PART U
ECHINODERMATA 3
ASTEROZOA—ECHINOZOA

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ECHINACEA

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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. *U*343), 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

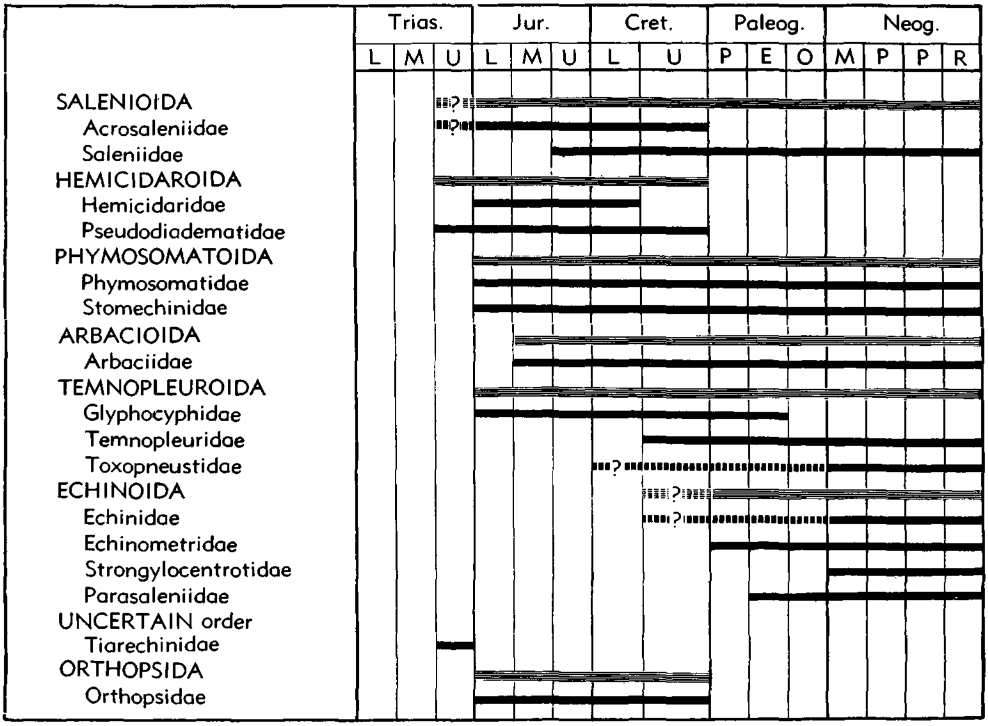

FIG. 272. Time ranges of families and orders of Echinacea and of Orthopsida (Echinacea or Diadematacea).

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,

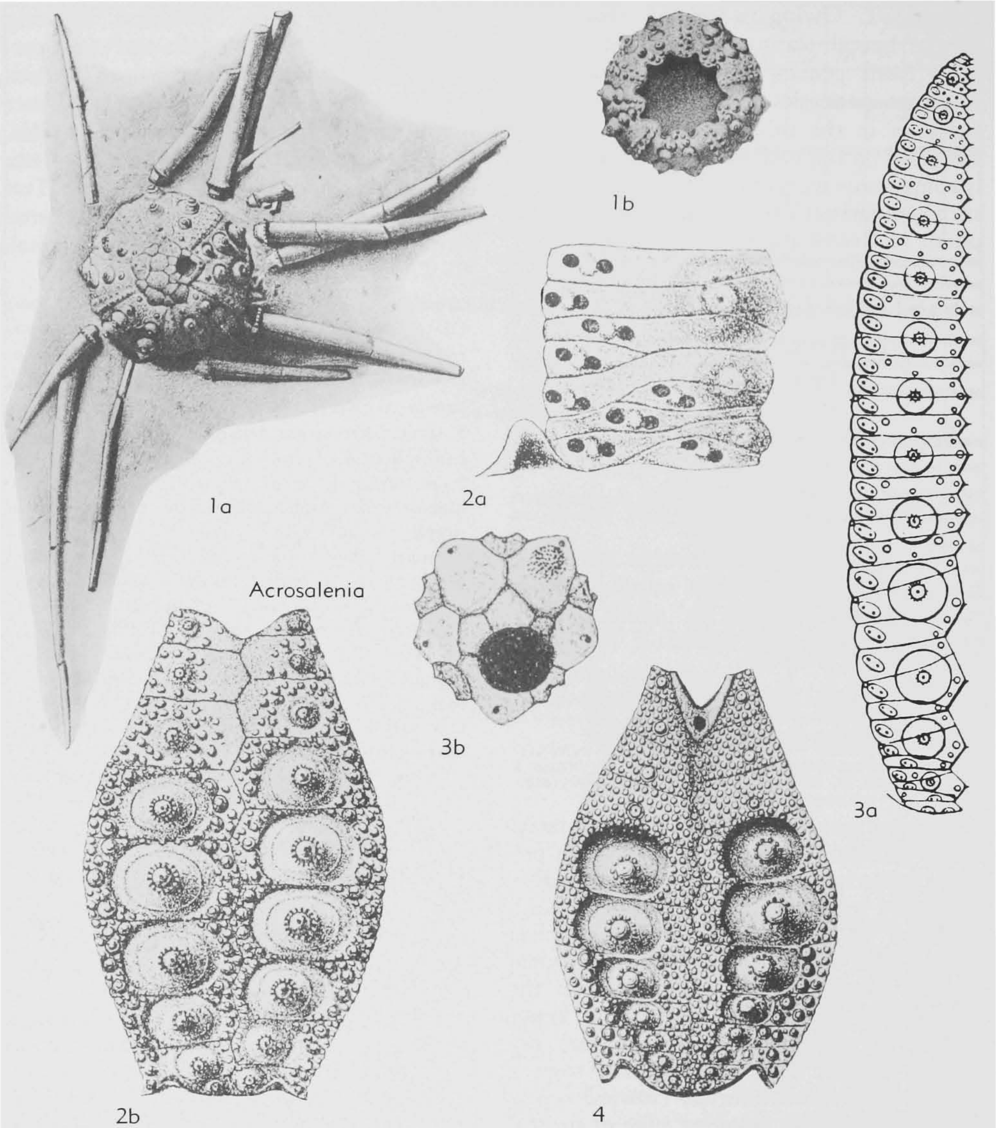

FIG. 273. Acrosaleniidae (p. U375).

*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.

