio.(Torton.),* Asia W.Pak.)-N.Afr.(Egypt).——FIG. 313,*3a,b.* **B. stellatus* (DUNCAN & SLADEN), *M.Mio.,* W.Pak.(W. Sind); *3a,b,* test, lat., detail, ×1.07, ×8 (47).——FIG. 313,*3c. B. gajensis* (DUNCAN & SLADEN), M.Mio., W.Pak.(W.Sind); test detail, ×8 (57).——FIG. 313,*3d. B. sadeki* FOURTAU, Mio., Egypt; apical system, ×7 (136d).

Desmechinus H. L. CLARK, 1923, p. 342 [**D. anomalus*; OD] [**Javanechinus* JEANNET, 1935, p. 49 (type, *J. rembangensis*)]. Medium-sized, depressed. Angular pores or pits lacking. Test sculpture in form of radiating ridges. Apical system obliquely elongate toward genital 1. Gill slits sharp, deep. Valves of globiferous pedicellariae without lateral teeth. Spines smooth. *Mio.,* Java; *Rec.,* Indonesia.——FIG. 314,*6.* **D. anomalus,* Rec., China Sea; *6a,b,* test plates (holotype), apical system, ×4 (136d).

Echinocyphus COTTEAU, 1860, p. 226 [**Glyphocyphus tenuistriatus* DESOR, 1857; OD]. Small, low, flattened above and below. Primary tubercles crenulate, forming regular series in each column in both areas. Horizontal interamb sutures with distinct elongate depressions. Angular pores or pits lacking. *U.Cret.(Turon.),* Eu.——FIG. 314, *2a-d.* **E. tenuistriatus* (DESOR), Fr.; *2a,* test, lat., ×1.3; *2b,c,* amb, interamb, ×4; *2d,* interamb plates, ×8 (27d).——FIG. 314,*2e. E. matronensis* LAMBERT & THIÉRY, Fr.; amb, ×4 (115).

Erbechinus JEANNET, 1935, p. 558 [**E. erbi*; OD]. Moderate in size, low, subconical. Angular pores or pits lacking. Sculpture in form of distinct multiple transversely elongate depressions in horizontal sutures. Interamb tubercles finely crenulate, forming horizontal series adorally. Apical system dicyclic. Gill slits small. *Plio.,* Java; *Rec.,* Indonesia (Kei Is.).——FIG. 314,*1.* **E. erbi,* Plio., Java; *1a-c,* test, lat., oral, aboral, ×1.3 (114).

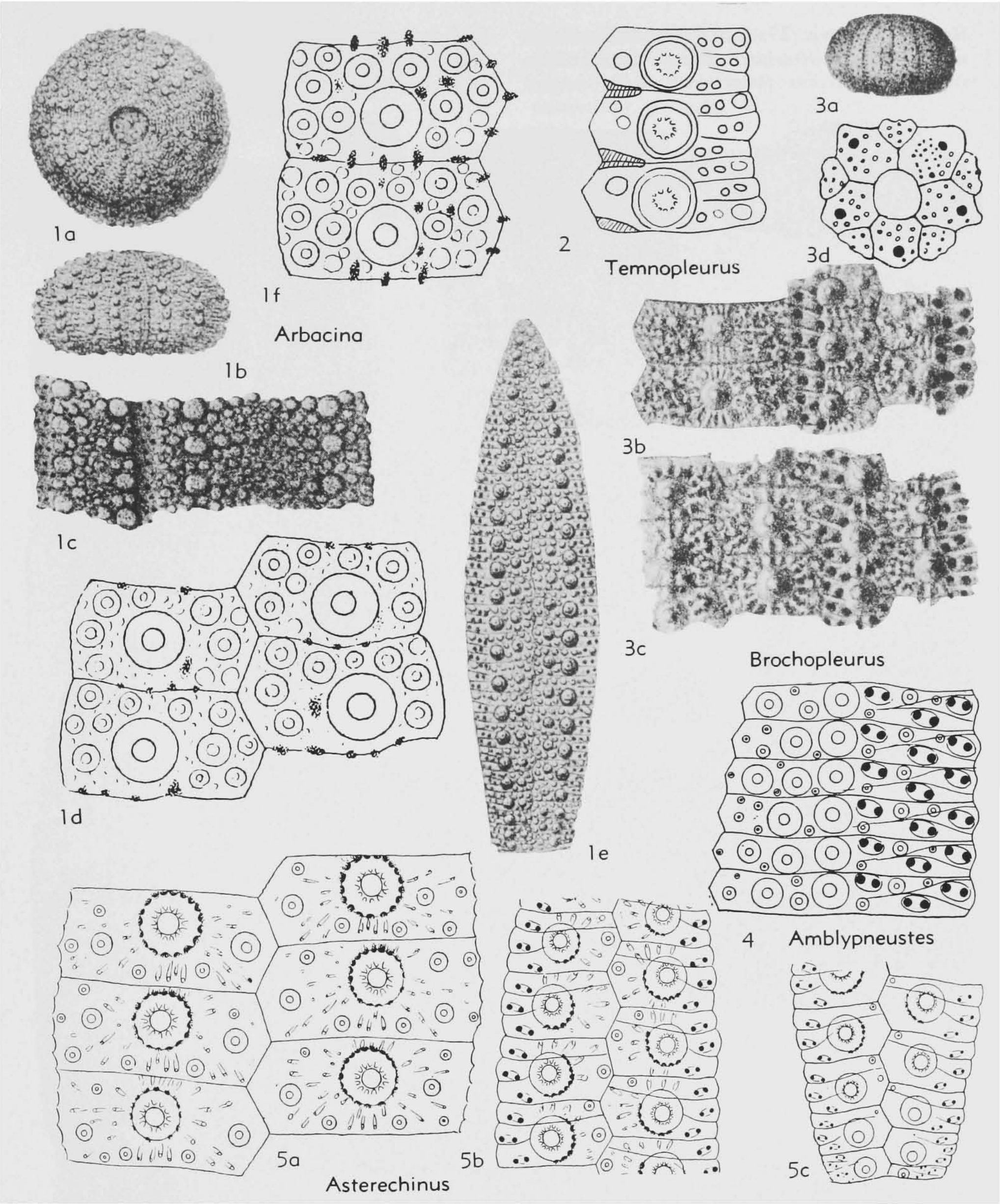

FIG. 313. Temnopleuridae (p. *U*418).

Genocidaris A. AGASSIZ, 1869, p. 262 [**G. maculata*; OD]. Small, regularly hemispherical. Tubercles noncrenulate, indented. Sculpture in form of small scattered depressions. Apical system dicyclic, oculars widely exsert. *Rec.*, Carib.-E.Atl.-Medit.

Glyptechinus DE LORIOL, 1873, p. 169 [**G. rochati*; OD]. Small, hemispherical. Primary tubercles noncrenulate, secondaries numerous. Horizontal sutures sunken. Interambs raised so as to form median keel, on which primary tubercles are situated. Gill slits small. *Cret.*, Eu.——FIG. 315,*1*. **G. rochati*, Urgon., Switz.; *1a*, test, lat., ×1.7; *1b,c*, amb, interamb, ×7 (119).

Goniosigma FELL, 1964, p. 201 [**Echinus enysi*

HUTTON, 1873, p. 39; OD]. Small to moderate in size. Small secondary tubercles of admedian angles of interamb plates arranged in vertical zigzag series, parallel to abradial sutures, so as to form sigmoid patterns on either side of interradius. Each ambital amb plate with single primary

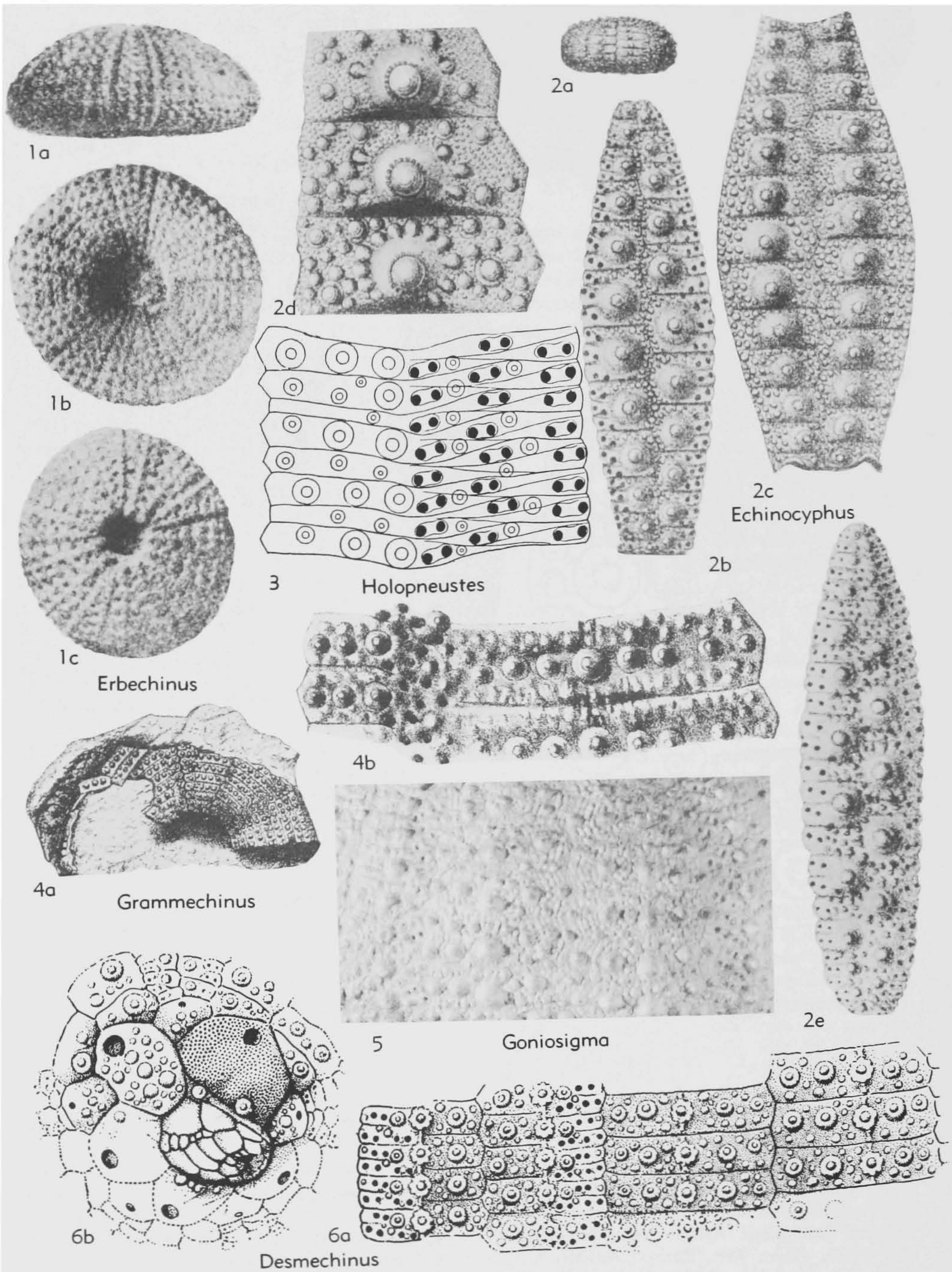

FIG. 314. Temnopleuridae (p. U418-U423).

tubercle and single secondary tubercle. Interamb plates as in *Grammechinus*. *L.Oligo.-M.Oligo.*, N.Z.——FIG. 314,5. **G. enysi* (HUTTON); part of test (holotype), ×4 (59).

Grammechinus DUNCAN & SLADEN, 1885, p. 82 [**G. regularis*; OD, M]. Moderate-sized, depressed. Tubercles noncrenulate. Interamb plates transversely elongate, with primary tubercle in

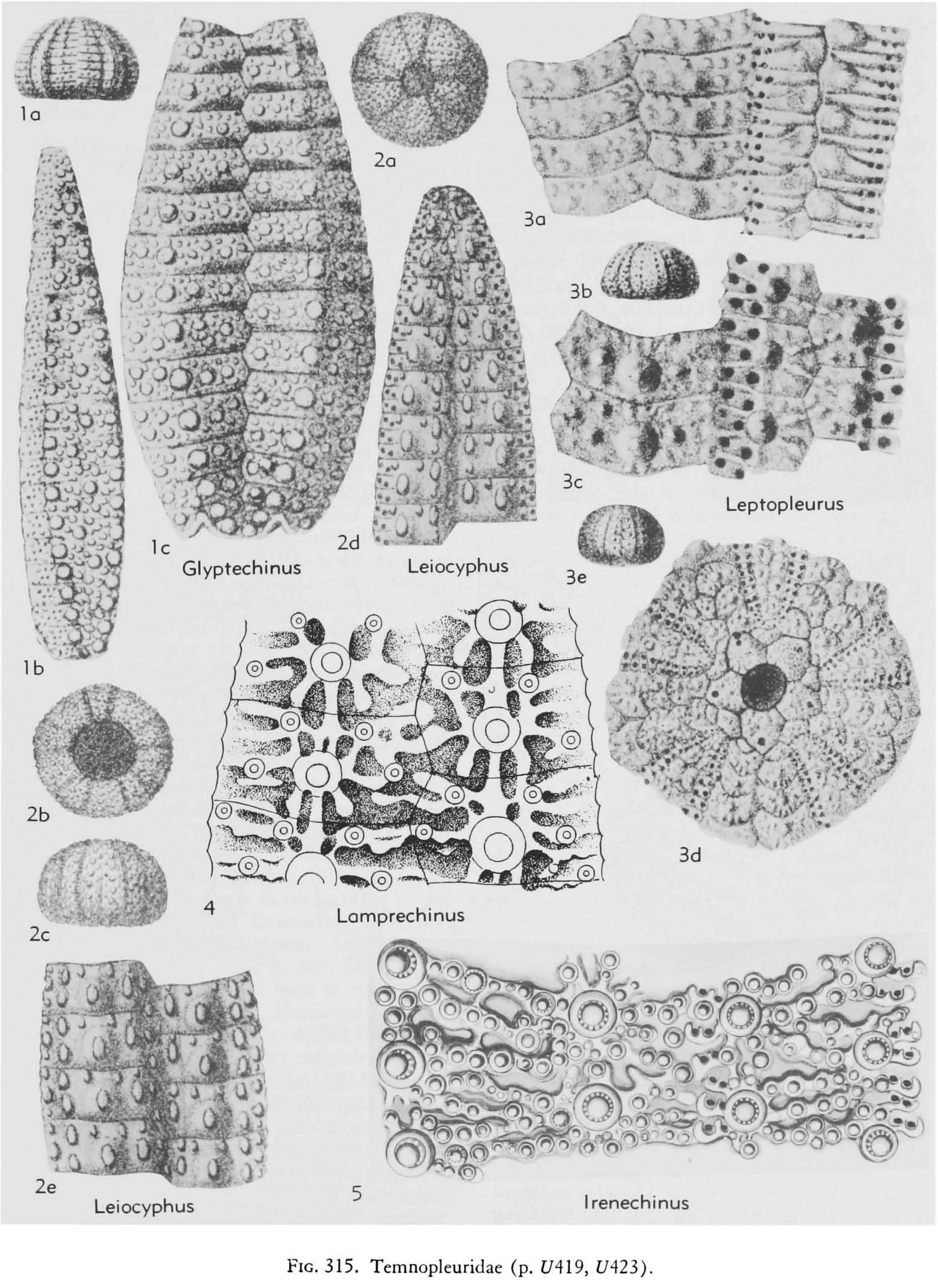

FIG. 315. Temnopleuridae (p. U419, U423).

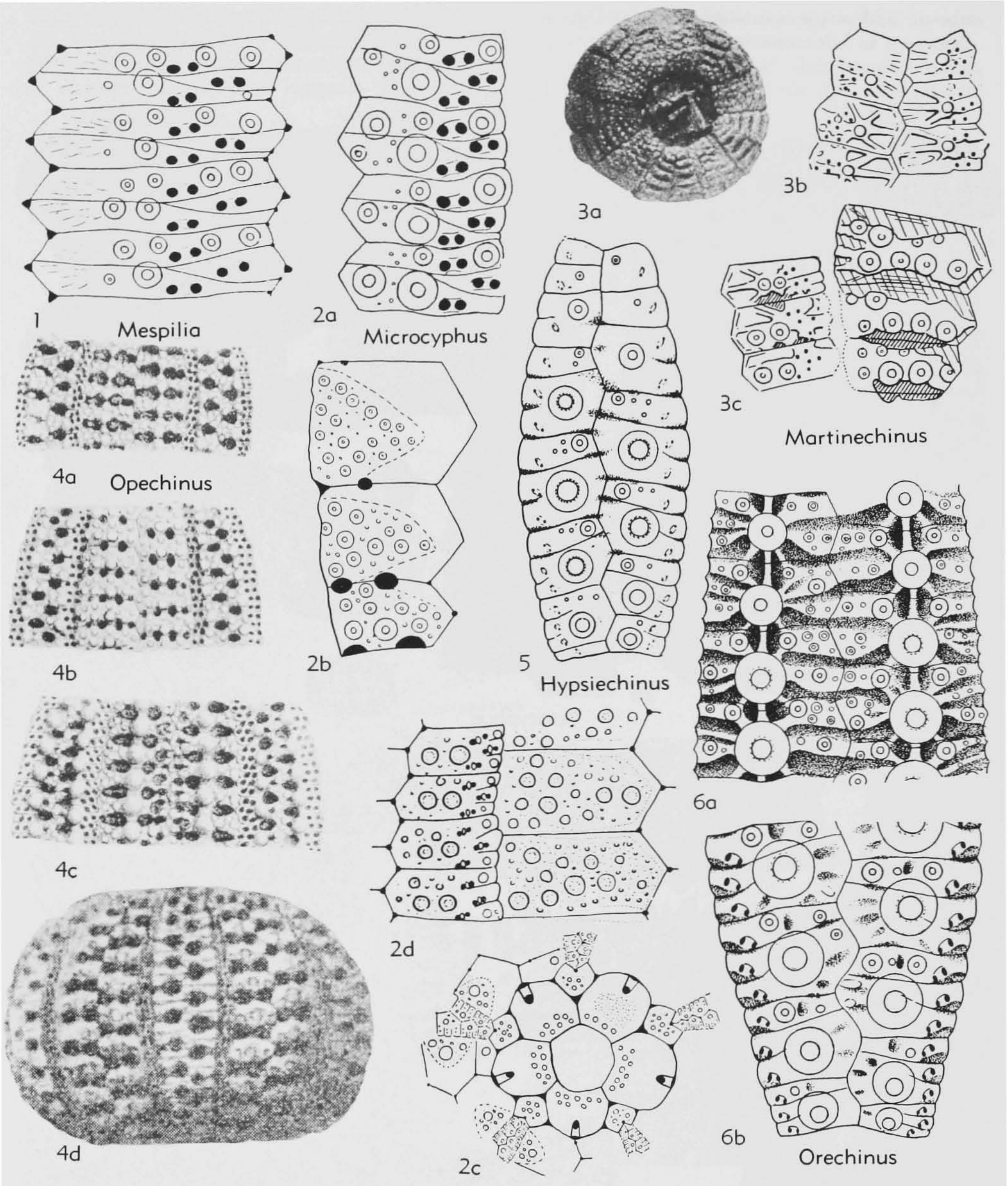

FIG. 316. Temnopleuridae (p. U423-U424).

middle of each plate; secondaries almost same size as primaries, lying on each side of them. Small tubercles near horizontal sutures elongate, some joining to form bridges across sutures. *Mio.*, Asia(W.Pak.).——FIG. 314,*4*. **G. regularis*; *4a*, test, adoral, ×0.74; *4b*, test plates, ×4 (48).

Graphepleurus H. L. CLARK, 1945, p. 315 [**G. granularis*; OD] [=*Graphechinus* H. L. CLARK, 1945, p. 317 (obj., *lapsus calami*)]. Ambs and interambs each with bare median area adapically; elsewhere on test epistroma moderately developed, with ridges between primary and larger secondary tubercles, and small shallow depressions. *Mio.*, Fiji.

Holopneustes L. AGASSIZ, 1841, p. ix [**H. porosissimus*; OD]. Medium-sized, globular. Small angular pores present. Every 2nd or 3rd amb plate with primary tubercle, primary amb tubercles occurring irregularly, not forming distinct longitudinal series. Pore zones broad, pore pairs in irregular series or 3 vertical series. Gill slits small and shallow. *Rec.*, Australia-Tasmania, N.Z.——FIG. 314,*3*. *H. inflatus* LUTKEN, N.Z.; amb plates, ×5.3 (136d).

Hypsiechinus MORTENSEN, 1903, p. 81 [**H. coronatus*; OD, M]. Very small, low, flattened above and below. Test sculpture visible but inconspicuous, taking form of small irregular depressions. Angular pores or pits lacking. Primary tubercles large, crenulate. Apical system large, dicyclic, raised into conspicuous knob in female. Buccal membrane wholly covered with plates. *Rec.*, N.Atl. (800-1350 m.).——FIG. 316,*5*. **H. coronatus;* amb, ×11.3 (136d).

Irenechinus FELL, 1964, p. 211 [**I. hentyi*; OD]. Like *Brochopleurus,* but with small to medium-sized test and distinctly crenulate tubercles, secondary tubercles of interambs carried on ridges of epistroma tending to form zigzag series between primary tubercles. *L.Oligo.-M.Oligo.*, N.Z.; *L.Mio.*, Australia.——FIG. 315,*5*. **I. hentyi,* L.Mio.(Batesford.), Victoria; test detail (holotype), ×7 (58).

Lamprechinus DÖDERLEIN, 1905, p. 622 [**L. nitidus*; OD]. Small, low hemispherical. Angular pores or pits lacking. Test sculptured. Tubercles noncrenulate. Apical system smooth, oculars widely exsert. Gill slits obsolete. Valves of globiferous pedicellariae with short open blades. *Rec.*, W.Pac.-IndoPac.——FIG. 315,*4*. *L. sculptus* MORTENSEN, Japan; interamb (holotype), ×7 (136d).

Leiocyphus COTTEAU, 1866, p. 760 [**Arbacia conjuncta* L. AGASSIZ, 1840; OD, M]. Small, hemispherical. Primary tubercles noncrenulate, forming regular series. Primaries and secondaries compressed, oval in outline. Small inconspicuous depressions present, no angular pores or pits. Apical system small, caducous. *U.Cret.*, Eu.——FIG. 315, *2*. **L. conjunctus* (L. AGASSIZ), Cenoman., Fr.; *2a-c,* test, aboral, oral, lat., ×1.3; *2d,e,* amb, interamb, ×7 (27a).

Leptopleurus LAMBERT & THIÉRY, 1910, p. 229 [*pro Lepidopleurus* DUNCAN & SLADEN, 1885, p. 306 (*non* RISSO, 1826; *nec* CLAPARÈDE, 1868; *nec* DALL, 1879)] [**Lepidopleurus hemisphaericus* DUNCAN & SLADEN, 1885, p. 306; OD]. Small hemispherical. Sculpture in form of ridges crossing interporiferous zones. Horizontal interamb sutures bend downward in middle, producing scalelike appearance. Primary tubercles smooth. Apical system dicyclic. *Mio.(Gaj.)*, W.Pak.-Egypt.——FIG. 315,*3a,b*. *?L. balli* (FOURTAU), Sinai; *3a,* detail of test, ×0.7; *3b,* test, lat., ×1.1 (64).——FIG. 315,*3c-e*. **L. hemisphaericus* (DUNCAN & SLADEN), W.Pak(W.Sind); *3c,d,* details of ambital region and aboral surface, ×?; *3e,* lat. aspect, ×1.2 (47).

Martinechinus JEANNET, 1937, p. 232 [**M. molengraaffi*; OD, M]. Moderate-sized. Sculpture comprises ridges radiating from ambulacral primaries, and depressions along interamb sutures. Depressions large, confluent at ambitus, reduced to small angular pores adapically. Peristome large, gill slits indistinct. *Plio.-Pleist.,* Timor.——FIG. 316,*3*. **M. molengraaffi*; *3a,* oral (holotype), ×0.8; *3b,c,* parts of amb, interamb (holotype), ×4 (91).

Mespilia DESOR, 1846, p. 357 [**Echinus globulus* LINNÉ, 1758, p. 664; OD]. Moderate-sized, globular or hemispherical. Sharply limited broad median interamb area naked aborally, this area carrying white striae. Small angular pores present, at least in juveniles. Each amb plate with primary tubercle. Globiferous pedicellariae with widened blades. *Rec.*, IndoPac.-W.Pac.(E. to Tonga and ?Hawaii).——FIG. 316,*1*. **M. globulus* (LINNÉ), Indonesia; amb plates, ×7 (136d).

Microcyphus L. AGASSIZ, 1846, p. 358 [**M. macalatus*; OD] [=*Anthechinus* A. AGASSIZ, 1863, p. 358 (type, *A. roseus*); *Salmacopsis* DÖDERLEIN, 1885, p. 21 (type, *S. olivacea*)]. Moderate-sized to small, hemispherical or high, ovate. Tubercles mostly confined to median part of plates, generally leaving very conspicuous naked area along both horizontal and vertical sutures. Angular pores very small, tubercles noncrenulate or weakly crenulate. Apical system compact, dicyclic. *Mio.*, Java; *Plio.(?Pleist.),* Timor; *Rec.*, W.Pac.-IndoPac.——FIG. 316,*2a*. **M. maculatus,* Rec., Mauritius; amb plates, ×7 (136d).——FIG. 316,*2b,c*. *M. javanus* JEANNET, Mio., Java; *2b,c,* interamb plates, apical system, ×4 (114).——FIG. 316,*2d*. *M.* sp., Plio., Timor; plates of ambital region, ×4 (91).

Opechinus DESOR, 1856, p. 107 [**Temnopleurus costatus* D'ARCHIAC & HAIME; SD POMEL, 1883, p. 85][=*Trumechinus* LAMBERT & THIÉRY, 1910, p. 218 (type, *T. batheri*); *Pseudopechinus* LAMBERT & THIÉRY, 1910, p. 232 (type, *Temnopleurus costatus* D'ARCHIAC & HAIME, 1853 *(nom. van.)* (obj.)]. Like *Erbechinus,* but with small to moderate-sized test, low hemispherical or almost globular. Interamb tubercles not forming horizontal series adorally. *Eoc.*, India; *Mio.-Plio.*, Indonesia; *Rec.*, Japan-Indonesia.——FIG. 316,*4c*. **O. costatus* (D'ARCHIAC & HAIME), Eoc., India; test plates, ×? (7).——FIG. 316,*4a*. *O. hookeri* (D'ARCHIAC & HAIME), Eoc., India; test plates, ×? (7).——FIG. 316,*4b*. *O. rousseaui* (D'ARCHIAC & HAIME), Eoc., India; test plates, ×? (7).——FIG. 316,*4d*. *O. gerthi* (LAMBERT), Plio., Timor; test, lat., ×1.3 (68).

Orechinus DÖDERLEIN, 1905, p. 622 [**Trigonocidaris monolini* A. AGASSIZ, 1879, p. 203; OD]. Small, low hemispherical, deeply sculptured, with ridges and furrows connecting primary tubercles; secondary tubercles may be weakly crenulate, little developed, not forming horizontal series. Apical system deeply sculptured, oculars widely exsert. Buccal membrane naked outside of buccal plates.

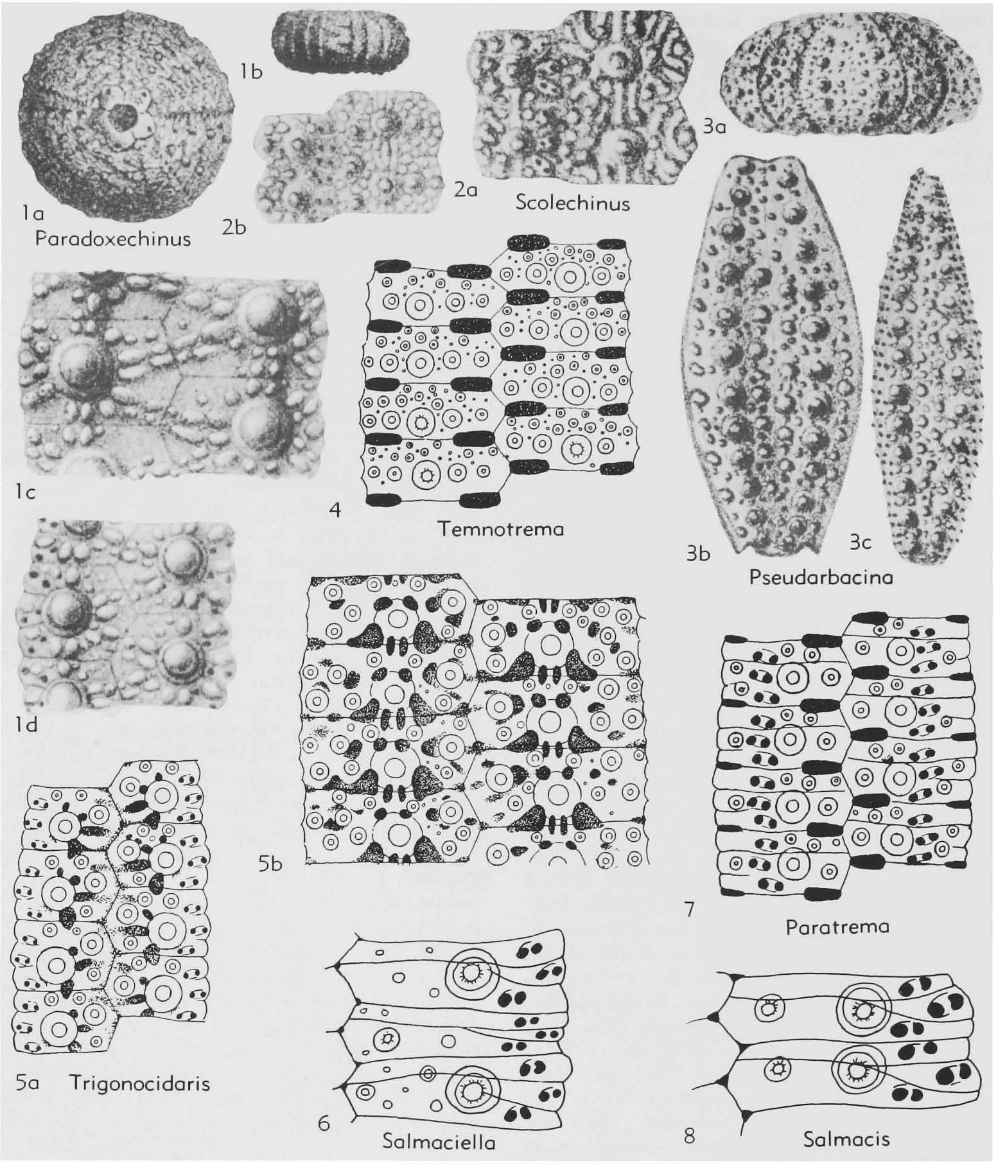

FIG. 317. Temnopleuridae (p. U424-U425).

Rec., W.Pac.-IndoPac. (450-2300 m.).——FIG. 316,6. **O. monolini* (AGASSIZ), Indonesia; *6a,b,* interamb, amb, ×8 (136d).

Paradoxechinus LAUBE, 1869, p. 186 [**P. novus*; OD] [=*Coptechinus* COTTEAU, 1883, p. 27 (type, *C. bardini*); *Ortholophus* DUNCAN, 1887, p. 414 (type, *Temnechinus lineatus* DUNCAN, 1876, =*P. novus*) (obj.)]. Small, flattened above and below. Primary tubercles noncrenulate, in both areas connected by oblique raised ridges, which form zigzag lines across median interamb area, spaces between ridges flat. No distinct secondary tubercles. Apical system dicyclic. *Eoc.,* Eu.; *Oligo.-Mio.,* Australia-Eu.——FIG. 317,*1a,b.* **P. novus,* Mio., S. Australia; *1a,* test, aboral, ×3.3 (15); *1b,* test, lat., ×1.1 (117).——FIG. 317,*1c,d. P. bardini* (COTTEAU), Mio., Fr.; *1c,d,* interamb, amb, ×12 (31).

Paratrema KOEHLER, 1927, p. 90 [**Pleurechinus döderleini* MORTENSEN, 1904, p. 90; OD]. Small, strong, low hemispherical or almost globular. Primary tubercles indistinctly crenulate, indented;

secondary tubercles smaller than primaries. Horizontal interamb sutures with deep pit at each end, horizontal amb sutures with deep pit at median end, and shallow pit at abradial end, anal opening central, periproct with small plates, no suranal plate. Only 5 buccal plates. *Rec.*, trop. W.Pac.-IndoPac.——Fig. 317,*7*. **P. doederleini* (Mortensen), Siam; amb plates, ×9.3 (136d).

Printechinus Koehler, 1927, p. 97 [**P. impressus*; OD]. Like *Opechinus*, but with depressions in horizontal sutures elongated vertically. *Plio.*, Java; *Rec.*, Ind.O.-Indonesia.

Prionechinus A. Agassiz, 1879, p. 202 [**P. sagittiger*; OD]. Small, hemispherical. No distinct sculpture on test, pores or pits lacking. Primary tubercles noncrenulate, forming regular series. Apical system regularly dicyclic, some distinctly sculptured. Spines coarsely thorny. Globiferous pedicellariae with single unpaired poison gland. [Bathyal-abyssal to 3,300 m.]*Rec.*, W.Pac.-IndoPac.

Pseudarbacina Fourtau, 1920, p. 22 [**Arbacina fraasi* Gauthier in Fourtau, 1902, p. 63; OD]. Like *Prionechinus*, but with simple granulation and no sculpture on test. Apical system, radioles and pedicellariae unknown. *L.Mio.*, N.Afr.——Fig. 317,*3*. **P. fraasi* (Gauthier), Helvet., Egypt; *3a*, test, lat., ×?; *3b,c*, interamb, amb, ×4.6 (64).

Pseudechinus Mortensen, 1903, p. 106, 138 [**Echinus albocinctus* Hutton, 1872, p. 12; OD] [=*Notechinus* Döderlein, 1905, p. 623 (type, *Echinus magellanicus* Philippi, 1857, p. 130)]. Small to moderate-sized, hemispherical to subconical, lacking angular pores. Sculpture indistinct, radiating about primary tubercles, present in juveniles. Primary tubercles noncrenulate or weakly crenulate. Apical system dicyclic or with 1 or 2 oculars insert. Suranal plate distinct. Radioles without thorns. *Plio.*, N.Z.-Australia; *Pleist.-Rec.*, N.Z.-Australia-S.Am.-subantarctic Is. ——Fig. 318,*1a,b*. **P. albocinctus* (Hutton), Rec., N.Z.; *1a*, test plates, adult, ×3.3; *1b*, adapical part of test, juvenile, ×10 (57).——Fig. 318,*1c,d*. *P. flemingi* Fell, Rec., N.Z.; *1c,d*, test plates, adult, immature, ×3.3 (57).

Pseudodicoptella Jeannet, 1935, p. 44 [**P. reicheli*; OD, M]. Very small (less than 3 mm. horiz. diam.), low hemispherical. Angular pits large, irregular, polygonal. Small depressions above primary tubercles in interamb plates. Primary tubercles prominent, noncrenulate. *Plio.*, Indon.——Fig. 319,*2*. **P. reicheli*, Ceram; *2a*, ambital part of amb, ×40; *2b*, adapical part of interamb, ×40 (114).

Salmaciella Mortensen, 1942, p. 226 [**Salmacis dussumieri* L. Agassiz, 1846, p. 359; OD]. Moderate-sized, low, subconical, deeply sunken at peristome. Angular pores distinct adapically. Tubercles crenulate. in regular series; adorally, one primary tubercle to each amb plate, aborally one primary tubercle on every 2nd amb plate. Anal opening excentric, near genital 5, ocular I, commonly insert. *Rec.*, W.Pac.-IndoPac.——Fig. 317,*6*. **S. dussumieri* (Agassiz), Japan; aboral amb plates, ×4.6 (136d).

Salmacis L. Agassiz, 1841, p. viii [**S. bicolor*; OD] [=*Melebosis* Girard, 1850, p. 364 (type, *M. mirabilis*, =*Echinus sphaeroides* Linné, 1758); *Diploporus* Troschel, 1866, p. 158 (type ?), *teste* Lambert & Thiéry, 1910, p. 217]. Like *Temnopleurus*, but with sutural pits reduced to small angular pores. *Plio.*, Java-Timor-E.Afr.; *Rec.*, W. Pac.-IndoPac.——Fig. 317,*8*. **S. bicolor*, Rec., Madag.; amb plates, ×4.6 (136d). [=*Malebosis* Cotteau, 1867, p. 813 *(nom. null.)*.]

Scolechinus Lambert & Thiéry, 1925, p. 570 [**S. dallonii*; OD]. Like *Brochopleurus* but with angular pores. *Oligo.-L.Mio.*, N.Afr.——Fig. 317,*2a*. **S. dallonii*, Alg.; test detail, ×? (115).——Fig. 317,*2b*. ?*S. catenata* (Desor), L.Mio., Fr.; test detail, ×? (109).

Temnechinus Forbes, 1852, p. 5 [**T. excavatus*; OD]. Small, subhemispherical. Angular pits present, broad and deep, with sloping edges. Primary tubercles noncrenulate, forming conspicuous vertical series; tubercles elevated, in middle of plates. Apical system compact, dicyclic, genital plates densely tuberculate. *Plio.*, Eng.

Temnotrema A. Agassiz, 1863, p. 358 [**T. sculptum*; OD] [=*Pleurechinus* A. Agassiz, 1872, p. 152, 464 (type, *P. bothryoides*) (*non* L. Agassiz, 1841); *Dicoptella* Lambert, 1907, p. 17 (type, *D. agassizi*, =*T. sculptum* A. Agassiz) (obj.); *Paradicoptella* Jeannet, 1935, p. 42 (type, *P. rutteni*)] [*non Temnotrema* Lambert & Jeannet, 1935 (=*Temnopleurus*)]. Like *Paratrema*, but with 10 buccal plates. *Mio.*, Java-Burma; *Plio.*, Indonesia; *Rec.*, W.Pac.-IndoPac. (Red Sea to Hawaii, Japan to Australia).——Fig. 317,*4*. *T. pulchellum* (Mortensen), Rec., Indonesia; interamb plates, ×7.3 (136d).

Trigonocidaris A. Agassiz, 1869, p. 263 [**T. albida*; OD]. Small, hemispherical or depressed. Angular pores or pits lacking. Sculpture in form of depressions and distinct ridges radiating from tubercles. Primary tubercles with indented areoles, some crenulate. Peristome covered by large imbricating plates. *Rec.*, W.Pac.-IndoPac.-N.Atl.——Fig. 317,*5*. *T. micropora* Mortensen, Indonesia; *5a,b*, amb, interamb, ×10 (136d).

Triplacidia Bittner, 1891, p. 143 [**Micropsis veronensis* Bittner, 1883, p. 1; OD] [=*Acrocircus* Lambert, 1911, p. 7 (type, *Micropsis biarritzensis* Cotteau, 1863)]. Large, hemispherical or subspherical. No sutural pits or sculpture on test. Primary interamb tubercles crenulate, imperforate, in horizontal and vertical series. Apical system dicyclic or monocyclic. *Eoc.*, W.Eu.-N.Afr.——Fig. 318,*3a*. **T. veronensis* (Bittner), N.Italy; amb plates, ×? (136d).——Fig. 318,*3b*. *T.*

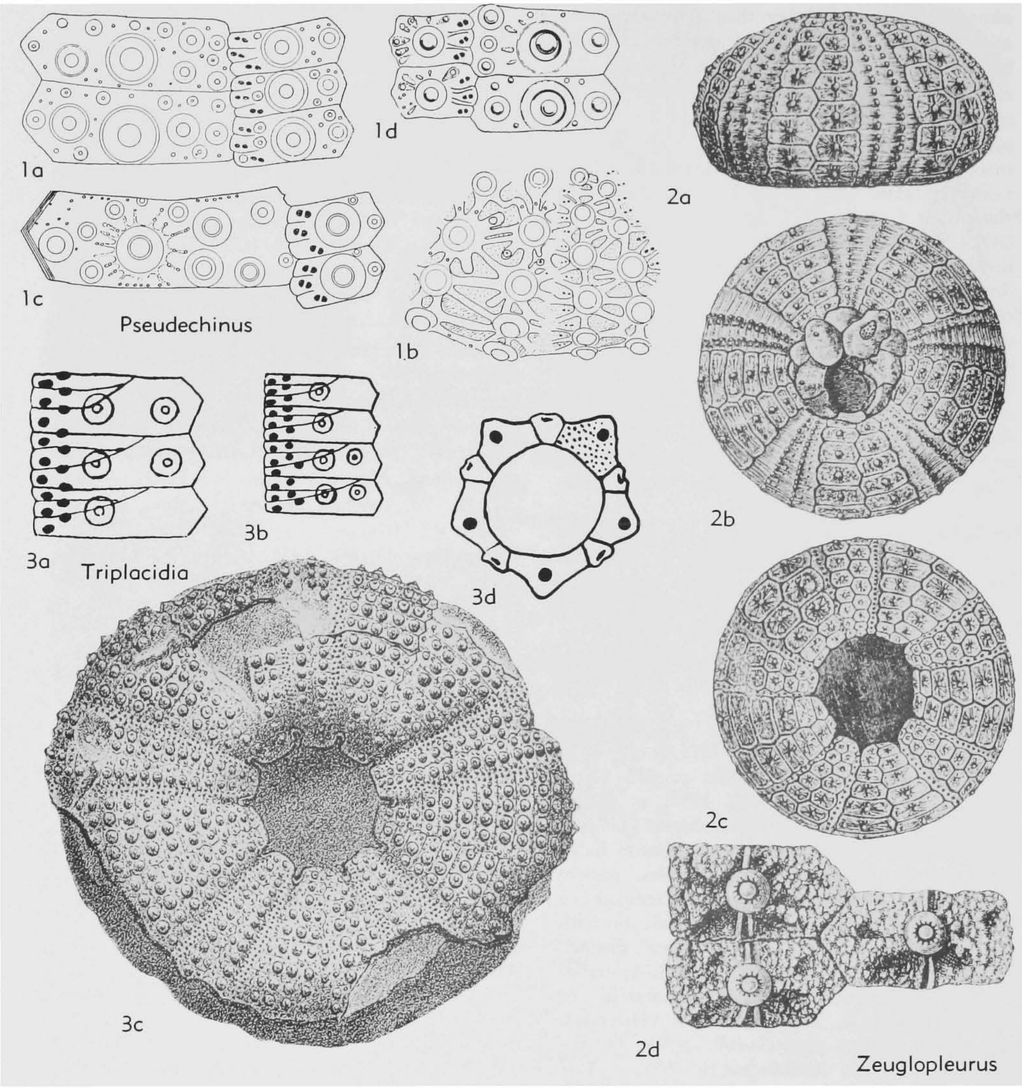

FIG. 318. Temnopleuridae (p. U425-U426).

stachei (BITTNER), N.Italy; amb plates, ×? (14).——FIG. 318,*3c*. *T. fraasi* (DE LORIOL), Egypt; test, oral, ×0.7 (121).——FIG. 318,*3d*. *T. biarritzensis* (COTTEAU), S.Fr., apical system, ×? (27e).

Zeuglopleurus GREGORY, 1889, p. 494 [**Z. costulatus*; OD]. Small, hemispherical. Angular pores or pits lacking. Sculpture in form of radiating ridges, no depressions in sutures. Tubercles crenulate, in regular series. Apical system elongate, periproct posterior, oculars I and V broadly insert. *U.Cret.*, W.Eu.——FIG. 318,*2*. **Z. costulatus*; Senon., Eng.; *2a-c*, test, lat., aboral, oral, ×3.7; *2d*, interamb plates, ×14.7 (70).

Family TOXOPNEUSTIDAE Troschel, 1872

[Toxopneustidae TROSCHEL, 1872, p. 38, *emend.* MORTENSEN, 1904, p. 135] [=Les Schizechiniens POMEL, 1883, p. 79]

Tubercles imperforate, noncrenulate. Test not sculptured. Ambs compounded in echinoid manner, trigeminate to polyporous, commonly conspicuously widened adorally. Gill slits narrow, distinct, in many very deep and divided by longitudinal keel. Pedicellariae of globiferous, triphyllous, ophicephalous, and tridentate types. *?Cret.-?Oligo., Mio.-Rec.*

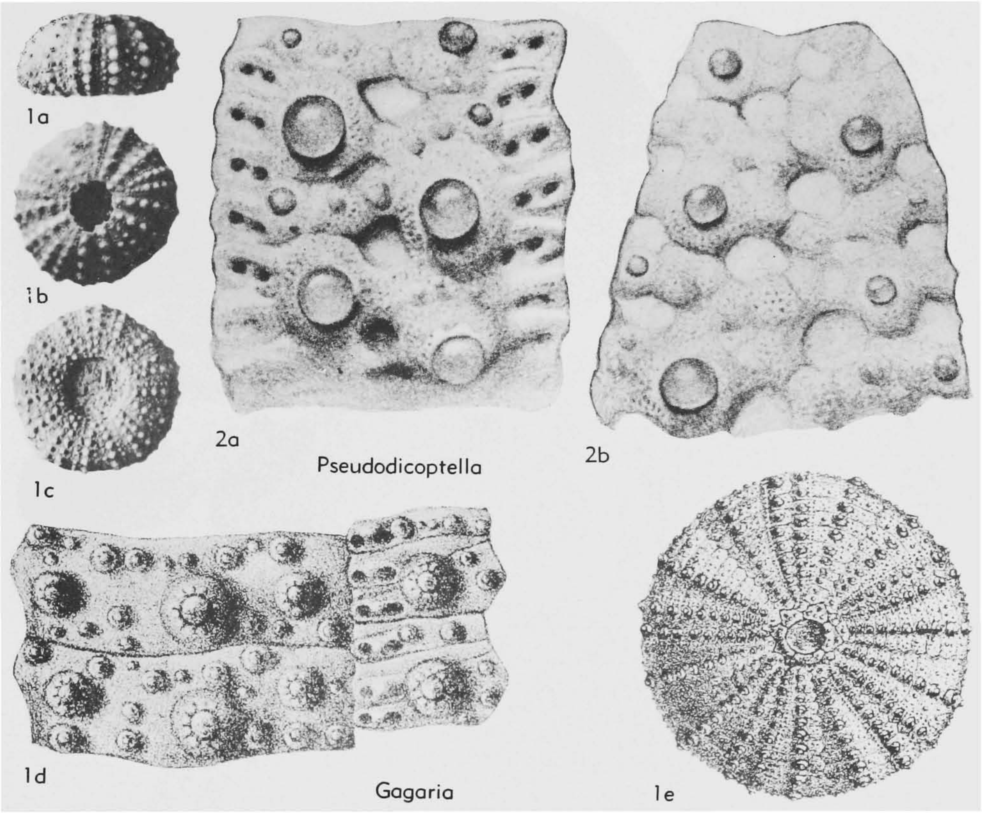

FIG. 319. Temnopleuridae *(2)*; Family Uncertain *(1)* (p. *U*425, *U*430-*U*431).

Toxopneustes A. AGASSIZ, 1841, p. 7 [**Echinus pileolus* LAMARCK, 1816, p. 45; OD] [=*Boletia* DESOR, 1846, p. 362 (obj.)]. Large, low hemispherical or subconical, flattened below. Amb plates trigeminate, primary tubercle lacking from every alternate amb plate; pore zones less than half width of interporiferous zone. Pore zones widened adorally. Apical system transversely elongate, usually oculars I and V broadly insert. *?Oligo.*, Eu.; *Pleist.*, Egypt; *Rec.*, W.Pac.-IndoPac.——FIG. 320, *1a*. **T. pileolus* (LAMARCK), Rec., Japan; adoral region, ×3.3 (136d).——FIG. 320,*1b*. *T. roseus* (A. AGASSIZ), Rec., Panama; amb, ×4 (136d). [=*Hemiechinus* GIRARD (MS name) AGASSIZ, 1872, p. 167.]

Cyrtechinus MORTENSEN, 1942, p. 229 [**Psammechinus verruculatus* LUTKEN, 1864, p. 98; OD, M]. Small, hemispherical. Amb plates trigeminate, each with primary tubercle; both ambs and interambs densely covered with tubercles; no naked areas aborally. Buccal membrane plated, though not densely so. *Rec.*, trop. W.Pac.-IndoPac.

Goniopneustes DUNCAN, 1889, p. 113 [**Amblypneustes pentagonus* A. AGASSIZ, 1872, p. 56; OD, M]. Medium-sized or large, thin, almost globular. Amb plates trigeminate, pores forming regular arcs; pore zones not widened adorally; primary tubercle on every 2nd or 3rd plate; secondary tubercles little developed; conspicuous naked median area aborally in both areas. *Rec.*, China Sea.

Gymnechinus MORTENSEN, 1903, p. 115 [**Echinus robillardi* DE LORIOL, 1883, p. 23; OD]. Small, depressed, almost discoidal. Amb plates trigeminate, each carrying primary tubercle; secondary interamb tubercles more or less developed, in some forming horizontal series at ambitus. Aboral side of test rather naked. Oculars I and II insert (anus displaced dextrally). *Rec.*, W.Pac.-IndoPac.

Lytechinus A. AGASSIZ, 1863, p. 24 [**Echinus variegatus* LAMARCK, 1816, p. 48; OD] [=*Psilechinus* LUTKEN, 1864, p. 26 (obj.)]. Medium-sized to large, low hemispherical. Amb plates trigeminate, each with primary tubercle; secondary amb tubercles not in regular series; conspicuous naked median space aborally in both areas. Buccal membrane bearing numerous plates, in addition to oral plates. *?Eoc.*, USA(Ala.); *Pleist.-Rec.*, trop.-subtrop., Americas (E.coast-W.coast), Cape Verde

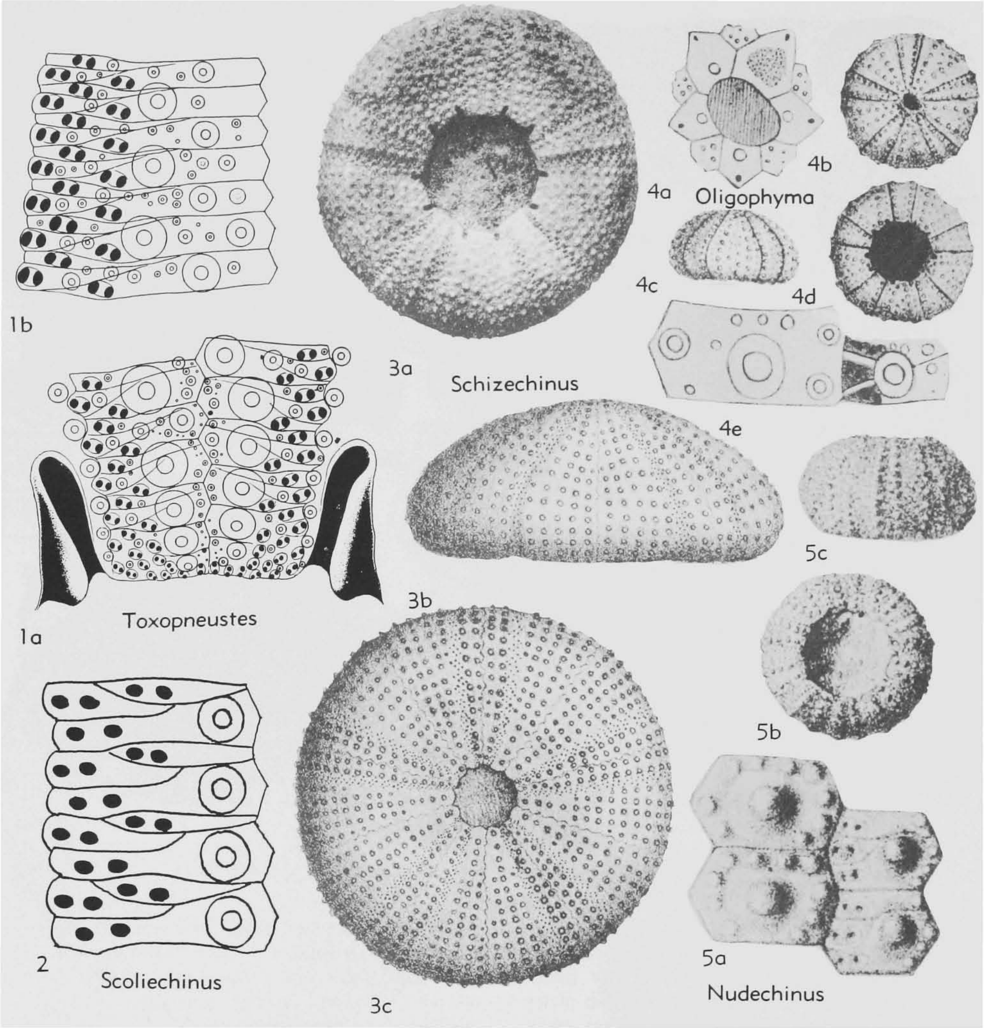

FIG. 320. Toxopneustidae (p. U427-U429).

Is.——FIG. 321,2. *L. euerces* H. L. CLARK, Rec., Gulf Mex.; amb, ×5.3 (136d).

Nudechinus CLARK, 1912, p. 276 [**N. scotiopremnus*; OD] [=*Taxophyma* LAMBERT, 1899, p. 36 (type, *Psammechinus lyonsi* GREGORY, 1898, p. 151)]. Small, regularly hemispherical. Amb plates trigeminate, each with primary tubercle; primary interamb tubercles in conspicuous vertical series. Apical system not excentric, genital I of normal form, carrying some tubercles of varying sizes, like adjoining genital plates. *Mio.*, Egypt; *Pleist.*, Egypt; *Rec.*, W.Pac.-IndoPac.——FIG. 320,*5*. *N. lyonsi* (GREGORY), Mio., Egypt; *5a*, plates, ×10.7; *5b,c*, test, adoral, lat., ×2.7 (75).

Oligophyma POMEL, 1869, p. 43 [**O. oranense*; SD LAMBERT & THIÉRY, 1911, p. 248]. Small. Amb plates trigeminate, pore pairs forming erect arcs; single series of larger tubercles in each column. Oculars I and V insert. *M.Mio.(Helvet.-Torton.)*, N.Afr.——FIG. 320,*4*. *O. cellense* POMEL, Helvet., Alg.; *4a*, apical system, ×?; *4b-d*, test, aboral, lat., oral, ×1; *4e*, amb and interamb plate, ×? (144).

Pseudoboletia TROSCHEL, 1869, p. 96 [**P. stenostoma*; OD]. Large, low, hemispherical or subconical. Amb plates polyporous (4 or 5 pore pairs to each arc), each plate with primary tubercle; conspicuous naked median space aborally in both areas; secondary tubercles forming horizontal series at ambitus. Oral plates with small spines. *Rec.*, IndoPac.-Carib.

Pseudocentrotus MORTENSEN, 1903, p. 122, 137 [**Toxocidaris depressa* A. AGASSIZ, 1863, p. 356; OD, M]. Large, low, oral side completely flattened.

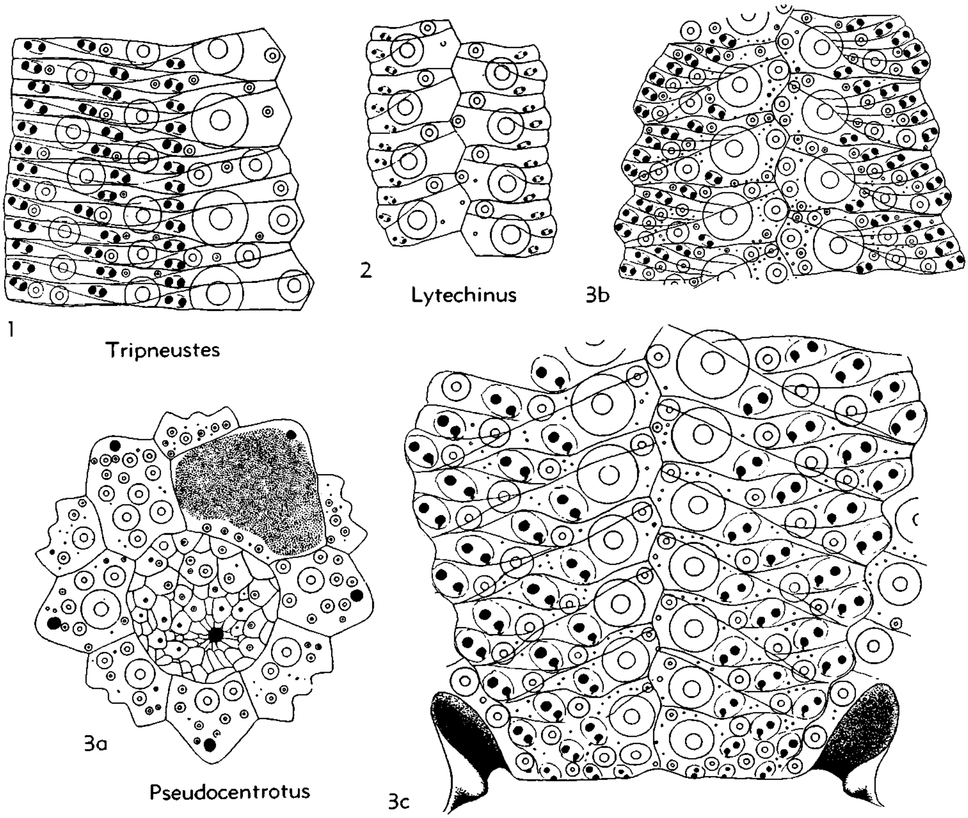

FIG. 321. Toxopneustidae (p. *U*427-*U*429).

Amb plates polyporous (6 or 7 pore pairs to each arc), pore zones narrow adorally, widening to become almost petaloid at ambitus. Secondary tubercles numerous, covering plates. *Rec.*, S.Japan. ——FIG. 321,*3*. **P. depressus* (AGASSIZ), Misaki Bay; *3a*, apical system, ×4.7; *3b,c*, amb aboral and adoral regions, ×5.3 (136d).

Schizechinus POMEL, 1869, p. 42 [**Anapesus tuberculatus* POMEL, 1887, p. 298; OD] [=*Toxophyma* LAMBERT & THIÉRY, 1925, p. 280 (no type designated)]. Large, more or less high hemispherical. Amb plates trigeminate, each with primary tubercle; secondary amb tubercles forming regular series parallel to primary series. Apical system with oculars I and V insert. *Mio.-Plio.*, Eu.-N.Afr.—— FIG. 320,*3a*. *S. duciei* (WRIGHT), Mio., Malta; test, oral, ×0.7 (38).——FIG. 320,*3b,c*. *S. tuberculatus* (POMEL), Mio., Alg.; *3b,c*, test, lat., aboral, ×0.8 (144).

Scoliechinus ARNOLD & CLARK, 1927, p. 23 [**S. axiologus*; OD, M]. Like *Lytechinus*, but with test flattened below and pore arcs inverse, pores of middle component being outermost. *?Cret.*, Jamaica.——FIG. 320,*2*. **S. axiologus*; amb detail, ×8 (136d).

Sphaerechinus DESOR, 1856, p. 134 [**Echinus granularis* LAMARCK, 1816, p. 44; OD, M]. Large, hemispherical, not conspicuously flattened below. Amb plates polyporous (4 to 6 pores in each arc), primary tubercle on each amb plate; secondary tubercles of same size as primaries, forming distinct horizontal series at ambitus. *Plio.*, Italy; *Rec.*, E.Atl.-Medit.

Tripneustes L. AGASSIZ, 1841, p. 8 [**Echinus ventricosus* LAMARCK, 1816, p. 44; OD] [=*Hipponoë* GRAY, 1840 *(nom. nud.)*; *Heliechinus* GIRARD, 1850, p. 364 (type, *H. gouldii*, =*T. ventricosus*) (obj.)]. Large, high, hemispherical to subspherical. Amb plates trigeminate, with primary tubercle on every 3 or 4 plates; pores arranged in 3 vertical series; conspicuous naked median space aborally in both areas. Apical system usually with oculars I and V broadly insert. *Mio.*, Eu.-Venez.-W.Pak.; *Plio.*, USA(Calif.); *Pleist.-Rec.*, IndoPac.-Carib. ——FIG. 321,*1*. **T. ventricosus* (LAMARCK), Rec., Carib.; amb, ×2.7 (136d).

Family UNCERTAIN

Gagaria DUNCAN, 1889, p. 91 [**Micropsis venustula* DUNCAN & SLADEN, 1884, p. 119; OD, M] [=*Leiopleurus* LAMBERT, 1902, p. 37 (type, *Psammechinus orbignyi* COTTEAU, 1883)]. Moderate-sized, low hemispherical. Angular pores and pits lacking. No distinct sculpture on test. Tubercles crenulate, not indented, forming regular

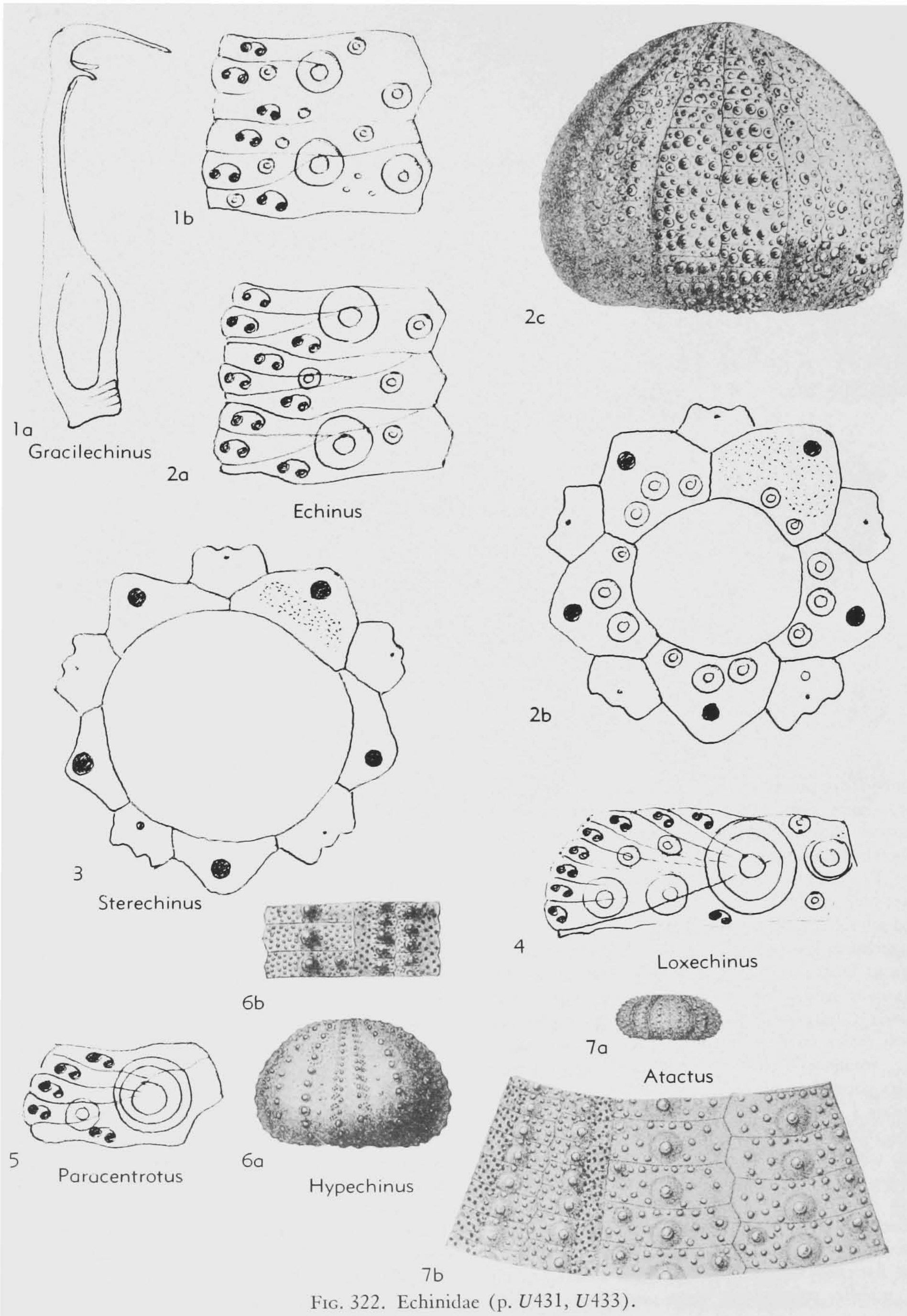

FIG. 322. Echinidae (p. U431, U433).

series in both areas. Apical system with only ocular I insert. *?Paleoc.*, N.Am.; *Eoc.*, W.Pak., *U.Oligo.*, N.Am.——FIG. 319,*1a-c*. *G. mossomi* COOKE, U.Oligo., USA(Fla.); *1a-c*, test, lat., aboral, oral, ×1 (24).——FIG. 319,*1d,e*. **G. venustula* (DUNCAN & SLADEN), Eoc., W.Pak.(W. Sind); *1d*, test detail, ×10; *1e*, test, aboral, ×2 (47).

Order ECHINOIDA Claus, 1876

[=Echinina MORTENSEN, 1942] [Materials for this order prepared by H. B. FELL and D. L. PAWSON, Victoria University of Wellington, N.Z.; transferred to Harvard University and Smithsonian Institution]

Lantern camarodont. Test not sculptured. Gill slits shallow. Tubercles imperforate, noncrenulate. Spines solid. *?U.Cret. (Cenoman.), Paleoc.-Rec.*

In MORTENSEN's (1943) classification, which is here adopted, four families are distinguished on the basis of structure of the globiferous pedicellariae. Such characters are almost always indeterminate in fossil material. Accordingly, the diagnoses for all genera of the order are here presented in such manner as to be mutually exclusive; this will permit generic identification of fossils (in most cases, at least) once the ordinal characters are recognized. Only after the generic determination has been made is it possible to determine the family, unless globiferous pedicellariae are preserved.

Family ECHINIDAE Gray, 1825

[*restr.* MORTENSEN, 1943] [=Triplechinidae A. AGASSIZ, 1872]

Globiferous pedicellariae with one or more lateral teeth on each side of blade. [See note with order Echinoida.] *?U.Cret. (Cenoman.), Mio.-Rec.*

Echinus LINNÉ, 1758, p. 663 [**E. esculentus*; SD FELL & PAWSON, herein (all other originally included species now assigned to other genera)]. Test widest at circular ambitus; amb plates trigeminate, with primary tubercle on every alternate (or every 3rd) amb plate. Buccal membrane containing scattered plates. Secondary radioles only slightly shorter than primary radioles, not very numerous or dense, very sparse in some forms; adradial zygopores not markedly separated from others by vertical series of enlarged secondary tubercles. Apical system dicyclic. *Plio.-Rec.*, Eu.-Atl.-Medit.-IndoPac.——FIG. 322,*2a,b*. **E. esculentus*, Rec., Eu.; *2a*, amb plates, ×3.4; *2b*, apical system, ×3.8 (136e).——FIG. 322,*2c*. *E. lamarckii* FORBES, Plio., Eng., test, ×0.7 (61).

Atactus POMEL, 1883, p. 79 [**Psammechinus fischeri* COTTEAU, 1880; OD] [=*Rotulechinus* LAMBERT & THIÉRY, 1914, p. 253 (obj.) (*nom. van. pro Atactus*, supposedly preocc. by *Atacta* SHINER, 1868)]. Like *Echinus*, but test low, flattened above, primary tubercle on every amb plate, pore arcs apparently almost horizontal, with interporiferous areas covered by small granules. Radioles unknown. *Plio.*, Rhodes.——FIG. 322,*7*. **A. fischeri* (COTTEAU); *7a*, test, ×0.8; *7b*, detail of test, ×7.7 (26).

Dermechinus MORTENSEN, 1942, p. 231 [**Echinus horridus* A. AGASSIZ, 1879, p. 203; OD]. Like *Echinus*, but with primary tubercle on every amb plate, and test high, height equaling or considerably exceeding horizontal diameter, in which case test is widest below ambitus; secondary radioles very numerous, densely arranged, with thorny shafts. Peristome smaller than apical system. *Rec.*, IndoPac.

Gracilechinus FELL & PAWSON, 1965, herein [**Echinus gracilis* A. AGASSIZ, 1869, p. 261; OD]. Like *Echinus* but with primary tubercle on every amb plate; peristome larger than apical system; secondary radioles with smooth shafts. Valves of globiferous pedicellariae with blade sharply differentiated from base, forming more or less tubular rostrum. [Fossils lacking pedicellariae cannot be distinguished from *Parechinus*.] *?Plio.*, Eng.; *Rec.*, Atl.-Medit.-IndoPac.——FIG. 322,*1a*. *G. acutus* (LAMARCK), *Rec.*, N.Atl.; valve of globiferous pedicellaria, ×77 (136e).——FIG. 322, *1b*. **G. gracilis* (A. AGASSIZ), *Rec.*, N.Am.(E. coast); amb plates, ×4.6 (136e).

Hypechinus DESOR, 1856, p. 130 [**Echinus patagonensis* D'ORBIGNY, 1842; OD]. Small (to 30 mm. diam.), similar to *Gracilechinus* but primary ambulacral tubercles reduced in size above ambitus and secondary granulation dense in some forms (resembling *Sterechinus*). *Mio.-Plio.*, Patagonia.——FIG. 322,*6*. **H. patagonensis* (D'ORBIGNY), Plio.; *6a*, test, lat., ×0.8; *6b*, detail of test, ×1.9 (44).

Isechinus LAMBERT, 1903, p. 476 [**Toxopneustes praecursor* ORTMANN, 1904, p. 53; SD LAMBERT & THIÉRY, 1914, p. 241]. Medium-sized (to 40 mm. diam.), subhemispherical, flattened below; amb plates trigeminate, zygopores in oblique arcs, forming 3 vertical series; pore zones not widened adorally; secondary interamb tubercles enlarged, resembling primaries and forming horizontal rows of 3 or 4 tubercles on each plate; radioles short. *Mio.*, Patagonia.——FIG. 323,*2*. **I. praecursor* (ORTMANN); *2a,b*, test, lat., adoral, ×1 (125); *2c*, amb plates, ×8 (136e).

Loxechinus DESOR, 1856, p. 136 [**Echinus albus* MOLINA, 1782, p. 200, 348; OD]. Widest at circular ambitus; amb plates polyporous, 7- to 10-geminate; radioles short; apical system dicyclic.

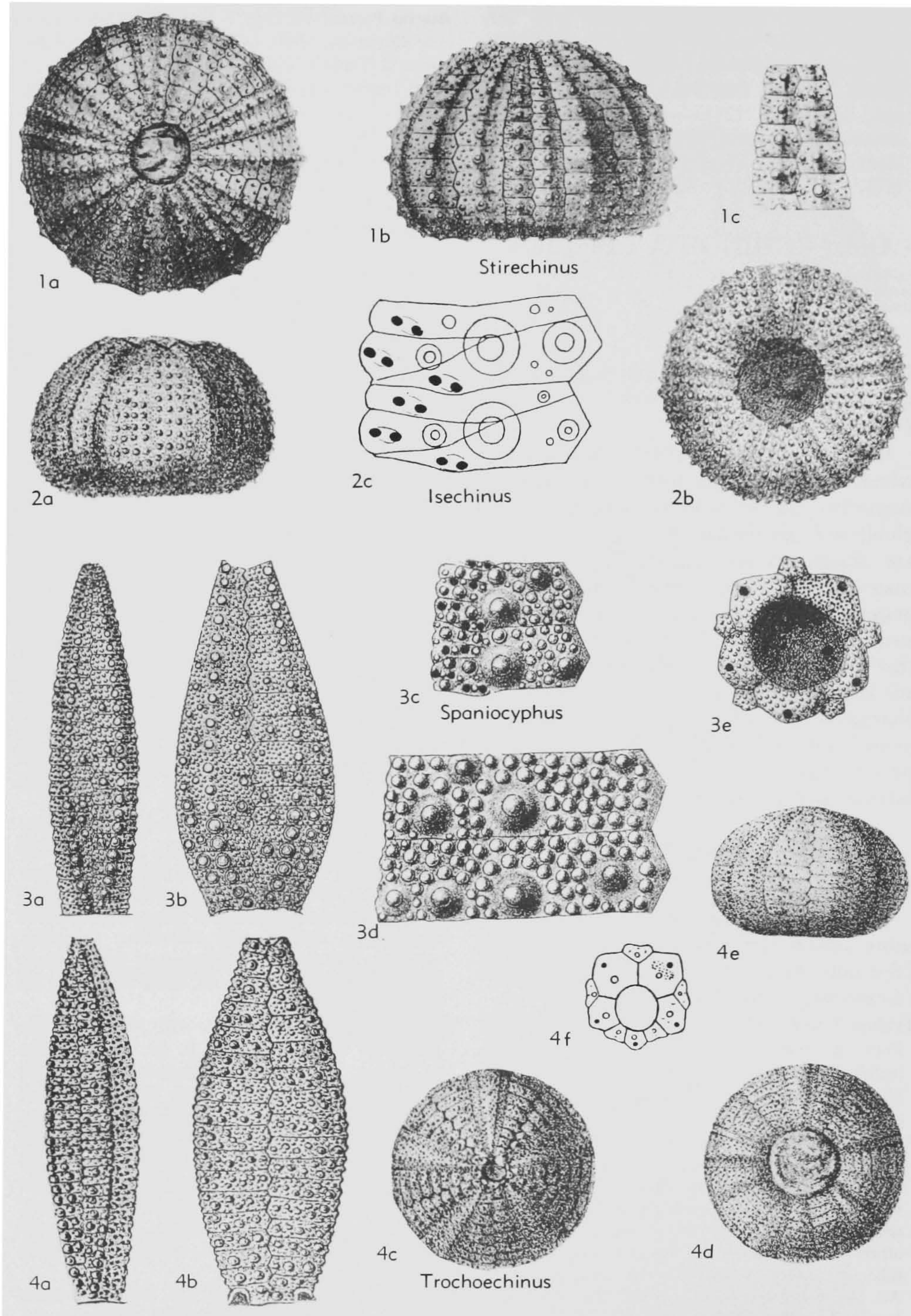

FIG. 323. Echinidae *(1-2)*; Family Uncertain *(3-4)* (p. *U*431, *U*433, *U*436).

Test green or whitish [Littoral.]. *Rec.*, Chile-S.Peru.——FIG. 322,*4*. **L. albus* (MOLINA), Chile; amb plate, ×4.6 (136e).

Paracentrotus MORTENSEN, 1903, p. 124, 135 [**Echinus lividus* LAMARCK, 1816, p. 50; OD]. Widest at circular ambitus; amb plates polyporous, 5-geminate; apical system regularly dicyclic, rarely with ocular I and V insert; radioles robust, as long as semdiiameter of test. *?Mio.*, Fr.; *?Plio.*, Eng.; *Rec.*, Medit.-N.Atl.——FIG. 322,*5*. **P. lividus* (LAMARCK), Rec., E.Atl.; amb plate, ×4.6 (136e).

Parechinus MORTENSEN, 1903, p. 108, 134 [**Cidaris angulosa* LESKE, 1778, p. 94; SD H. L. CLARK, 1912, p. 272] [=*Protocentrotus* DÖDERLEIN, 1906, p. 204 (obj.)]. Like *Gracilechinus* but valves of globiferous pedicellariae triangular, with blade not sharply differentiated from base. [Fossils lacking pedicellariae cannot be distinguished from *Gracilechinus*.] *Rec.*, S.Afr.(Mozambique-Cape-Angola).

Polyechinus MORTENSEN, 1942, p. 231 [**Paracentrotus agulhensis* DÖDERLEIN, 1905, p. 623; OD]. Like *Paracentrotus* but amb plates 4-geminate and test hemispherical, large (to 80 mm. diam.); radioles shorter than semidiameter of test. *Rec.*, S.Afr.

Psammechinus L. AGASSIZ & DESOR, 1846, p. 368 [**Echinus miliaris* P. L. S. MÜLLER, 1771, p. 108; SD LAMBERT & THIÉRY, 1910, p. 239] [*non Psammechinus* MORTENSEN, 1903, p. 136, =*Lytechinus* A. AGASSIZ]. Widest at circular ambitus; amb plates trigeminate, with primary tubercle on each; buccal membrane densely plated, with contiguous or even imbricated plates; secondary radioles numerous, smooth; apical system dicyclic. *?Cret.; ?Mio.* (numerous species recorded but without evidence of buccal plates); *Plio.*, Eu.; *Pleist.-Rec.*, N.Atl.-Medit.

Sterechinus KOEHLER, 1901, p. 8 [**S. antarcticus*; OD]. Like *Echinus* but secondary spines very numerous and dense, with thorny shafts; adoral radioles flattened, primary radioles relatively distinct, larger and more conspicuous than the matted secondaries which surround them; apical system with oculars I and V insert, or monocyclic. Test and spines bright red in life, but bleaching to olive or white in spirits. *Rec.*, Antarctic.——FIG. 322,*3*. **S. antarcticus*; apical system, ×4.6 (136d).

Stirechinus DESOR, 1856, p. 131 [**S. scillae*; OD] [=*Styrechinus* DESOR, 1856, p. 131 *(nom. null.)*] [*non Sterechinus* KOEHLER, 1901, p. 8]. Like *Gracilechinus* but primary tubercles of ambs and interambs linked by vertical ridges forming conspicuous meridional keels on each column. *Mio.-Plio.*, Fr.-Italy(Sicily)-Malta; *Rec.*, S.Atl.-W.Atl. ——FIG. 323,*1*. **S. scillae*, Plio., Sicily; *1a,b*, test, aboral, lat., ×0.8; *1c*, amb, ×1.6 (44).

Family ECHINOMETRIDAE Gray, 1825

[*nom. correct.* BELL, 1881 (*pro* Echinometradae GRAY, 1855)]

Blade of globiferous pedicellariae with unpaired lateral tooth. [See note with order Echinoida.] *Paleoc.-Rec.*

Echinometra GRAY, 1825, p. 426 [**Echinus lucunter* LINNÉ, 1758, p. 665; OD] [=*Ellipsechinus* LUTKEN, 1864, p. 165 (type, *E. macrostomus*, =*Echinometra vanbrunti* A. AGASSIZ, 1863, p. 21); *Plagiechinus* POMEL, 1883, p. 78 (type, *Echinometra prisca* COTTEAU, 1875, p. 12); *Mortensenia* DÖDERLEIN, 1906, p. 233 (type, *Echinus oblonga* DE BLAINVILLE, 1825, p. 95)]. Ambitus oblong or elliptical, longer transverse axis passing through ocular I and genital 3; amb plates polyporous, 4- to 10-geminate, exceptionally (in *E. prisca*) trigeminate; spines equal to or shorter than test diameter, acuminate but not otherwise modified. *Paleoc.*, India; *Oligo.*, Cuba; *Mio.*, Fr.; *Plio.*, Calif.-Fiji; *Pleist.-Rec.*, trop. Atl.-IndoPac. ——FIG. 324,*6*. **E. lucunter* (LINNÉ), *Rec.*, Carib.; amb plate, ×5 (136e). [=*?Ellipsocidaris* POMEL, 1869 *(nom. nud.)*.]

Anthocidaris LUTKEN, 1864, p. 164 [**Toxocidaris crassispina* A. AGASSIZ, 1863, p. 356; OD]. Widest at circular ambitus; amb plates polyporous, 7- to 9-geminate, amb at peristome wider than interamb; radioles elongate (some as long as horiz. diam. of test) unequally developed, usually much longer on one side of body (and usually so elongated on either anterior amb or posterior interamb); oculars I and V insert. Dark purple epidermis. *Rec.*, Japan-China.——FIG. 324,*5*. **A. crassispina* (A. AGASSIZ), Japan; amb plates, ×5 (136e).

Caenocentrotus H. L. CLARK, 1912, p. 348 [**Echinus gibbosus* L. AGASSIZ & DESOR, 1840, p. 367; OD]. Widest at circular ambitus; amb plates polyporous, 4- to 5-geminate; anus displaced to left, hence oculars IV and V insert; spines shorter than semidiameter of test. *Rec.*, Galapagos-Peru-Chile. [Almost all tests deformed aborally by the parasitic crab *Fabia chilensis*, which inhabits the rectum.].

Colobocentrotus BRANDT, 1835, p. 65 [**C. mertensii*; OD]. Ambitus oblong or elliptical, longer transverse axis passing through ocular II and genital 4; amb plates polyporous, 8- to 12-geminate, zygopores arranged in single arcs; aboral spines rounded, button-shaped, but not forming continuous mosaic; subambital enlarged spines forming marginal fringe. *Rec.*, cosmop. [=*Colobocentrus* GRAY, 1840, p. 52 *(nom. van.)*.]

Echinostrephus A. AGASSIZ, 1863, p. 20 [**E. aciculatus*; OD] [=*Perinatus* A. AGASSIZ, 1872, p. 119 *(nom. nud.)*; *Raphidechinus* LAMBERT & THIÉRY, 1914, p. 241 (type, *Echinus molaris* DE BLAIN-

VILLE, 1815, p. 88)]. Widest above circular ambitus; aboral spines very long and slender; amb plates 3- to 4-geminate; apical system dicyclic. [Blackish reef-dwelling forms.]. *Rec.,* trop. Indo-Pac.——Fig. 324,*4*. *E. molaris* (DE BLAINVILLE), Indon.; amb plates, ×6.7 (136e).

Evechinus VERRILL, 1871, p. 583 [**Echinus chloroticus* VALENCIENNES, 1846, pl. 7; OD]. Widest

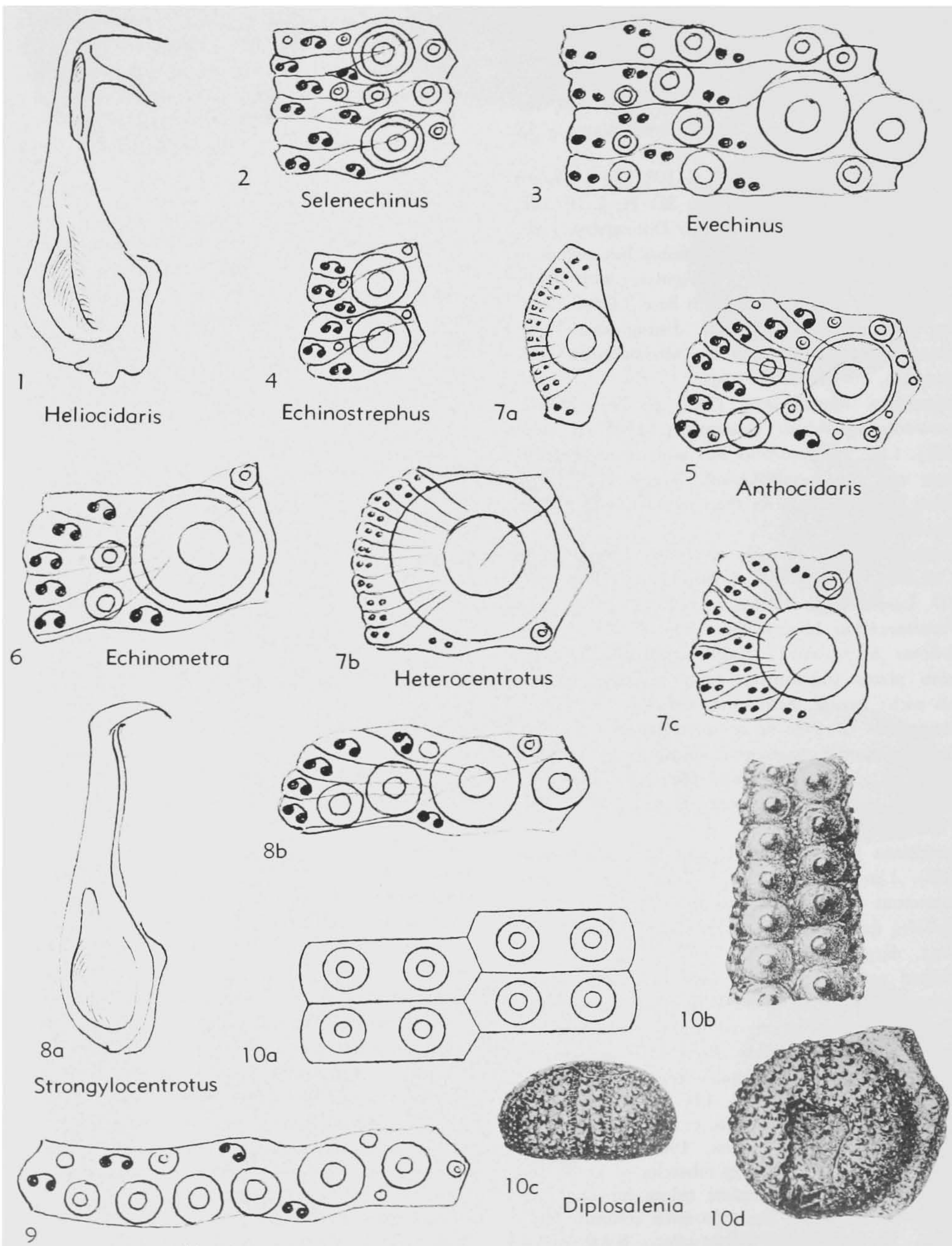

Fig. 324. Echinometridae *(1-7)*; Strongylocentrotidae *(8-9)*; Parasaleniidae *(10)* (p. *U*433-*U*436).

at circular ambitus; amb plates trigeminate, with primary tubercle on only every 2nd, 3rd, or 4th plate; buccal membrane containing scattered plates; secondary spines only slightly shorter than primary spines; adradial zygopores separated from others by rather conspicuous vertical series of secondary tubercles, zygopores tending to form 3 vertical series in each area. [Littoral, green forms restricted to New Zealand.] *Pleist.-Rec.*, N.Z.-Kermadec Is.——FIG. 324,*3*. **E. chloroticus* (VALENCIENNES), Rec., N.Z.; amb plates, ×5 (136e).

Heliocidaris L. AGASSIZ & DESOR, 1846, p. 371 [**Echinus tuberculatus* LAMARCK, 1816, p. 50; OD] [=*Toxocidaris* A. AGASSIZ, 1863, p. 22 (type, *Toxopneustes delalandi* L. AGASSIZ & DESOR, 1846, p. 367, =*Echinus erythrogrammus* VALENCIENNES, 1846, pl. 7] [*non Heliocidaris* POMEL, 1883 (MORTENSEN, 1903; LAMBERT & THIÉRY, 1914) (=*Evechinus*)]. Widest at circular ambitus; amb plates polyporous, 7- to 10-geminate; spines long and robust (in length reaching half horiz. diam. of test), brownish, ambital spines flattened distally; oculars I and V usually insert. [Littoral reef-dwelling forms.] *Rec.*, Australia-N.Z.——FIG. 324,*1*. *H. erythrogramma* (VALENCIENNES), E.Australia; valve of globiferous pedicellaria, ×83 (136e).

Heterocentrotus BRANDT, 1835, p. 65 [**Echinus mammillatus* LINNÉ, 1758, p. 664; SD POMEL, 1883, p. 77] [=*Acrocladia* L. AGASSIZ & DESOR, 1846, p. 373 (type, *Echinus trigonarius* LAMARCK, 1816, p. 51; SD POMEL, 1883, p. 77)]. Ambitus elliptical, longer transverse axis passing through ocular II and genital 4; apical system normally dicyclic; amb plates polyporous, 9- to 16-geminate, zygopores of some species arranged in double arcs; primary spines very thick and massive, subcylindrical or prismatic, carried on greatly enlarged primary tubercles; no marginal fringe of ambital spines, aboral spines not modified as scales or plates. *?Mio.*, Madag.; *Plio.-Pleist.*, Suez-Indonesia; *Rec.*, IndoPac.-W.Pac.——FIG. 324, *7a,b*. **H. mammillatus* (LINNÉ), Rec., W.Pac.; *7a*, aboral amb plate, ×8.3; *7b*, ambital amb plate, ×3.3 (136e).——FIG. 324,*7c*. *H. trigonarius* (LAMARCK), Rec., W.Pac.; amb plate showing double pore arcs, ×4.2 (136e). [=*Holocentronotus* GRAY, 1855, p. 37 *(nom. van.)*.]

Pachycentrotus H. L. CLARK, 1912, p. 349 [**Sphaerechinus australiae* A. AGASSIZ, 1872, p. 55; OD] [=*Cryptopora* A. AGASSIZ, 1872, p. 55 (obj.); *Pachechinus* A. AGASSIZ, 1872, p. 159 (obj.)]. Widest at circular ambitus; amb plates mostly polyporous (4-geminate), but several adoral plates and few others trigeminate; oculars I and V insert and in some forms II and IV also; radioles very short, length scarcely reaching 4th of horiz. diam. [Littoral to 70 m.] *Rec.*, S.Australia.

Podophora L. AGASSIZ, 1840, p. 19 [**Echinus atratus* LINNÉ, 1758, p. 665; OD]. Like *Colobocentrotus* but aboral spines converted into flat polygonal plates arranged in basaltiform mosaic. [Intertidal reefs.] *Rec.*, trop. IndoPac.-W.Pac.

Selenechinus DE MEIJERE in DELAGE & HÉROUARD, 1903, p. 246 [**Echinus armatus* DE MEIJERE, 1902, p. 5; OD]. Widest at circular ambitus; amb plates trigeminate, with primary tubercle on every 2nd or 3rd plate except adorally; buccal membrane containing scattered plates; secondary spines only slightly shorter than primary spines; adradial zygopores not separated from others and not forming 3 distinct vertical series; secondary tubercles very small or lacking on amb plates except adorally. Test white or red. *Rec.*, ?Philippine Is. ——FIG. 324,*2*. **S. armatus* (DE MEIJERE); amb plates, ×5 (136e).

Zenocentrotus A. H. CLARK, 1931, p. 5 [**Z. kellersi*; OD]. Like *Hetrocentrotus* but primary radioles not much enlarged, with marginal fringe of conspicuous subambital radioles, rather longer than others; apical system with oculars I and V insert or dicyclic. *Rec.*, S.Polynesia.

Family STRONGYLOCENTROTIDAE Gregory, 1900

[*emend.* MORTENSEN, 1943]

Test circular at ambitus. Blade of globiferous pedicellariae without lateral teeth. [See note with order Echinoida.] *Mio-Rec.*

Strongylocentrotus BRANDT, 1835, p. 63 [**S. chlorocentrotus* (=*Echinus droebachiensis* O. F. MÜLLER, 1776, p. 235); OD] [=*Euryechinus* VERRILL, 1866, p. 341 (obj.)]. Widest at circular ambitus; amb plates polyporous, 5- to 10-geminate, amb at peristome wider than interamb; length of spines not exceeding semidiameter of test. *Mio.*, USA (Ore.); *Plio.*, USA(Calif.); *Rec.*, mainly N.Pac. (1 N.Atl. species believed to be late migrant from N.Pac. by way of Arctic). [Records from European *Mio.-Plio.* probably misidentifications of *Paracentrotus*.] —— FIG. 324,*8*. **S. droebachiensis* (O. F. MÜLLER), Rec., Arctic circumpolar; *8a*, valve of globiferous pedicellaria, ×62; *8b*, amb plate, ×6.7 (136e).

Allocentrotus MORTENSEN, 1942, p. 232 [**Strongylocentrotus fragilis* JACKSON, 1912, p. 128; OD]. Like *Strongylocentrotus* but amb plates always 5-geminate and amb at peristome distinctly narrower than interamb, spines slender and short, not exceeding 4th diameter of test in length. *Rec.*, W.N.Am.(Vancouver to L.Calif.).

Hemicentrotus MORTENSEN, 1942, p. 231 [**Sphaerechinus pulcherrimus* A. AGASSIZ, 1863, p. 357; OD]. Like *Strongylocentrotus* but amb plates 4-geminate, zygopores arranged in 4 vertical series. [Littoral.]. *Rec.*, Japan-N.China.——FIG. 324,*9*. **H. pulcherrimus* (A. AGASSIZ), Japan; amb plate, ×7.5 (136e). [=*?Discaster* AGASSIZ, 1872, p. 178.]

Family PARASALENIIDAE Mortensen, 1903

[*nom. transl. et correct.* MORTENSEN, 1943 (*ex* Parasaleninae MORTENSEN, 1903]

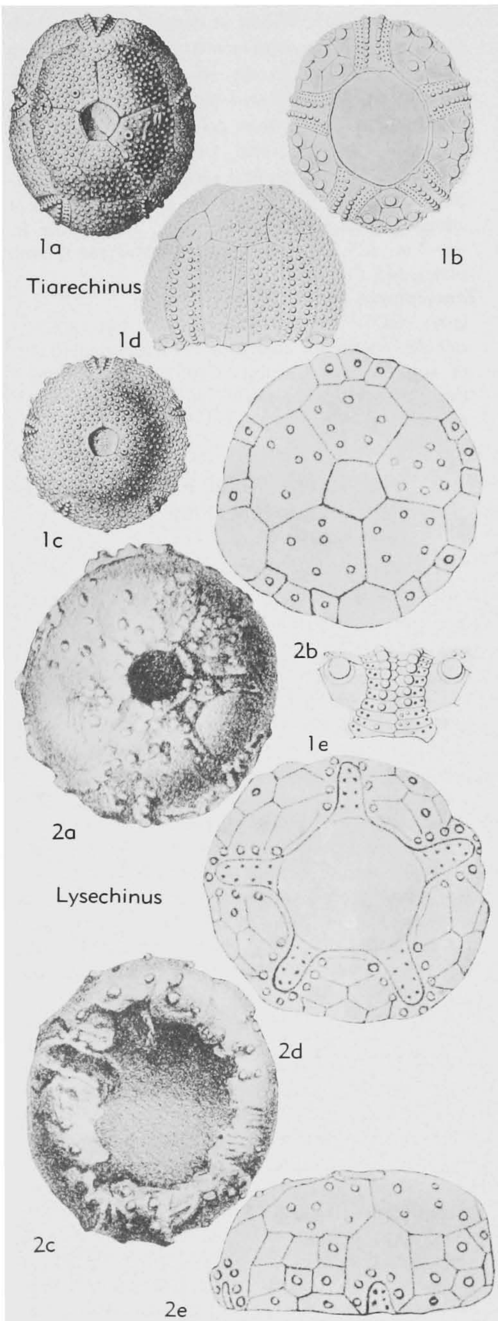

FIG. 325. Tiarechinidae (p. U437).

Test elliptical at ambitus. Blade of globiferous pedicellariae without lateral teeth. [See note with order Echinoida.] *Eoc.-Rec.*

Parasalenia A. AGASSIZ, 1863, p. 22 [**P. gratiosa*; OD] [=*Cladosalenia* A. AGASSIZ, 1872, p. 148 (obj.)]. Ambitus elliptical, longer transverse axis passing approximately through ocular III and genital 5; amb plates trigeminate; apical system dicyclic; single series of primary interamb tubercles in each column. *L.Mio.(Aquitan.),* Fr.; *Rec.,* Indo-Pac.-W.Pac.

Diplosalenia MORTENSEN, 1942, p. 232 [**Parasalenia gosseleti* COTTEAU, 1894, p. 633; OD]. Like *Parasalenia* but with double series of primary tubercles in each interamb column. *Eoc.,* Eu.——FIG. 324, *10.* **D. gosseleti* (COTTEAU), Fr.; *10a,* interamb plates of holotype, ×3.3 (136e); *10b,* amb, ×3.3; *10c,d,* test, lat., aboral, ×0.8 (27e).

Family UNCERTAIN

Spaniocyphus POMEL, 1883, p. 81 [**Echinus fallax* L. AGASSIZ; SD SAVIN, 1905, p. 191]. Small (*ca.* 10 mm. diam.), low hemispherical; amb plates trigeminate, ambs conspicuously widened adorally, with numerous secondary granules and primary tubercle on each plate, forming vertical meridional series. [Ambulacral structure not precisely known, possibly not echinoid; if diadematoid, genus should probably be referred to Stomechinidae.] *L.Cret.-U.Cret.,* Eu.——FIG. 323,*3.* **S. fallax* (L. AGASSIZ), L.Cret.(Valangin.), Switz.; *3a,b,* amb, interamb, ×3.2; *3c-e,* amb, interamb, apical system, ×9.6 (27a).

Trochoechinus DE LORIOL, 1909, p. 234 [**Psammechinus zumoffeni* DE LORIOL, 1902; OD]. Like *Psammechinus* but apical system with oculars I and V insert. [Ambulacral structure not precisely known, possibly not echinoid; if diadematoid, genus should probably be referred to Stomechinidae.] *U.Cret.(Cenoman.),* Asia Minor; *Mio.,* Malta.——FIG. 323,*4a-e.* **T. zumoffeni* (DE LORIOL), Syria; *4a,b,* amb, interamb, ×2 (125); *4c-e,* test, aboral, oral, lat., ×1 (126).——FIG. 323,*4f.* ?*T. tortonicus* (GREGORY), Mio., Malta; apical system, ×2 (72).

Order PLESIOCIDAROIDA Duncan, 1889

[Plesiocidaroida DUNCAN, 1889, p. 19] [=Blastoéchinides MUNIER-CHALMAS, 1895] [Materials for this order prepared by H. B. FELL, except diagnosis by J. W. DURHAM]

Test rigid, peristome large; gill slits absent or distinct; tubercles small, noncrenulate; primordial interambulacral plates persistent, followed by three plates; apical system very large. [This small group seems to be ancestral to the Arbacioida and thus is referred to the Echinacea, even though the lantern is unknown.] *U.Trias.(Carn.).*

Family TIARECHINIDAE Gregory, 1896

[Tiarechinidae GREGORY, 1896, p. 1003]

Lantern unknown, probably stirodont. Primary tubercles imperforate, noncrenulate. Test small (up to 7 mm. horiz. diam.), flattened below, hemispherical above, plates firmly fused together. Primordial interamb plate persisting, succeeded by 3 series of interamb plates. Amb plates simple throughout, zygopores uniserial. Apical system very large, occupying most of aboral surface, dicyclic, oculars strongly exsert. Periproct small, pentagonal in outline, probably covered by 5 valvular plates, as in Arbacioida. Peristome large, without gill slits. *U.Trias.*

Tiarechinus NEUMAYR, 1881, p. 169 [**T. princeps*; OD, M] [=*Haueria* LAUBE, unpub. MS *(nom. nud.) (non* D'ORBIGNY, 1846)]. Very small (test 5 mm. diam.). Oral side flat, upper side high, arched. Amb plates simple, each with distinct tubercle, pore pairs uniserial. Primary tubercles confined to oral side. Ambulacra continuing halfway up sides of test. *U.Trias.*, Eu.——FIG. 325,*1*. **T. princeps*; Carn., N.Austria; *1a-d,* test, aboral (2 specimens), oral, lat., ×4; *1e,* detail of adoral part of amb, ×7 (128).