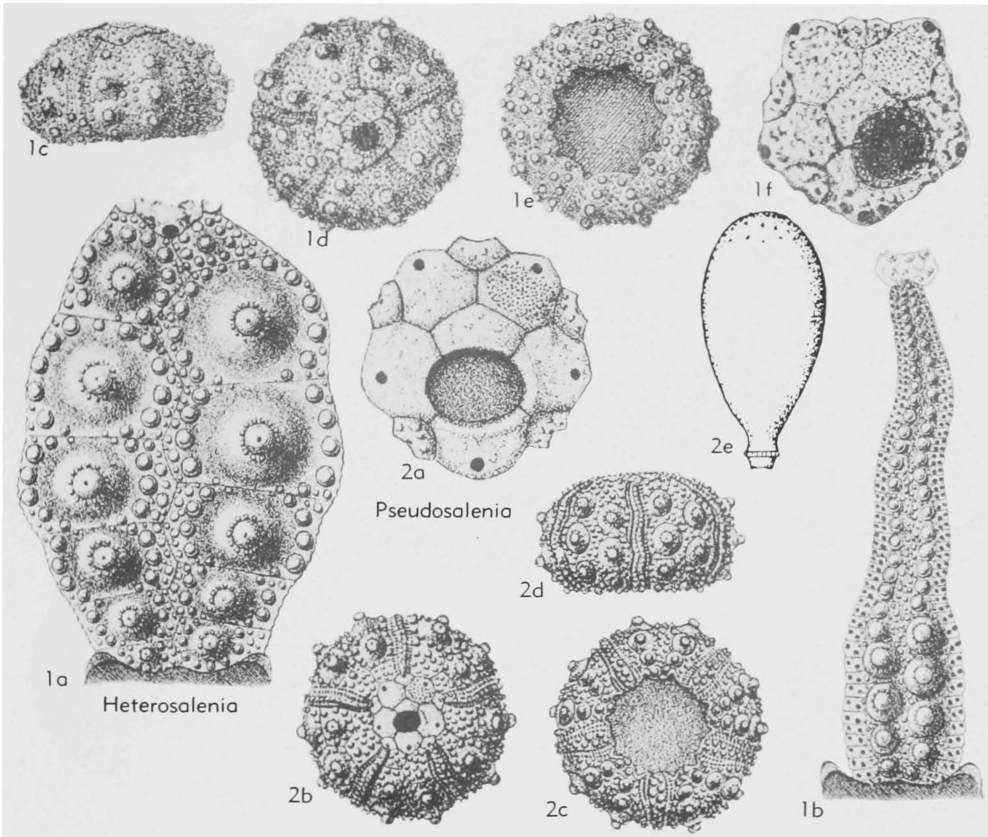

FIG. 274. Acrosaleniidae (p. *U375-U376*).

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-

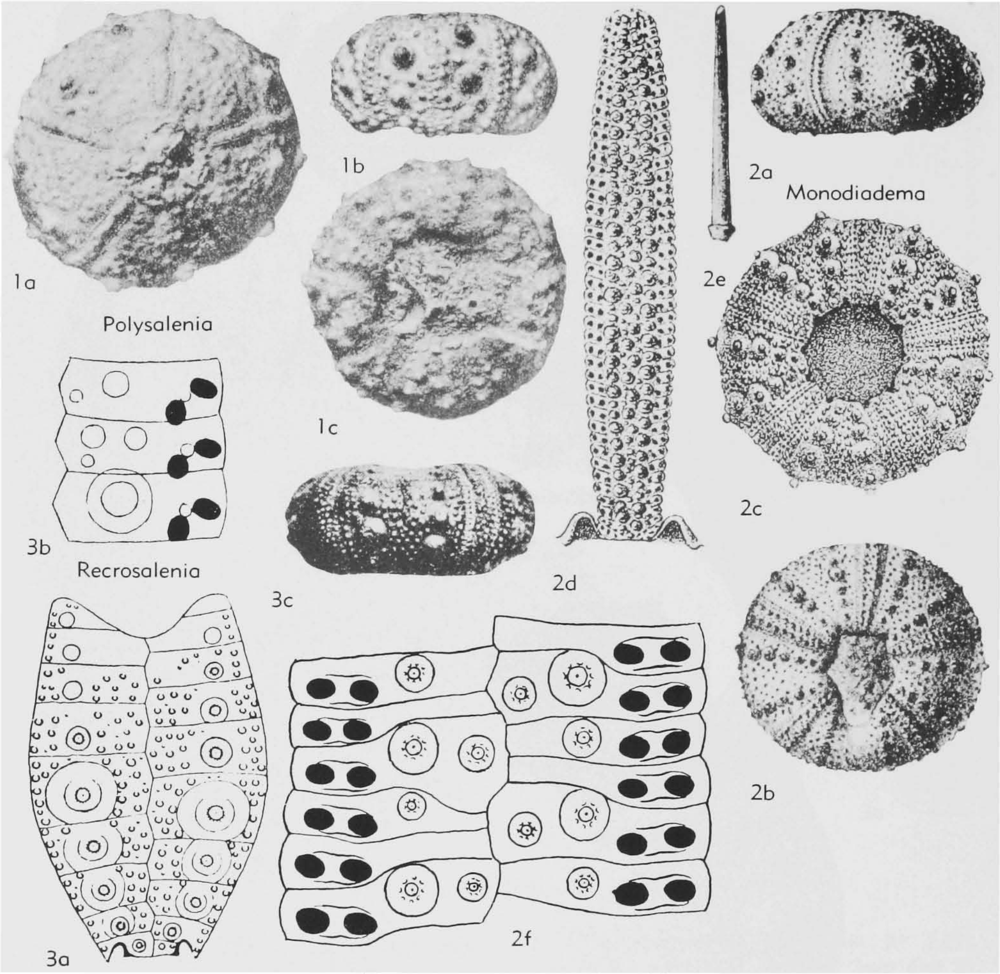

FIG. 275. Acrosaleniidae (p. U375-U377).

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).——

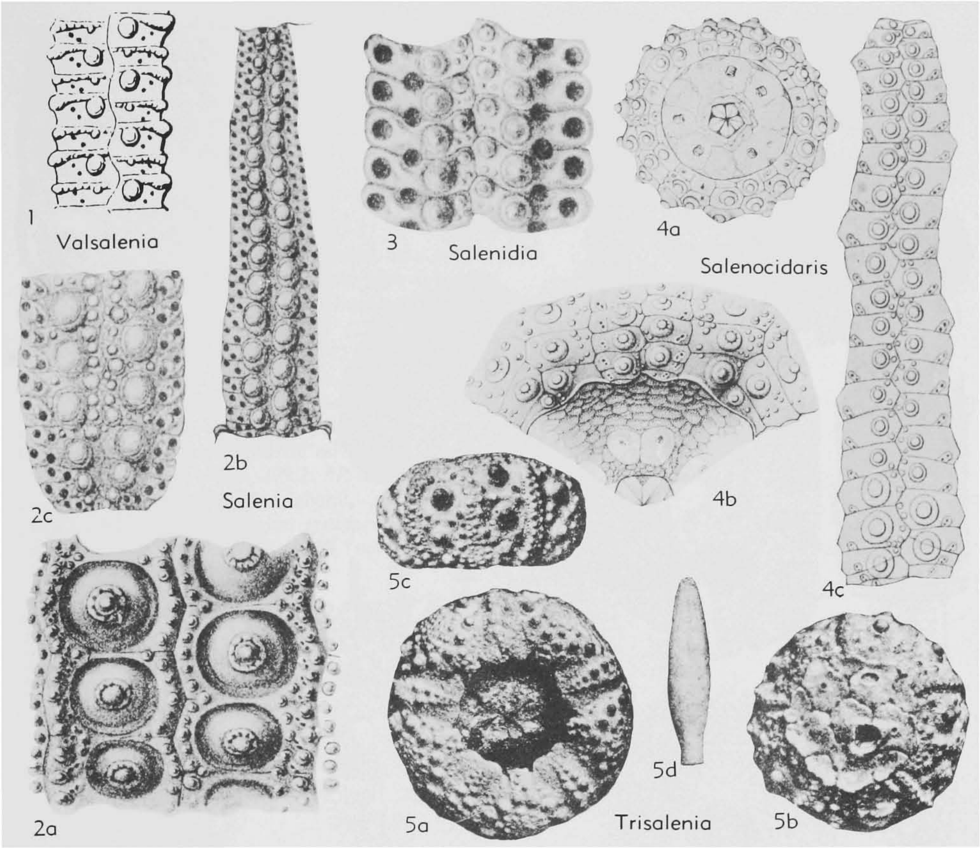

FIG. 276. Saleniidae (Saleniinae) (p. *U377-U379*).