Lysechinus GREGORY, 1896, p. 1000 [**L. incongruens*; OD, M]. Like *Tiarechinus* but less specialized, with no distinct primary tubercles, but small granules, not confined to oral side, but found scattered also adapically. Ambulacra almost wholly confined to oral side. *U.Trias.*, Eu.——FIG. 325,*2*. **L. incongruens,* Carn., N.Austria; *2a,b,* test, aboral; ×4.7; *2c,d,* test, oral, ×4.7; *2e,* test, lat., ×4.7 (73).

Superorder UNCERTAIN (ECHINACEA or DIADEMATACEA)

Order ORTHOPSIDA Mortensen, 1942

[*nom. transl.* FELL & PAWSON, herein (*ex* suborder Orthopsina MORTENSEN, 1942, p. 225)]

Lantern camarodont (known only in *Orthopsis*). Ambulacra simple, without compounded plates, at most with only incipient triads; zygopores arranged in straight meridians. Tubercles perforate, noncrenulate. Apical system dicyclic, exceptionally with posterior oculars insert. Spines unknown. *L.Jur.-U.Cret.*

The characters of the tubercles and ambs point to an aulodont derivation of the camarodont Orthopsida, which possibly share a common ancestry with Pedinoida. The remaining camarodont orders, on the other hand, evidently derive from a stirodont ancestry. Until fuller information is available on the morphology of Orthopsida, it is impossible to assign them to any defined superorder, but it seems probable that they represent an independent camarodont assemblage of superordinal status.

Family ORTHOPSIDAE Duncan, 1889

[*nom. transl.* GREGORY, 1900, p. 308 (*ex* Orthopsinae DUNCAN, 1889, p. 59)]

Characters of order. Test small or large, regularly hemispherical or globular (apparent ovoid form of *Gymnodiadema* probably a post-mortem distortion). *L.Jur.-U.Cret.*

Orthopsis COTTEAU, 1864, p. 550, 563 [**Cidarites miliaris* D'ARCHIAC, 1835; OD] [=*Stephanopsis* LAMBERT, 1900, p. 29 (type, *O. similis* STOLICZKA, 1873, p. 46) (*non* CAMBRIDGE, 1869, *nec* BEDOT, 1896); *Stephomma* STECHOW, 1921, p. 263 (*pro Stephanopsis* LAMBERT, 1900); *Arialopsis* LAMBERT & THIÉRY, 1925, p. 566 (obj.) (syn. of *Stephomma*); *?Miorthopsis* POMEL, 1883, p. 100 (type, *O. flouesti* COTTEAU, 1867)]. Moderate in size, usually flattened above and below. Amb plates imperfectly trigeminate, primary plates remaining distinct, with tubercles in regular series; pore zones straight, uniserial. Primary interamb tubercles perforate, noncrenulate; secondary tubercles well developed, but not as large as primaries and not continuing throughout. Apical system dicyclic. Lantern camarodont. *M.Jur.(Bathon.)-U.Cret. (Senon.),* Eu.-Asia-Afr.-N.Am.——FIG. 326,*1a-e*. **O. miliaris* (D'ARCHIAC), Senon., Fr.; *1a,b,* test, aboral, oral, ×0.87 (27a); *1c,* apical system, ×2.7 (27a); *1d,e,* amb, interamb, ×2.7 (27a).——FIG. 326,*1f*. *O. flouesti* COTTEAU, Cenoman., Fr.; test, lat., ×0.8 (31).——FIG. 326,*1g*. *O. globosa* COTTEAU & GAUTHIER, Senon., Iran; amb detail, approx. ×5.3 (34).——FIG. 326,*1h*. *O. ruppelli* (DESOR), Cenoman., Egypt; test, aboral, ×0.8 (121).——FIG. 326,*1i*. *O. casanovai* COOKE, Senon., USA(Tex.); test, lat., ×1 (23).

Brochechinus LAMBERT & THIÉRY, 1908, p. 21 [**B. elisae*; OD, M]. Small, hemispherical. Pores in arcs of 3 adorally, in single series aborally; each amb primary tubercle occupying 2 plates; interambs with single series of perforate, noncrenulate tubercles in each column, but also with granules connected by ridges, forming network. Apical system dicyclic. *U.Jur.,* Eu.——FIG. 326,*2*. **B. elisae,*

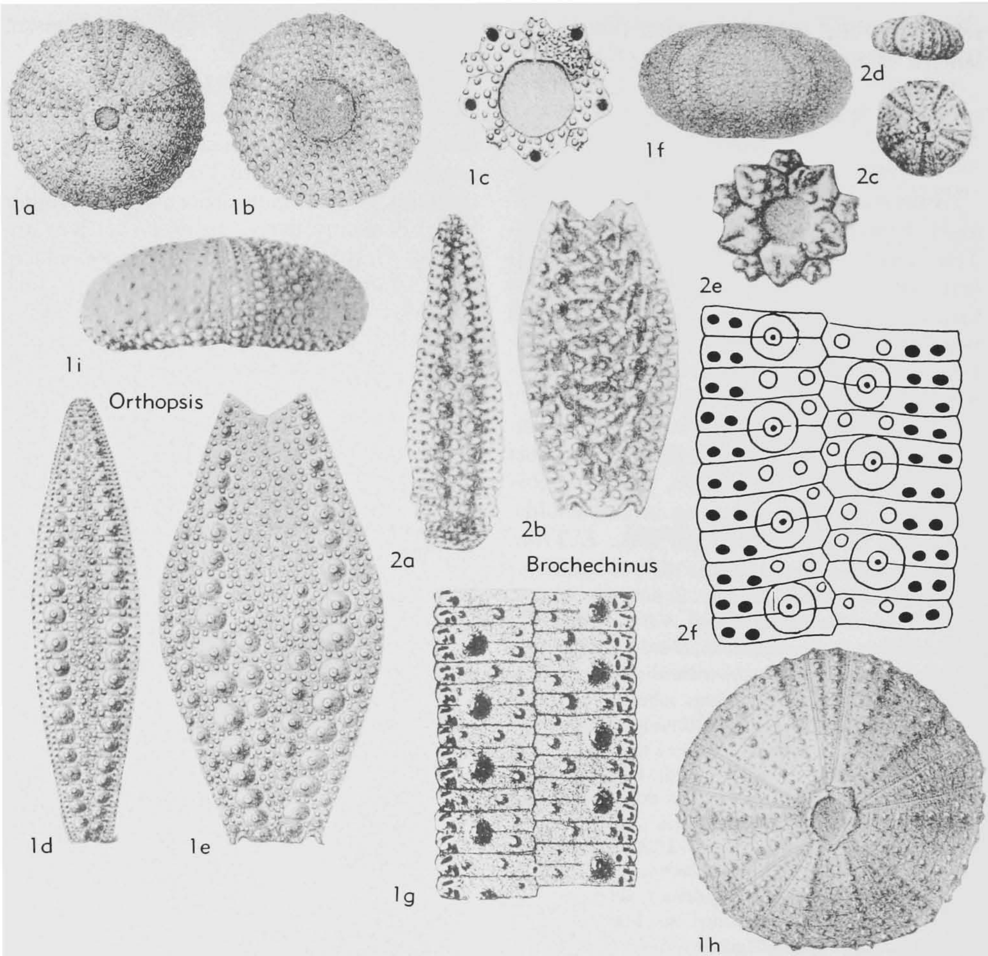

FIG. 326. Orthopsidae (p. U437-U438).

Oxford., Fr.; *2a,b,* amb, interamb, ×5.3; *2c,d,* test, aboral, lat., ×1.2; *2e,* apical system, ×5.3 (115); *2f,* amb, detail, ×10 (136d).

Dubarechinus LAMBERT, 1937, p. 62 [**D. despujolsi*; OD]. Small to medium-sized, subglobular. Amb plates bigeminate adorally, merely primaries adapically. Interamb plates with very small primary tubercles. Amb plates granuliferous, *L.Jur. (Domer.),* Morocco.

Gymnodiadema DE LORIOL, 1884, p. 606 [**G. choffati*; OD, M]. Like *Dubarechinus,* but with amb plates all primaries, with some perforate tubercles near peristome; interamb plates also with distinct perforate tubercles near peristome. *M.Jur. (Bathon.-Callov.),* Eu.——FIG. 327,*1.* **G. choffati,* Port.; *1a,b,* test, lat., aboral, ×0.7 (124); *1c,* amb plates, ×4 (125); *1d,* detail of test, ×2 (124); *1e,* adoral part of interamb, ×2 (125).

Orthocidaris COTTEAU, 1862, p. 182 [**Hemicidaris inermis* A. GRAS, 1848; OD, M]. Moderate in size to large, subspherical. Amb plates simple primaries with many small tubercles; pore pairs in single series throughout, except near peristome; interambs each with single series of perforate, noncrenulate tubercles in each column. *L.Cret.,* Eu.——FIG. 328,*2.* **O. inermis* (A. GRAS), Valangin., Fr.; *2a-c,* test, aboral, oral, lat., ×0.7 (27a); *2d,* test, lat. (large specimen), ×0.7 (31); *2e,* amb, ×2 (27a); *2f,g,* amb plates, adoral, aboral, ×4 (31).

Scaptodiadema DE LORIOL, 1891, p. 4 [**S. matheyi*; OD, M]. Like *Brochechinus* but with spaces between primary tubercles covered by small imperforate irregular tubercles. *U.Jur.,* Eu.——FIG. 328,*1.* **S. matheyi,* Oxford., Switz.; *1a,b,* amb, interamb, ×3.3; *1c-e,* test aboral, oral, lat., ×1.2; *1f,* apical system, ×4 (126).

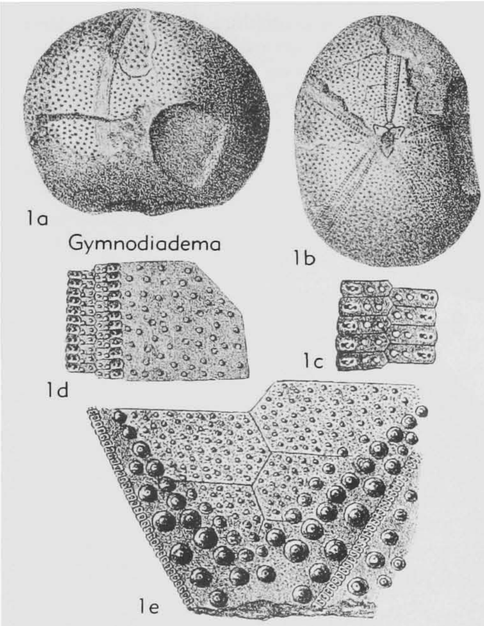

FIG. 327. Orthopsidae (p. *U*438).

DOUBTFUL GENERA OF REGULAR ECHINOIDS

Besairecidaris LAMBERT, 1936, p. 117 [**B. ankarensis*; OD]. Recorded as cidarid but probably some hemicidarid. Description inadequate. [See Mortensen, Mon., v. 5 (2), p. 557, 1951)] *Jur.*, Madag.

Bramus DE GREGORIO, 1930, p. 29 [**B. simplex*; OD]. Minute spines (possibly of a miocidarid). *Perm.*, Sicily.

Crinocidaris DE GREGORIO, 1930, p. 29 [**C. unicus*; OD].

Dallonia LAMBERT in DALLONI, 1920, p. 154 [**D. squamosa*; OD]. Algeria. [Supposed diadematacean, but probably consisting of fragments of some spatangoid.]

Echinopluteus MORTENSEN, 1897, p. 5 (type not specified). Erected for echinoid larval forms of unknown parentage, binomial, comparable to *Leptocephalus,* hence valid under Article 17 (4) of *Code,* and having status under the Law of Priority. Opinion 44 is relevant.

Firmacidaris LAMBERT, 1937, p. 45 [**Sphaerotiaris precincta* LAMBERT, 1933; OD]. Supposed cidaroid near *Besairecidaris* considered by MORTENSEN (1951, p. 558) as probably a hemicidarid, but indeterminate.

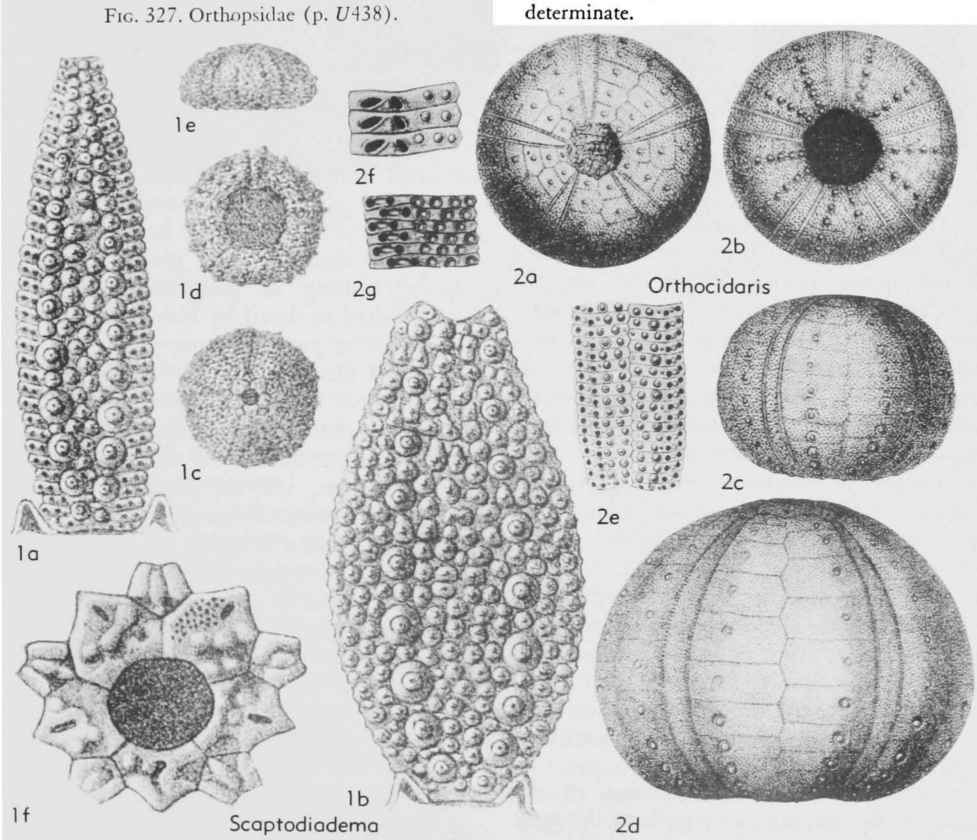

FIG. 328. Orthopsidae (p. *U*438).

Gajechinus LAMBERT & THIÉRY, 1914, p. 242 [**Echinus subcrenatus* DUNCAN & SLADEN, 1885, p. 317; OD]. Considered by MORTENSEN (Mon., v. 3 (2), p. 392, 1943) as *nom. delend.*

Ombria QUENSTEDT, 1873, p. 298.

Pleurechinus L. AGASSIZ, 1841, p. 7 [**Cidaris bothryoides* KLEIN, 1754, Tab. VI, H (prelinnean); SD LAMBERT, 1907, p. 15] [*non Pleurechinus* A. AGASSIZ, 1872, p. 152 =*Temnotrema* A. AGASSIZ]. Based on internal cast of unidentifiable echinoid, holotype now lost, figure unrecognizable. Declared by MORTENSEN (Mon., v. 3 (2), p. 370, 1943) a *genus delendum.*

Pleurocidaris POMEL, 1883, p. 111 [?type]. Genus based on fragmentary fossils probably referable to *Phyllacanthus, Prionocidaris,* and other genera, diagnostic character being not of generic value. [See Mortensen, Mon., v. 1, 1928, p. 489.]

Protocidaris DE GREGORIO, 1930, p. 20 [**P. bencontestus*; OD]. Minute spines (possibly of some miocidarid). *Perm.,* Sicily.

Radiolus (auctt.). Name used in binomial manner for unidentifiable fossil spines, comparable with *Otolithus.* Permissible under Article 17 (4) of *Code,* by way of establishing formal nomenclature for fragments of uncertain systematic position.

Rhabdechinus LAMBERT, 1910, p. 5 [**Cidaris belone* D'ORBIGNY]. Discussed by MORTENSEN (Mon., v. 3 (1), p. 365, 1930), who concludes that the genus is possibly based on cidarid spines, which are indeterminate, plus a fragment of test of what may be *Phymotaxis.*

Vernius DE GREGORIO, 1930, p. 18 [**V. elaboratus;* OD]. Minute spines (possibly of some miocidarid). *Perm.,* Sicily.

Superorder GNATHOSTOMATA Zittel, 1879

[Diagnosis by J. W. DURHAM]

Corona rigid; periproct outside apical system; no compound ambulacral plates; primary tubercles usually perforate and crenulate; spines hollow; lantern and girdle usually present in adult, teeth keeled; apical system and peristome usually approximately opposite. *Jur.-Rec.*

HOLECTYPOIDS

By CAROL D. WAGNER and J. WYATT DURHAM

[University of California (Berkeley)]

INTRODUCTION

The holectypoids comprise a group of morphologically highly variable echinoids which appear, in part at least, to bridge the gap between the "regular" and "irregular" groups. Within the order, the position of the periproct varies from well above the ambitus (e.g., *Anorthopygus*) to immediately adjacent to the peristome (e.g., *Echinoneus*). Variation of most morphological characters of systematic importance is so extreme as to render overall relationships obscure and classification tenuous. In the Cretaceous genera, in particular, a genus may exhibit very progressive development of one or more characters accompanied by morphological features which undoubtedly are nonprogressive. Although general trends of morphological change are observable within the order, distinct levels of evolution are not easily recognized.

Relative shape and disposition of the plates of the ambulacra are perhaps the most significant phylogenetic characters. An overall trend from simple primaries throughout to reduced plates adorally and for an increasing distance adapically is notable. The pattern of association of plates in triads ("plate crushing" or "plate reduction") has been studied in detail by HAWKINS (1920). The resulting group of three plates is not a compound plate, as the three are not bound together by a single tubercle. The adapical member of the triad is a relatively high primary, the next adorally a smaller primary or a demiplate, and the adoralmost member a much reduced demiplate. Species in which this pattern is highly developed commonly have pore-pairs disposed in more or less distinct arcs of three. However, in all genera, including those in which the triad grouping extends to the adapical terminus of the ambulacrum, the earliest plates adjacent to the peristome are usually relatively high primaries. In some later genera, distinct petaloid tendencies appear with rare demiplates on the oral side only.

Character of interambulacral ornament has played an important role in most classi-

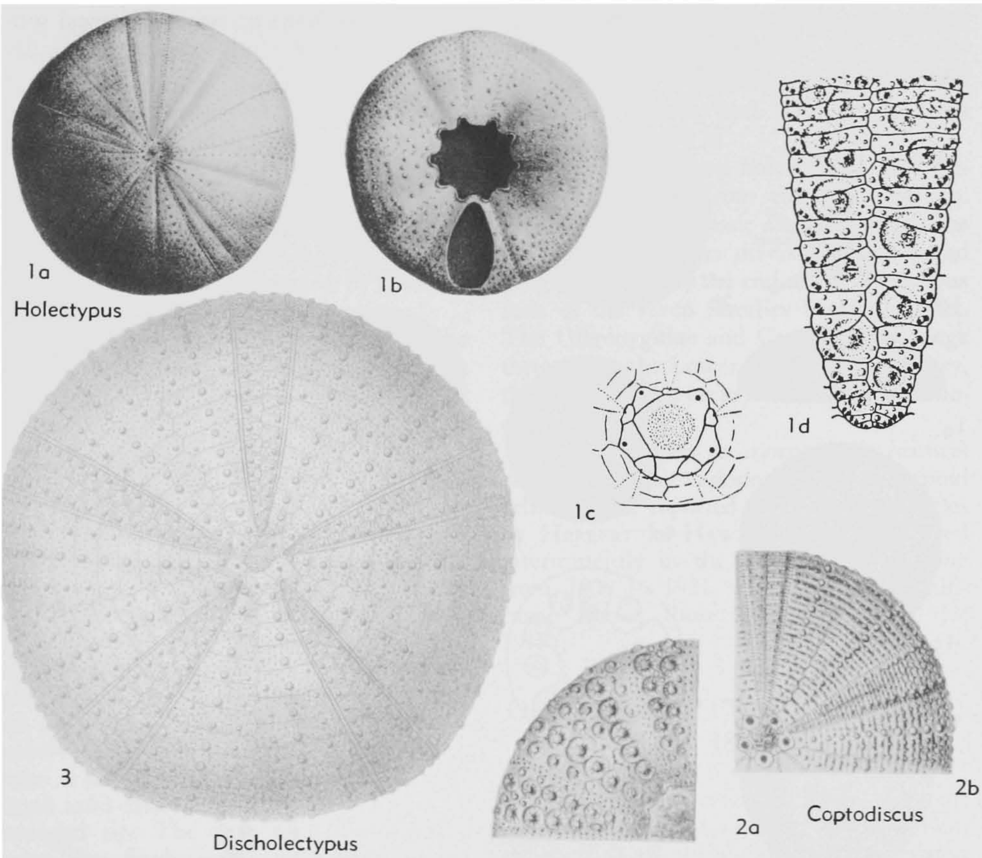

FIG. 329. Holectypidae (p. *U*444).

fications of the group. In genera with orderly ornament one large primary tubercle is situated slightly adradial and adoral to the center of each interambulacral plate, forming distinct meridional rows over the corona. Tubercles of essentially the same size occur in transverse or diagonal rows toward the interradial suture and in diagonal rows adradial to the central tubercle. In the more advanced groups, orderliness of tubercle placement breaks down and a condition of numerous, equal-sized, deeply scrobiculate scattered tubercles is attained. Earlier representatives of the order have perforate and crenulate tubercles; later genera may have perforate or nonperforate tubercles, all of essentially the same size.

The perignathic girdle is highly variable. Auricles of *Holectypus* are short rodlike structures not connected by interradial ridges. In the Discoididae and Conulidae the earlike auricles are connected by ridges. In geologically younger groups the girdle is highly specialized, rudimentary, or absent in the adult. Lantern supports in *Haimea, Oligopygus,* and *Bonaireaster* consist of flat, rectangular structures interradial in position in the adult but radial in origin. In the Conoclypidae the auricles are elongate, flaring structures mounted on a high oral funnel; these are also interradial in position but radial in origin.

Internal buttresses are present, though poorly developed, in *Holectypus*. They are highly developed in the Discoididae, extending outward from the ridges of the perignathic girdle slightly adradial to the center of the interambulacral column and continuing some distance above the ambitus. *Conulus* shows no trace of internal supports and none are found in the geologically younger groups.

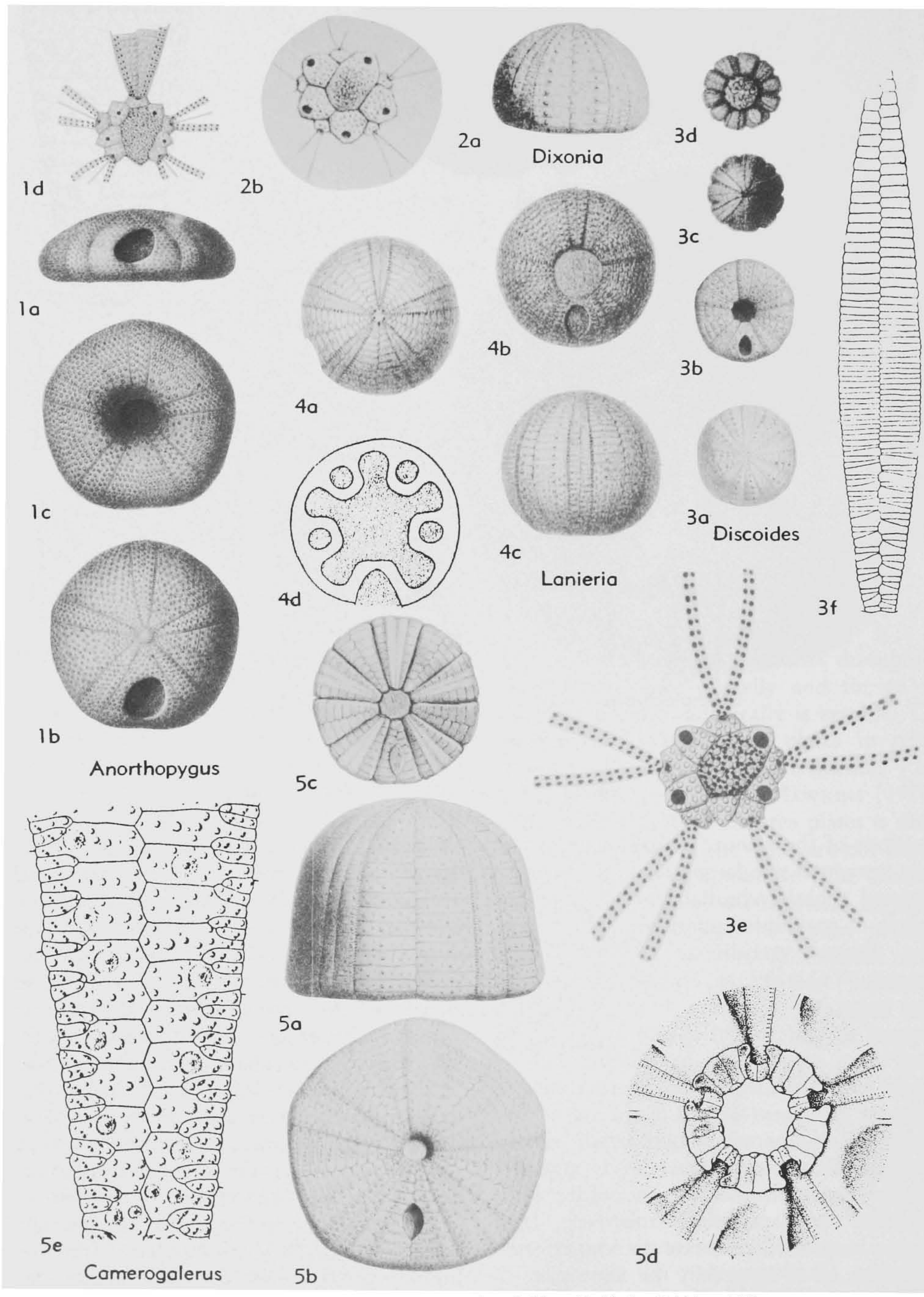

FIG. 330. Anorthopygidae *(1)*; Discodeidae *(2-5)* (p. *U*444-*U*445).

A general trend is observable in the progressive changes of the apical system. The Holectypidae and Discoididae have five genital plates; genital plate 5 may be perforate or not. *Conulus,* the Galeritidae, and most members of the Echinoneidae have four perforate genital plates. *Anorthopygus* has an ethmolytic apical system. *Echinoneus* and representatives of the Oligopygidae and Conoclypidae are characterized by a monobasal system with four genital pores.

Overall shape of the test ranges from the highly vaulted *Conulus* with flat oral side and relatively sharp ambitus to the globular *Lanieria* and to the ovoid *Oligopygus* with rounded ambitus and pulvinate oral side.

Spines and pedicellariae are not well known. Primary spines of *Holectypus depressus* are relatively short aborally, longer orally, with blunt tip, slender striated shaft, prominent, commonly oblique milled ring and long, tapering base. They have a hollow axis and no cuticle. Short hairlike miliaries are also present. Tridentate and globiferous pedicellariae have been observed on *Holectypus.* Primary spines of *Echinoneus,* which are short and fairly strong, form a dense, uniform cover; they have a small axial cavity and terminate in a simple, rounded tip. The very numerous miliary spines are finely serrate. Globiferous, tridentate, triphyllous, and ophicephalous pedicellariae are present.

Studies on the crystallographic c-axis orientation of the calcite plates (Raup, 1959, 1960) shed useful light on relationships within the Holectypoida. The families Holectypidae, Galeritidae, Echinoneidae, and Conoclypidae have the c-axis normal to the test. In *Conulus albogalerus* c-axis orientation varies ontogenetically; in *Camerogalerus cylindrica* the c-axis is tangential to the test. The orientation in the Oligopygidae and Anorthopygidae is unknown as yet.

Inasmuch as *Echinoneus* and *Micropetalon* are the only living Holectypoida, ecologic evaluations are necessarily largely inferential. *Echinoneus* is mainly littoral, living buried in coarse substrates, often beneath rocks or coral. *E. cyclostomus* has been recorded from depths of 120 meters. Most fossil records are from fine, calcareous sediments. Faunas including holectypoids commonly exhibit great diversity and contain elements of known warm-water affinity. At present, *Echinoneus* is tropicopolitan; *Micropetalon* is known only from the Hawaiian Islands and China Sea from depths of 40 to 70 m.

The earliest known holectypoid *(Holectypus)* is reported from the Pliensbachian. During the late Jurassic and throughout the Cretaceous the order diversified and spread geographically. By the end of the Cretaceous four of the seven families became extinct. The Oligopygidae and Conoclypidae range throughout the Lower and Middle Tertiary, the latest known occurrence being late Miocene.

Detailed studies on morphologic features and phylogenetic relationships of holectypoid echinoids are reported in a series of articles by Herbert L. Hawkins which appeared intermittently in the *Geological Magazine* from 1909 to 1921. Of particular significance among those are Hawkins (1911, 1918).

Order HOLECTYPOIDA Duncan, 1889

[Holectypoida Duncan, 1889, p. 135]

Test hemispherical to globular or ovoid; ambulacra petaloid or not, narrower than interambulacra throughout; apical system monobasal or with 4 or 5 genital plates; girdle with or without interradial ridges, well developed or rudimentary or lacking in adult; teeth with lateral flanges; gill slits present or not; periproct supramarginal to inframarginal. *L.Jur.(Pliensbach.)-Rec.*

Suborder HOLECTYPINA Duncan, 1889

[*nom. transl.* Wagner & Durham, herein (*ex* Holectypoida Duncan, 1899, p. 135)]

Ambulacra nonpetaloid; auricles radial; gill slits distinct; interambulacral ornament orderly; 5 genital plates except in Anorthopygidae. *L. Jur. (Pliensbach.) - U. Cret. (Senon.).*

Family HOLECTYPIDAE Lambert, 1899

[*nom. transl.* Lambert & Thiéry, 1914 (*ex* Holectypinae Lambert, 1899, table opp. p. 50)]

Genital plate 5 present; peristome and periproct regular in outline. *L.Jur.(Pliensbach.)-U.Cret.(Senon.).*

Holectypus Desor, 1842, p. 65 [**Discoidea depressa* Agassiz, 1839, p. 88 (*=*Echinites depressus* Leske, 1778, p. 164); OD] [=*Temnodiscus* Lambert & Thiéry, 1911, p. 280 (*non* Koken, 1896); *Temnholectypus* Lambert & Thiéry, 1925, p. 576 (type, *Holectypus circularis* Cotteau & Gauthier, 1895, p. 75)]. Oral side flat or concave; ambulacral plates in groups of 3 orally; genital plate 5 imperforate; branchial slits well developed; periproct large, marginal or inframarginal; internal buttresses poorly developed. *L. Jur.(Pliensbach.)-U. Cret. (Senon.),* Eu.-N.Am.——Fig. 329,*1a-c*. **H. depressus* (Leske), M.Jur.(Bajoc.), Eng.; *1a,b,* aboral, oral, ×0.7 (172); *1c,* apical system, enlarged (196a).——Fig. 329,*1d*. *H. hemisphaericus* (Lamarck), M.Jur.(Bajoc.), Eng.; adoral detail of ambulacrum, enlarged (81).

Coenholectypus Pomel, 1883, p. 75 [**Holectypus macropygus* Desor, 1842, p. 173; SD Hawkins, 1912, p. 450] [=*Caenholectypus* Pomel, 1883, p. 125 *(nom. null.)*]. Similar to *Holectypus* but genital 5 perforate. *Cret.*, Eu.-N.Am.-S.Am.

Coptodiscus Cotteau & Gauthier, 1895, p. 108 [**C. nomiae*; OD]. Similar to *Coenholectypus* except for deep pits on plates and in sutures on oral side. *U. Cret. (Cenoman. - Senon.),* Iran - Arabia-Spain.——Fig. 329,*2*. **C. nomiae,* Senon., Iran; *2a,* part of oral surface; *2b,* part of aboral surface, ×0.7 (210).

Discholectypus Pomel, 1883, p. 75 [**Holectypus meslei* Gauthier, 1876, p. 84; OD]. Subhemispherical; ambulacral plates in groups of 3 throughout; lantern and girdle unknown; primary interambulacral tubercles large, in distinct vertical rows. *L.Cret.,* Alg.-S.Fr.——Fig. 329,*3*. **D. meslei* (Gauthier), Alb., Alg.; aboral, ×1 (35).

Metholectypus Hawkins, 1923, p. 201 [**M. trechmanni*; OD]. Small, subglobular; ambulacra of simple primaries throughout; apical system minute, genital plate 5 imperforate; periproct inframarginal, close to peristome; lantern and girdle unknown. *Cret.,* Jamaica.

Family ANORTHOPYGIDAE Wagner & Durham, n. fam.

Apical system ethmolytic; peristome transversely elongate; periproct variable in outline. *Cret.(Alb.-Cenoman.).*

Anorthopygus Cotteau, 1869, p. 648 [**Nucleolites orbicularis* Grateloup, 1836, p. 180; OD] [=*Pseudopileus* de Loriol, 1901, p. 29 (type, *Anorthopygus zumoffeni* de Loriol, 1901, p. 30; OD]. Ambulacra of simple primaries throughout or with reduced plates orally; periproct large, marginal or supramarginal, oblique, subrounded or pyriform; pore pairs uniserial. *Cret.(Alb.-Cenoman.),* Eu.-N.Am.——Fig. 330,*1*. **A. orbicularis* (Grateloup), Cenoman., Fr.; *1a-c,* post., aboral, oral, ×1; *1d,* apical system, enlarged (27a).

Family DISCOIDIDAE Lambert, 1899

[*nom. correct.* Wagner & Durham, herein (*pro* Discoidesidae Smiser, 1935, p. 35, *nom. transl. ex* Discoidinae Lambert, 1899, table opp. p. 50)]

Oral side flat; ambulacra with reduced plates from peristome to ambitus or slightly above ambitus, pore pairs uniserial adapically, in arcs of 3 orally; high ridges on perignathic girdle; well-developed internal buttresses; ornament orderly adapically, tending to concentric pattern orally; periproct inframarginal; gill slits distinct. *Cret.*

Discoides Parkinson, 1811, p. 20 [**Echinites subuculus* Leske, 1778, p. 171; OD] [=*Discodea* Gray, 1825, p. 429 (obj.); *Discoidea* Agassiz, 1835, p. 137 *(nom. van.)*; *Protocyamus* Gregory in Lankester, 1900, p. 316 (obj.)]. Aboral side conical to subconical; ambulacra with reduced plates from peristome to ambitus; genital plate 5 imperforate, madreporite may extend to all genital plates. *Cret. (Apt.-Turon.),* Eu.-N. Am.——Fig. 330,*3*. **D. subucula* (Leske), Cenoman., Eng. *(3a,b,f)*; Fr.*(3c-e)*; *3a,b,* aboral, oral, ×1 (173); *3c,d,* int. mold, aboral and oral views, ×1 (27a); *3e,* apical system, enlarged (27a); *3f,* amb. plates, enlarged (81).

Camerogalerus Quenstedt, 1873, p. 411 [**Galerites cylindricus* Lamarck, 1816, p. 23; OD] [=*Pithodia* Pomel, 1883, p. 75 (obj.); *Pseudodiscoides* Lambert & Thiéry, 1914, p. 282 (obj.)]. Medium-sized to large, aborally highly inflated; ambulacral plates numerous, reduced plates irregularly above ambitus, demiplates much reduced below ambitus; apical system small, genital plate 5 imperforate. *U.Cret.(Cenoman.),* Eu.——Fig. 330,*5*. **C. cylindrica* (Lamarck), Eng.; *5a-c,* lat., oral, int. mold oral view, ×0.7 (173); *5d,* perignathic girdle, enlarged (196b); *5e,* part of ambulacrum, enlarged (81).

Dixonia Wagner & Durham, 1964, p. 170 [**Discoidea dixoni* Forbes in Dixon, 1850, p. 341]. Test small; aboral side conical to subconical; ambulacra with reduced plates from peristome to above ambitus; genital plate 5 perforate. *Cret. (Apt.-Turon.),* Eu.——Fig. 330,*2*. **D. dixoni* (Forbes), Turon., Eng.; *2a,* lat., ×1; *2b,* apical system, enlarged (173).

Lanieria Duncan, 1889, p. 158 [**Echinoconus lanieri* Cotteau, 1881, p. 11; OD]. Small, globular to subglobular; ambulacral plates in groups of 3 except close to oculars; 5 perforate genital plates; peristome small, gill slits present; primary tubercles in horizontal and vertical rows. *U.Cret.,* Cuba-USA.——Fig. 330,*4*. **L. lanieri* (Cotteau), Cuba; *4a-c,* aboral, oral, lat., ×1 (30); *4d,* cross sec., radiating walls connecting auricles with test,

×1.8 (136f). [=*Hawkinsia* LAMBERT, 1928, p. 21, *nom. correct.* JEANNET, 1936, p. 581, *pro Hawkensia* LAMBERT, 1928 (type, *Coenholectypus cubae* HAWKINS, 1913, p. 202).]

Suborder ECHINONEINA H. L. Clark, 1925

[Echinoneina H. L. CLARK, 1925, p. 176; *emend.* WAGNER & DURHAM, herein]

Ambulacra nonpetaloid; auricles radial or lantern and girdle absent in adult; gill slits indistinct or absent; interambulacral ornament not orderly except in *Conulus;* apical system tetra- or monobasal, 4 genital pores. *M.Jur.(Callov.)-Rec.*

Family ECHINONEIDAE Agassiz & Desor, 1847

[*nom. correct.* WAGNER & DURHAM, herein (*pro* Échinonéides AGASSIZ & DESOR, 1847, p. 143)]

Ambulacra with reduced plates in part or throughout; lantern and girdle absent in adult (present in young of *Echinoneus*); peristome oblique or elongate. *U.Cret.-Rec.*

Echinoneus LESKE, 1778, p. 173 [**E. cyclostomus*; SD H. L. CLARK, 1917, p. 101] [=*Echinanaus* GRAY, 1825, p. 7 *(nom. van.)* (obj.); *Pseudohaimea* POMEL, 1885, p. 118 (type, *Haimea delagei* POMEL; SD WAGNER & DURHAM, herein); *Koehleraster* LAMBERT & THIÉRY, 1921, p. 331 (type, *Echinoneus abnormalis* DE LORIOL, 1883, p. 41)]. Ovoid; ambulacral plates in groups of 3, pore pairs uniserial adapically, in groups of 3 adorally, pore zones slightly sunken; apical system monobasal; peristome oblique, irregular, buccal membrane with small plates; periproct inframarginal; tubercles perforate or imperforate, noncrenulate; globiferous, tridentate, ophicephalous, and triphyllous pedicellariae. [*Echinoneus* VAN PHELSUM, 1774, not accepted because the work of this author is not consistently binomial (ICZN Code, 1961, Art. 11c).] *Oligo.-Rec.*, Eu.-W.Indies-IndoPac.-Australia.——FIG. 331,*2*. **E. cyclostomus,* Rec., Lord Howe Is.; *2a,b,* aboral, lat., ×1 (136f).

Micropetalon A. AGASSIZ & H. L. CLARK, 1907, p. 251 [**M. purpureum*; OD]. Like *Echinoneus* except genital plates distinct; pore zones not depressed, pore pairs without peripodia; primary tubercles imperforate. *Rec.*, Hawaii.——FIG. 331, *5*. **M. purpureum; 5a,b,* aboral, oral, ×2 (323).

Paleoechinoneus GRANT & HERTLEIN, 1938, p. 105 [**P. hannai*; OD]. Ovoid; ambulacral plates in groups of 3 throughout, pore pairs uniserial adapically, in arcs of 3 adorally; pore zones not depressed; peristome elongate along III-5 axis; apical system tetrabasal; periproct marginal, slightly oblique; primary tubercles numerous, perforate, scrobiculate. *U.Cret.*, USA(Calif.)-Mex.

Family CONULIDAE Lambert, 1911

[*nom. correct.* WAGNER & DURHAM, herein (*pro* Conulusidae LAMBERT, 1911, p. 27)]

Ambulacra with reduced plates; girdle continuous, ridges low; pore pairs uniserial or in arcs of 3 orally; ornament not orderly except *Conulus*; peristome round to oblique. *M.Jur.(Callov.)-Eoc.*

Conulus LESKE, 1778, p. 161 [**C. albogalerus*; OD] [=*Echinites* LESKE, 1778, p. xviii (type, *E. albogalerus*=*Conulus albogalerus;* SD WAGNER & DURHAM, herein) (obj.) (*non* MÜLLER & TROSCHEL, 1844, *nec* DUNCAN, 1889); *Pyrina* DESMOULINS, 1835, p. 192 (see following note) (type, *Nucleolites castanea* BRONGNIART, 1822; SD COOKE, 1946, p. 220); *Conulopyrina* HAWKINS, 1921, p. 420 (type, *C. anomala*)]. Oral side flat, aborally hemispherical to highly conical; apical system ethmophract; peristome slightly elongate along III-5 axis, gill slits rudimentary, auricles low; periproct ovate, inframarginal, larger than peristome; 4 genital plates, perforate; interambulacral tubercles numerous, in diagonal pattern adradially and interradially to central tubercle. *U. Cret.*, Eu.-N.Afr.-Asia-N.Am.——FIG. 331,*4*. **C. albogalerus,* Senon., Eng.; *4a,b,* lat., oral, ×0.7 (191a); *4c,* perignathic girdle, ×3 (196b); *4d,* adoral part of ambulacrum, enlarged (81).

[Contrary to the opinions of LAMBERT (1911), HAWKINS (1919), and MORTENSEN (1948), *Pyrina petrocoriensis* DESMOULINS, 1837, cannot be the type of *Pyrina* DESMOULINS, 1835, as it was not included in the original list of species assigned to the genus. COOKE'S 1946 designation of *Nucleolites castanea* BRONGNIART, 1822, one of the species originally referred to the genus, makes *Pyrina* DESMOULINS, 1835, *(non auctorum)* a subjective synonym of *Conulus* LESKE, inasmuch as *N. castanea* has long been accepted as a typical member of *Conulus*.]

Galeraster COTTEAU, 1890, p. 548 [**G. australiae*; OD]. Test rounded or slightly elongate posteriorly; apical system unknown in type-species, in other species with 4 perforate genital plates; periproct marginal; tubercles perforate, crenulate. *Cret.-Eoc.*, sunken; tubercles perforate, crenulate. *Eoc.*, Australia-Fr.——FIG. 331,*6*. **G. australiae*; *6a,b,* oral, post., ×0.75 (136f).

Globator AGASSIZ, 1840, p. 7, 16 [**G. nucleus*; OD] [=*Pyrina auctt.* (*non* DESMOULINS, 1835, see note under *Conulus*); *Pseudopyrina* LAMBERT, 1908, p. 49 (type, *Nucleolites ovulum* LAMARCK; OD)]. Test round or elongate, orally flattened to slightly concave; pore pairs uniserial, pore zones flush to slightly sunken; 4 genital plates; peristome round or oblique; periproct marginal or supramarginal; tubercles perforate, crenulate. *Cret.-Eoc.*, Eu.-Medit.-Madagascar-India-W.Indies-Brazil-USA.——FIG. 331,*1*. **G. nucleus,* Senon., Belg.; *1a-c,* aboral, oral, post., ×1.3 (142).

Pygopyrina POMEL, 1883, p. 54 [**Desorella icaunensis* COTTEAU, 1855, p. 711 (=*Desoria icaunensis* COTTEAU, 1855, p. 224); OD] [=*Conodoxus* POMEL, 1883, p. 74 (genus without species);

Nucleopyrina POMEL, 1883, p. 53 (type, *Pyrina cylindrica* GRAS, 1848, p. 45)]. Like *Globator* except pore pairs in arcs of 3 adorally; periproct supramarginal. *M. Jur. (Callov.)-U. Cret. (Ceno-man.)*, Eu.-Asia.——FIG. 331,*3*. **P. icaunensis* (COTTEAU), U.Jur., Oxford., Fr.; aboral, ×1 (27b).

Family GALERITIDAE Gray, 1825

[Galeritidae GRAY, 1825, p. 428]

Ambulacra of simple primaries throughout; pore pairs uniserial; interambulacral ornament not orderly; 4 genital pores. *U. Cret.(Senon.)*.

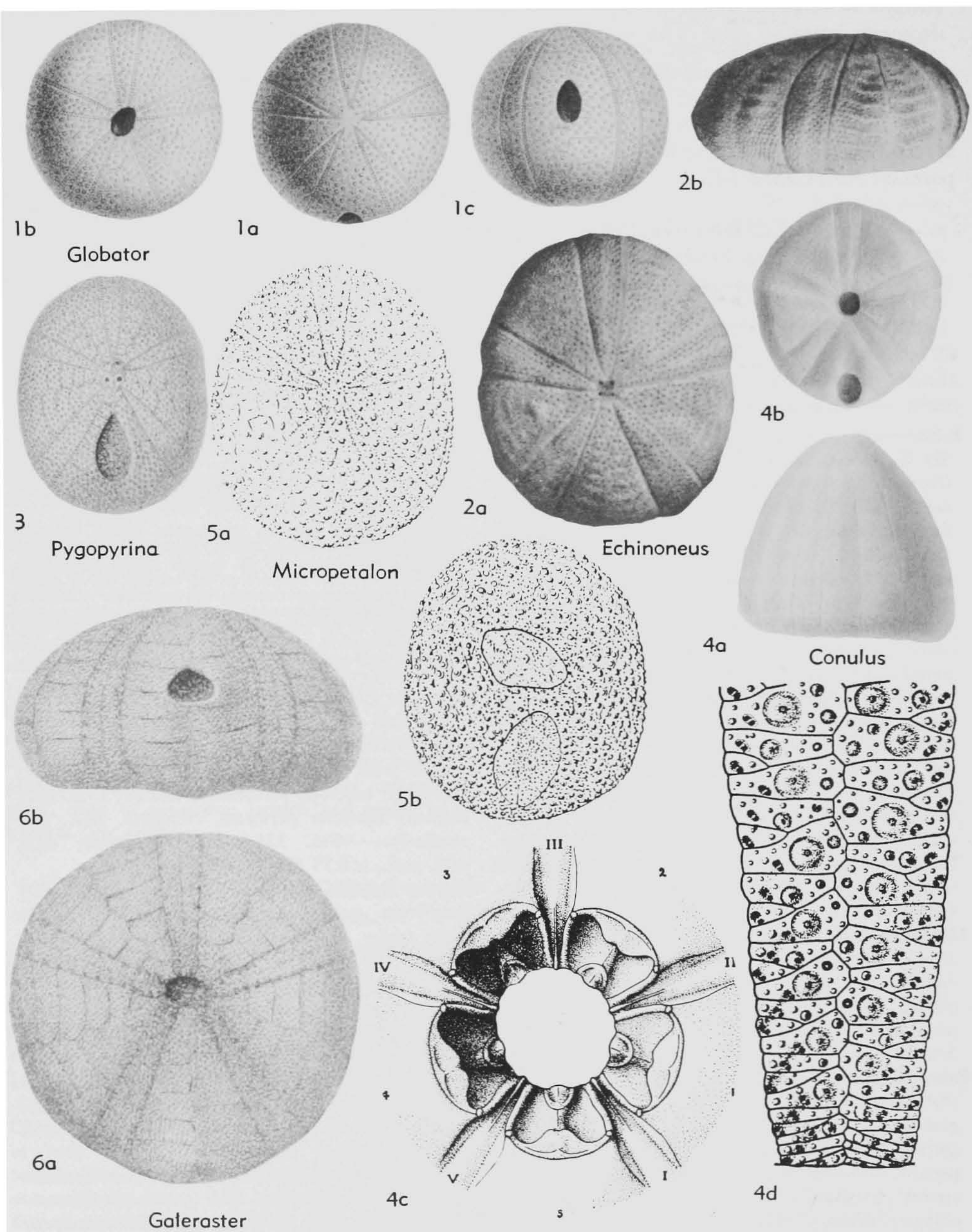

FIG. 331. Echinoneidae *(2,5)*; Conulidae *(1,3-4,6)* (p. U445-U446).

Galerites LAMARCK, 1801, p. 19 [**Echinites vulgaris* LESKE, 1778, p. 165; OD] [=*Adelopneustes* GAUTHIER, 1889, p. 52 (type, *A. lamberti* THOMAS & GAUTHIER, 1889, p. 53); *Pironaster* MUNIER-CHALMAS, 1890, p. 181 (type, *Echinoconus roemeri* D'ORBIGNY, 1855, p. 545); *Conulopsis* HAWKINS, 1912, p. 455 (obj.)]. Hemispherical to subconical; pore pairs diagonal, pores minute adorally; peristome round or pentagonal; rudimentary bourrelets present in some; periproct inframarginal, round; tubercles perforate, crenulate. *U.Cret.(Senon.)*, Eu.——FIG. 332,*1a,b*. **G. vulgaris* (LESKE), Ger.; *1a,b*, aboral, oral, ×1 (186).——FIG. 332,*1c,d*. *G. roemeri* D'ORBIGNY, Ger.; *1c,d*, details of ambulacrum, adoral, adapical, ×8 (136f).[=*Echinoconus* D'ORBIGNY, 1853, p. 29 (obj.).]

Family UNCERTAIN

Cluniaster JEANNET, 1934, p. 6 [**C. rhenanus*; OD]. Ovoid to subglobular; ambulacra of directly opposed primary plates, pore pairs uniserial; apical system unknown; indistinct branchial slits; periproct in slight groove. [Genus based on 2 poor specimens; peculiar structure possibly due to preservation.] *L.Cret.(Hauteriv.)*, Switz.——FIG. 332,*3*. **C. rhenanus*; diagram of part of ambulacrum, enlarged (198).

Mattsechinus THIÉRY in COLLIGNON & LAMBERT, 1928, p. 269 [**M. collignoni*; OD]. Globular; ambulacra of small primary plates only, pore pairs in irregular triads; periproct inframarginal; peristome somewhat sunken; tubercles perforate, in vertical series aborally. *U.Cret.(Senon.)*, Eu.(Aus.).——FIG. 332,*2*. **M. collignoni*; *2a,b*, aboral, post., ×1 (182).

Suborder CONOCLYPINA Haeckel, 1896

[*nom. correct.* DURHAM & MELVILLE, 1957, p. 256 (erroneously credited to ZITTEL, corrected on p. 270) (*pro* Conoclyparia HAECKEL, 1896, p. 486)]

Ambulacra petaloid or subpetaloid; pores of petals at least partly conjugate; auricles interradial; ornament not orderly; apical system monobasal, 4 genital pores. *U.Cret. (Senon.)-Mio.*

Family CONOCLYPIDAE Zittel, 1879

[Conoclypidae ZITTEL, 1879, p. 515]

Corona large, hemispherical; ambulacra petaloid; bourrelets conspicuous; periproct large; peristome with oral funnel; pores widely separated in petals, outer pore elongate. *Eoc.-Mio.*

Conoclypus AGASSIZ, 1839, p. 61 [**Clypeus conoideus* LESKE, 1778, p. 159; SD LAMBERT & THIÉRY, 1914, p. 286]. Test slightly elongated posteriorly,

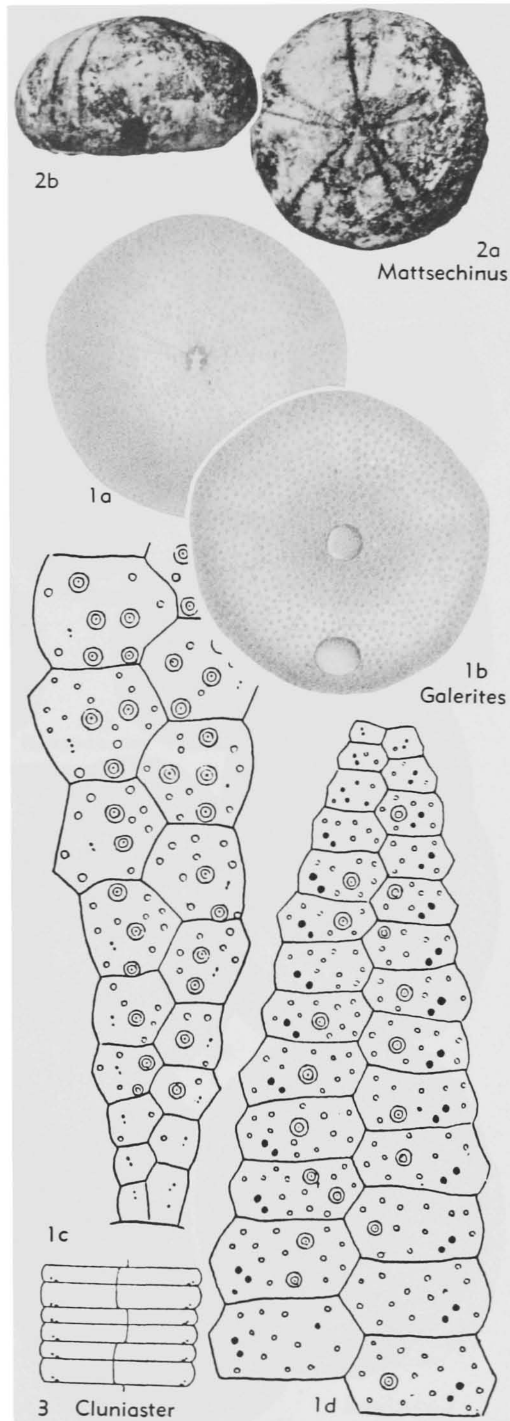

FIG. 332. Galeritidae *(1)*; Family Uncertain *(2-3)* (p. *U*447).

high, flattened orally, margin fairly sharp; ambulacral plates all primaries except near peristome, periproct inframarginal, oval; primary tubercles perforate, crenulate. *Eoc.*, Medit.-Madag.-India-?Brazil; *Mio.*, Italy.——Fig. 333,*1a,b*. **C. conoideus* (Leske), M.Eoc., Fr.; *1a,b,* aboral, oral, ×0.3 (27f).——Fig. 333,*1c,d*. *C. aequidilatatus* Agassiz, Eoc., Eu.(Aus.); *1c,* half test int. with auricles and funnel, ×0.8; *1d,* vert. sec. showing funnel and auricle, ×0.8 (52).

Oviclypeus Dames, 1877, p. 44 [**O. lorioli*; OD]. Similar to *Conoclypeus* but lower, margin more rounded; periproct marginal; outer pore only slightly larger than inner pore; petals terminate more abruptly distally. *Eoc.*, Italy.——Fig. 333,*2*. **O. lorioli*; *2a,b,* aboral, oral, ×0.3 (41).

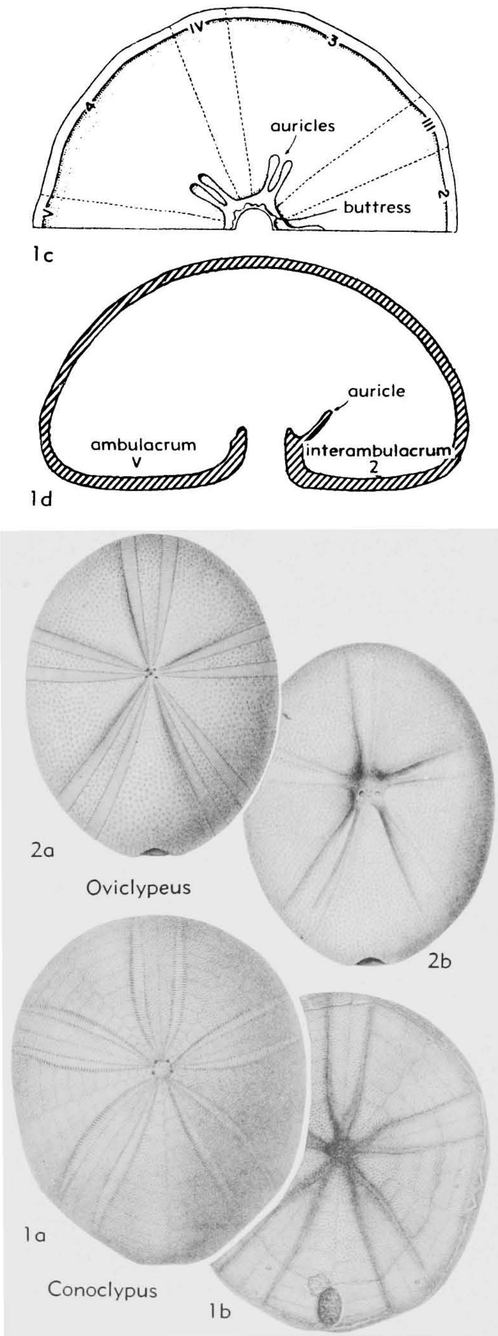

Fig. 333. Conoclypidae (p. *U*447-*U*448).

Family OLIGOPYGIDAE Duncan, 1889

[*nom. transl.* Wagner & Durham, herein (*ex* Oligopyginae Duncan, 1889, p. 173)]

Small to medium-sized; periproct small; without oral funnel; auricles partially recumbent. *U.Cret.(Senon.)-Oligo.*

Oligopygus de Loriol, 1887, p. 394 [**O. wetherbyi*; OD]. Slightly concave orally, deep depression around peristome; anterior petal usually longest, pores subequal, conjugate; apical system subcentral; periproct inframarginal; tubercles imperforate, noncrenulate. *U.Eoc.-Oligo.*, trop. Am.——Fig. 334,*5*. **O. wetherbyi,* U.Eoc., USA(Fla.); *5a-c,* aboral, oral, lat., ×0.7 (205b).

Bonaireaster Pijpers, 1933, p. 84 [**B. rutteni*; OD]. Test rounded pentagonal, orally flat; ambulacra petaloid, pores conjugate; periproct inframarginal; peristome small, round; auricles small, separate; tubercles very small, dense, deeply scrobiculate. *Eoc.*, W.Indies.——Fig. 334,*6*. **B. rutteni*; *6a,b,* aboral, oral, ×1 (215); *6c,* peristome and girdle, ×2 (52).

Haimea Michelin, 1851, p. 56 [**H. caillaud*; OD] [=*Pauropygus* Arnold & Clark, 1927, p. 30 (type, *P. platypetalus*)]. Ovoid; ambulacra subpetaloid to petaloid, pore pairs conjugate; peristome pentagonal; periproct inframarginal; tubercles numerous, small, scattered. *Eoc.*, W.Indies-Senegal.——Fig. 334,*4*. **H. caillaudi,* W.Indies; *4a-c,* aboral, oral, lat., ×1 (209).

Microlampas Cotteau, 1889, p. 101 [**M. conicus*; OD] [=*Microsoma* Cotteau, 1887, p. 7 (obj.) (*non Microsoma* Cotteau, 1886)]. Outline round, oral side flat, peristome sunken; petals long, narrow, pores subequal, faintly conjugate, from near ambitus to peristome single pores only; apical system monobasal; peristome pentagonal; periproct round, marginal. *Eoc.*, Spain.——Fig. 334,*3*. **M. conicus*; *3a,b,* aboral, post., ×1.5 (33).

Ovulechinus Lambert, 1918, p. 19 [**O. pilula*; SD Lambert, 1920, p. 4]. Ovoid to semiglobular; ambulacral slightly petaloid; periproct marginal; tubercles very small, scrobiculate. *U.Cret.(Senon.),* Fr.——Fig. 334,*1*. **O. pilula*; *1a,b,* aboral, oral, ×1 (110). [Transfer to p. *U*523.]

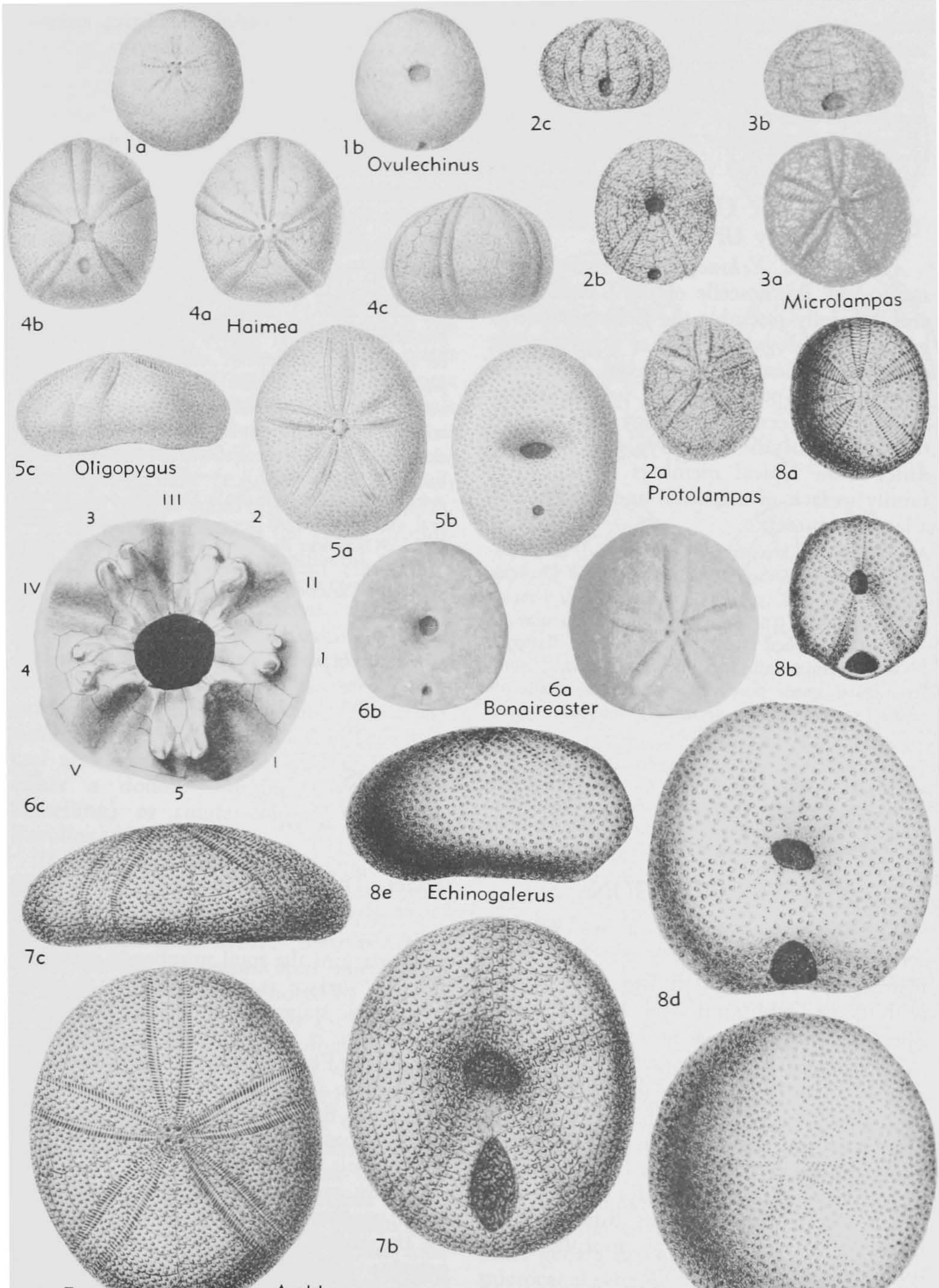

FIG. 334. Oligopygidae *(1-6)*; Family Uncertain *(7-8)* (p. U448, U450).

Protolampas LAMBERT, 1918, p. 37 [**Echinolampas arnaudi* COTTEAU, 1891, p. 155; OD]. Outline oval, oral side pulvinate; pores conjugate, outer pore elongate; apical system anterior; periproct marginal. *Paleog.(Dan.)*, Fr.——FIG. 334,2. **P. arnaudi* (COTTEAU); *2a-c*, aboral, oral, post., ×1 (136f).

Suborder UNCERTAIN

Family UNCERTAIN

Amblypygus, Echinogalerus, and *Rhopostoma* lack the floscelle of the Cassiduloida and generally resemble the Echinoneidae in gross morphology and lack of a lantern but differ from them in having the ambulacra more or less petaloid. The petaloid character and general morphology also suggest *Oligopygus* of the Oligopygidae, but they differ from typical members of the latter family in lack of a lantern and presence of a large periproct.

Amblypygus L. AGASSIZ, 1840, p. 5, 17 [**A. dilatatus* AGASSIZ & DESOR, 1847, p. 167; SD DUNCAN & SLADEN, 1883, p. 15] [=*Semiclypeus* EYMAR, 1898, p. 48 (type, *S. pretiosus*)]. Circular to ovate, low-arched to high subconical, flattened orally, margin tumid; ambulacra petaloid, pores conjugate, outer pore elongate, pores small adorally; apical system apparently tetrabasal; peristome sunken, subrounded to oblique; periproct large, pyriform, inframarginal; tubercles perforate, crenulate; no evidence of girdle or lantern in adult. *Eoc.-Oligo.*, Circummedit.-Madag.-India-W.Indies-USA(Fla.-Calif.).——FIG. 334,7. **A. dilatatus* (AGASSIZ & DESOR), Eoc., Fr.; *7a-c*, aboral, oral, profile views, ×1 (27e).

Echinogalerus KÖNIG, 1825, p. 171 [**Echinites peltiformis* WAHLENBERG, 1818, p. 49; SD LAMBERT, 1897, p. 20] [=*Caratomus* L. AGASSIZ, 1840, p. 7, 16 (type, *Catopygus avellana* DUBOIS, 1843, pl. 1, fig. 19-21) (=*Caratomella* STRAND, 1928, p. 38, *nom. subst.*)]. Small, outline round or oval, low-arched aborally, slightly convex orally, may be subrostrate posteriorly; ambulacra subpetaloid, pores not conjugate, pore pairs uniserial throughout; apical system tetrabasal; periproct subtriangular or transverse oval, inframarginal; peristome elongate or oblique. *U.Cret.(Cenoman.-Senon.)*, Eu.-N. Am.(Baja Calif.).——FIG. 334,*8a,b*. **E. peltiformis* (WAHLENBERG), Sweden; *8a,b*, aboral, oral views, ×1 (142).——FIG. 334,*8c-e*. *E. truncatus* D'ORBIGNY; *8c-e*, aboral, oral, profile views, ×2.5 (142). [=*Rostrogalerus* LAMBERT, 1911, p. 30 (type, *Caratomus rostratus* DESOR, 1842, p. 38; OD).]

Rhopostoma COOKE, 1959, p. 26 [**Ananchytes cruciferns* MORTON, 1830, p. 245; OD]. Like *Echinogalerus* except periproct supramarginal. *Paleoc.*, USA.

CLYPEASTEROIDS

By J. WYATT DURHAM
[University of California (Berkeley)]

INTRODUCTION

The clypeasteroids are a well-circumscribed group of echinoids that live on or beneath the surface of the sea floor, largely within the sublittoral and littoral zones. Species that live in a horizontal position are approximately symmetrical. A few species typically live in an inclined position with the anterior part of the test buried in sediments and the posterior part projecting above the floor. Such species (e.g., *Dendraster excentricus* and rotulinids) have the anterior and posterior regions differentiated, either in symmetry or by morphological modifications.

The shape of the test varies from ovoid (e.g., *Fibularia*), to campanulate (e.g., *Clypeaster*), to discoid (e.g., *Clypeaster, Dendraster*). Internal supports are most highly developed in extremely flattened species. The ambitus in the flattened genera varies from rounded (e.g., *Laganum*) to acute (e.g., *Echinodiscus*). In species with acute margins the total number of plates on the oral surface is established at an early ontogenetic stage, and thereafter growth on this surface is by enlargement of pre-existing plates (Fig. 335). On the aboral surface new plates are added throughout life and it appears that relative ages can be established by comparing numbers of plates within the petals (51).

During ontogeny the plates, particularly those on the oral surface and marginally on the aboral surface, may change shape greatly. These changes are greatest in the highly flattened species and least in those with ovoid tests. They are necessitated by the change from the immediate post-metamorphosis depressed spherical test to a discoidal test.

The petals (Fig. 336,*1*) are restricted to the aboral surface and distally they vary from wide open to closed. Within the petals all plates may be primaries (Fig. 336,*2*) or they may include both demiplates (Fig. 336,*3*) and primaries. Inasmuch as groups of primary and demiplates are not bound together by a single large primary tubercle as in regular echinoids, this condition is here termed **pseudocompound.** Although sutures between most plates are normal to the surface, the adradial suture around the petals is inclined, with ambulacral plates overlapping the interambulacral. The pores for the respiratory tube feet within the petals are always paired. They are simple in some genera (e.g., *Echinocyamus*), but in more specialized genera (e.g., *Encope, Scutella*) the outer pore is subdivided (see Fig. 337).

In some clypeasteroids the single primordial (basicoronal) interambulacral plate is separated from subsequent interambulacrals by enlargement of adjacent ambulacral plates during ontogeny (Fig. 335). Once developed, this condition (discontinuous interambulacra) is characteristic of a given stock and persistent in adults (Fig. 338). Adapically, the clypeasteroid interambulacral area may terminate (see Fig. 339) in either a double column (Clypeasterina, Scutellina) or single column (Laganina, Rotulina) of plates.

The distribution, occurrence, and character of the clypeasteroid accessory tube feet (see Fig. 340, 341), except in the family Arachnoididae where they occur in bands parallel to conspicuous linear rows of tubercles, have been ignored by most investigators, with the notable exceptions of Mortensen, Lovén, and Nichols. The size of the pores for these tube feet varies greatly, even in the same species (see Fig. 340,*6*), but they are invariably smaller than pores for the respiratory tube feet. Their distribution varies greatly, but has not been systematically studied. They are present within and around the petals in many groups (see Fig. 340,*1,5,7*) but are absent in this area in the family Mellitidae (see Fig. 341,*1a*). Preliminary surveys appear to indicate that their distribution is significant at all taxonomic levels, including species.

Although poorly known, an interconnected system of canals occurs in the interior of both ambulacral and interambulacral plates of many genera. Schaffer (150) has described this system in some species of *Scutella* and named it the **microcanal system** (see Fig. 342). Unpublished observations by Wagner on *Encope* show that these canals are occupied by extensions of the coelomic cavity and that branches of the water-vascular system leading to the accessory tube feet ramify through them; also, the ampullae for these tube feet are suspended within them. It seems probable that the "double wall" of the test present in some species of *Clypeaster* and a few other genera is another modification of this microcanal system.

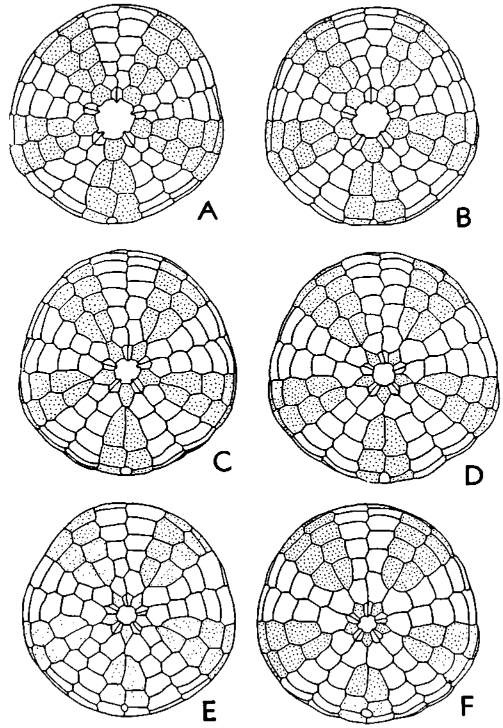

Fig. 335. *Dendraster excentricus* (Eschscholtz). Ontogeny of oral surface. Growth series from diameter of 4 mm. *(A)* to 21 mm. *(F)* enlarged to standard size to show changes in shape and relationships of plates produced by differential peripheral growth of plates (51).

Internal supports of the test are absent in *Fibularia,* but in flattened genera they may be exceedingly complex in distribution and construction. Schaffer (150) has termed the resulting pattern of internal cavities between the upper and lower walls of the test the **macrocanal system.** He has also provided a detailed system of nomenclature for ramifications of both canal systems.

No resorption occurs around the peristome, and as a result, the primordial plates are also the basicoronal plates. Within the different stocks development of the primor-

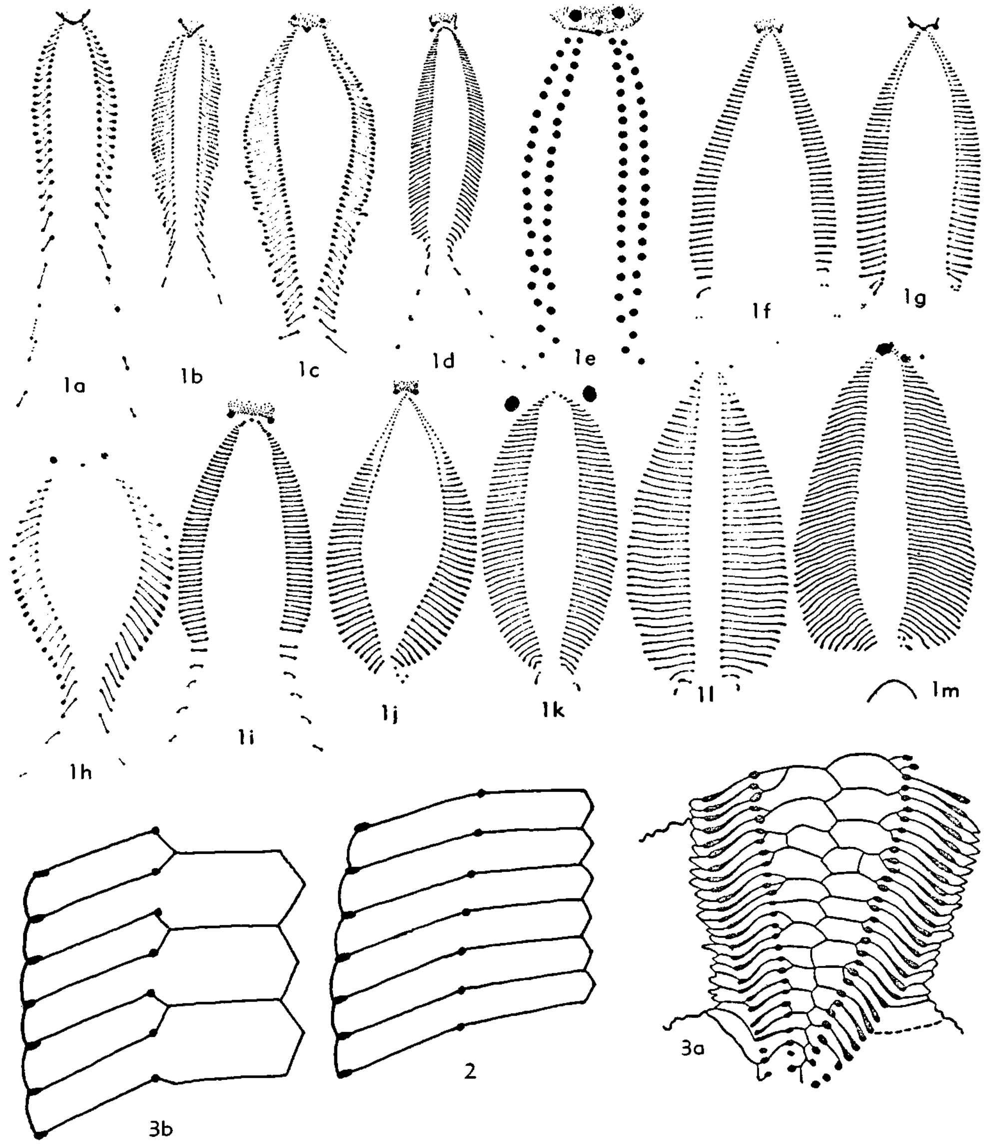

FIG. 336.——*1.* Morphology of clypeasteroid petals: *1a, Heliophora orbiculus* (LINNÉ), amb III (×2.8); *1b, Rotula deciesdigitata* (LESKE), amb V (×1.8); *1c, Laganum laganum* (LESKE), amb II (×2.4); *1d, Dendraster excentricus* (ESCHSCHOLTZ), amb IV (×0.9); *1e, Mortonia australis* (DESMOULINS), amb IV (×8.6); *1f, Fellaster zelandiae* (GRAY), amb IV (×2.1); *1g, Clypeaster ravenelii* (A. AGASSIZ), amb IV (×1.0); *1h, Jacksonaster depressum* (LESSON), amb IV (×2.3); *1i, Echinarachnius parma* (LAMARCK), amb IV (×2.3); *1j, Clypeaster prostratus* (RAVENEL), amb IV (×1.9); *1k, Leodia sexiesperforata* (LESKE), amb IV (×2.5); *1l, Mortonella quinquefaria* (SAY), amb IV (×2.5); *1m, Astriclypeus manni* (VERRILL), amb I (×1.7) (51).——*2.* Diagram of primary plates in petal of laganid clypeasteroid (136g).——*3.* Diagram of pseudocompound plates in petals of clypeasteroids; *3a,* neolaganid *(Weisbordella)*; *3b,* clypeasterid *(Clypeaster)* (*3a,* 51; *3b,* 136g).

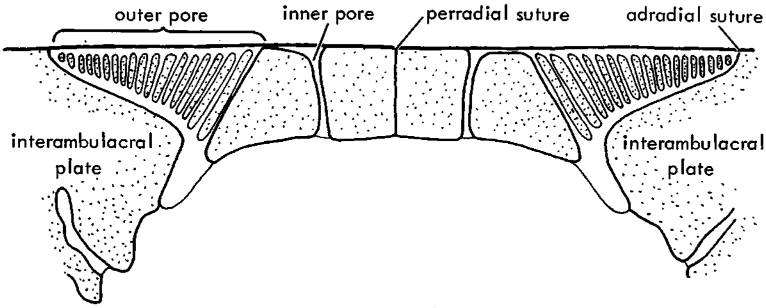

FIG. 337. Cross section of pores for respiratory tube feet in *Scutella* (after SCHAFFER, 217).

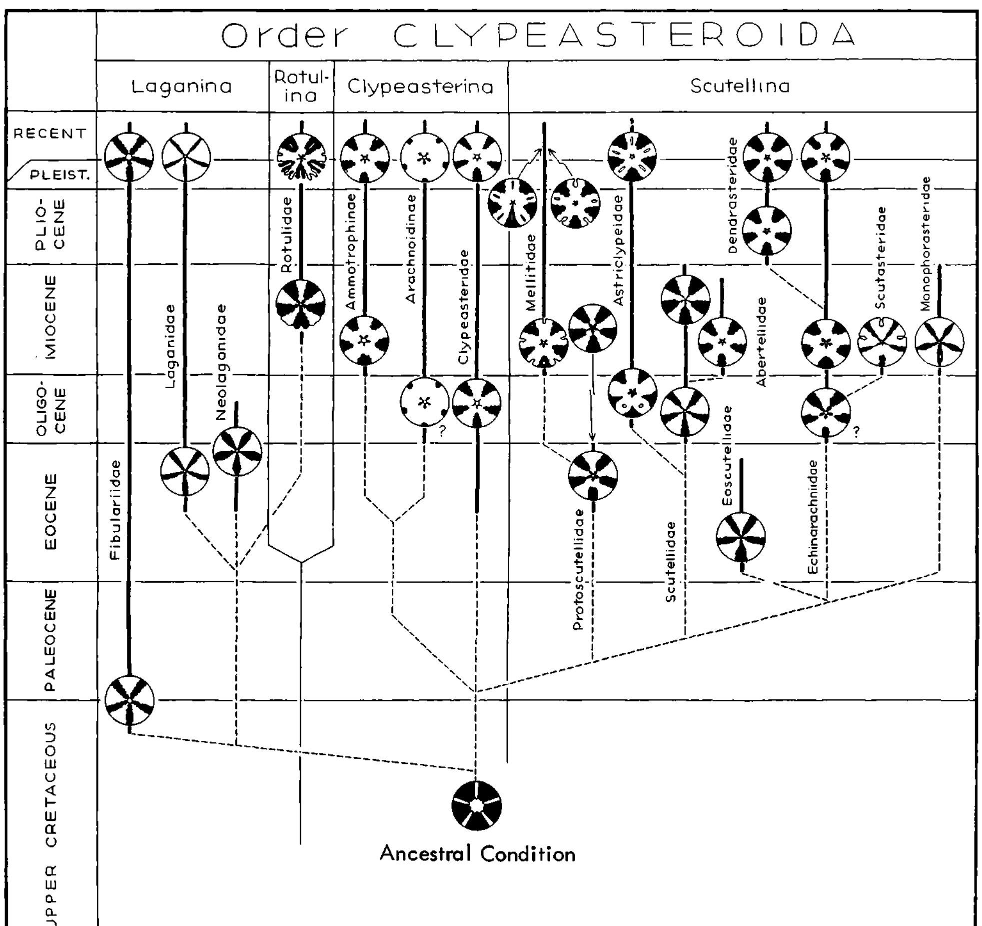

FIG. 338. Evolution of interambulacra on oral surface of Clypeasteroida. Interambulacra in black; vertical spacing proportional to time except for Pleistocene (Durham, n).

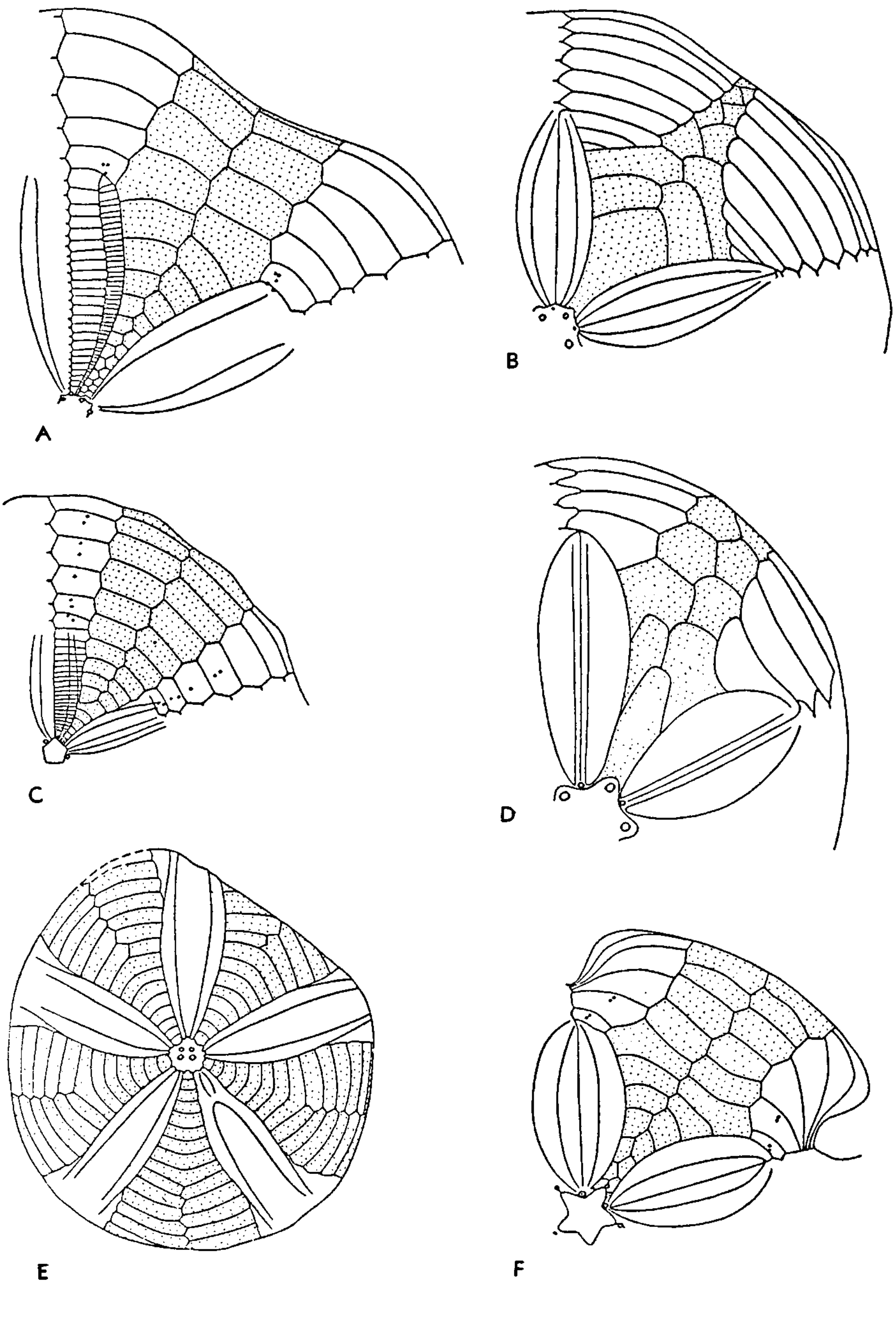

FIG. 339. Apical termination of clypeasteroid interambulacra (enlarged): *A, Clypeaster ravenelii* (A. AGASSIZ), Recent, Gulf of Mexico; *B, Laganum laganum* (LESKE), Recent, New Hebrides; *C, Heliophora orbiculus* (LINNÉ), Recent, Loanda, Angola; *D, Sanchezella sanchezi* (LAMBERT), upper Eocene, Cuba; *E, Tarphypygus clarki* (LAMBERT), upper Eocene, Cuba; *F, Encope grandis* L. AGASSIZ, Recent, Gulf of California. Interambulacral areas stippled (51).

dial plates is very characteristic. The arrangement in *Echinocyamus* (see Fig. 343, *1a*) and other fibulariids is primitive and reminiscent of that in regular echinoids. Among clypeasterids the primordial ambulacral plates (see Fig. 344,*1*,*2*) are much larger than the interambulacral plates, but in remaining families the trend is toward increasing size of the interambulacral plate. In the astriclypeid genus *Amphiope* (see Fig. 345,*4*) the size relationships are almost completely reversed from those in *Cly-*

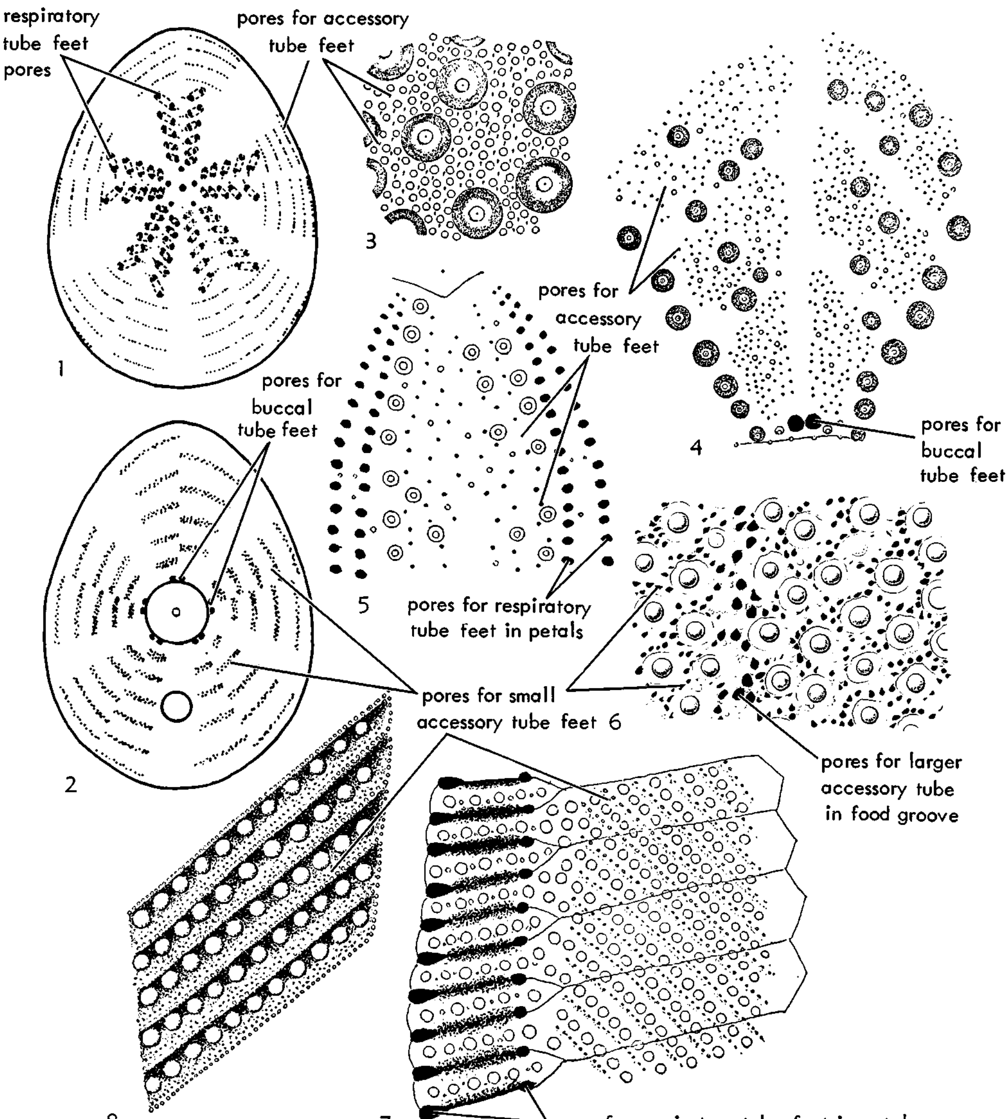

FIG. 340. Pores for accessory tube feet in Clypeasteroida (pores in black): *1,2, Echinocyamus pusillus* (MÜLLER), aboral, oral, ×9 (211a); *3, Clypeaster ochrus* CLARK, adorally, interambulacrum 5, ×18 (136g); *4,5, Laganum laganum* (LESKE), adapical and adoral ends of ambulacrum, ×15 (136g); *6, Leodia sexiesperforata* (LESKE), portion of interambulacrum, including branch of food groove, on oral surface, ×50 (Durham, n); *7,8, Arachnoides placenta* (LINNÉ), "combed" area in petal, oral "combed" area, ×20 (136g).

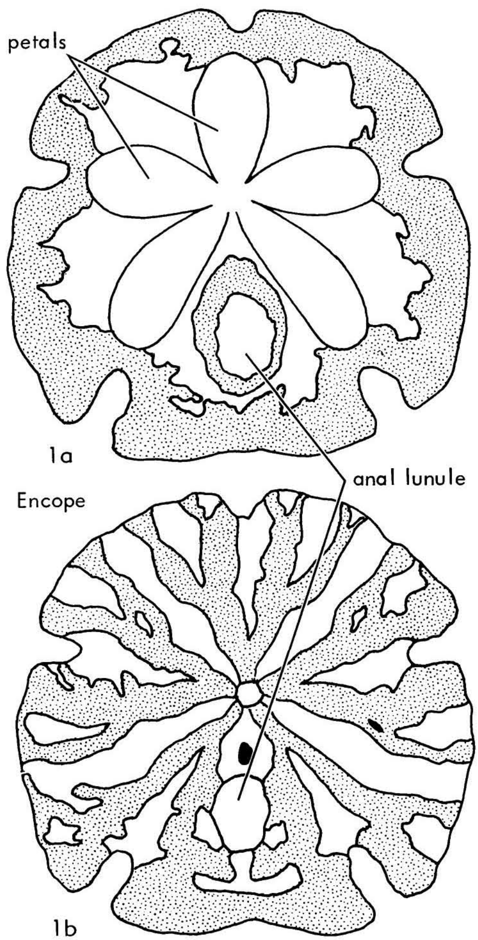

FIG. 341. *1a,b, Encope grandis* AGASSIZ, aboral and oral surfaces, showing distribution (stippled areas) of accessory tube feet, ×0.67 (Wagner, n).

FIG. 342. Microcanal system in interambulacral and adjacent ambulacral plates on oral side of *Scutella vindobonensis secunda* SCHAFFER, ×0.7 (217).

peaster. In all groups except the rotulinids only the usual ten ambulacral and five interambulacral basicoronal plates are present, but in the Rotulina 20 plates occur (see Fig. 344,*4*). Seemingly, one of the first postprimordial plates here has become incorporated into the row around the peristome. The means by which this insertion occurs has not yet been studied, but examination of an ontogenetic sequence should furnish the necessary information.

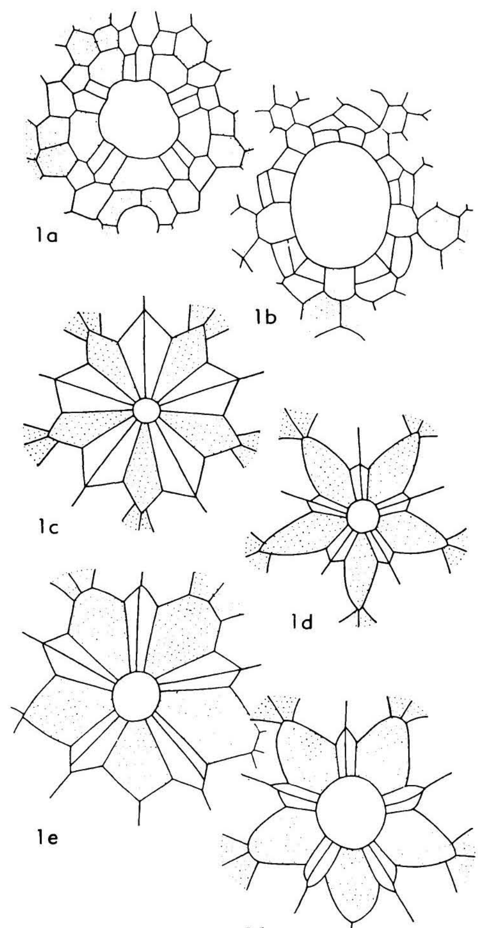

FIG. 343. Clypeasteroid basicoronal plates (enlarged): *1a, Echinocyamus pusillus* (MÜLLER), Recent, Europe; *1b, Tarphypygus clarki* (LAMBERT), upper Eocene, Cuba; *1c, Scutella subrotunda* (LESKE), "Oligo-Miocene," Malta; *1d, Periarchus lyelli pileussinensis* (RAVENEL), upper Eocene, Georgia; *1e, Remondella gabbii* (RÉMOND), upper Miocene, California; *1f, Astrodapsis brewerianus* (RÉMOND), upper Miocene, California. Interambulacral plates stippled (51).

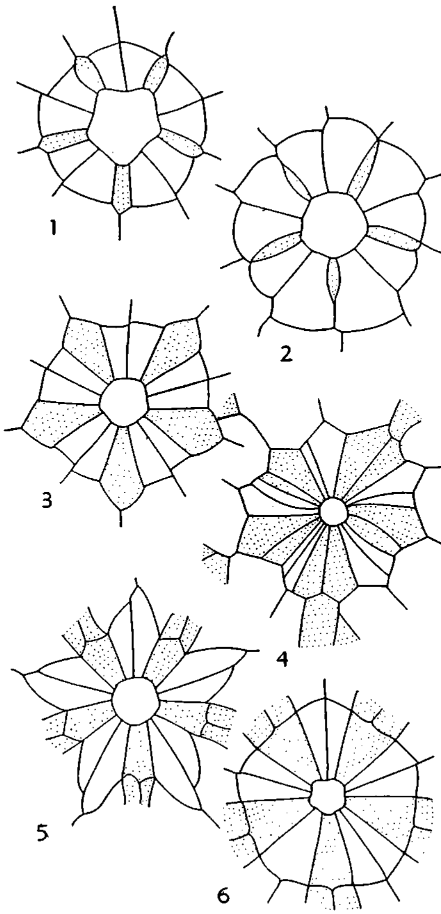

Fig. 344. Clypeasteroid basicoronal plates (enlarged): *1, Clypeaster rosaceus* (Linné), Recent, Florida; *2, Clypeaster reticulatus* (Linné), Recent, Philippine Islands; *3, Arachnoides placenta* (Linné), Recent, east coast of Sumatra; *4, Heliophora orbiculus* (Linné), Recent, Loanda, Angola; *5, Laganum laganum* (Leske), Recent, New Hebrides; *6, Neolaganum archerensis* (Twitchell), upper Eocene, Florida. Interambulacral plates stippled (51).

The periproct varies in position from supramarginal to close to the peristome (Fig. 346). Food grooves (Fig. 347) leading to the peristome are absent in a few fibulariids and clypeasterids but become exceedingly complex and well marked in scutellinids. Their presence is apparently correlated with the development of numerous small accessory tube feet outside the petals as a food-gathering mechanism.

The primary spines (see Fig. 348) vary from very dense to scattered, but all adults have several to a plate. Terminally the spines may be either pointed or club-shaped, the latter type producing a mosaic pavement effect in some forms (Fig. 349). The primary spines are usually longer on the oral surface. The miliary spines (see Fig. 350) are smaller and shorter and of considerable value in recognition of suborders.

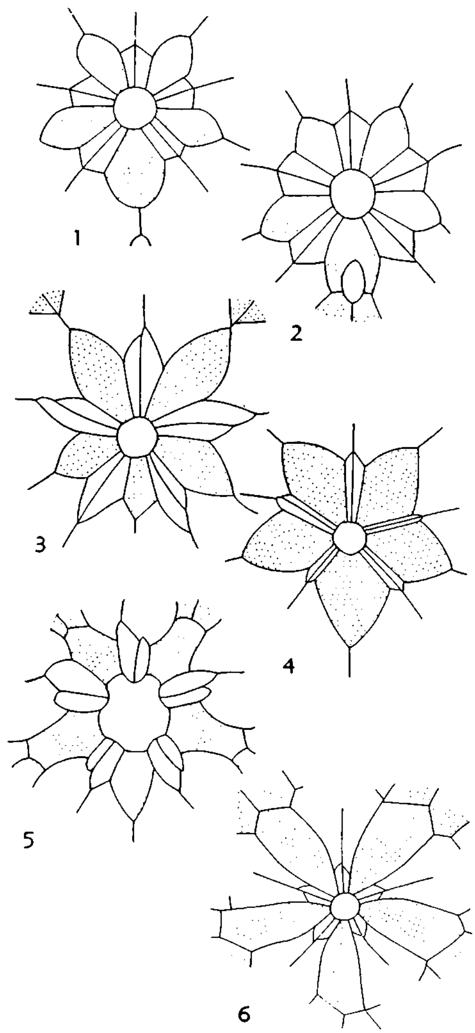

Fig. 345. Clypeasteroid basicoronal plates (enlarged): *1, Encope emarginata* (Leske), Recent, Gulf of Mexico; *2, Mellita quinquiesperforata* (Leske), Recent, Gulf of Mexico; *3, Vaquerosella vaquerosensis* (Kew), lower Miocene, California; *4, Amphiope bioculata* (Desmoulins), Miocene, Europe; *5, Pseudoastrodapsis nipponicus* (Nisiyama), "Mio-Pliocene," Japan; *6, Eoscutella coosensis* (Kew), upper Eocene, Oregon. Interambulacral plates stippled (51).

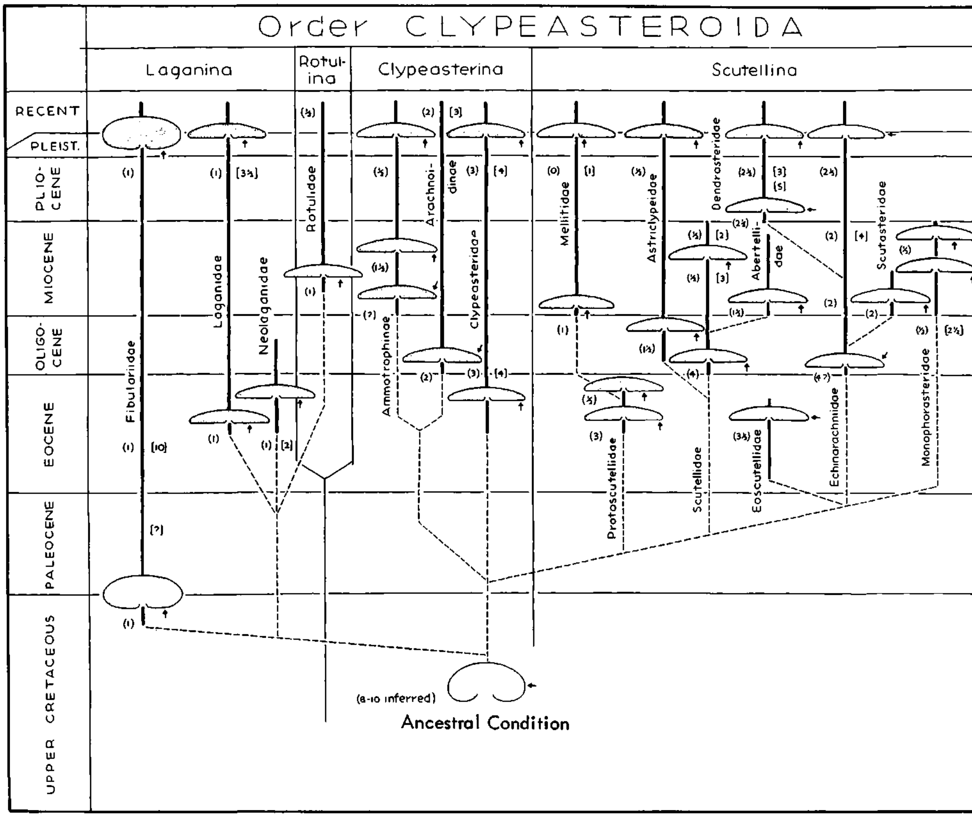

FIG. 346. Evolution of periproct position in Clypeasteroida. Diagrammatic profiles with position of periproct indicated by arrow. Minimum (in parentheses) and maximum (in brackets) numbers of plates between periproct and primordial plates indicated for each; vertical spacing proportional to time except for Pleistocene (Durham, n).

In cross section the primary spines have a hollow axis and are quite diverse in their structure (see Fig. 351). Pedicellariae (see Fig. 352) include tridentate, ophicephalous, triphyllous, and globiferous types. The last-named type has been recorded only in the genus *Fibulariella.* The tubercles for attachment of the primary spines are usually perforate and crenulate, but it is difficult to determine their character on many minute species.

Internally, the auricles (see Fig. 353) for attachment of muscles from the lantern are separate as in most echinoids and rest on the margins of the primordial ambulacral plates in the Clypeasterina (see Fig. 353, *3,5,6*) but are fused together forming one process and rest on the primordial interambulacral plates in the remaining suborders (see Fig. 353,*1,2,4,7,8*).

Characteristic calcareous spicules and plates of various sorts (Fig. 354) are present in the tube feet, internal organs, and periproctal region and on the buccal membrane, but have not yet been reported as fossils.

As recorded to date, clypeasteroid genera increase in abundance from two in the latest Cretaceous to a maximum of 36 in Miocene and then wane to the 24 currently recognized in the living fauna (see Fig. 355). Knowledge of the group in temperate latitudes of the southern hemisphere is very limited.

The group seems to have been derived from some member of the suborder Holectypina in the Late Cretaceous. The clypeasteroid species (of *Fibularia* and *Echinocyamus*) reported from the late Senonian already have the periproct in a specialized

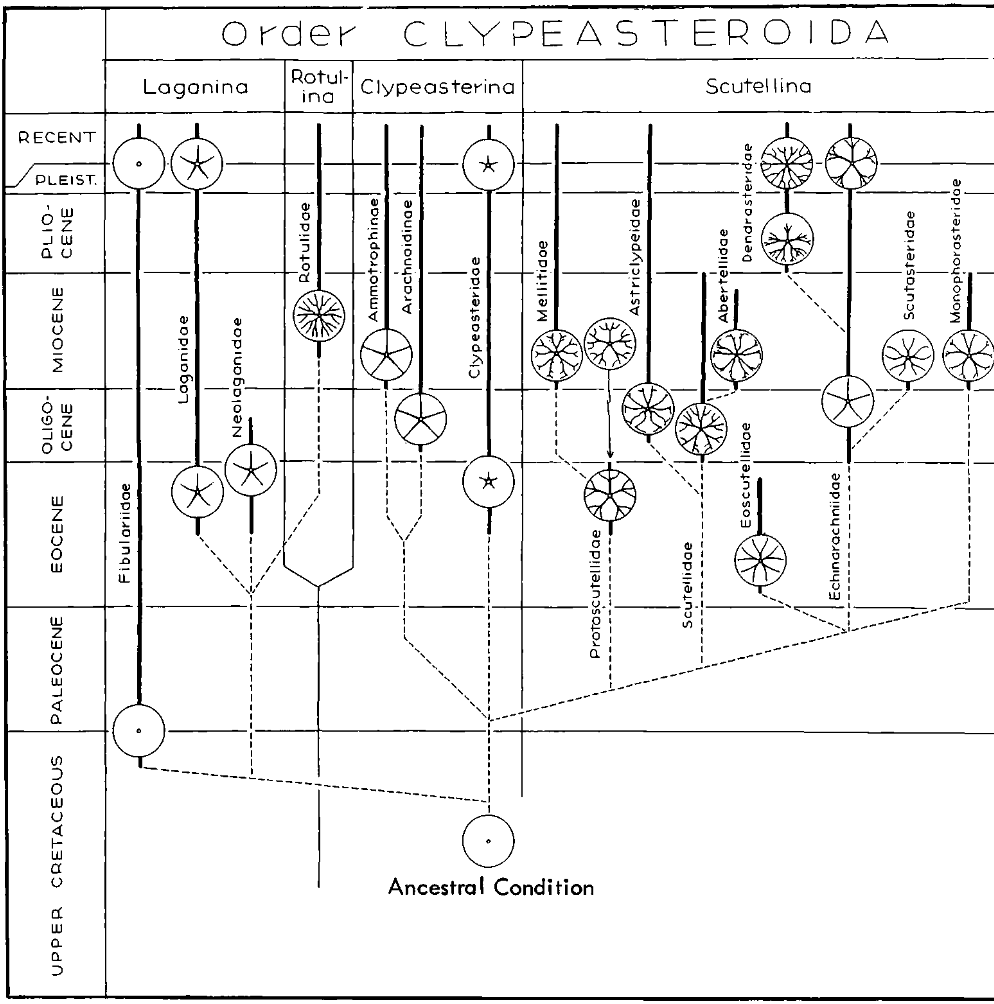

FIG. 347. Development and evolution of food grooves on oral surface in Clypeasteroida. Vertical spacing proportional to time except for Pleistocene (Durham, n).

position and presumably have only a single interambulacral plate adapically, thus indicating that more primitive genera are to be searched for in the Cretaceous.

The inferred phylogeny of the group indicates that three of the four suborders were already very distant from one another by mid-Eocene time (see Fig. 356). The fibulariids, often considered to represent the ancestral stock of other clypeasteroids, are primitive in most characters but have fused auricles and the periproct in a specialized (adoral) position by the latest Cretaceous and thus the known members cannot be ancestral to other groups where these characters are less advanced. This interpretation implies that members of the suborders Clypeasterina and Scutellina, as well as less specialized laganinids, are still to be discovered and that many of the intermediates between these groups are still unknown. The Late Cretaceous and Paleocene are intervals that should be particularly rewarding in the search for these "missing links."

Members of this order have been considered in detail by L. AGASSIZ (1841), DURHAM (1955), LAMBERT & THIÉRY (1909-1925), and MORTENSEN (1948). A previously unrecognized morphological feature (the microcanal system) was recently described by SCHAFFER (1962).

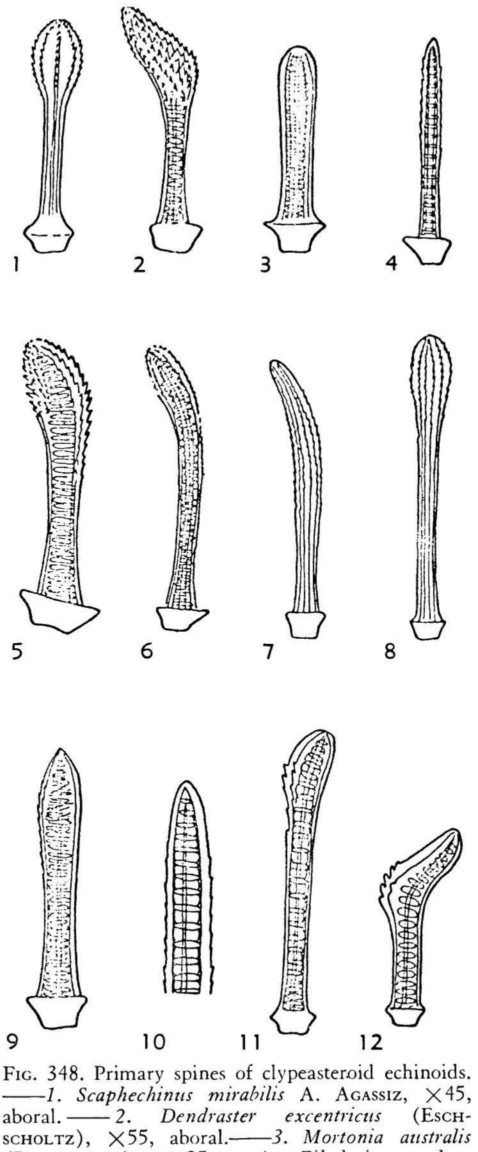

FIG. 348. Primary spines of clypeasteroid echinoids.——*1. Scaphechinus mirabilis* A. AGASSIZ, ×45, aboral.——*2. Dendraster excentricus* (ESCHSCHOLTZ), ×55, aboral.——*3. Mortonia australis* (DESMOULINS), ×25.——*4. Fibularia ovulum* LAMARCK, ×45.——*5. Echinodiscus bisperforatus* LESKE, ×80, aboral.——*6. Echinodiscus bisperforatus* LESKE, ×80, oral.——*7. Arachnoides placenta* (LINNÉ), ×40, interambulacral.——*8. Arachnoides placenta* (LINNÉ), ×55, from combed area.——*9. Clypeaster rotundus* (A. AGASSIZ), ×55, aboral.——*10. Jacksonaster depressum* (LESSON), ×100, point only.——*11. Heliophora orbiculus* (LINNÉ), ×75, aboral.——*12. Rotula deciesdigitata* (LESKE), ×75, aboral (51, after 136g).

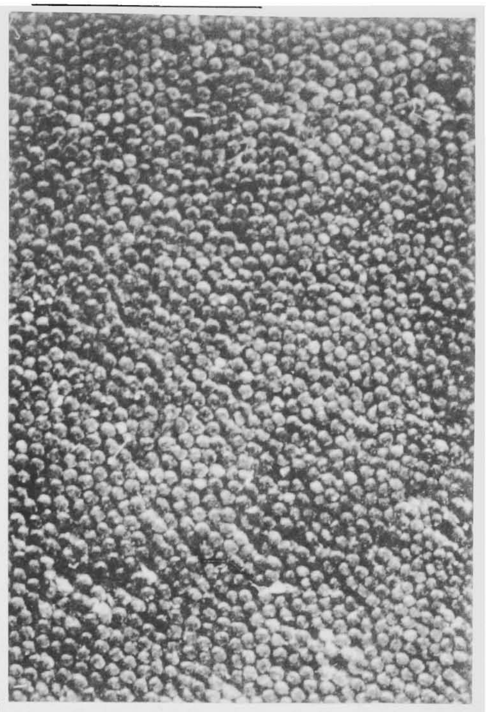
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FIG. 349. Mosaic pavement effect produced by enlargement of tip of spines in *Encope wetmorei* CLARK (180).

Order CLYPEASTEROIDA A. Agassiz, 1872

[*nom. transl.* DURHAM & MELVILLE, 1957, p. 259 (*ex* suborder Clypeastridae A. AGASSIZ, 1872, p. 304, 375)]

Test ovoid to flattened, with petaloid ambulacra invariably as wide or wider than interambulacra on oral surface; genital plates fused; primary tube feet respiratory, restricted to petals; accessory tube feet numerous, extending outside petals, in some forms reaching into interambulacra; peristome small, no gill slits; lantern without compass, teeth without lateral flanges; test usually with internal supports; spines small, short, numerous, of two types; pedicellariae tridentate, ophicephalous, triphyllous, and globiferous. *U.Cret.(Maastricht.)-Rec.*

Suborder CLYPEASTERINA A. Agassiz, 1872

[*nom. correct.* DURHAM & MELVILLE, 1957, p. 259 (*pro* suborder Clypeastridae AGASSIZ, 1872, p. 304, 375)]

Test with internal supports; petals with pseudocompound plates; interambulacra

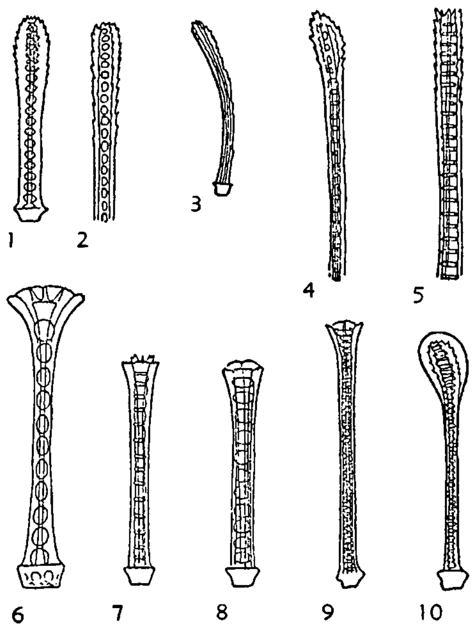


FIG. 350. Miliary spines of clypeasteroids (51, after 136g).——*1,2. Clypeaster*; *1, C. japonicus* DÖDERLEIN, ×55; *2, C. rotundus* (A. AGASSIZ), ×65.——*3. Arachnoides placenta* (LINNÉ), ×55.——*4. Scaphechinus mirabilis* A. AGASSIZ, ×100, aboral.——*5. Echinarachnius parma* (LAMARCK), ×100, aboral.——*6. Peronella japonica* MORTENSEN, ×150.——*7. Fibularia ovulum* LAMARCK, ×105.——*8. Mortonia australis* (DESMOULINS), ×105.——*9. Heliophora orbiculus* (LINNÉ), ×75.——*10.* Scutellinid, ×75.

discontinuous, terminated adapically by pair of plates; apical system pentagonal or stellate, apices interambulacral; auricles separate; aboral miliary spines simply pointed. *U.Eoc.-Rec.*

The petals consist of regularly alternating primary plates and demiplates. The primordial interambulacral plate is separated from the younger plates by one and a half or more pairs of adjacent ambulacral plates. The earliest known species (Auversian) have discontinuous interambulacra, while all possible ancestors have continuous interambulacra, indicating that intermediate species are yet to be found.

The known Arachnoididae (except *Fossulaster*) have the pores for accessory tube feet outside the petals arranged in linear groups (Fig. 340,7-8), alternating with rows of tubercles, producing a characteristic "combed" effect.

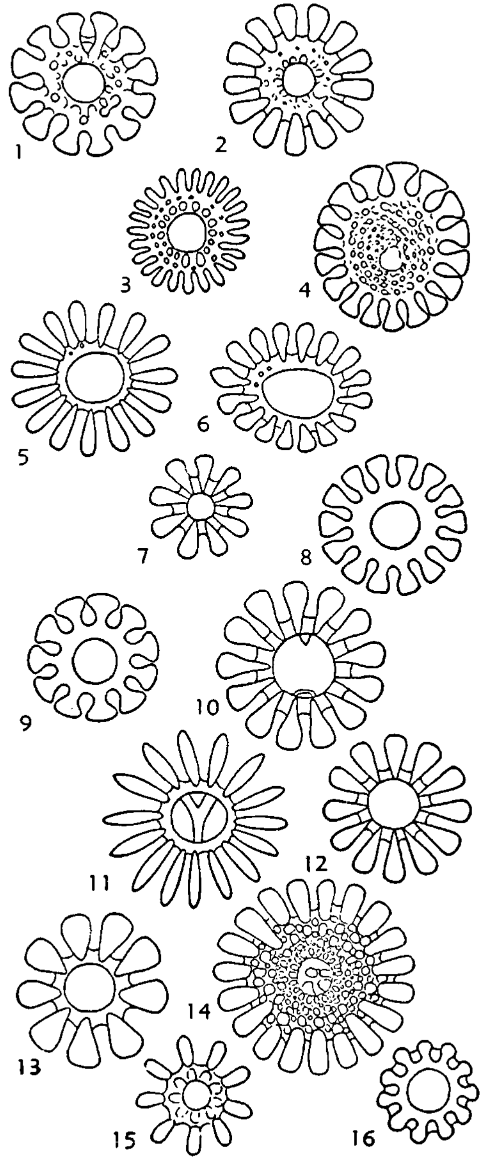


FIG. 351. Primary spines of clypeasteroid echinoids in cross section.——*1-4. Clypeaster reticulatus* (LINNÉ), ×150; *C. humilis* (LESKE), ×105; *C. annandalei* KOEHLER, ×90; *C. lamprus* H. L. CLARK, ×80.——*5. Arachnoides placenta* (LINNÉ), ×135.——*6. Fellaster zelandiae* (GRAY), ×135.——*7. Mortonia australis* (DESMOULINS), ×180.——*8. Jacksonaster depressum* (LESSON), ×180.——*9. Hupea decagonalis* (LESSON), ×180.——*10. Dendraster excentricus* (ESCHSCHOLTZ), ×150.——*11. Scaphechinus mirabilis* A. AGASSIZ, ×150.——*12. Echinarachnius parma* (LAMARCK), ×150.——*13. Heliophora orbiculus* (LINNÉ), ×275.——*14-15. Clypeaster rosaceus* (LINNÉ), ×65; *C. humilis* (LESKE), ×140, aboral.——*16. Peronella japonica* MORTENSEN, ×150.

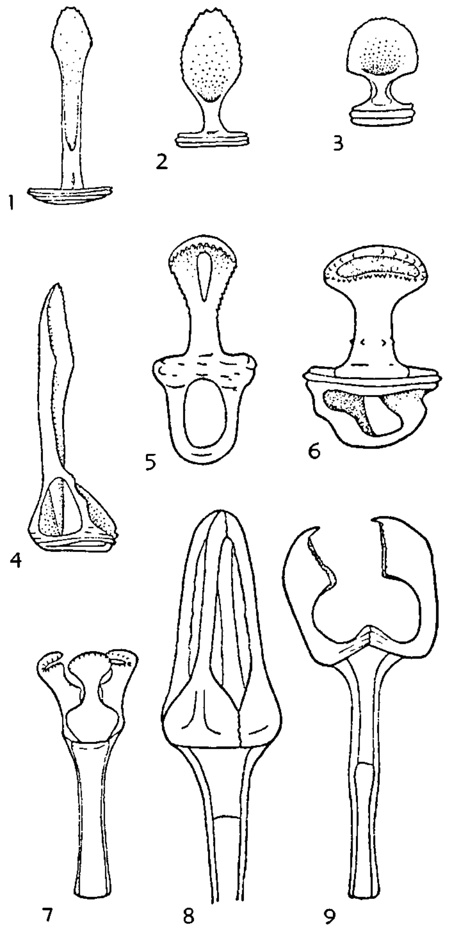


FIG. 352. Pedicellariae of clypeasteroid echinoids (51, after 136g).——*1. Jacksonaster depressum* (LESSON), ×80.——*2. Laganum fudsiyama* DÖDERLEIN, ×125.——*3,4. Clypeaster australasiae* (GRAY), ×180; *C. fervens* KOEHLER, ×42.——*5. Laganum dickersoni keiense* MORTENSEN, ×125.——*6-8. Clypeaster australasiae* (GRAY), ×180; *C. rarispinus* DE MEIJERE, ×70; *C. subdepressus* GRAY, ×27.——*9. Leodia sexiesperforata* (LESKE), ×160. [Figs. *1, 4, 8,* tridentate; *2, 3,* triphyllous; *5-7,* ophicephalous; *9,* "bidentate"; *1-6,* single valves; *7-9,* complete valves; *8,* 4-valved, tridentate type.]

Family CLYPEASTERIDAE L. Agassiz, 1835

[*nom. correct.* D'ORBIGNY, 1851, p. 121 (*pro* Clypèastres L. AGASSIZ, 1835, p. viii)]

Five genital pores; food grooves simple, poorly defined; buccal membrane naked; primordial interambulacral plates usually greatly reduced; no "combed" areas. *U.Eoc.(Auvers.)-Rec.*

Clypeaster LAMARCK, 1801, p. 341 [**C. rosaceus* (=**Echinus rosaceus* LINNÉ, 1758, p. 665); SD DESMOULINS, 1835, p. 183] [=*Scutum* SCHUMACHER, 1817, p. 33 (obj.); *Echinanthus* GRAY, 1825, p. 427 (*non* LESKE, 1778) (obj.); *Nyctimene* GISTL, 1848, p. 175 (*non* BORKHAUSEN, 1797; *nec* MORRIS, 1837) (obj.); *Rhaphidoclypus* A. AGASSIZ, 1863, p. 25 (type, *R. scutiformis* A. AGASSIZ, =*Echinus reticulatus* LINNÉ, 1758, p. 666; SD LAMBERT & THIÉRY, 1914, p. 301); *Stolonoclypus* A. AGASSIZ, 1863, p. 25 (type, *S. placunarius* A. AGASSIZ, =*Echinanthus humilis* LESKE, 1778, p. 185; SD LAMBERT & THIÉRY, 1914, p. 301); *Alexandria* PFEFFER, 1881, p. 63 (type, *A. magnifica*); *Echinorodorum* POMEL, 1883, p. 68 (obj.); *Pavaya* POMEL, 1883, p. 68 (type, *Clypeaster corwini* PAVAY, 1874, p. 98); *Anomalanthus* BELL, 1884, p. 43 (type, *Echinanthus tumidus* WOODS, 1878, p. 169); *Bunactus* POMEL, 1887, p. 204 (type, *Clypeaster scillae* DESMOULINS, 1837, p. 64; SD LAMBERT, 1912); *Laganidea* POMEL, 1887, p. 172 (type, *Clypeaster scutellaeformis* POMEL, 1885, p. 30); SD LAMBERT, 1912); *Miophyma* POMEL, 1887, p. 260 (type, *Clypeaster altus* LAMARCK, 1816, p. 14 (=*Echi-*

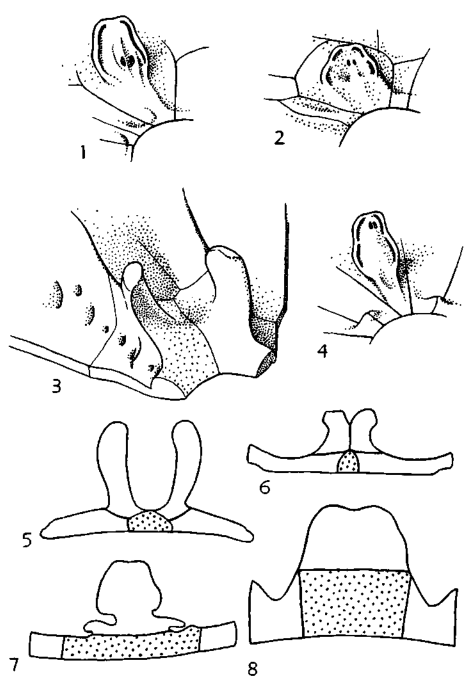


FIG. 353. Clypeasteroid auricles (Durham, n).——*1. Echinarachnius parma* (LAMARCK).——*2. Echinocyamus pusillus* (MÜLLER).——*3. Clypeaster ravenelii* (A. AGASSIZ).——*4. Hupea decagonalis* (LESSON).——*5. Clypeaster.*——*6. Arachnoides.*——*7. Encope.*——*8. Echinocyamus* [*5, 6, 7. 8,* in profile, interambulacral plates stippled].

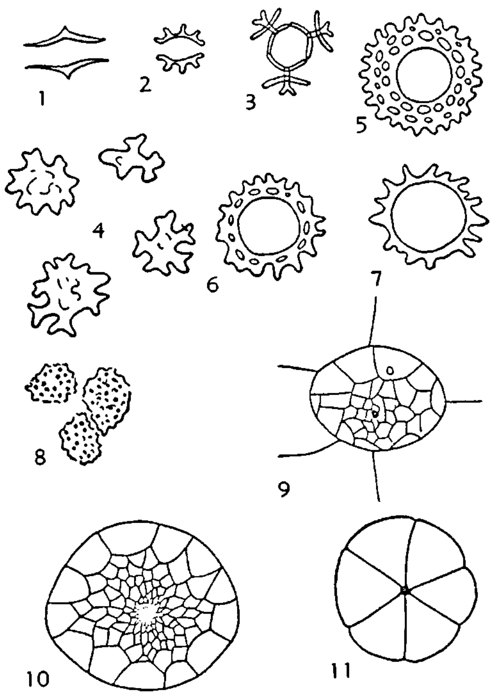


FIG. 354. Spicules, buccal plates, and periproctal plates of clypeasteroid echinoids (51, after 136g). *1. Echinarachnius parma* (LAMARCK), ×180, spicules from sucking disc of tube foot.——*2. Echinodiscus auritus* LESKE, ×210, spicules from sucking disc of tube foot.——*3. Heliophora orbiculus* (LINNÉ), ×265, spicules from sucking disc of tube foot.——*4-7. Clypeaster rotundus* (A. AGASSIZ), ×100, spicules from buccal membrane; *C. rangianus* DESMOULINS, ×135, spicule from sucking disc of tube foot; *C. rotundus* (A. AGASSIZ), ×180, spicule from sucking disc of tube foot; *C. latissimus* (LAMARCK), ×180, spicule from sucking disc of tube foot.——*8. Heliophora orbiculus* (LINNÉ), ×70, plates from buccal membrane.——*9. Fellaster zelandiae* (GRAY), ×10, periproctal plates.——*10. Peronella japonica* MORTENSEN, ×10, periproctal plates.——*11. Echinocyamus elongatus* H. L. CLARK, ×15, periproctal plates.

nanthus altus LESKE, 1778, p. 189); SD DURHAM, 1955); *Oxypleura* POMEL, 1887, p. 221 (*non* AMYOT & SERVILLE, 1843); *Paratina* POMEL, 1887, p. 190 (*non* MIK, 1874); *Platypleura* POMEL, 1887, p. 174 (*non* AMYOT & SERVILLE, 1843); *Pliophyma* POMEL, 1887, p. 247 (type, *Clypeaster atlas* POMEL, 1887, p. 252; SD LAMBERT, 1912); *Diplothecanthus* DUNCAN, 1889, p. 153 (obj.); *Plesianthus* DUNCAN, 1889, p. 154 (type, *Echinanthus testudinarius* GRAY, 1851, p. 35); *Biarritzella* BOUSSAC, 1911, p. 30 (type, *B. marbellensis*); *Dactylanthus* LAMBERT, 1912, p. 89 (*non* CARLGREN, 1911); *Eurycoila* LAMBERT, 1912, p. 90 (type, *Clypeaster intermedius* DESMOULINS, 1837, p. 64); *Eurypleura* LAMBERT, 1912, p. 90 (*non* KAUP, 1858); *Paleanthus* LAMBERT, 1912, p. 89 (type, *Clypeaster breunigi* LAUBE, 1868, p. 19); *Coronanthus* LAMBERT, 1913, p. 123 (type, *Clypeaster microstoma* LAMBERT, 1914, p. 91); *Oxclypeina* LAMBERT & THIÉRY, 1913, p. 122 (*pro Oxypleura* POMEL, 1887) (type, *Clypeaster doma* POMEL, 1887, p. 223; SD LAMBERT, 1912); *Paratinanthus* LAMBERT & THIÉRY, 1913, p. 122 (*pro Paratina* POMEL, 1887) (type, *Clypeaster confusus* POMEL, 1887, p. 190; SD LAMBERT & THIÉRY, 1914); *Platyclypeina* LAMBERT & THIÉRY, 1913, p. 122 (*pro Platypleura* POMEL, 1887) (type, *Clypeaster marginatus* LAMARCK, 1816, p. 14; SD LAMBERT, 1912); *Tholeopelta* LAMBERT & THIÉRY, 1913, p. 122 (*pro Eurypleura* LAMBERT, 1912) (type, *Clypeaster duchassaingi* MICHELIN, 1861, p. 107); *Alexandraspis* LAMBERT & THIÉRY, 1914, p. 315 (*pro Alexandria* PFEFFER, 1881, *non Alexandrium* MOLIN, 1860) (type, *Alexandria magnifica* PFEFFER, 1881, p. 63); *Guebhardanthus* LAMBERT, 1914, p. 17 (type, *Clypeaster priscus* OPPENHEIM, 1901, p. 92); *Laubeanthus* LAMBERT, 1914, p. 19 (type, *Clypeaster breunigi* LAUBE); *Leptoclypus* KOEHLER, 1922, p. 31 (type, *Clypeaster annandalei* KOEHLER, 1922, p. 16); *Rhaphydoclypus* CHECCHIA-RISPOLI, 1925, p. 63 (*nom. van.*); *Orthanthus* MORTENSEN, 1948, p. 34 (type, *Clypeaster euclastus* CLARK, 1941, p. 120); *Zanolettia* SÁNCHEZ ROIG, 1951, p. 39 (type, *Z. zanolettii*); *Herrerasia* SÁNCHEZ ROIG, 1952, p. 137 (type, *Clypeaster profundus* SÁNCHEZ ROIG, 1949, p. 91) *non C. profundus* L. AGASSIZ, 1840); *Rojasaster* SÁNCHEZ ROIG, 1952, p. 135 (type, *Clypeaster hernandezi* SÁNCHEZ ROIG)]. Medium-sized to large, test flattened to highly campanulate, margin rounded to flattened and inflated; peristome usually in deep infundibulum; oral surface flat to concave; petals variable, closed and rounded to open or sublyrate, with outer pores elongate, inner ones rounded, commonly connected by groove; periproct usually inframarginal, rarely marginal, situated between 3rd and 4th, or 4th and 5th pair of coronal plates; buccal membrane naked, with imbedded irregular spicules; internal supports variable in abundance, consisting of thin laminae and pillars; wall of test sometimes double, separated by pillars. [Variation in external test morphology and shape of petals is very great, more than 400 nominal taxa existing in the literature, but no systematic basis for subgeneric groupings can be recognized.] *U. Eoc.(Auvers.)-Rec.*, worldwide.——FIG. 357,*1a-e*. Lateral profiles of *Clypeaster*, ×0.7; *1a, C. altus alticostatus* MICHELIN, Mio., Malta; *1b*, **C. rosaceus* (LINNÉ), Rec., Carib.; *1c, C. euclastus* CLARK, Rec., Carib.; *1d, C. reticulatus* (LINNÉ), Rec., IndoPac.; *1e, C. latissimus* (LAMARCK), Rec., E. Indies (Durham, n).——FIG. 357,*1f,g*. **C. rosaceus* (LINNÉ), Rec., Carib.; *1f,g*, aboral, int. ab-

Order CLYPEASTEROIDA: Stratigraphic Distribution of Genera					
	Laganina	Rotulina	Clypeasterina	Scutellina	TOTAL GENERA
Recent	9	2	4	9	24
Pleistocene	7	2	4	9	22
Pliocene	7	3	3	12	25
Miocene	7	2	5	22	36
Oligocene	4	-	2	7	13
Eocene	18	-	1	6	25
Paleocene	3	-	-	-	3
U. Cretaceous	2	-	-	-	2
TOTAL GENERA	28	3	7	34	72

FIG. 355. Recorded stratigraphic distribution of clypeasteroid genera (Durham, n).

oral, ×0.7 (136g).——FIG. 357,*1h-k*. Plates of oral surface of *Clypeaster* (interamb. stippled), *1h-j* (reduced), *1k* (enlarged); *1h*, **C. rosaceus* (LINNÉ), Rec., Carib.; *1i*, *C. ravenelii* (A. AGASSIZ), Rec., USA(Tex.); *1j*, *C. europacificus* CLARK, Rec., Gulf Calif.; *1k*, *C. reticulatus* (LINNÉ), Rec., Philippine Is. (51). [See also Figs. 336,*1g,1j,3b*; 339,A; 340,*3*; 344,*1,2*; 348,*9*; 350,*2*; 351,*1-4,14,15*; 352,*3-4,6-8*; 353,*3,5*; 354,*4-7*.]

Family ARACHNOIDIDAE Duncan, 1889

[*nom. transl.* H. L. CLARK, 1914, p. 43 (*ex* Arachnoidinae DUNCAN, 1889, p. 158)]

Test flattened, outline usually rounded; ambitus moderately thin; petals open; ambulacral food grooves simple, well defined, no secondary tube feet in grooves; accessory tube feet outside petals usually in dense oblique series ("combs"), restricted to ambulacral areas; 4 genital pores; peristome not sunken; buccal membrane plated; primordial interambulacral plates externally larger than ambulacral plates. *Oligo.-Rec.*

Subfamily ARACHNOIDINAE Duncan, 1889

[Arachnoidinae DUNCAN, 1889, p. 158]

Periproct supramarginal; petals raised above interambulacra, pore pairs conjugate; combed areas large; food grooves extending to apical system; internal supports in outer marginal zone only. *Oligo.-Rec.*

Arachnoides LESKE, 1778, p. 218 [*nom. conserv.* ICZN, 1954] [**Echinus placenta* LINNÉ, 1758, p. 666, ICZN, 1954] [=*Echinarachnius* LESKE, 1778, p. 217 (suppressed ICZN, 1954)]. Narrow groove from periproct to basicoronal plates; periproct slightly supramarginal, edge of test notched; only one pair of interambulacral plates on oral surface; periproct between 2nd and 3rd pair of coronal plates; combed areas extend over all ambulacral areas except along suture between areas on oral surface. *Plio.-Rec.*, IndoPac.——FIG. 358,*1*. **A. placenta* (LINNÉ), Rec., Java (*1a,b*), Sumatra (*1c*); *1a,b*, aboral, oral, ×1; *1c*, plates on oral surface (interamb. stippled), ×0.6 (6, 51). [See also figs. 340, *7-8*; 344,*3*; 348,*8*; 350,*3*; 351,*5*.]

Fellaster DURHAM, 1955, p. 125 [**Arachnoides zelandiae* GRAY, 1855, p. 14 (=*Echinarachnius zelandiae* GRAY, 1843, p. 264); OD]. No groove from periproct to basicoronal plates; periproct supramarginal, at junction between 3rd and 4th pairs of coronal plates; no marginal notch for periproct; 2 or 3 coronal interambulacral plates on oral surface; combed areas about 0.7 width of ambulacral plates. *Oligo.-Rec.*, N.Z.——FIG. 358,*2*. **F. zelandiae* (GRAY), Rec.; *2a*, oral with spines,

×0.5 (136g); *2b,* oral without spines, ×0.7 (136g); *2c,* plates of oral surface, ×0.7 (51). [See also Figs. 336,*1f*; 351,*6*; 354,*9*.]

Subfamily AMMOTROPHINAE Durham, 1955

[Ammotrophinae DURHAM, 1955, p. 127]

Combed areas small; internal supports

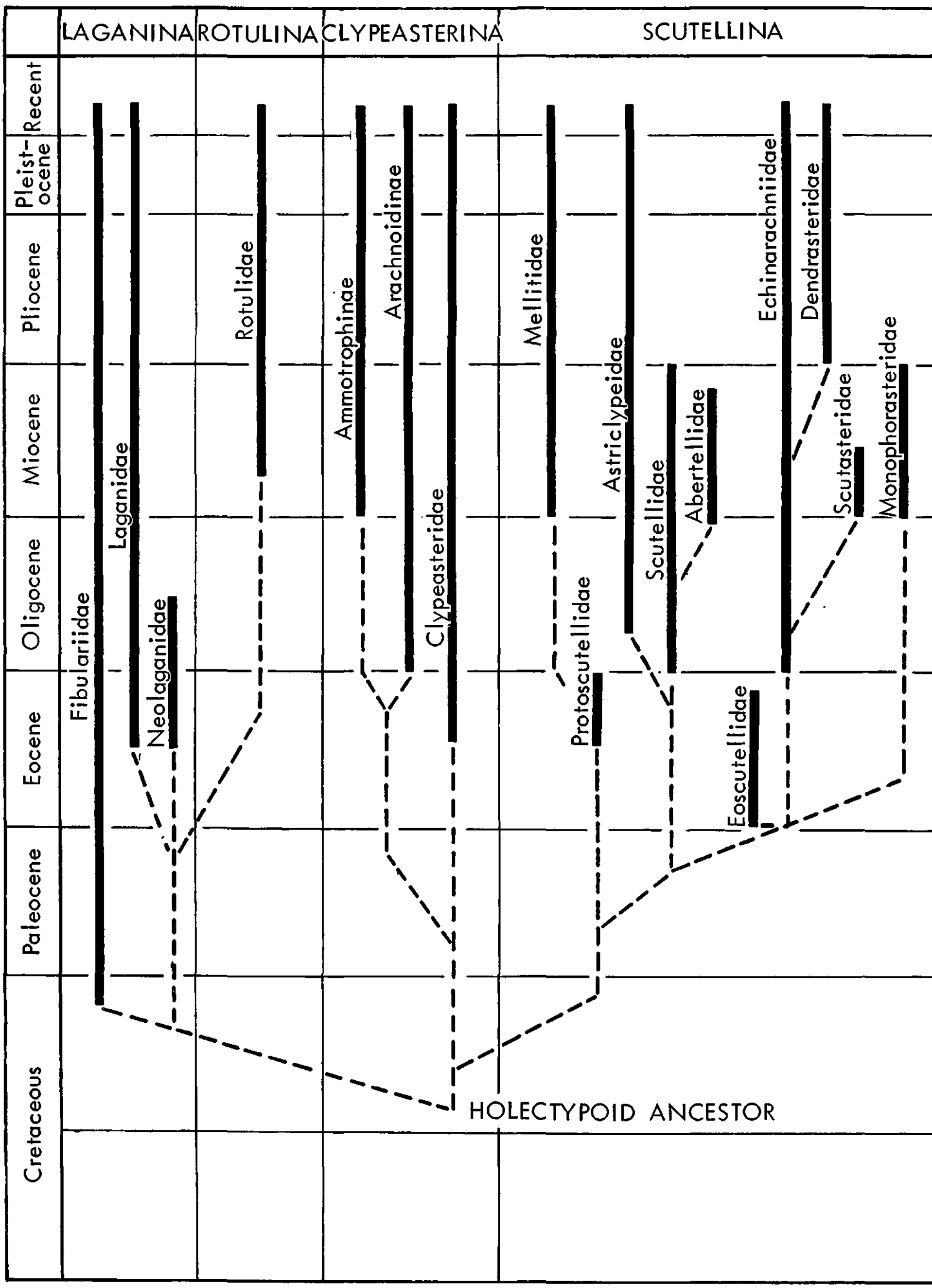


FIG. 356. Inferred phylogeny of the families of clypeasteroid echinoids (Durham, n).

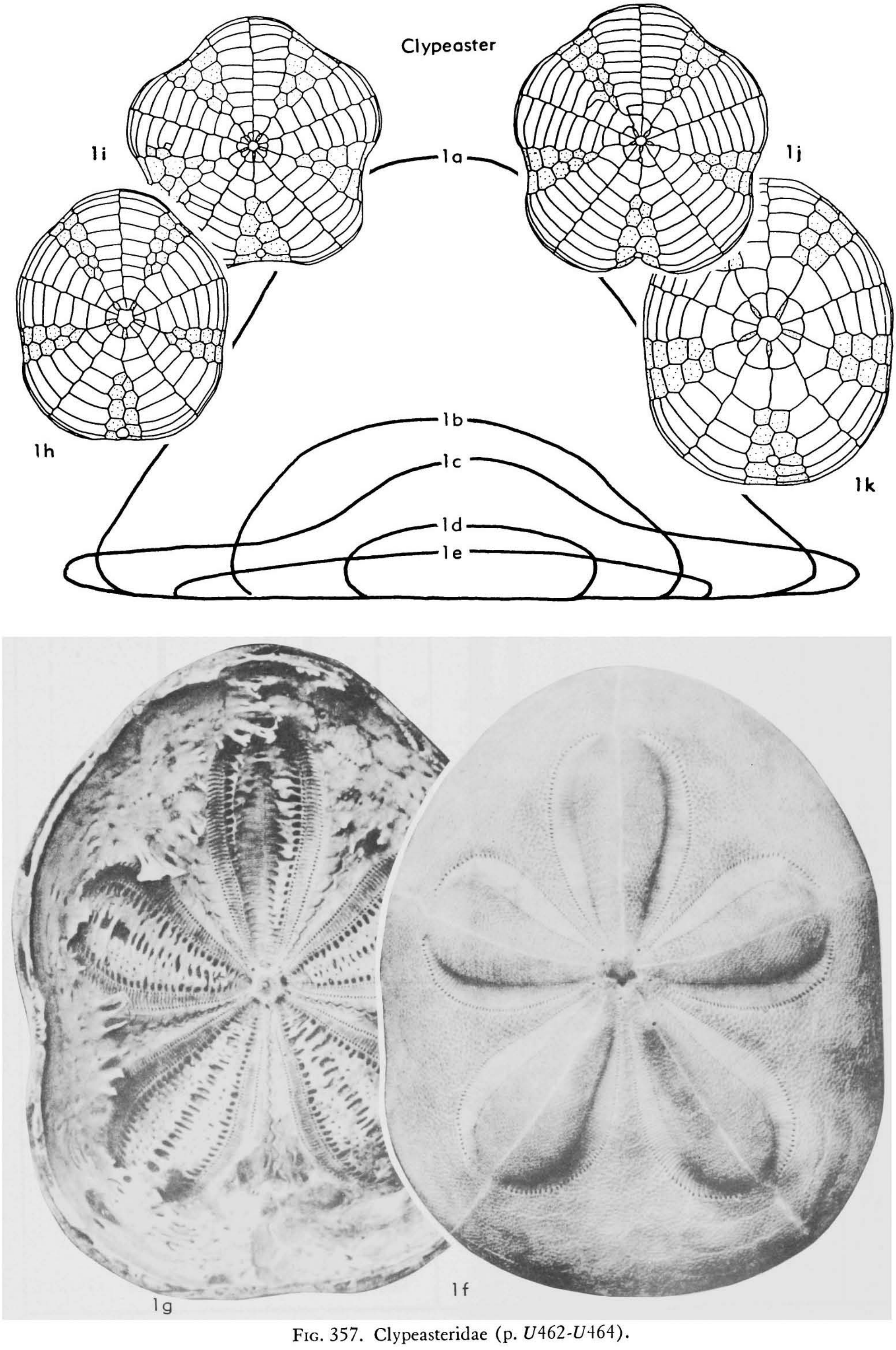


FIG. 357. Clypeasteridae (p. U462-U464).

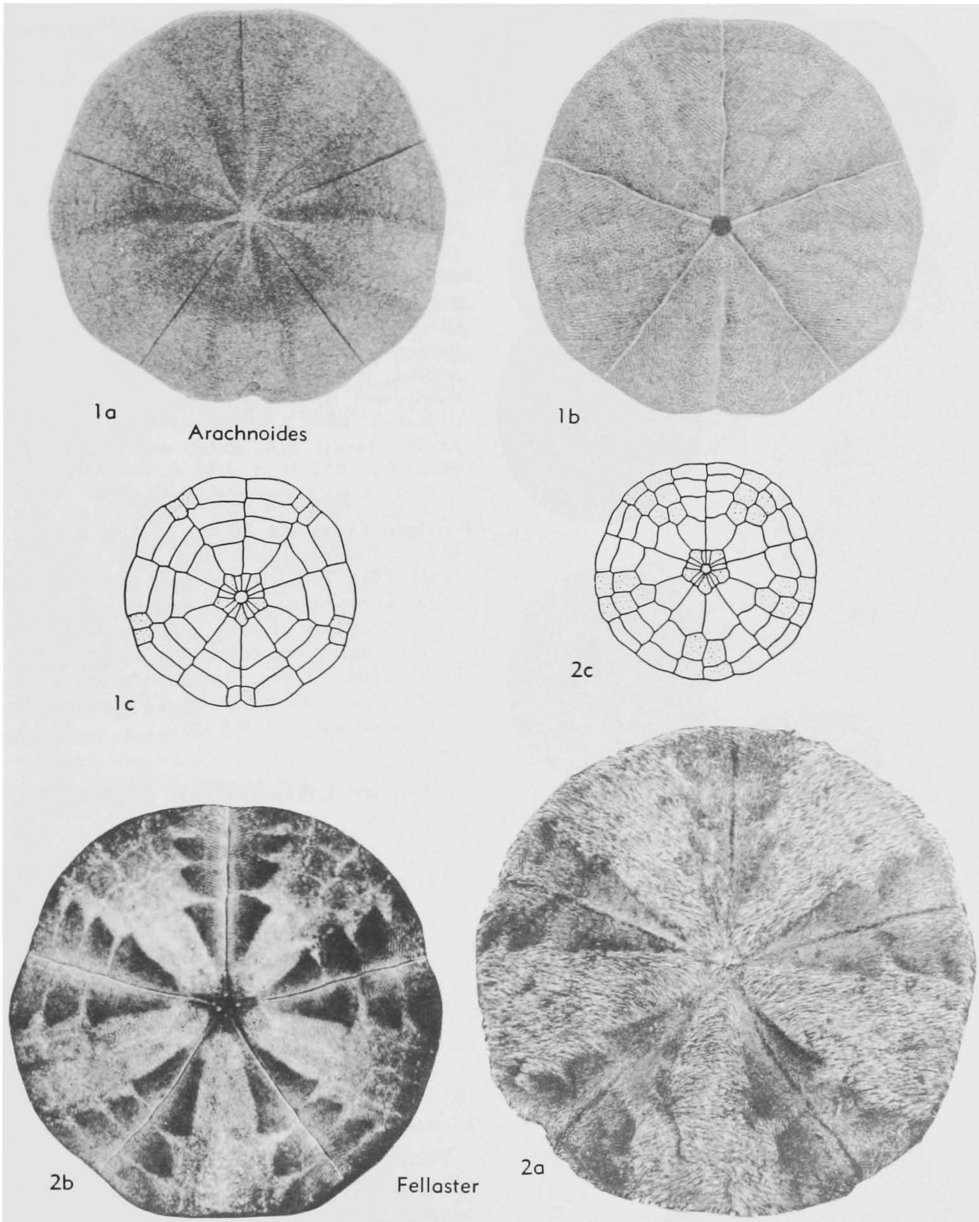


FIG. 358. Arachnoididae (Arachnoidinae) (p. *U*464).

both marginal and around peristome, concentric peripherally; periproct usually oral; no groove from periproct to basicoronal plates. *Mio.-Rec.*

Ammotrophus H. L. CLARK, 1928, p. 471 [**A. cyclius*; OD] [=*Hesperaster* H. L. CLARK, 1938, p. 411 (type, *H. arachnoides*)]. Combed areas adjacent to food grooves on apical surface and in small triangular areas on oral surface; food grooves extending to apical system; 3 or 4 coronal interambulacral plates on oral surface; periproct 0.3 distance from margin, between 1st pair of coronal plates. *Pleist.-Rec.,* S. Australia-W. Australia.——FIG. 359,*4*. **A. cyclius,* Rec., S. Australia; *4a,b,* aboral view, plates on oral surface (interamb. stippled), ×0.7 (51, 136g).

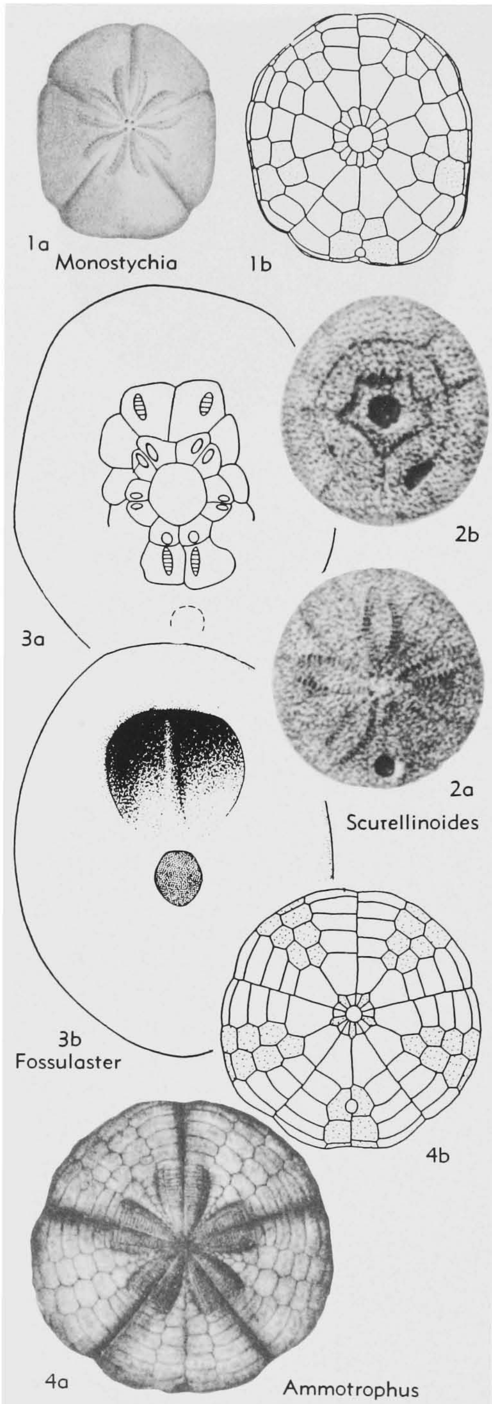


FIG. 359. Arachnoididae (Ammotrophinae) *(1-2,4)*, (Subfamily Uncertain) *(3)* (p. U467-U468).

Monostychia LAUBE, 1869, p. 188 [**M. australis*; OD]. Test rounded to elongate; ambitus with ambulacral indentations; food grooves extending to apical system; combed areas small, poorly defined; 2 coronal interambulacral plates on oral surface; periproct just submarginal, between 2nd pair of coronal plates. *Mio.*, S.Australia-Tasmania.——FIG. 359,*1*. **M. australis*, S.Australia; *1a*, aboral view, ×1 (15); *1b*, plates on oral surface (interamb. stippled), ×0.7 (51).

Scutellinoides DURHAM, 1955, p. 128 [**Scutellina patella* TATE, 1891, p. 275 (*non* HALL, 1908); OD]. Test depressed conical; periproct supramarginal, distant about 2 pairs of plates from ambitus; pore pairs not conjugate; petals moderately well developed, extending 0.75 distance to margin. *Mio.*, S.Australia.——FIG. 359,*2*. **S. patella* (TATE); *2a,b*, aboral, oral views, ×1.5 (31).

Subfamily UNCERTAIN

Fossulaster LAMBERT & THIÉRY, 1925, p. 577 [**F. halli* (=*Scutellina patella* HALL, 1908, *non* TATE, 1891); OD]. Test ovate; periproct supramarginal; petals inconspicuous; only 2 pairs of inner radial internal supports; females with well-developed bipartite anterior oral marsupium; no recognizable food grooves. *?L.Mio.*, Australia.——FIG. 359,*3*. **F. halli*; *3a,b*, oral surface int. (♂), oral surface with marsupium (♀), ×6 (51).

Suborder LAGANINA Mortensen, 1948

[Laganina MORTENSEN, 1948, p. 156]

Flattened or inflated; with internal supports when flattened; petaloid ambulacral plates simple or pseudocompound; interambulacra narrow, continuous, terminated adapically by single plate; apices of apical system opposite interambulacra; auricles fused; aboral miliary spines with terminal crown; usually no spicules in tube feet. [Mostly tropical, some temperate.] *U.Cret.(Senon.)-Rec.*

Pseudocompound plates (Fig. 336,*3a*) are present only in the Neolaganidae. The adapical termination of the narrow interambulacra in a single plate or series of plates is a striking feature shared only with the rotulinids. The late Senonian species of *Fibularia* and *Echinocyamus* (not examined), if correctly assigned to these genera, should have this feature (present in Eocene species); if so, they are precluded from the ancestry of later clypeasterinids, and scutellinids. Also, lower and middle Eocene species of this suborder already have their characteristic features well developed, indicating that, despite their simple petals and test morphology, none of the known Eocene species can be ancestral to the clypeasterinids and scutellinids.

Family FIBULARIIDAE Gray, 1855

[*nom. correct.* DUNCAN, 1889, p. 144 (*pro* Fibularina GRAY, 1855, p. 65)] [includes Fistularina GRAY, 1855, p. 27]

Shape variable; petals variable, indistinct or simple, open; pore pairs not conjugate, pores rounded; food grooves absent or indistinct; primordial plates simple; internal supports absent or radial partitions only. [Temperate and tropical regions.] *U.Cret. (Senon.)-Rec.*

Fibularia LAMARCK, 1816, p. 16 [**F. ovulum*; SD ICZN, 1950] [=*Echinocyamus* GRAY, 1825, p. 428, and LAMBERT, 1891, p. 749 (*non* LESKE, 1778)]. Test ovate, inflated; periproct close to peristome; hydropores in groove; no internal supports; 5 large periproctal plates; buccal membrane naked; no calcareous disc in tube feet. *U.Cret.(U. Senon.)-Rec.*, worldwide as fossil, living IndoPac. only.——FIG. 360,*1*. **F. ovulum*, Rec., E.Indies (Kei Is.); *1a,b*, aboral, oral views, ×2.5 (136g). [See also figs. 348,*4*; 350,*7*.]

Cyamidia LAMBERT & THIÉRY, 1914, p. 288 [**Echinocyamus nummulitica* DUNCAN & SLADEN, 1884, p. 132; OD]. Like *Echinocyamus*, small, variably inflated; petals well defined, inner member of pore pair smaller than outer; periproct radially elongate, midway on oral surface; single hydropore. *Eoc.*, India-Pak.-Australia.——FIG. 360,*2*. **C. nummulitica* (DUNCAN & SLADEN), Pak.; *2a,b*, aboral, oral, ×3; *2c*, apical region, enlarged (47).

Echinocyamus VAN PHELSUM, 1774, p. 131 [**Echinocyamus pusillus* MÜLLER, 1776, p. 236 (=*Spatagus pusillus* MÜLLER, 1776, p. 236); SD ICZN, 1950] [=*Anaster* SISMONDA, 1841, p. 45 (type, *A. studeri*); *Fibularia* LAMBERT, 1891, p. 749 (suppressed ICZN) (*non* LAMARCK, 1816)]. Test moderately flattened; hydropores few, not in groove; periproct between 1st and 2nd pair of coronal plates; petals poorly defined in some forms, pore pairs usually oblique; no spicules in tube feet; 5 pairs of internal radiating partitions; in some species females with aboral marsupium. *U. Cret.(Senon.)-Rec.*, worldwide as fossil, living Eu.-IndoPac.——FIG. 360,*5*. **E. pusillus* (MÜLLER), Rec., Eu.; *5a-c*, aboral, oral, oral int., ×4 (135). [=*Echinocentrotus* CHECCHIA-RISPOLI, 1907, pl. 17 *(nom. null.)*.]

Eoscutum LAMBERT, 1914, p. 293 [**Porpitella doncieuxi* LAMBERT, 1905, p. 136; OD]. Small, flattened, apical system slightly elevated; petals well developed, nearly closed, slightly more than half length of radius; periproct just supramarginal; 10 internal radial partitions. *Eoc.*, Eu.——FIG. 360,*3*.

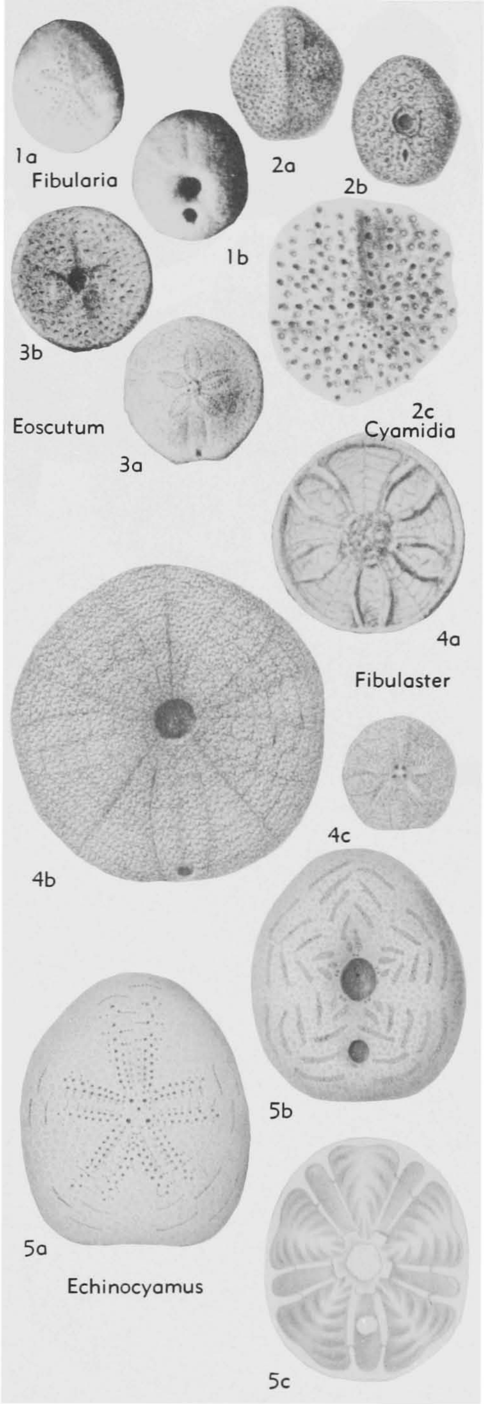


FIG. 360. Fibulariidae (p. *U469*, *U471*).

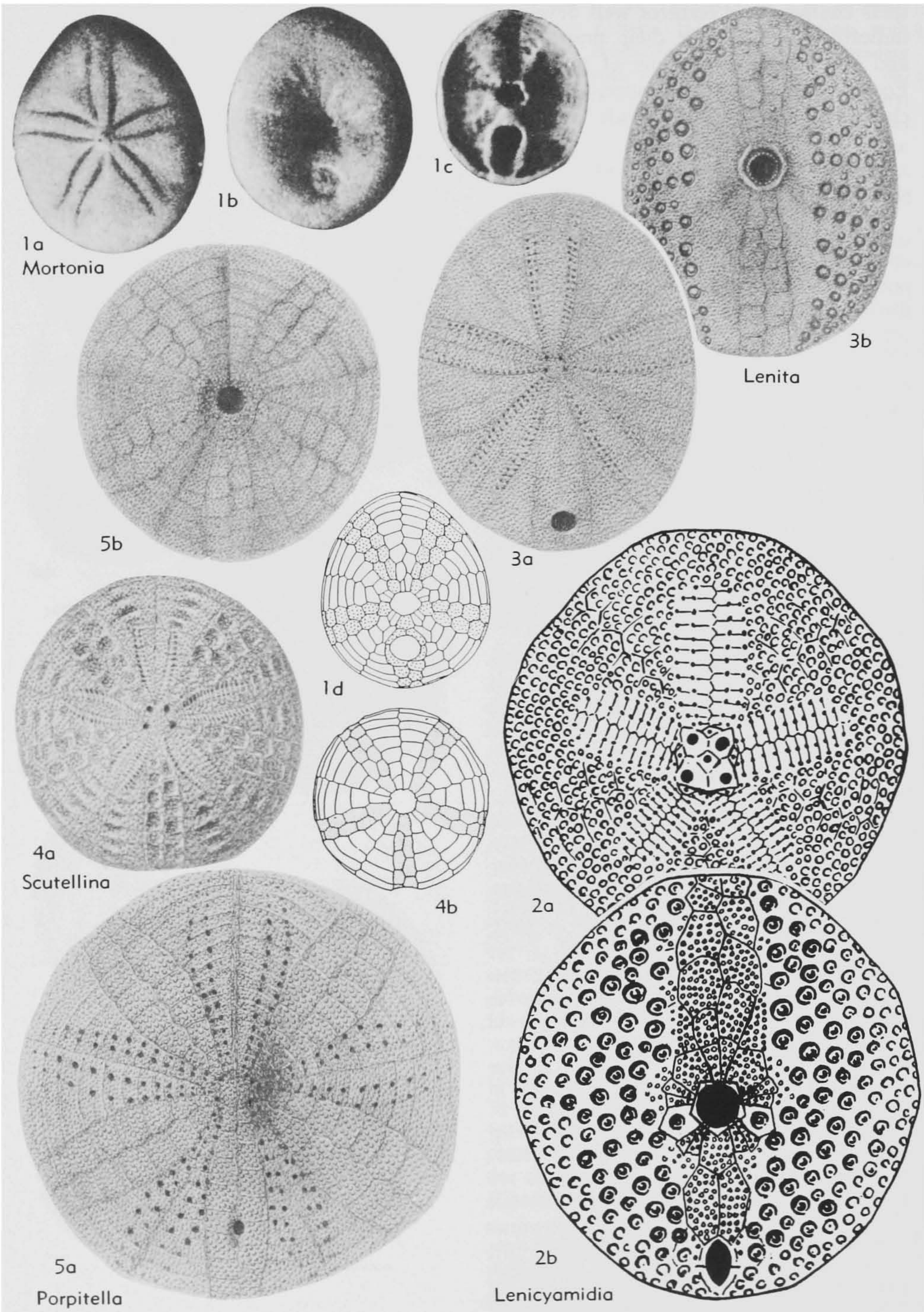


FIG. 361. Fibulariidae (p. U471).

*E. doncieuxi (LAMBERT), Fr.; 3a,b, aboral, oral, ×2.5 (203b).

Fibulariella MORTENSEN, 1948, p. 6 [**Fibularia acuta* YOSHIWARA, 1898, p. 60; OD]. Like *Fibularia* but periproct elongated, with numerous small periproctal plates; calcareous disc in tube feet; no groove for hydropores. *Rec.*, IndoPac.

Fibulaster LAMBERT & THIÉRY, 1914, p. 296 [*pro Crustulina* POMEL, 1883, p. 72 (*non* MENGE, 1867)] [**Sismondia michelini* COTTEAU, 1861, p. 49; SD COTTEAU, 1892, p. 309]. Like *Scutellina* but margin thicker; internal radial partitions adambulacrally curved; submarginal periproct between 6th and 7th pairs of coronal plates. *Eoc.*, Eu.——FIG. 360,*4*. **F. michelini* (COTTEAU), Fr.; *4a,b*, int. oral, oral, ×2.6; *4c*, aboral view, ×1 (27).

Lenicyamidia BRUNNSCHWEILER, 1962, p. 165 [**L. compta*; OD]. Like *Cyamidia* but with median granulate area and lateral zones having deeply scrobiculate tubercles on oral surface. *L.Eoc.*, Australia.——FIG. 361,*2*. **L. compta*; *2a,b*, aboral, oral, ×7 (179).

Lenita DESOR, 1847, p. 142 [**Lenita patellaris* DESOR, 1847, p. 84 (=*Echinus patellaris* GMELIN, 1791, p. 301, =*Echinites patellaris* LESKE, 1778, p. 256); SD DESOR, 1858, p. 222]. Small, flattened ovoid, slightly arched along longitudinal axis; petals open, extending nearly to margin; periproct supramarginal, 1 or 2 plates from margin; 10 well-developed internal radial partitions, with 5 less well developed interradially; oral surface with lateral zones of large tubercles having sunken areoles, median area without tubercles; small tubercles only on apical surface. *Eoc.*, Eu.-?N.Am.——FIG. 361,*3*. **L. patellaris* (LESKE), Fr.; *3a,b*, aboral, oral, ×3 (27).

Mortonia GRAY, 1852, p. 38 [**Fibularia australis* DESMOULINS, 1837, p. 86; OD]. Like *Echinocyamus* but with single posterior pair of partitions only; oral surface concave; petals open, with radial ridge between members of pore pairs; single hydropore. *Rec.*, IndoPac.——FIG. 361,*1*. **M. australis* (DESMOULINS), Hawaii; *1a-c*, aboral, oral, oral int., ×2.5; *1d*, plates of oral surface (interamb. stippled), ×2 (51, 136g). [See also Figs. 336,*1e*; 348,*3*; 350,*8*; 351,*7*.]

Porpitella POMEL, 1883, p. 72 [**Scutellina hayesiana* L. AGASSIZ, 1847, p. 82 (=*S. supera* L. AGASSIZ, 1841, p. 103, =*Cassidulus Hayesianus* DESMOULINS, 1837, p. 246); SD LAMBERT, 1905, p. 138]. Small, irregular ovoid, slightly arched along longitudinal axis; petals well defined, long, moderately open; periproct supramarginal, about 4 plates from ambitus; 15 internal radiating partitions. *Eoc.*, Eu.——FIG. 361,*5*. **P. hayesianus* (DESMOULINS), Fr.; *5a,b*, aboral, oral, ×4 (27).

Scutellina L. AGASSIZ, 1841, p. 98 [**S. nummularia* (=*Scutella nummularia* DEFRANCE, 1827, p. 231, =*S. lenticularis* LAMARCK, 1816, p. 10; OD)]. Small, flattened, outline circular, margin thin; petals well defined, anterior petal open, posterior petals tending to close; periproct marginal; interambulacra about 0.25 width of ambulacra at ambitus. *Eoc.*, Eu.-N.Afr.——FIG. 361,*4*. **S. lenticularis* (LAMARCK), Fr.; *4a,b*, aboral, plates of oral surface (interamb. stippled), ×3 (27, 51).

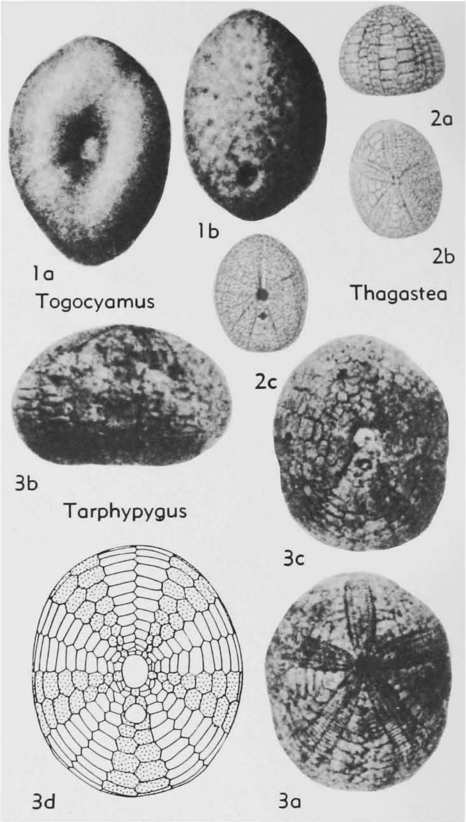


FIG. 362. Fibulariidae (p. *U*471-*U*472).

Tarphypygus ARNOLD & H. L. CLARK, 1927, p. 42 [**T. ellipticus*; OD]. Ovoid to subglobular; petals well defined, open; periproct on oral surface, between 1st and 2nd coronal plates; basicoronal plates small; about 11 pairs of ambulacral and 7 pairs of interambulacral coronal plates on oral surface; ambulacra about 1.5 times as wide as interambulacra at ambitus; interambulacra terminated adapically by series of single plates. *Eoc.*, Jamaica-Cuba.——FIG. 362,*3a-c*. **T. ellipticus*, Jamaica; *3a-c*, aboral, lat., oral, ×1 (9).——FIG. 362,*3d*. *T. clarki* (LAMBERT), Cuba; plates of oral surface (interamb. stippled), ×2 (51). [See also Figs. 339,*E*; 343,*1b*.]

Thagastea POMEL, 1888, p. 373 [**T. wetterlei*; OD] [=*Thegaster* DUNCAN, 1889, p. 294 (*nom. null.*)]. Inflated, subconical, flattened orally; petals well defined, pore pairs not inclined; hydropores several; periproct close to peristome, between 2nd

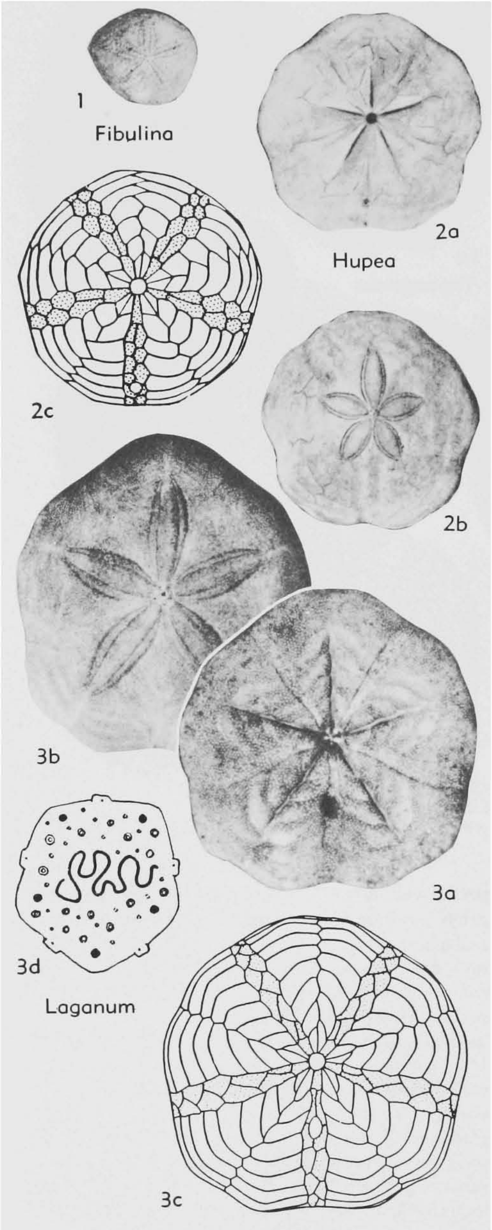


FIG. 363. Laganidae (p. U472-U473).

and 3rd pair of coronal plates; no internal supports; interambulacra terminated adapically by series of single plates; no food grooves. *Eoc.*, Eu.-N.Afr.——FIG. 362,*2*. **T. wetterlei*, Tunisia; *2a-c*, lat., aboral, oral, ×1 (27).

Togocyamus OPPENHEIM, 1915, p. 228 [**Echinocyamus (Togocyamus) seefriedi*; OD]. Very small, like *Fibularia*, but periproct supramarginal; 10 internal partitions. *Paleoc.*, Fr.W.Afr.——FIG. 362, *1*. **T. seefriedi* (OPPENHEIM); *1a,b*, oral, aboral, ×10 (213).

Family LAGANIDAE A. Agassiz, 1873

[*nom. transl. et correct.* A. AGASSIZ, 1873, p. 516 (*pro* Tribu des Laganes DESOR, 1858, p. 216)] [*emend.* DURHAM, 1954, p. 677]

Test flattened, outline angulated to rounded; petals well developed, open, outer member of pore pair slightly elongated, pores usually conjugate; ambulacral food grooves present, simple, not reaching margin; interambulacra very narrow on oral surface, terminal apical plate rhomboidal; basicoronal plates forming pentameral star with ambulacral plates at apices of rays; no abrupt change in size of oral ambulacral plates; ambulacral plates not pseudocompound in petals; internal supports both radial and concentric; periproct oral. [Tropical.] *Eoc.*, Eu.; *Oligo.-Rec.*, IndoPac.

Laganum LINK, 1807, p. 161 [**L. petalodes* (=*Echinodiscus laganum* LESKE, 1778, p. 204); OD] [=*Lagana* GRAY, 1825, p. 427 (type, *L. minor* (=*Echinodiscus laganum* LESKE) (obj.); *Echinodiscus* LAMBERT & THIÉRY, 1914, p. 311 (*non* LESKE, 1778)]. Medium-sized to large, apical area slightly raised; petals about 0.7 length of radius; genital pores 5, hydropores in groove; periproct elongated, midway between 1st and 2nd pair of coronal plates; basicoronal interambulacral plates about as wide as ambulacral plates; 5 or 6 coronal interambulacral plates to column on oral surface. *Eoc.*, Eu.; *Mio.-Rec.*, IndoPac.——FIG. 363,*3*. **L. laganum* (LESKE), Rec., Indonesia(Kei Is.); *3a-c*, oral, aboral, plates of oral surface (interamb. stippled), ×0.7; *3d*, apical system with groove for hydropores, ×6 (51, 136g). [See also Figs. 339,*B*; 340,*4*,*5*; 344,*5*.]

Fibulina TORNQUIST, 1904, p. 327 [**F. gracilis*; OD]. Similar to *Fibularia* but with 5 furrows (ambulacral food grooves?) radiating from peristome. [Description indicates that it is a laganid.] *Eoc.*, Madag.——FIG. 363,*1*. **F. gracilis*; aboral, ×1 (221).

Hupea POMEL, 1883, p. 69 [**Laganum decagonale* POMEL, 1883, p. 69 (=*Scutella decagonalis* LESSON, 1827, p. 48); OD]. Outline slightly polygonal; apical area raised; petals small, about 0.5 length of radius; 5 genital pores; hydropores not in groove; periproct submarginal, distant its diameter from margin, between 3rd and 4th pairs of coronal plates; 4 or 5 coronal interambulacral plates per column on oral surface. *Plio.-Rec.*, Malaysia-Polynesia.——FIG. 363,*2*. **H. decagonale* (LESSON), Rec., Malaysia; *2a,b*, oral, aboral, ×0.75; *2c*, plates of oral surface (interamb. stippled), ×0.7 (51, 136g). [Also Fig. 353,*4*.]

Jacksonaster LAMBERT & THIÉRY, 1914, p. 313 [**Echinarachnius conchatus* M'CLELLAND, 1840, p. 181, =*Laganum depressum* LESSON, L. AGASSIZ, 1841, p. 110; OD]. Medium-sized to large, apical area slightly raised, central; 5 genital pores; petals open, length 0.7 of radius; hydropores in groove; periproct oral, about 0.25 distance from margin, commonly transversely elliptical, between 1st and 2nd pair of coronal plates; about 5 ambulacral and 3 or 4 interambulacral coronal plates on oral surface. *Mio.-Rec.*, IndoPac.——FIG. 364,*3*. **J. conchatus* (M'CLELLAND), Rec., Malaya; *3a,b*, aboral, oral with spines, ×0.8; *3c*, plates of oral surface (interamb. stippled), ×1.5 (51, 136g). [See also Figs. 336,*1h*; 348,*10*; 351,*8*; 352,*1*.]

Peronella GRAY, 1855, p. 13 [**Laganum peronii* L. AGASSIZ, 1841, p. 123; OD]. Like *Laganum* but with 4 genital pores, hydropores not in groove

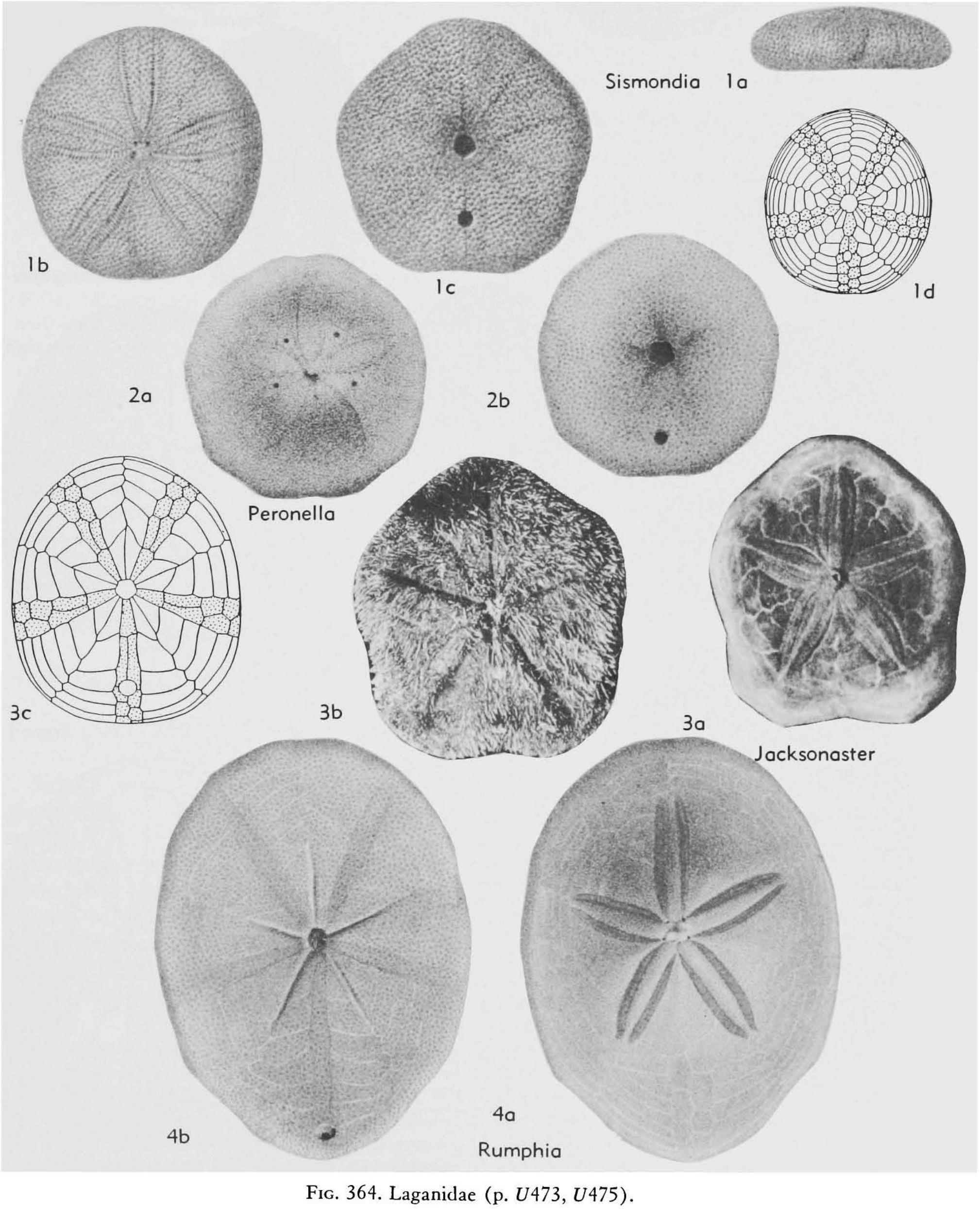


FIG. 364. Laganidae (p. *U*473, *U*475).

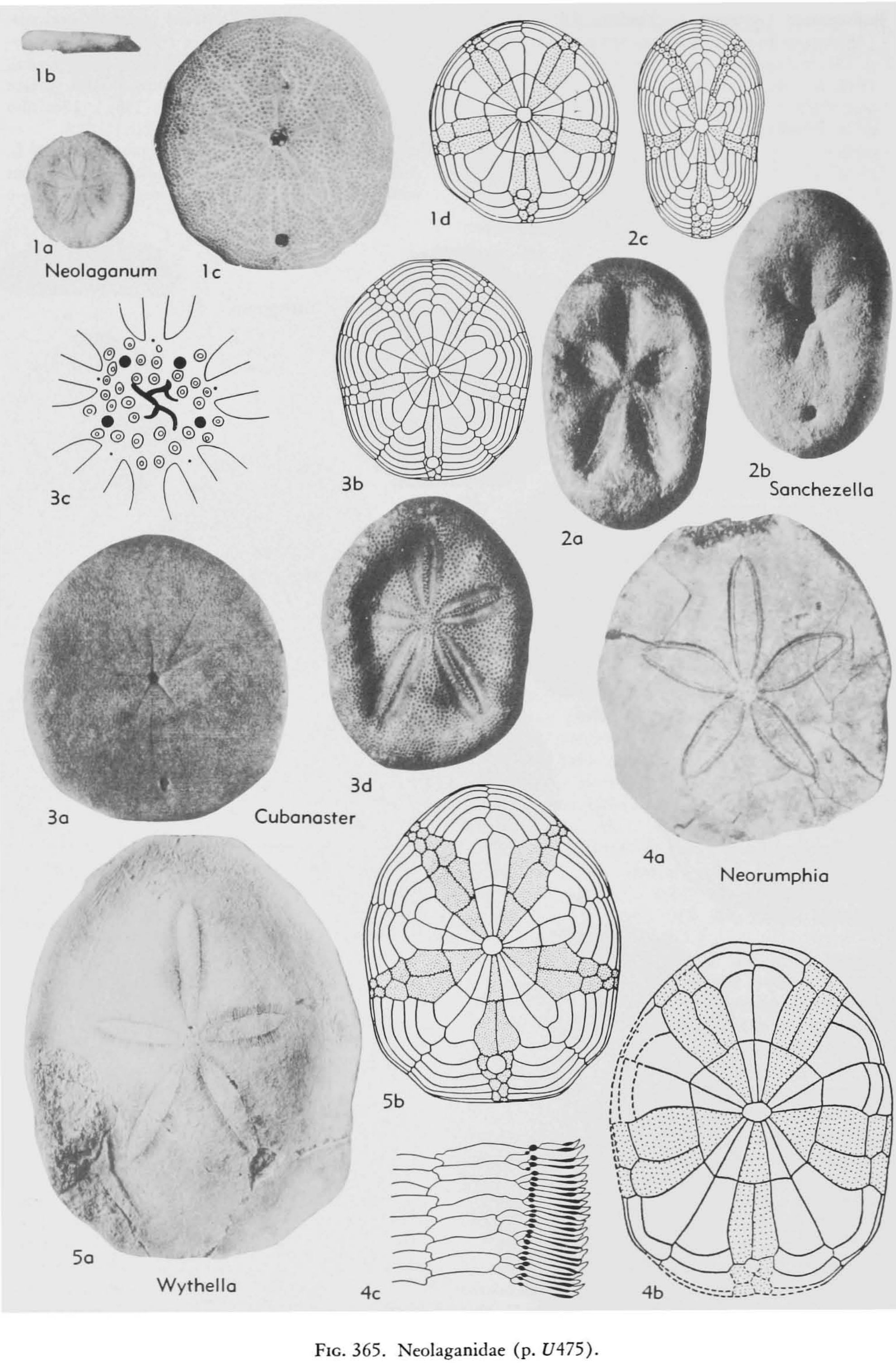


FIG. 365. Neolaganidae (p. U475).

and periproct 0.4 distance from margin; 3 to 5 interambulacral and 5 or 6 ambulacral coronal plates to column on oral surface. *U.Mio.-Rec.*, IndoPac.——Fig. 364,*2*. **P. peronii* (Agassiz), Rec.; *2a,b*, aboral, oral, ×1 (6).

Peronellites Hayasaka & Morishita, 1947, p. 101 [**Peronella (Peronellites) ovalis*; OD]. Test elliptical; 4 genital pores; apical system raised; petals short, about 0.5 of radius, anterior petal longest, anterior paired petals shortest, poriferous zones "very narrow." *Mio.*, Formosa.

Rumphia Desor, 1858, p. 229 [**Laganum rostratum* L. Agassiz, 1841, p. 118; OD] [=*Michelinia* Dujardin & Hupé, 1862, p. 560 (*non* de Koninck, 1842), *pro Polyaster* Michelin, 1859, p. 397 (*non* Gray, 1840)]. Medium-sized to large, elongate; apical area raised, slightly anterior; petals elongate, open, length 0.7 of radius; 4 genital pores; hydropores not in groove; periproct oral, close to margin; about 7 coronal ambulacral plates to column on oral surface, number of interambulacral plates uncertain. *Mio.-Rec.*, IndoPac.——Fig. 364,*4*. **R. rostratum* (Agassiz), N.Z.; *4a,b*, aboral, oral, ×0.7 (6).

Sismondia Desor, 1858, p. 225 [**Scutella occitana* Defrance, 1827; SD Pomel, 1883, p. 72]. Small, margin inflated; petals open, slightly lyrate, length about 0.75 of radius; 4 genital pores, hydropores in groove; periproct 0.4 distance from margin; between 1st and 2nd pair coronal plates; food grooves indistinct; about 6 interambulacral and 8 ambulacral coronal plates per column on oral surface; internal radial partitions well developed, concentric supports incipient, basicoronal interambulacral plates larger than ambulacral. *Eoc.*, Eu.-Afr.-Asia; *Oligo.-Mio.*, IndoPac.-Australia. ——Fig. 364,*1*. **S. occitana* (Defrance), Fr.; *1a-d*, lat., aboral, oral, plates of oral surface (interamb. stippled), ×1 (27, 51).

Family NEOLAGANIDAE Durham, 1954

[Neolaganidae Durham, 1954, p. 680]

Similar to Laganidae, but usually with pseudocompound plates in petals, outer member of pore pairs greatly elongated, basicoronal plates in regular pentagon with ambulacral plates at apices, first pair of coronal plates markedly larger than succeeding plates, and terminal adapical interambulacral plate rectangular. *Eoc.-Oligo.*, Gulf Mexico-Carib. [See Figs. 336,*3a*; 339,*D*; 344,6.]

Neolaganum Durham, 1954, p. 680 [**Laganum archerensis* Twitchell, p. 161; OD]. Small to medium-sized; petals nearly closed, length 0.7 of radius; plates within petals in dyads and triads; 4 genital pores; hydropores in branching groove; periproct oral, about 0.25 distance from margin; 4 or 5 ambulacral and 3 or 4 interambulacral coronal plates per column on oral surface. *Eoc.*, Gulf Mexico.——Fig. 365,*1*. **N. archerensis* (Twitchell), USA(Fla.); *1a,b*, aboral, lat. views, ×1; *1c,d*, oral, plates of oral surface (interamb. stippled), ×1.3 (22, 51, 190).

Cubanaster Sánchez Roig, 1952, p. 3 [**Jacksonaster torrei* Lambert, 1962, p. 61; OD]. Small to medium-sized; petals elongate, slightly open, length about 0.75 of radius; some dyads in petals, other plates simple; 4 genital pores; hydropores in groove; periproct oral, large, about 0.17 of distance from margin, between 2nd pair of coronal plates; 7 or 8 ambulacral and 5 or 6 interambulacral coronal plates per column on oral surface. *U.Eoc.*, W.Indies-Panama.——Fig. 365, *3a-c*. **C. torrei* (Lambert), Cuba; *3a,b*, oral, plates of oral surface (interamb. stippled), ×1; *3c*, apical system with groove for hydropores, ×10 (51, 216d).——Fig. 365,*3d*. *C. acunai* (Sánchez Roig), Cuba; aboral, ×0.8 (167).

Neorumphia Durham, 1954, p. 681 [**Rumphia elegans* Sánchez Roig, 1949, p. 100; OD]. Large, elongate, posteriorly truncated; ambitus thick, adapical surface raised centrally; petals almost closed, pointed, plates mostly triads and tetrads, length about 0.75 of radius; 4 genital pores; hydropores in branching groove; periproct large, about 0.17 of distance from margin, between 2nd pair coronal plates; orally with about 3 ambulacral and 2 or 3 interambulacral coronal plates per column. *U.Oligo.*, Cuba.——Fig. 365,*4*. **N. elegans* (Sánchez Roig); *4a,b*, aboral, plates of oral surface (interamb. stippled), ×0.6; *4c*, pseudocompound plates in petal I, ×3 (51, 216b).

Sanchezella Durham, 1954, p. 682 [**Jacksonaster sanchezi* Lambert, 1926, p. 61; OD]. Medium-sized, elongate, thickened; both oral and apical surfaces moderately concave; ambitus thick, rounded; petals depressed, elongate, open, with some dyads; 4 genital pores; hydropores in groove; periproct large, 0.25 of distance from margin, between 2nd pair coronal plates; numerous plates on oral surface. *U.Eoc.*, W.Indies.——Fig. 365,*2*. **S. sanchezi* (Lambert), Cuba; *2a-c*, aboral, oral, plates of oral surface (interamb. stippled), ×0.8 (51, 167).

Weisbordella Durham, 1954, p. 682 [**Peronella caribbeana* Weisbord, 1934, p. 52; OD]. Like *Neolaganum* but with larger periproct and without groove for hydropores; oral surface slightly concave. *U.Eoc.*, W.Indies.

Wythella Durham, 1954, p. 682 [**Laganum eldridgei* Twitchell, 1915, p. 160; OD]. Similar to *Cubanaster* but larger, margin thinner, petals raised and interambulacral areas widened midway on oral surface; also similar to *Neorumphia* but interambulacra much narrower at ambitus. *U.Eoc.*, Gulf Mex.——Fig. 365,*5*. **W. eldridgei* (Twitchell), USA(Ga.); *5a*, aboral, ×0.7; *5b*, plates of oral surface (interamb. stippled), ×1 (22, 51).

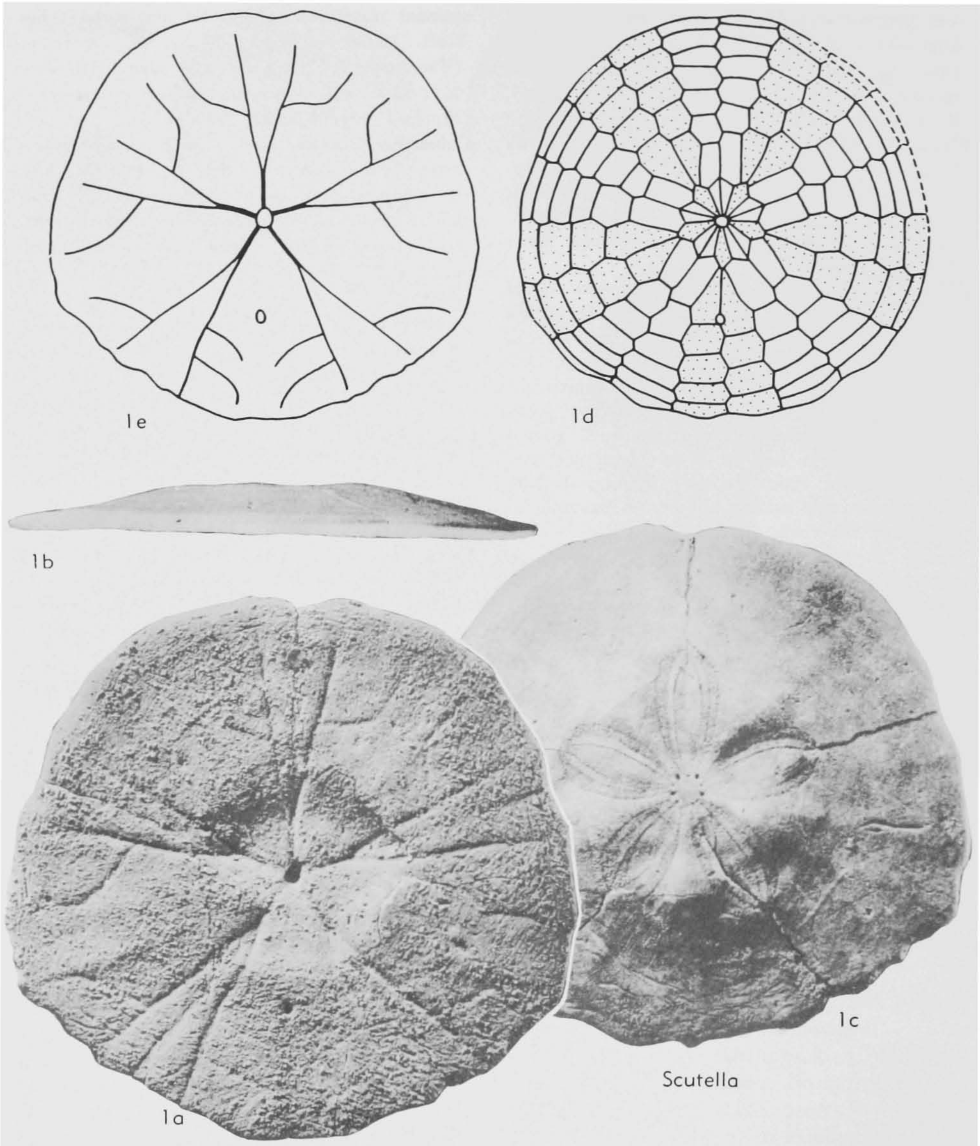


FIG. 366. Scutellidae (p. U477).

Suborder SCUTELLINA Haeckel, 1896

[*nom. correct.* DURHAM & MELVILLE, 1957, p. 259 (*pro* Scutellaria HAECKEL, 1896, p. 488)]

More or less flattened; concentric and radial internal supports; ambulacra petaloid adapically, no pseudocompound plates, outer member of pore pair elongated; interambulacra terminating adapically in pair of plates, usually discontinuous in later genera; apical system pentagonal or stellate, apices interambulacral; auricles fused; basicoronal interambulacral plates as large as ambulacral plates, commonly larger; with ambulacral food grooves; aboral miliary spines terminating in glandular bag; buccal membrane naked; 2 spicules in sucking disc of tube feet. *Eoc.-Rec.*

The oldest recorded genus *(Eoscutella, L.Eoc.)* in the Pacific area is already specialized in its elongate basicoronal plates, thin ambitus, bifurcating food grooves, and highly developed internal supports. In Europe, *Proescutella* of similar age but uncertain suborder, is a generally less specialized but not closely related genus with a groove for the hydropores, and an advanced position for the periproct. In the Gulf of Mexico area the Eocene *Protoscutella* has simple food grooves, but the specialized basicoronal plates and discontinuous posterior interambulacrum show that it is not closely related to the other two genera. These points indicate that ancestral scutellinids should be present in the Paleocene, if not in the Late Cretaceous.

Family SCUTELLIDAE Gray, 1825

[Scutellidae Gray, 1825, p. 527] [*emend.* Durham, 1955, p. 150]

Medium-sized to large, flattened, internal supports well developed; petals closed, outer member of pore pair subdivided; interambulacra continuous, usually as wide as ambulacra at ambitus; primordial ambulacral and interambulacral plates about equal; 4 genital pores; periproct on oral surface; food grooves bifurcating close to peristome. *Oligo.-Mio.*

Scutella Lamarck, 1816, p. 7 [**S. subrotunda* (=**Echinodiscus subrotundus* Leske, 1778); SD L. Agassiz, 1841, p. 5] [=?*Lambertiella* Checchia-Rispoli, 1917, p. 57]. Large, thin, petals about half corresponding radius, anterior petal longer than posterior petals; 6 or 7 ambulacral and 4 or 5 interambulacral plates to column on oral surface; periproct midway on oral surface, between 1st pair coronal plates. *?U.Oligo., Mio.,* Eu.——Fig. 366,*1*. **S. subrotunda* (Leske), Mio., Malta; *1a-c,* oral, lat., aboral, ×0.6; *1d,e,* plates of oral surface (interamb. stippled), food grooves, ×0.5 (189).

Parascutella Durham, 1953, p. 349 [**Scutella leognanensis* Lambert, 1903, p. 173; OD]. Large, thin; petals about 0.7 length of radius, anterior petal shorter than posterior; 5 or 6 ambulacral and 4 or 5 interambulacral plates on oral surface; periproct submarginal, between 3rd pair of coronal plates. *Mio.,* Eu.——Fig. 367,*2*. **P. leognanensis* (Lambert), Fr.; *2a,b,* aboral, oral, ×0.7; *2c,* plates of oral surface (interamb. stippled), ×0.6 (6, 189).

Parmulechinus Lambert, 1910, p. 63 [*pro Stenaster* Lambert, 1905, p. 140 (*non* Billings, 1858)] [**Stenaster labrei* Lambert, 1905 (=*Scutella agassizi* Oppenheim, 1902, =*S. striatula* L. Agassiz, 1841, *non* de Serres, 1829); OD]. Medium-sized to large, thin; petals small, about 0.5 length of radius; ambitus broadly indented at interambulacra; 6 or 7 ambulacral and 4 or 5 interambulacral coronal plates on oral surface; interambulacra about half width of ambulacra at ambitus; periproct marginal to submarginal, approximately between 4th and 5th coronal plates. *Oligo.-L.Mio.,* Eu.——Fig. 367,*1*. **P. agassizi* (Oppenheim), Oligo., Eu.; *1a,b,* aboral, oral ×0.7 (6).

Family PROTOSCUTELLIDAE Durham, 1955

Moderate-sized to large, moderately flattened; petals partly open; paired interambulacra barely in contact with basicoronal plates, posterior interambulacrum variable; interambulacra about as wide as ambulacra at ambitus; 5 genital pores; periproct on oral surface; primordial interambulacral plates much larger than ambulacral. *Eoc.*

Protoscutella Stefanini, 1924, p. 843 [**Scutella mississippiensis* Twitchell, 1915, p. 124; OD]. Test low, ambitus thin, usually with posterior periproctal notch; petals equal, length about half of radius; periproct submarginal, between 3rd and 4th coronal plates; food grooves simple, unbranched; posterior interambulacrum discontinuous; 6 or 7 ambulacral and 3 to 5 interambulacral coronal plates on oral surface. *M.Eoc.-U.Eoc.,* Gulf Mex.-SE.USA.——Fig. 368,*2*. **P. mississippiensis* (Twitchell), M.Eoc., USA(Miss.); *2a,b,* aboral, plates of oral surface (interamb. stippled), ×0.8 (22, 51).

Mortonella Pomel, 1883, p. 231 [*pro Mortonia* Desor, 1858, p. 231, *non* Gray, 1851)] [**Scutella quinquefaria* Say, 1825, p. 228 (=*Scutella rogersi* L. Agassiz, 1841, *non* Morton, 1834); SD ICZN, 1955]. Like *Periarchus* but test thick, margin rounded, petals broader, and periproct midway on oral surface. *U.Eoc.,* GulfMex., SE.USA-Cuba.——Fig. 368,*4*. **M. quinquefaria* (Say), USA (Ga.); *4a-c,* aboral, oral, lat., ×0.8 (22).

Periarchus Conrad, 1866, p. 21 [**Sismondia alta* Conrad, 1865, p. 74; OD]. Test raised apically, ambitus thin; petals open, slender, length slightly over half of radius, anterior longest; periproct oral, nearly half distance from peristome, between 1st pair coronal plates; food grooves bifurcate about midway on oral surface; all interambulacra continuous; usually 7 ambulacral and 4 or 5 interambulacral coronal plates on oral surface. *U.Eoc.,* Gulf Mex.-SE. USA-Cuba.——Fig. 368,*3a,b*. **P. alta* (Conrad), USA(N.Car.); *3a,b,* aboral, lat., ×0.8 (22).——Fig. 368,*3c*. *P. lyelli pileussinensis* (Ravenel), USA(Ga.); plates of oral surface (interamb. stippled), ×0.7 (51).