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*;

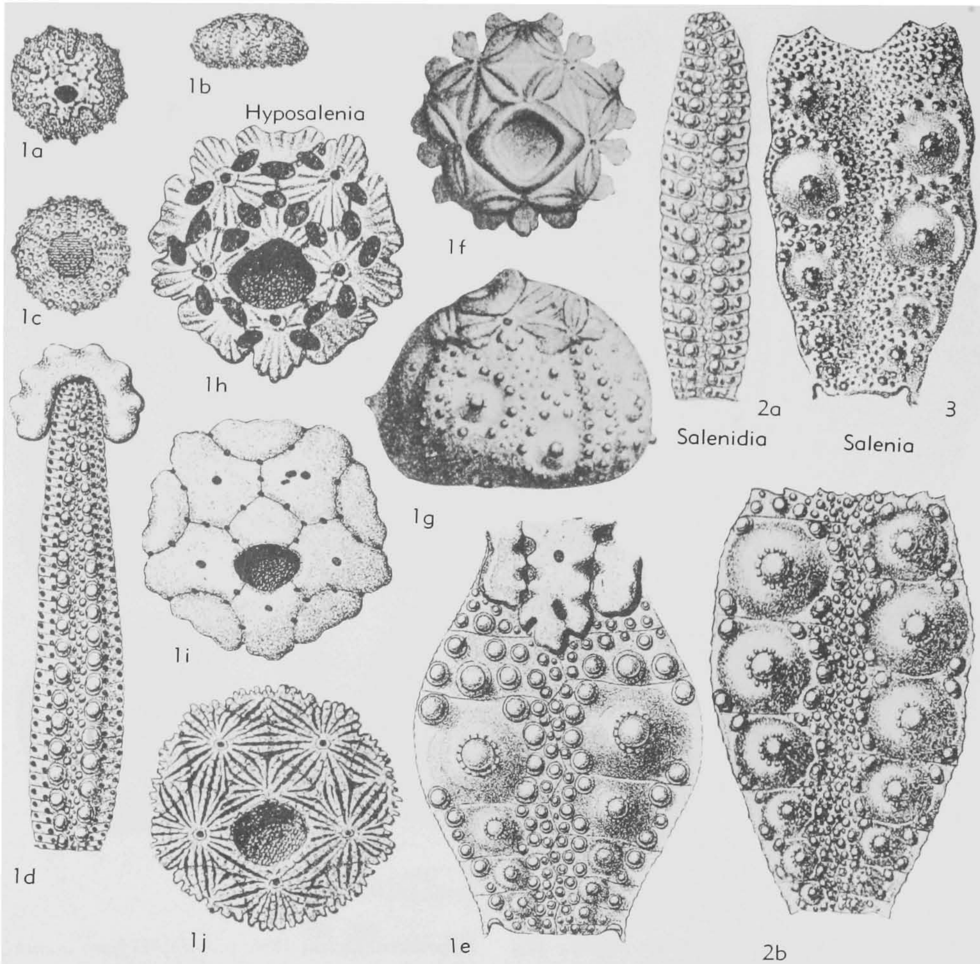

FIG. 277. Saleniidae (Saleniinae) *(2-3)*, (Hyposaleniinae) *(1)* (p. *U*377-*U*379).

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, crenu-

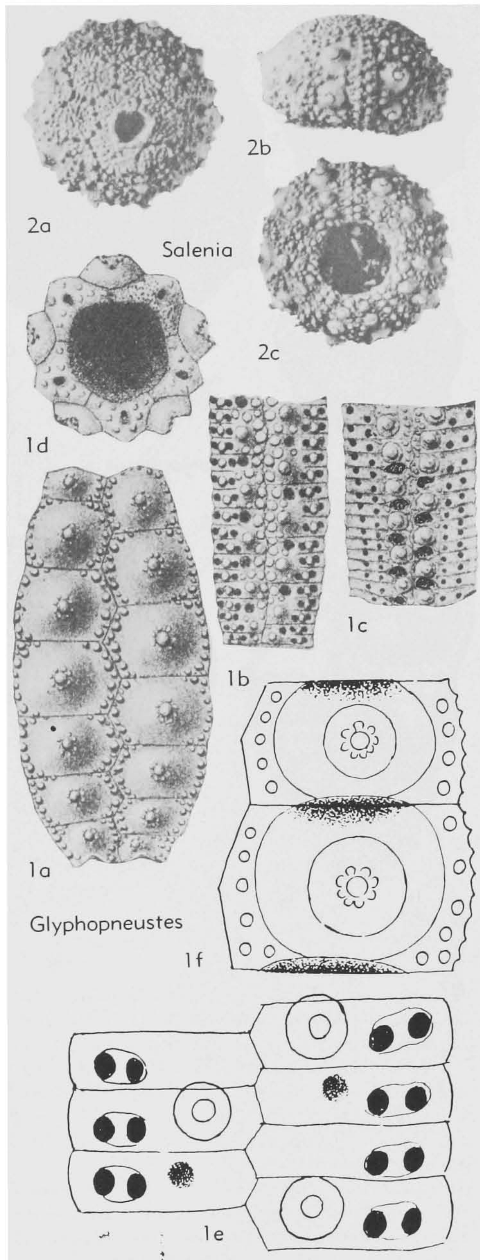

FIG. 278. Saleniidae (Saleniinae) *(2)*, (Hyposaleniinae) *(1)* (p. *U377-U378*, *U380*).

late; 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*.

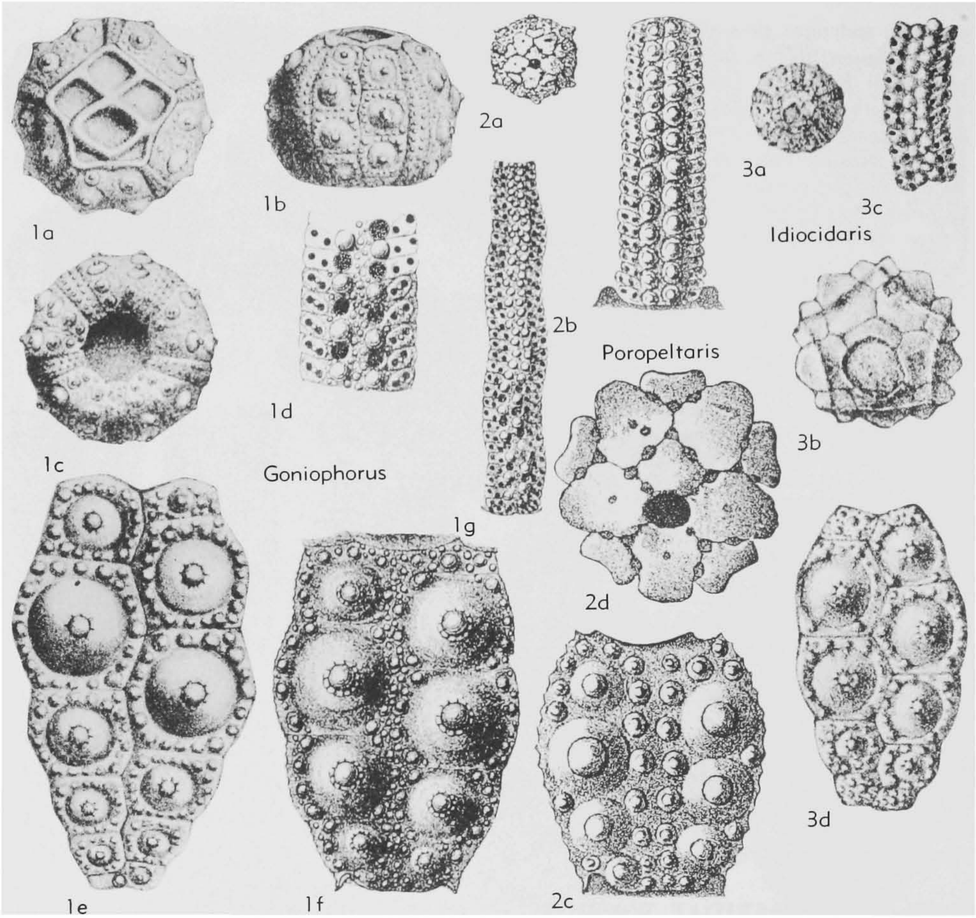

FIG. 279. Saleniidae (Hyposaleniinae) (p. U379-U381).

**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

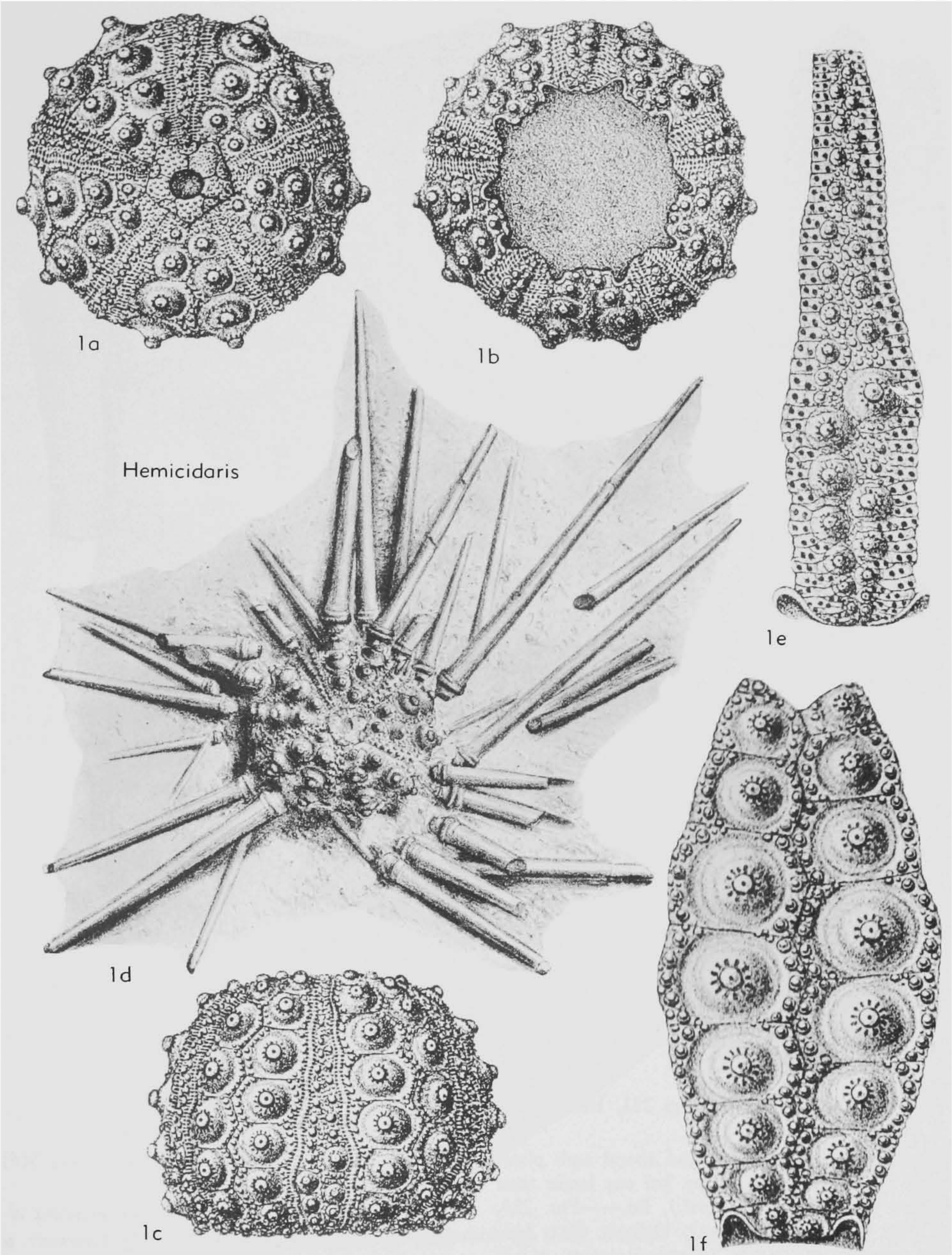

FIG. 280. Hemicidaridae (p. U381-U382).

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

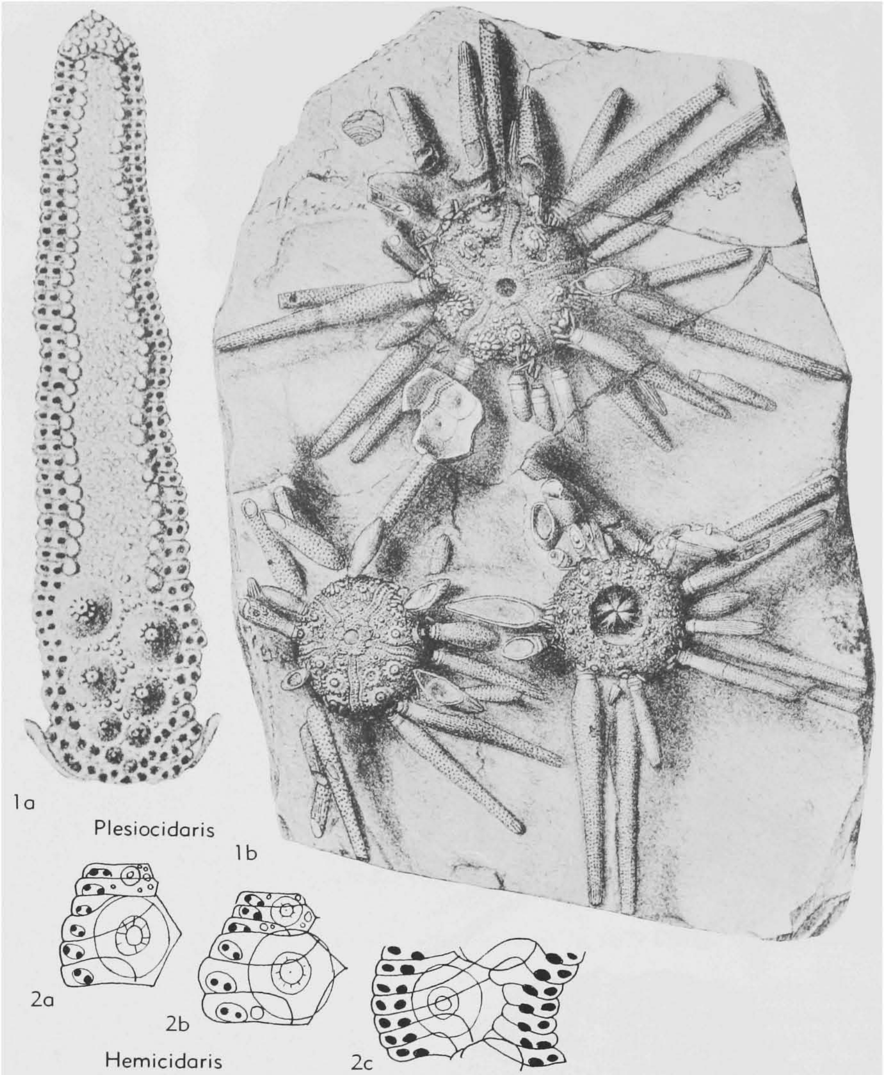

FIG. 281. Hemicidaridae (p. U381-U382, U384).

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).