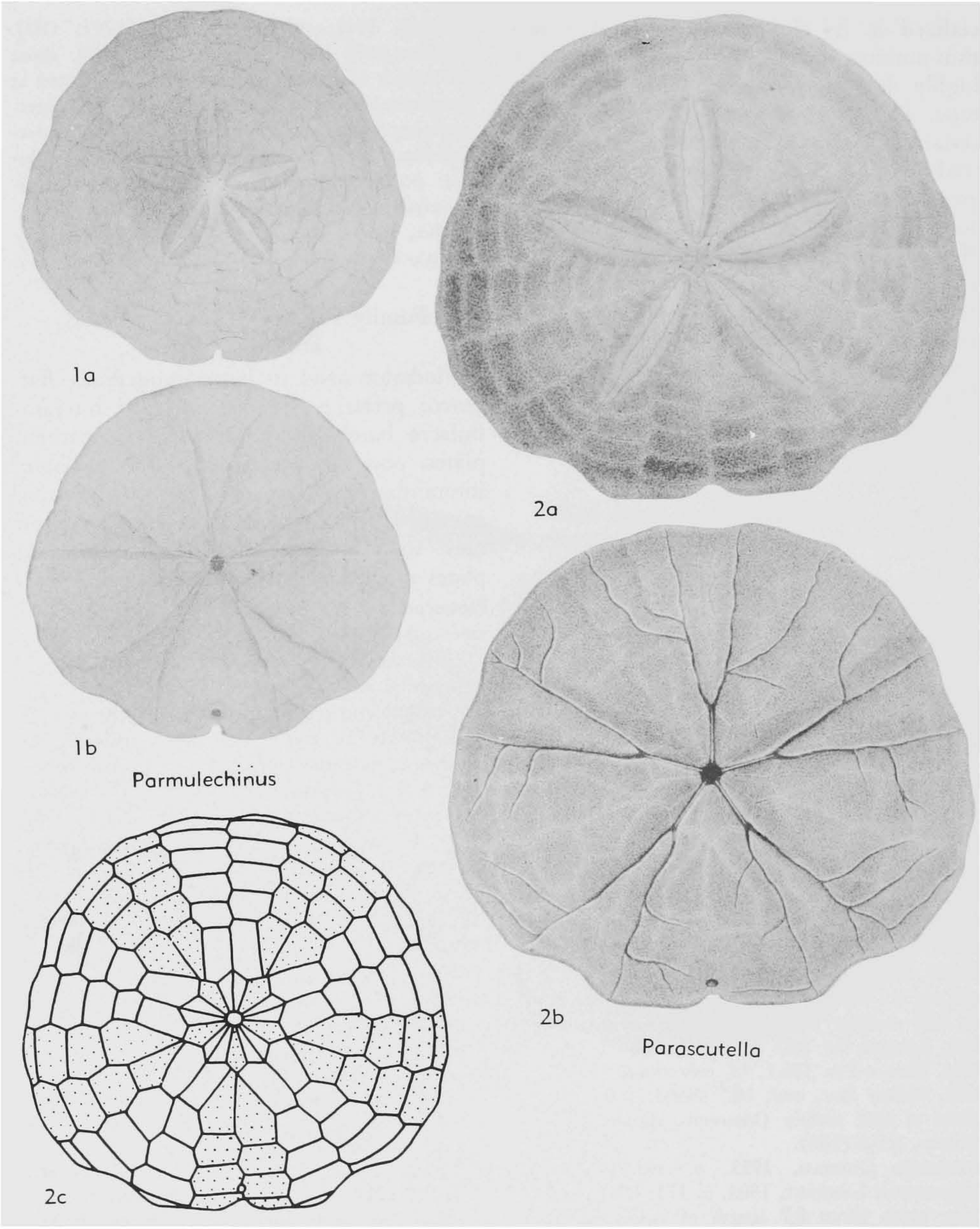


FIG. 367. Scutellidae (p. U477).

Family EOSCUTELLIDAE Durham, 1955

[Eoscutellidae DURHAM, 1955, p. 156]

Moderate-sized, flattened, thin, width greater than length; petals moderately closed; 4 genital pores; food grooves bifurcating close to peristome; interambulacra continuous, about half width of ambulacra at ambitus; periproct marginal. *Eoc.*

Eoscutella GRANT & HERTLEIN, 1938, p. 54 [**Scutella coosensis* KEW, 1920, p. 65; OD]. Petals about half length of anterior radius; margin very thin; broad anal notch; primordial interambulacral plates about 3 times length of ambula-

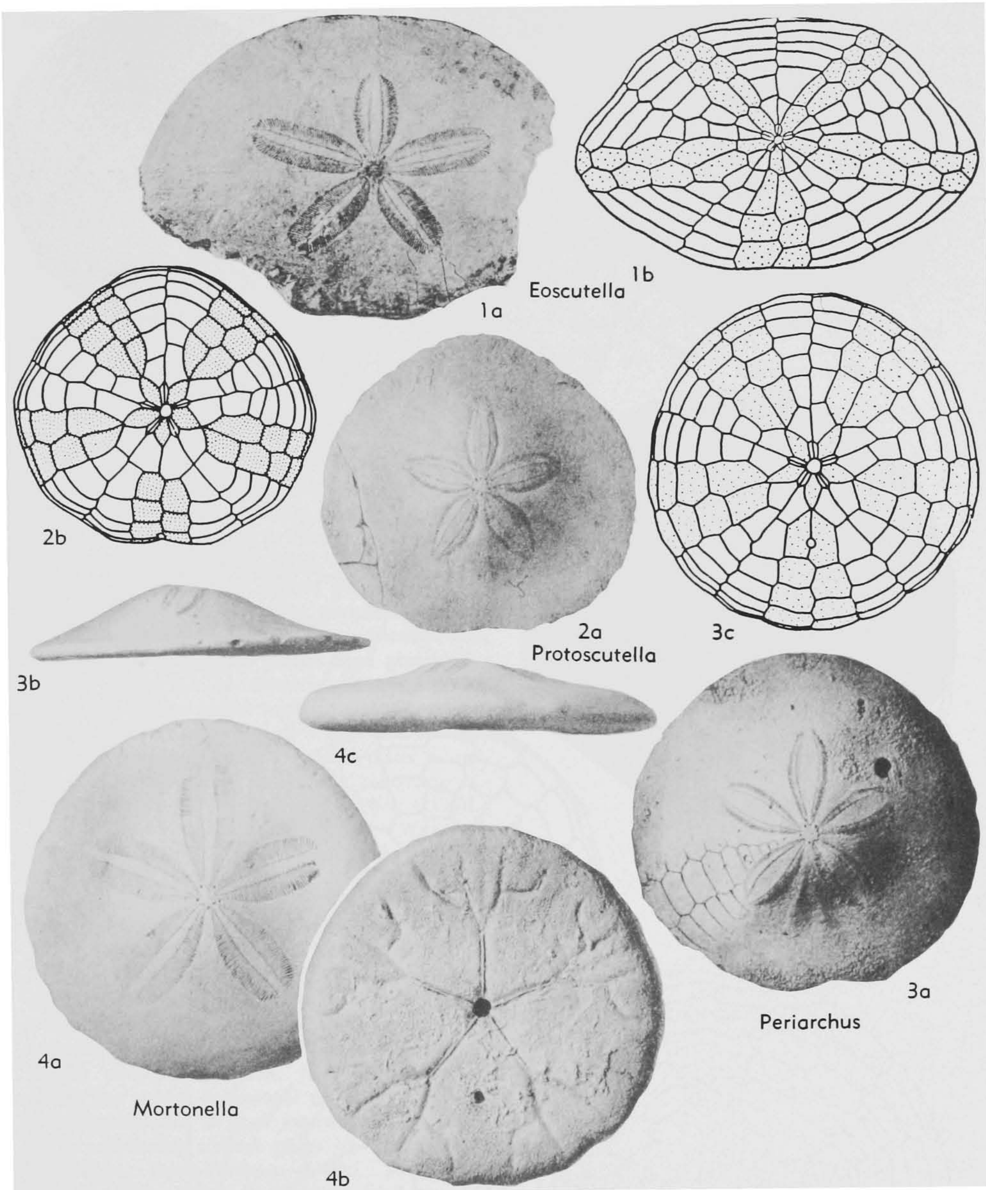


FIG. 368. Protoscutellidae (2-4); Eoscutellidae (1) (p. U477-U479).

cral plates; internal supports highly developed. *Eoc.*, W.USA.——FIG. 368,*1*. **E. coosensis* (KEW), USA(Ore.); *1a*, aboral, ×0.8; *1b*, plates of oral surface (interamb. stippled), ×0.7 (51, 200).

Family DENDRASTERIDAE Lambert, 1889

[Dendrasteridae LAMBERT, 1889, opp. p. 50] [*emend.* DURHAM, 1955, p. 157]

Medium-sized to large; petals well developed; anterior petal more widely open than paired petals; interambulacrum 5 discontinuous; interambulacra nearly as wide as ambulacra at ambitus; 4 genital pores; food grooves bifurcating or trifurcating; periproct inframarginal to supramarginal. *Plio.-Rec.*

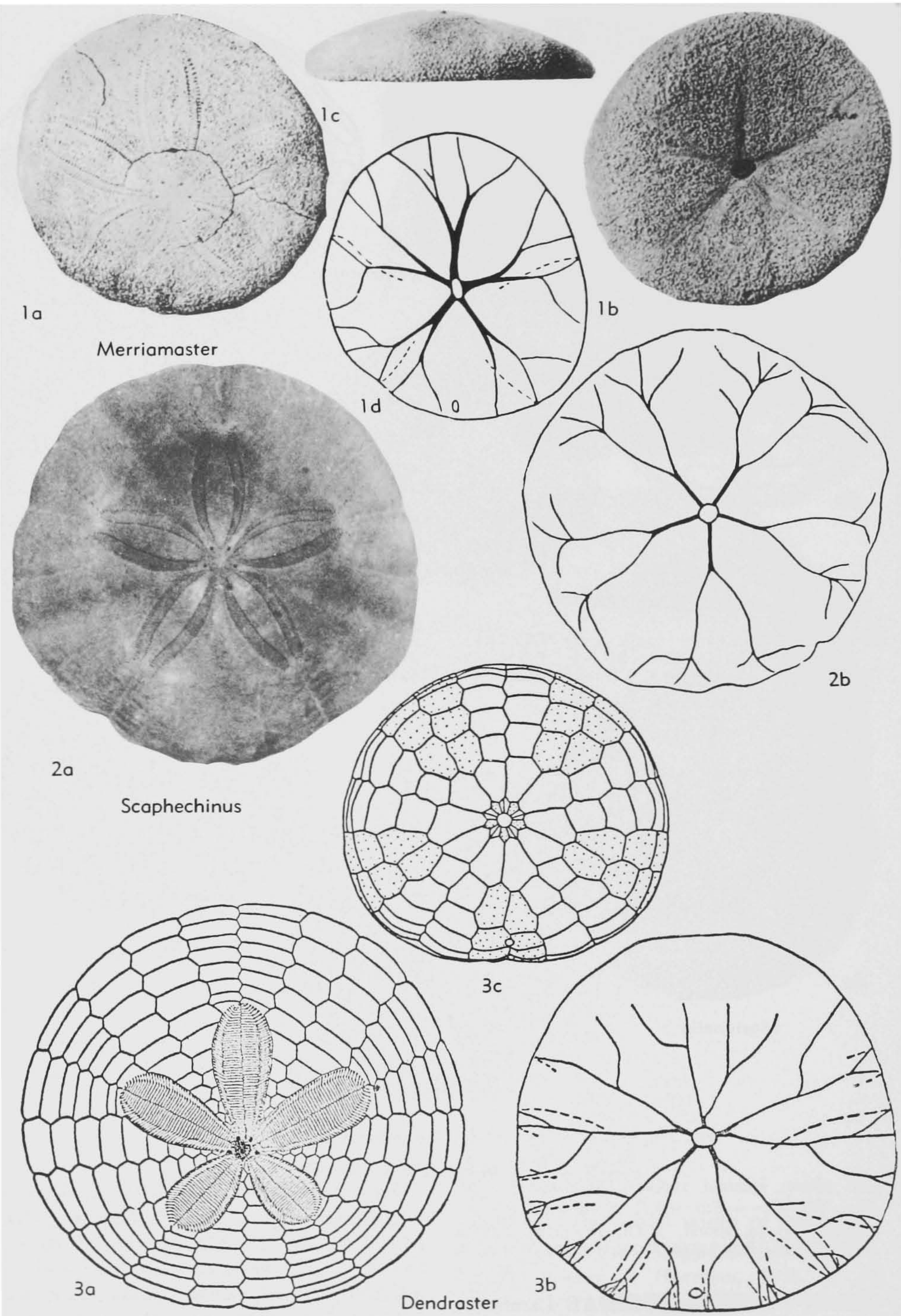


FIG. 369. Dendrasteridae (p. U481).

Dendraster L. Agassiz, 1847, p. 135 [**D. excentricus* (=*Echinarachinus excentricus* Valenciennes, 1846, pl. 10, =**Scutella excentricus* Eschscholtz, 1831, p. 19); OD]. Apical system commonly excentric posteriorly; margin of test moderately thin; anterior petal elongated; periproct inframarginal, between 2nd and 3rd pair coronal plates; food grooves bifurcating, complex, usually extending onto apical surface and best developed posteriorly; interambulacra all discontinuous with 3 or 4 coronal plates on oral surface; ambulacra with 5 or 6 posterior and 7 or 8 anterior coronal plates on oral surface. *Plio.-Rec.,* USA(GulfCalif.-Puget Sound).——Fig. 369,*3*. **D. excentricus* (Eschscholtz), Rec., USA(Calif.-Wash.); *3a,b,* aboral, food grooves, ×1, ×0.8; *3c,* plates of oral surface (interamb. stippled), ×0.6 (51, 69). [See also Figs. 335; 336,*1d*; 348,*2*; 351,*10*.]

Merriamaster Lambert, 1911, p. 64 [**Scutella perrini* Weaver, 1908, p. 273 (=*Orchoporus koehleri* Lambert & Thiéry, 1914, p. 293); OD] [=*Orchoporus* Lambert & Thiéry, 1914, p. 293, =?*Twitchellia* Lambert, 1916, p. 171]. Margin rounded; apical system slightly posterior; length of petals about 0.75 of radius; periproct just submarginal, often on slight rostrum, between 2nd and 3rd pair of coronal plates; food grooves bifurcate about 0.3 of distance from peristome, extending on to apical surface in large adults; interambulacra discontinuous; 3 or 4 interambulacral and 5 to 7 ambulacral coronal plates to column on oral surface; radial and concentric internal supports simple. *?M.Plio., U.Plio.,* C.Calif.-BajaCalif.——Fig. 369,*1*. **M. perrini* (Weaver), U.Plio., USA(Calif.); *1a-c,* aboral, oral, lat., ×1; *1d,* food grooves, ×0.8 (51, 200).

Scaphechinus A. Agassiz, 1863, p. 359 [**S. mirabilis* (=*Chaetodiscus scutella* Lütken, 1864, p. 172); OD] [=*Chaetodiscus* Lütken, 1864, p. 172 (obj.)]. Apical system central, petaloid region slightly depressed, with interambulacral depressions extending to ambitus; ambitus commonly indented at sutures; length of petals about 0.7 of radius; periproct marginal; food grooves bifurcating just outside basicoronal plates; interambulacra discontinuous; 3 or 4 interambulacral and 4 or 5 ambulacral coronal plates on oral surface. *Plio.-Rec.,* Japan-Formosa.——Fig. 369,*2*. **S. mirabilis,* Rec., Japan; *2a,b,* aboral, food grooves, ×0.8 (*2a*, 212a; *2b*, 51). [See also Figs. 348,*1*; 350,*4*; 351,*11*.]

Scutellaster Cragin, 1895, p. 90 [**S. cretaceus* (*=*Scutella interlineata* Stimpson, 1856, p. 153); OD] [=*Calaster* Kew, 1920, p. 130 (type, *Scutella interlineata* Stimpson) (obj.); *Anorthoscutum* Lambert & Thiéry, 1914, p. 319 (type, *Scutella interlineata* Stimpson) (obj.)]. Margin of test thin to thick; apical system slightly posterior; outline of test rounded to indented interambulacrally; petals about 0.75 length of radius; periproct supramarginal, between 2nd pair of plates from ambitus;

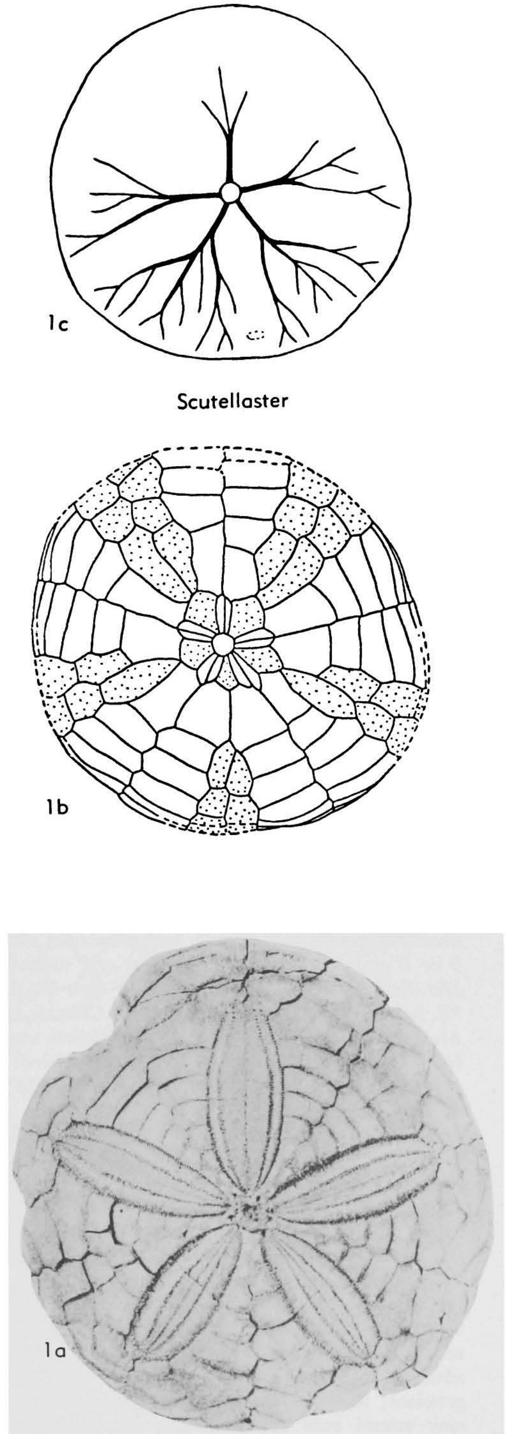


Fig. 370. Dendrasteridae (p. *U*481-*U*482).

food grooves trifurcating 0.3 distance from peristome, poorly developed anteriorly; both columns of anterior, and posterior column only of posterior paired interambulacra in contact with basicoronal plates; 2 or 3 interambulacral and 4 or 5 ambulacral coronal plates on oral surface. *Plio.*, USA (C.Calif.-Alaska)-?Sakhalin.——FIG. 370,*1a,b*. *S. interlineatus* (STIMPSON), U.Plio., USA(Calif.); *1a,b,* aboral, plates of oral surface (interamb. stippled), ×0.7 (51, 200).——FIG. 370,*1c*. *S. major* (KEW), U.Plio., USA(Calif.); food grooves, ×0.7 (51).

Family ECHINARACHNIIDAE Lambert, 1914

[Echinarachniidae LAMBERT, 1914, p. 314] [*emend.* DURHAM, 1955, p. 163]

Medium-sized to large; petals well developed, anterior petal more open than paired petals; interambulacrum 5 may be discontinuous; interambulacra 0.7 or less, width of ambulacra at ambitus; 4 genital pores; periproct marginal to inframarginal; food grooves with central trunk. *Oligo.-Rec.*, N. Pac.; *Rec.*, NE.N.Am.

Echinarachnius GRAY, 1825, p. 428 [*nom. conserv.* ICZN, 1954] [**Scutella parma* LAMARCK, 1816, p. 11; SD L. AGASSIZ, 1841, p. 5] [=*Phelsumia* POMEL, 1883, p. 70 (obj.); *Phelsumaster* LAMBERT & THIÉRY, 1914, p. 316 (obj.)]. Petals lyrate, about 0.6 length of radius; periproct marginal, between 3rd pair coronal plates; food grooves with straight trunk, 2 equal lateral branches near margin; contact of coronal interambulacral plates with primordial plates very variable; posterior area usually discontinuous; 3 or 4 interambulacral and 5 or 6 ambulacral coronal plates on oral surface. *Mio.-Rec.*, N.Pac.; *Rec.*, NE.N.Am.——FIG. 371,*4*. **E. parma* (LAMARCK), Rec., N.Am.(E.Can., *4a,b*; Alaska, *4c*); *4a-c,* aboral, oral, plates of oral surface (usual arrangement, interamb. stippled), ×0.8 (6, 51). [See also Figs. 336,*1i*; 350,*5*; 351,*12*.]

Astrodapsis CONRAD, 1856, p. 315 [**A. antiselli* (*non* KEW, 1920); OD] [=*Asterodapsis* A. AGASSIZ, 1872, p. 172 *(nom. van.)*; *Astrodaspis* LAMBERT & THIÉRY, 1914, p. 314 *(nom. null.)*]. Medium-sized to large, outline rounded, elongate or pentagonal; margin thin to inflated, most strongly indented at posterior ambulacra; periproct marginal to just submarginal; petals slightly to strongly raised, apical system not raised; petals usually broad, more or less open; apical surface of advanced species with broad interambulacral depressions; food grooves as in *Echinarachnius* but may extend onto apical surface; interambulacra continuous in early and discontinuous in later species; 4 or 5 interambulacral and 5 to 9 ambulacral coronal plates on oral surface. *M.Mio.-L.Plio.*, USA(Calif.).——FIG. 371,*2*. **A. antiselli*, L.Plio.; *2a-d,* aboral, oral, lat., plates of oral surface (interamb. stippled), ×0.8 (51, 200).

Kewia NISIYAMA, 1935, p. 136 [**Scutella blancoensis* KEW, 1920, p. 64; OD] [=*Kewia* NISIYAMA, 1934, p. 489 *(nom. nud.)*]. Small to medium-sized; anterior petal open, paired petals moderately closed; petals about 0.7 length of radius; periproct supramarginal, close to margin; food grooves simple; posterior interambulacrum discontinuous, paired interambulacra usually continuous; 2 or 3 interambulacral and 3 to 5 ambulacral coronal plates on oral surface. *Oligo.-Mio.*, N.Am.-N.Pac. ——FIG. 371,*1*. **K. blancoensis* (KEW), M.Mio., USA(Ore.); *1a-d,* aboral, lat., oral, plates of oral surface (interamb. stippled), ×1 (51, 200).

Nipponaster DURHAM, 1952, p. 844 [**Astrodapsis nipponicus* NISIYAMA, p. 602; OD] [=*Pseudoastrodapsis* DURHAM, 1953, p. 756 (obj.]. Margin rounded, outline slightly elongate; petals open, slightly raised, length about 0.75 of radius; periproct submarginal between 2nd and 3rd pair coronal plates; food grooves simple; paired interambulacra continuous, posterior discontinuous; interambulacra about 0.25 width of ambulacra at ambitus. *"Mio.-Plio.,"* Japan-?Sakhalin-?Kamchatka.——FIG. 371,*3*. **N. nipponicus* (NISIYAMA), Japan; *3a-d,* aboral, oral, lat., plates of oral surface (interamb. stippled), ×1.5 (51, 212b).

Remondella DURHAM, 1955, p. 168 [**Clypeaster gabbi* RÉMOND, 1863, p. 53; OD]. Like *Kewia,* but periproct marginal, and ambulacra with more numerous plates near ambitus on oral surface. *U.Mio.-L.Plio.*, USA(Calif.).——FIG. 372,*2*. **R. gabbii* (RÉMOND), U.Mio.; plates of oral surface (interamb. stippled), ×1.2 (51).

Tenuirachnius DURHAM, 1955, p. 169 [**Scutella gabbi* var. *tenuis* KEW, 1915, p. 71 (=*Echinarachnius gabbii kleinpelli* GRANT & HERTLEIN, 1938, p. 60, =*Scutella gabbi tenuis* KEW, *non Echinarachnius tenuis* YOSHIWARA, 1898); OD]. Like *Kewia,* but periproct barely supramarginal, test thin and flattened, and 3 pairs of oral coronal plates in interambulacrum 5. *U.Mio.*, USA(Calif.). ——FIG. 372,*1*. **T. kleinpelli* (GRANT & HERTLEIN); *1a,b,* plates of oral surface, aboral view, ×1 (51, 200).

Vaquerosella DURHAM, 1955, p. 166 [**Scutella andersoni* TWITCHELL, 1915, p. 183; OD]. Small to large, width commonly greater than length; ambitus indented at ambulacra, most strongly posteriorly; petals more or less raised, anterior petal open, paired petals slightly closed, 0.7 to 0.75 length of radius; periproct marginal; food grooves simple; posterior interambulacra discontinuous, anterior paired interambulacra variable; orally 3 or 4 coronal plates in paired interambulacra and 2 in posterior; 5 or 6 coronal oral plates in anterior

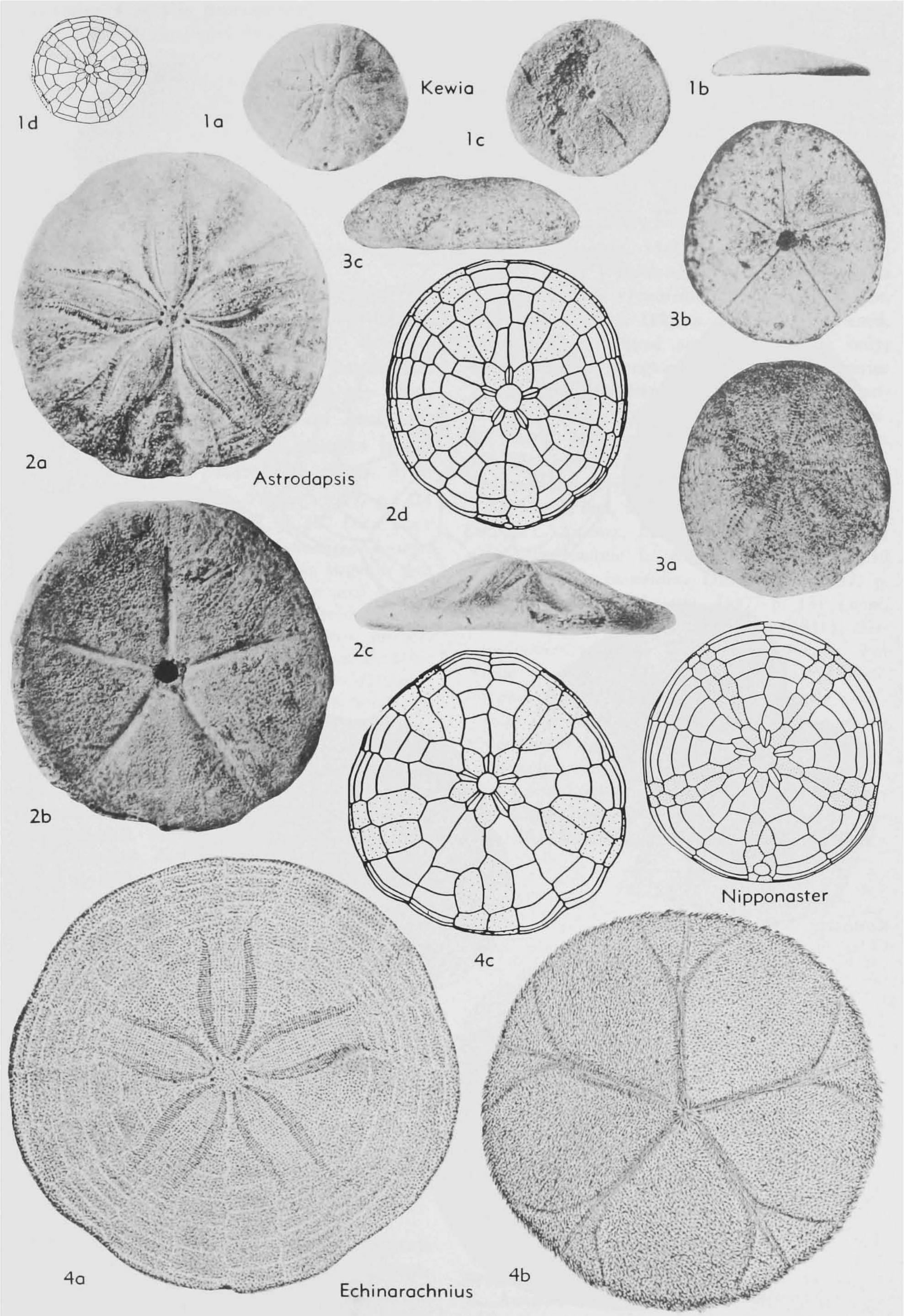


FIG. 371. Echinarachniidae (p. *U*482).

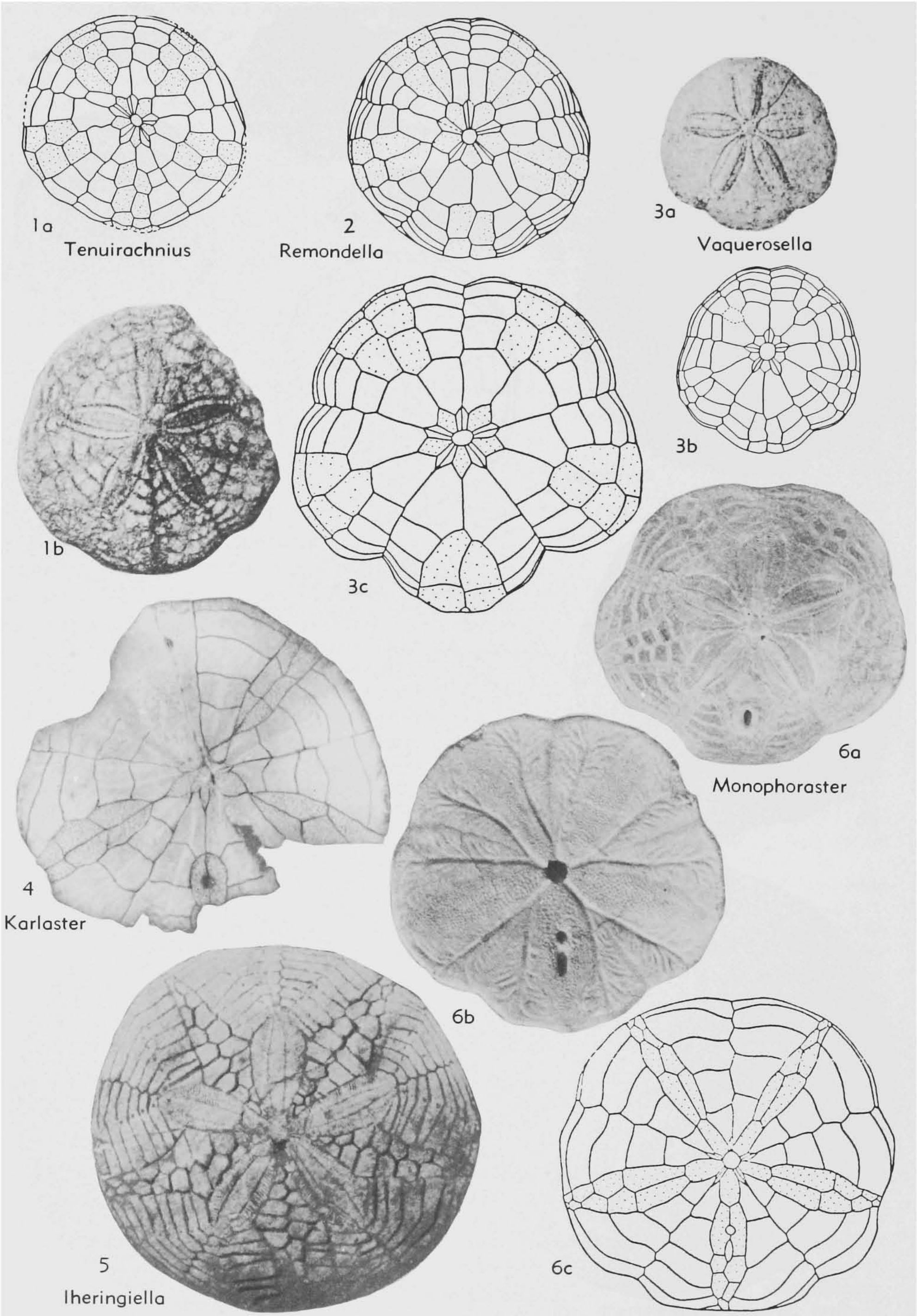


FIG. 372. Echinarachniidae *(1-3)*; Monophorasteridae *(4-6)* (p. U482, U485).

ambulacra, 4 or 5 in posterior ambulacra. *L.Mio.*, USA(Calif.)-Mexico(BajaCalif.).——FIG. 372,*3a,b*. **V. andersoni* (TWITCHELL), Calif.; *3a,b*, aboral view, plates of oral surface (interamb. stippled), ×1 (51, 200).——FIG. 372,*3c*. *V. norrisi* (PACK), Calif.; plates of oral surface (interamb. stippled), ×1 (51).

Family MONOPHORASTERIDAE Lahille, 1896

[Monophorasteridae LAHILLE, 1896, p. 441 (*emend.* DURHAM, 1955, p. 169)]

Medium-sized to large, flattened; well-defined but variably open petals; interambulacra continuous, narrower at ambitus than midway on oral surface; primordial interambulacral plates much larger than ambulacral plates; periproct on oral surface; 4 genital pores; food grooves bifurcating just outside primordial plates. *Mio.*

Monophoraster LAMBERT & THIÉRY, 1921, p. 324 [*pro Monophora* DESOR, 1847, p. 287 (*non* BORY DE ST. VINCENT, 1804)] [**Monophora darwini* DESOR, 1847, p. 287; OD]. Petals large, length 0.7 radius, anterior longest; posterior anal lunule; periproct between lunule and peristome; interambulacra greatly constricted at ambitus; primordial interambulacral plates much elongated. *Mio.*, Arg.-Chile.——FIG. 372,*6*. **M. darwini* (DESOR), Arg.; *6a,b*, aboral, oral views, ×0.8; *6c*, plates of oral surface (interamb. stippled), ×0.6 (51, 202a).

Iheringiella BERG, 1898, p. 16 [*pro Iheringia* LAHILLE, 1898, p. 437 (*non* KEYSERLING, 1891)] [**Scutella patagoniensis* DESOR, 1847, p. 287; OD] [=*Iheringiana* BERG, 1898, p. 41 (obj.); *Iheringina* LAHILLE, 1899, p. 395 (obj.)]. Petals partly closed to lyrate, length 0.7 radius; no lunules; periproct submarginal, between 2nd and 3rd pair coronal plates; 3 or 4 interambulacral, and 4 or 5 ambulacral coronal plates per column on oral surface. *Mio.*, Arg.——FIG. 372,*5*. **I. patagoniensis* (DESOR); aboral view, ×1 (202b).

Karlaster MARCHESINI SANTOS, 1958, p. 16 [**K. pirabensis*; OD]. Like *Monophoraster* but with posterior interambulacrum discontinuous orally, and food grooves trifurcating (?) near peristome. *Mio.*, Brazil.——FIG. 372,*4*. **K. pirabensis*; plates of oral surface, ×0.8 (207).

Family MELLITIDAE Stefanini, 1911

[Mellitidae STEFANINI, 1911, p. 749 (*emend.* DURHAM, 1955, p. 171)]

Medium-sized to large, flattened; petals well defined, moderately closed, outer member of pore pair greatly elongated; internal supports well developed; posterior interambulacral and paired ambulacral lunules or notches; paired interambulacra not continuous, posterior interambulacrum variable; on oral surface interambulacra widest at ambitus, about as wide as ambulacra; basicoronal plates small; periproct oral, between posterior lunule and peristome; food grooves bifurcating just outside primordial plates. [Tropical and warm temperate Americas.] *L.Mio.-Rec.*

Mellita L. AGASSIZ, 1841, p. 34 [*nom. conserv.* ICZN, 1956] [**Echinodiscus quinquiesperforatus* LESKE, p. 197 (=*Mellita testudinata* KLEIN, 1734); SD POMEL, 1883, p. 71]. Thin, flattened, ambitus sharp; paired ambulacral lunules only; lunules narrow, elongate, normally closed; anterior paired petals shortest, others about equal; peristome and apical system slightly anterior; 4 genital pores; posterior interambulacrum continuous. *Mio.-Rec.*, N.Am.-S.Am.-W.Indies.——FIG. 373,*1*. **M. quinquiesperforata* (LESKE), Rec., Puerto Rico; *1a-c*, aboral, oral, lat. views, ×0.7 (6).

Encope L. AGASSIZ, 1840, p. 6, 17 [**E. grandis*; OD] [=*Moulinia* L. AGASSIZ, 1841, p. 3, 139 (type, *Scutella cassidulina* DESMOULINS, 1837, p. 78); *Moulinsia* L. AGASSIZ, 1847, p. 139 (*nom. van. pro Moulinia*) (*non* GRATELOUP, 1841); *Desmoulinaster* LAMBERT & THIÉRY, 1914, p. 294 (type, *Scutella cassidulina* DESMOULINS); *Echinoglyphus* GRAY, 1852, p. 37 (type, *Scutella emarginata* LAMARCK, 1816, p. 9, =*Echinodiscus emarginatus* LESKE, 1778, p. 200; SD, herein); *Echinoglycus* GRAY, 1855, p. 24 (*nom. null.?*); *Ravenellia* LÜTKEN, 1864, p. 168 (type, *Scutella macrophora* RAVENEL, 1843, p. 81); *Macrophora* CONRAD, 1865, p. 134 (type, *Scutella macrophora* RAVENEL, 1843, p. 81)]. Like *Mellitella*, but with apical system and peristome slightly anterior; posterior petals longest; posterior interambulacrum continuous; posterior lunule more than half inside line connecting ends of petals. *L.Mio-Rec.*, N. Am.-S. Am.-W. Indies.——FIG. 373,*4*. **E. grandis*, Rec., Gulf Calif.; *4a,b*, aboral, oral views, ×0.6; *4c*, plates of oral surface (interamb. stippled), ×0.5 (1, 51). [See also Figs. 339,*F*; 341,*1a,b*.]

Leodia GRAY, 1852, p. 36 [**L. richardsoni* (=**Echinodiscus sexiesperforatus* LESKE, 1778, p. 199, =*Echinus hexaporus* GMELIN, 1789, p. 3189, =*Scutella sexforis* LAMARCK, 1816, p. 9); OD]. Like *Mellita* but with 5 closed ambulacral lunules. *U.Mio.-Rec.*, E. N. Am.-E. S. Am.——FIG. 373,*2*. **L. sexiesperforatus* (LESKE), Rec., E. USA; plates of oral surface (interamb. stippled), ×0.6(51). [See also Figs. 336, *lk*; 340,*6*; 352,*9*.]

Mellitella DUNCAN, 1889, p. 162 [**Encope stokesii* L. AGASSIZ, 1841, p. 59; OD]. Margin thick or thin; 5 ambulacral lunules, open or closed; posterior interambulacral lunule outside petals; apical

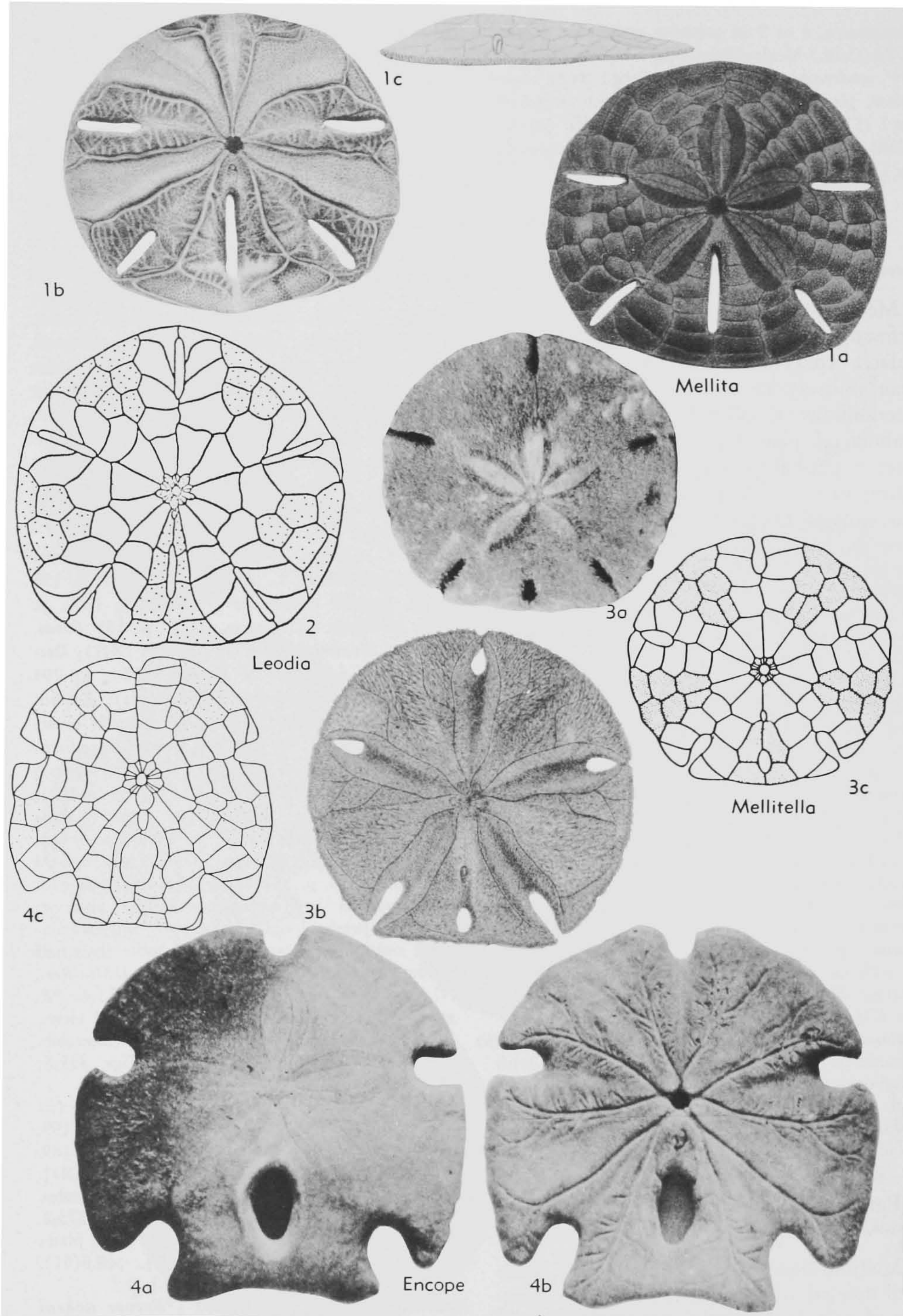


FIG. 373. Mellitidae (p. U485, U488).

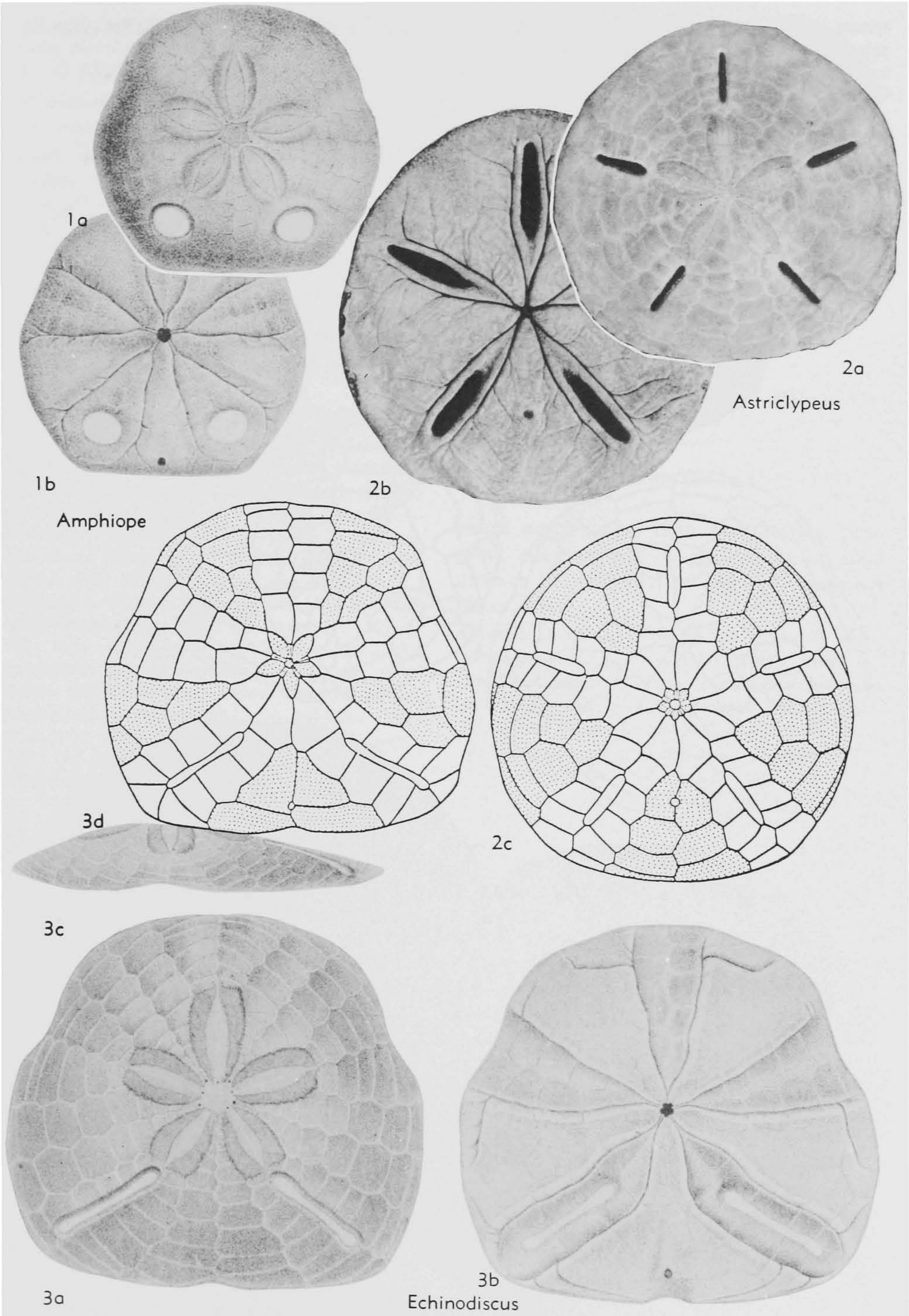


FIG. 374. Astriclypeidae (p. U489).

system and peristome slightly posterior· posterior paired petals shortest; 5 genital pores; posterior interambulacrum discontinuous. *Mio.-Plio.*, E.Pac., Carib. (neotropical); *Rec.*, E. Pac. (tropical).——

FIG. 373,3. *M. *stokesii* (AGASSIZ), Rec., Ecuador; *3a,b,* aboral, oral views, ×0.8, ×0.6; *3c,* plates of oral surface (interamb. stippled), ×0.8 (6, 51, 136g).

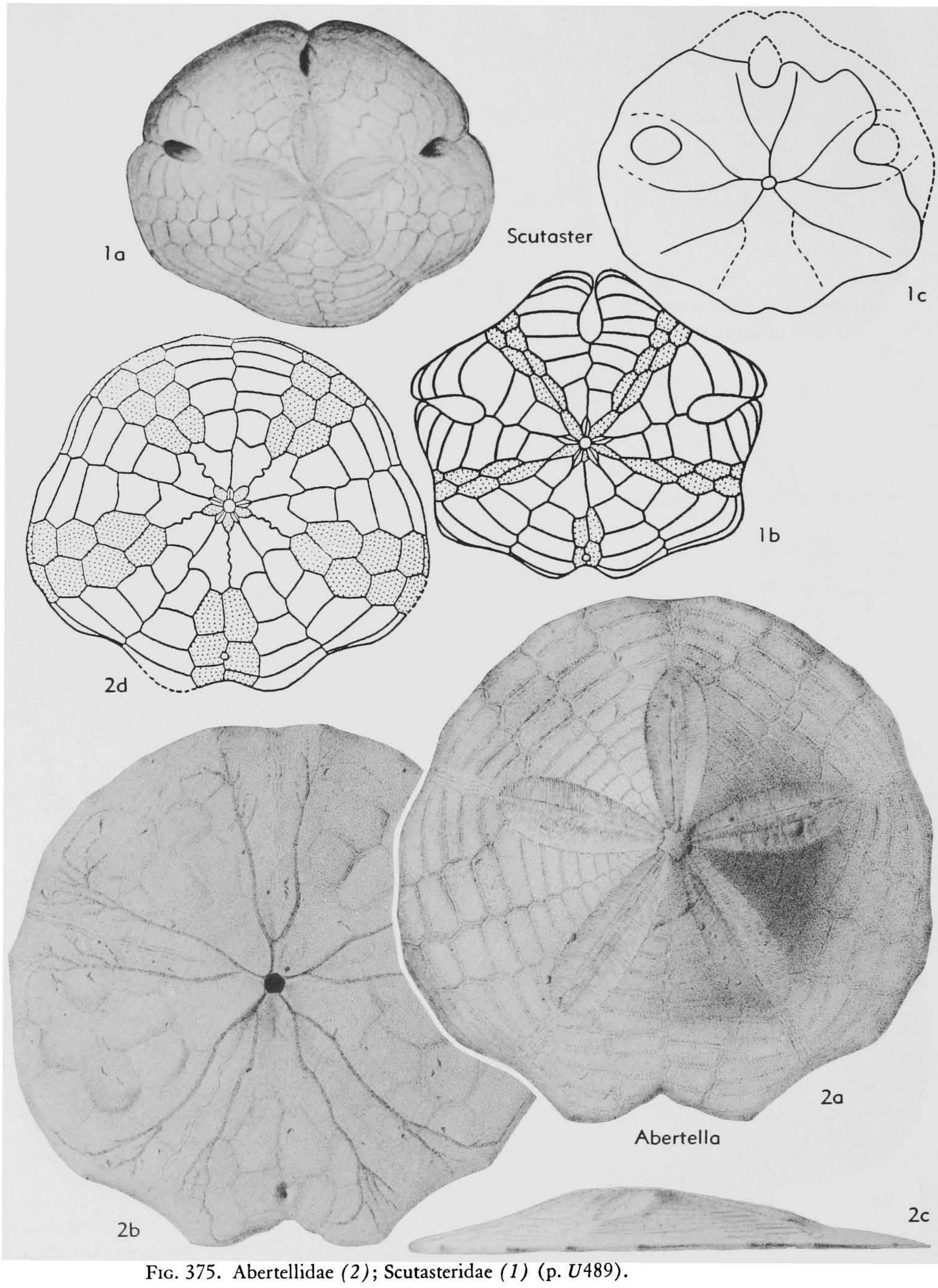


FIG. 375. Abertellidae *(2)*; Scutasteridae *(1)* (p. U489).

Family ASTRICLYPEIDAE Stefanini, 1911

[Astriclypeidae STEFANINI, 1911, p. 747]

Medium-sized to large, flattened, margin thin; internal supports well developed, with paired posterior ambulacral lunules or notches; anterior ambulacral lunules present in some forms; petals well defined; posterior interambulacra discontinuous, others variable; interambulacra about as wide as ambulacra at ambitus; primordial interambulacral plates much larger than ambulacrals; 4 genital pores; periproct on oral side; food grooves bifurcating just outside primordial plates. *Oligo.-Rec.*

Astriclypeus VERRILL, 1867, p. 311 [**A. manni*; OD] [=*Crustulum* TROSCHEL, 1868, p. 1 (obj.)]. Five ambulacral lunules; apical system central; all interambulacra discontinuous; periproct midway on oral surface. *Mio.-Rec.*, Cambodia-S.Japan.——FIG. 374,*2*. **A. manni*, Rec., S. Japan; *2a-c*, aboral, oral views, plates of oral surface (interamb. stippled), ×0.5 (51,136g). [See also FIG. 336,*1m*.]

Amphiope L. AGASSIZ, 1840, p. 6, 17 [**Scutella bioculata* DESMOULINS, 1835; SD LAMBERT, 1907, p. 49]. Like *Echinodiscus* but lunules broad and transversely (except Oligocene species) oval, apical system slightly anterior. *Oligo.-Mio.*, Eu.; *Mio.*, Angola-India.——FIG. 374,*1*. **A. bioculata* (DESMOULINS), Mio., Fr.; *1a,b,* aboral, oral views, ×0.8 (6). [See also Fig. 345,*4*.]

Echinodiscus LESKE, 1778, p. 195 [**E. bisperforatus* (=*Echinoglycus irregularis* LESKE, 1778, p. 197, =*Lobophora bifora* L. AGASSIZ, 1841, p. 64); SD ICZN, 1950][=*Echinoglycus* LESKE, 1778, p. 197 (obj.); *Lobophora* L. AGASSIZ, 1841, p. 64 (obj.) (*non* CURTIS, 1825); *Tretodiscus* POMEL, 1883, p. 71 (obj.); *Tetrodiscus* LAMBERT & THIÉRY, 1921, p. 323 *(nom. van.)*]. Two elongate, narrow posterior ambulacral lunules, open or closed; apical system central; anterior petal longest, posterior petals shortest; periproct about 0.2 distance from ambitus, between 1st and 2nd coronal plates; anterior interambulacra usually discontinuous. *Mio.-Rec.*, IndoPac.——FIG. 374,*3*. **E. bisperforatus,* Rec., IndoPac.; *3a-c,* aboral, oral, lat. views, ×0.7; *3d,* plates of oral surface (interamb. stippled), ×0.6 (6, 51). [See also Figs. 348,*6*; 354,*2*.]

Family ABERTELLIDAE Durham, 1955

[Abertellidae DURHAM, 1955, p. 177]

Medium-sized to large; internal supports well developed; margin with broad ambulacral and anal indentations; petals well defined, nearly closed; interambulacra all discontinuous; basicoronal interambulacral

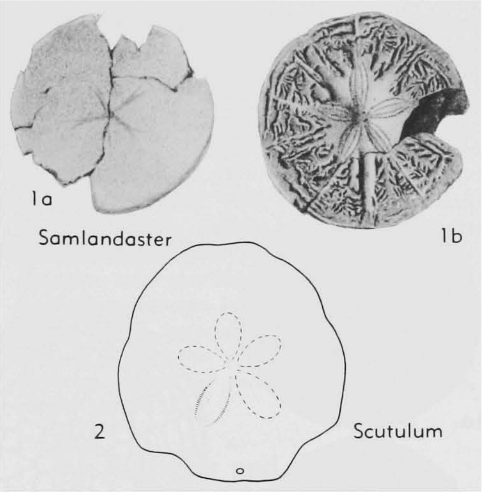


FIG. 376. Family Uncertain (p. *U*489-*U*491).

plates much larger than ambulacrals; periproct submarginal; 4 genital pores; food grooves bifurcating just outside primordial plates. *Mio.*

Abertella DURHAM, 1953, p. 350 [**Scutella aberti* CONRAD, 1842, p. 194; OD]. Petals about 0.7 length of radius; posterior marginal indentations most prominent; periproct between 2nd pair postbasicoronal plates; interambulacra about 0.5 width of ambulacra at ambitus. *Mio.*, N.Am.(Md.)-C. Am.——FIG. 375,*2*. **A. aberti* (CONRAD), USA (Md.); *2a-c,* aboral, oral, lat. views, ×0.5; *2d,* plates of oral surface (interamb. stippled), ×0.4 (22, 51).

Family SCUTASTERIDAE Durham, 1955

[Scutasteridae DURHAM, 1955, p. 178]

Medium-sized to large; internal supports well developed; with 3 ovate anterior ambulacral lunules or indentations; anterior petal more open than paired petals which are moderately closed; posterior interambulacrum discontinuous; 4 genital pores; periproct submarginal; food grooves bifurcating just outside primordial plates. *L.Mio.*

Scutaster PACK, 1909, p. 278 [**S. andersoni*; OD]. Posterior anal notch; periproct just submarginal; interambulacra very narrow, on oral surface; apical system and peristome slightly posterior; primordial plates of paired interambulacra elongated. *L.Mio.*, USA(Calif.).——FIG. 375,*1a*. **S. andersoni*; aboral view, ×0.8 (200).——FIG. 375,*1b,c*. *S. vaquerosensis* LOEL & COREY; *1b,c,* plates of oral surface (interamb. stippled), food grooves, ×0.6 (51).

Family UNCERTAIN

Samlandaster Lambert & Thiéry, 1914, p. 293 [**Scutella germanica* von Beyrich, 1847, p. 101; OD]. Small, thin; petals narrow, 0.3 length of radius; ambulacral pores nearly equal; apical system central, 4 genital pores; periproct supramarginal; food grooves bifurcating near peristome; internal supports highly developed. *U.Eoc.*, Eu.——Fig. 376,*1*. **S. germanica* (Beyrich), Pol.; oral view, ×0.8 (141).

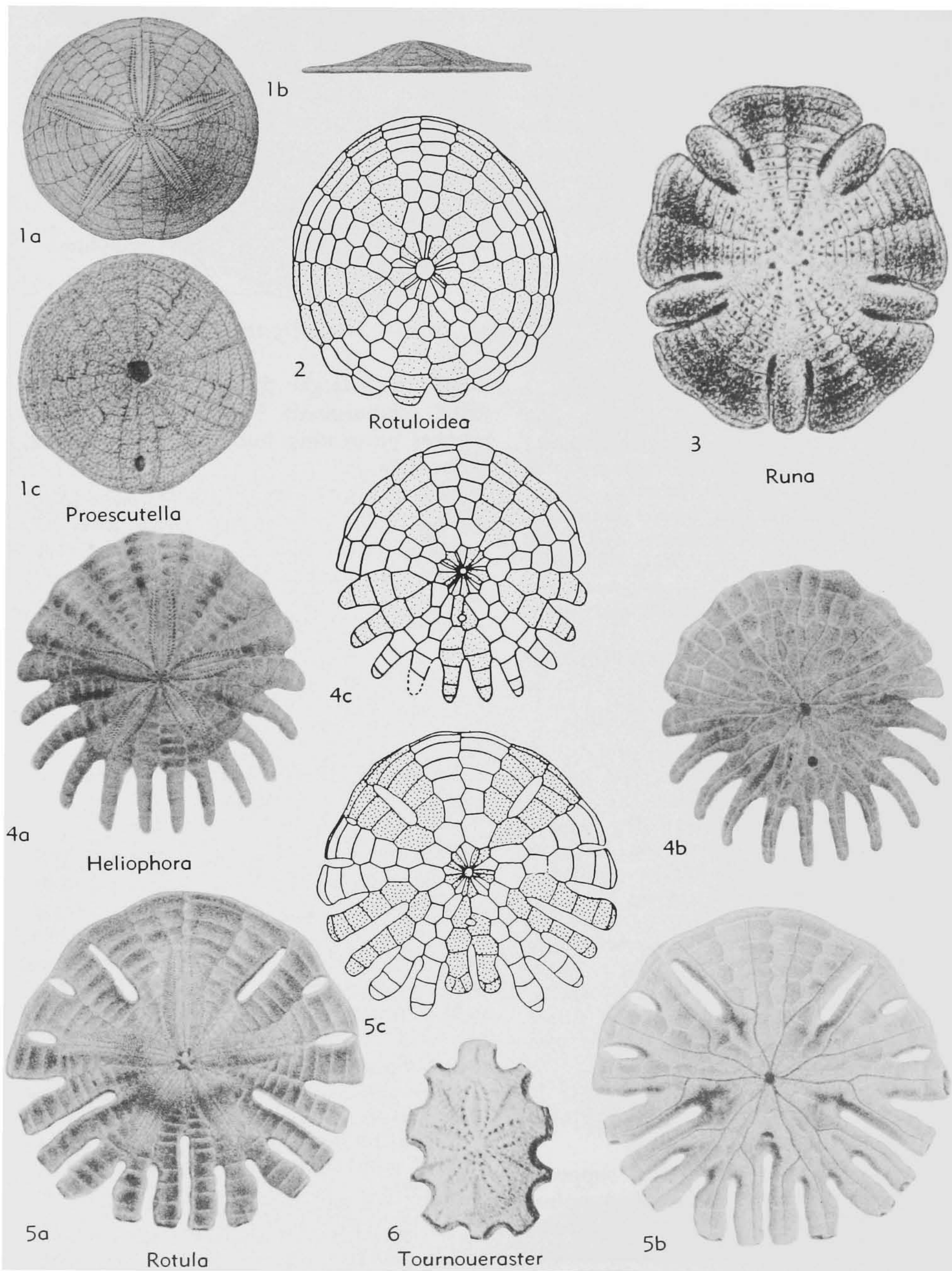


Fig. 377. Rotulidae *(2,4,5)*; Family Uncertain *(1,3,6)* (p. *U*491).

Scutulum TOURNOUER, 1869, p. 981 [**S. parisiense*; OD] [=*Scutellum* FRITEL, 1910, p. 209 *(nom. null.)* (*non* PUSCH, 1833)]. Small, thin, flattened; ambitus indented ambulacrally; petals about 0.5 length of radius, shortest anteriorly, moderately closed; 4 genital pores; periproct supramarginal; food grooves bifurcating about 0.3 distance from peristome. *Oligo.*, Fr.——FIG. 376,*2*. **S. parisiense*; sketch of aboral surface, ×1.5 (51).

Suborder ROTULINA Durham, 1955

[Rotulina DURHAM, 1955, p. 183]

Test flattened, posteriorly dentate or digitate; concentric and radial internal supports; ambulacra petaloid adapically; petals well defined, anterior most widely open, pore pairs mostly conjugate; no pseudocompound plates; posterior interambulacrum continuous, others variable; interambulacra about as wide as ambulacra at ambitus, terminating adapically in series of single plates; apical system compact, stellate, apices ambulacral; 4 genital pores; periproct oral; 20 basicoronal plates, including 5 reduced interambulacral plates, remaining 5 primary interambulacral plates as large as ambulacral plates; auricles fused; food grooves bifurcating near peristome; aboral miliary spines smooth, terminating in crown; 3 spicules in sucking disc of tube feet. *Mio.-Rec.*

Family ROTULIDAE Gray, 1855

[*nom. transl.* DURHAM, 1955, p. 183 (*ex* Rotulina GRAY, 1855, p. 65); *emend.* DURHAM, 1955, p. 183]

Characters of suborder. *Mio.-Rec.*

Rotula SCHUMACHER, 1817, p. 33, 84 [**R. multiloba* (=*Echinodiscus octiesdigitatus* LESKE, 1778, p. 211, =*Echinus orbiculus* var. β LINNÉ, 1758, p. 666, =*Rotula augusti* auctt.); SD DESOR, 1858, p. 238] [=*Echinotrochus* POMEL, 1883, p. 72 (obj.)]. Test unequally digitate posteriorly, with paired anterior interambulacral lunules; pore pairs conjugate, outer pore elongate and subdivided, periproct oral; between 1st pair of coronal plates; paired interambulacra usually discontinuous. *Mio.-Rec.*, W.Afr.——FIG. 377,*5*. **R. octiesdigitatus* (LESKE), Rec.; *5a-c*, aboral, oral, plate of oral surface (interamb. stippled), ×0.6 (6, 51).

Heliophora L. AGASSIZ, 1840, p. 17 [**Echinus orbiculus* var. α LINNÉ, 1758, p. 666 (=*Rotula rumphii* auctt.); SD LAMBERT, 1906, p. 126] [=*Hemiheliopsis* LAMBERT, 1906, p. 128 (type, *H. fonti*); *Radiorotula* LAMBERT & THIÉRY, 1921, p. 321 (obj.)]. Posteriorly equally digitate, no lunules; pore pairs conjugate, outer pore simple; periproct oral, between 1st pair of coronal plates; paired interambulacra usually discontinuous, but variable. *Mio.-Rec.*, W.Afr.——FIG. 377,*4*. **H. orbiculus* (LINNÉ), Rec.; *4a-c*, aboral, oral, plates of oral surface (interamb. stippled), ×0.8 (6, 51). [See also Figs. 336,*1a*; 339,*C*; 344,*4*; 348,*11*; 350,*9*; 351,*13*; 354,*3,8*.]

Rotuloidea ETHERIDGE, 1872, p. 98 [**R. fimbriata*; OD]. Posteriorly dentate, no lunules; margin thick; petals elongate, pore pairs only partially conjugate, outer pore simple; periproct midway on oral surface, between 1st and 2nd pair of coronal plates; paired interambulacra continuous. *Mio.-Plio.*, W.Afr.——FIG. 377,*2*. **R. fimbriata*, Plio., Morocco; plates of oral surface (interamb, stippled), ×1 (51).

Suborder and Family UNCERTAIN

Proescutella POMEL, 1883, p. 70 [**Scutella cailliaudi* COTTEAU, 1861, p. 46; OD] [=*Praescutella* POMEL, 1883, p. 130 *(nom. null.)*]. Medium-sized, scutellid-like, flattened, apical system raised, margin thin; petals open, length 0.8 of radius; pore pairs conjugate, outer pore elongate, simple; 4 genital pores; periproct oral, 0.25 of distance from margin, between 4th pair of coronal plates; food grooves not well defined, ?simple; interambulacra about 0.3 width of ambulacra at ambitus, continuous; hydropores in groove. [The hydropores in a groove suggest that this genus may be an early member of the Laganina.] *M.Eoc.*, Fr.——FIG. 377,*1*. **P. cailliaudi* (COTTEAU); *1a,b*, aboral, lat. views, ×0.7; *1c*, oral view, ×1 (27).

Runa L. AGASSIZ, 1841, p. 32 [**R. comptoni*; SD LAMBERT & THIÉRY, 1914, p. 294]. Based on internal mold. Unrecognizable; probably a fibulariid. *Mio.*, Italy.——FIG. 377,*3*. **R. comptoni*; aboral view, ×2.5 (6).

Tournoueraster LAMBERT, 1914, p. 294 [**Scutella decemfissus* DESMOULINS, 1835; OD]. Based on internal mold, markedly different from *Runa*; unrecognizable. *L.Oligo.*, Fr.——FIG. 377,*6*. **T. decemfissus* (DESMOULINS); aboral view, ×8 (222).

Superorder ATELOSTOMATA Zittel, 1879

[Diagnosis prepared by J. WYATT DURHAM]

Corona rigid; periproct outside apical system; no compound ambulacral plates; lantern, girdle, and branchial slits absent in adult; apical system and peristome rarely opposite; primary tubercles usually perforate and crenulate; primary spines hollow; interambulacra invariably wider than ambulacra on oral surface. *Jur.-Rec.*

CASSIDULOIDS

By Porter M. Kier
[Smithsonian Institution, United States National Museum]

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.

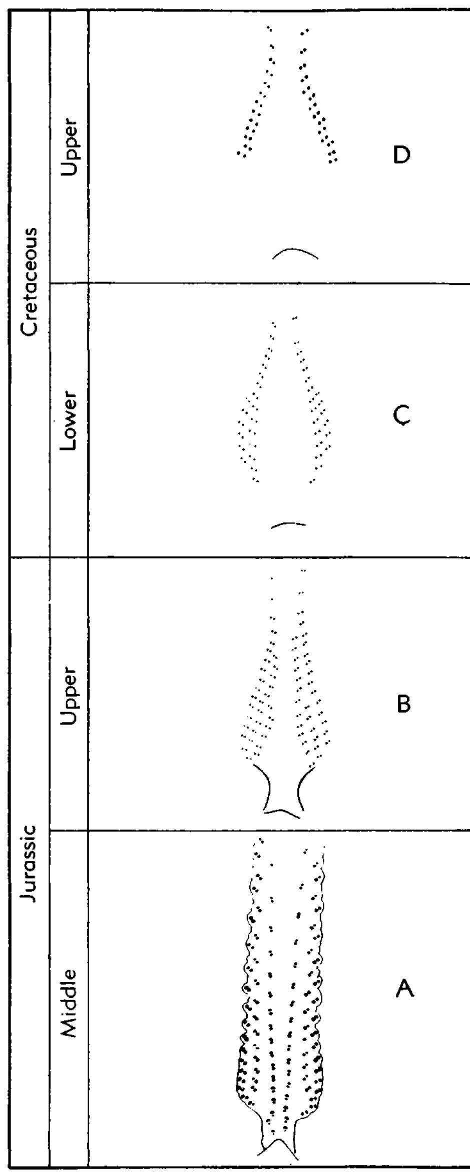


Fig. 378. Evolution of pygurid type of phyllode, trend toward decrease in number of pores, widening of phyllodes, and increase in distance between pores and edge of peristome shown in four species of *Pygurus* (not to scale) (Kier, n).

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.

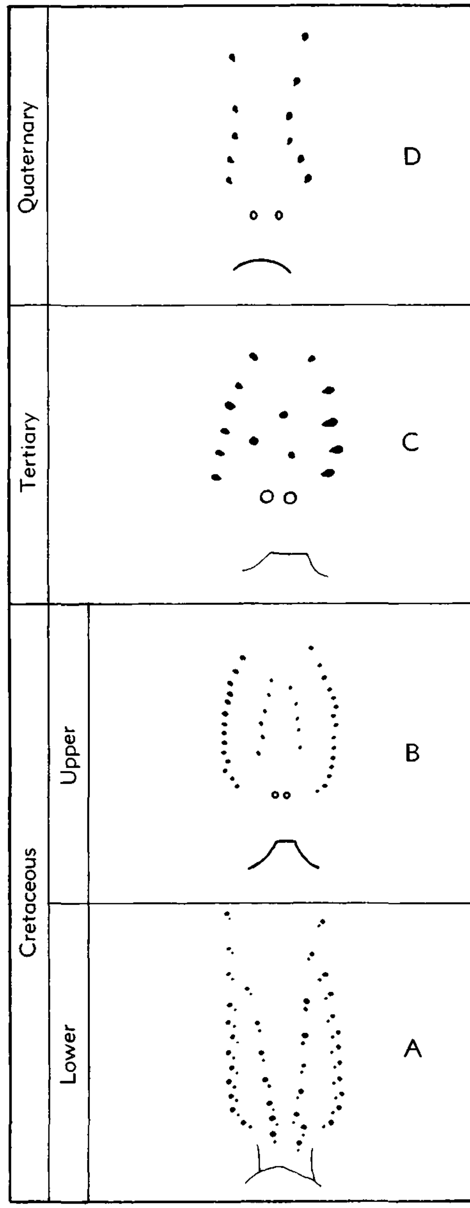


FIG. 379. Evolution of nucleolitid type of phyllode, trend toward widening of phyllodes, reduction from pore pairs to single pores, and introduction of buccal pores shown in four species (*A, Pygorhynchus obovatus* (AGASSIZ); *B, Petalobrissus lefebvrei* (FOURTAU); *C, Pliolampas gauthieri* (COTTEAU);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

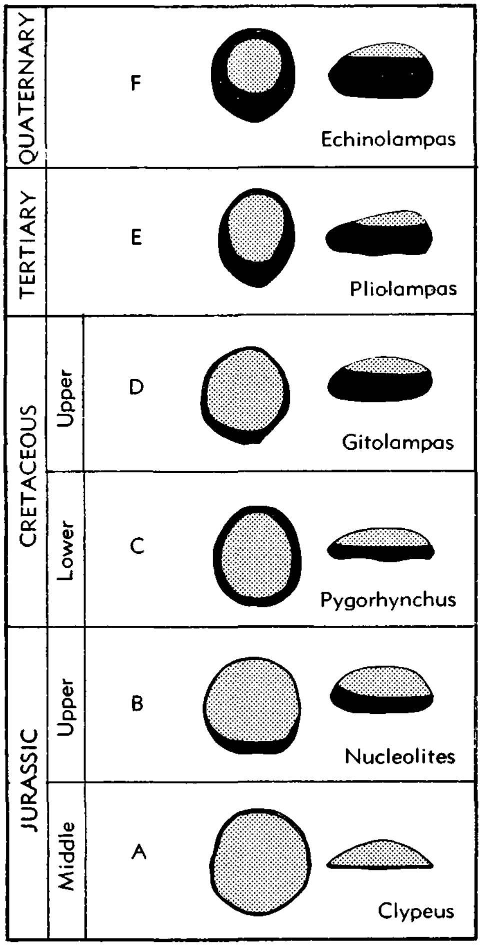


FIG. 380. Aboral and side view of some important cassiduloid genera showing change in shape of test and length of petals (petaloid area shaded, area below petals solid black) (Kier, n).

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

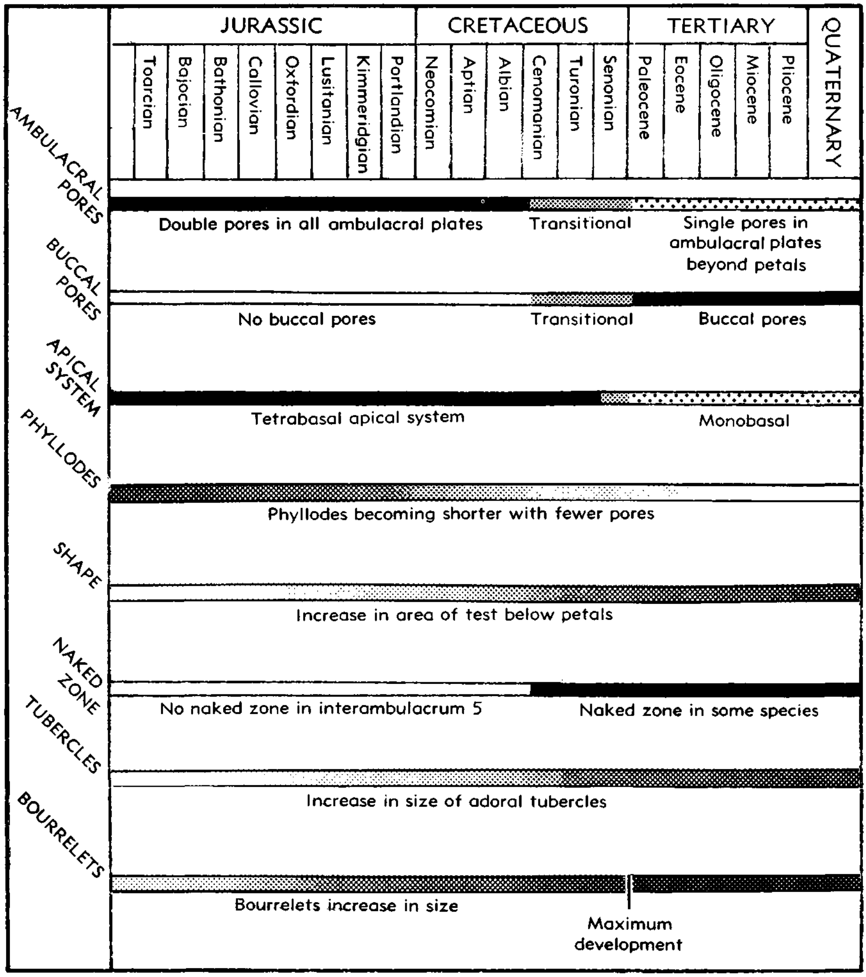


Fig. 381. Evolutionary trends in Cassiduloida (Kier, n).

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

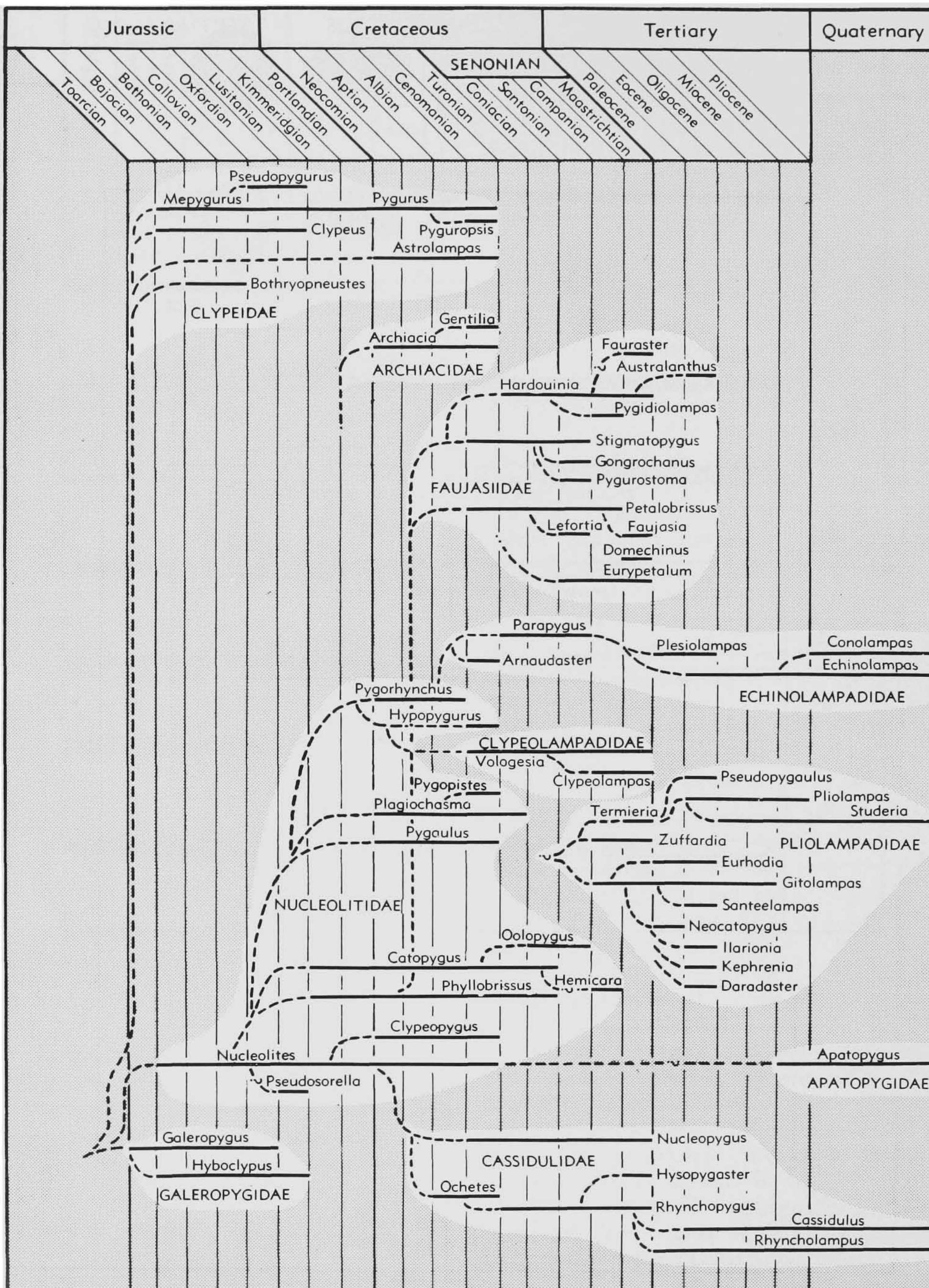


FIG. 382. Phylogeny of Cassiduloida (98).

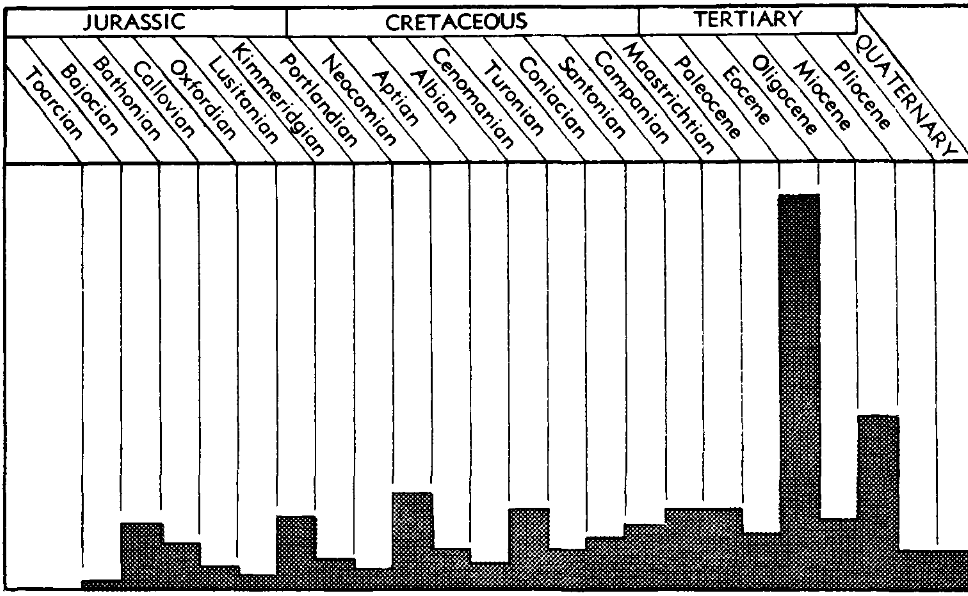


FIG. 383. Relative abundance of cassiduloid species in successive divisions of Jurassic and post-Jurassic time (scale arbitrary) (98).

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

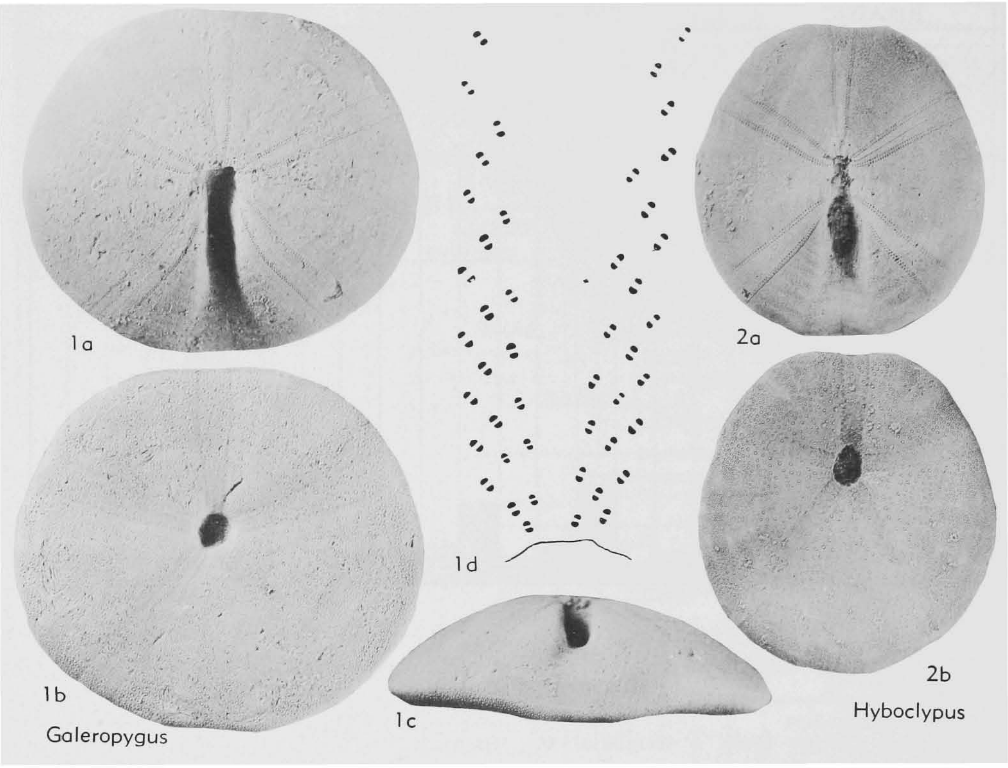


FIG. 384. Galeropygidae (p. U499).

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).

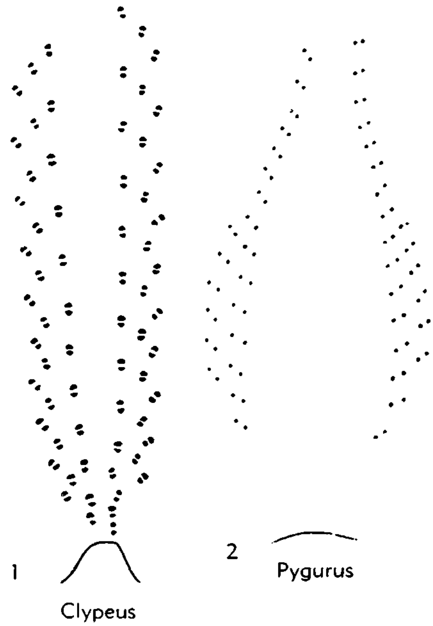


Fig. 385. Clypeidae (p. *U*499).

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.*

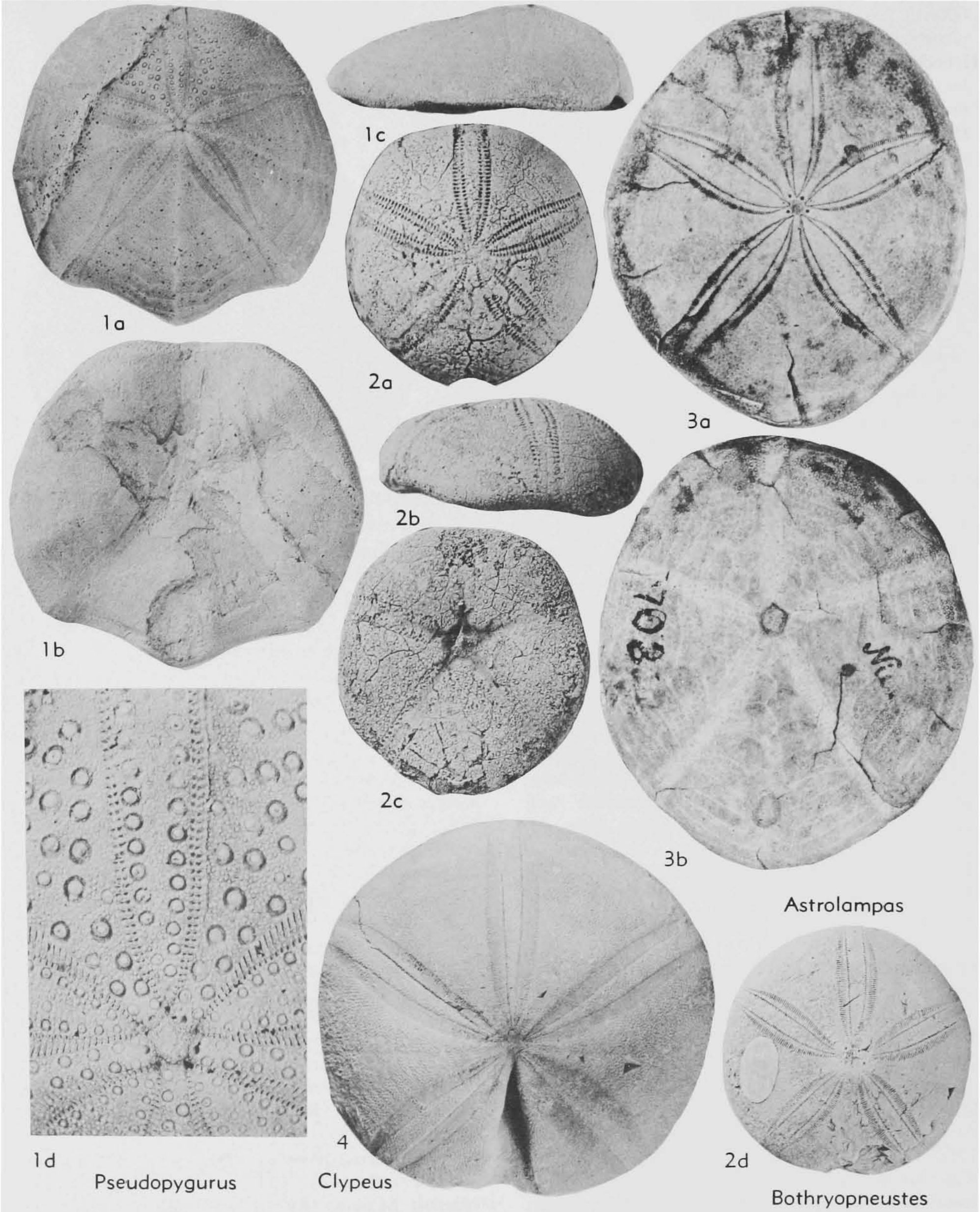


FIG. 386. Clypeidae (p. U499).

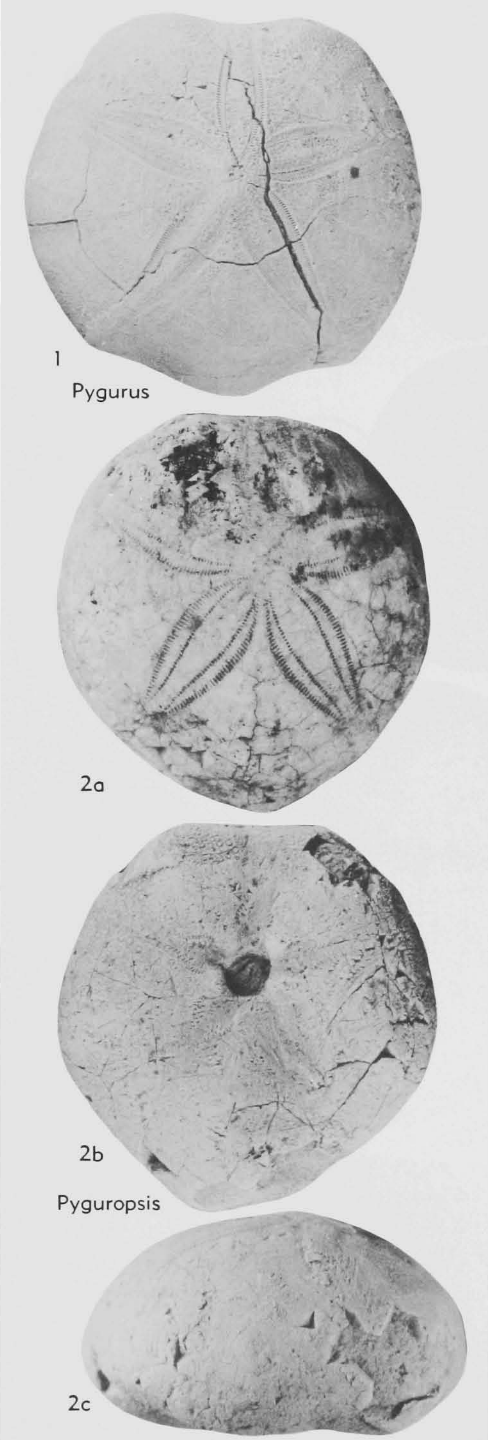


FIG. 387. Clypeidae (p. *U*499-*U*500).

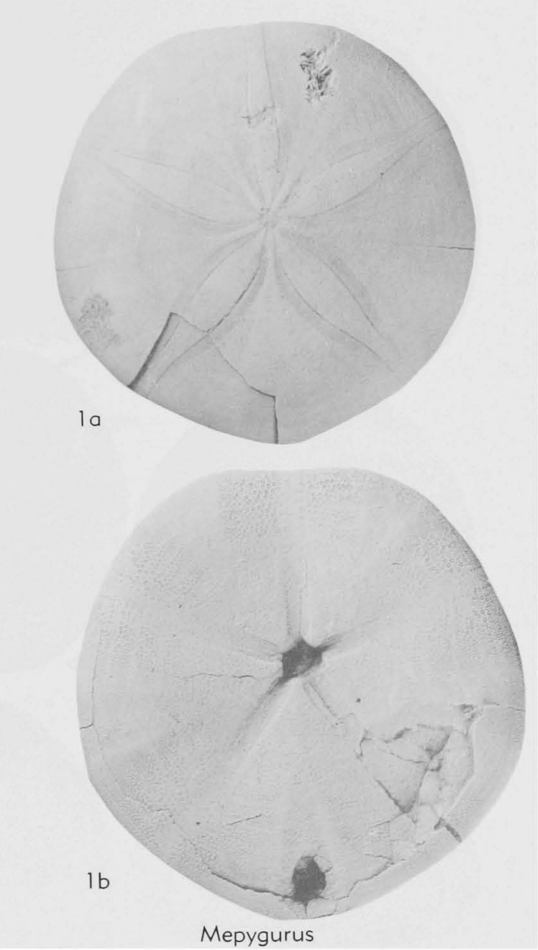


FIG. 388. Clypeidae (p. *U*499-*U*500).

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-

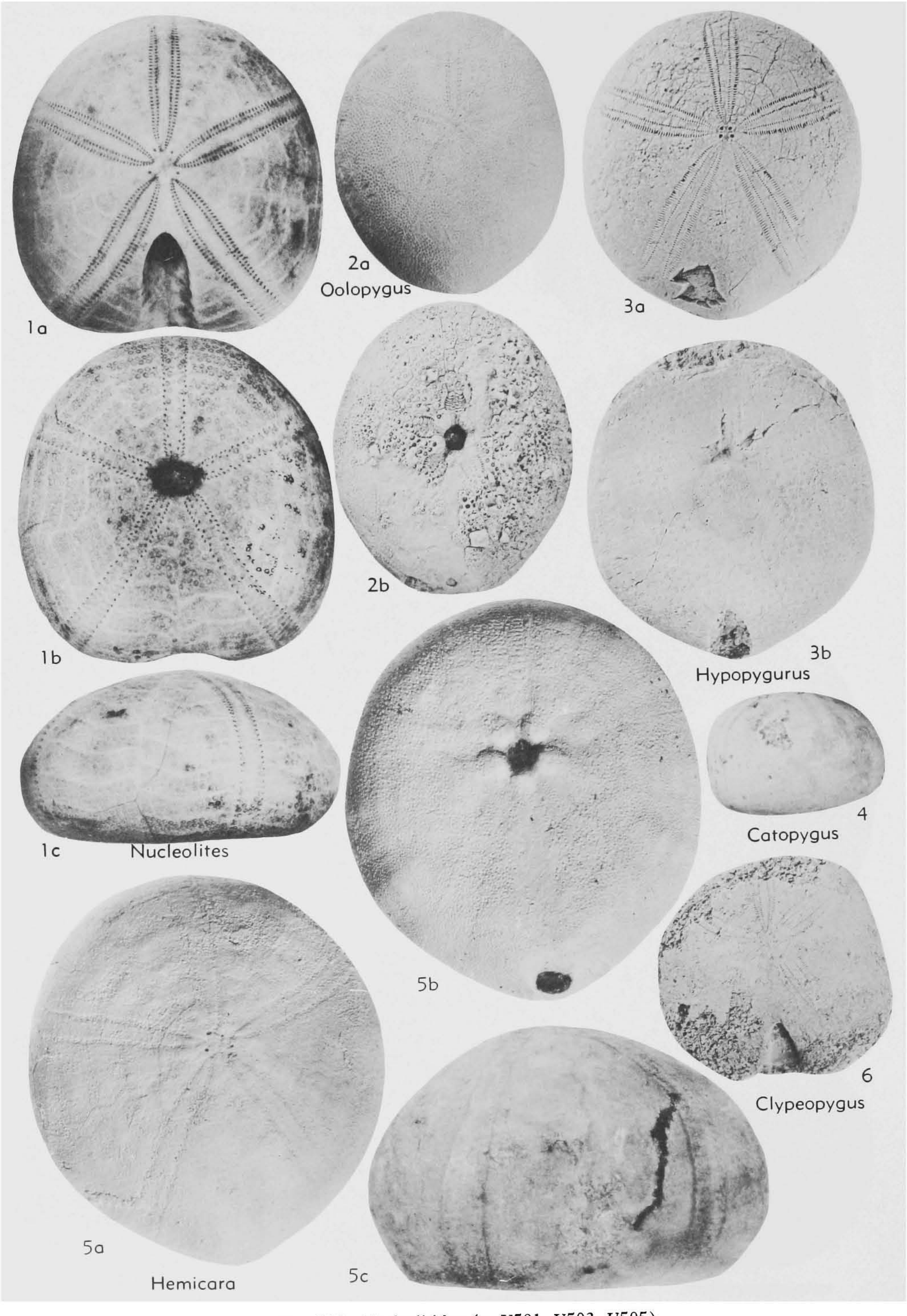


FIG. 389. Nucleolitidae (p. U501, U503, U505).

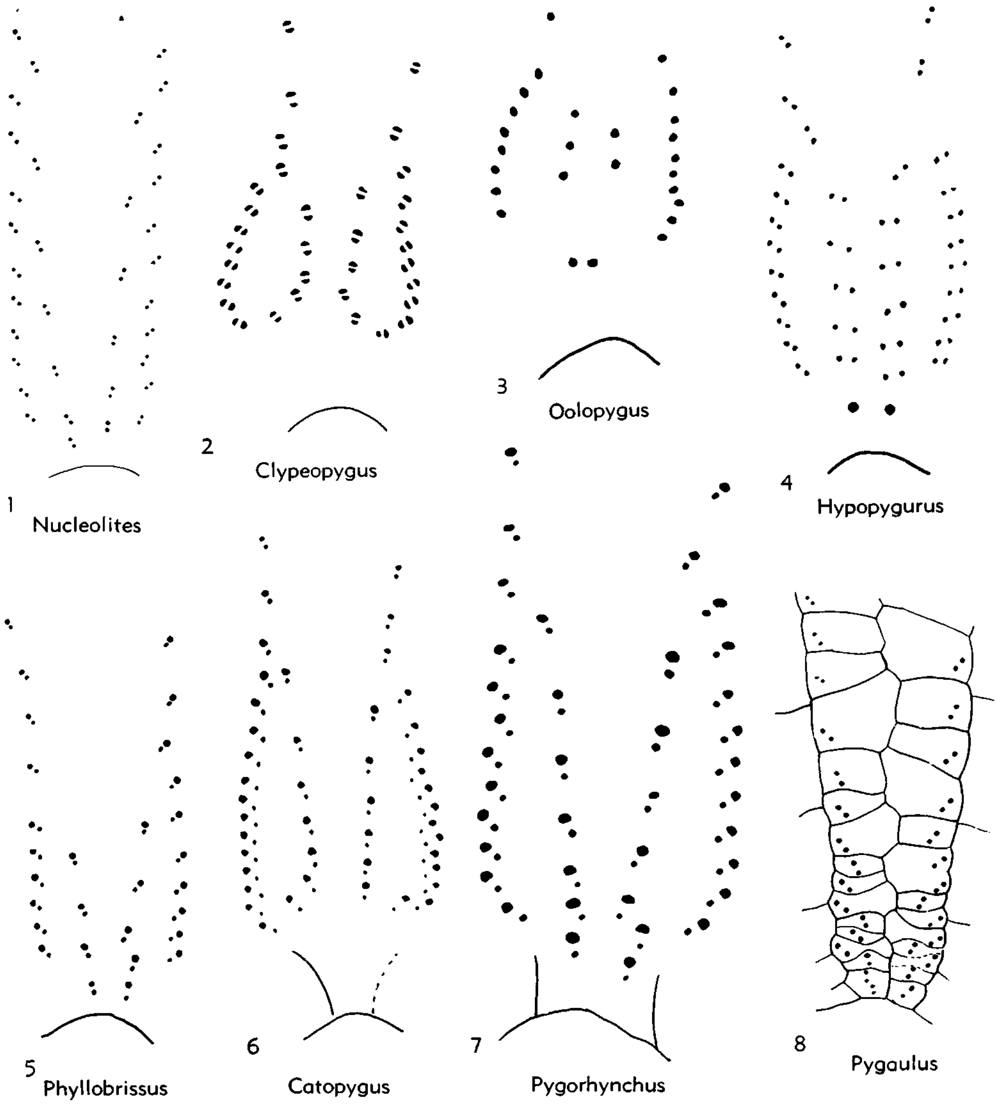


FIG. 390. Nucleolitidae (p. *U*501, *U*503, *U*505-*U*506).

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,

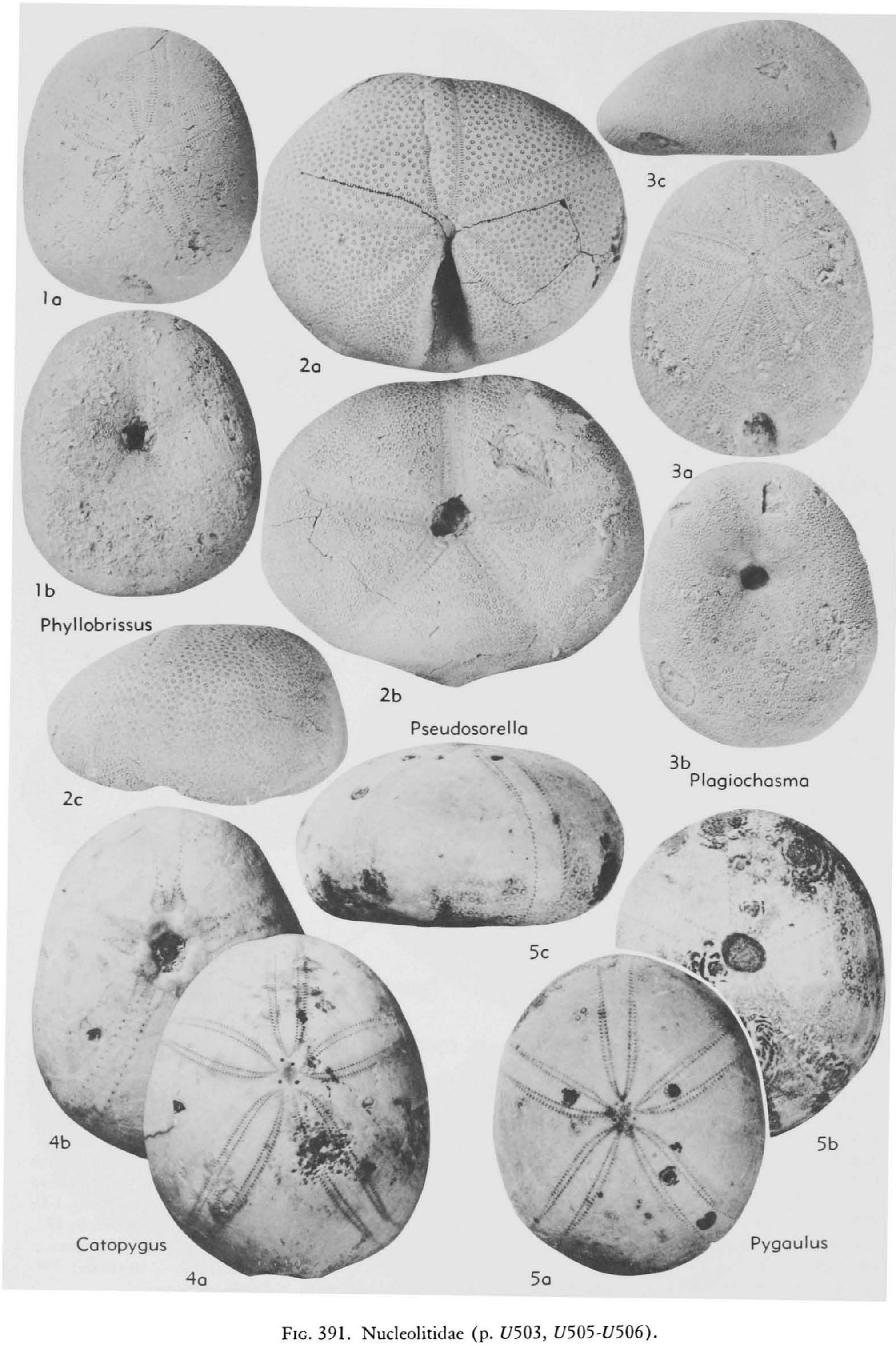


Fig. 391. Nucleolitidae (p. *U*503, *U*505-*U*506).

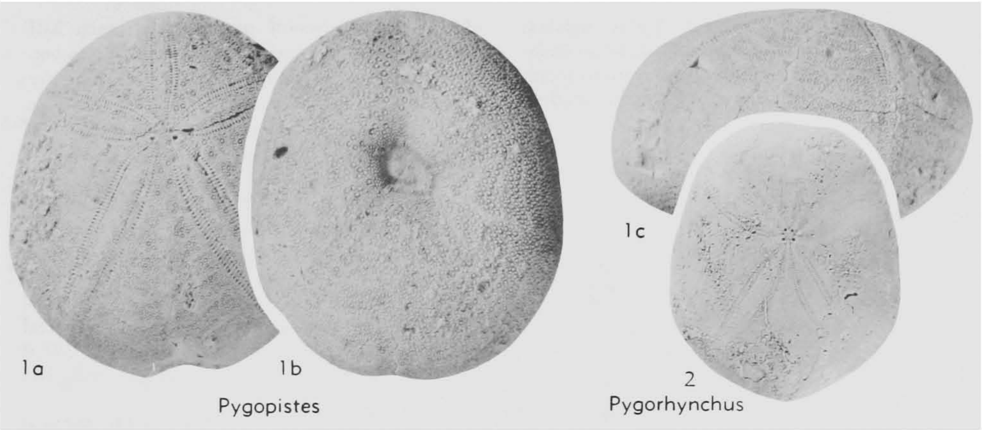


FIG. 392. Nucleolitidae (p. *U*506).

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,

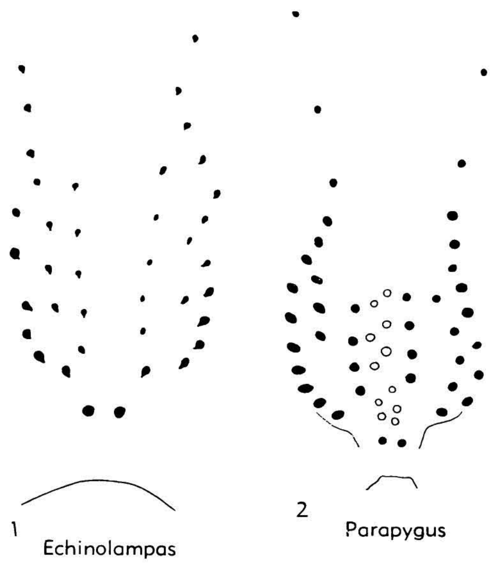


FIG. 394. Echinolampadidae (p. U506-U508).

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.

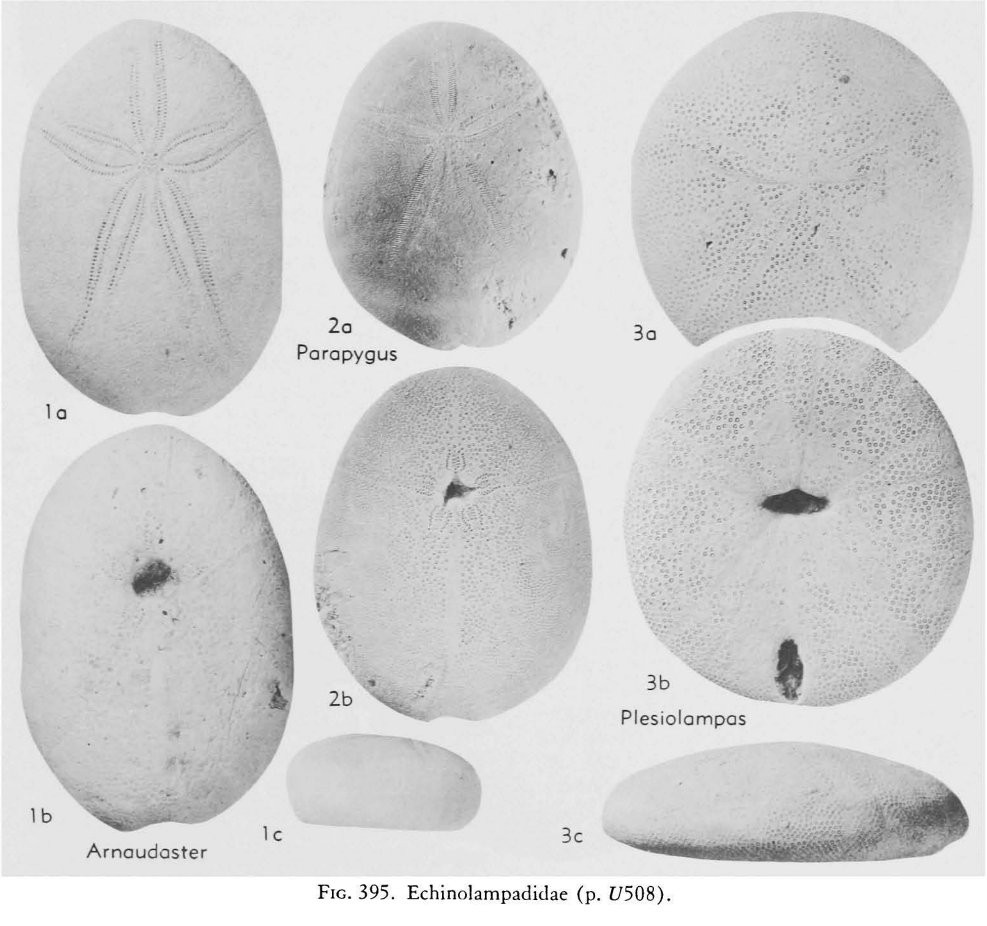
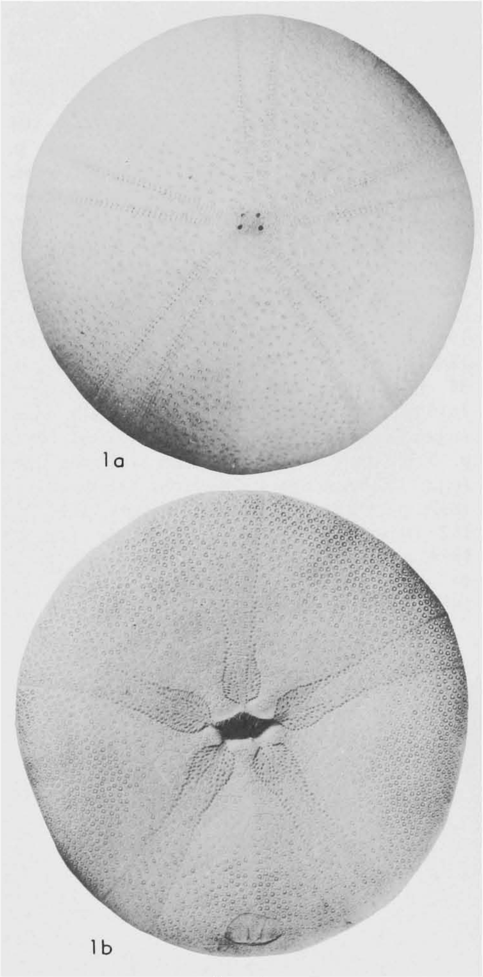


FIG. 395. Echinolampadidae (p. U508).



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,

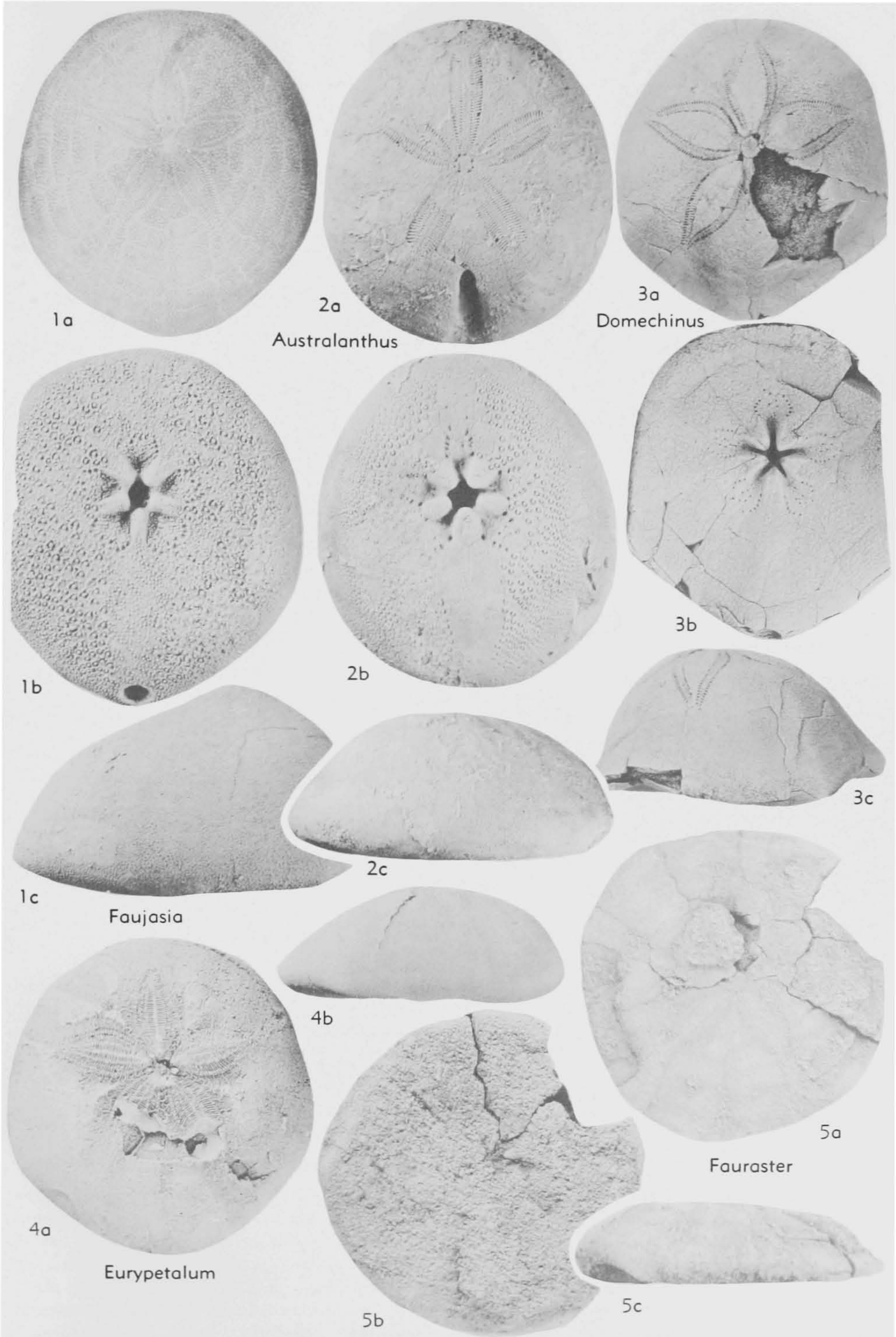


FIG. 397. Faujasiidae (p. U510, U512).

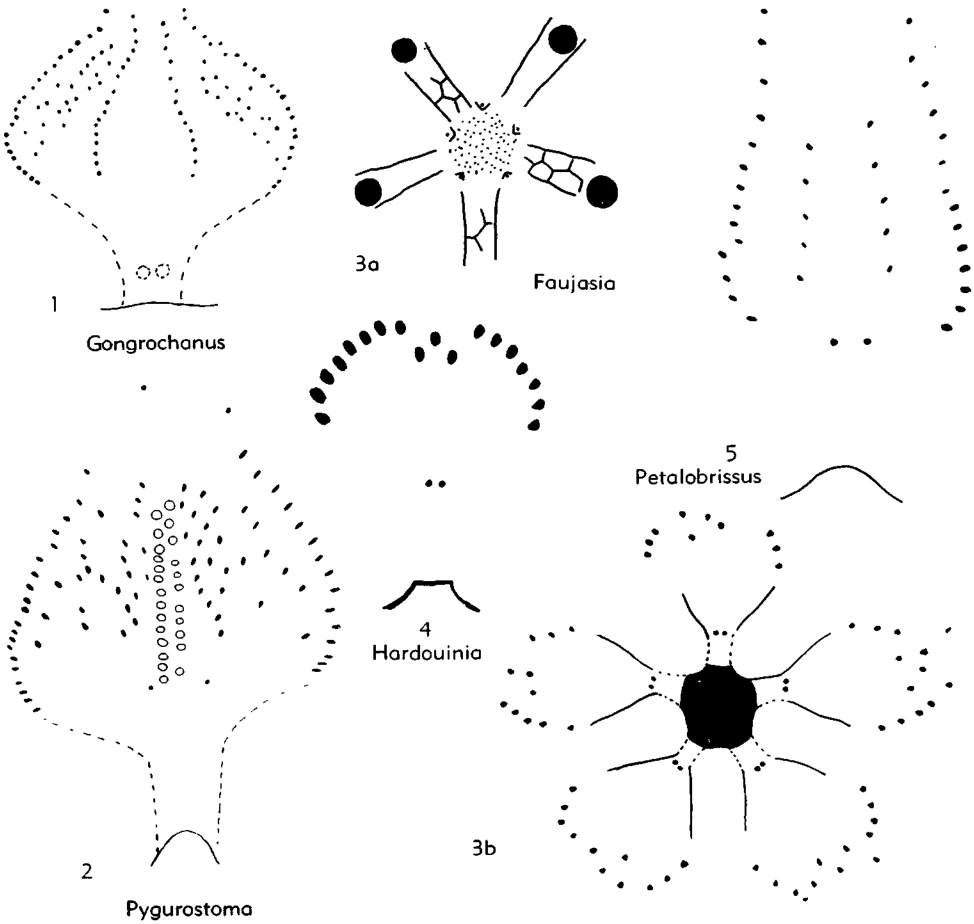


FIG. 398. Faujasiidae (p. U510, U512).

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.-*

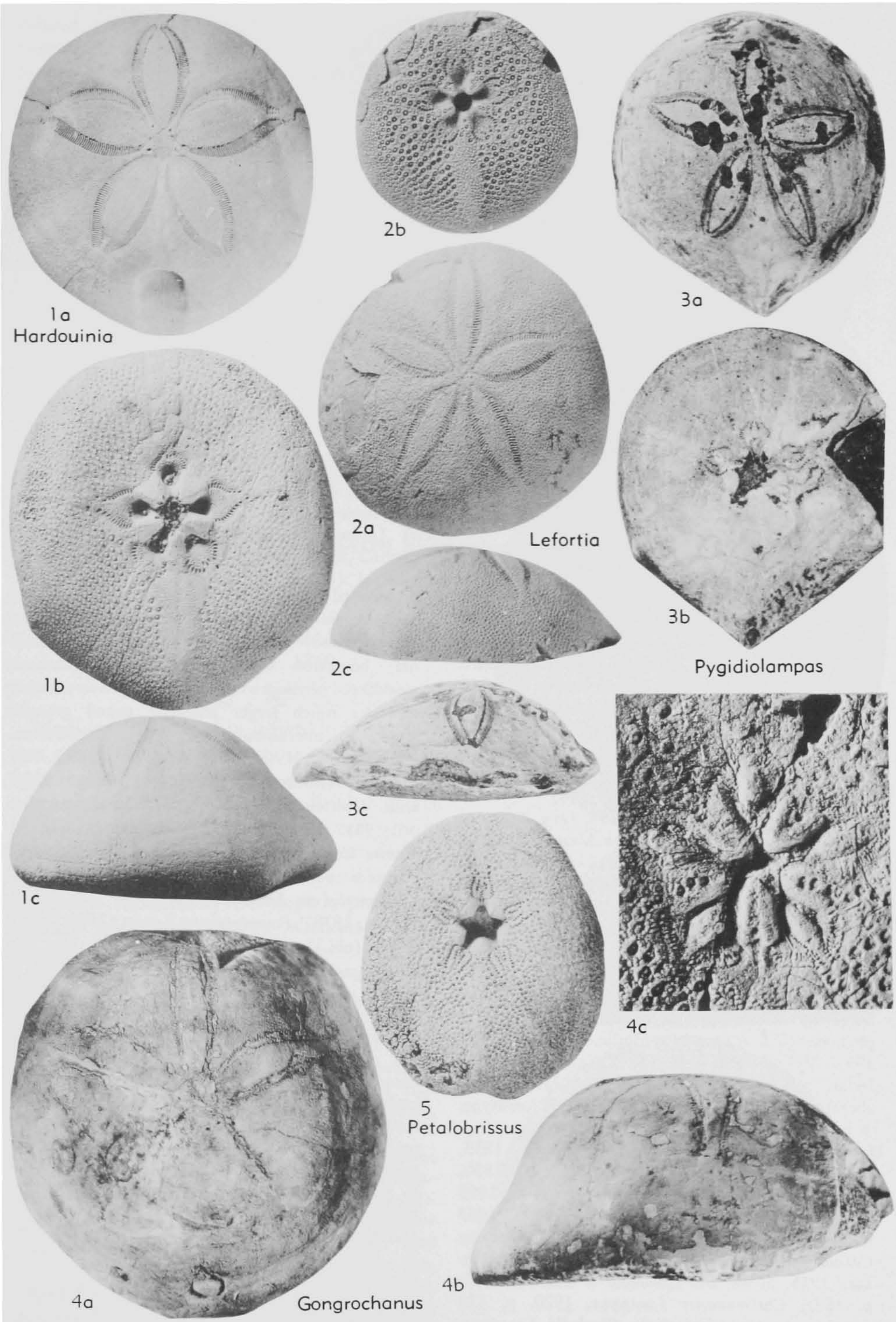


FIG. 399. Faujasiidae (p. U512-U513).

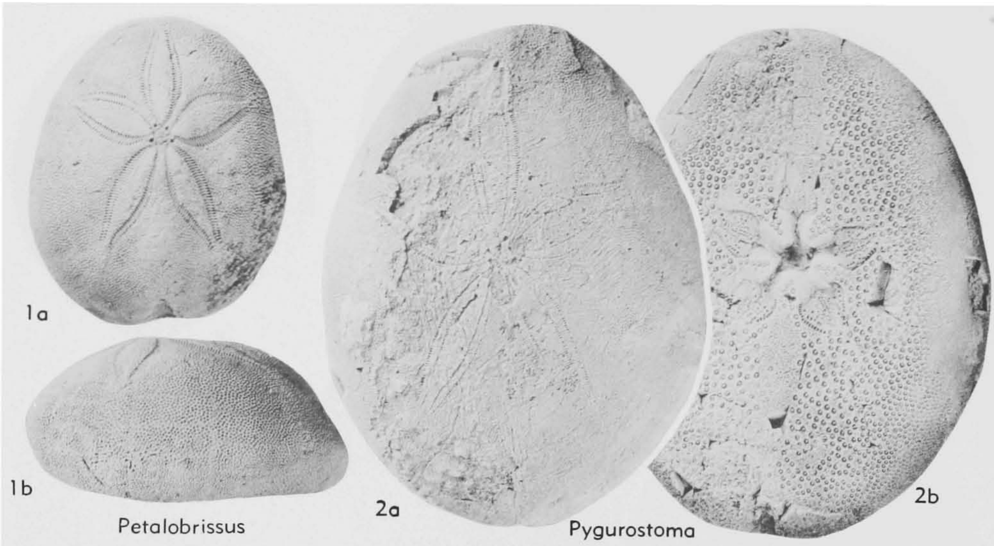


FIG. 400. Faujasiidae (p. U512-U513).

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).

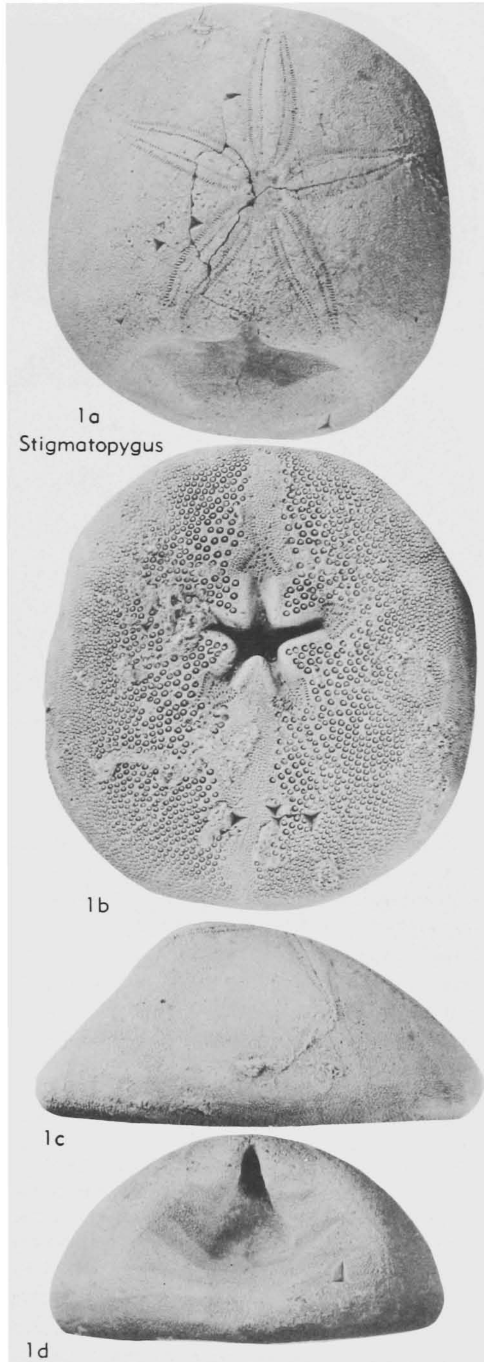


Fig. 401. Faujasiidae (p. *U*513).

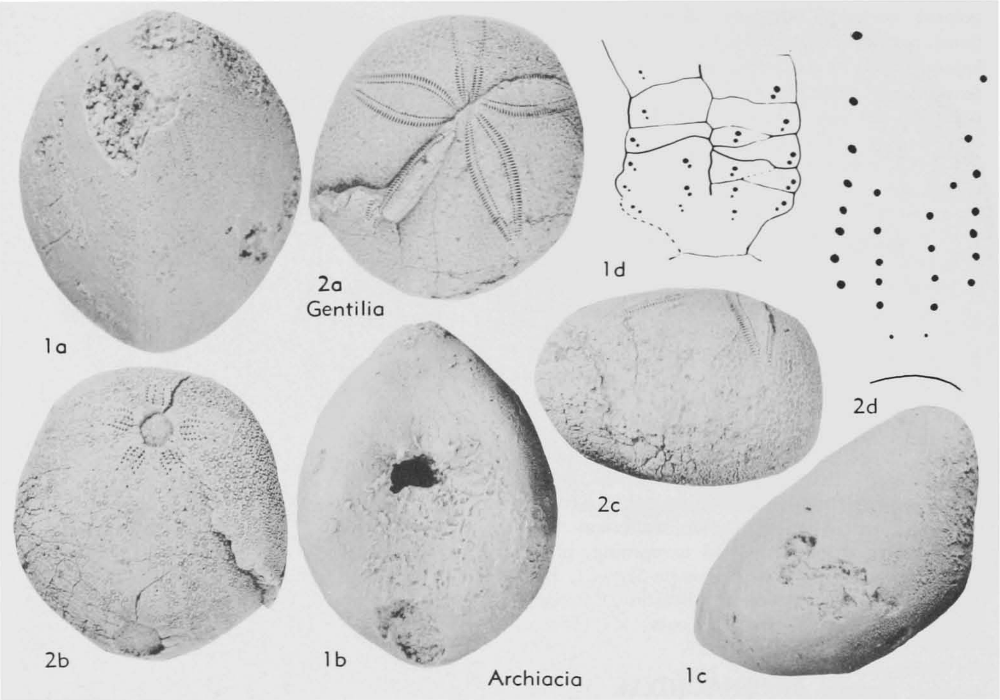


FIG. 402. Archiaciidae (p. U513).

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-*

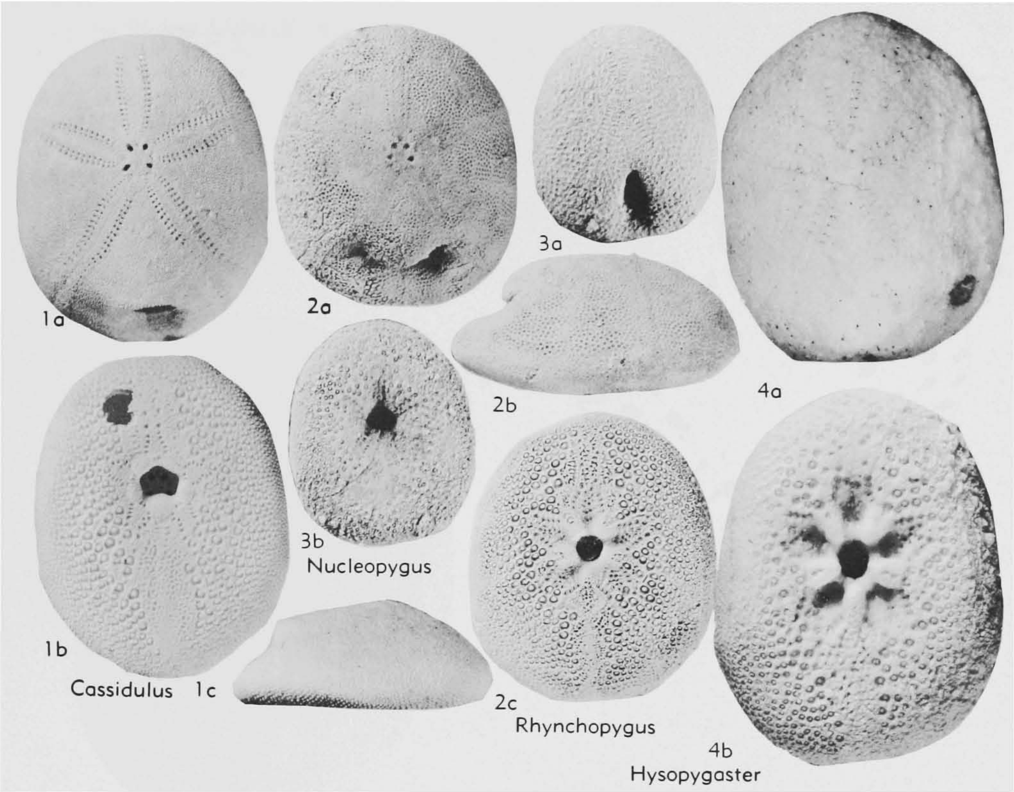


FIG. 403. Cassidulidae (p. U514-U515).

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*

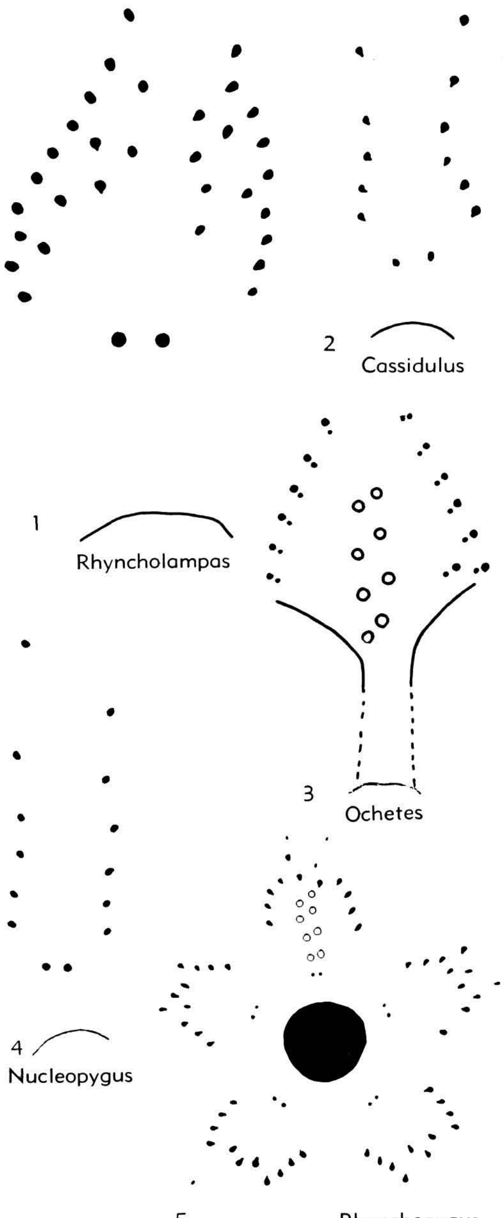


FIG. 404. Cassidulidae (p. U514-U515).

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).

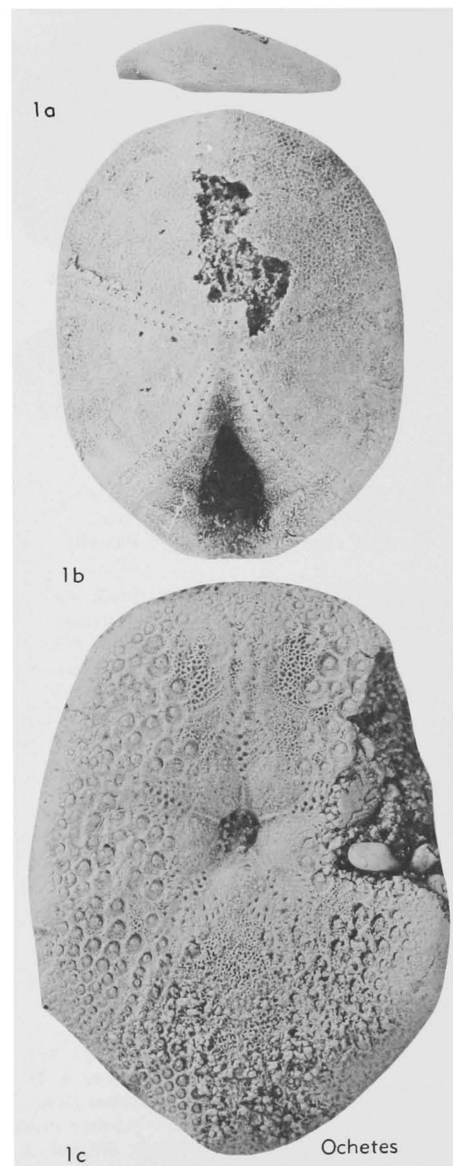


FIG. 405. Cassidulidae (p. U514).

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.*

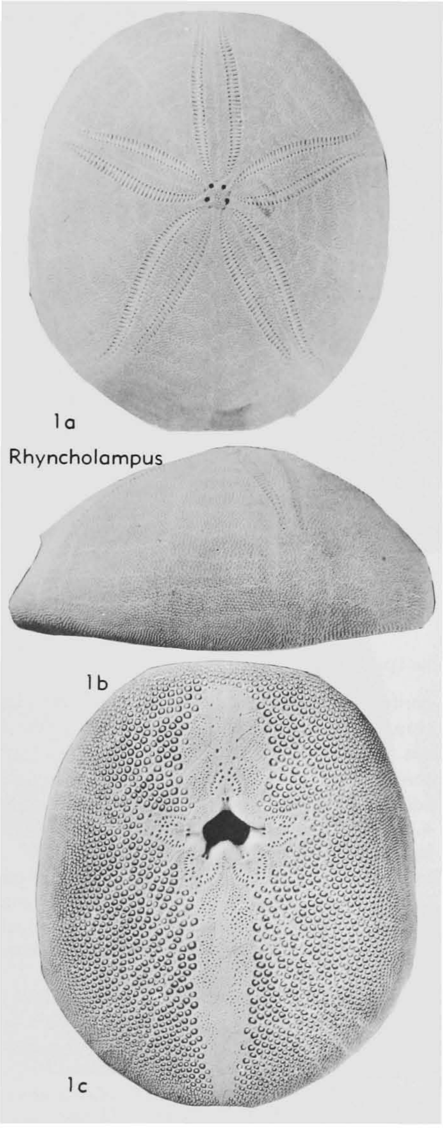


FIG. 406. Cassidulidae (p. *U*515).

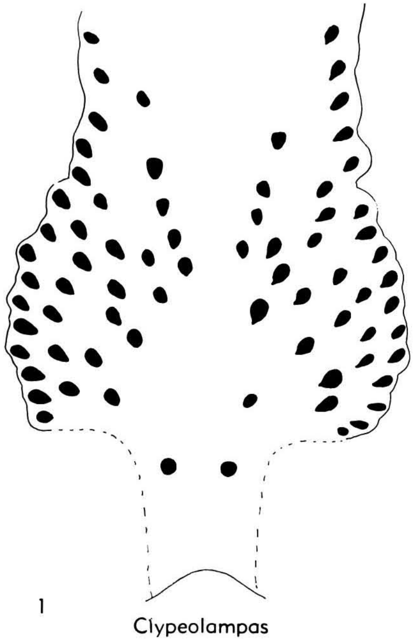


FIG. 407. Clypeolampadidae (p. *U*515-*U*516).

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).

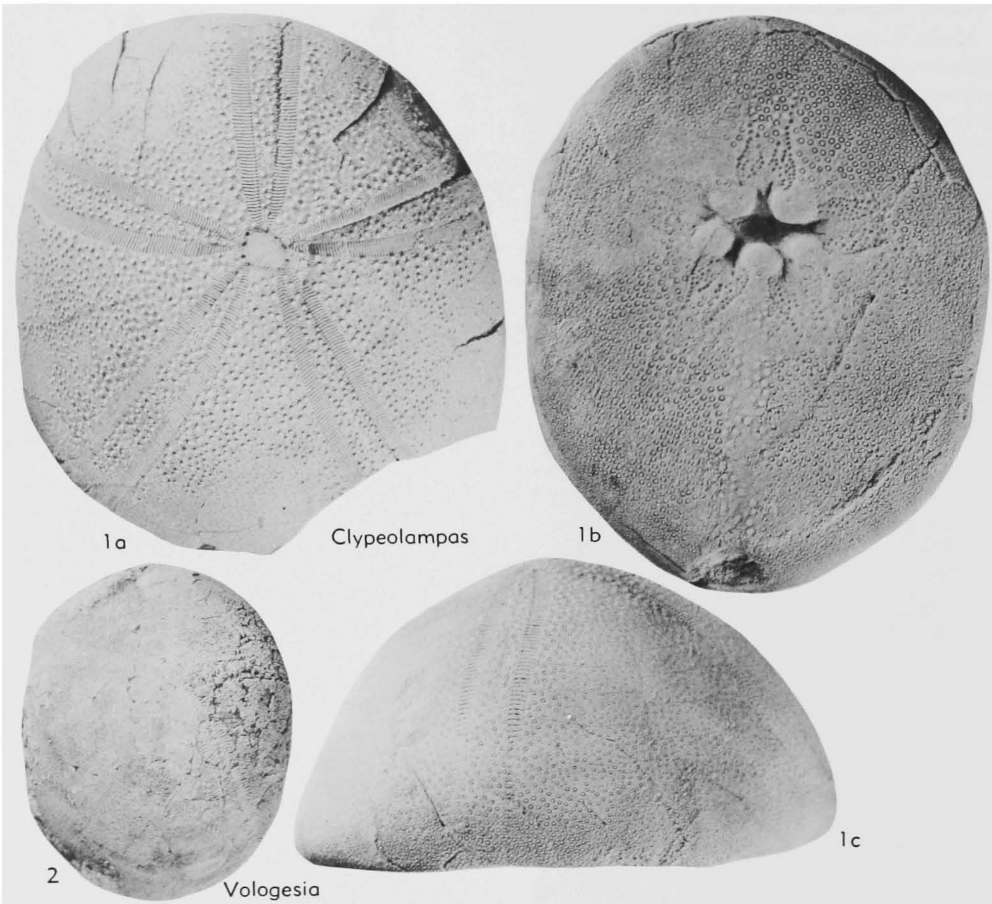


FIG. 408. Clypeolampadidae (p. U515-U516).

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.*-

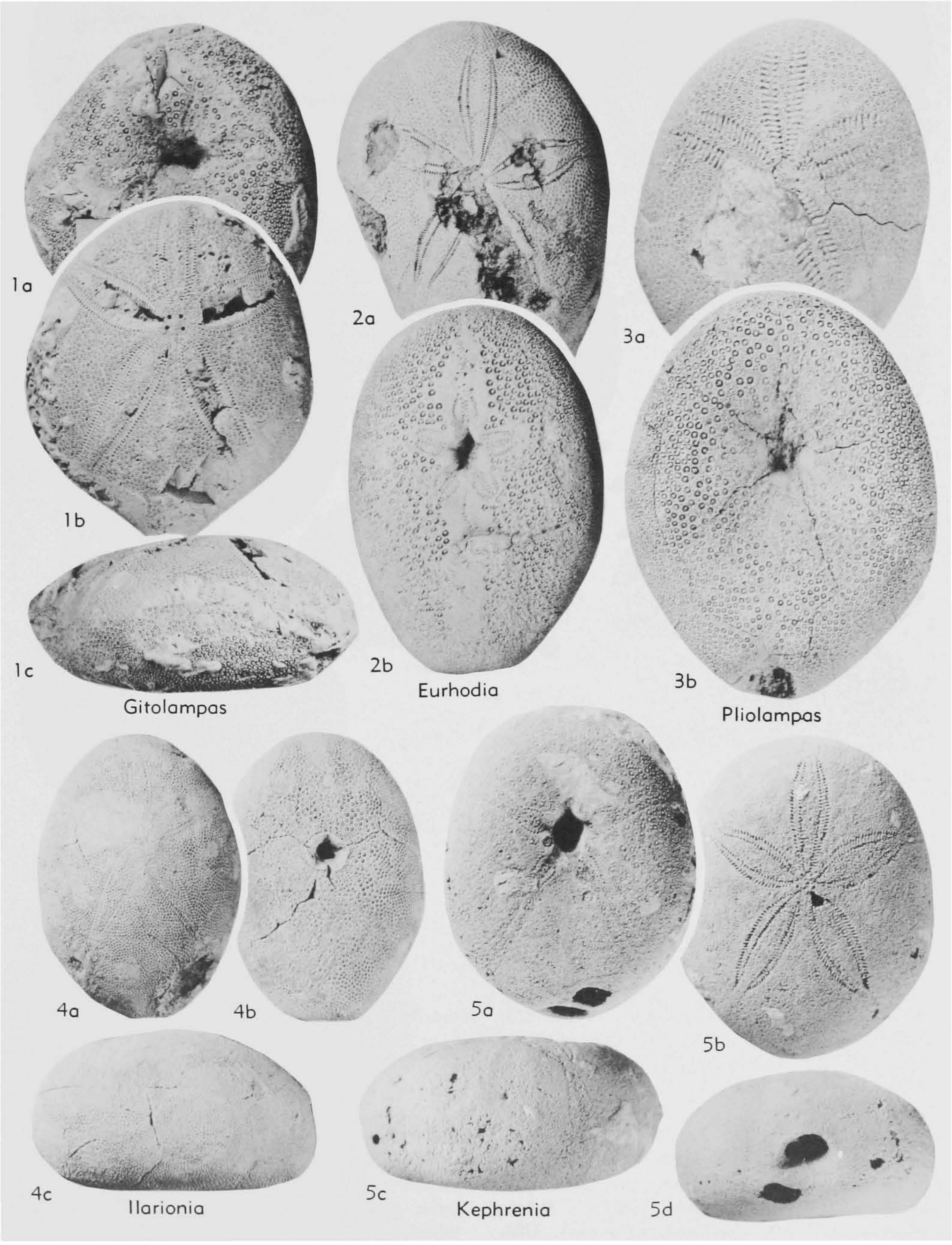


Fig. 409. Pliolampadidae (p. *U*517-*U*518).

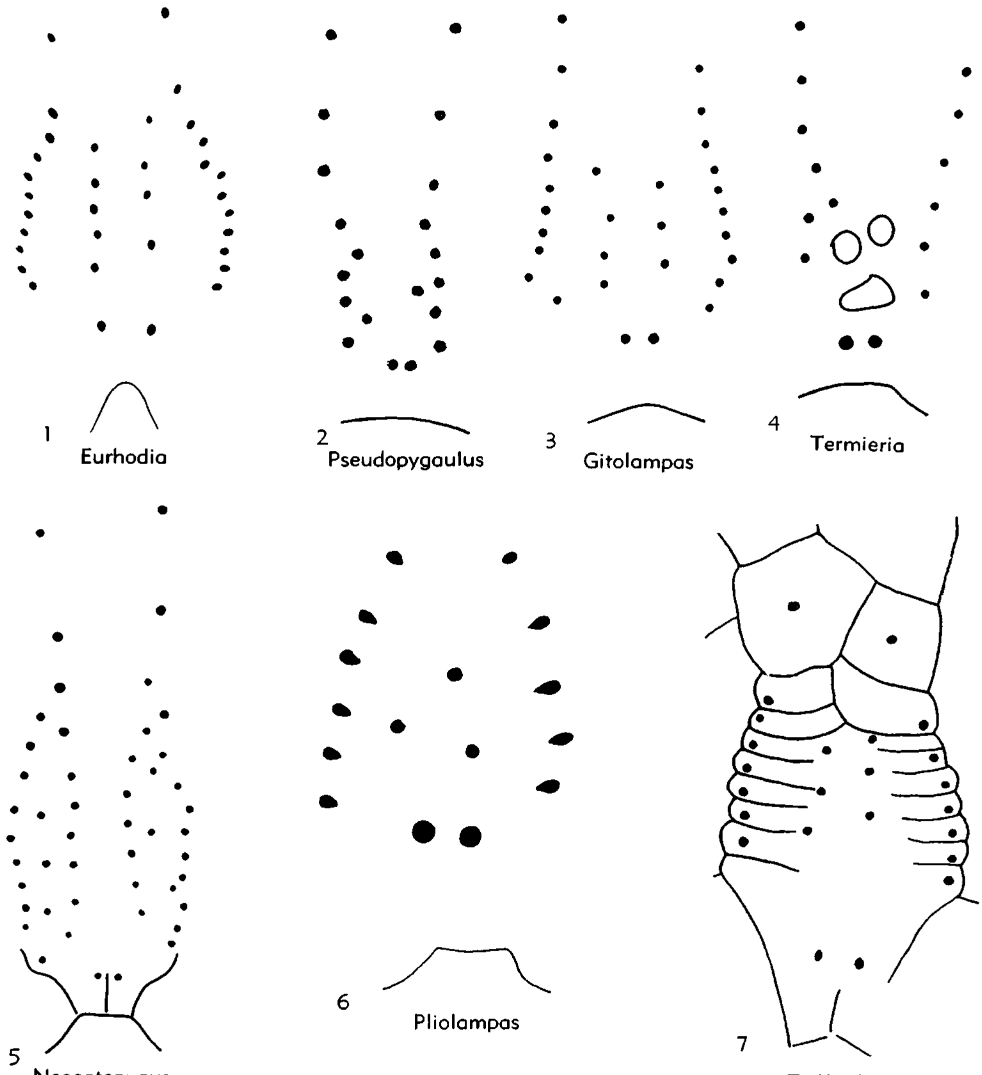


FIG. 410. Pliolampadidae (p. U517-U520, U522).

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-

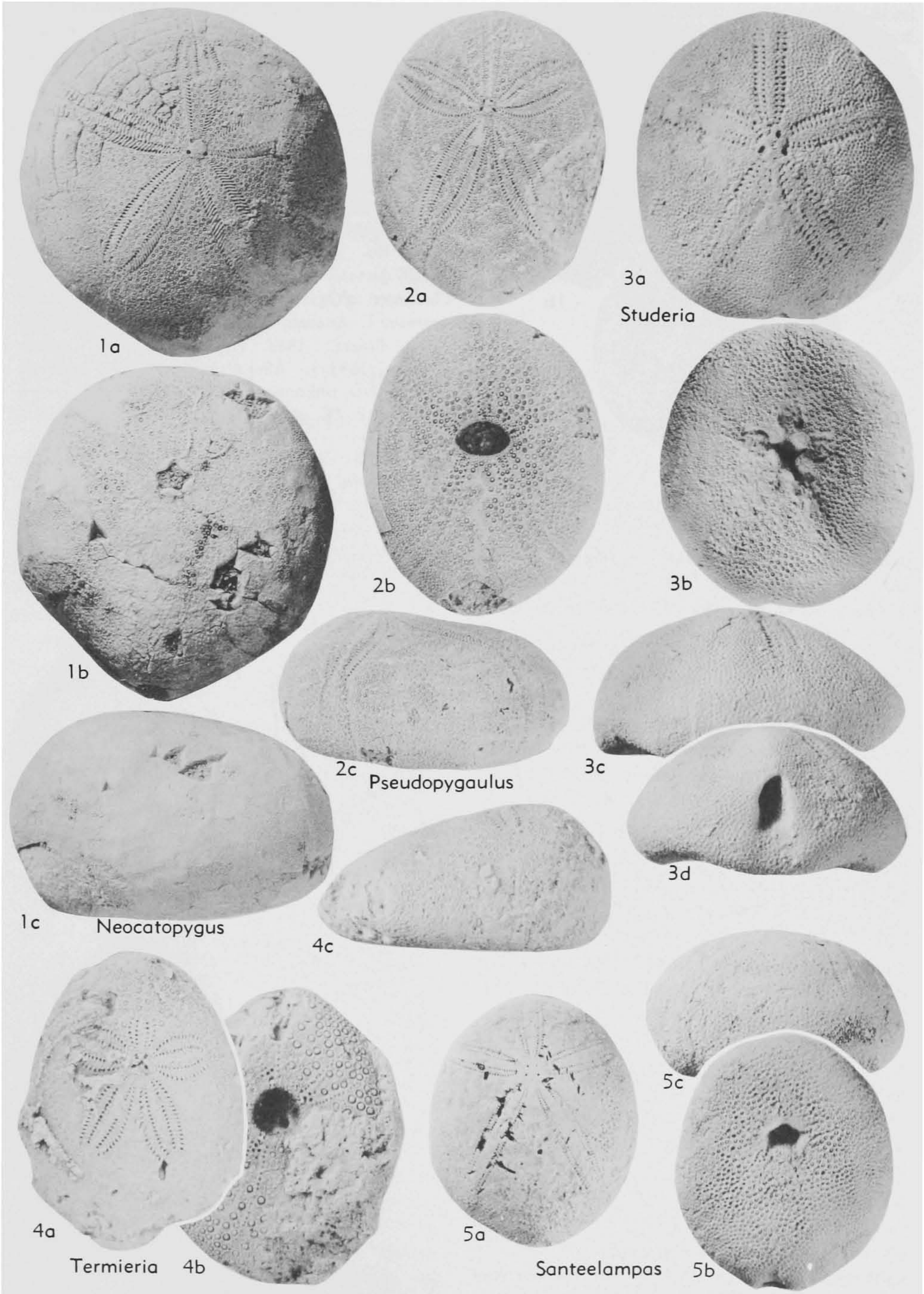


FIG. 411. Pliolampadidae (p. U517-U520, U522).

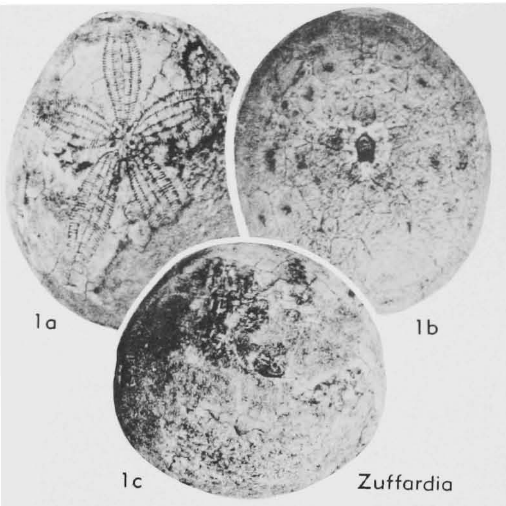


FIG. 412. Pliolampadidae (p. U522).

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.

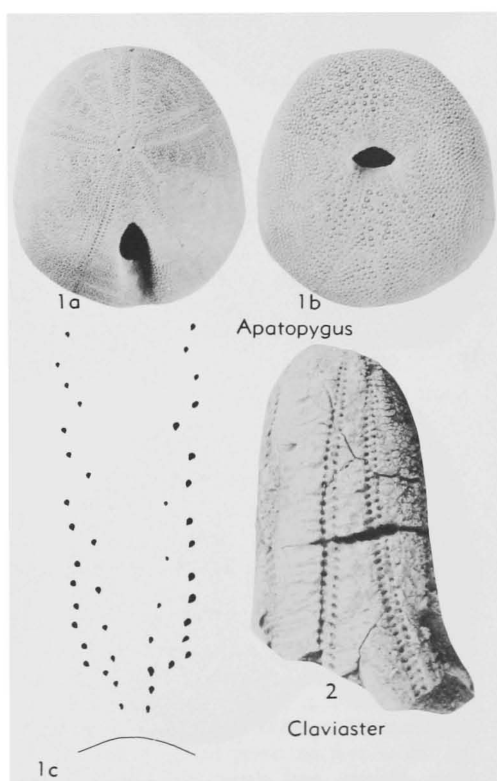


FIG. 413. Apatopygidae *(1)*; Family Uncertain *(2)* (p. U522).

[**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

By CAROL D. WAGNER and J. WYATT DURHAM
[University of California (Berkeley)]

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.*

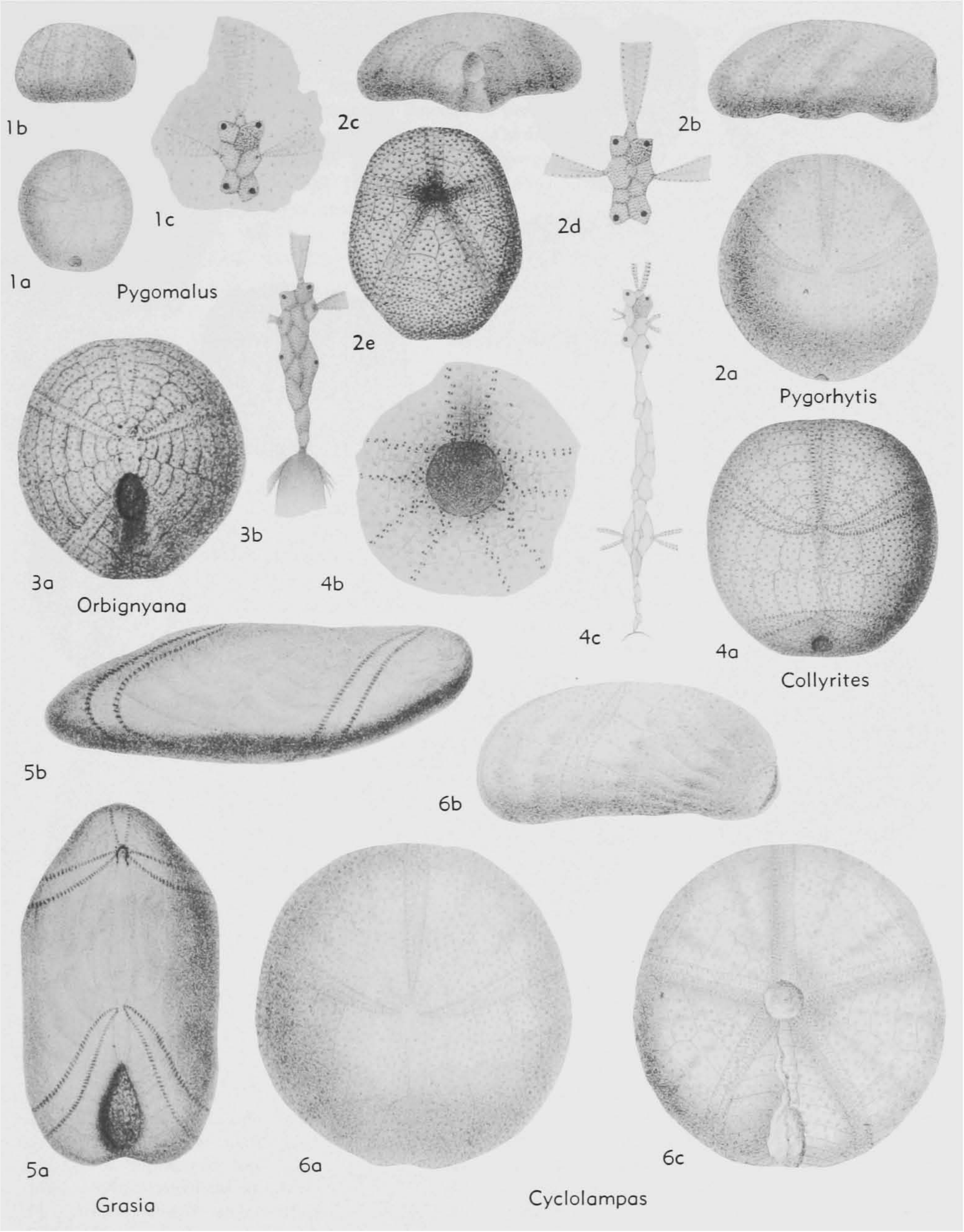


FIG. 414. Collyritidae (p. *U525-U527*).

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*

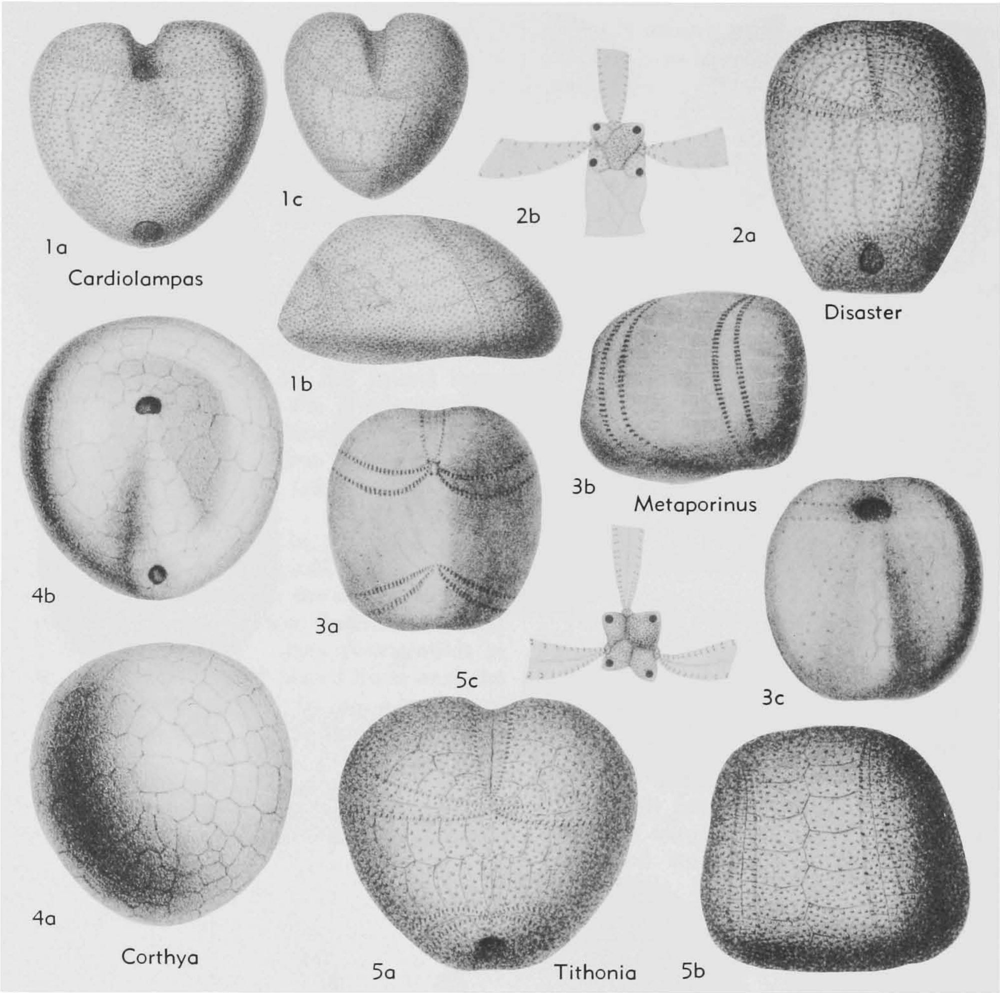


FIG. 415. Disasteridae (p. *U*527-*U*528).

(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).

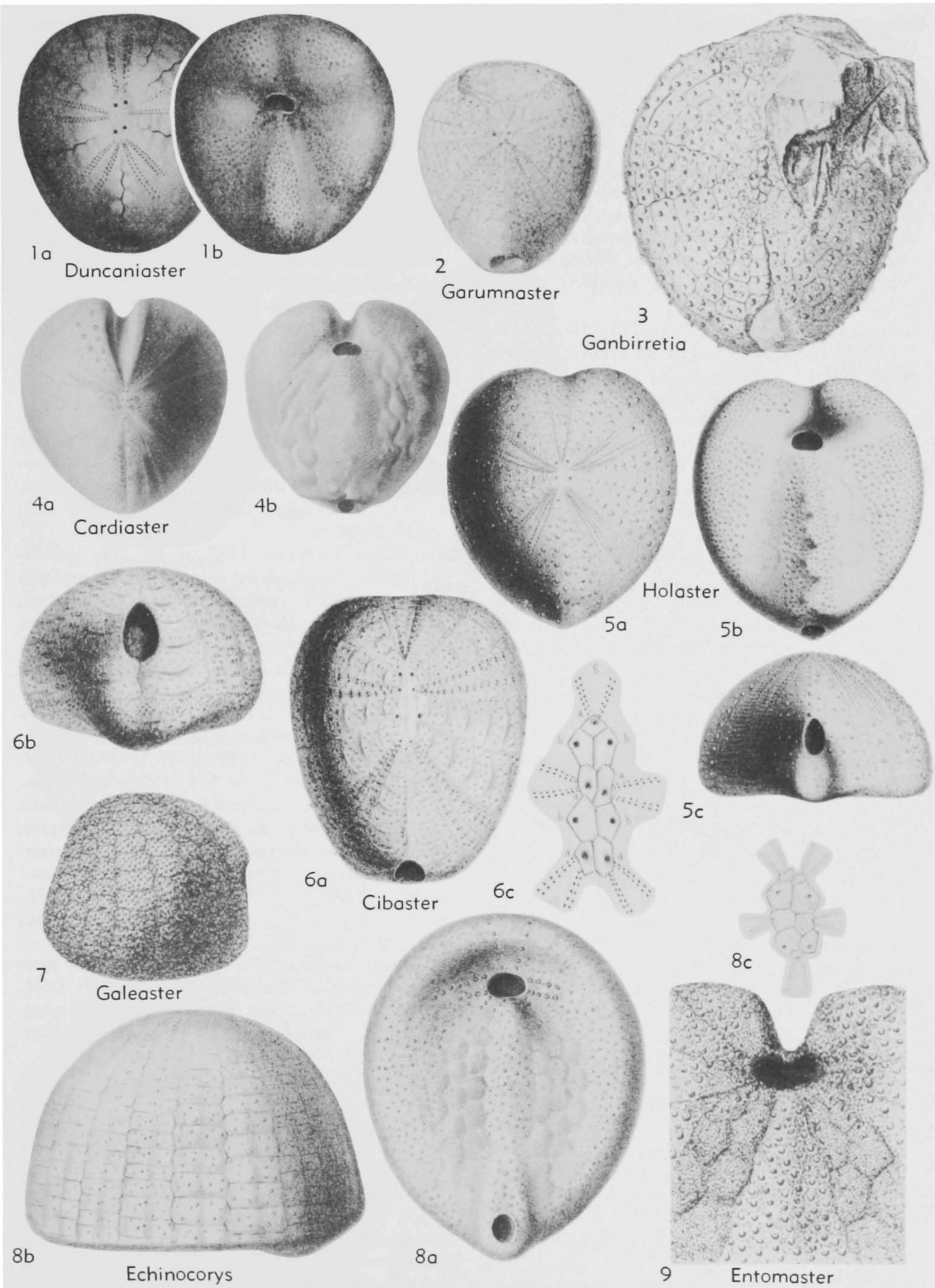


FIG. 416. Holasteridae (p. U528, U530).

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 cavity; 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

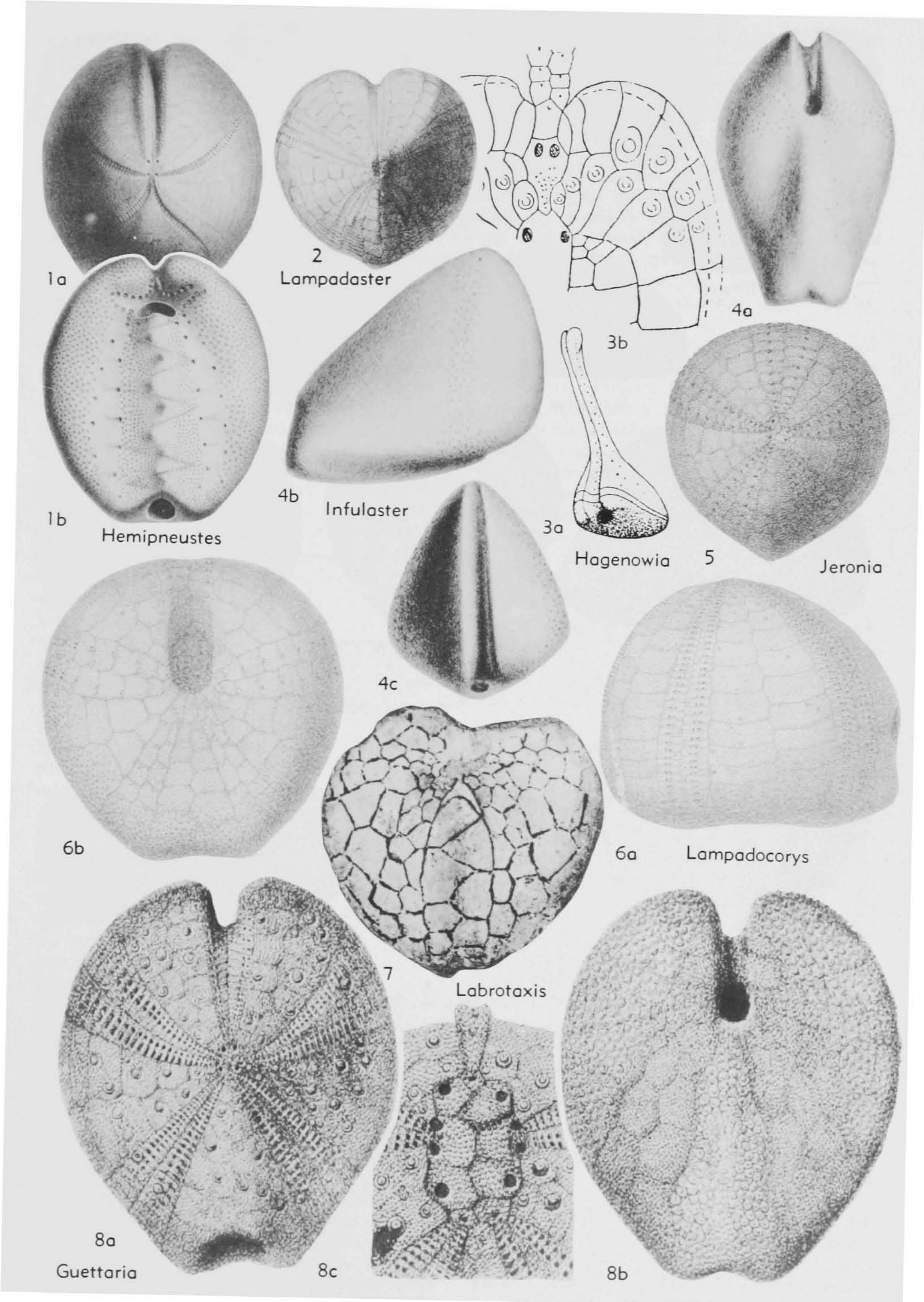


FIG. 417. Holasteridae (p. U530).

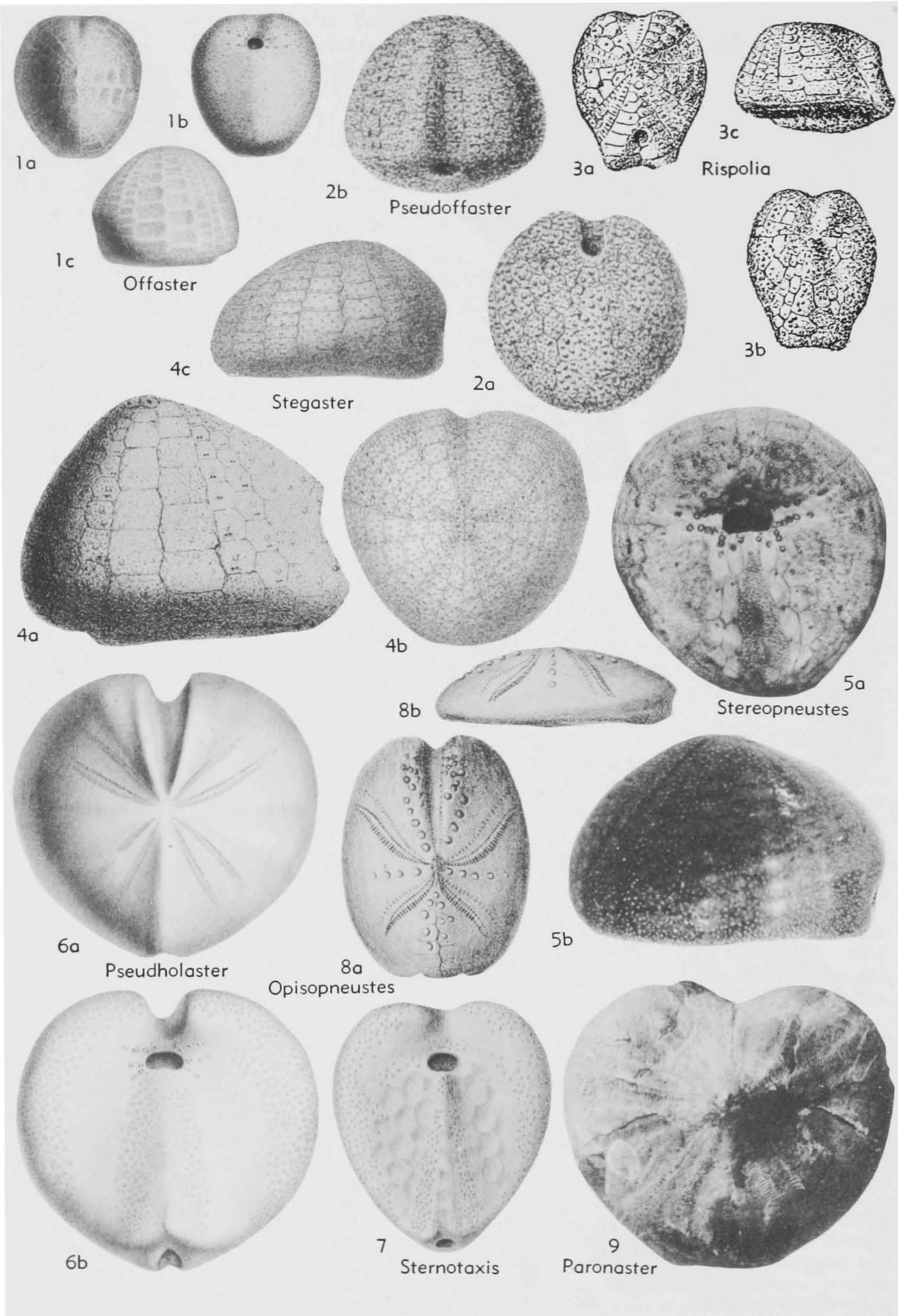


FIG. 418. Holasteridae (p. U530, U533).

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] [=*Cragin-aster* 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).

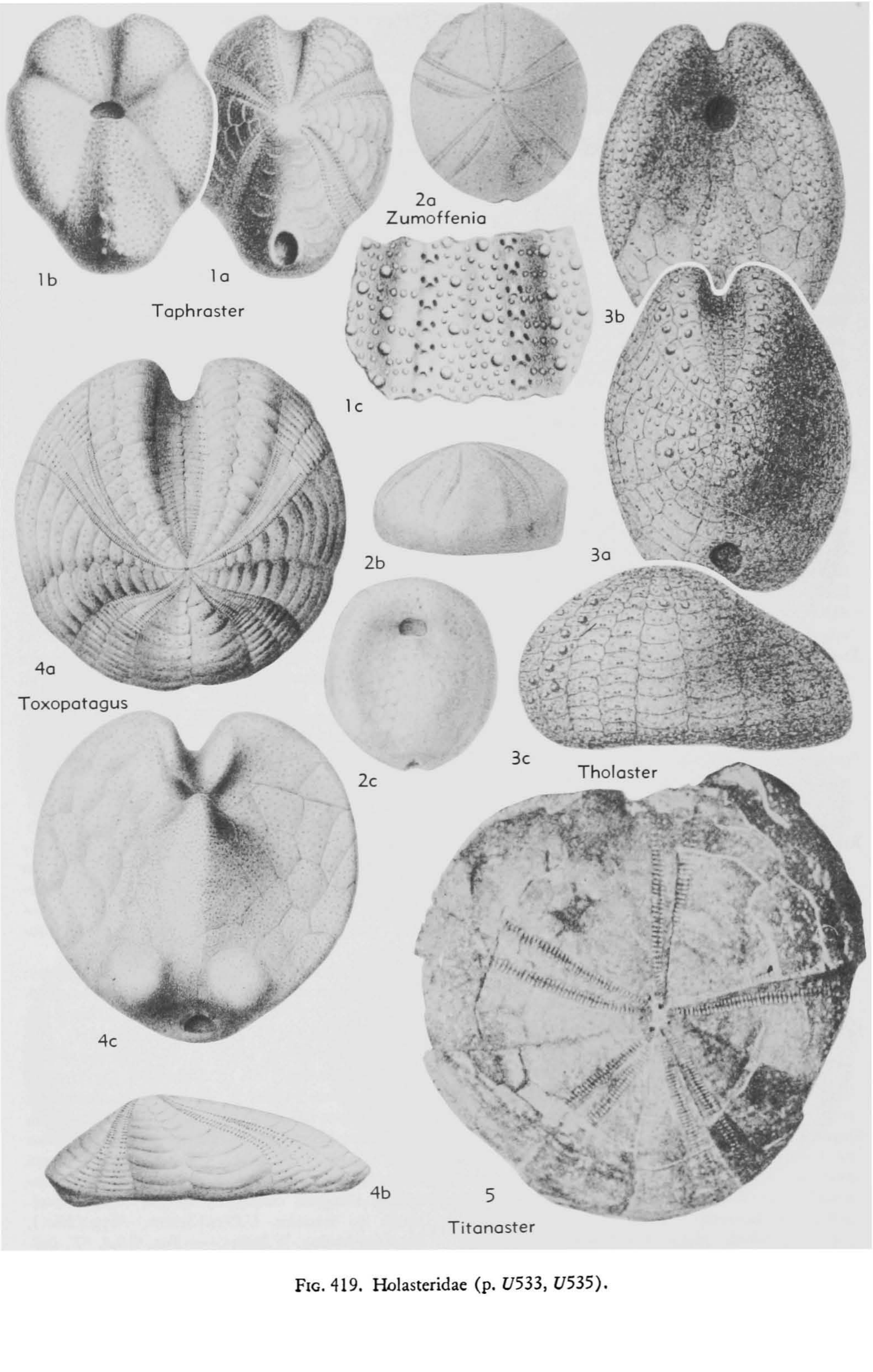


FIG. 419. Holasteridae (p. U533, U535).

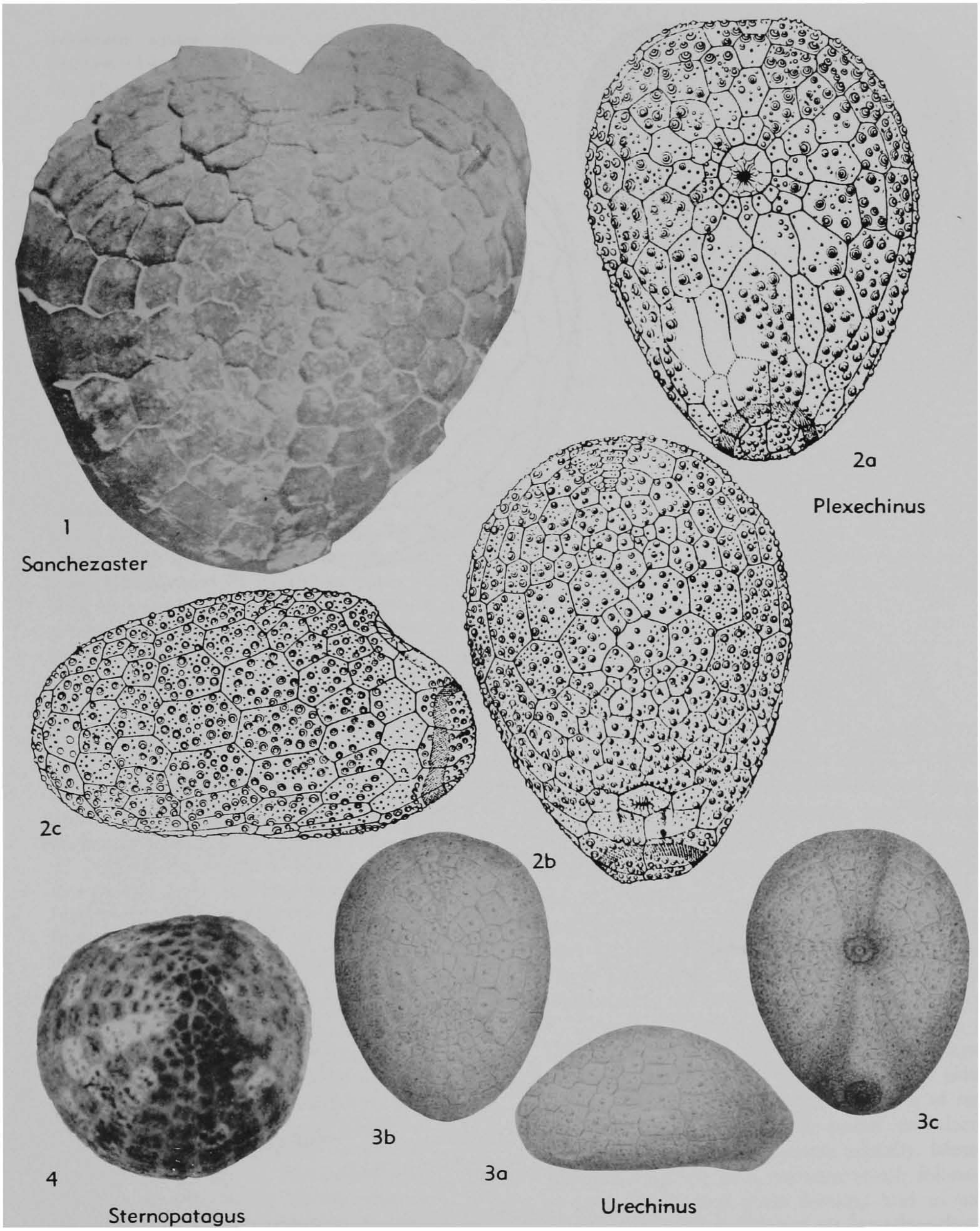


FIG. 420. Urechinidae (p. *U*536-*U*537).

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

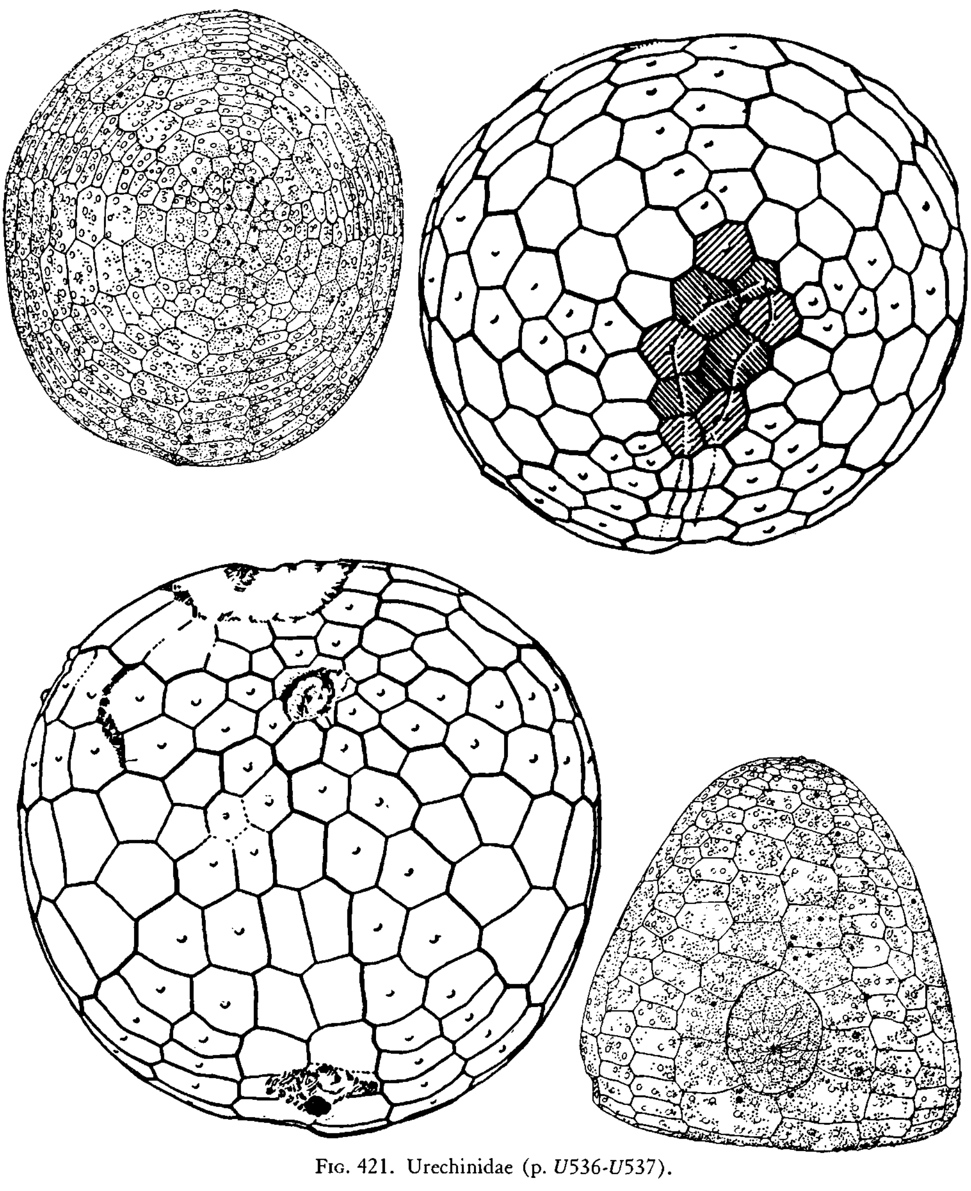


FIG. 421. Urechinidae (p. U536-U537).

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, nonpetaloid, 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.*

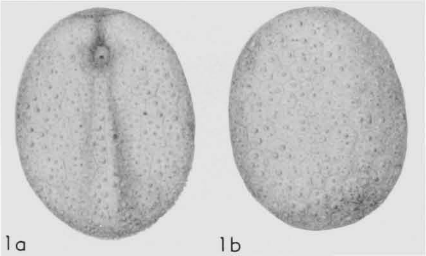


FIG. 422. Calymnidae (p. U537).

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).

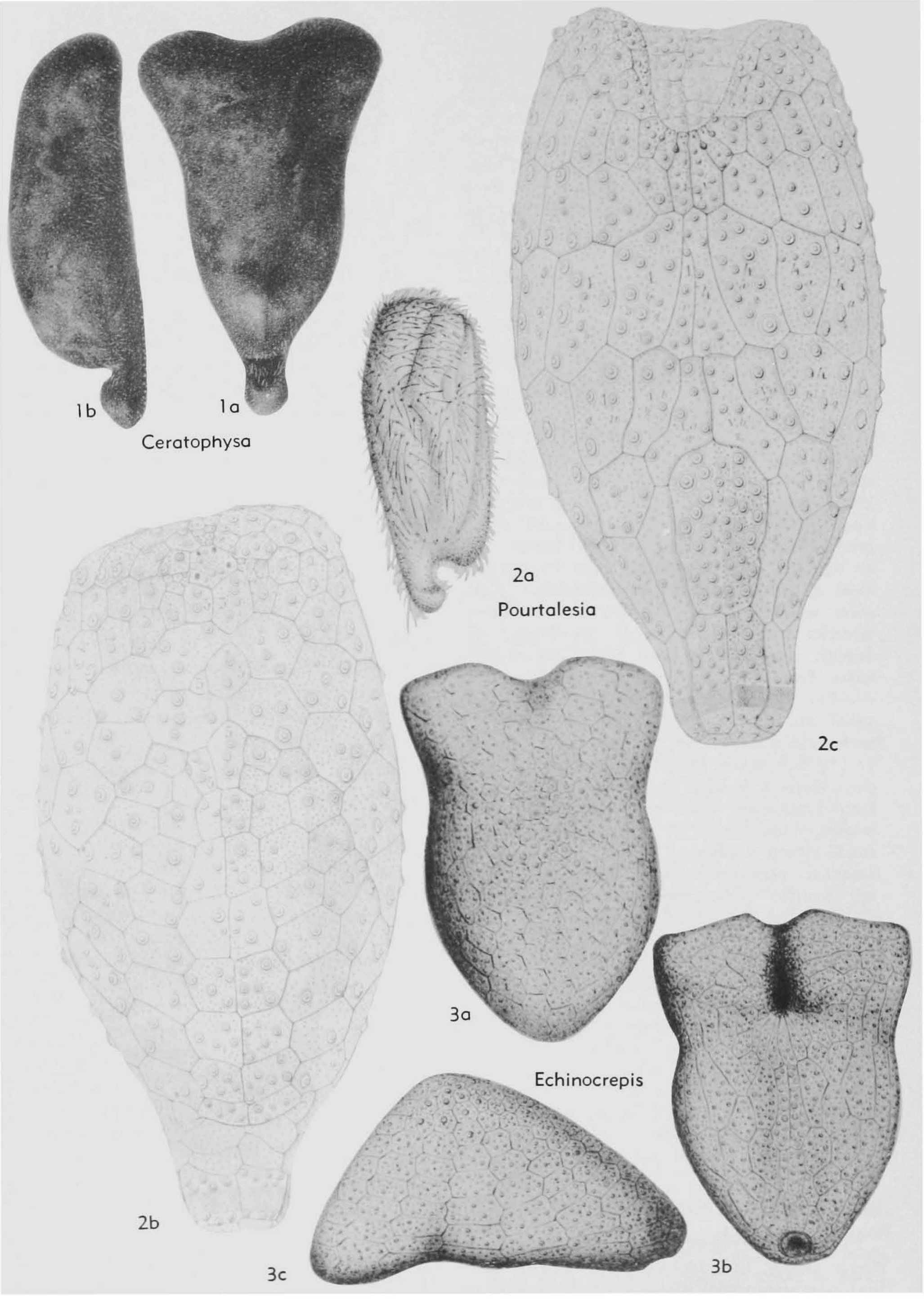


FIG. 423. Pourtalesiidae (p. U537, U539).

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).

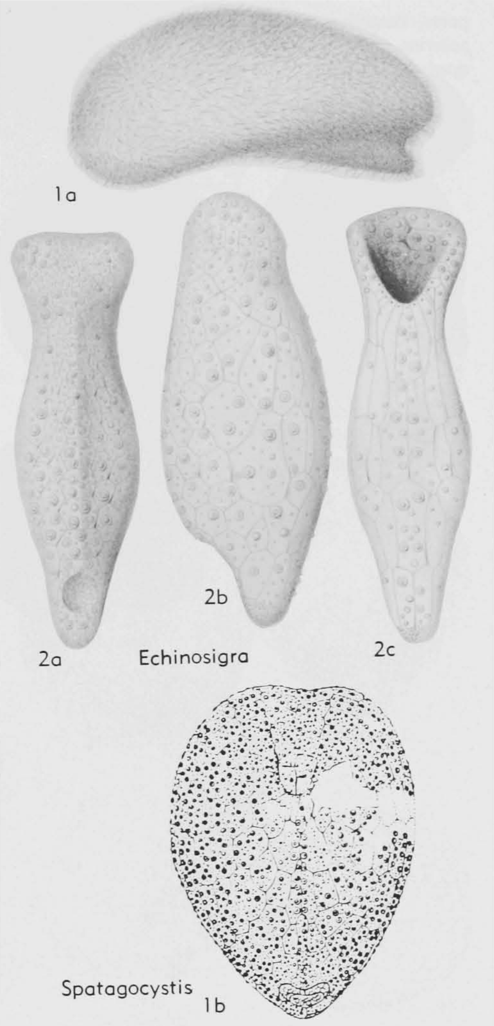


Fig. 424. Pourtalesiidae (p. *U*539).

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).

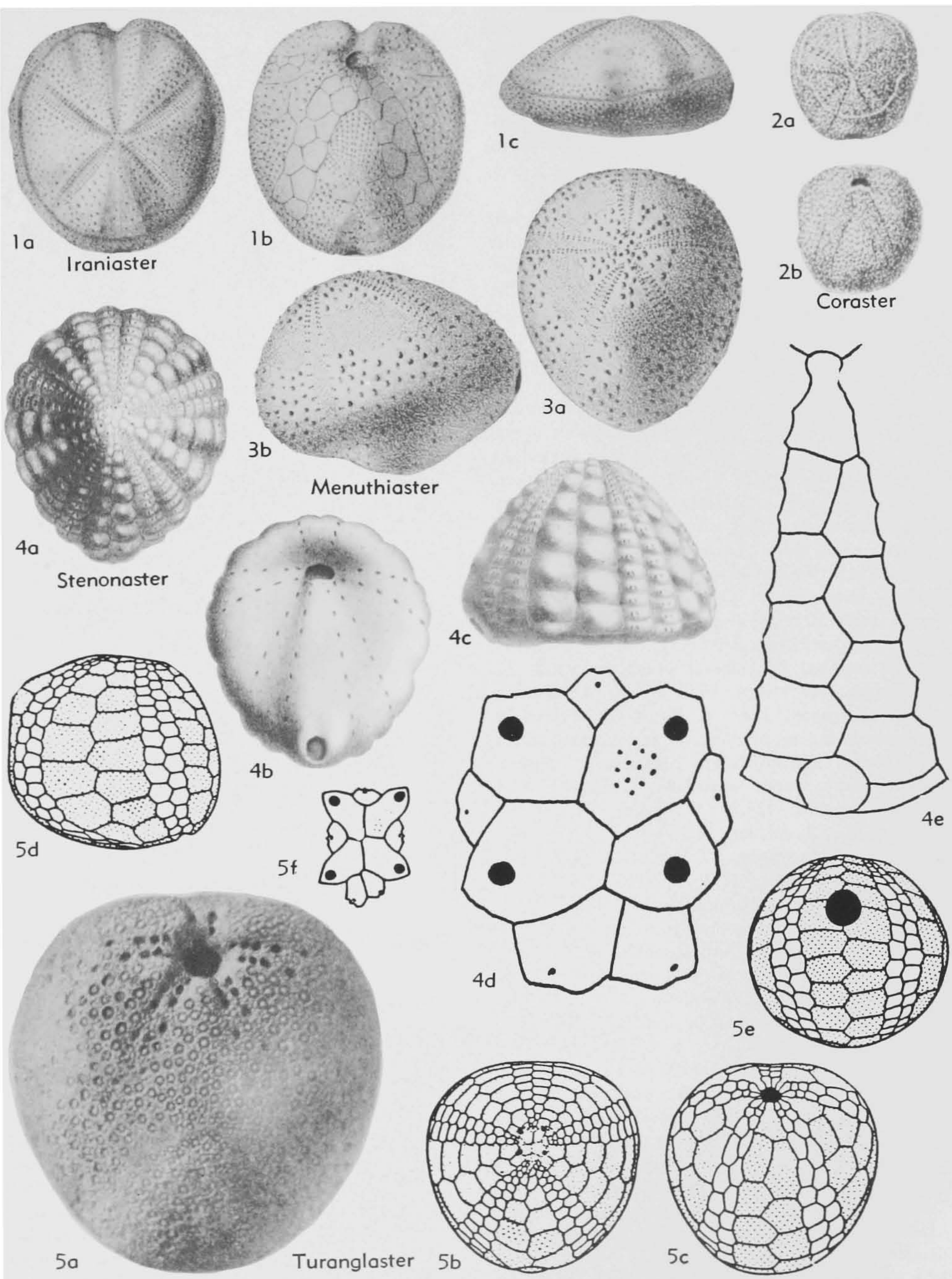


FIG. 425. Stenonasteridae *(4)*; Somaliasteridae *(1)*; Family Uncertain *(2-3,5)* (p. U539-U543).

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).

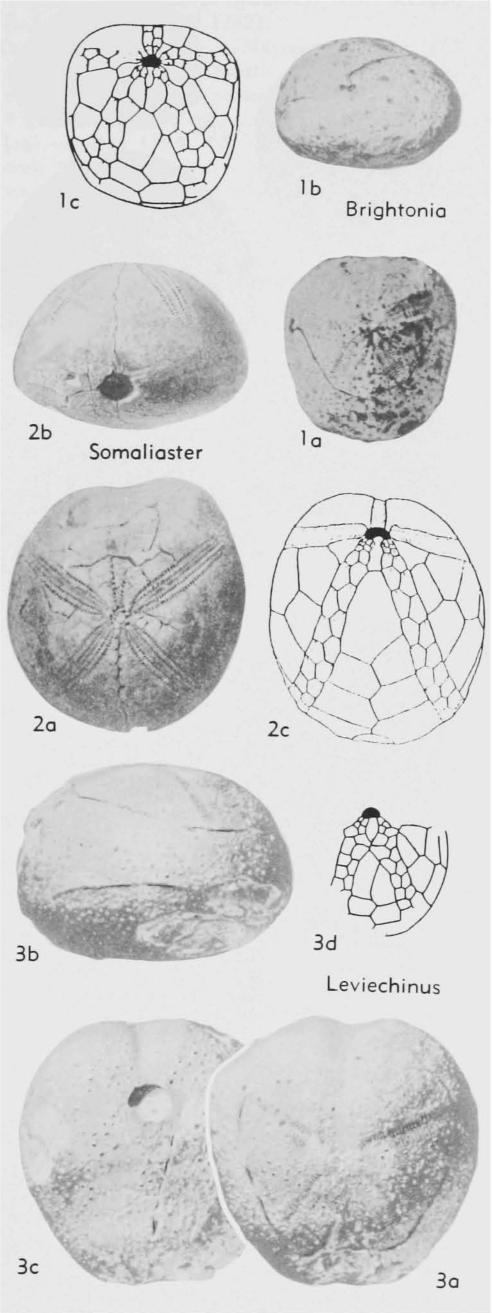


Fig. 425A. Somaliasteridae (p. U541-U542).

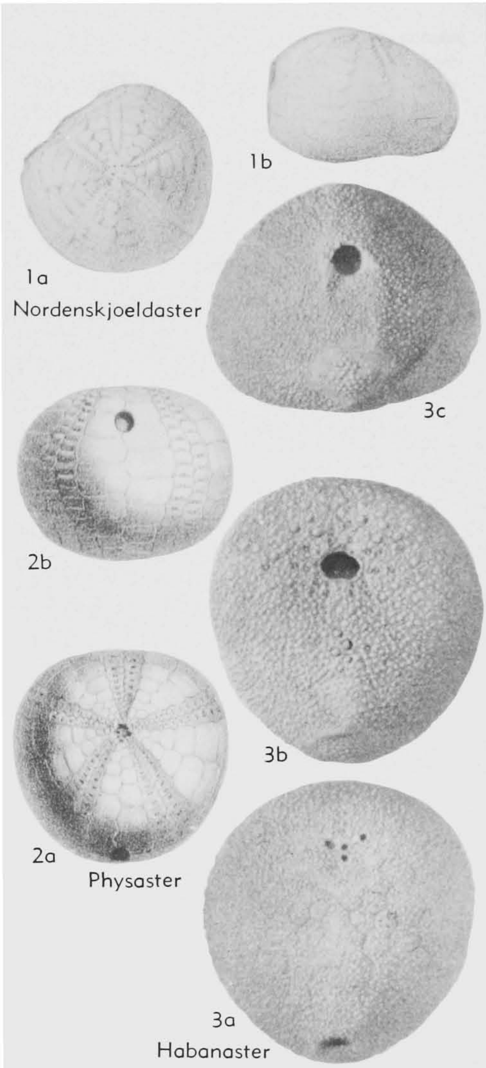


FIG. 426. Family Uncertain (p. *U*542-*U*543).

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
[Princeton University]

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

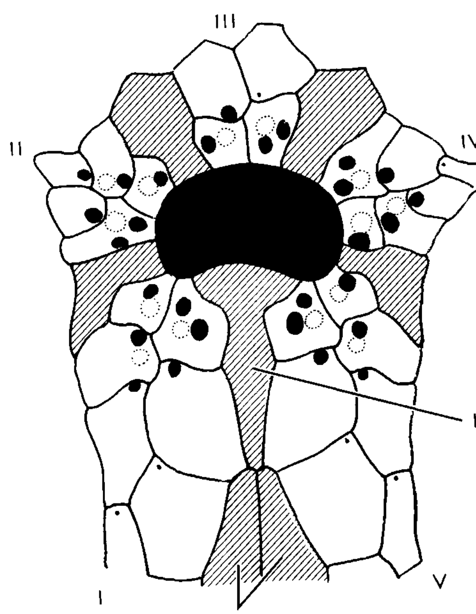


FIG. 427. Peristomial region of *Lovenia elongata* (mod. from Mortensen). [Explanation: peristome (large black area) with peristomial plates omitted; interambulacral plates shaded; *l,* labrum; *s,* sternal plates. Ambulacral plates near peristome with large feeding tube feet set into pits (black) and 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,

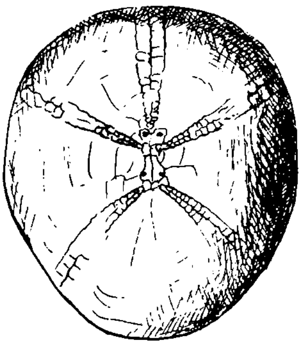


FIG. 428. *Toxaster laffittei* DEVRIÈS, possible link between collyritid holasteroids and toxasterid spatangoids. L.Cret.(Berrias.), N.Afr., ×2 (after Devriès).