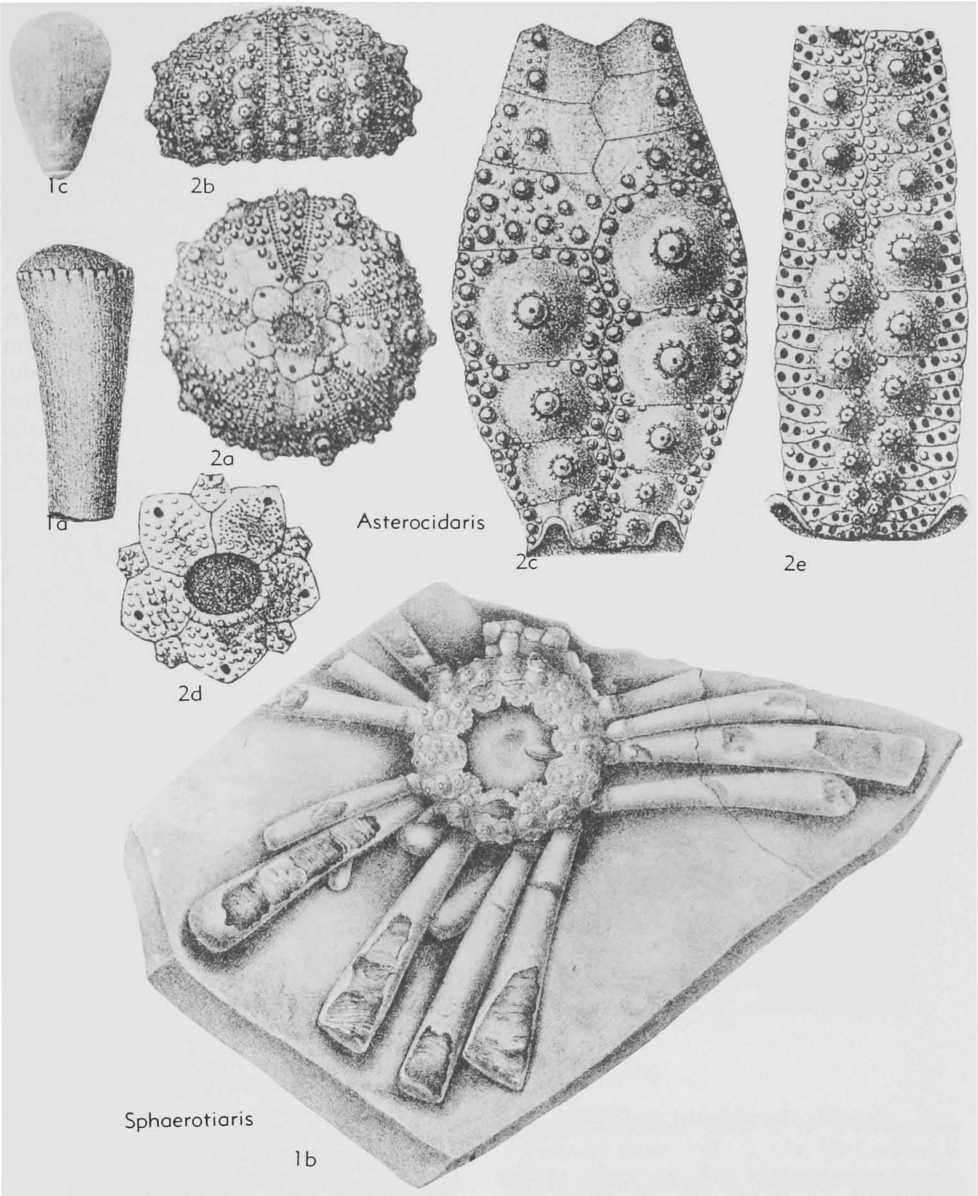

FIG. 282. Hemicidaridae (p. U382, U386).

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).

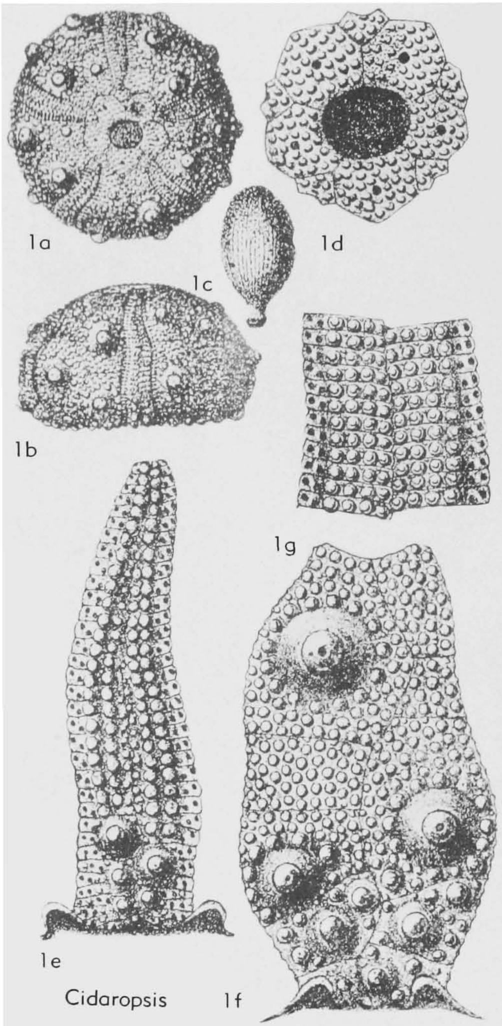

FIG. 283. Hemicidaridae (p. U382).

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

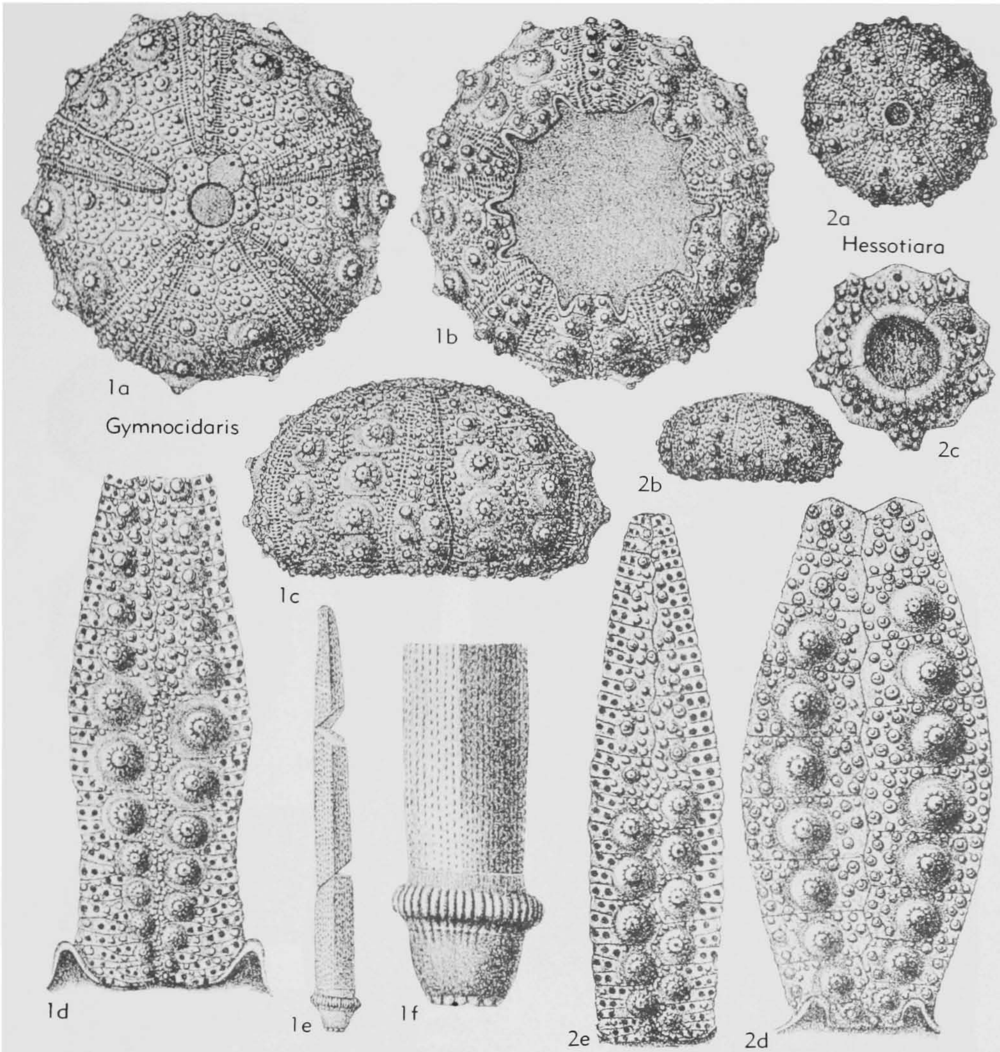

FIG. 284. Hemicidaridae (p. *U*382-*U*384).

(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-

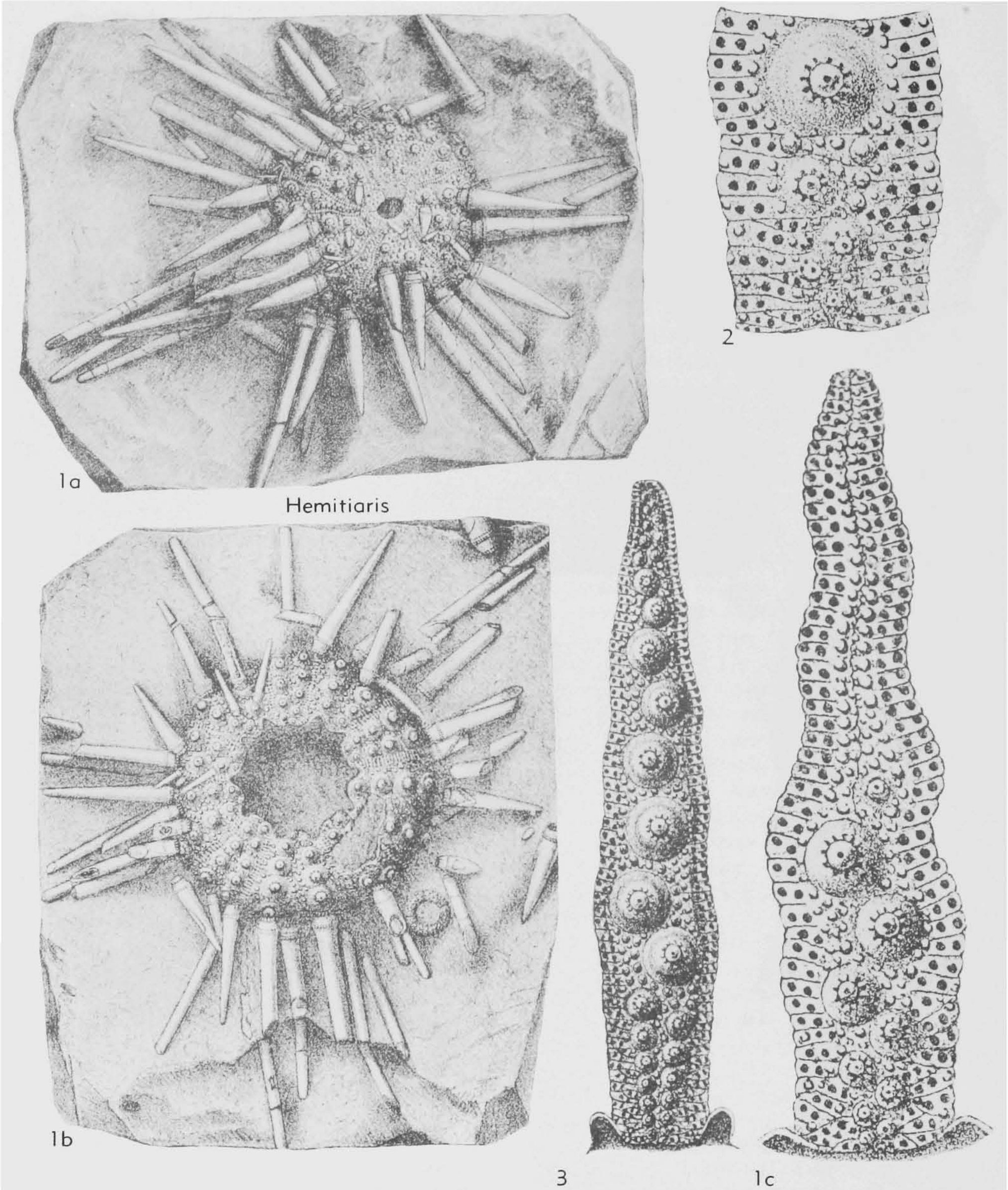

FIG. 285. Hemicidaridae (p. U382-U383).

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

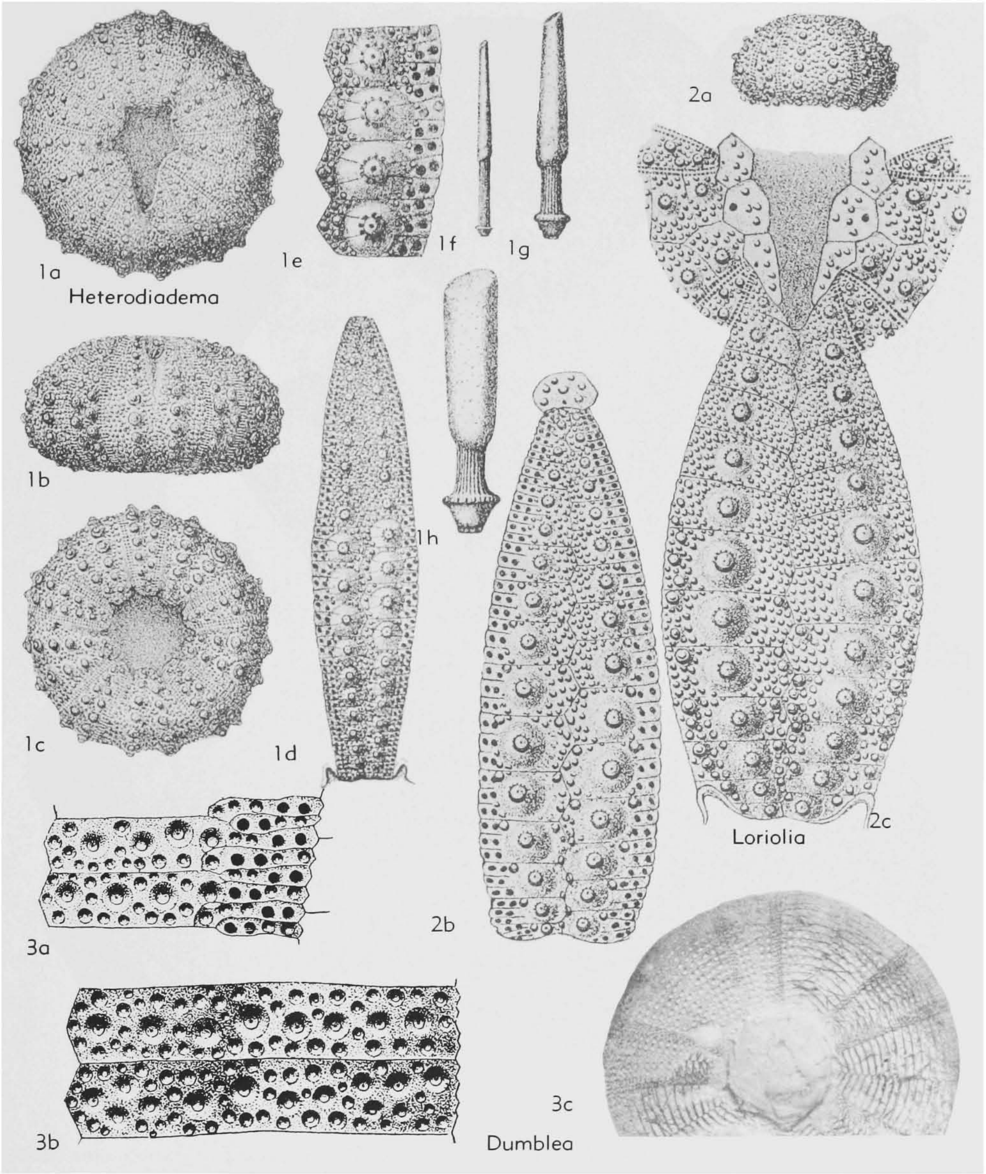

FIG. 286. Hemicidaridae *(1)*; Pseudodiadematidae *(2-3)* (p. *U*384, *U*387-*U*388).