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

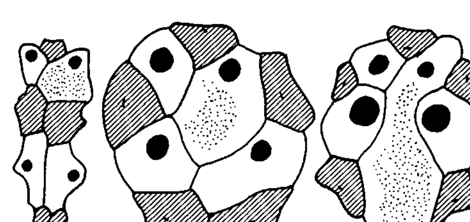


FIG. 429. Three evolutionary stages of spatangoid apical system.——*A*. Primitive elongate condition (*Toxaster lafittei*) (after Devriès).——*B*. Ethmophract condition (*Hemiaster*) (after Mortensen).——*C*. Ethmolytic condition (*Brissus*) (after Mortensen).

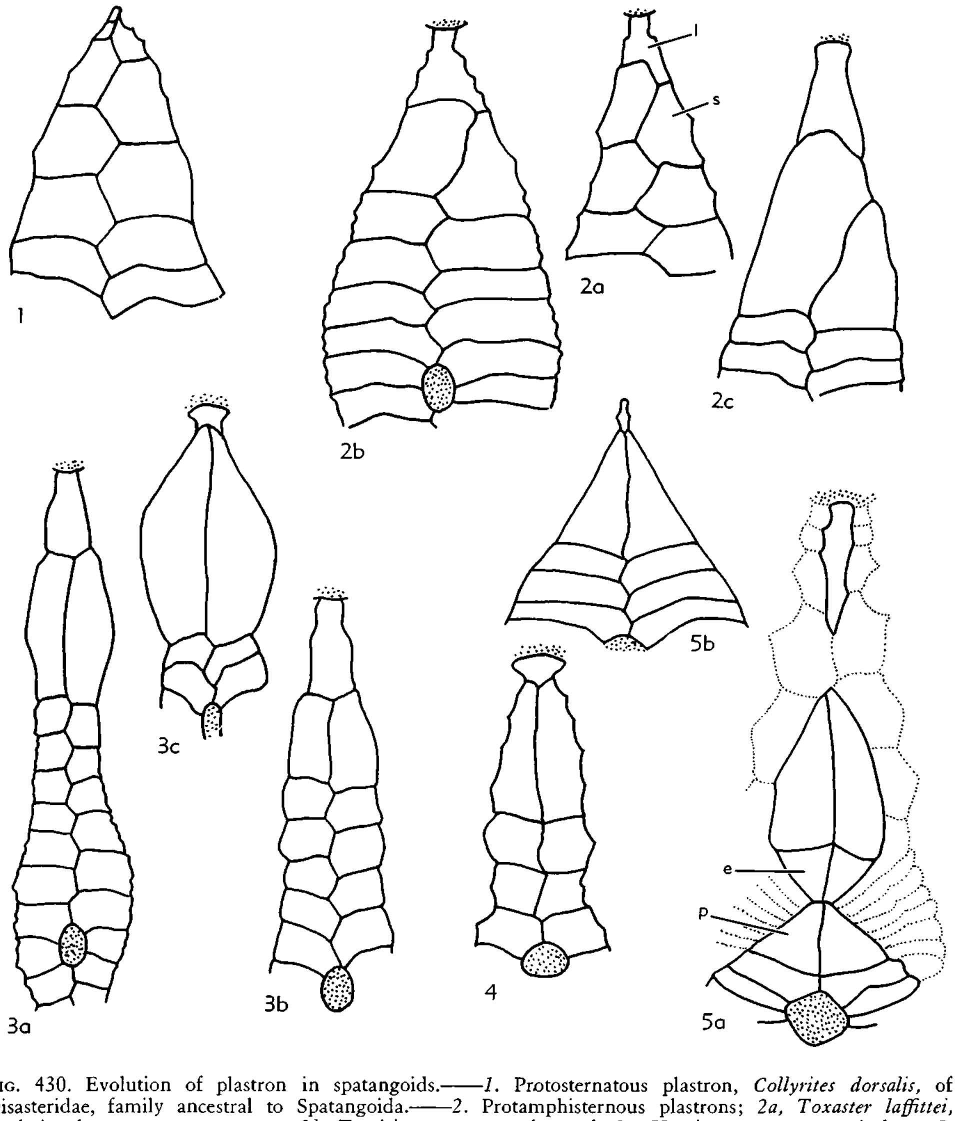


FIG. 430. Evolution of plastron in spatangoids.——*1.* Protosternatous plastron, *Collyrites dorsalis,* of Disasteridae, family ancestral to Spatangoida.——*2.* Protamphisternous plastrons; *2a, Toxaster laffittei,* gradational to protosternous type; *2b, T. africanus,* more advanced; *2c, Hemiaster texanus,* 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

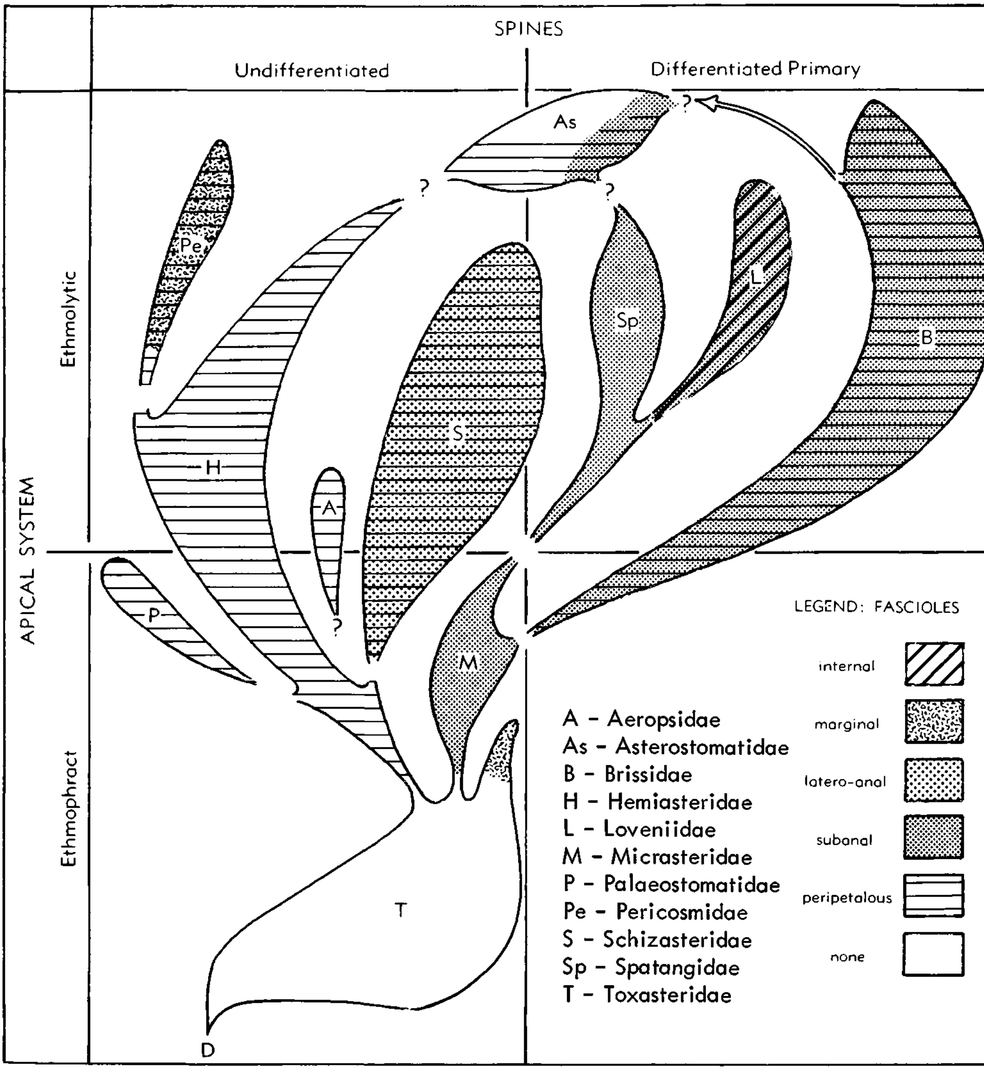


FIG. 431. Spatangoid family tree indicated by structure of apical system and differentiation of spines and fascioles. Primitive Toxasteridae are inferred to have given rise to two main branches, distinguished as the hemiasterid stock (suborder Hemiasterina) at left and the micrasterid stock (suborder 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

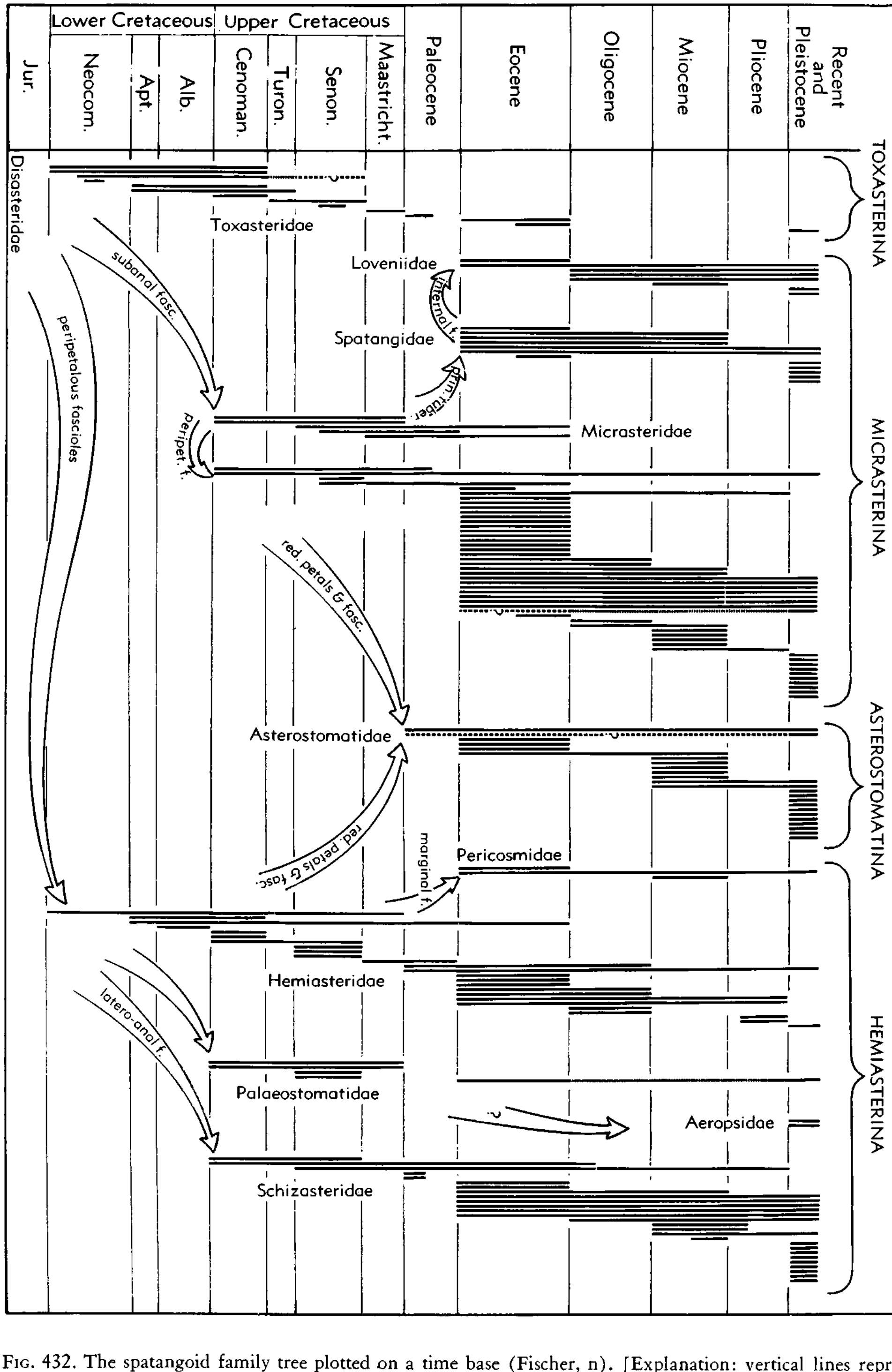


FIG. 432. The spatangoid family tree plotted on a time base (Fischer, n). [Explanation: vertical lines represent individual genera; total number of genera per stage and per 40-million-year intervals plotted at right.]

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.-Cenoman.),* 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).

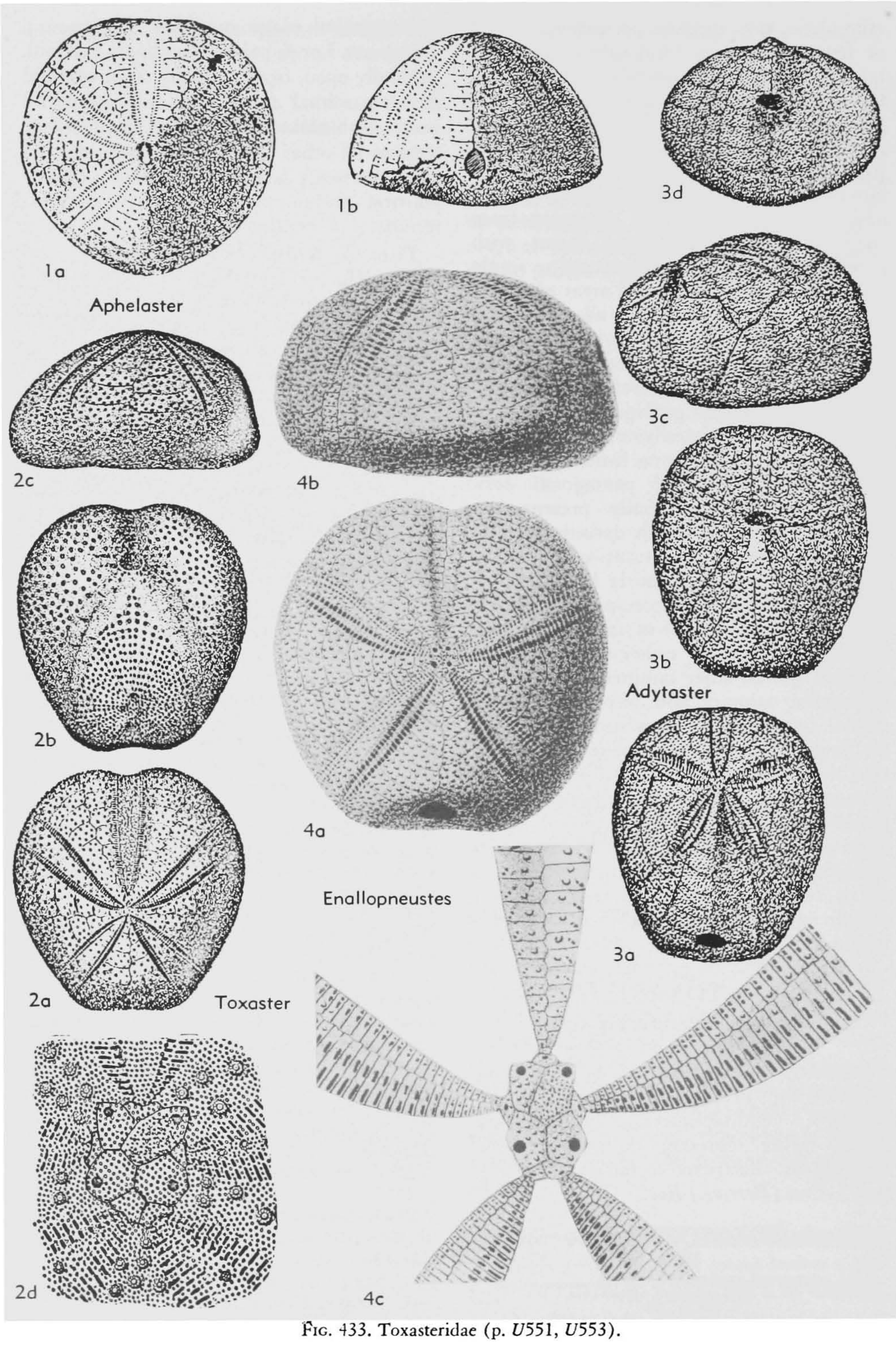


FIG. 433. Toxasteridae (p. *U551*, *U553*).

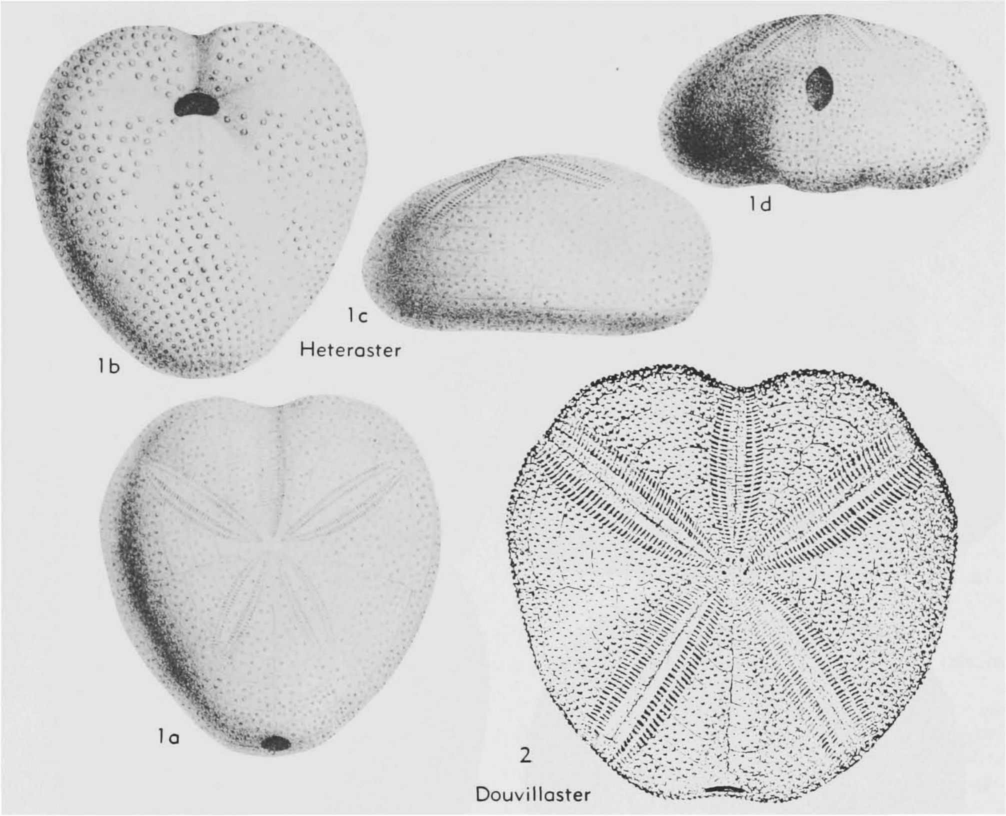


FIG. 434. Toxasteridae (p. U553).

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).

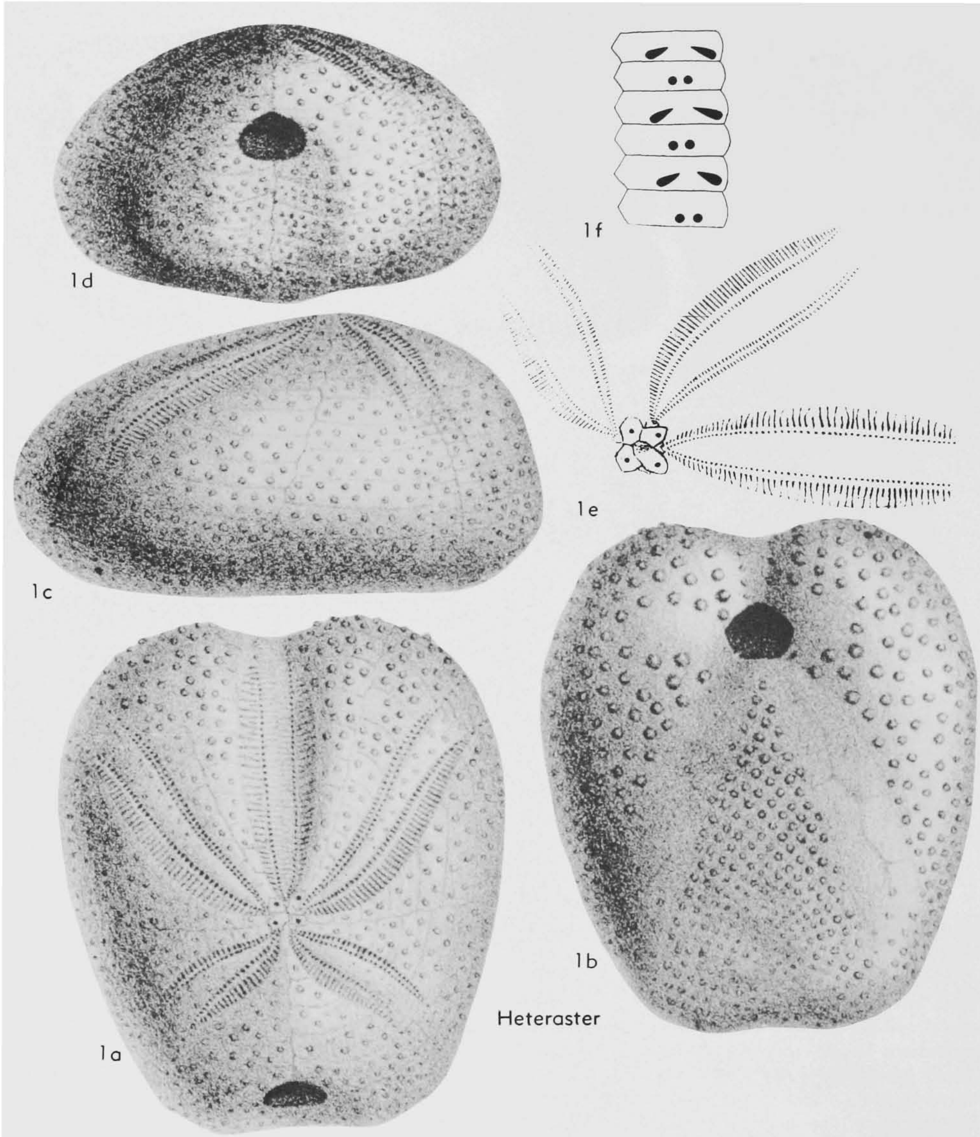


FIG. 435. Toxasteridae (p. *U*553).

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

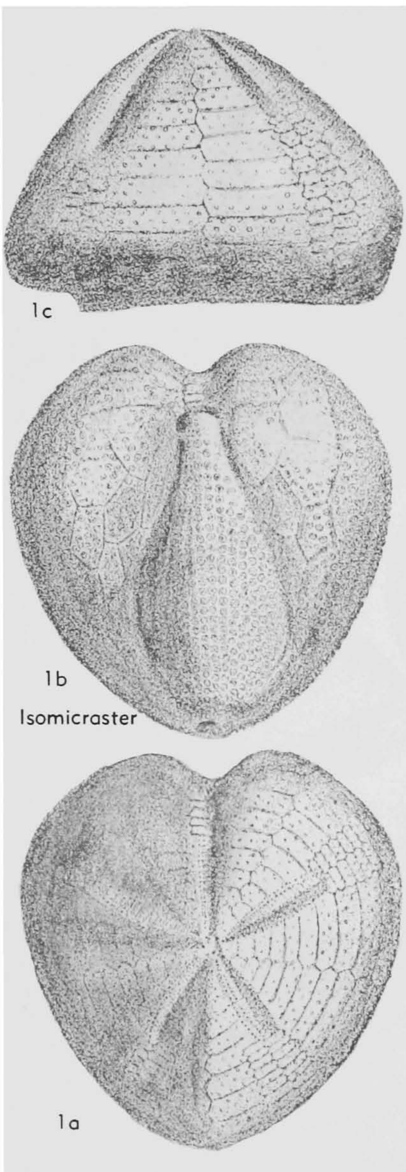


Fig. 436. Toxasteridae (p. U554).

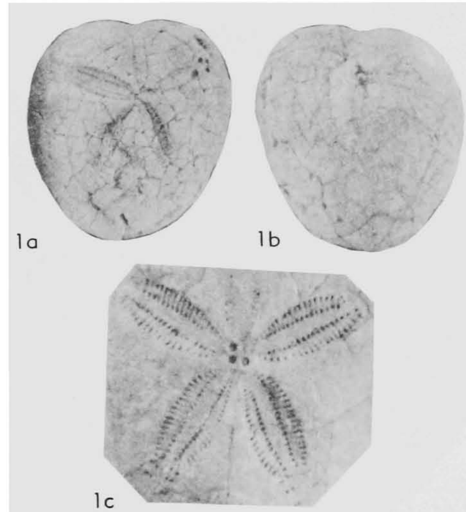


Fig. 437. Toxasteridae (p. U555).

(Roemer, 1888); *2c*, detail of apex, enlarged (136h).

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).

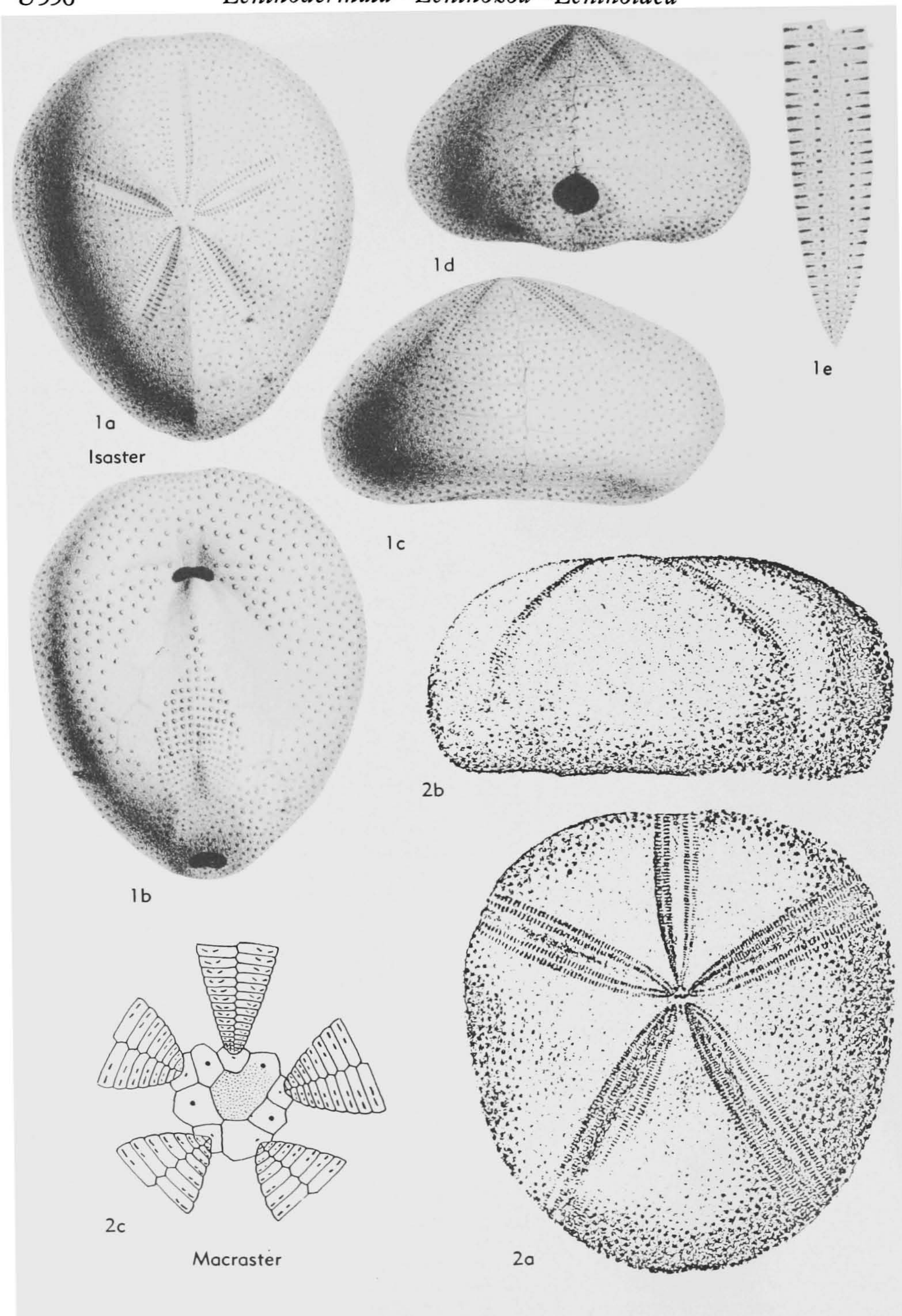


FIG. 438. Toxasteridae (p. U554-U555).

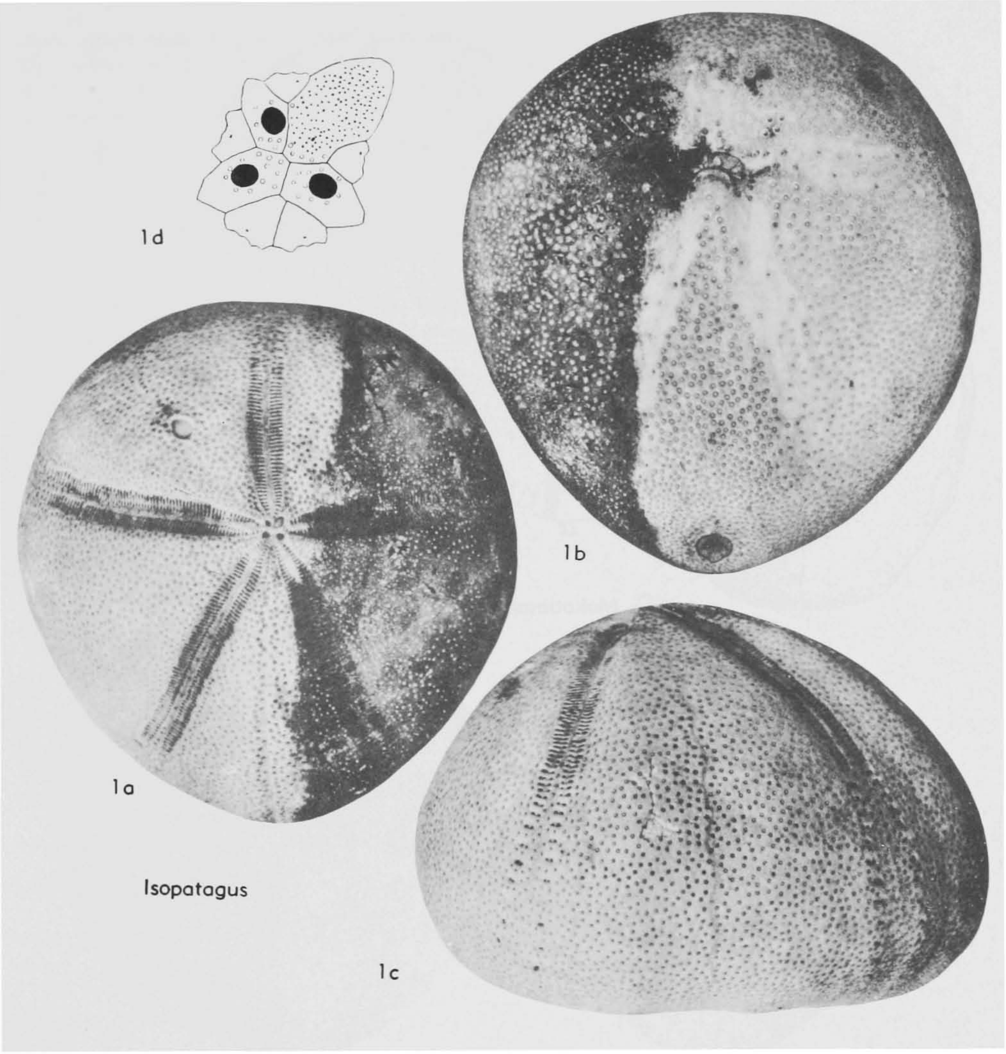


FIG. 439. Toxasteridae (p. U554).

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.

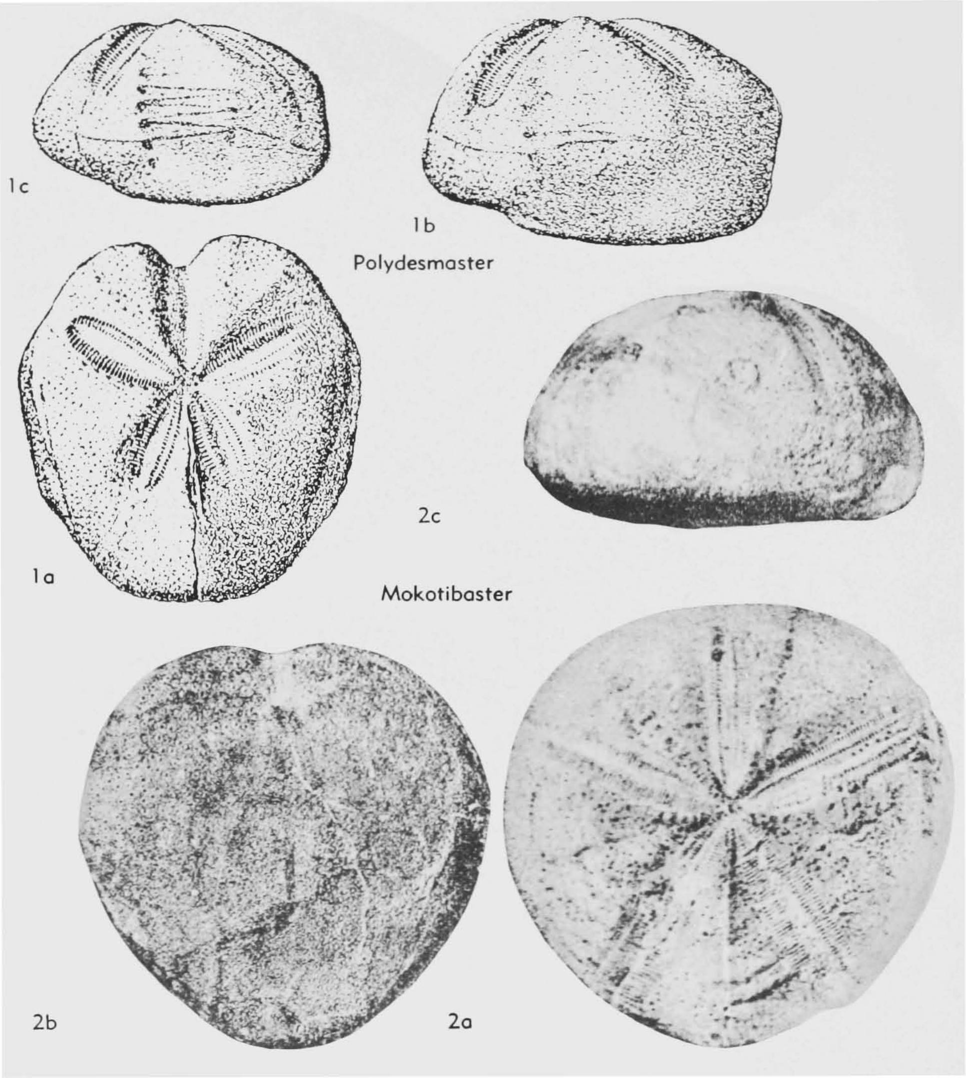


FIG. 440. Toxasteridae (p. U555).

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).

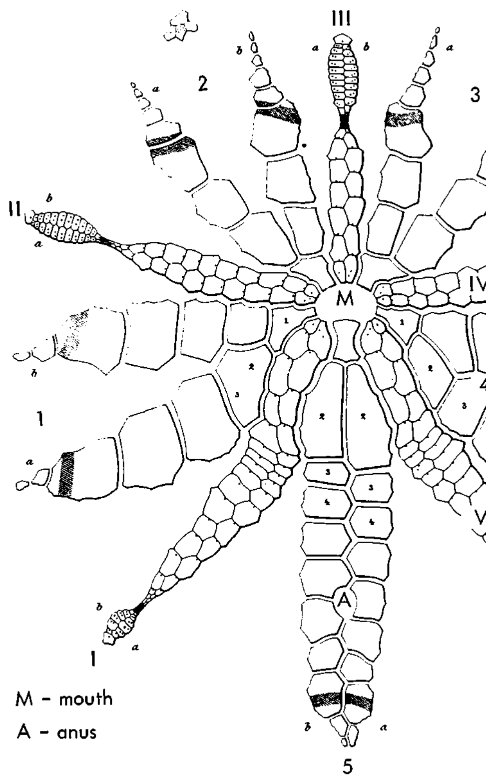


FIG. 441. Plate diagram of *Hemiaster* (Lovén).

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*

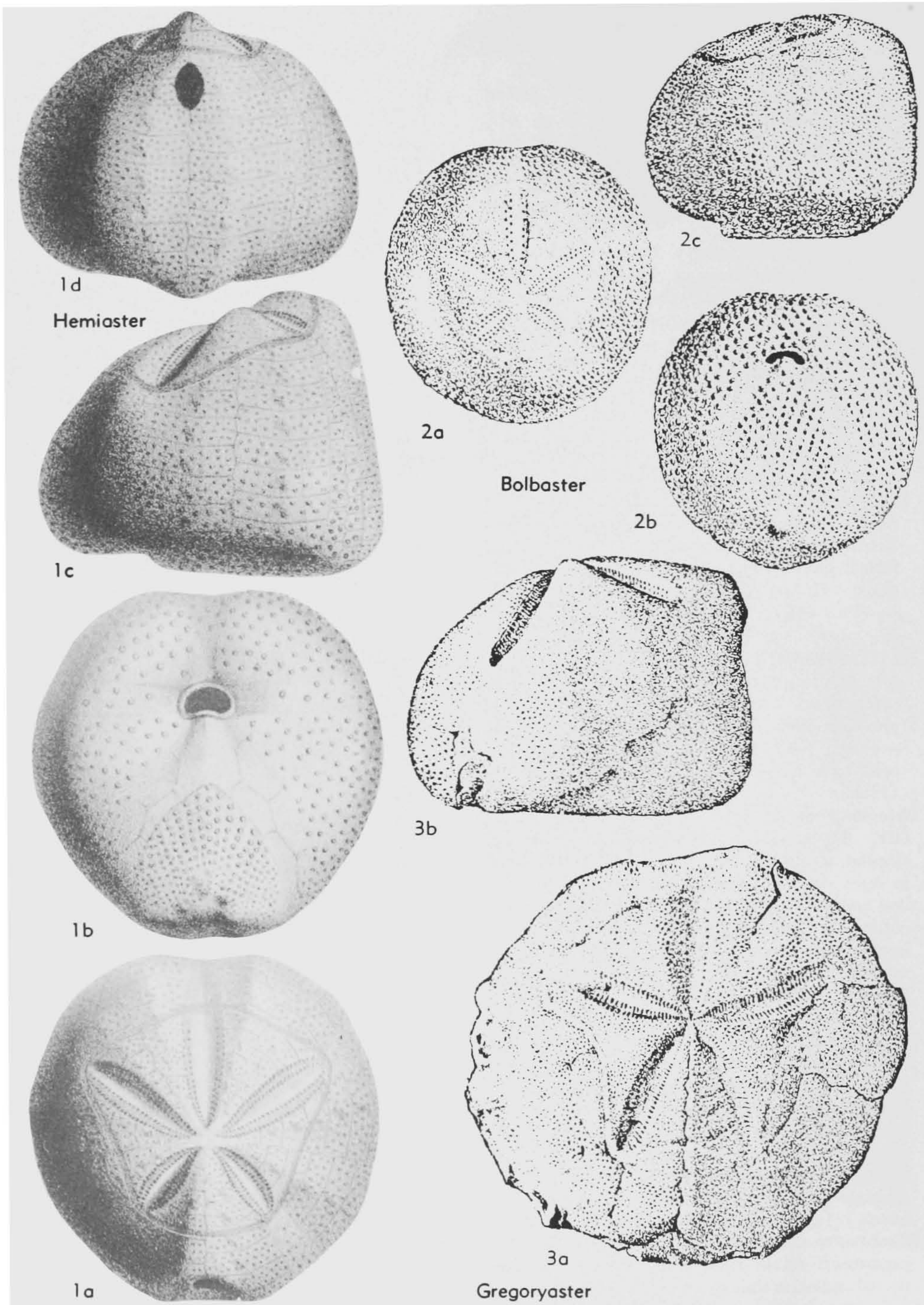


Fig. 442. Hemiasteridae (p. U558-U559).

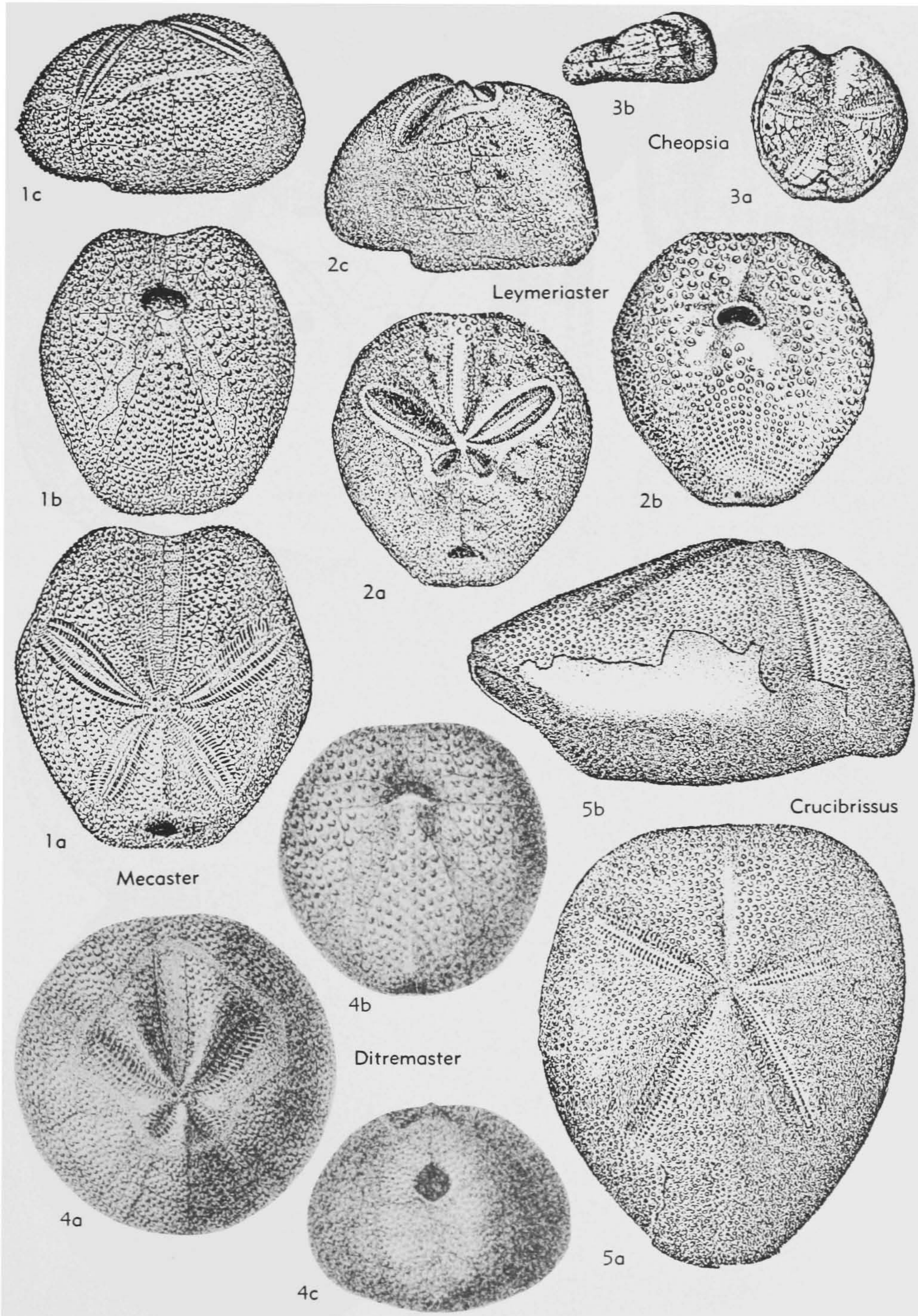


FIG. 443. Hemiasteridae (p. U559).

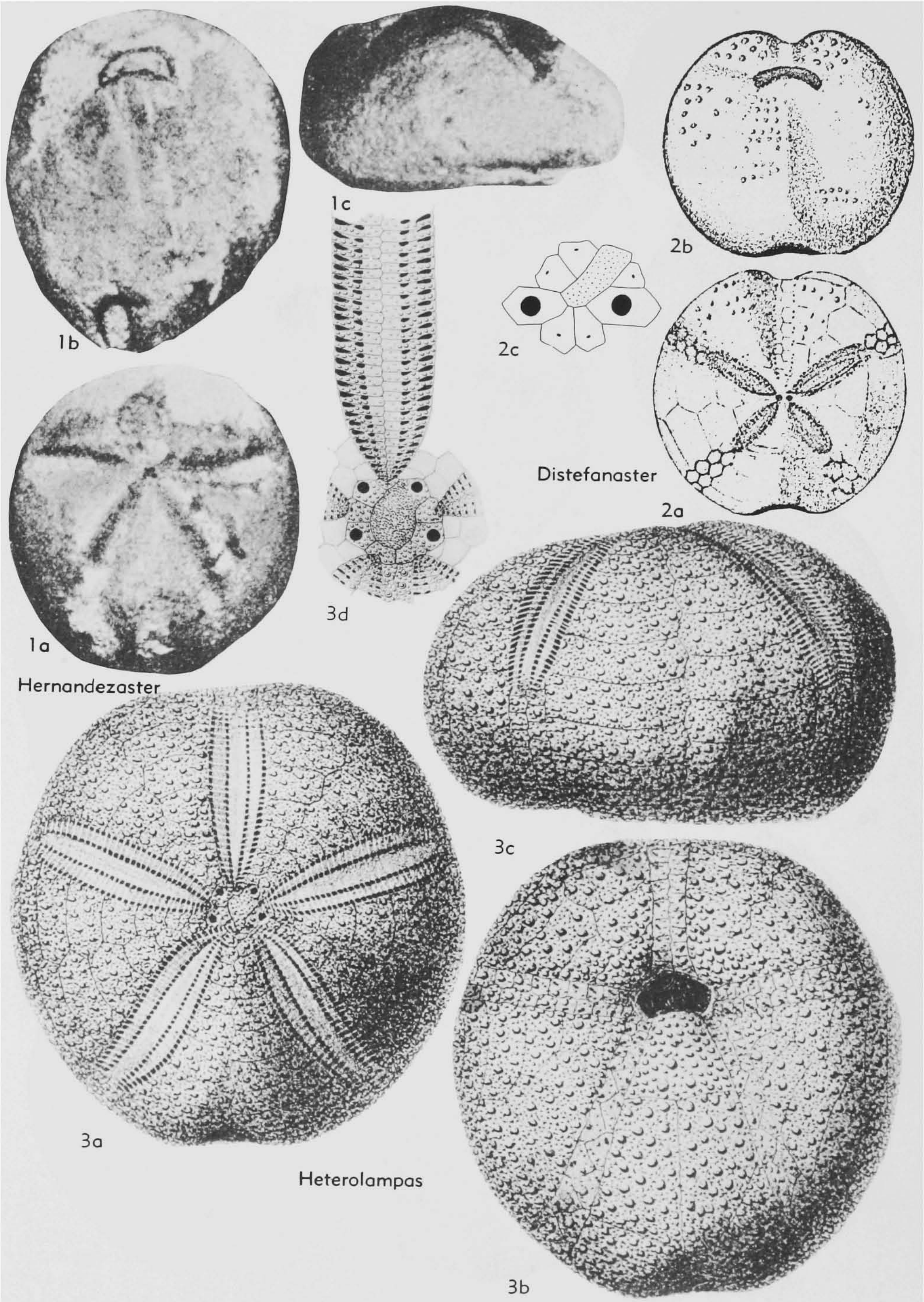


FIG. 444. Hemiasteridae (p. U559, U564).

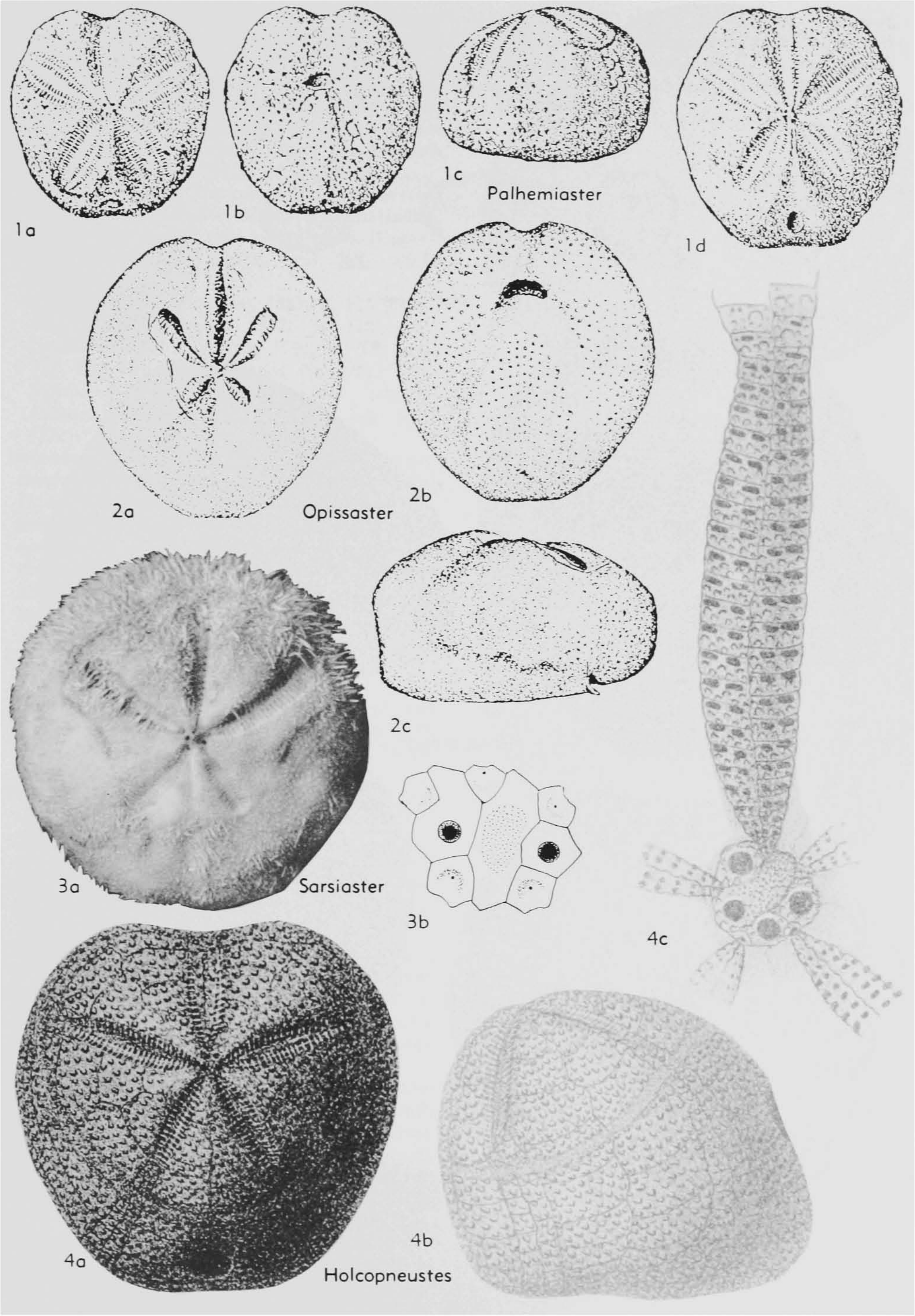


FIG. 445. Hemiasteridae (p. *U*564-*U*565).

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).

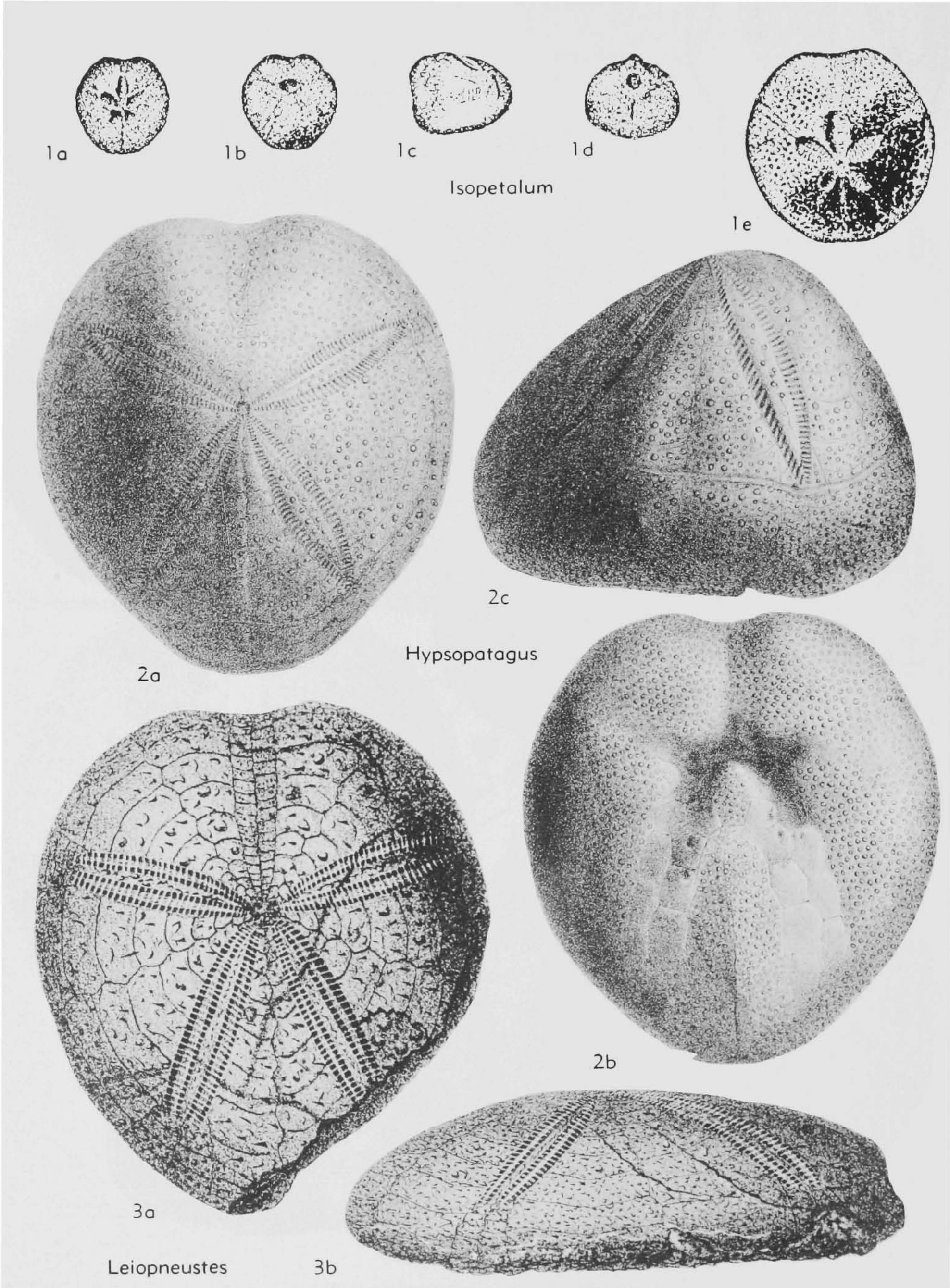


FIG. 446. Hemiasteridae (p. U565)

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).

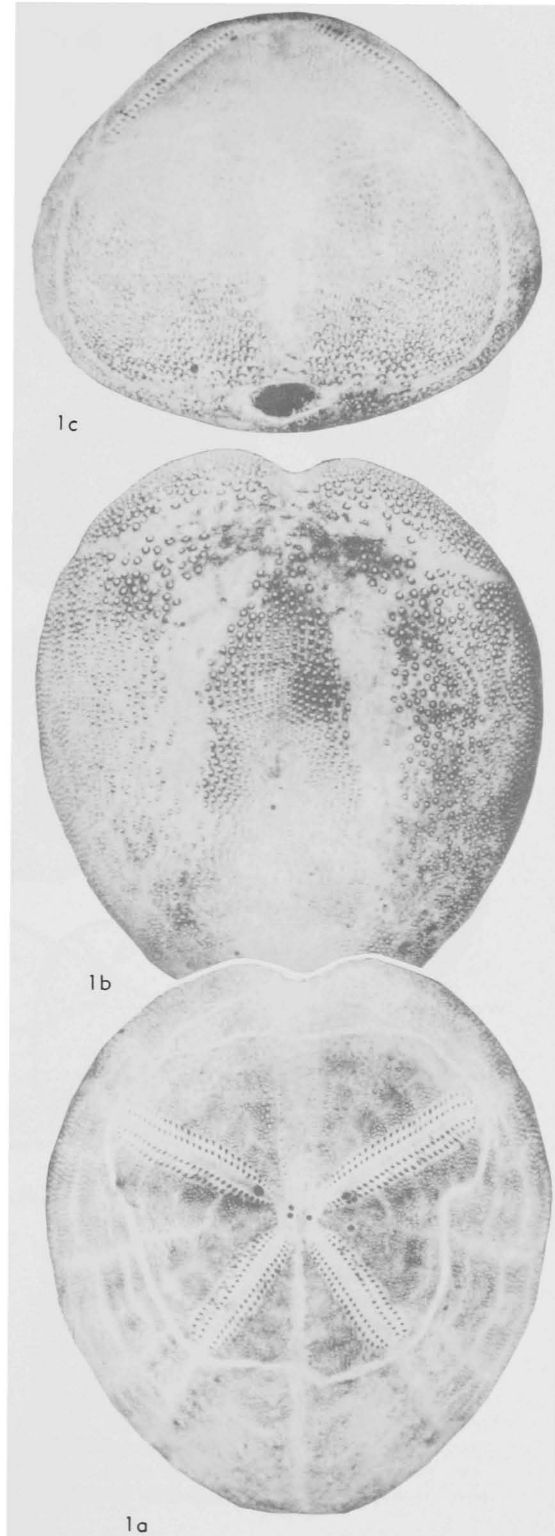
Isopetalum LAMBERT, 1911, p. 188 [**Linthia pseudoverticale* OPPENHEIM, 1900, p. 107; OD] [=*Homoianthoides* LAMBERT, 1920, p. 162]. Small, globose test with truncated rear; apical system unknown; 5 small petals, posterior pair shortest; peripetalous fasciole present; probably a hemiasterid. *Oligo.*, 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. *U*576).

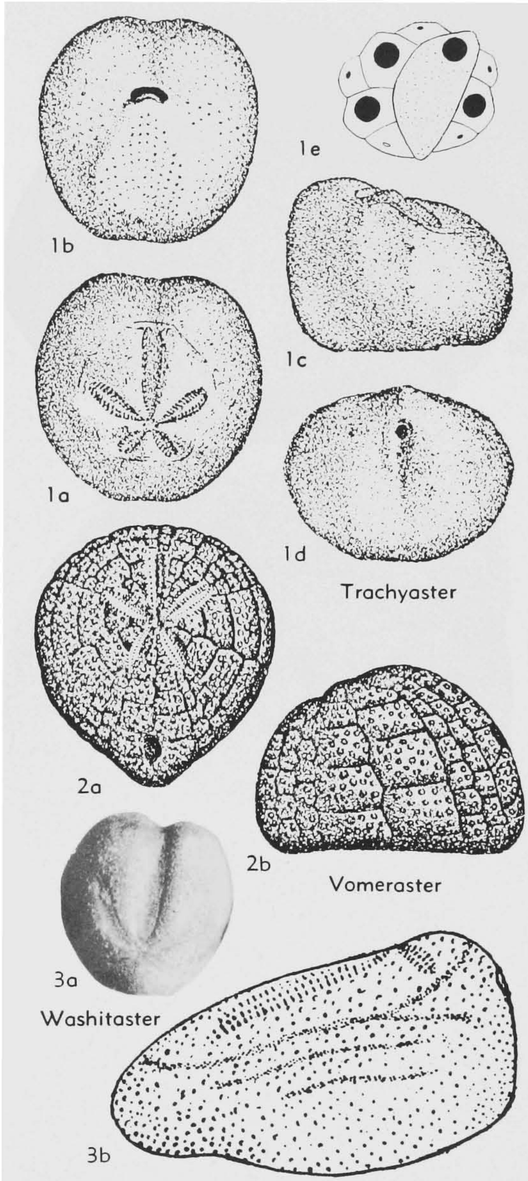


FIG. 448. Hemiasteridae (p. *U559*, *U565*, *U566*).

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.

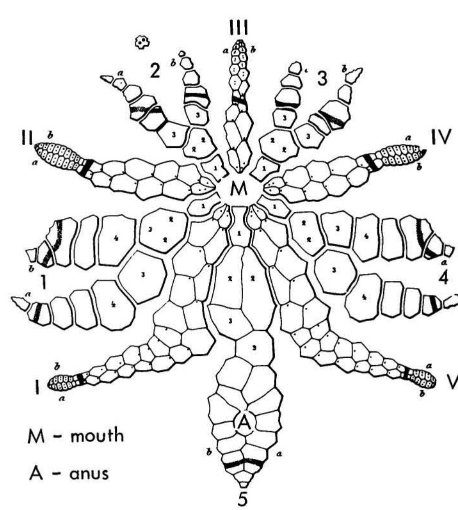


FIG. 449. Plate diagram of *Palaeostoma* (Lovén).

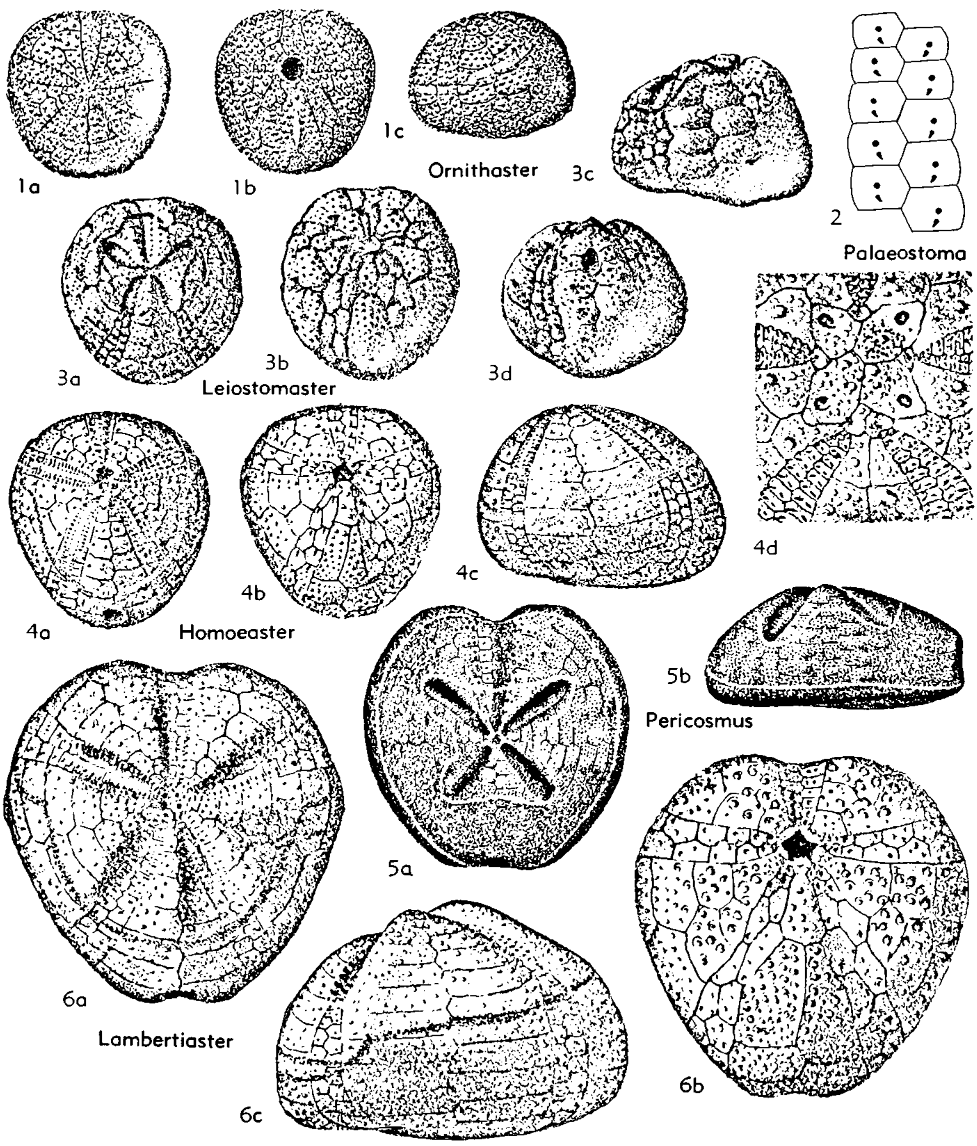


FIG. 450. Palaeostomatidae *(1-4,6)*; Pericosmidae *(5)* (p. U566-U568).

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-

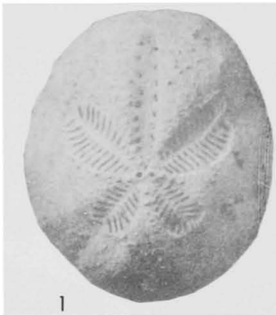


FIG. 451. Palaeostomatidae (p. *U566-U567*).

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).

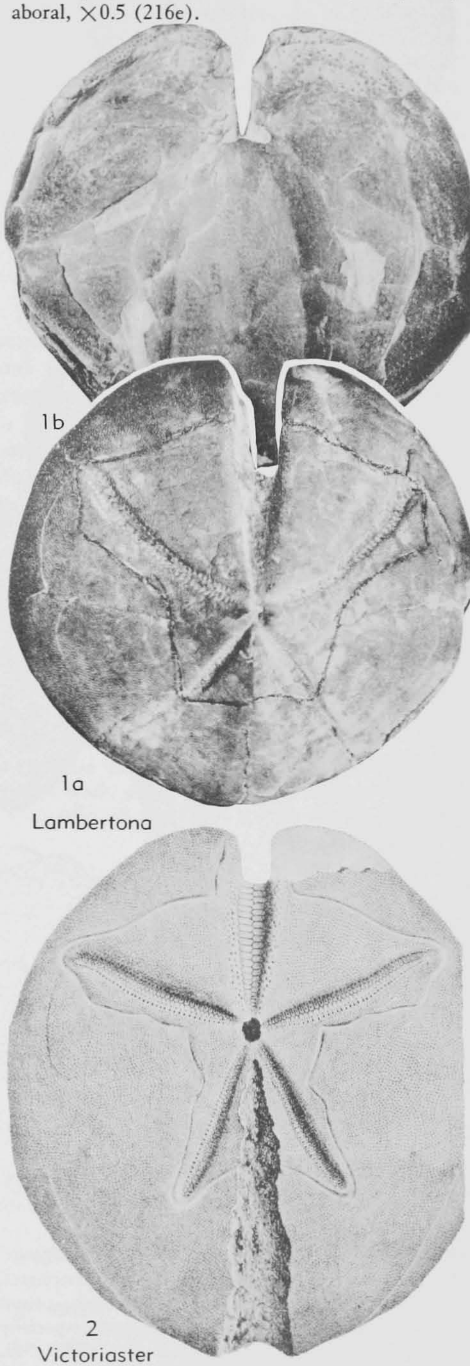


FIG. 452. Pericosmidae (p. *U568-U569*).

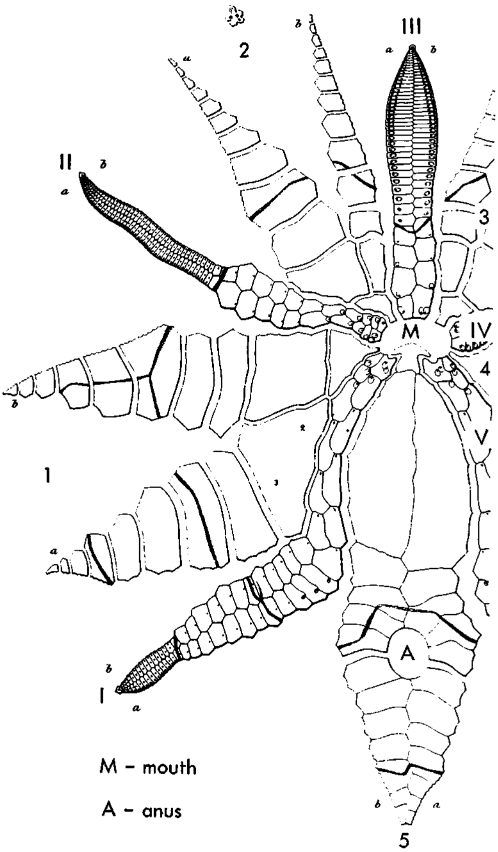


FIG. 453. Plate diagram of *Schizaster* (Lovén).

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.*

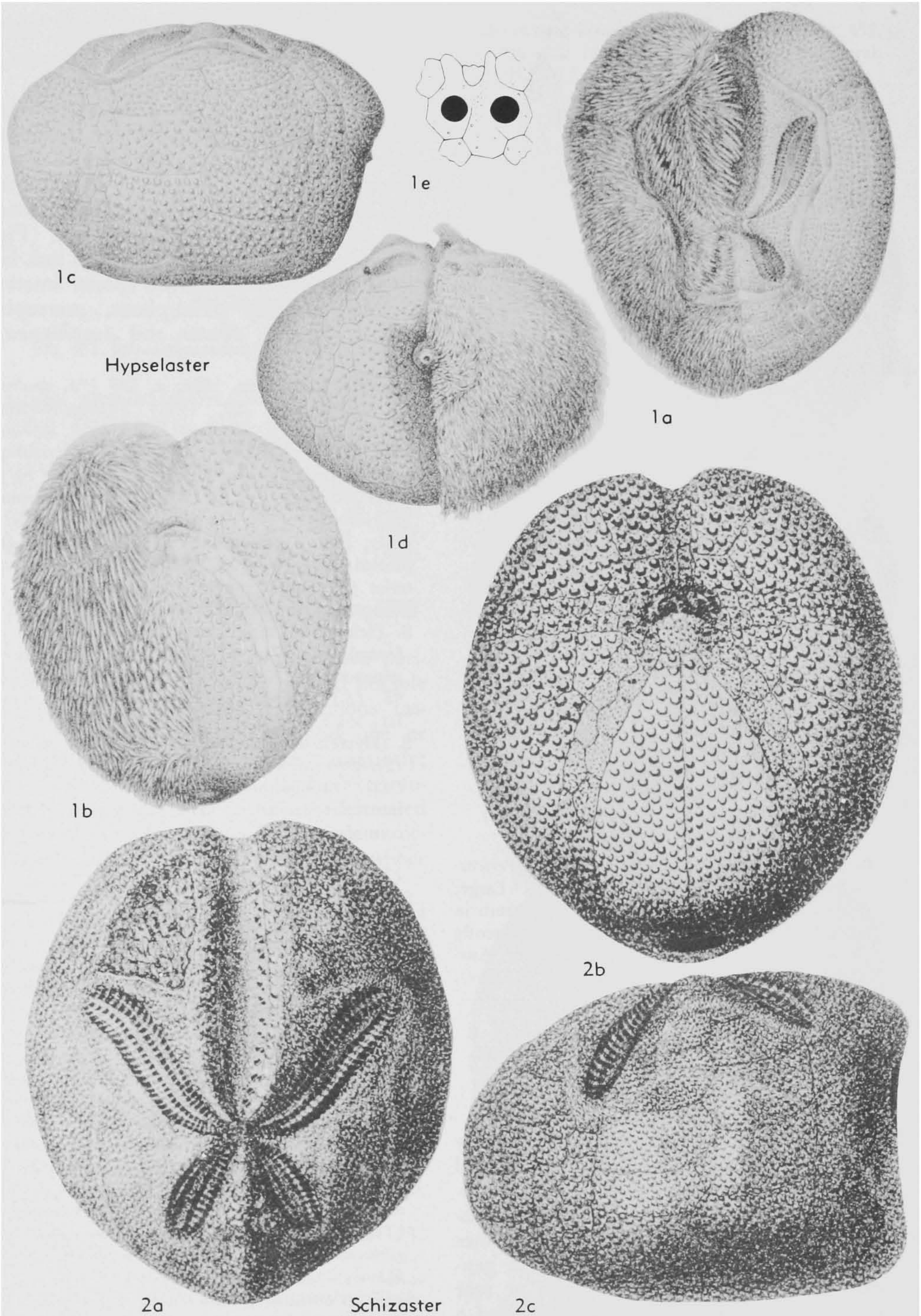


FIG. 454. Schizasteridae (p. U569).

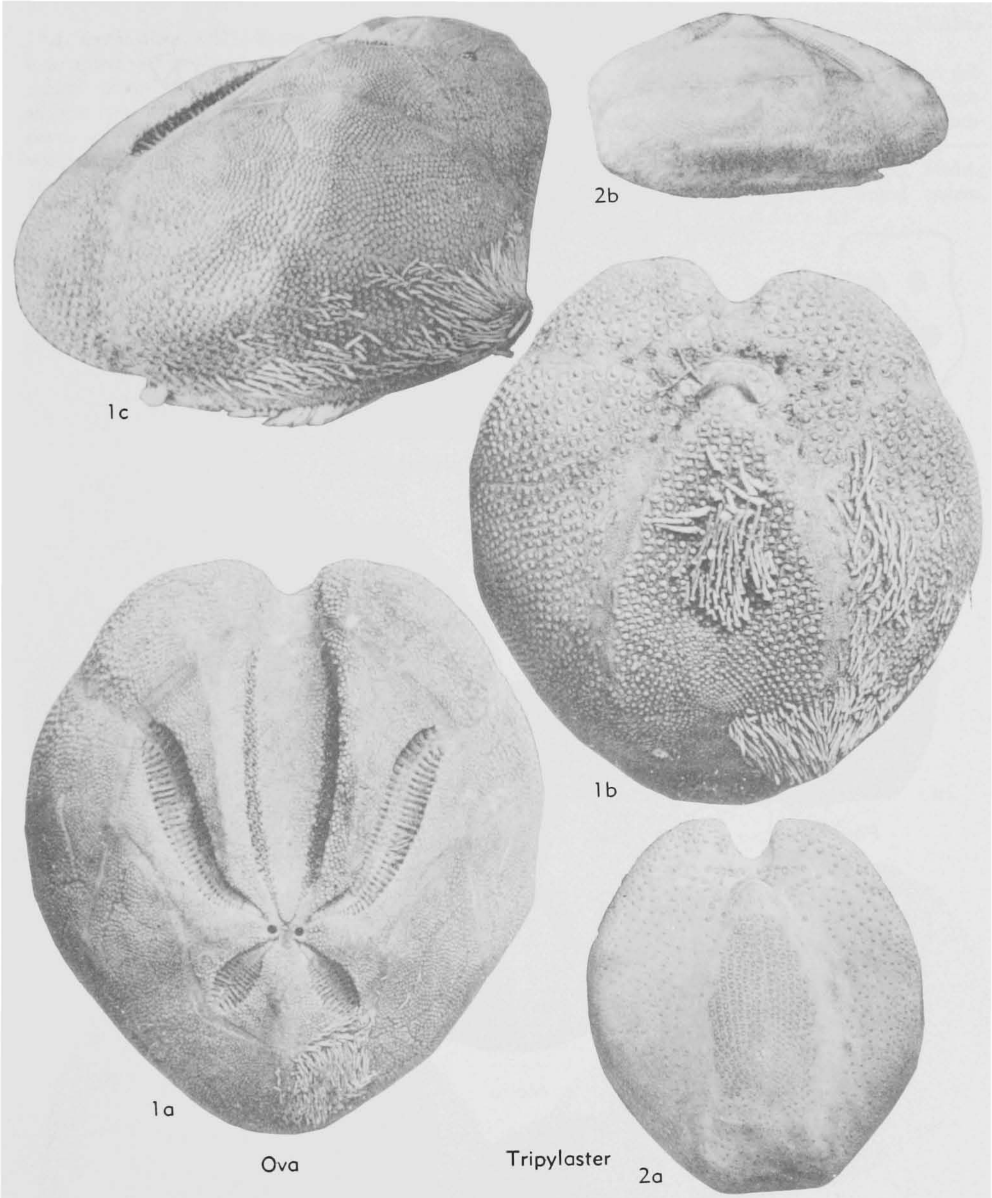


FIG. 455. Schizasteridae (p. U569).

(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)]

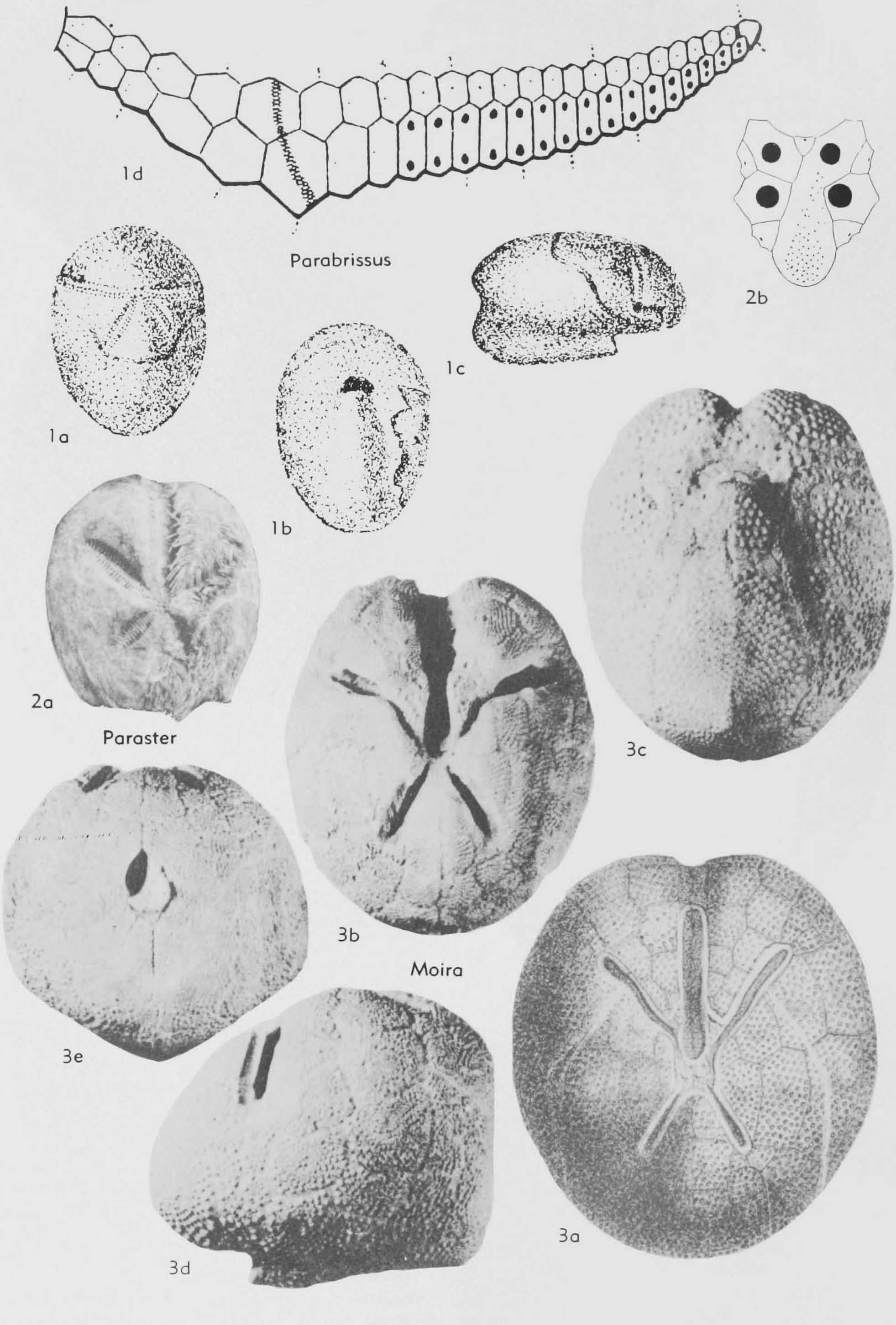


FIG. 456. Schizasteridae (p. U569, U576).

[**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,

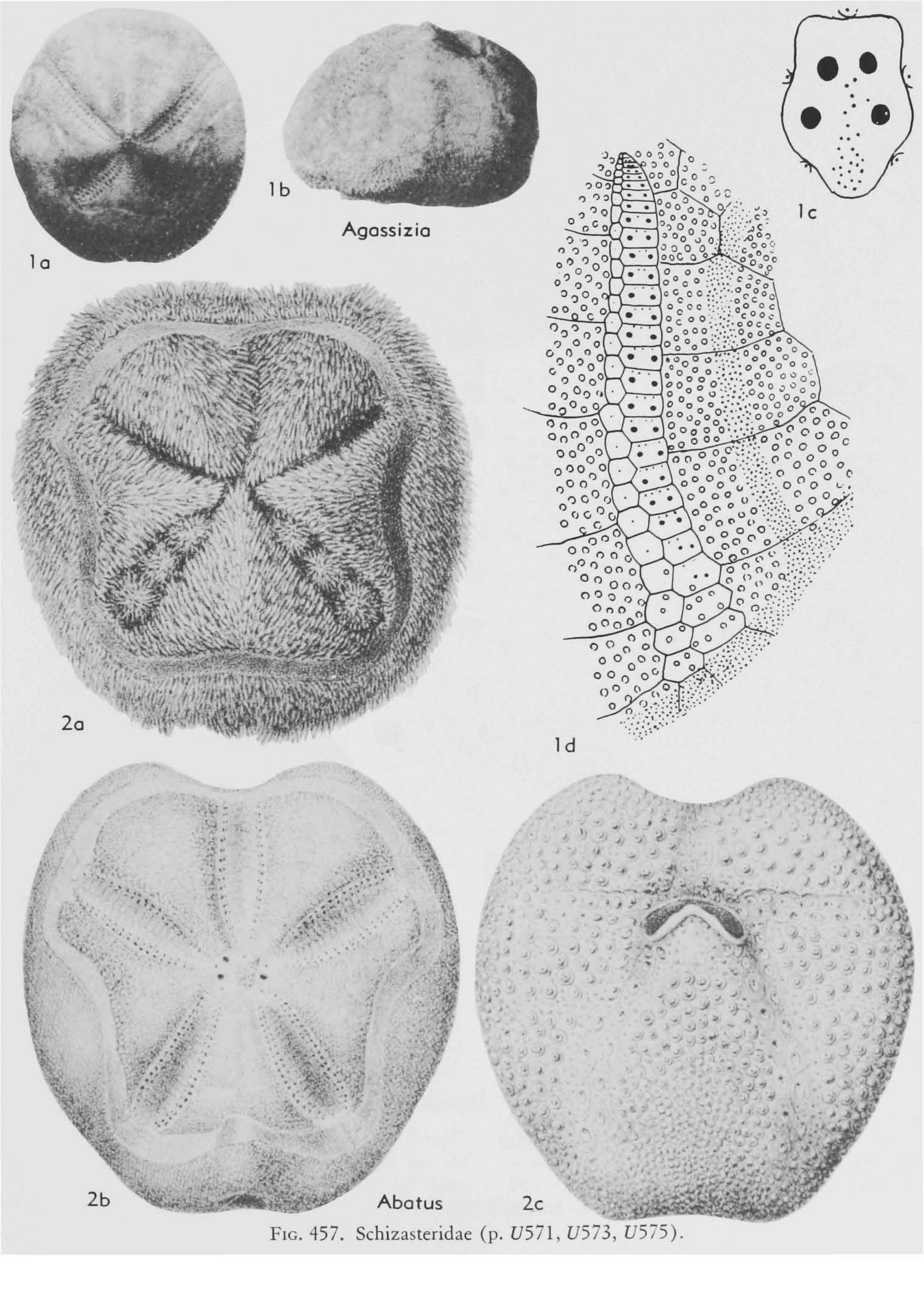


FIG. 457. Schizasteridae (p. *U*571, *U*573, *U*575).

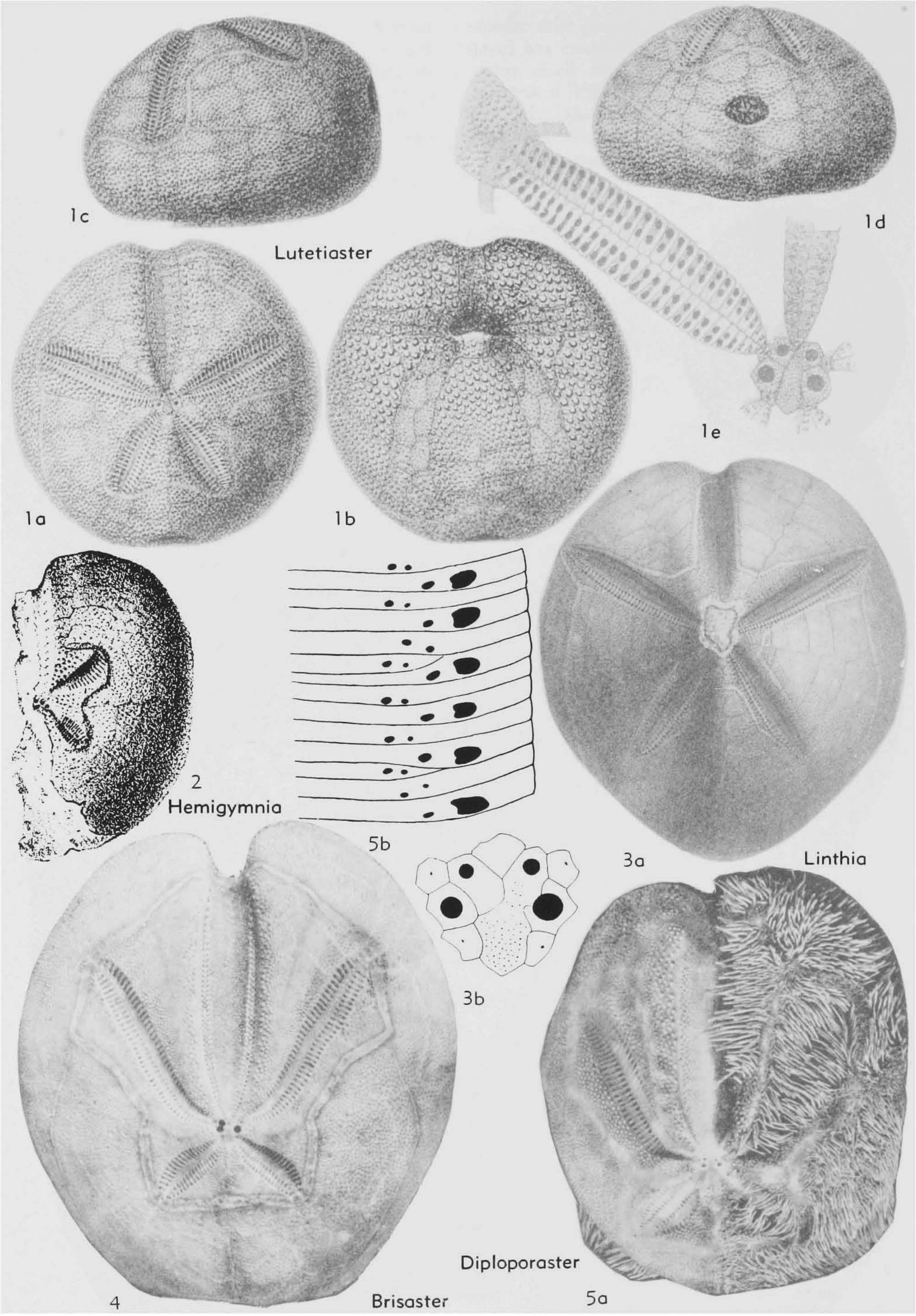


FIG. 458. Schizasteridae (p. U575-U576).

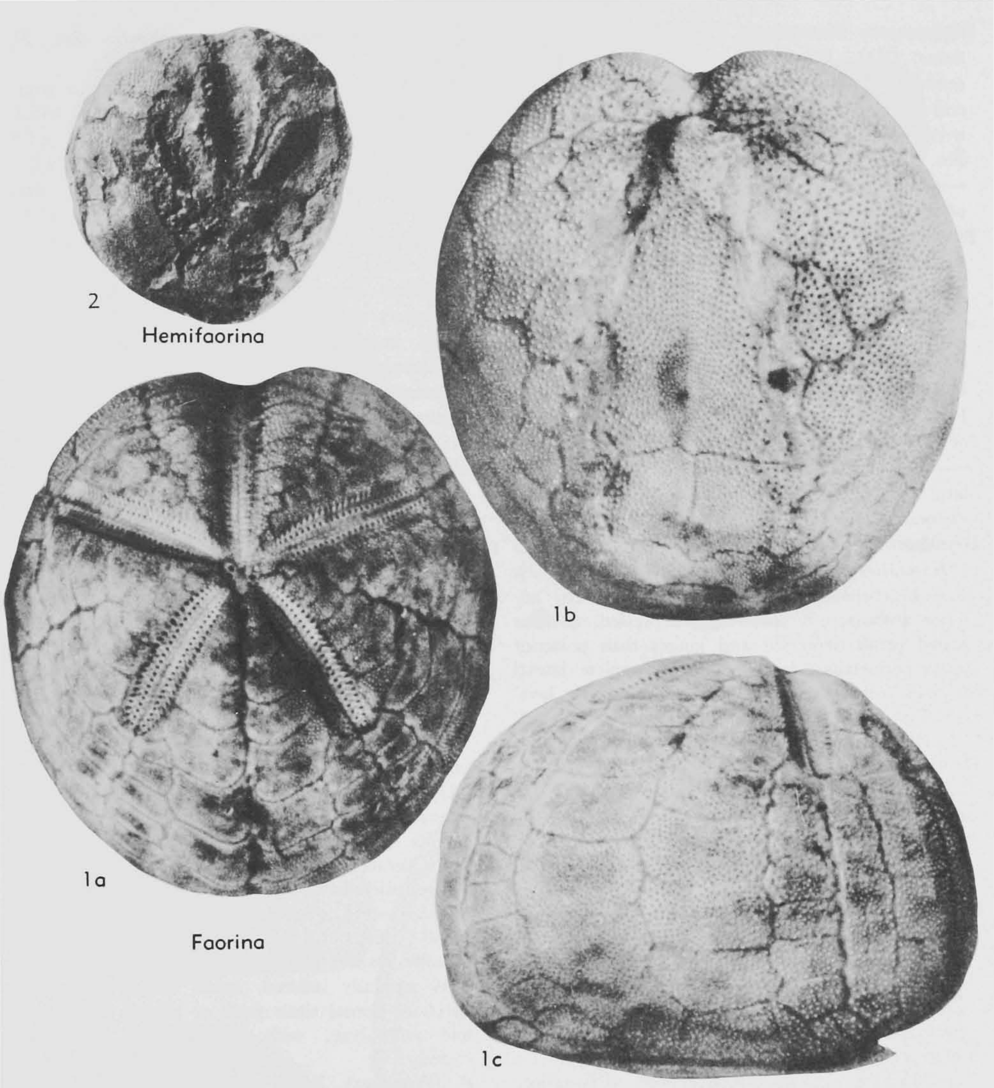


FIG. 459. Schizasteridae (p. *U576*).

×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.).

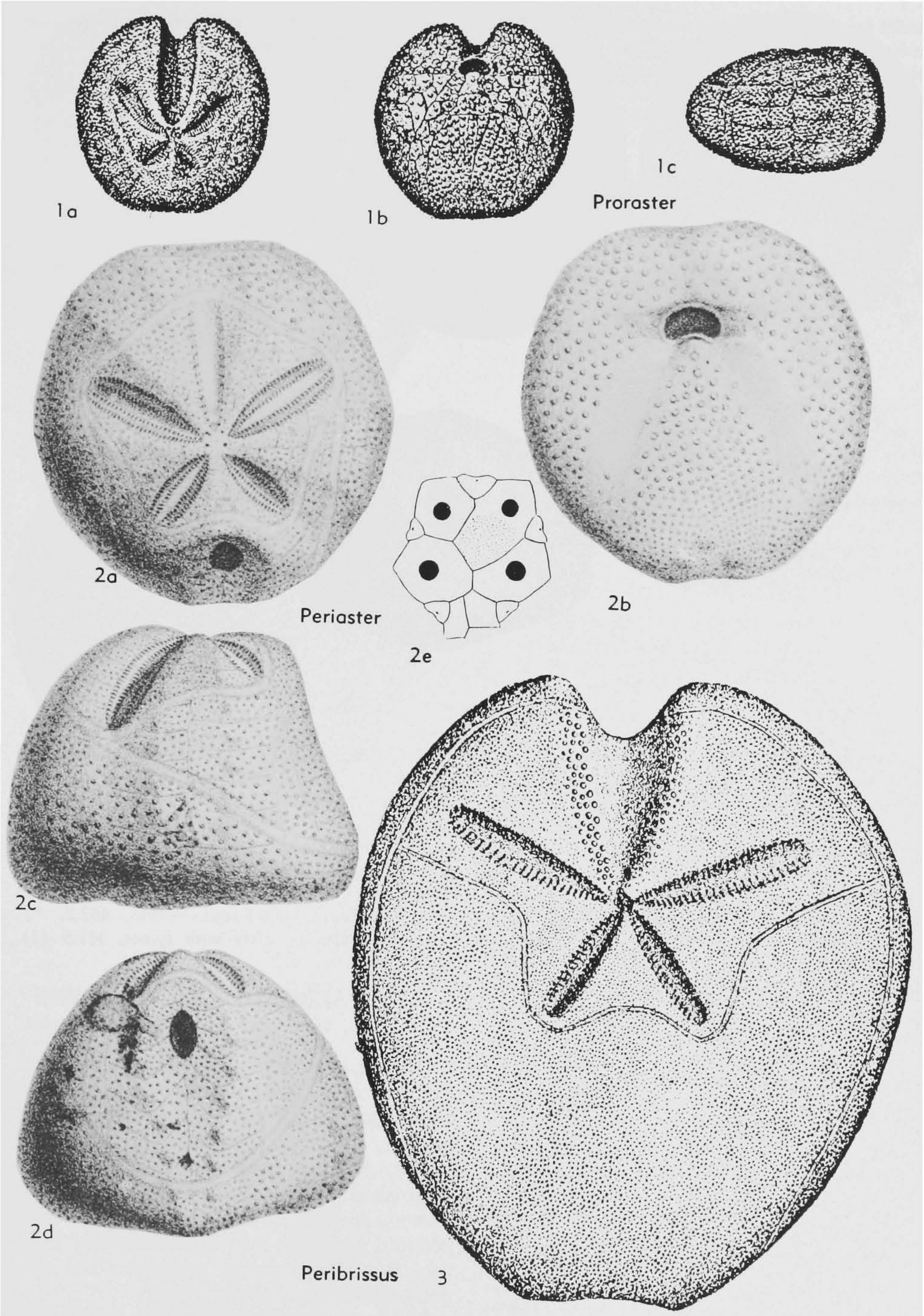


FIG. 460. Schizasteridae (p. U576, U578).

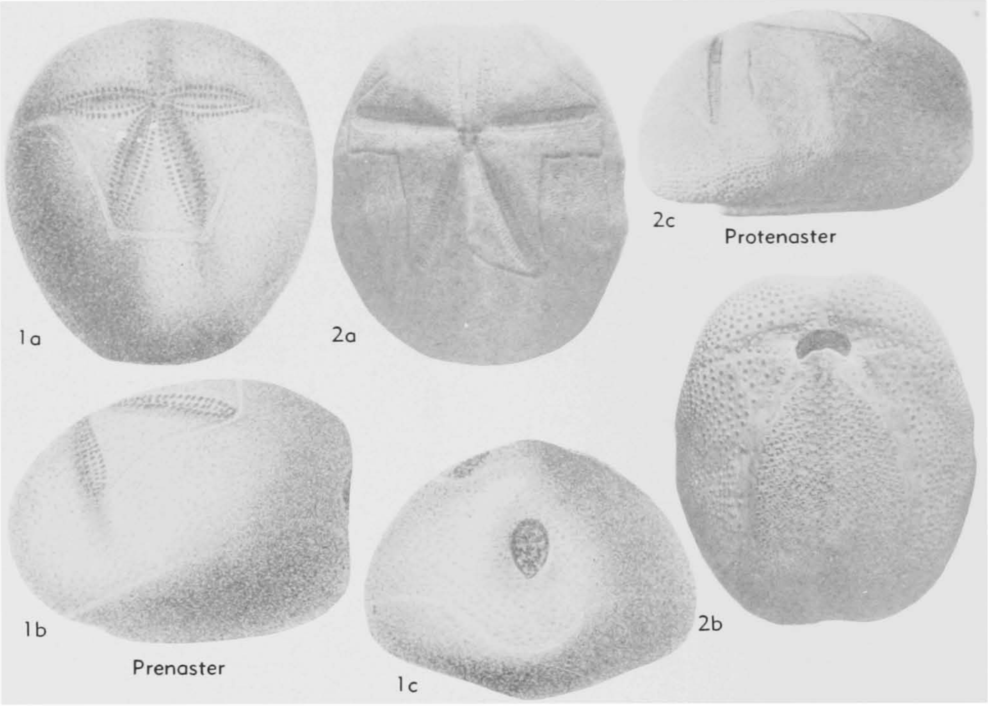


FIG. 461. Schizasteridae (p. U576).