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.*

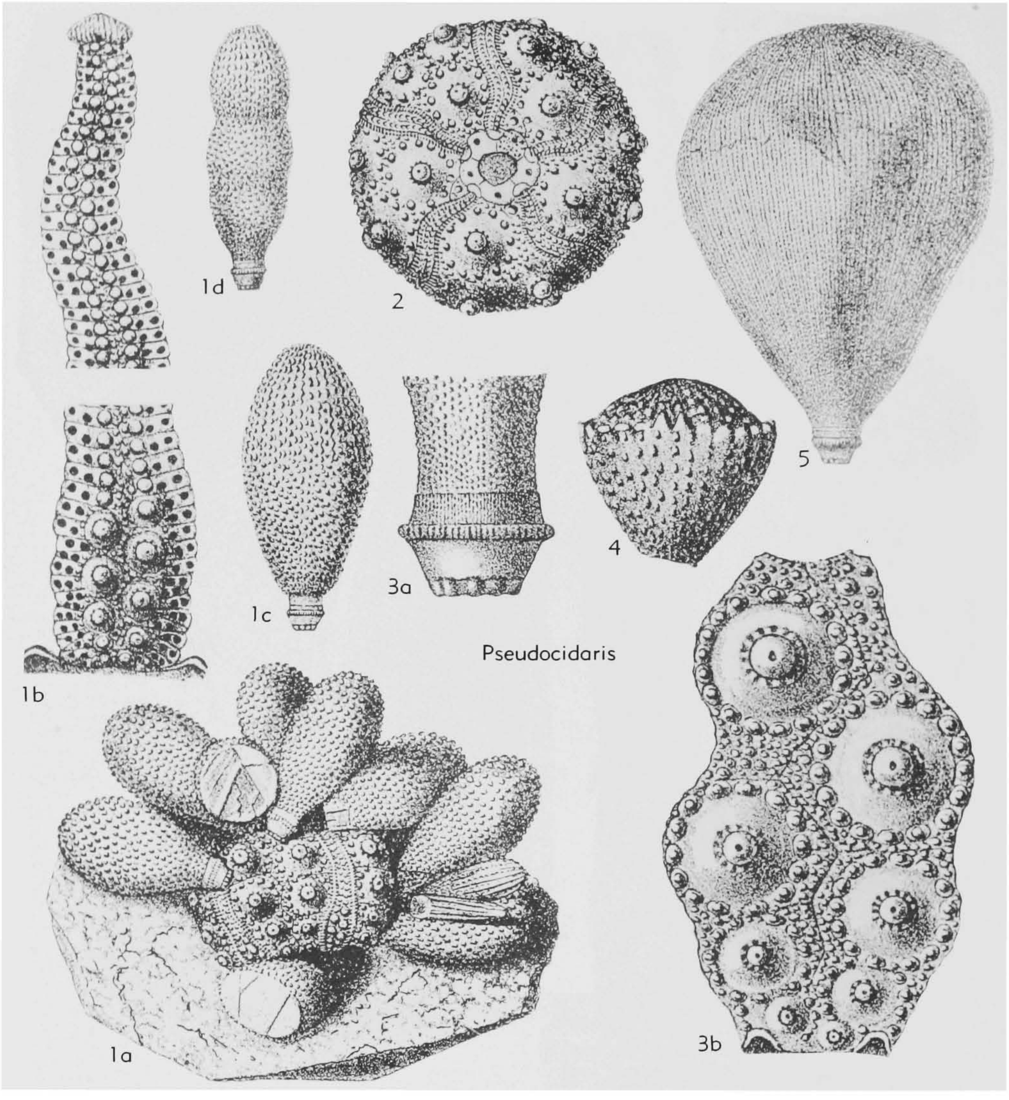

FIG. 287. Hemicidaridae (p. U385).

(*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.;

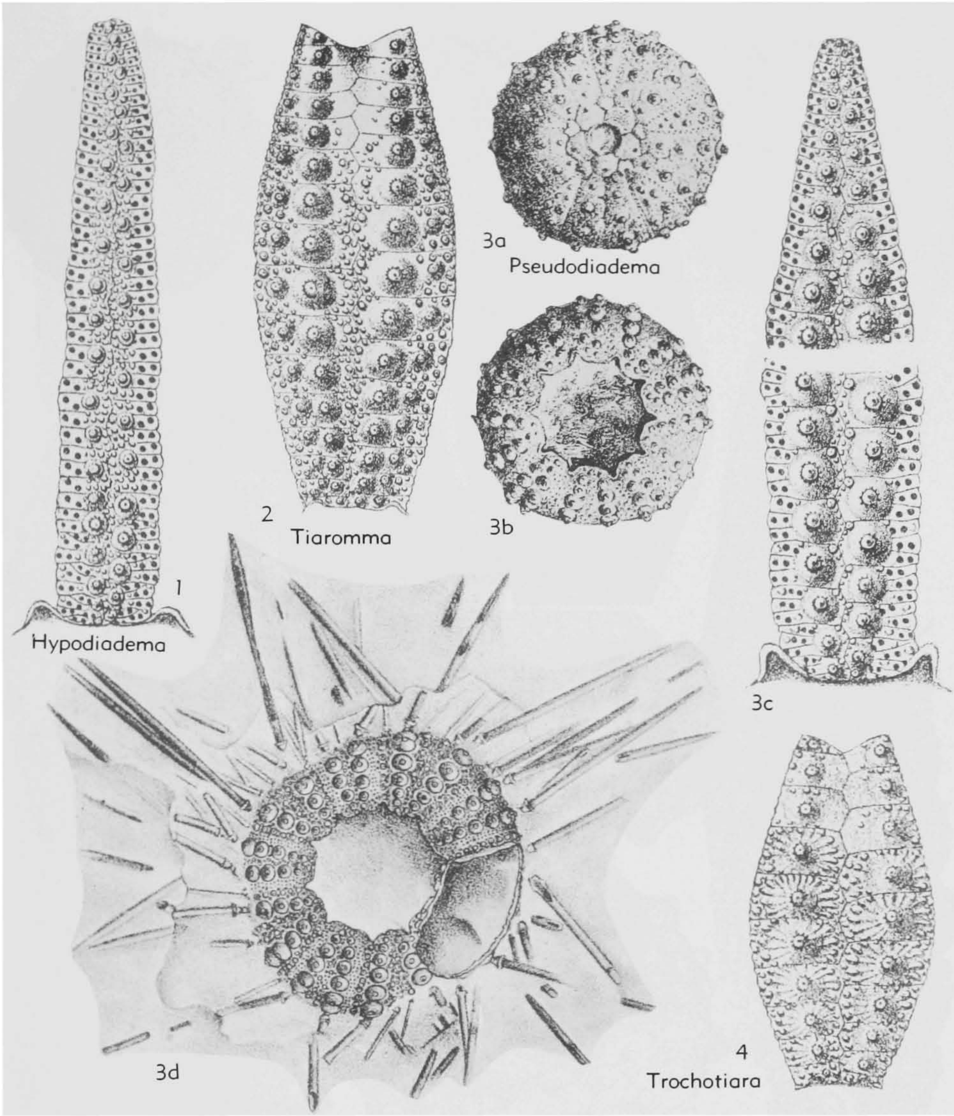

FIG. 288. Pseudodiadematidae (p. *U386-U387, U391*).