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);

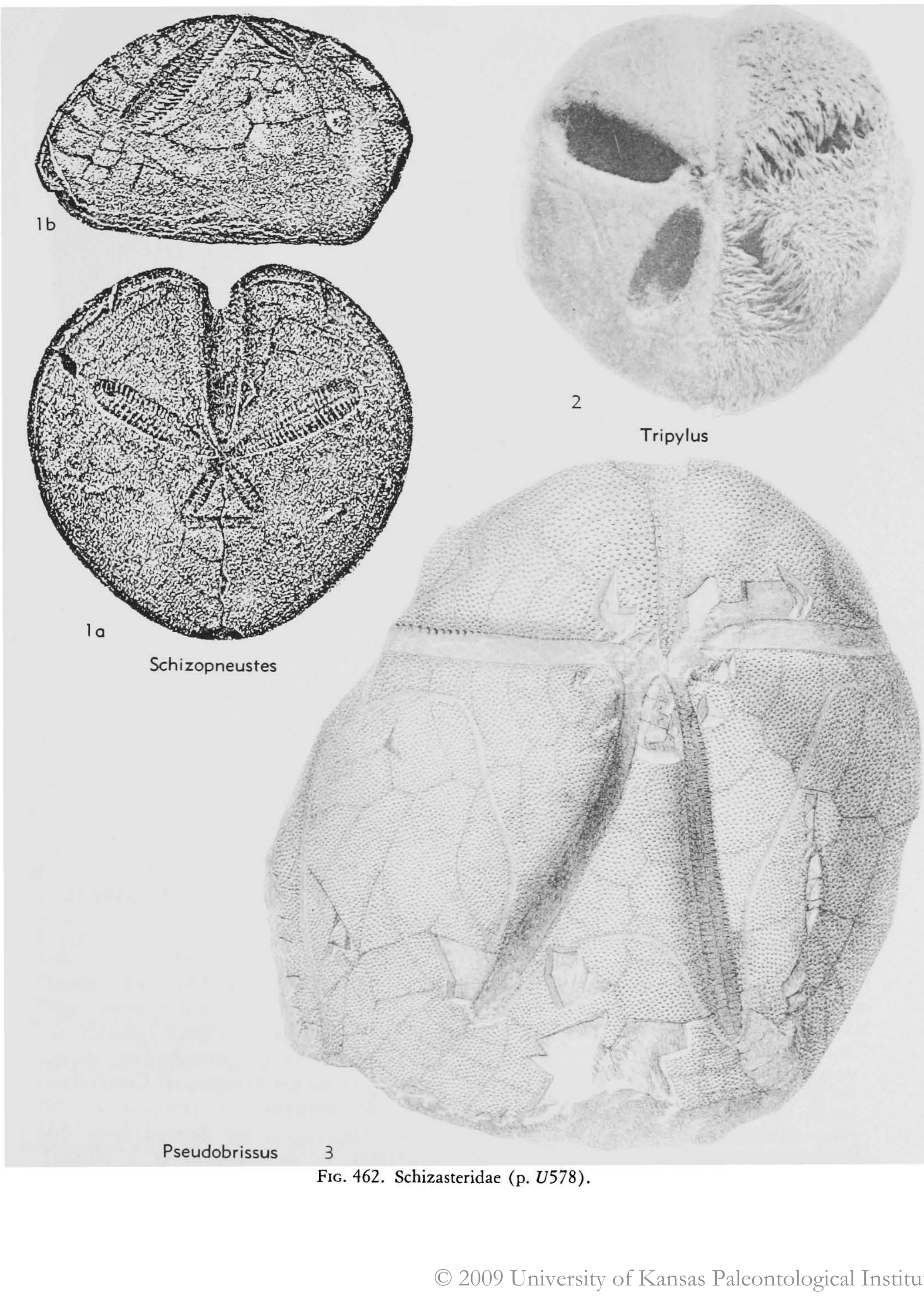


FIG. 462. Schizasteridae (p. *U*578).

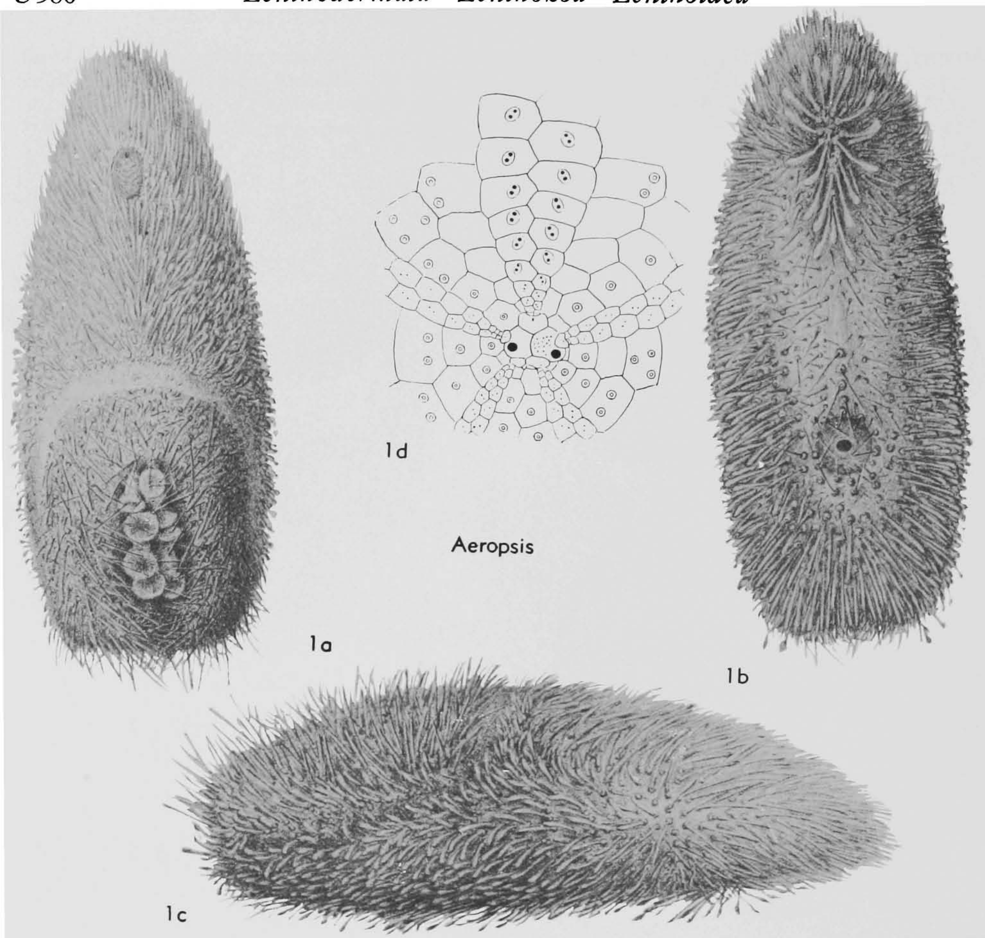


FIG. 463. Aeropsidae (p. U578-U579).

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

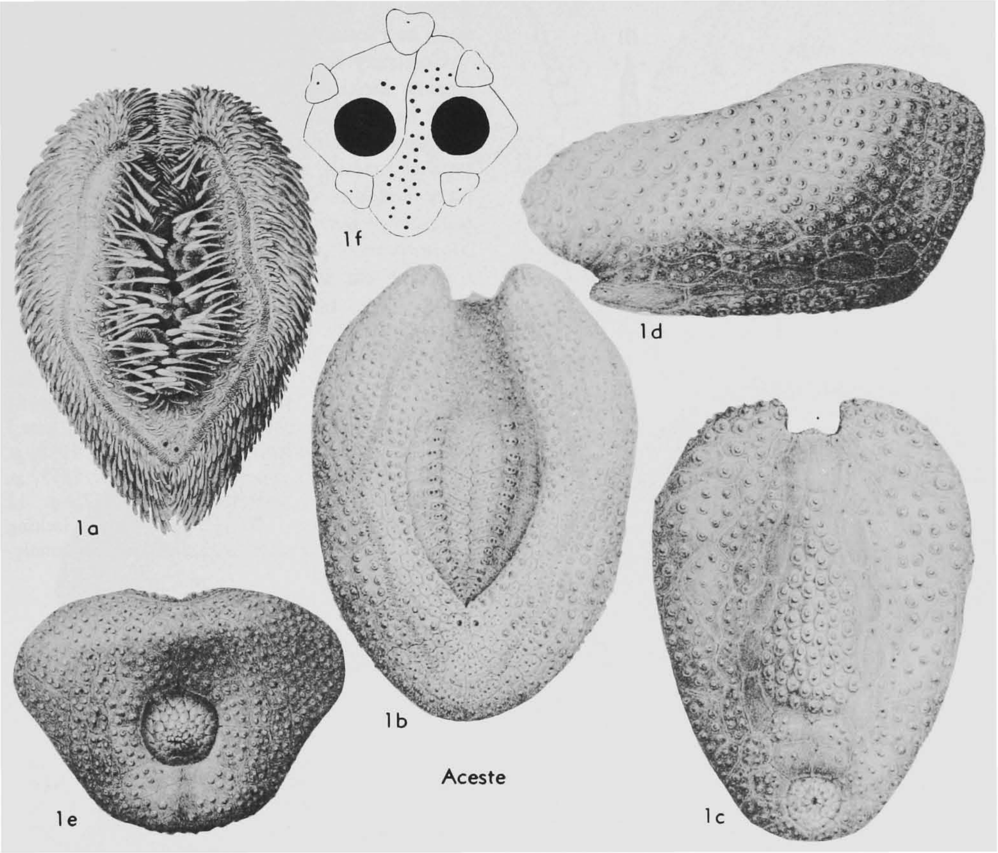


FIG. 464. Aeropsidae (p. *U*580).

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*;

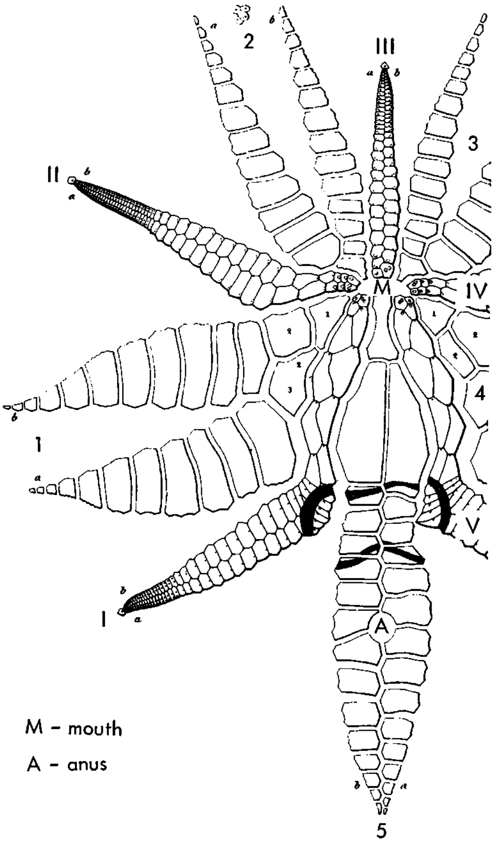


FIG. 465. Plate diagram of *Micraster* (Lovén).

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-

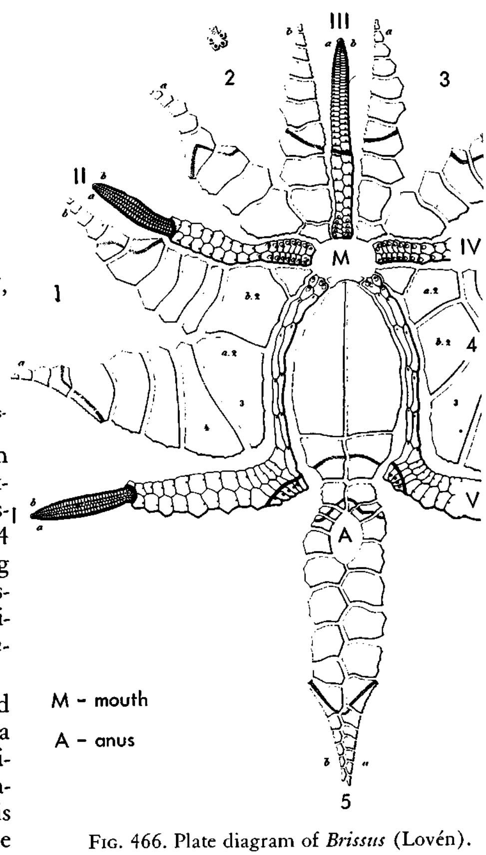


FIG. 466. Plate diagram of *Brissus* (Lovén).

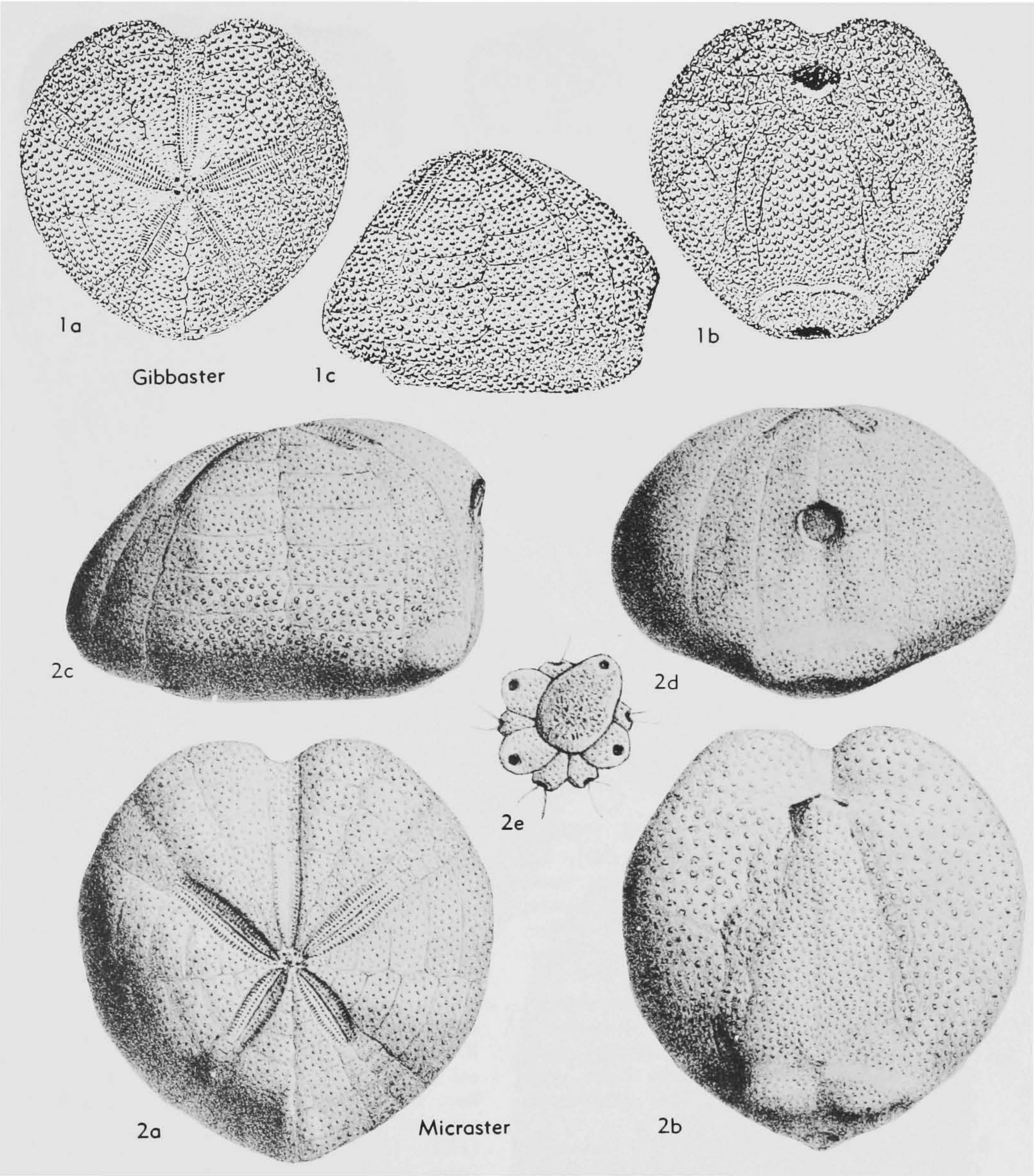


FIG. 467. Micrasteridae (p. *U*581).

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.*,

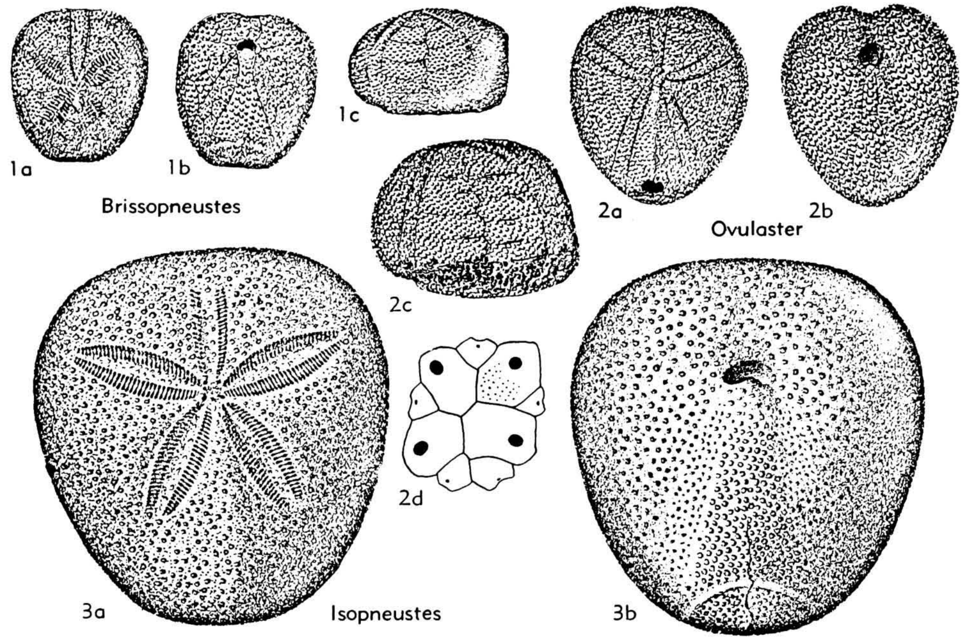


FIG. 468. Micrasteridae (p. U581).

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.).]

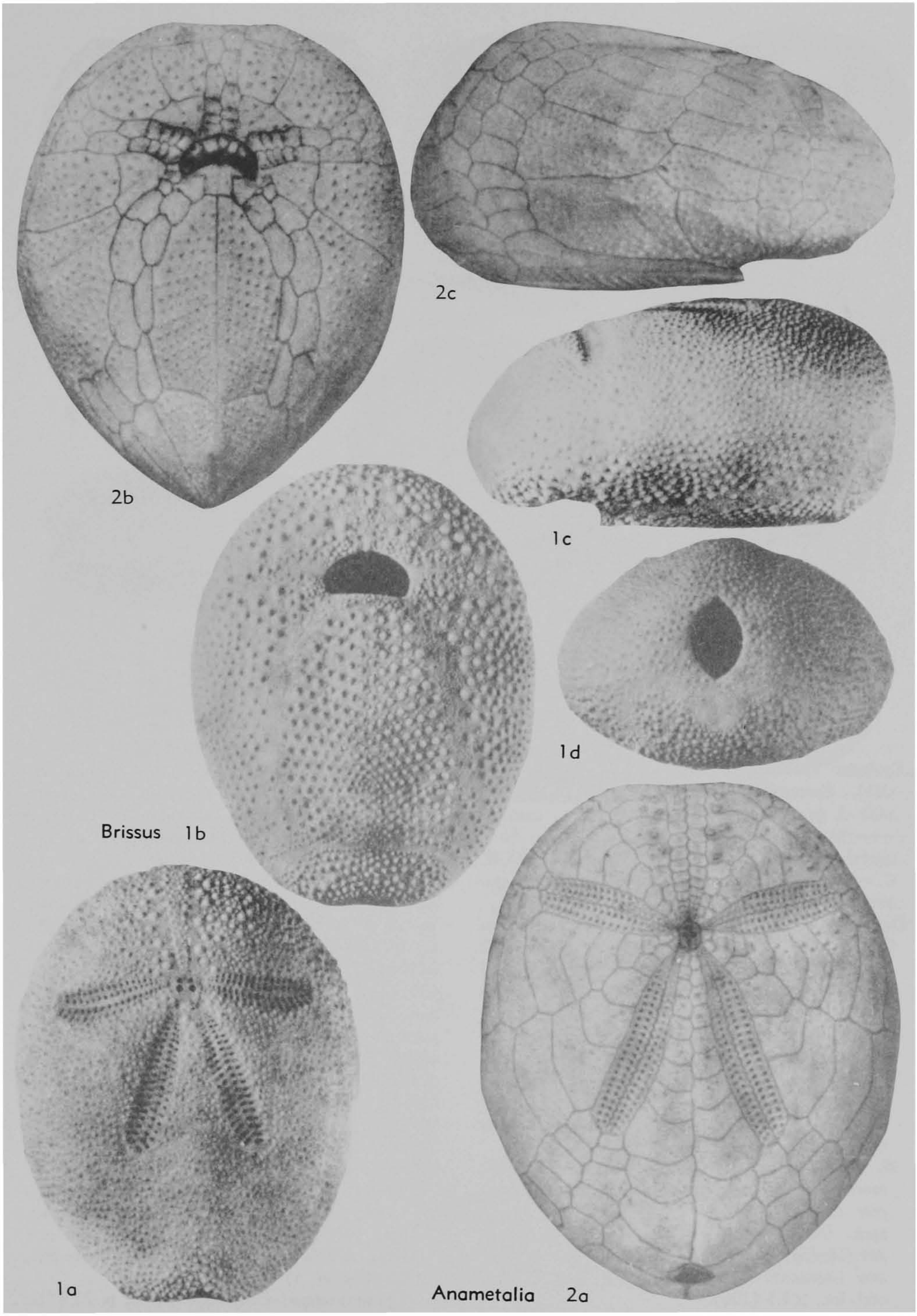


FIG. 469. Brissidae (p. U582-U584).

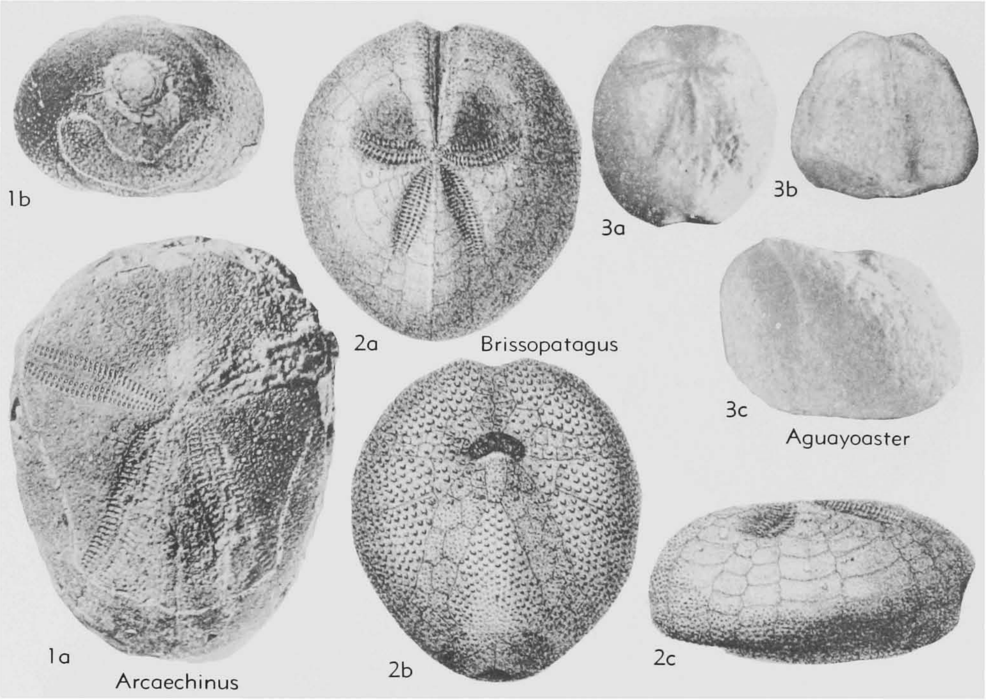


FIG. 470. Brissidae (p. *U*583-*U*584).

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.

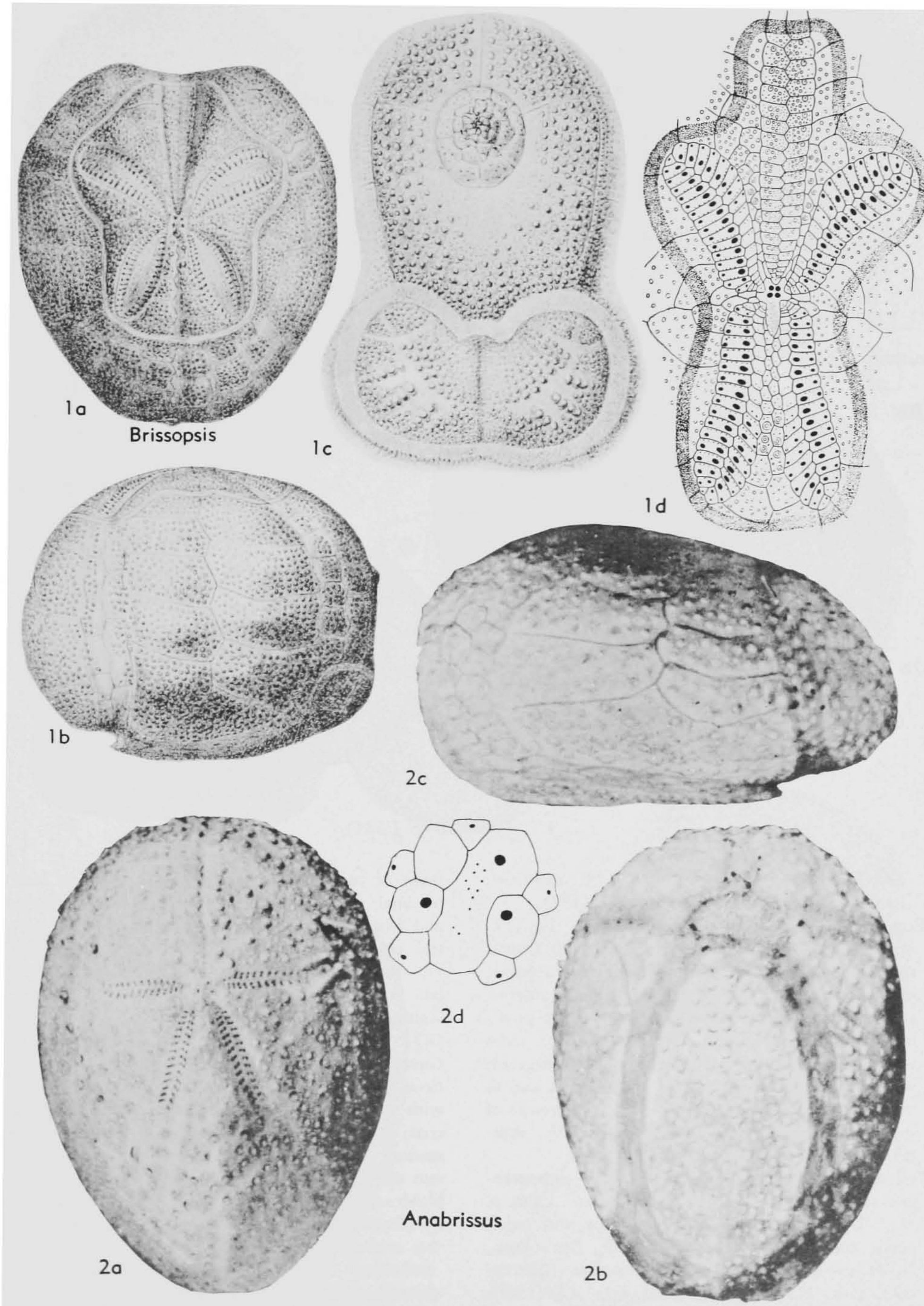


FIG. 471. Brissidae (p. *U*583-*U*584).

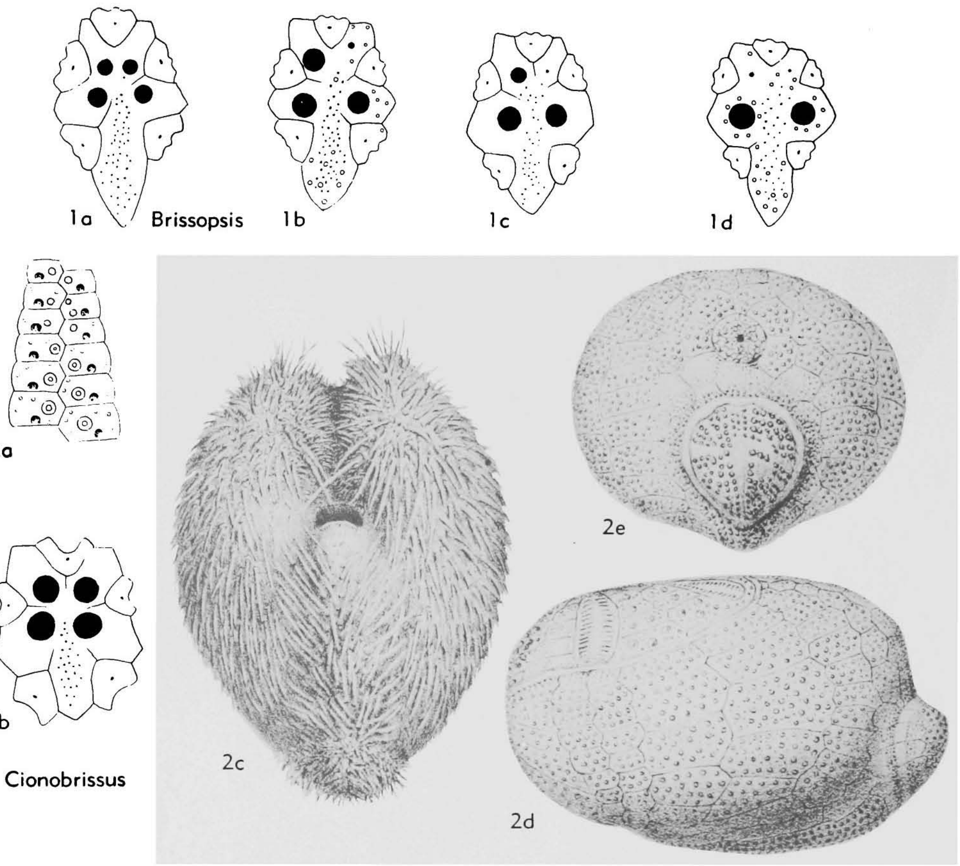


FIG. 472. Brissidae (p. U584).

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-*

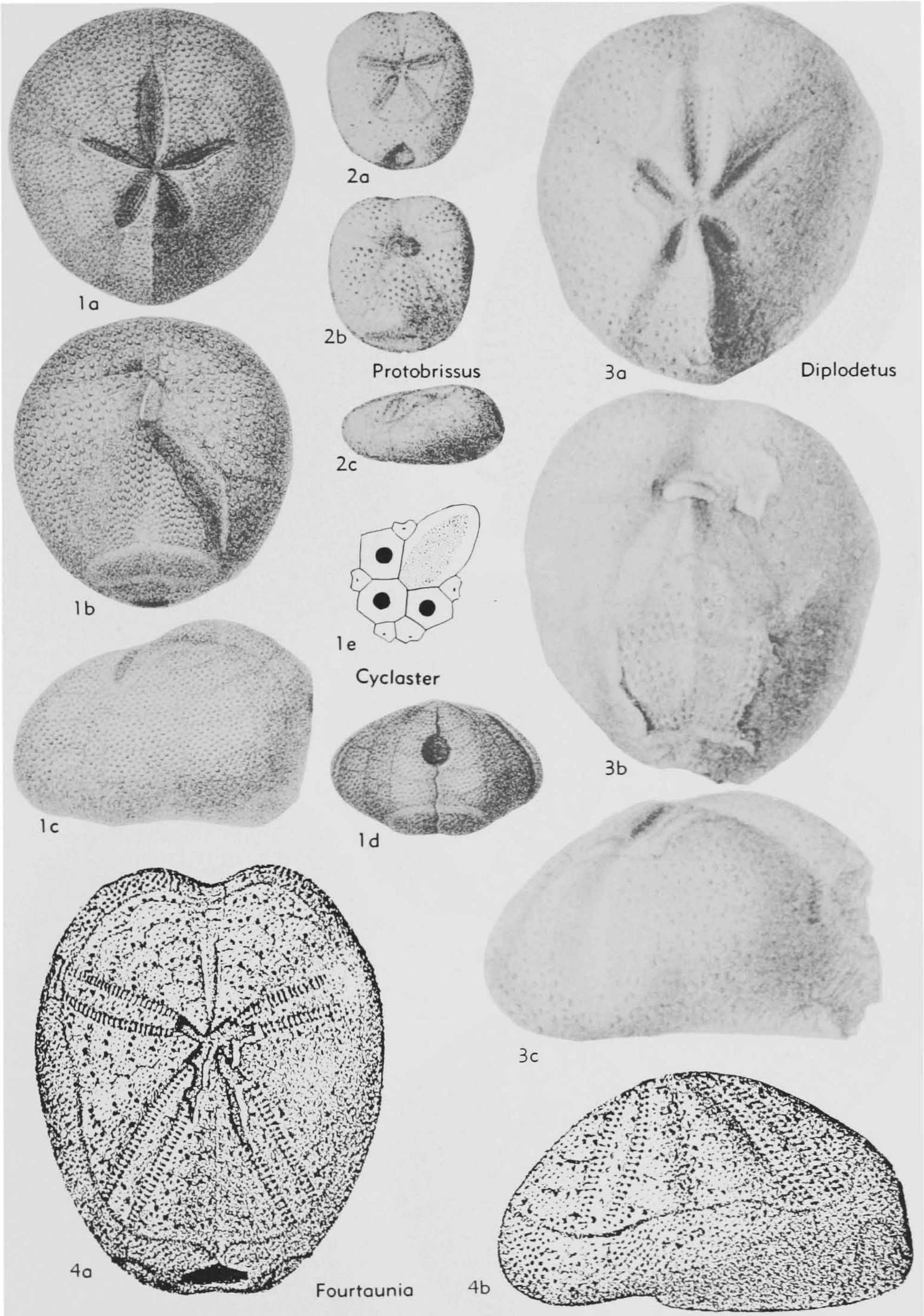


FIG. 473. Brissidae (p. *U*586, *U*588).

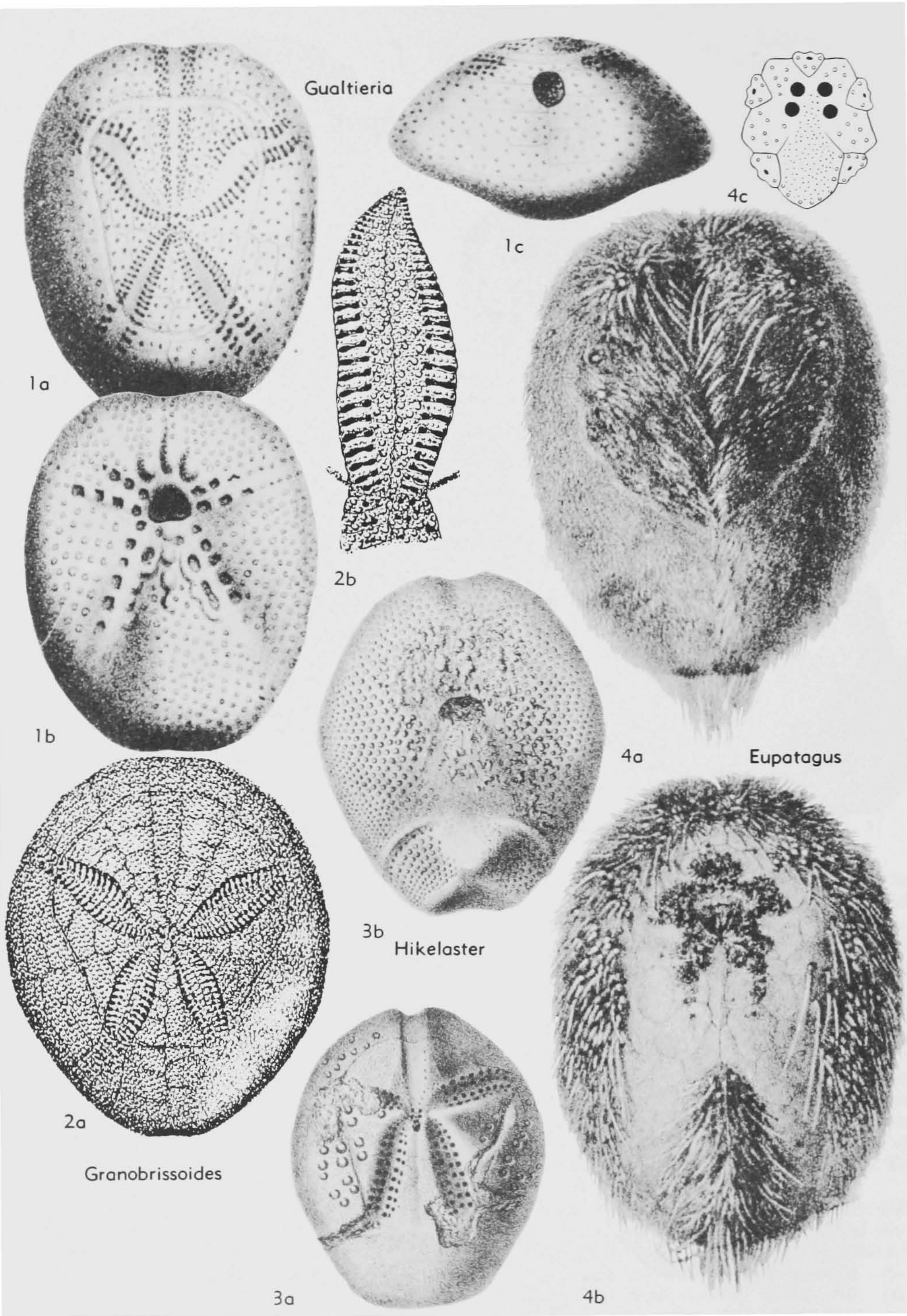


FIG. 474. Brissidae (p. U586, U588, U591).

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-*

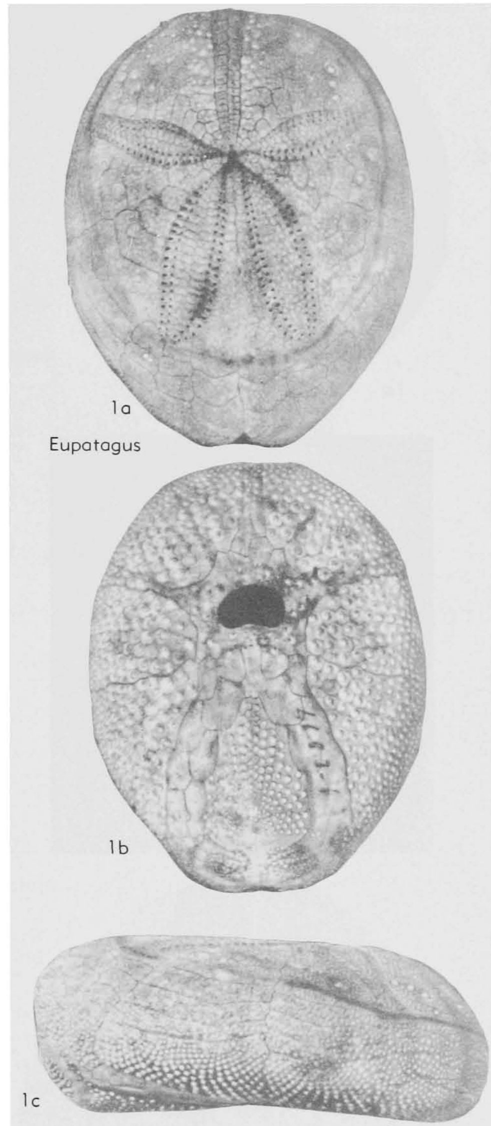


FIG. 475. Brissidae (p. U586).

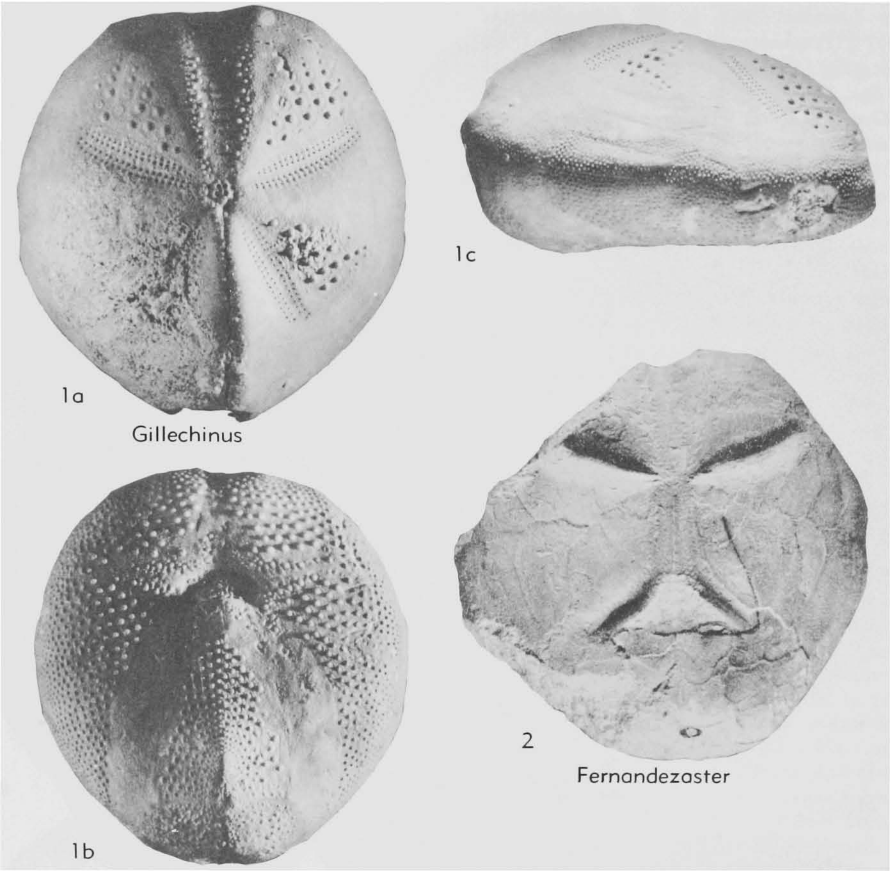


FIG. 476. Brissidae (p. U588).

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.,*

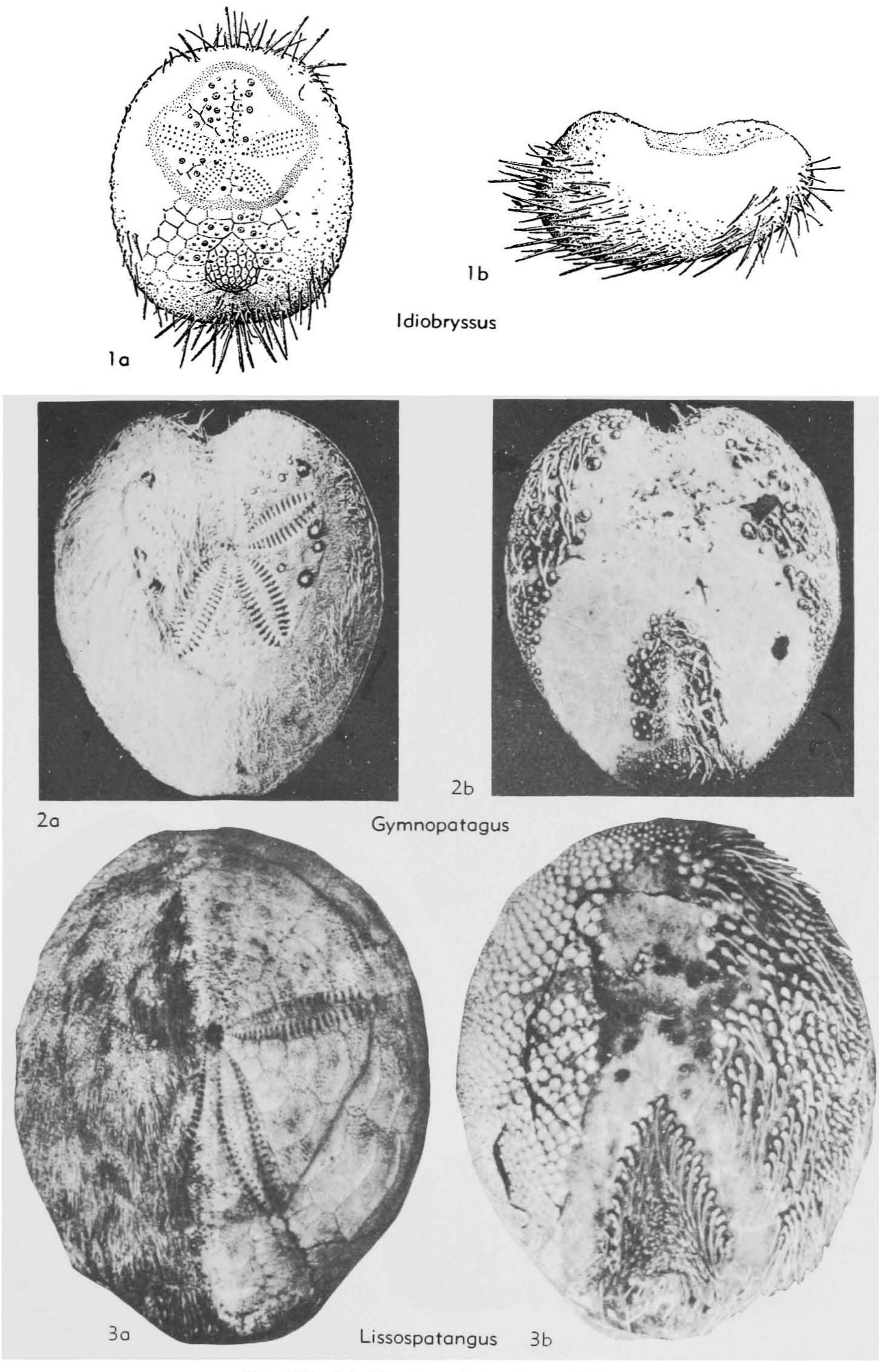


FIG. 477. Brissidae (p. *U*586, *U*588, *U*591).

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].

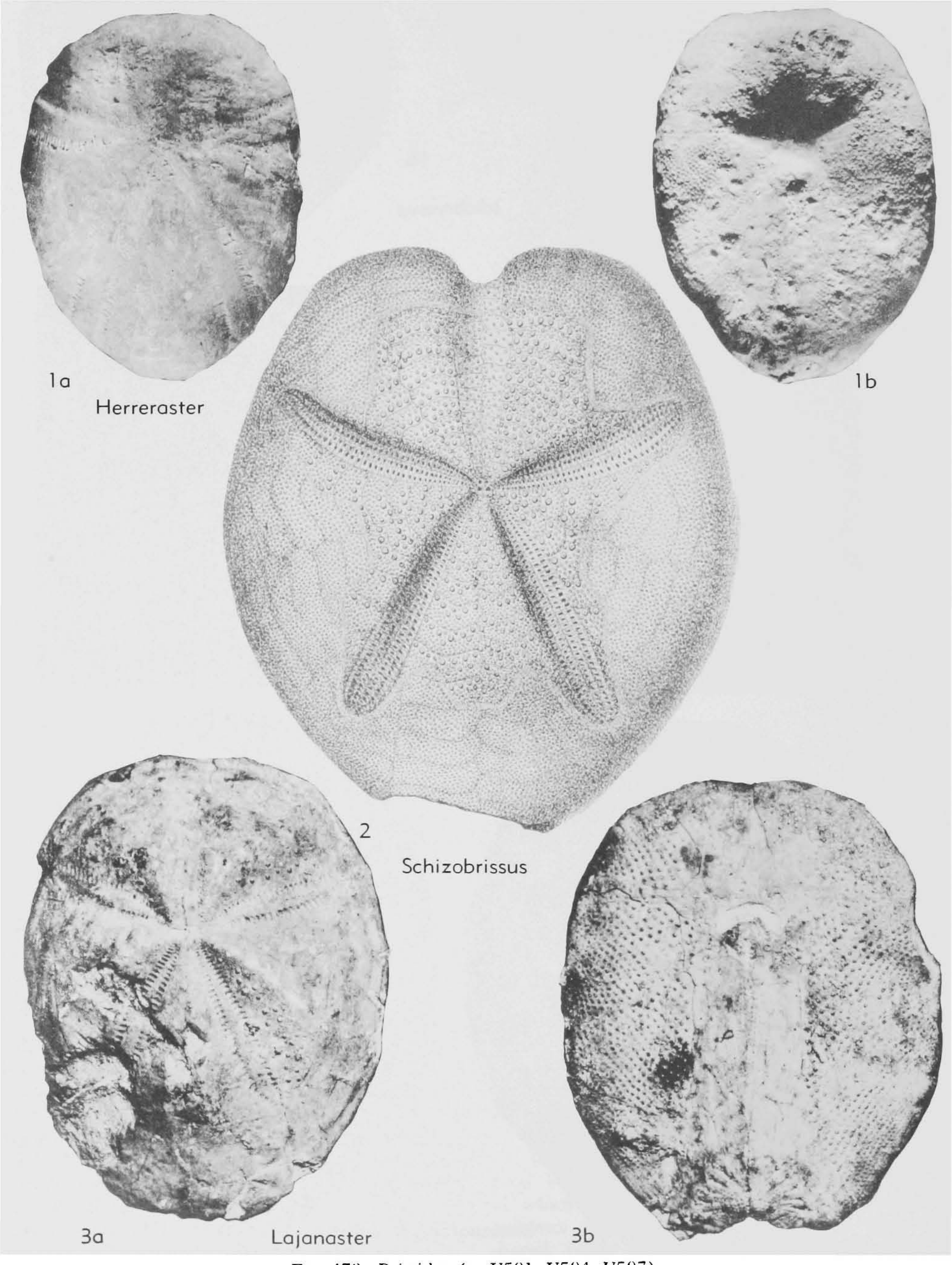


FIG. 478. Brissidae (p. U591, U594, U597).

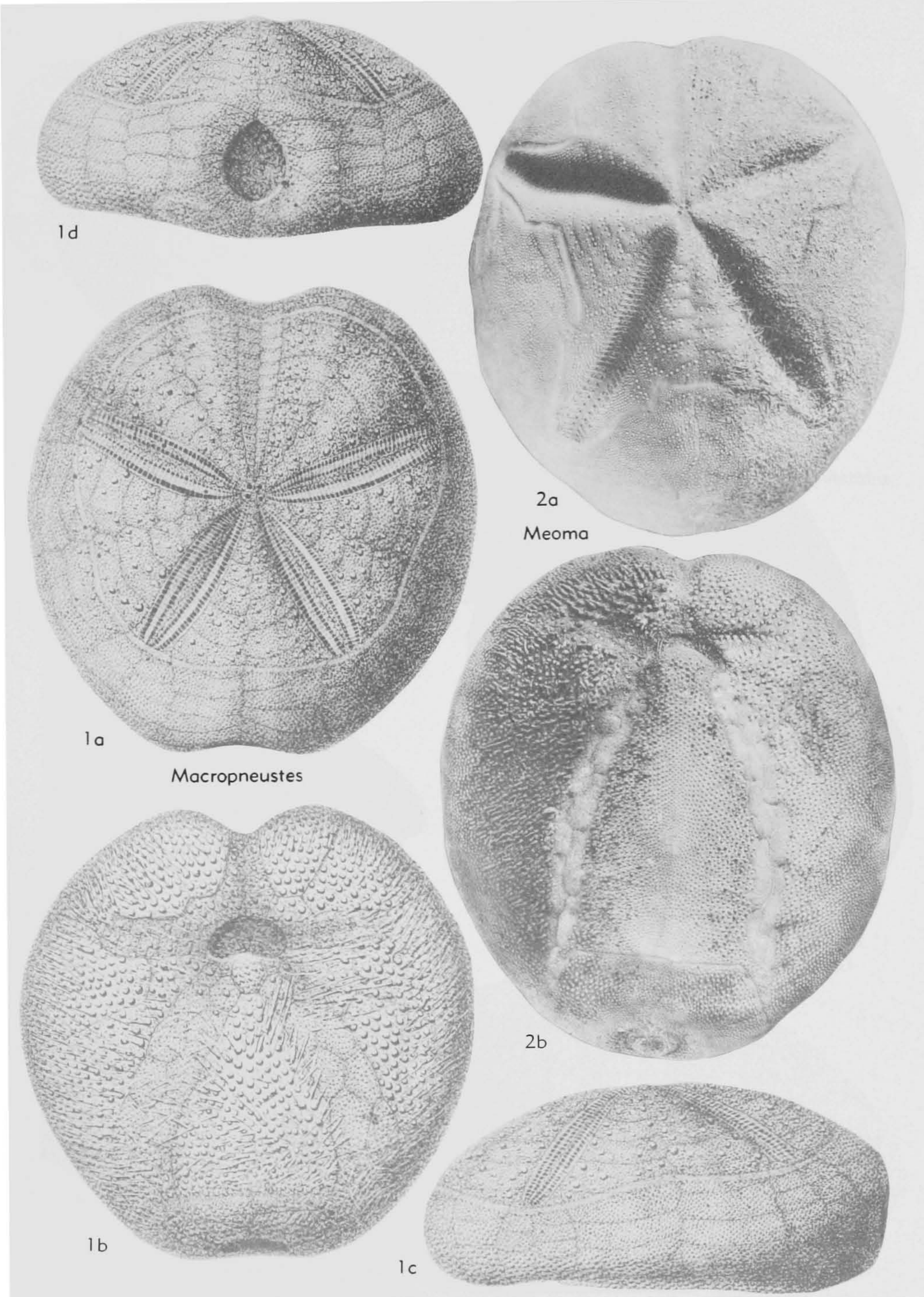


FIG. 479. Brissidae (p. U591-U592).

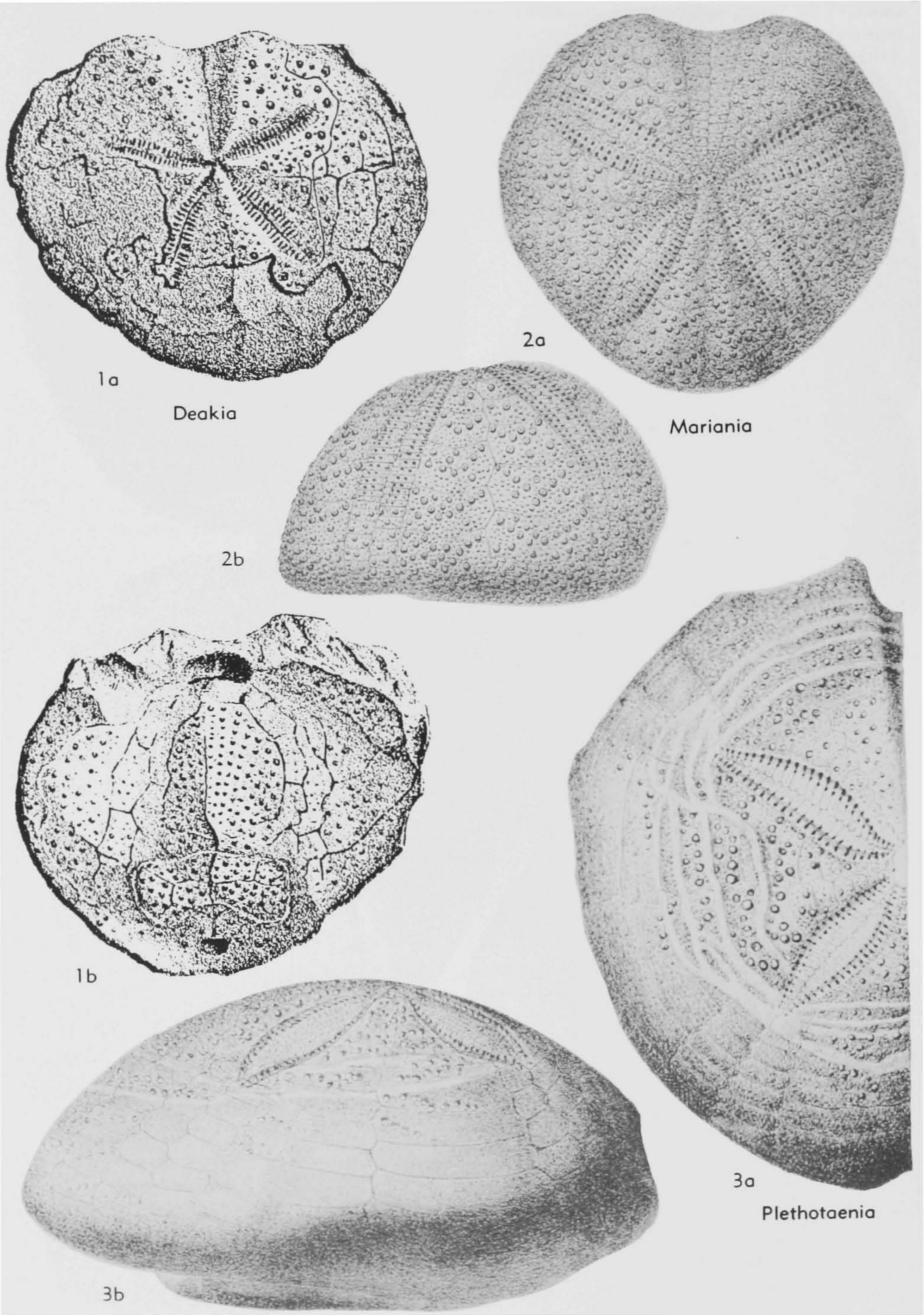


FIG. 480. Brissidae (p. U591-U592, U594).

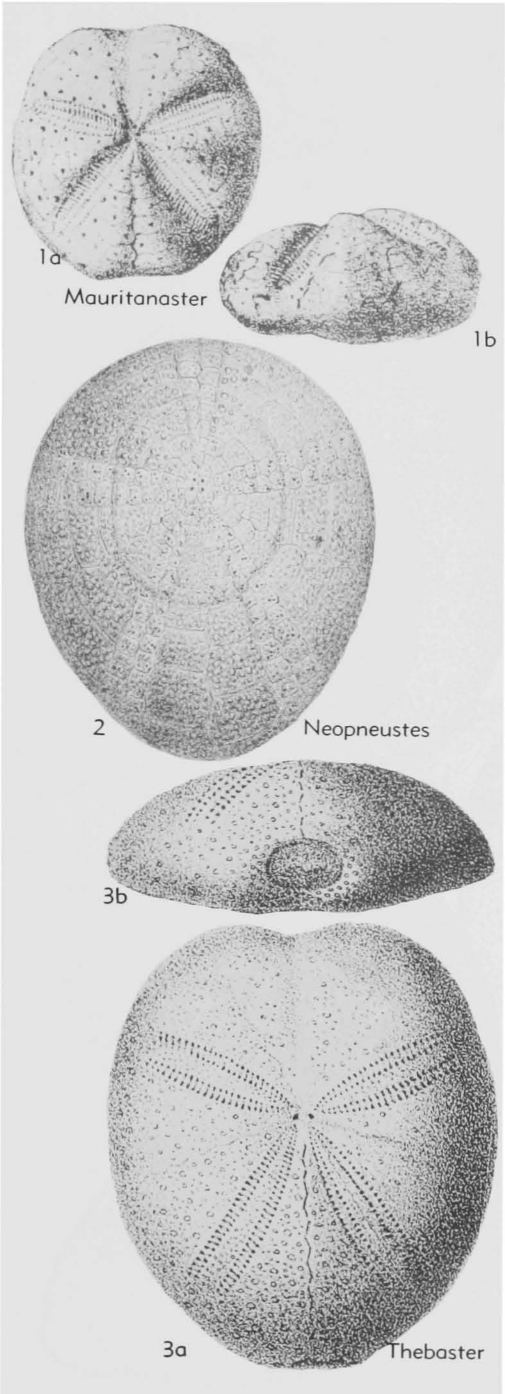


FIG. 481. Brissidae (p. *U*592, *U*600-*U*602).

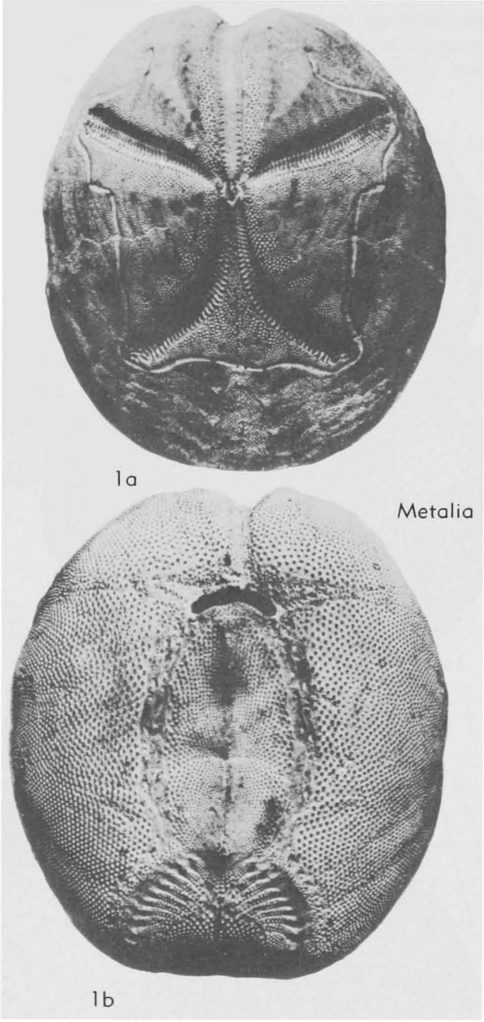


FIG. 482. Brissidae (p. *U*597, *U*599).

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.

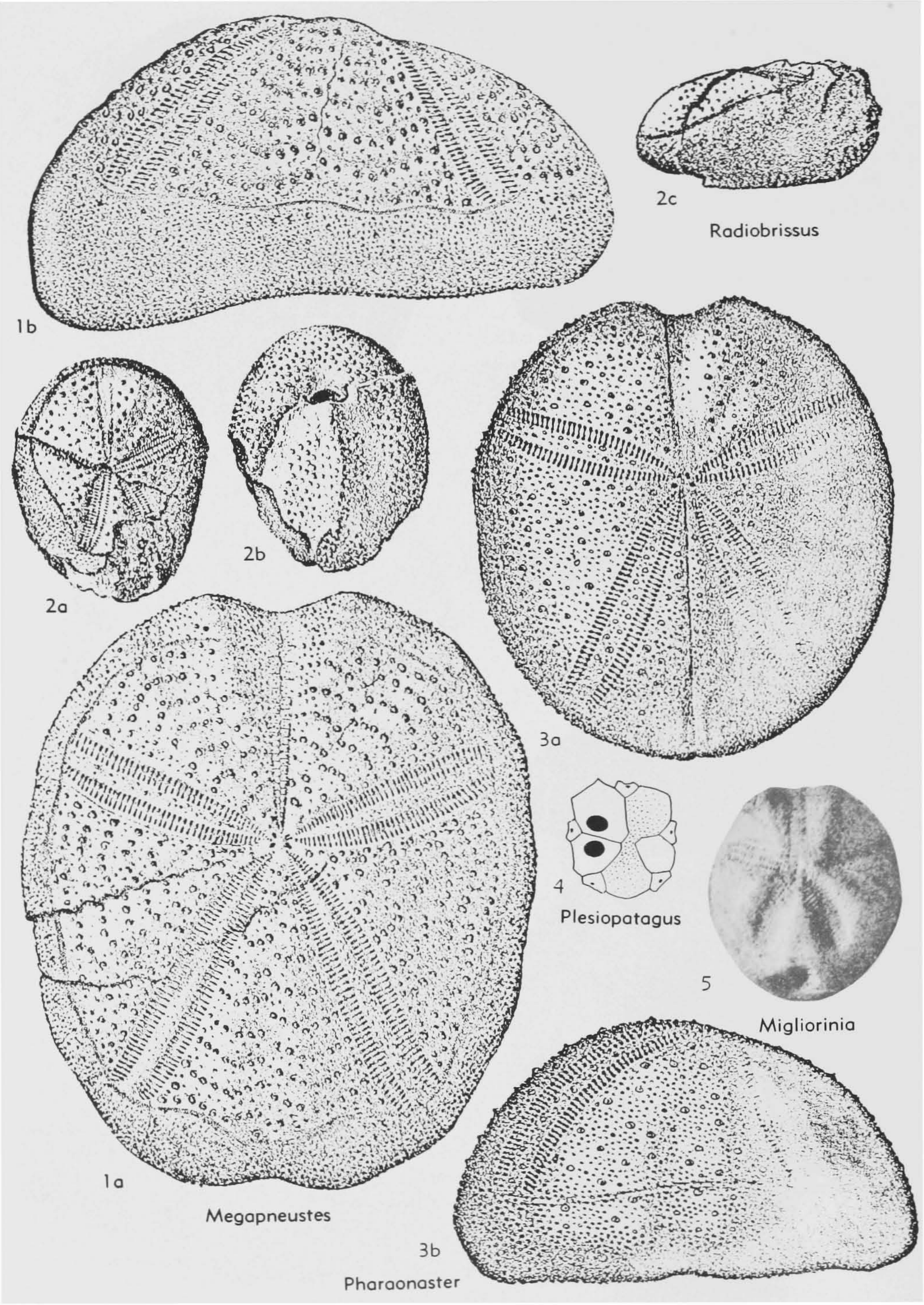


FIG. 483. Brissidae (p. U592, U599-U601, U603).

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

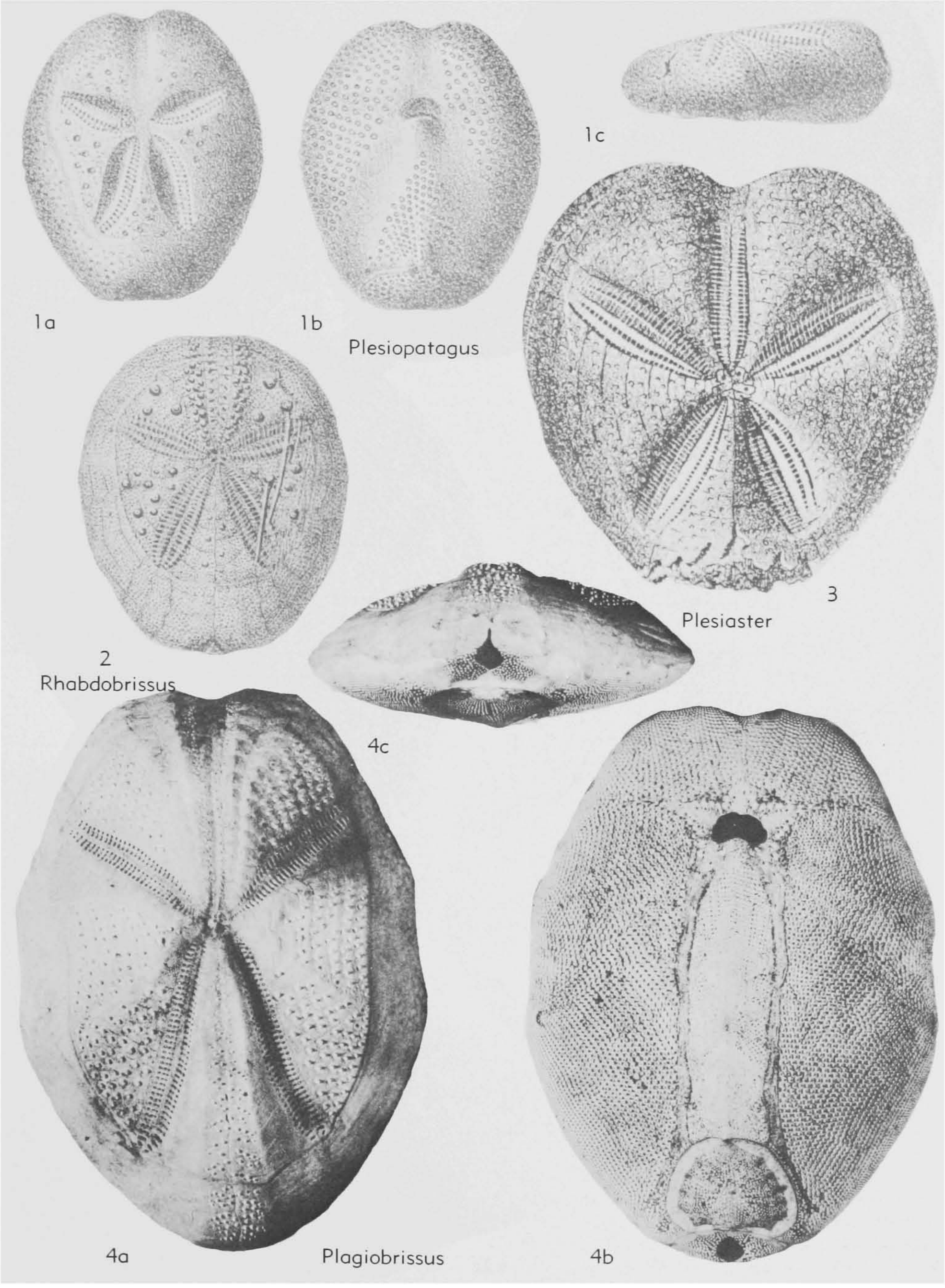


FIG. 484. Brissidae (p. *U*602-*U*603).

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.*,

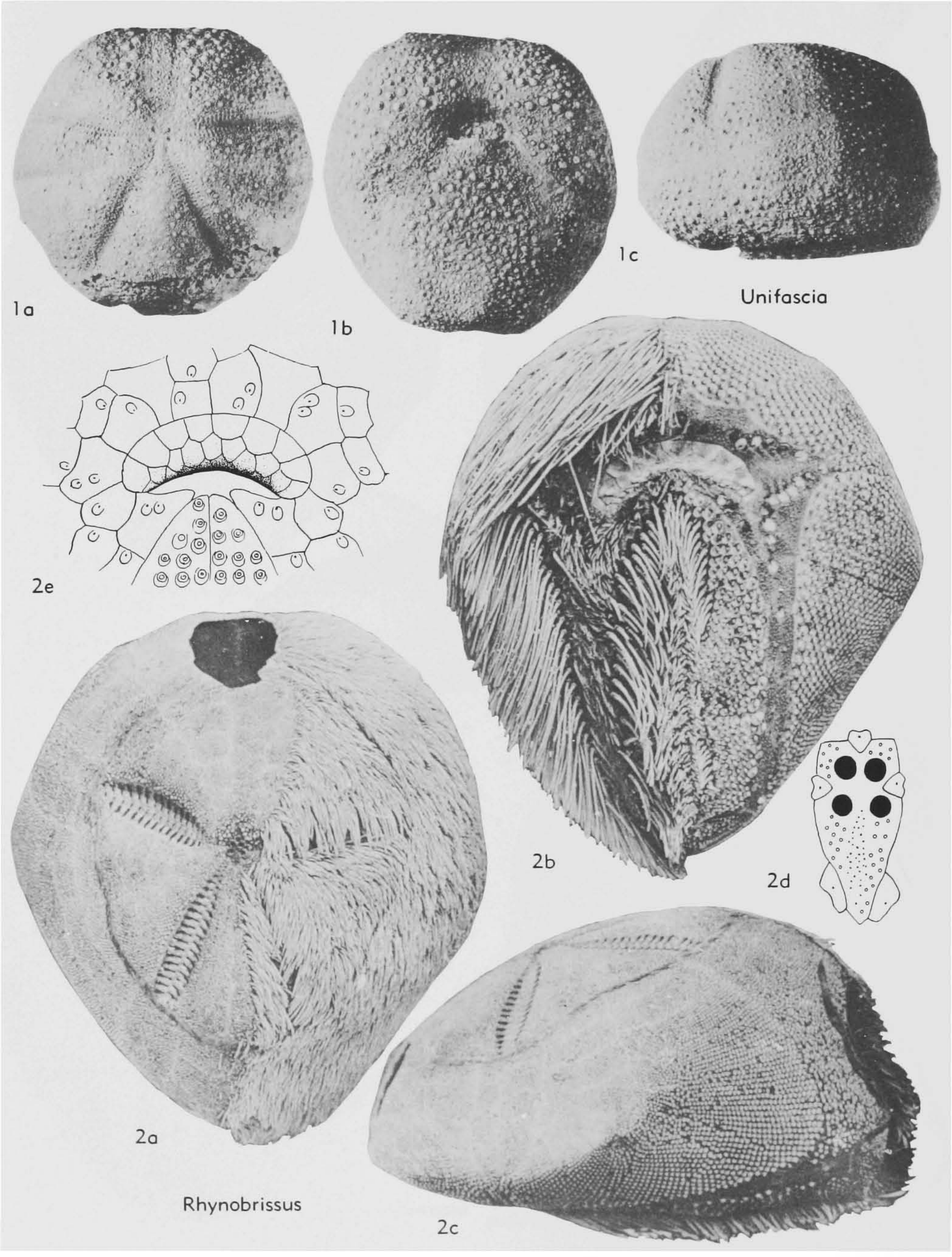


FIG. 485. Brissidae (p. U604-U605).

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

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

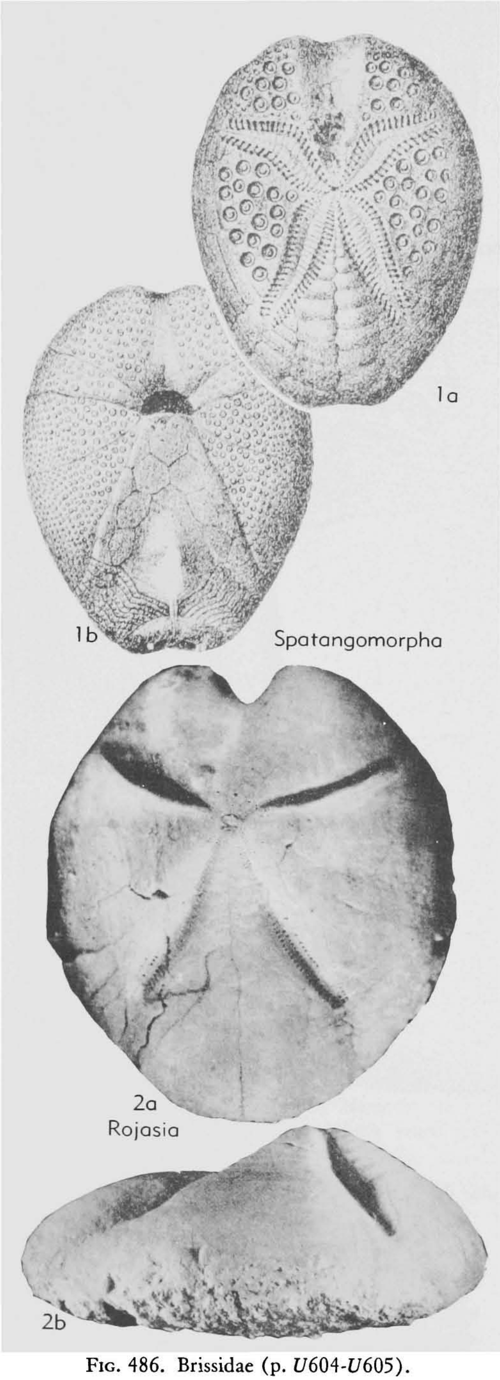


Fig. 486. Brissidae (p. *U*604-*U*605).

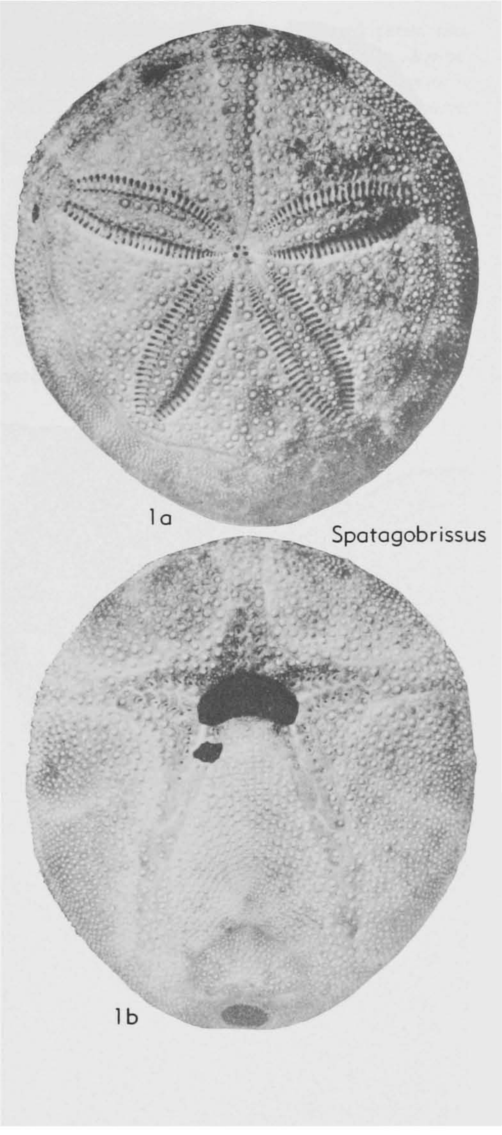


Fig. 487. Brissidae (p. *U*605).

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

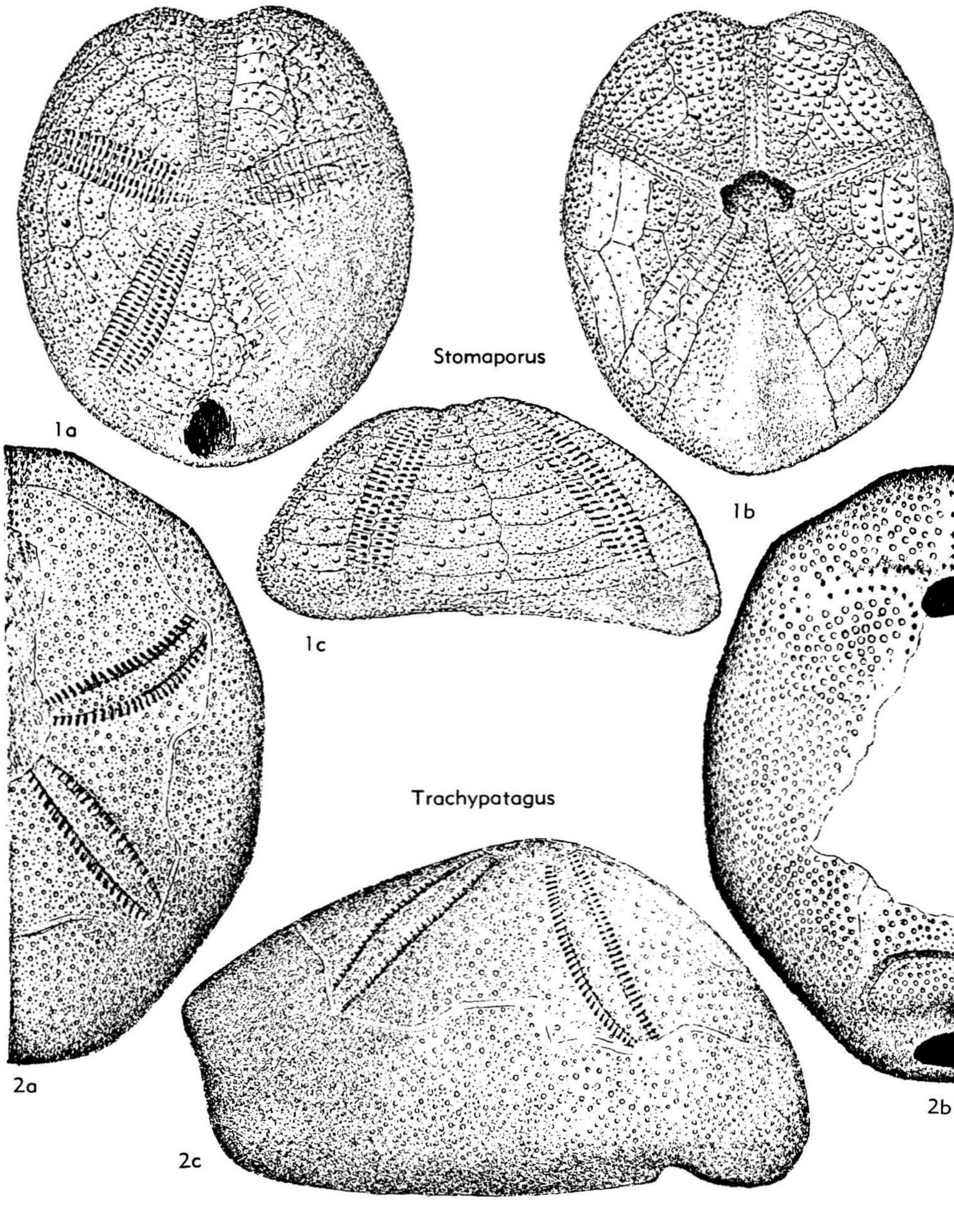


FIG. 488. Brissidae (p. *U*605).

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.

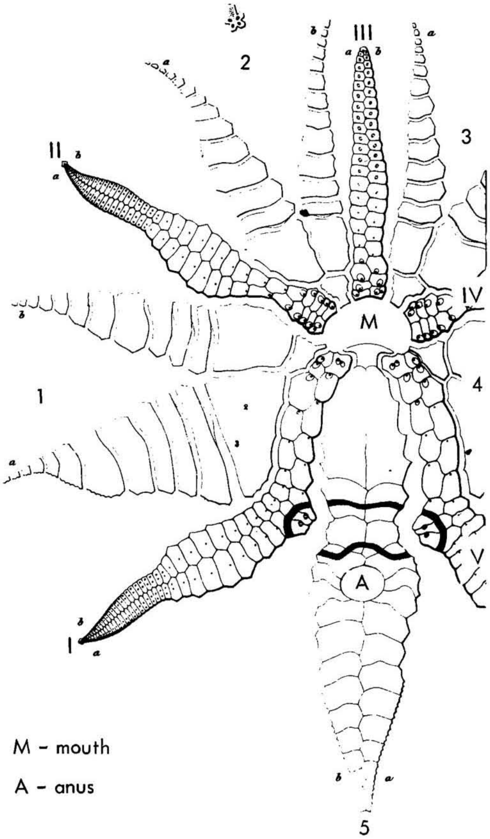


FIG. 489. Plate diagram of *Spatangus* (Lovén).

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).

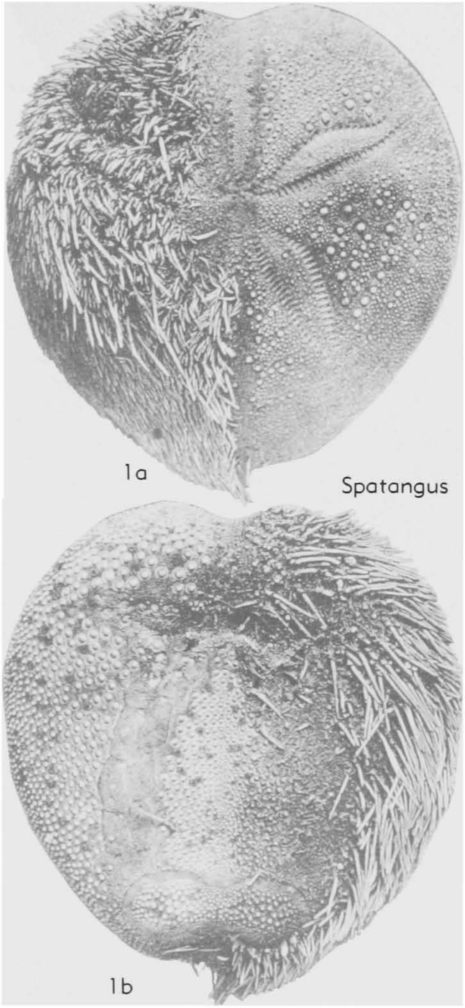


FIG. 490. Spatangidae (p. *U605*, *U608*).

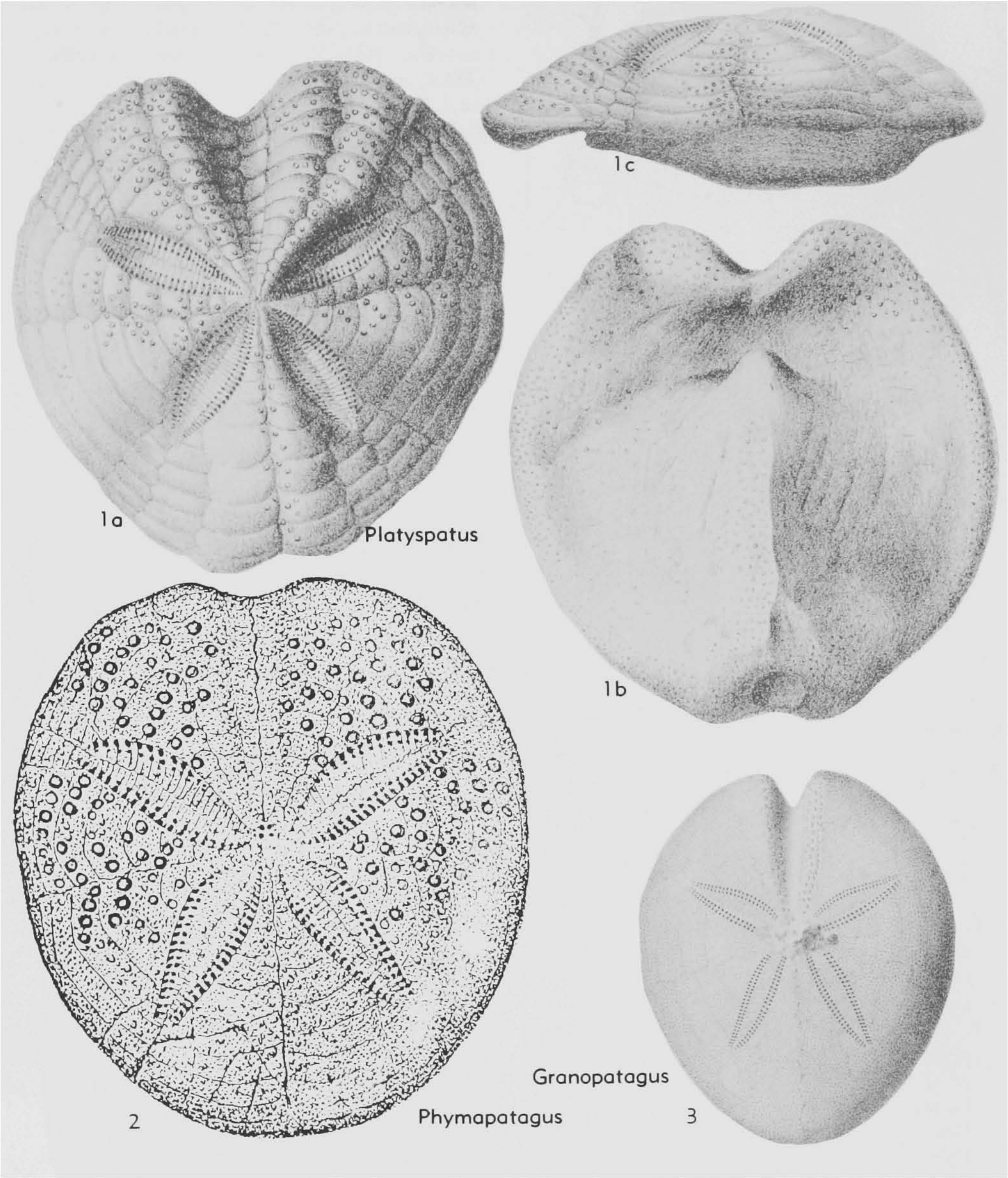


FIG. 491. Spatangidae (p. U608).

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

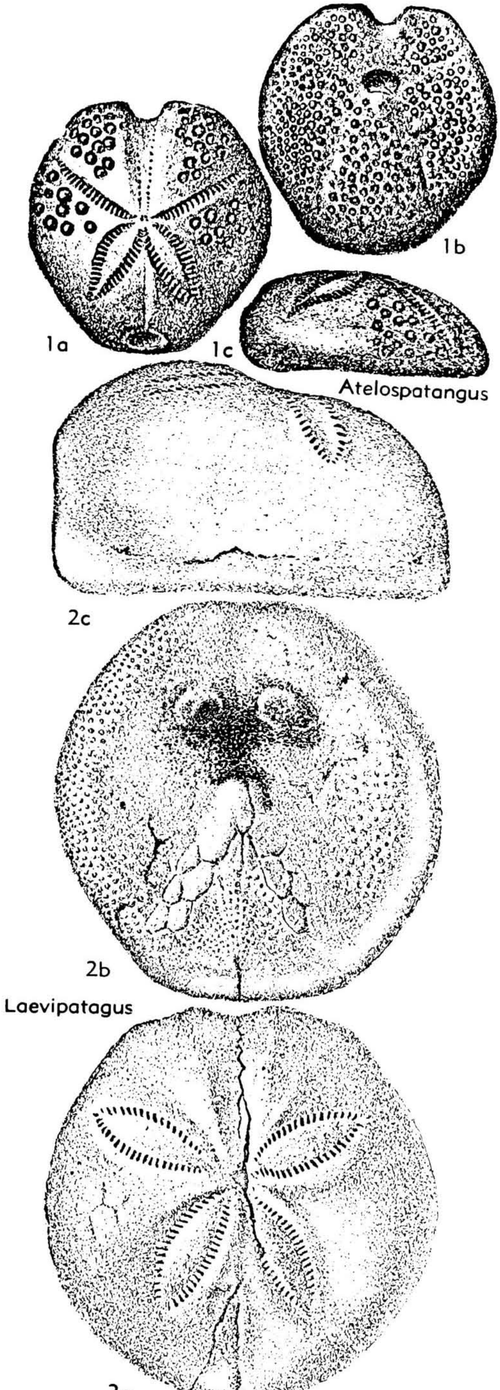


FIG. 492. Spatangidae (p. U608-U609).

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.

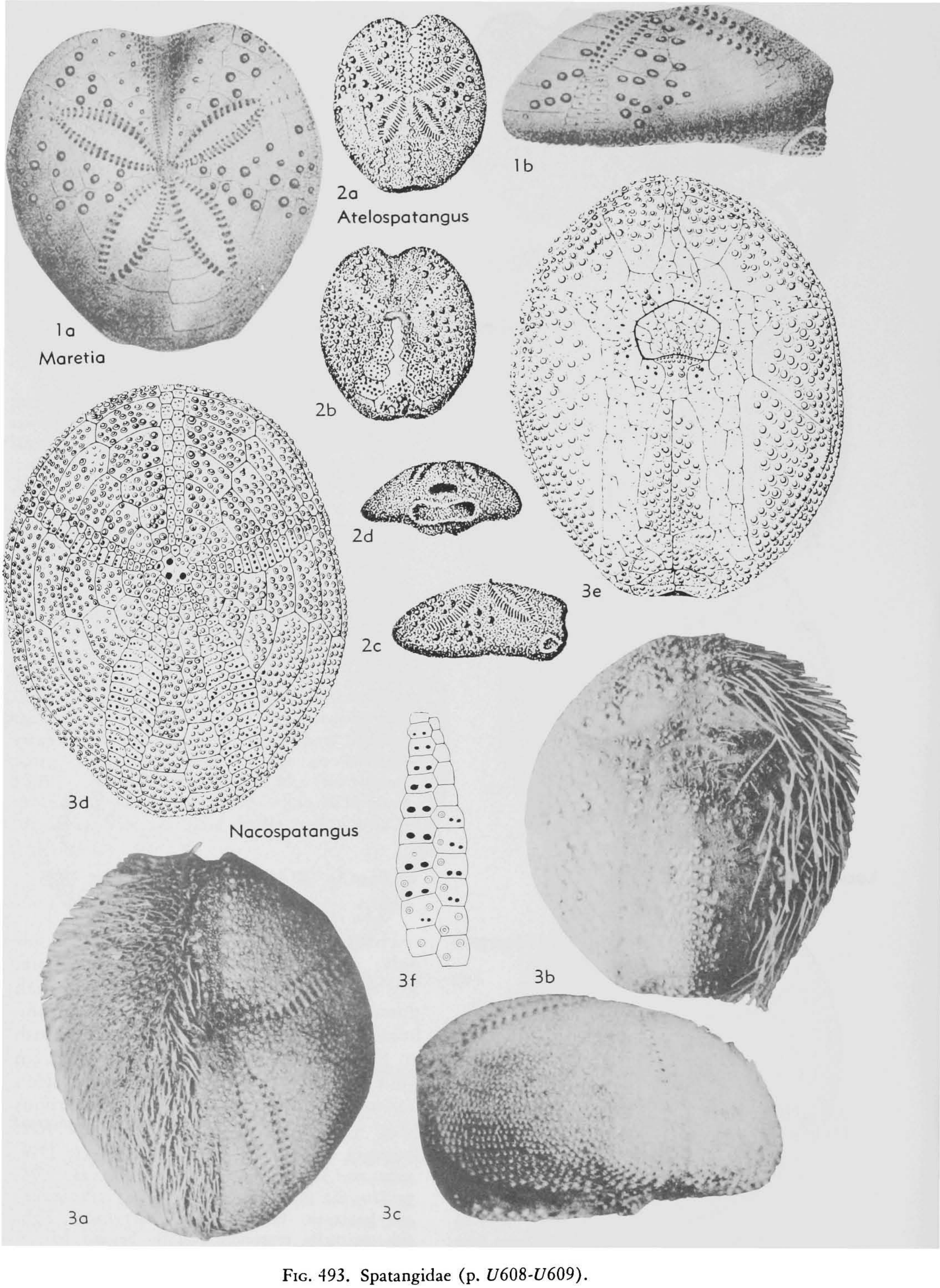


FIG. 493. Spatangidae (p. U608-U609).

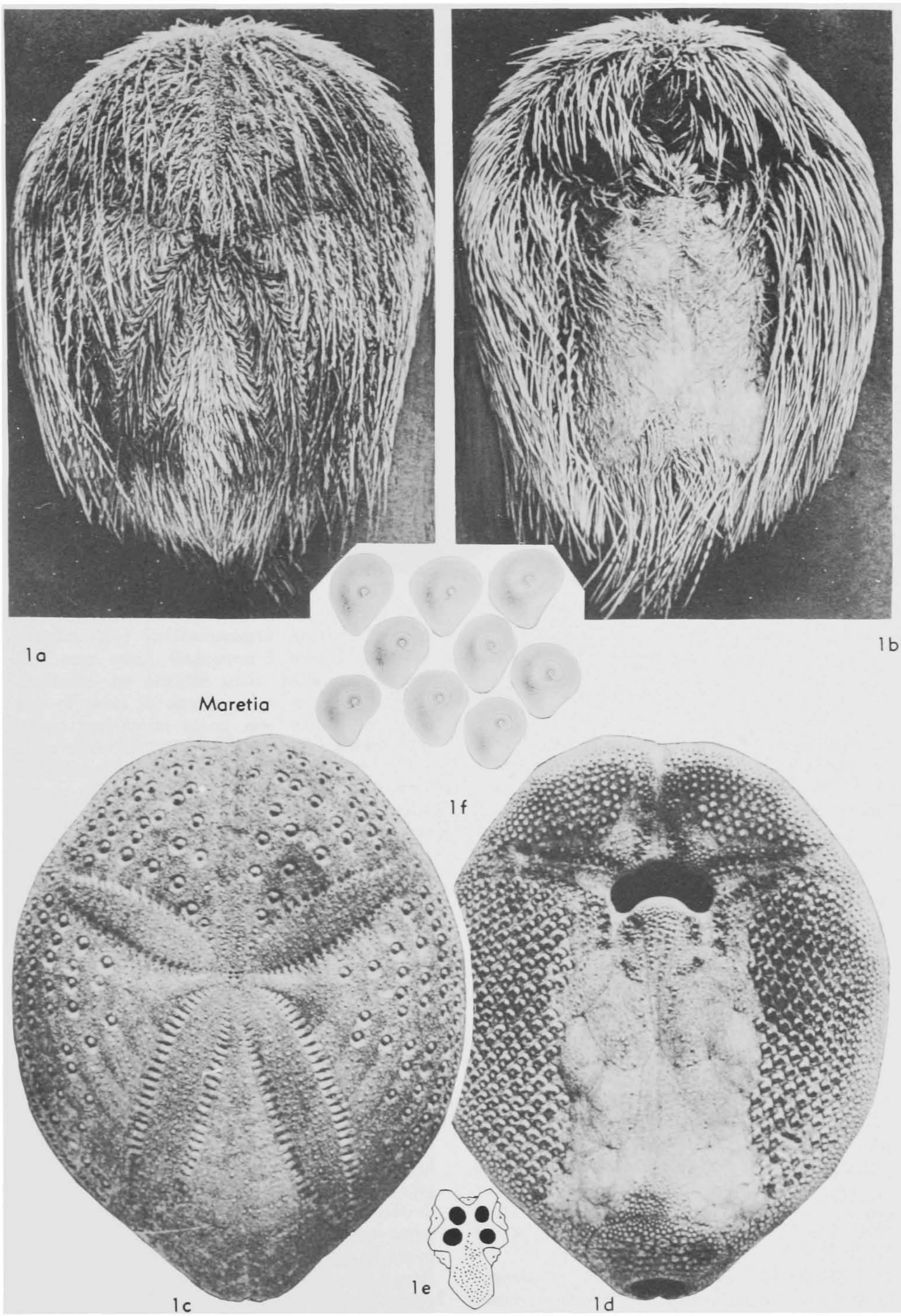


FIG. 494. Spatangidae (p. U609).

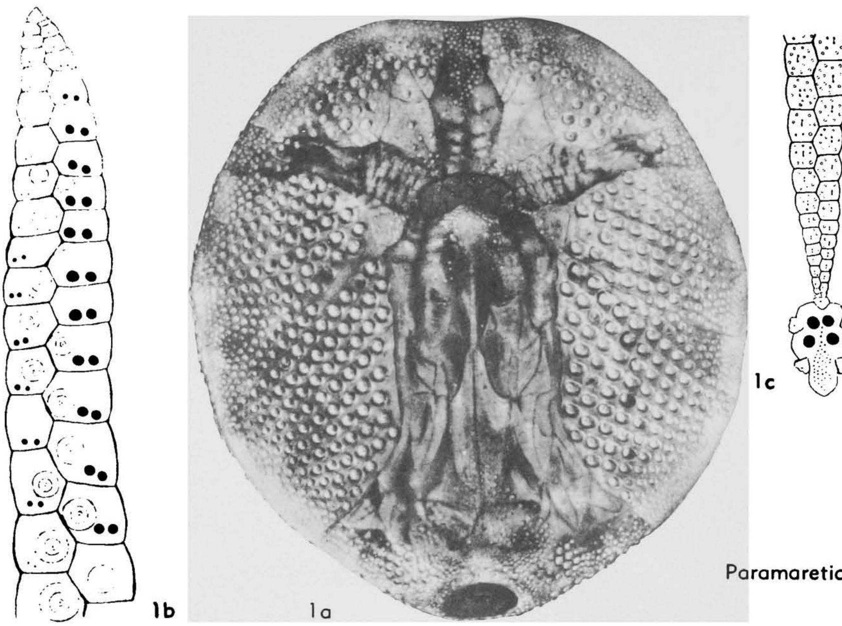


FIG. 495. Spatangidae (p. U609).

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

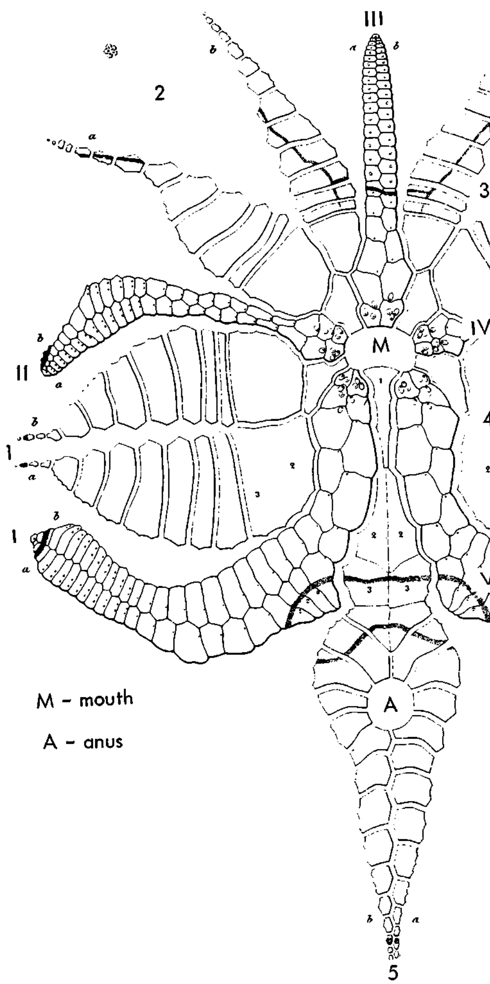


FIG. 496. Plate diagram of *Lovenia* (Lovén).

sinus; anterior petals long, open, somewhat depressed, posterior petals short, broad, closed, flush; phyllodes not well developed. *U.Eoc.,* Hung.

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-

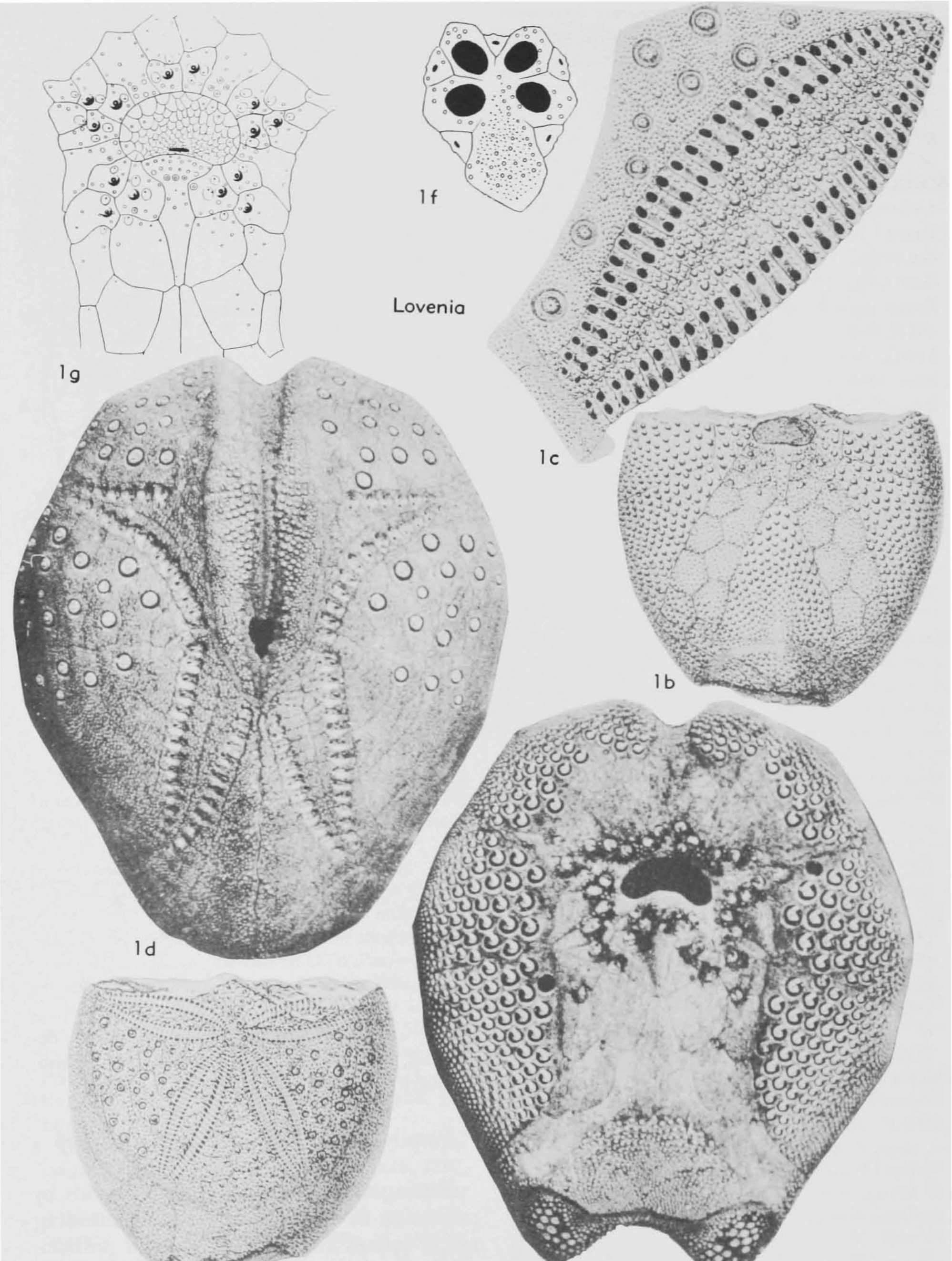


FIG. 497. Loveniidae (p. U613).

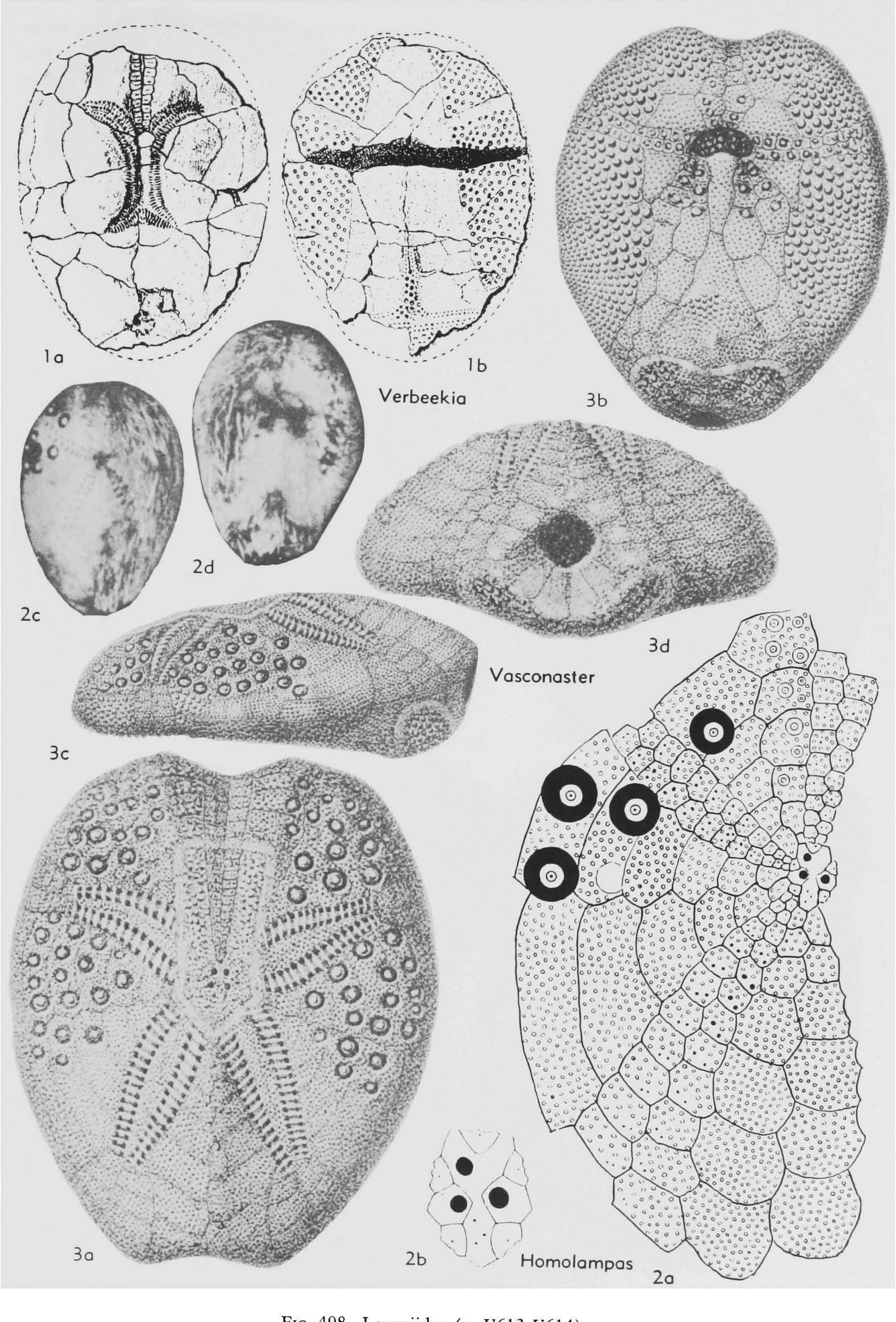


FIG. 498. Loveniidae (p. U613-U614).

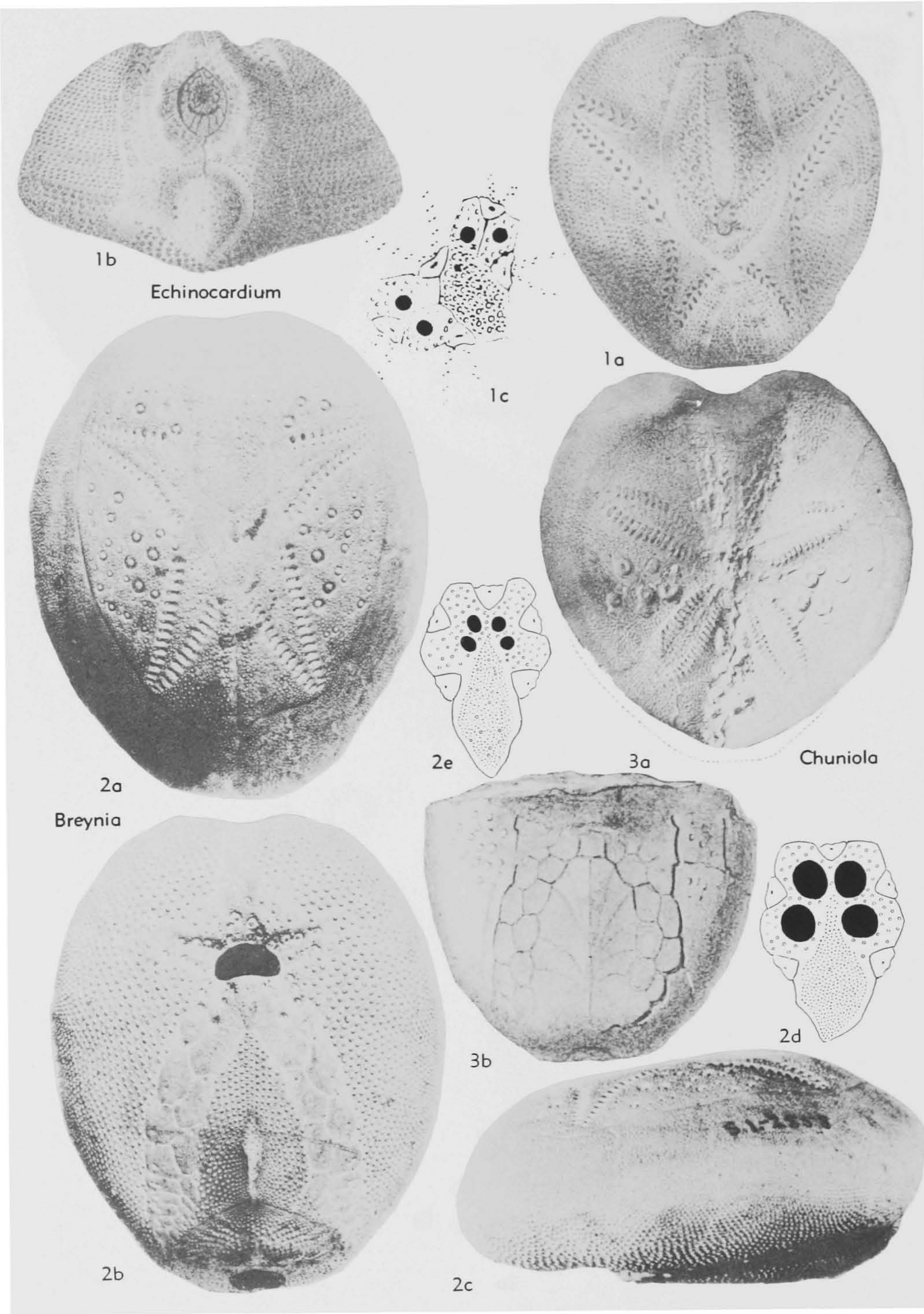


FIG. 499. Loveniidae (p. U613).

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 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).

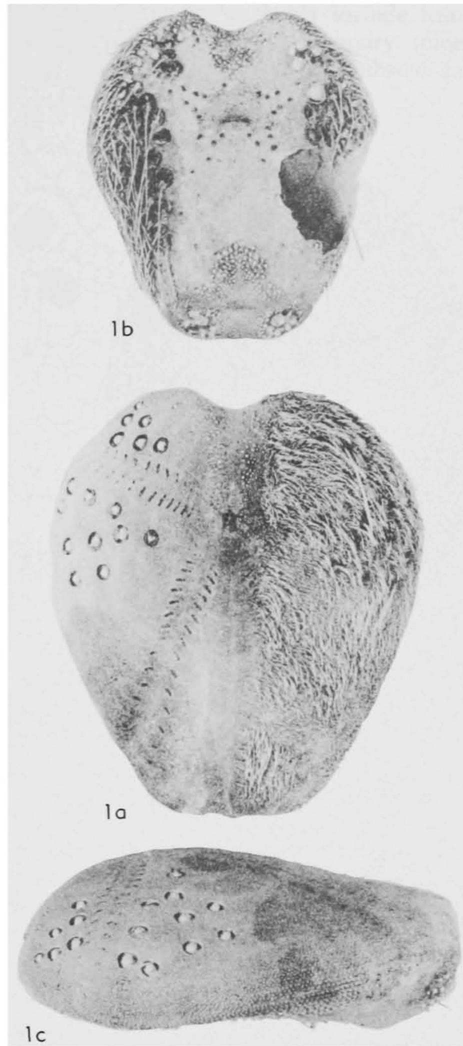


FIG. 500. Loveniidae (p. U614).

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-

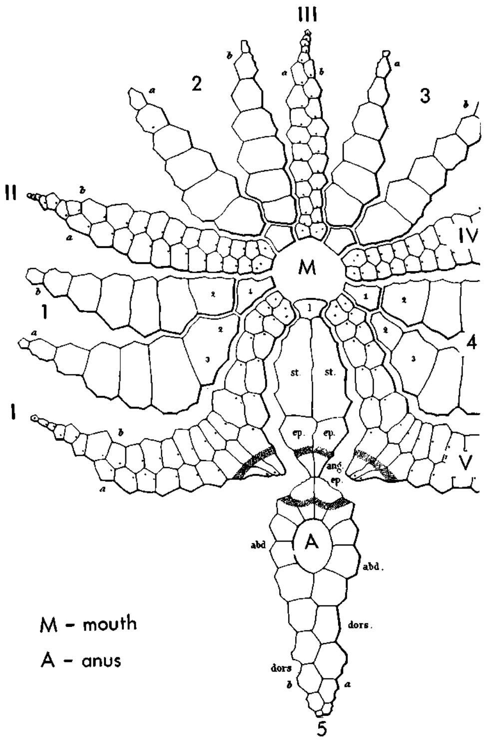


FIG. 501. Plate diagram of *Palaeotropus* (Lovén).

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-

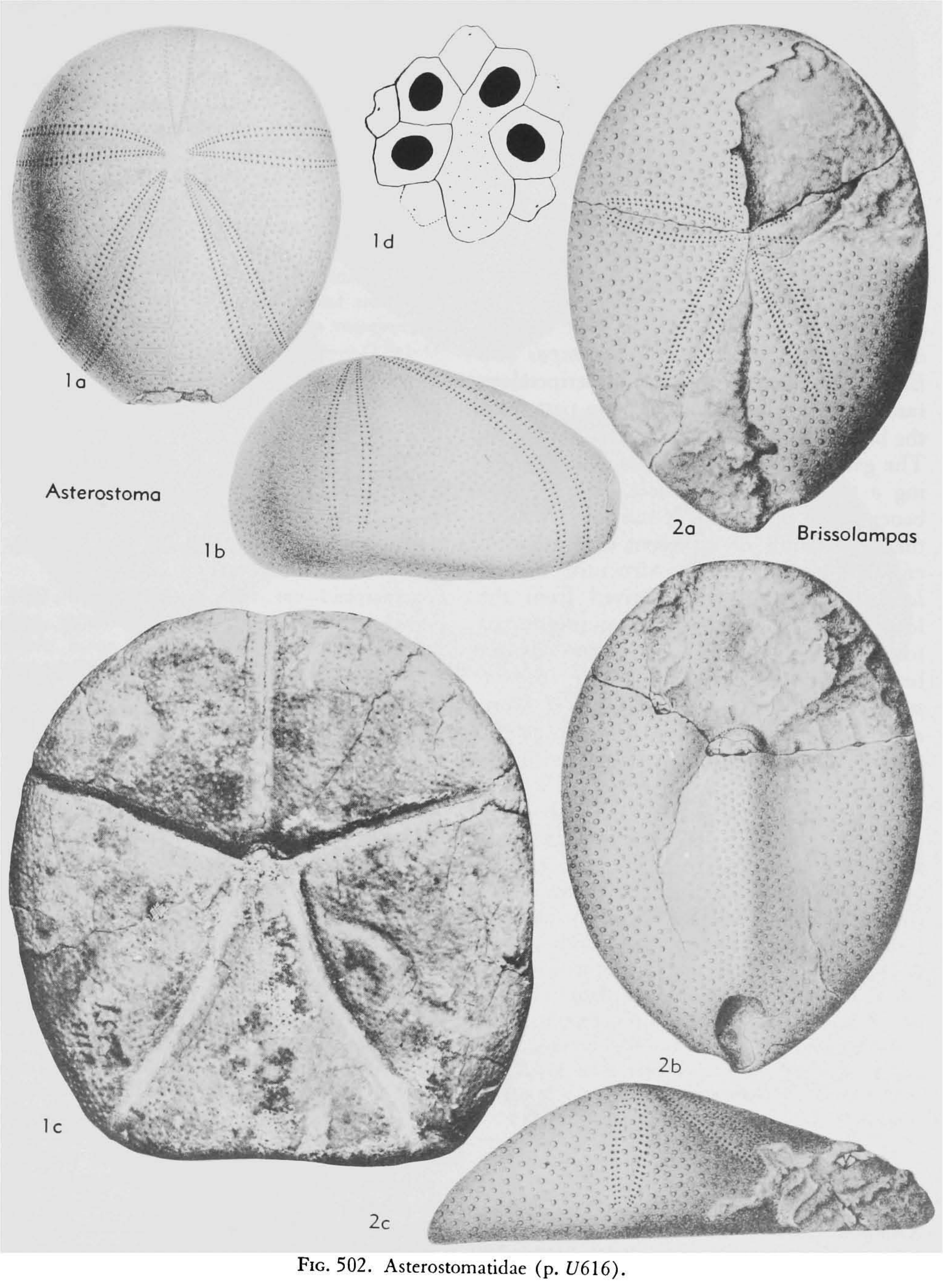


FIG. 502. Asterostomatidae (p. *U616*).

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.

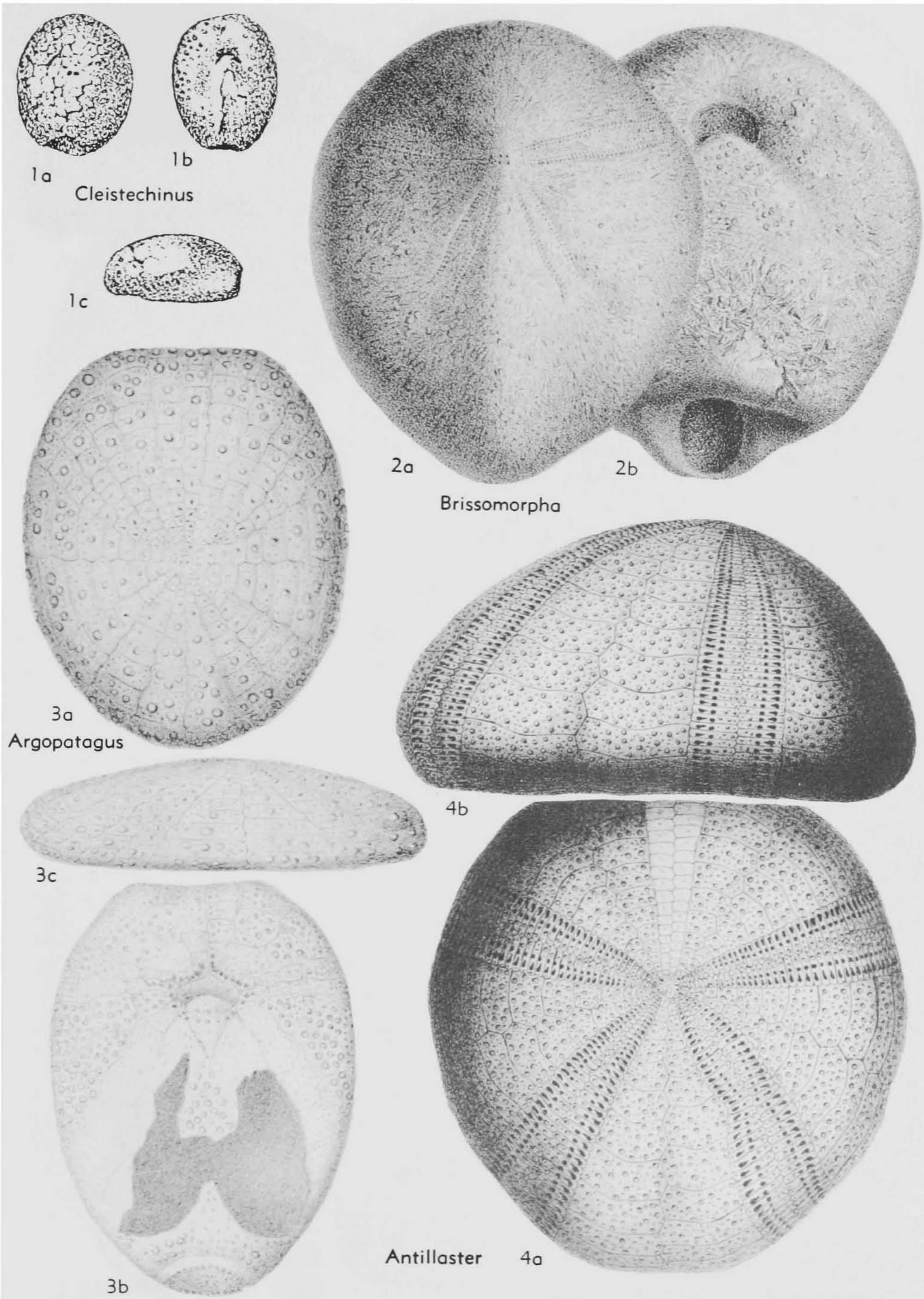


FIG. 504. Asterostomatidae (p. *U*616).

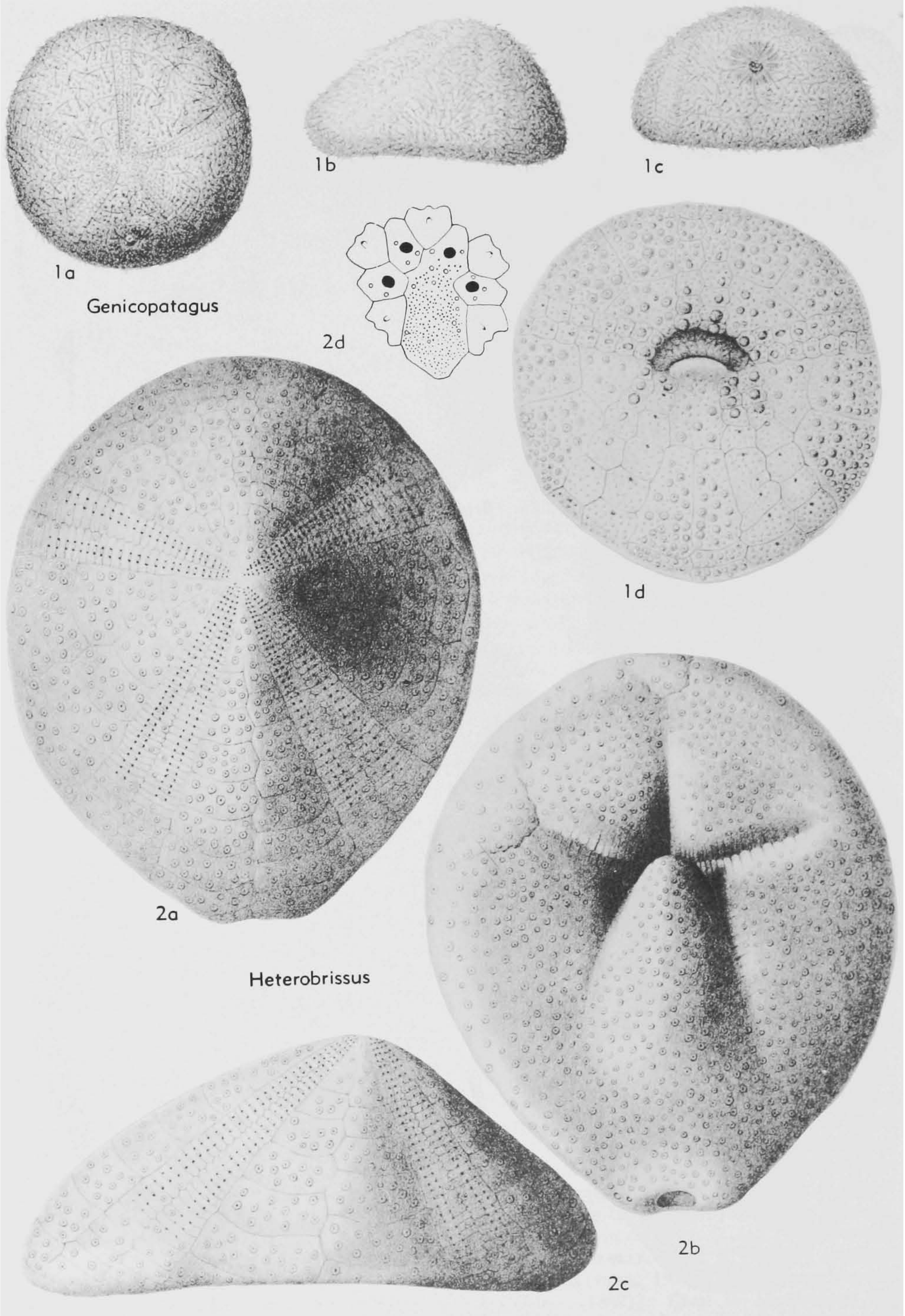


Fig. 505. Asterostomatidae (p. U622).

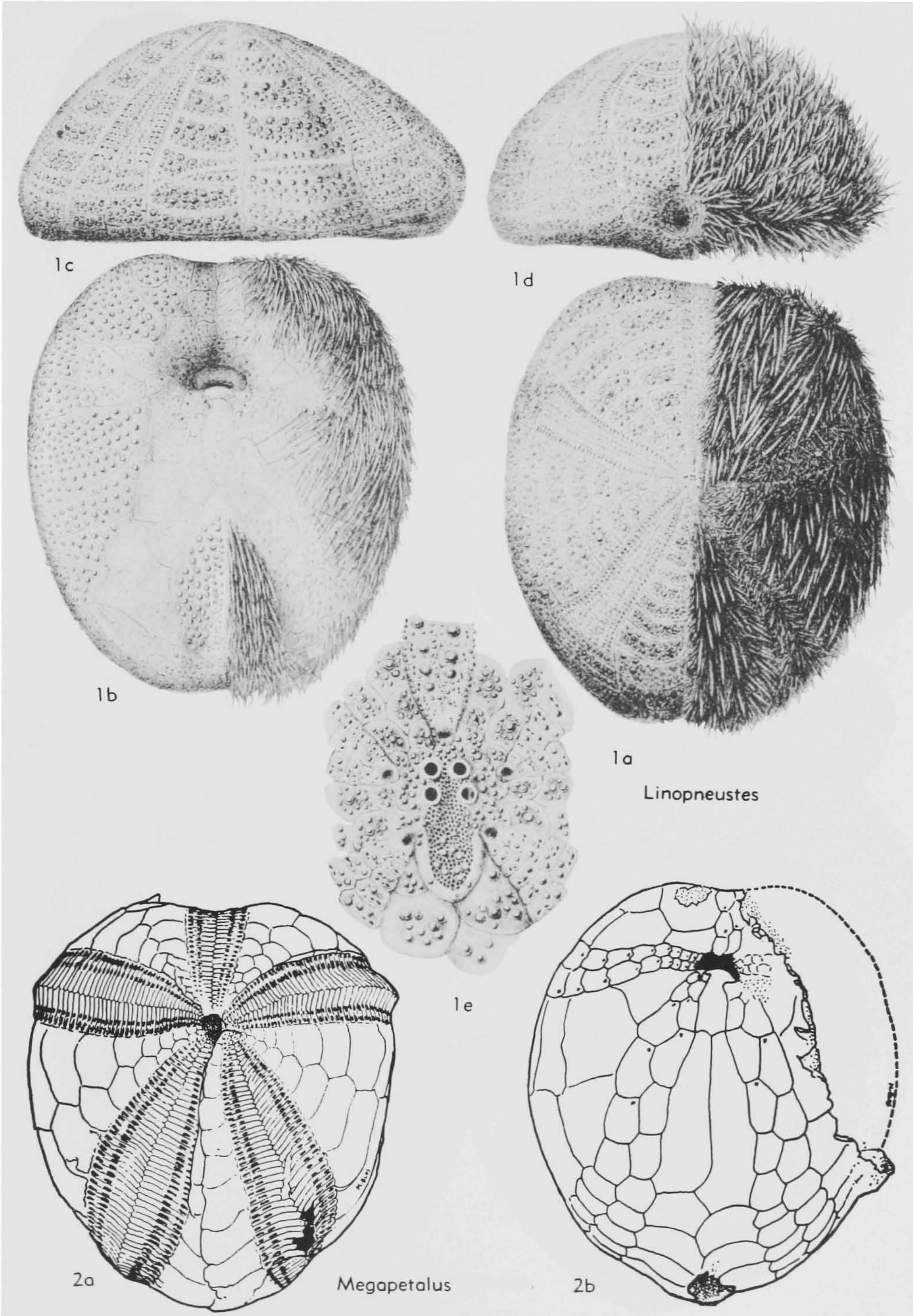


FIG. 506. Asterostomatidae (p. *U*622).

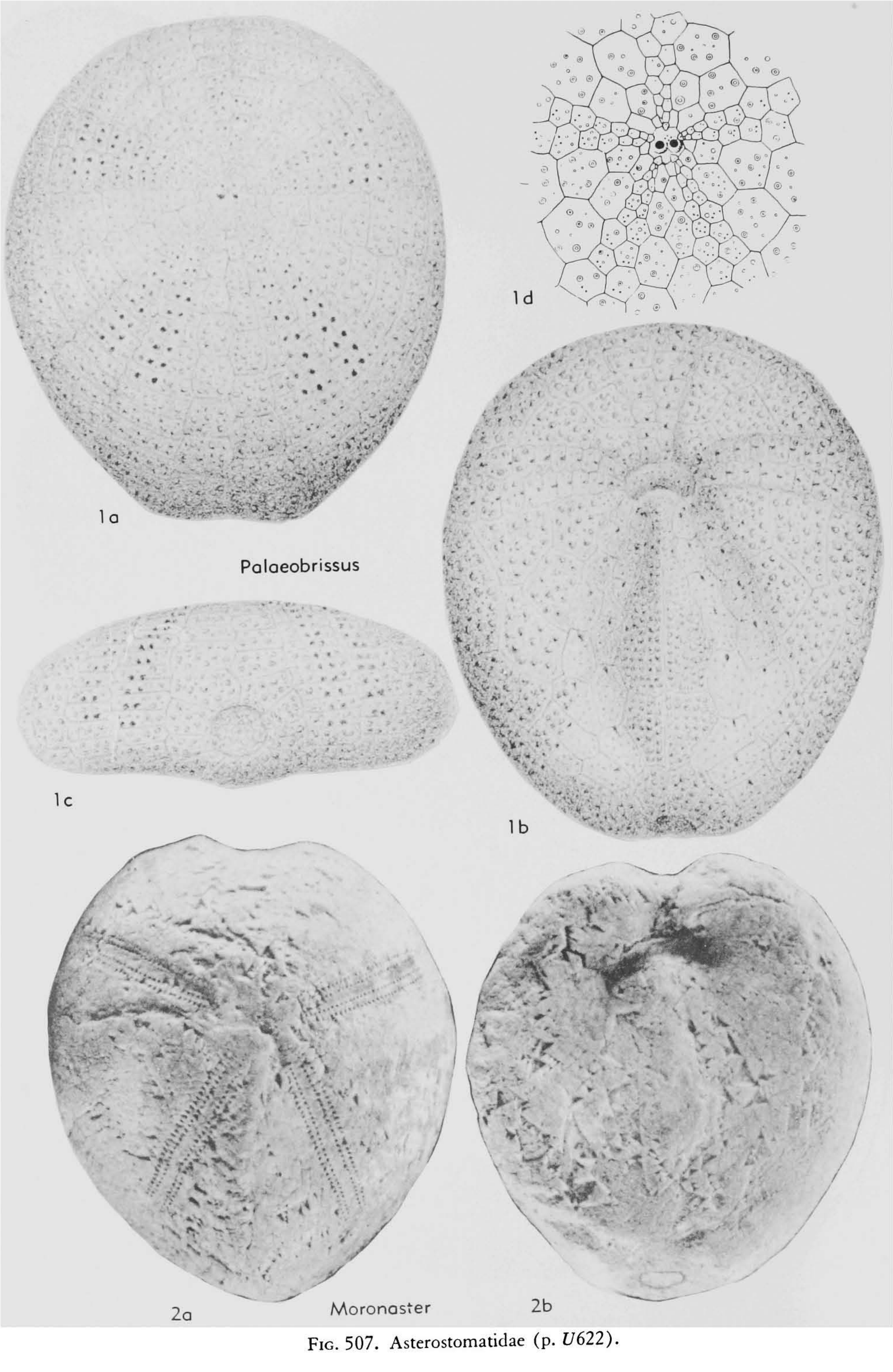


FIG. 507. Asterostomatidae (p. U622).

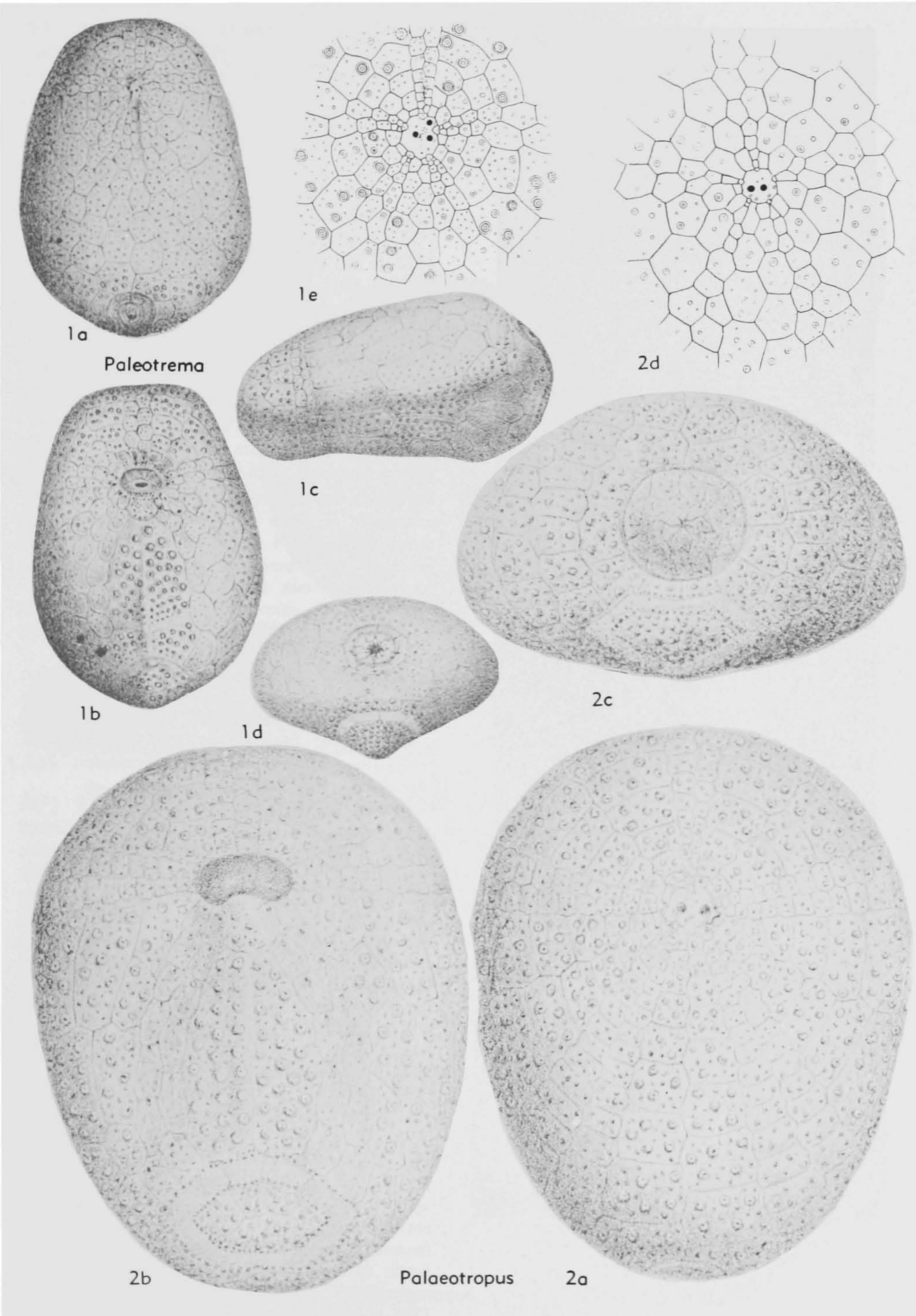


FIG. 508. Asterostomatidae (p. U622, U624).

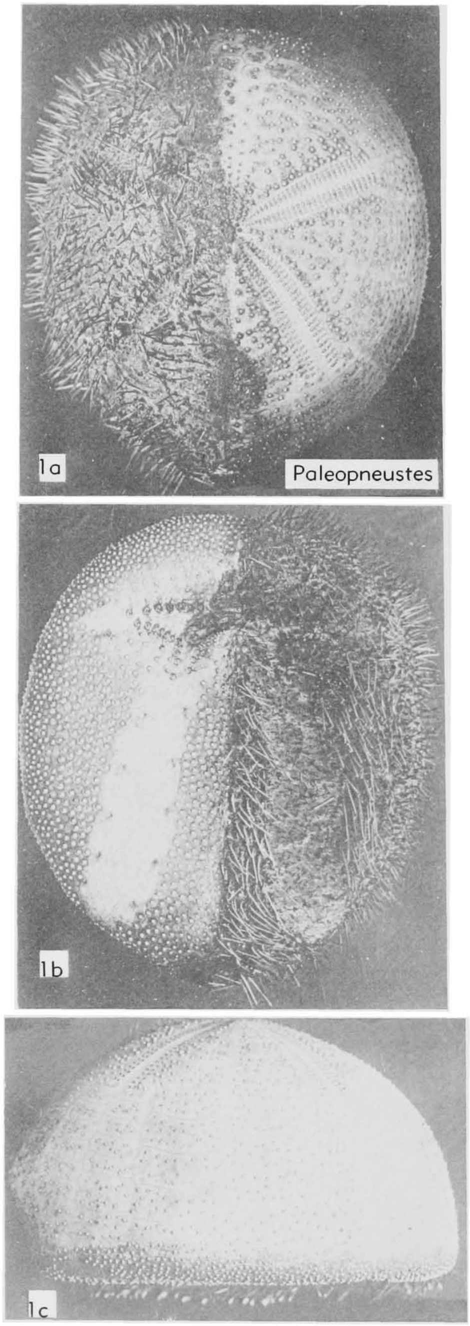


FIG. 509. Asterostomatidae (p. U624).

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-

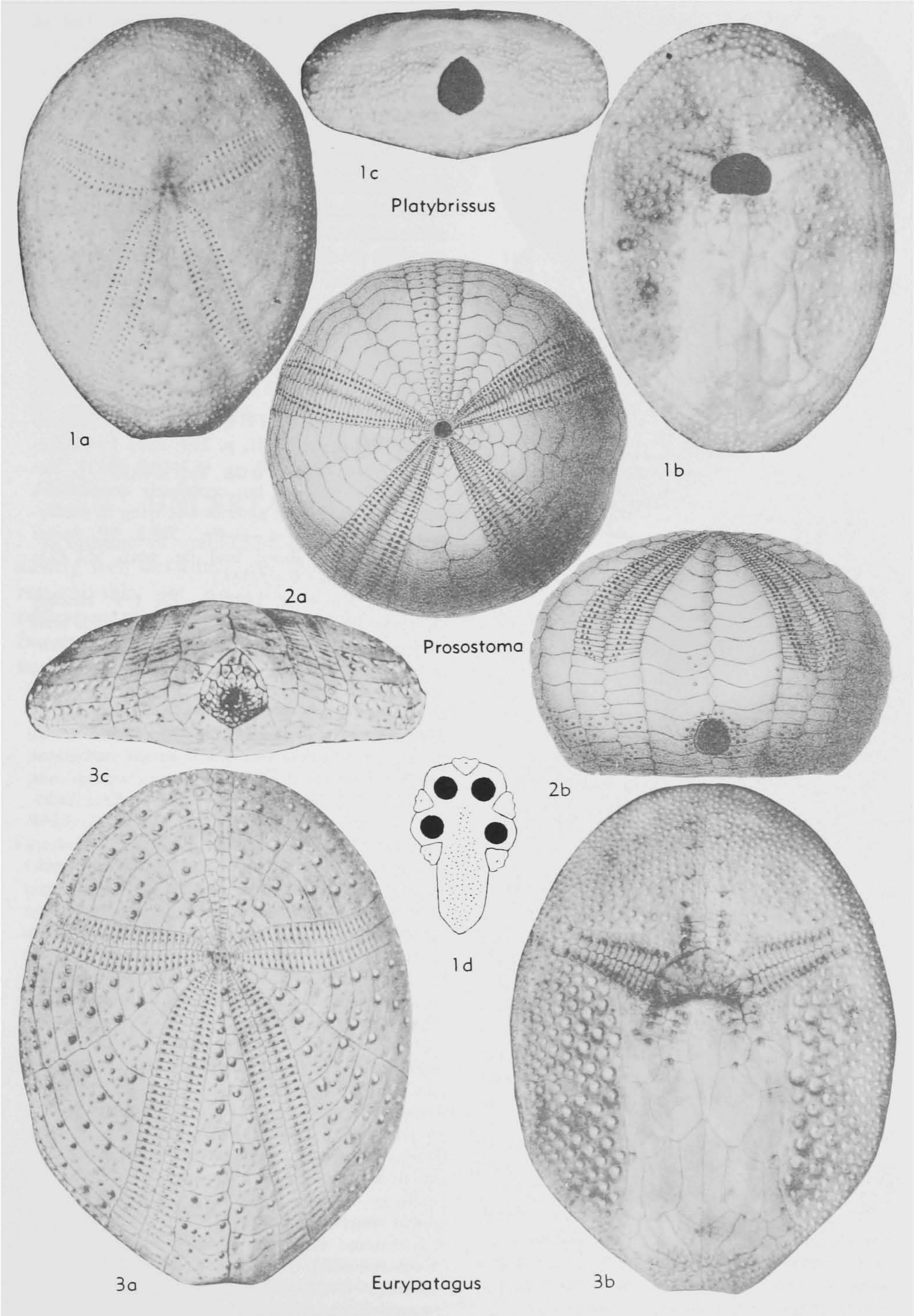


FIG. 510. Asterostomatidae (p. *U624-U625*).

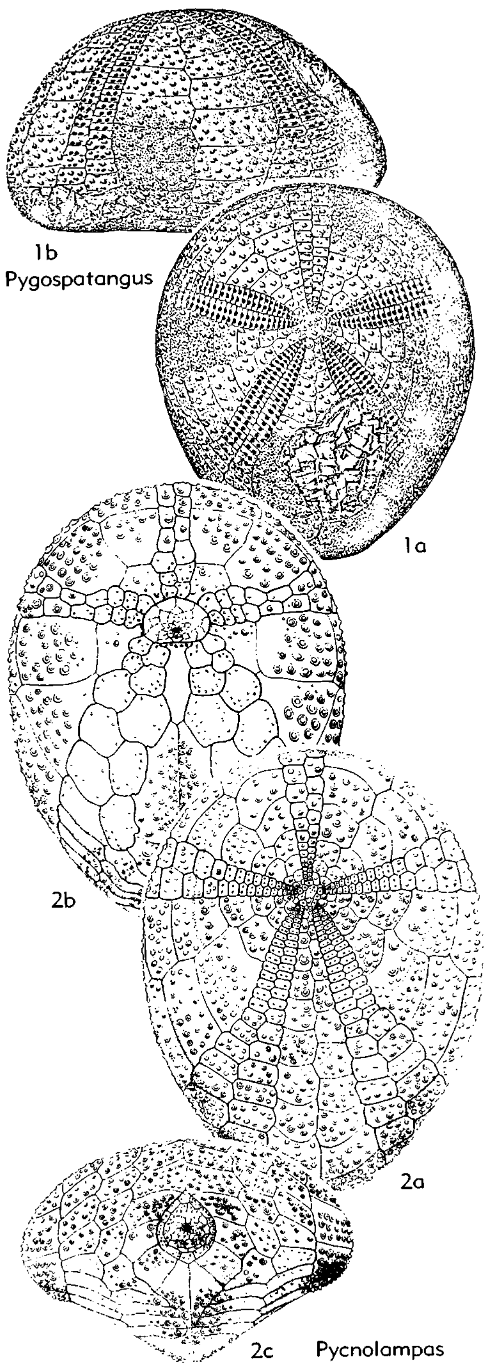


FIG. 511. Asterostomatidae (p. U625).

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.

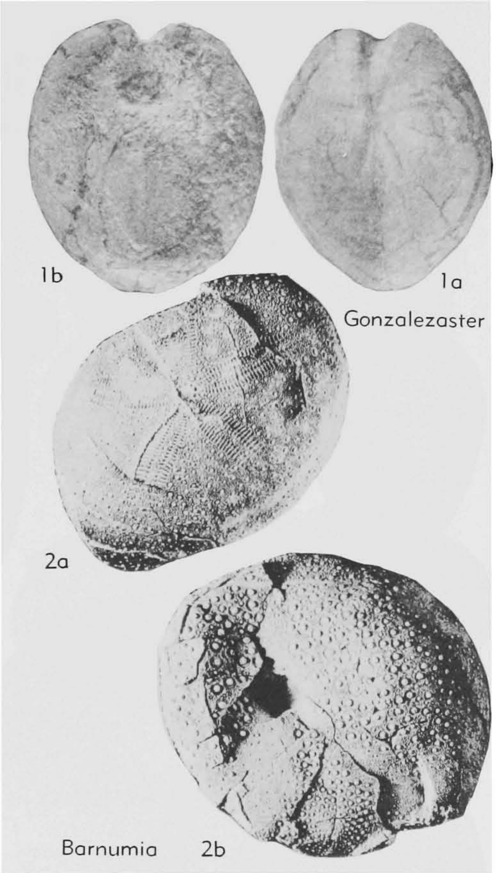


FIG. 512. Spatangoida, Suborder and Family Uncertain (p. *U*625).

Oligo., Italy.——FIG. 514,*1*. **E. oblongus*; *1a,b,* aboral, lat., ×1.5 (205a).

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).

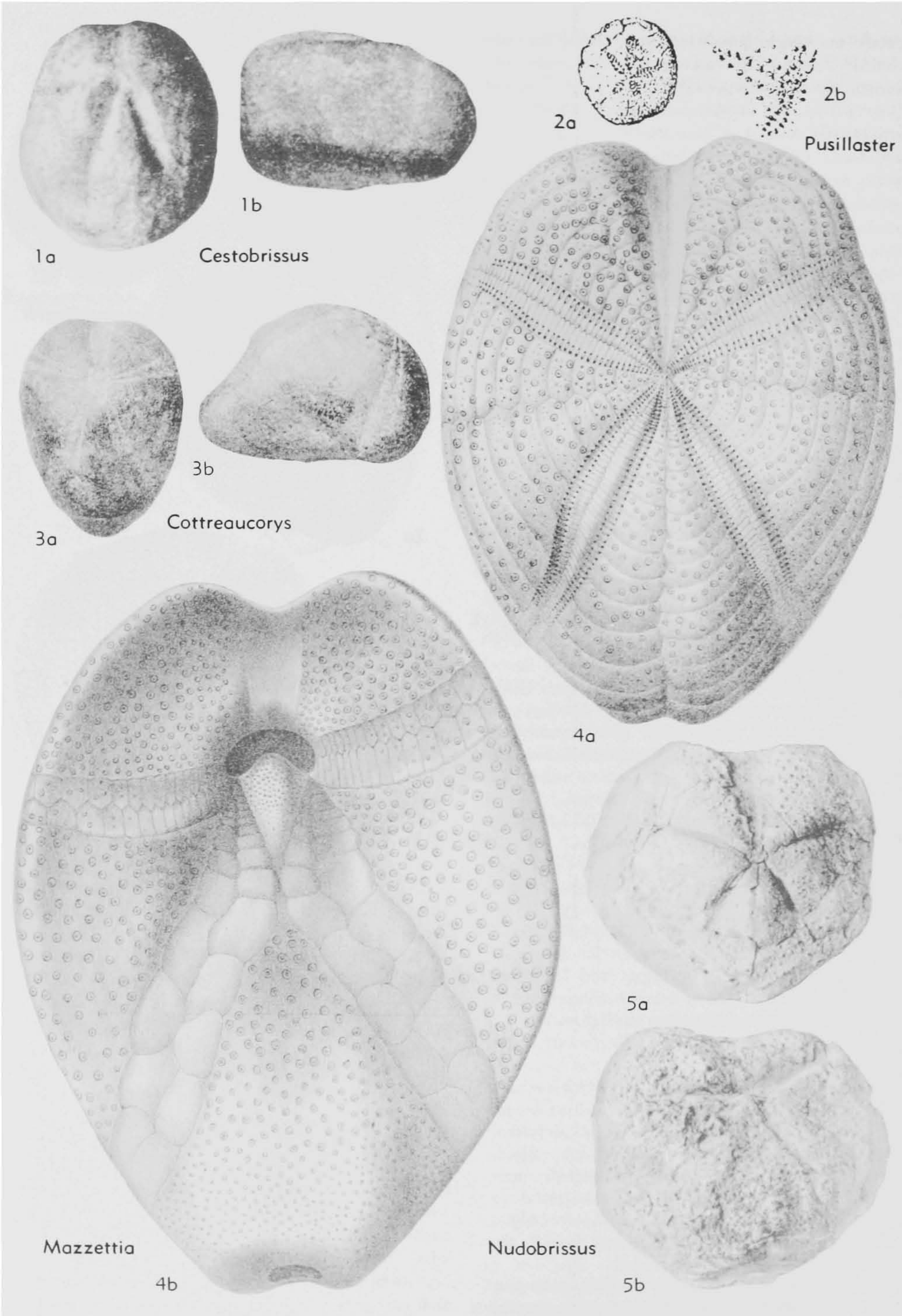


FIG. 513. Spatangoida, Suborder and Family Uncertain (p. *U625*, *U627*).

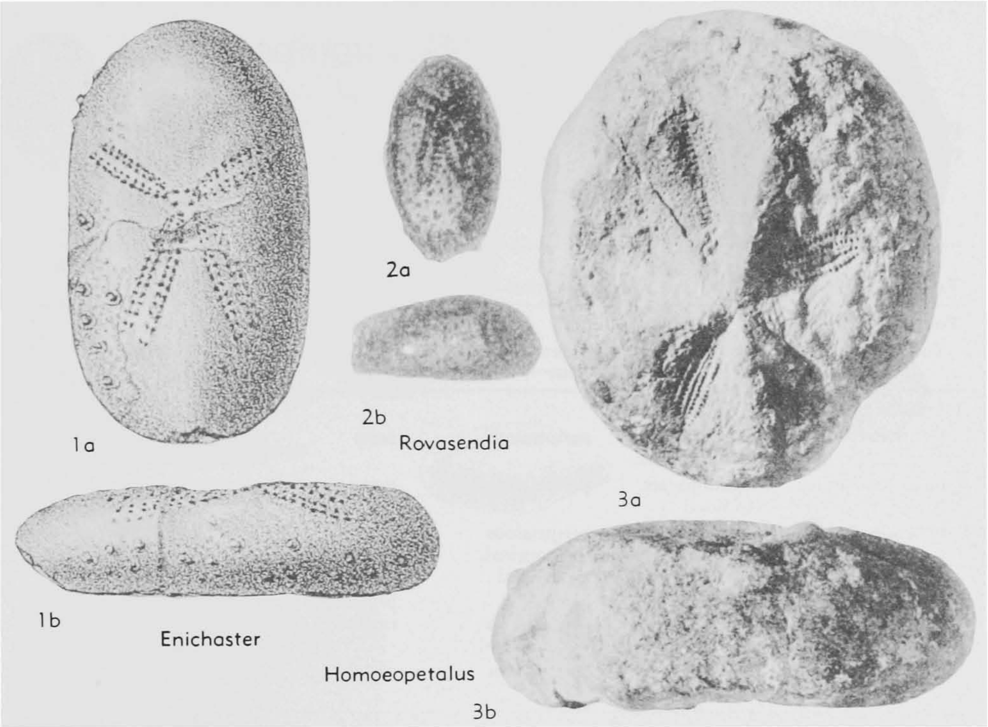


FIG. 514. Spatangoida, Suborder and Family Uncertain (p. *U*625, *U*627).

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*

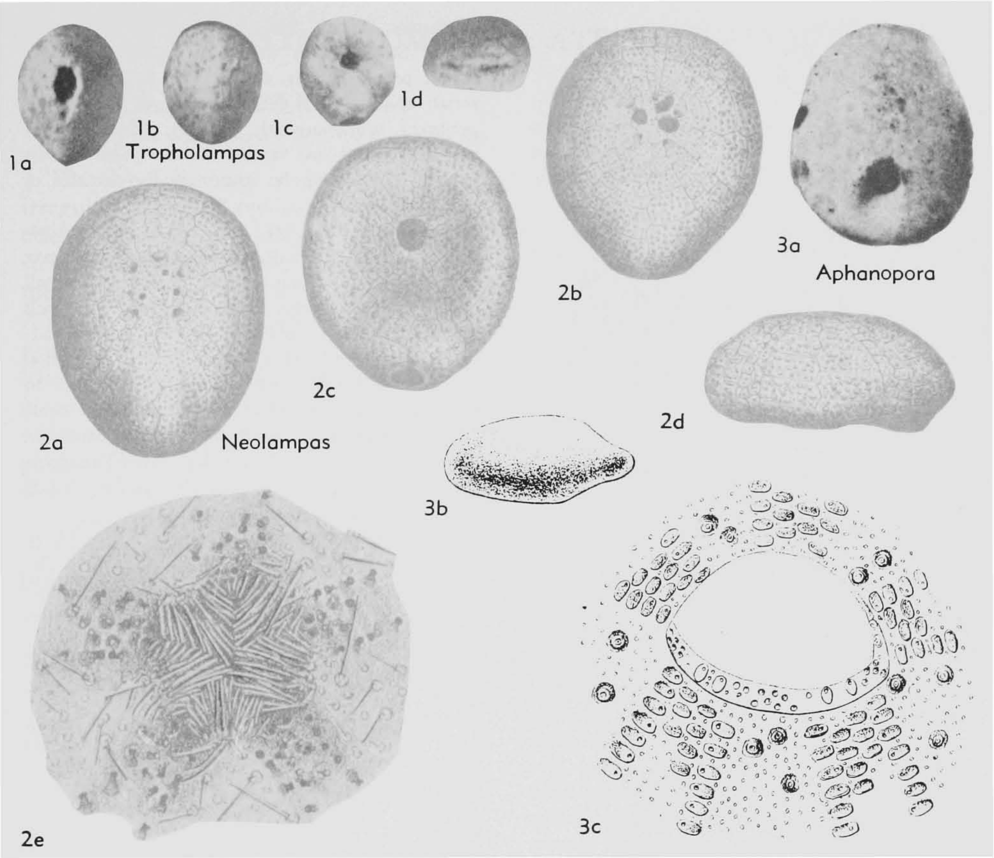


FIG. 515. Neolampadidae (p. U630).

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.*

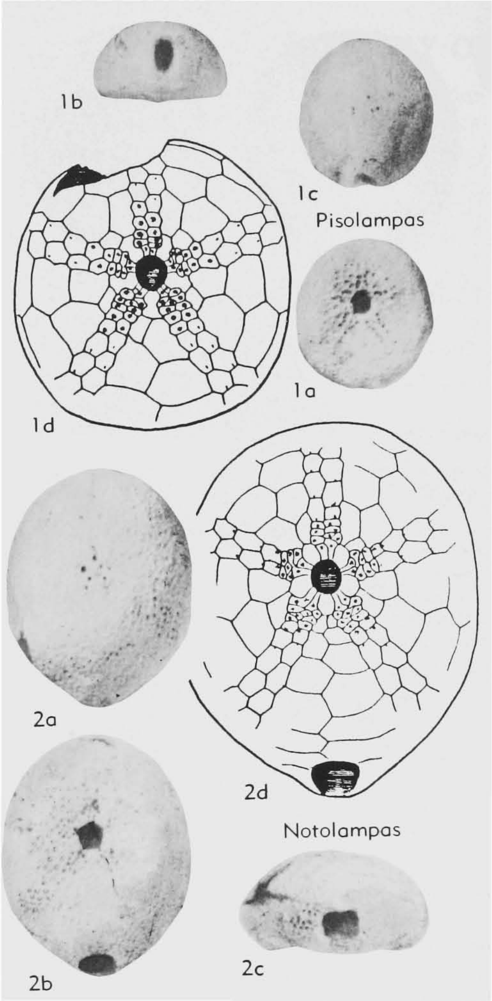


FIG. 516. Neolampadidae (p. U630).

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).

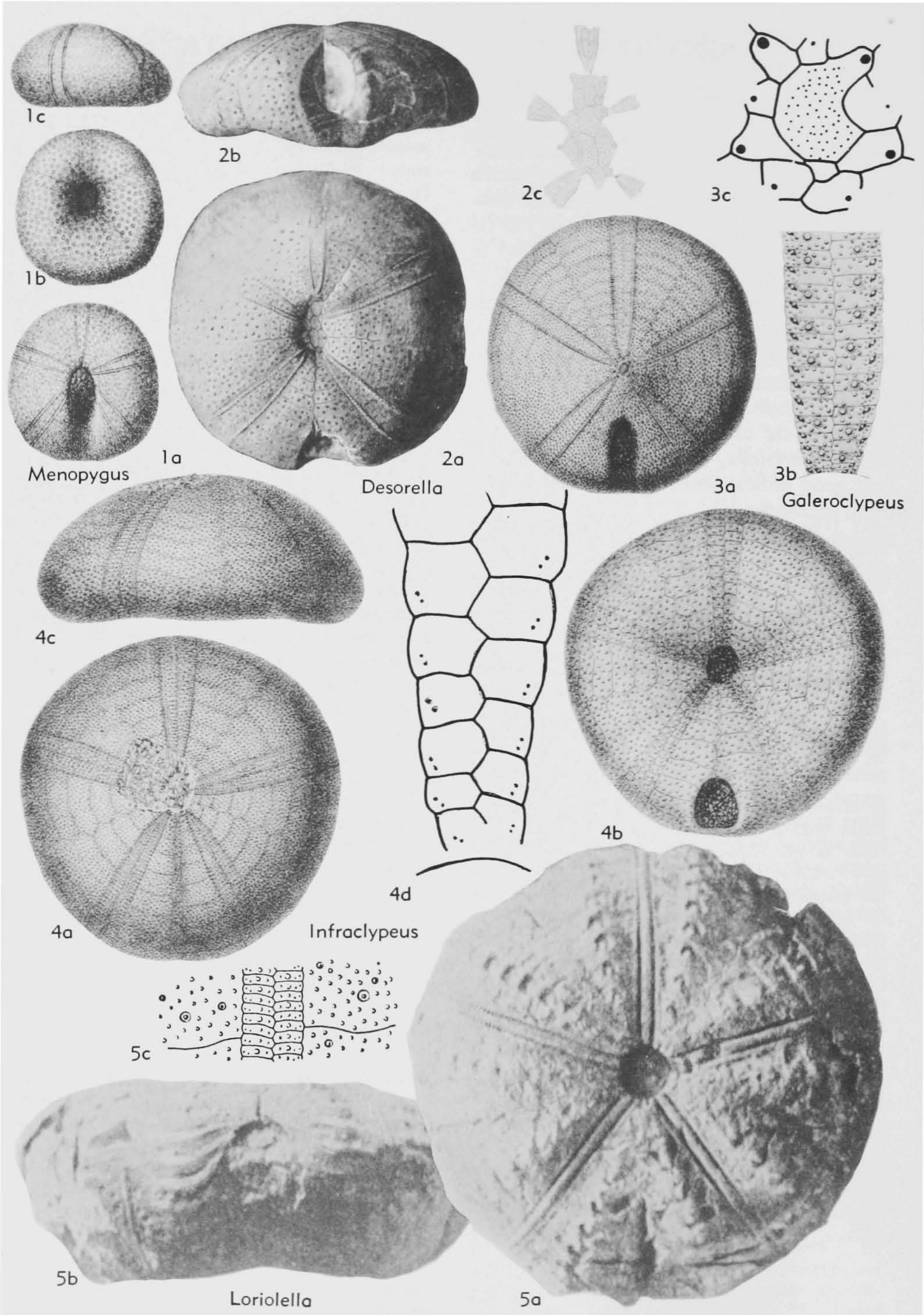


FIG. 517. Gnathostomata or Atelostomata, Order Uncertain (p. U631).

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 [=*Insufflaster* 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 noncidaroid.]
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

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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

[Smithsonian Institution]

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,

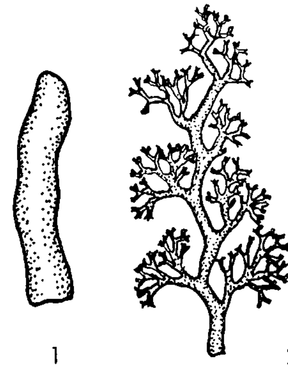

FIG. 518. Holothuroid tentacles (diagram.) (PAWSON & FELL, n).——*1*. Simple finger-like tentacle of dactylochirote.——*2*. Complexly branched tentacle of dendrochirote.

with mouth and anus close together, at the top of the "neck."

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

Don L. Frizzell[1] and Harriet Exline[2]

[[1]Professor of Geology, University of Missouri at Rolla, Rolla, Missouri; [2]Mrs. Don L. Frizzell, Rolla, Missouri; Research Associate, California Academy of Sciences, San Francisco, California]

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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

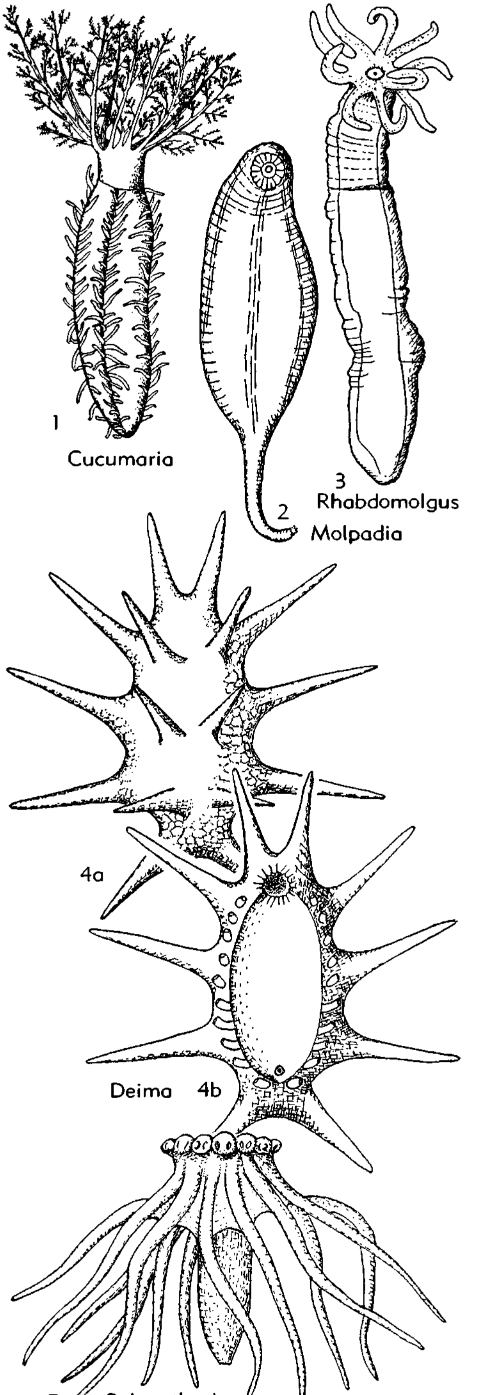

FIG. 519. Representative Recent holothurians (14, fig. 1-5).——*1. "Cucumaria" planci* (BRANDT).——*2. Molpadia musculus* (RISSO).——3. *Rhabdomolgus ruber* KEFERSTEIN.——*4a,b. Deima atlanticum* HÉROUARD.——*5. Pelagothuria natatrix* LUDWIG.

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

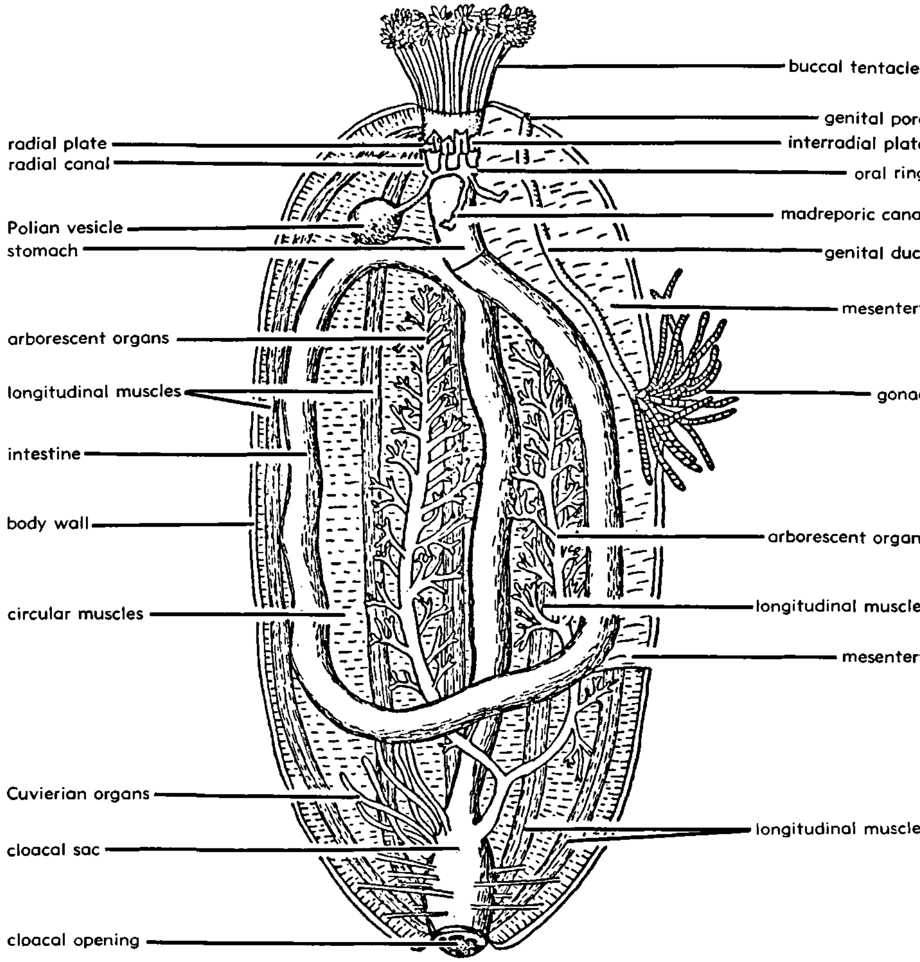

FIG. 520. Morphology of a typical holothurian (14, fig. 6, modified from Parker & Haswell, after Leuckart).

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.

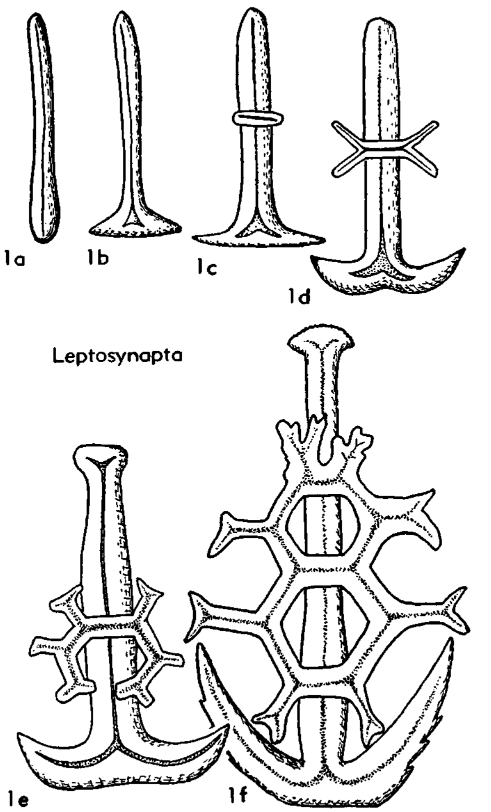

FIG. 521. Successive stages in development of anchor and anchor plate of *Leptosynapta inhaerens* (O. F. MÜLLER) (14, fig. 7a-f).

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* (FORSKÅL).

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

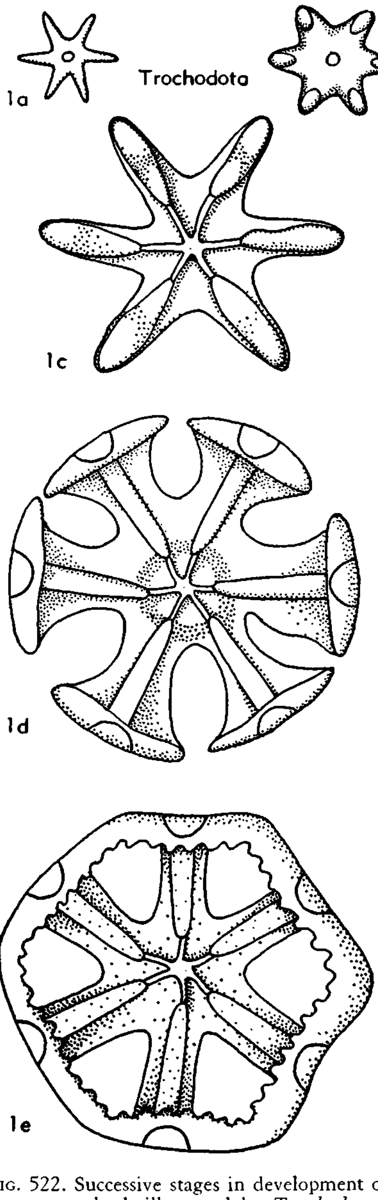

FIG. 522. Successive stages in development of *Chiridota*-type wheel, illustrated by *Trochodota venusta* (SEMON) (14, fig. 8a-e).

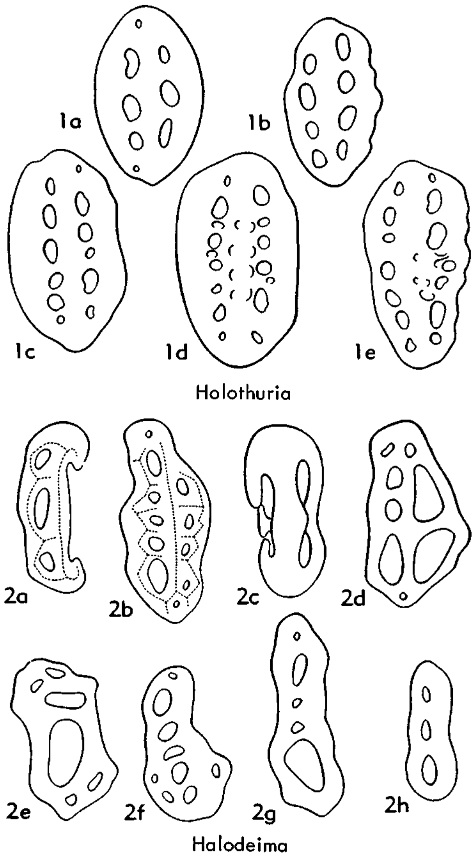

FIG. 523. Intraspecific variability of sclerites in *(1a-e) Holothuria umbrina* RÜPPELL & LEUCKART and *(2a-h) Halodeima insignis* (LUDWIG) (14, fig. 9a-e, 10a-h).

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.

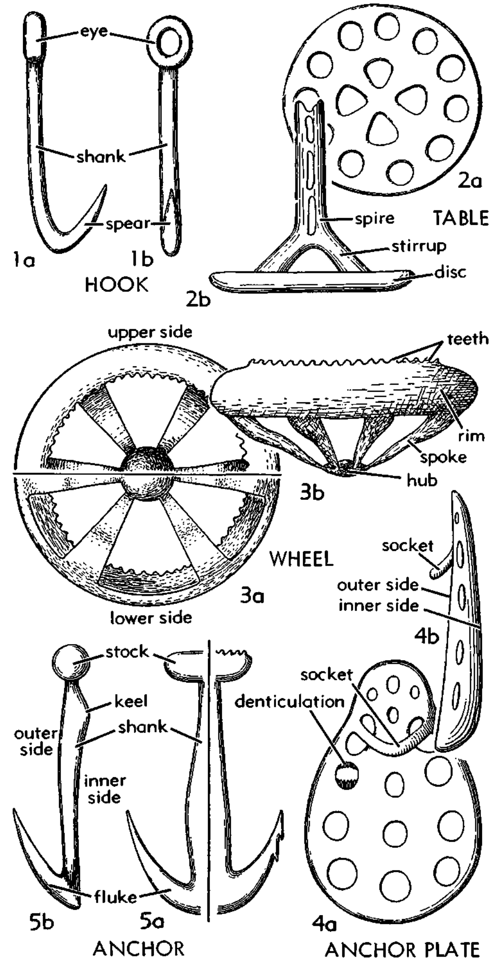

FIG. 524. Terminology of holothurian sclerites (14, fig. 17-21).

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.;

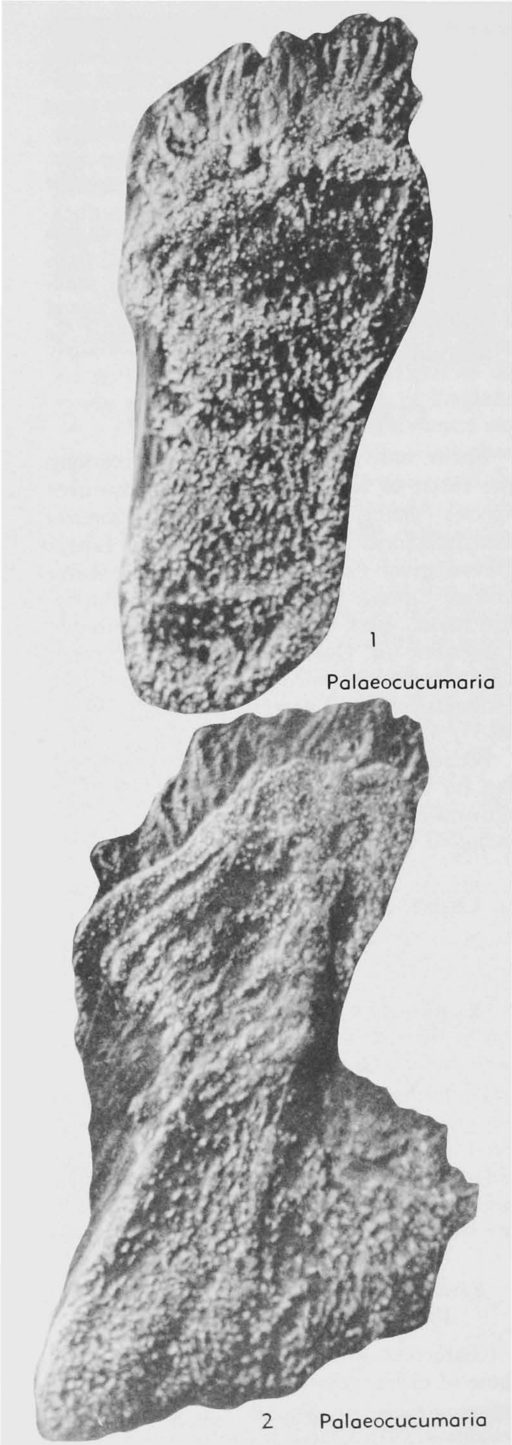

FIG. 525. *Palaeocucumaria hunsrueckiana* LEHMANN (42, pl. 10, fig. 2a,3).

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).

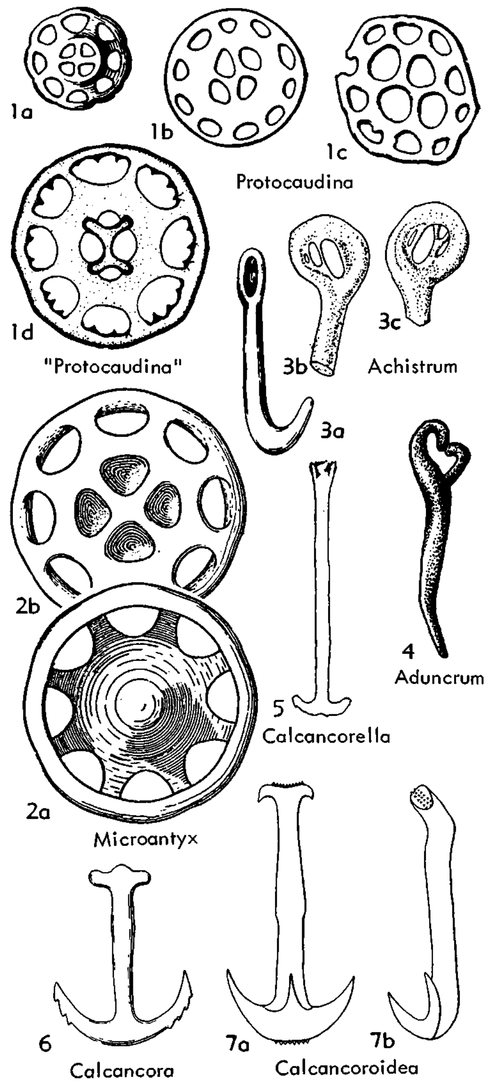

FIG. 527. Morphological features of holothurian sclerites (various sources).

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.

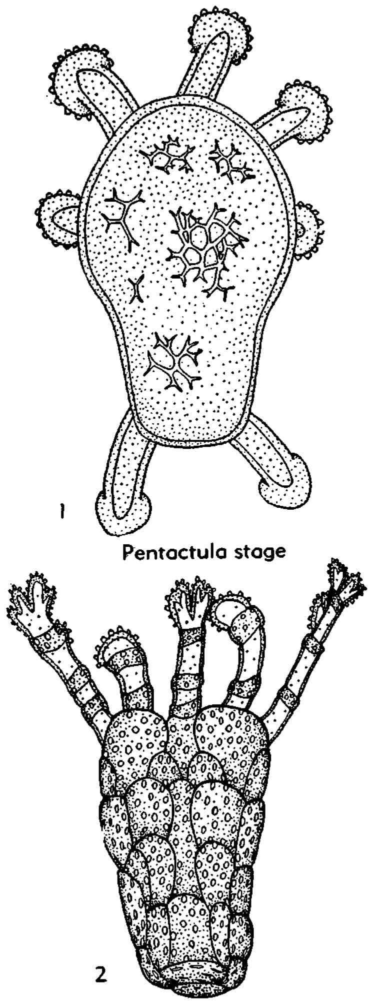

FIG. 528. Larval stages (*Cucumaria chronhjelmi* THÉEL) (14, fig. 15-16).——*1. Pentactula.*——*2.* 21-day larva.

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

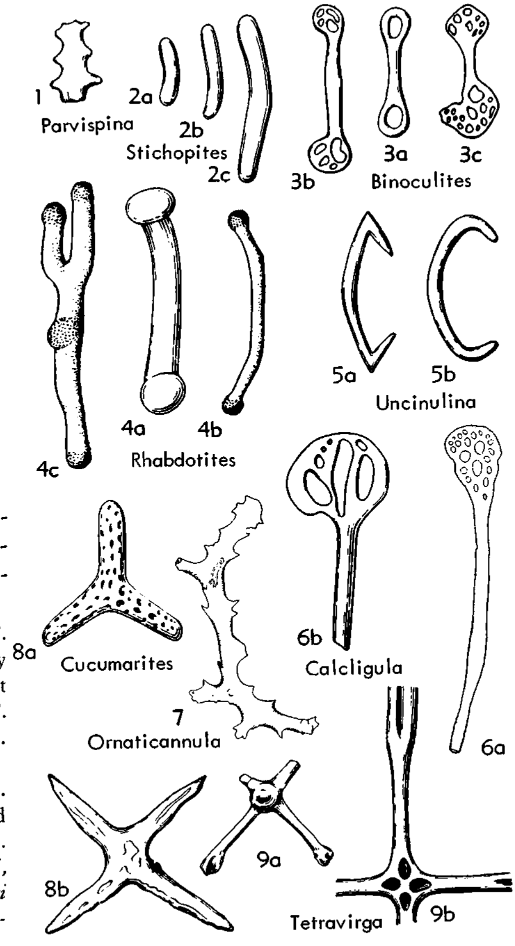

Fig. 529. Stichopitidae (p. *U662-U664*).

and branches. *Jur.-Pleist.*, Eu.——Fig. 529,*7*. **O. bonheurei*, Jur., Fr.; ×170 (10).

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].

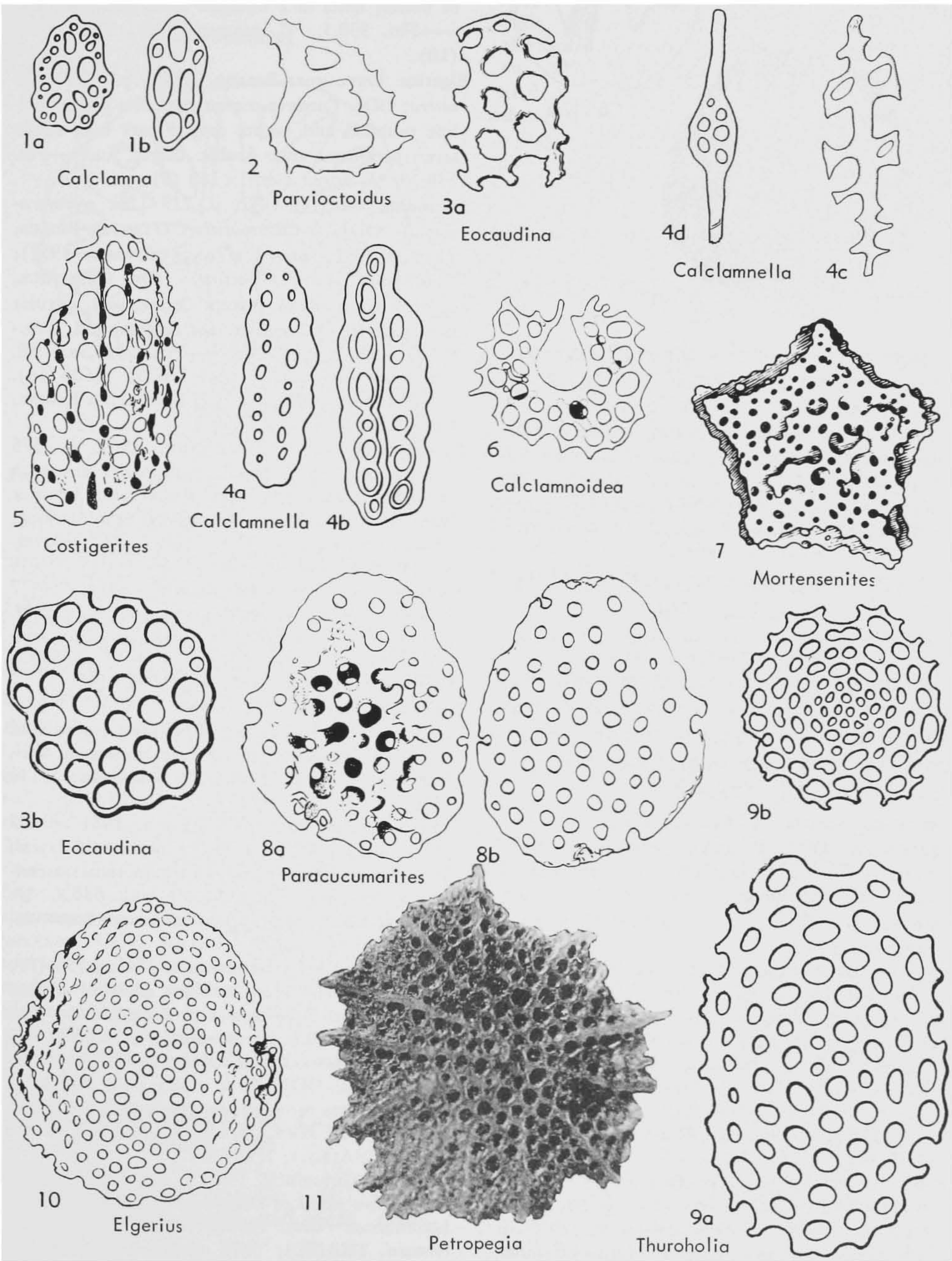

Fig. 530. Calclamnidae (p. *U664-U665*).

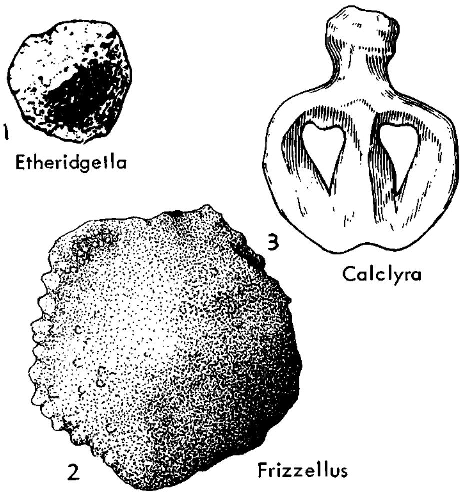

FIG. 531. Etheridgellidae *(1,2)*; Calclyridae *(3)* (p. *U665-U666*).

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).

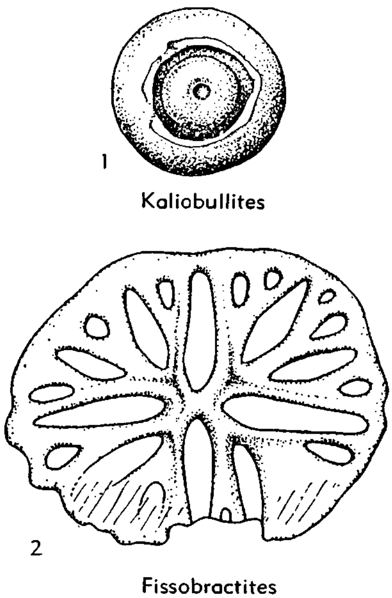

FIG. 531A. Calclamnidae *(2)*; Kaliobullitidae *(1)* (p. *U*664, *U*670).

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).

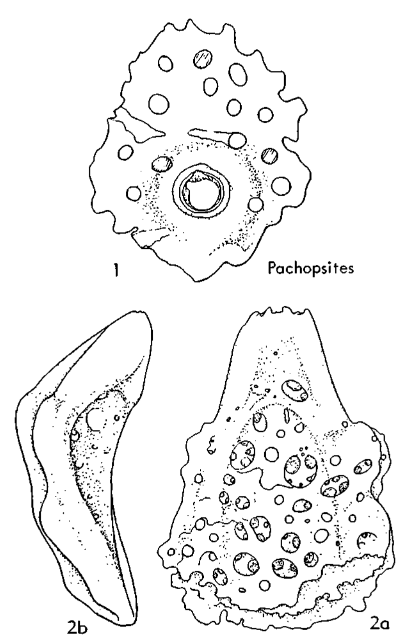

FIG. 531B. Calclamnidae *(1)*; Alexandritidae *(2)* (p. *U*664, *U*668).

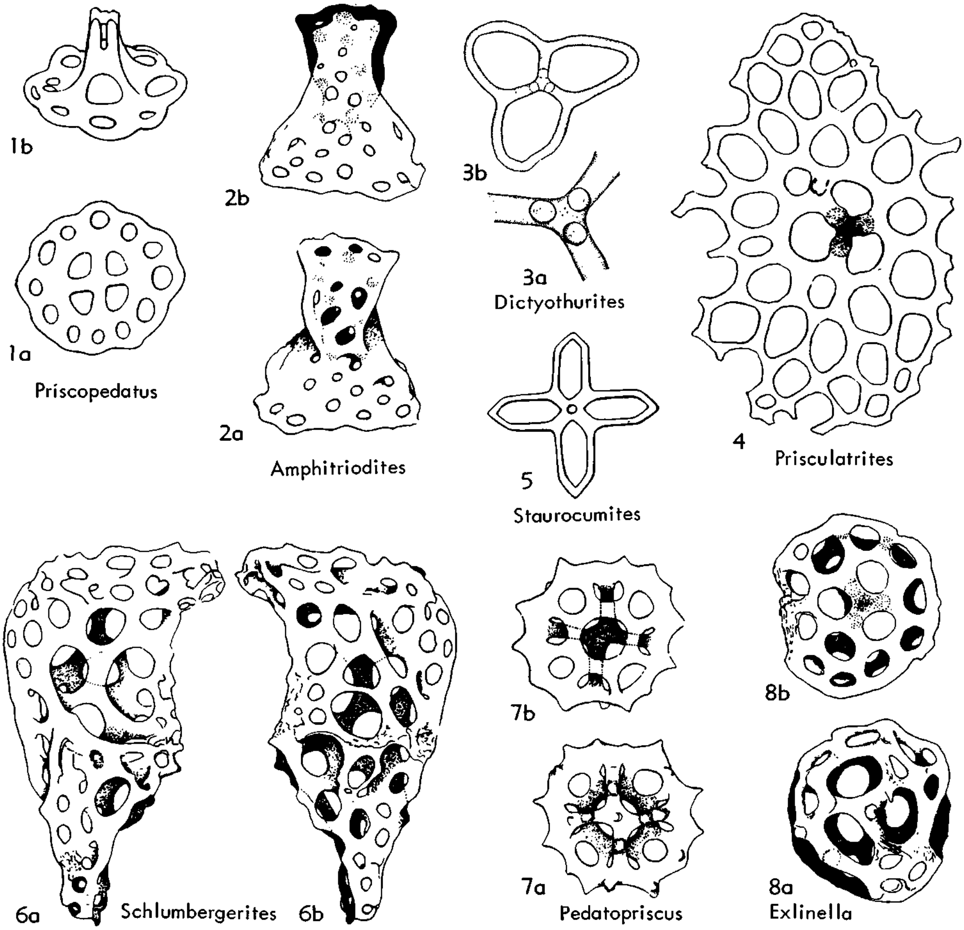

FIG. 532. Priscopedatidae *(1,3-5)*; Exlinellidae *(7-8)*; Schlumbergeritidae *(2,6)* (p. *U666-U667*).

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).

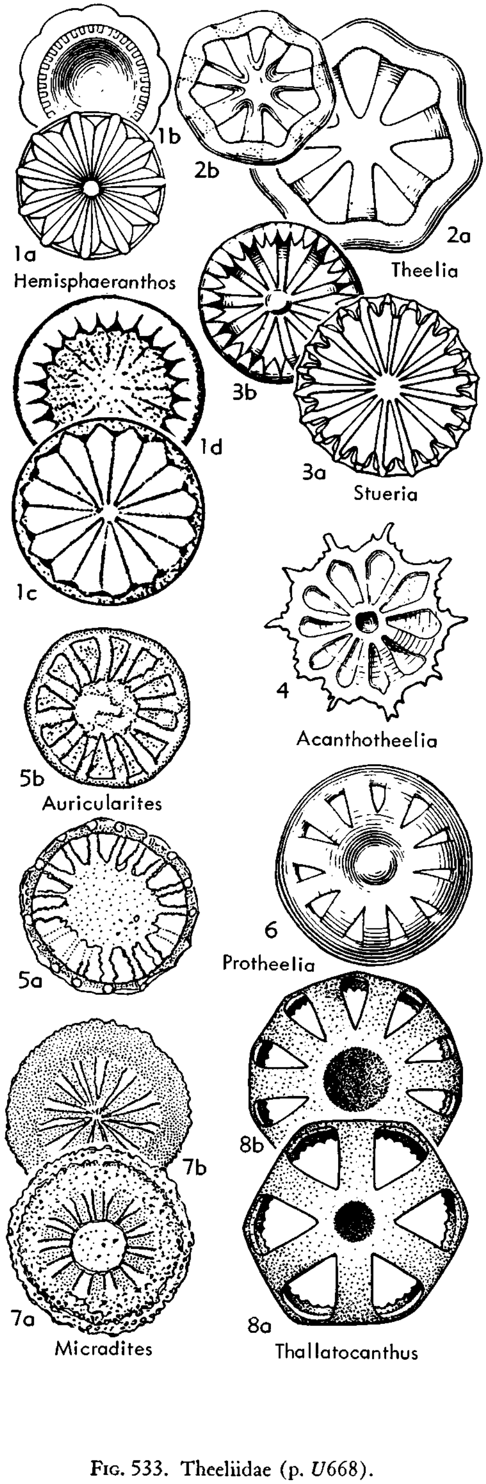

FIG. 533. Theeliidae (p. *U668*).

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*

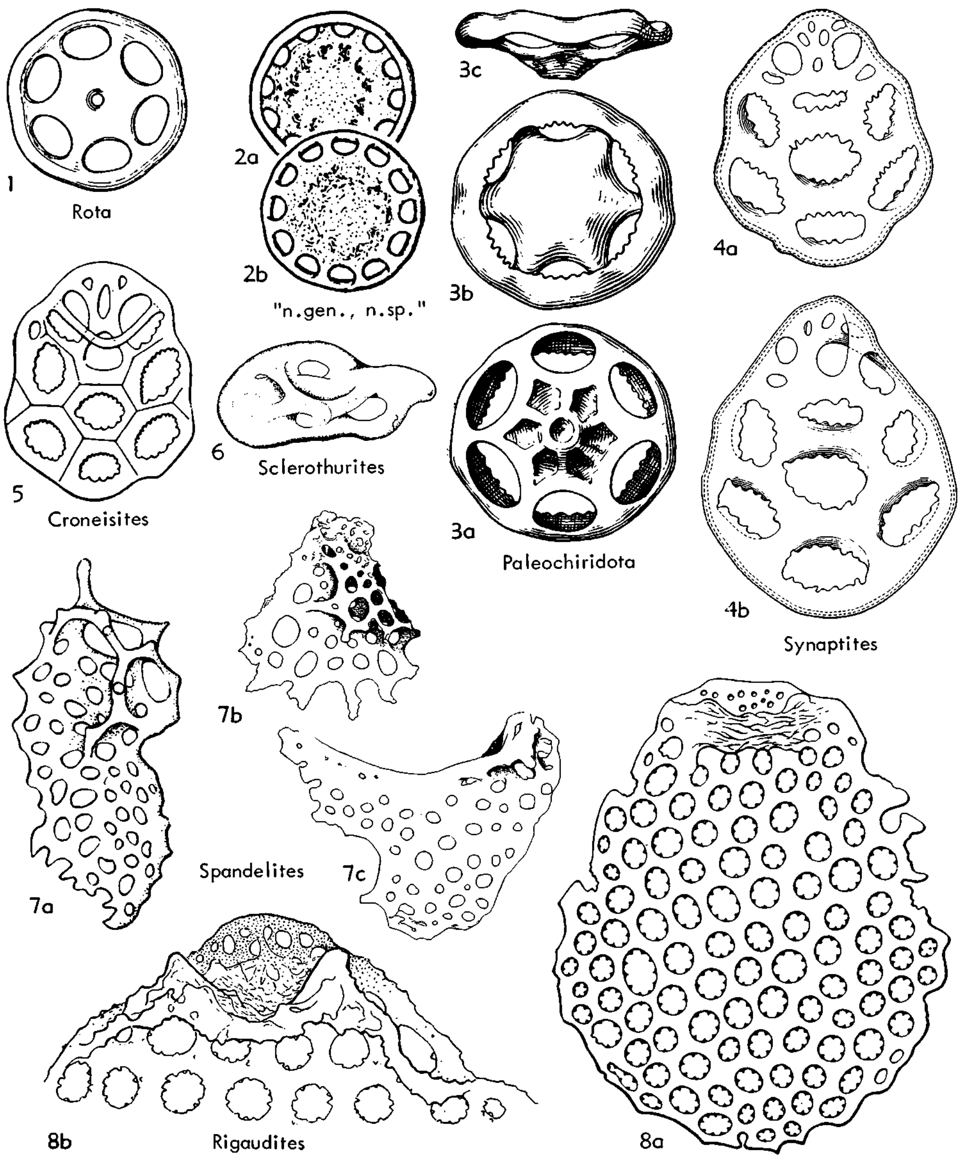

FIG. 534. Paleochiridotidae *(1-3)*; Synaptitidae *(4-5, 7-8)*; Family Uncertain *(6)* (p. *U*670-*U*671).

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).

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Printed in the U.S.A. by Malloy Lithographing, Inc., Ann Arbor, Michigan