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).

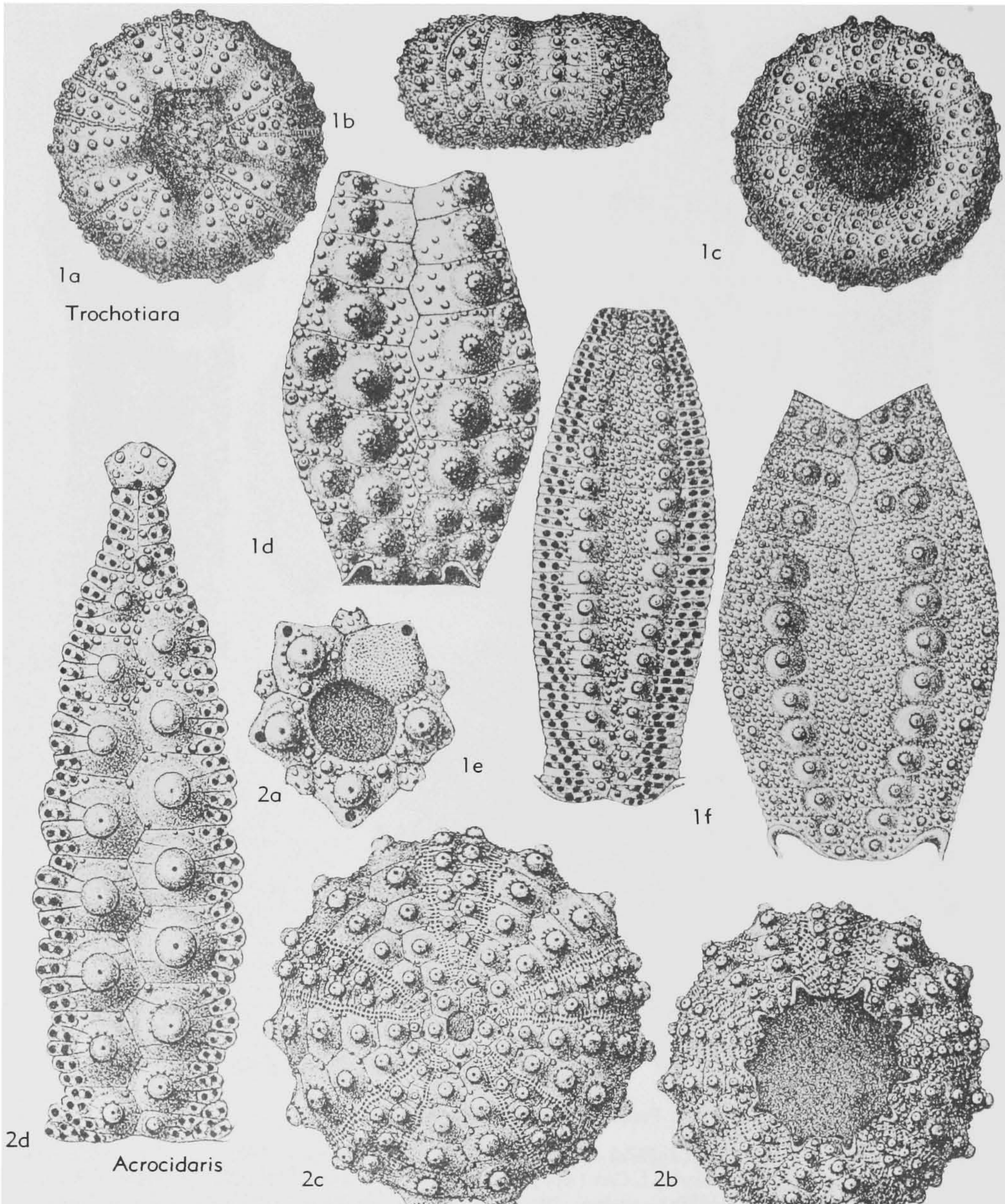

FIG. 289. Pseudodiadematidae (p. U386, U391).

——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,

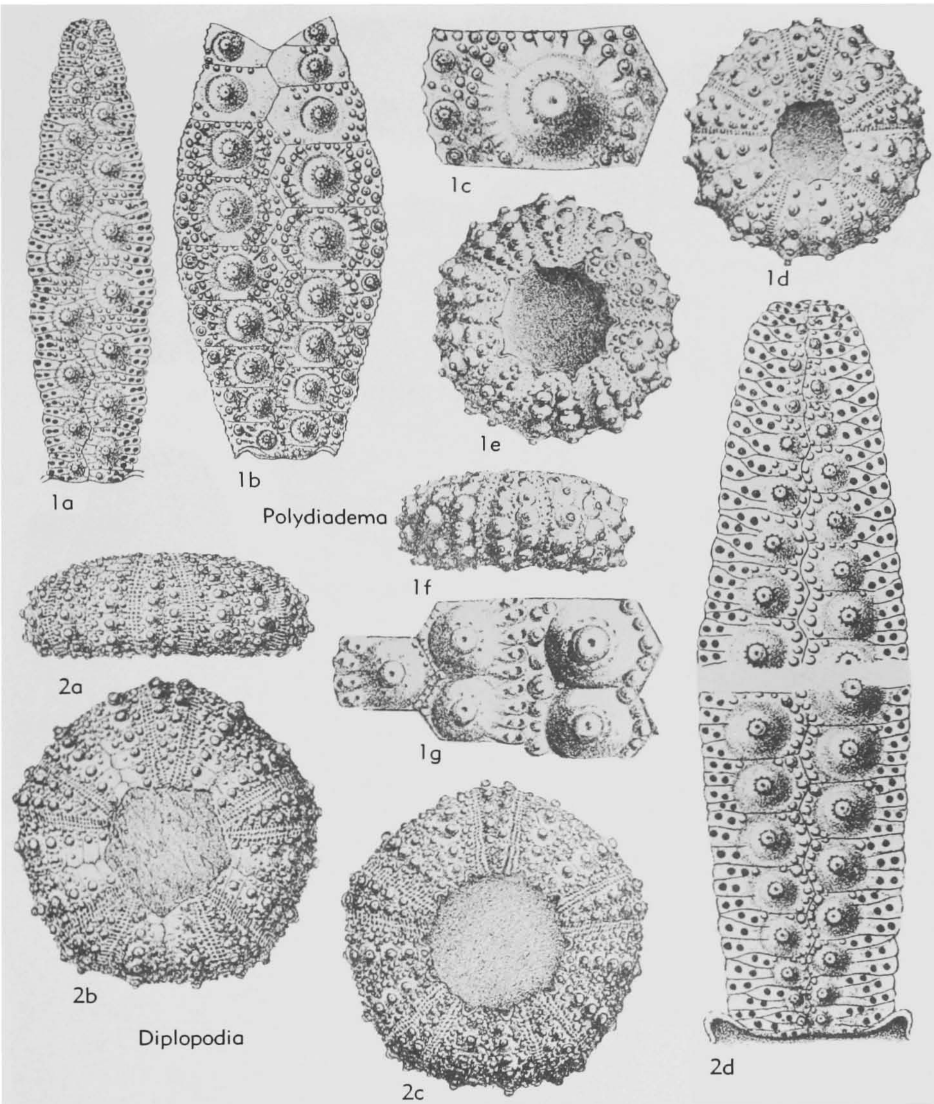

FIG. 290. Pseudodiadematidae (p. *U386-U387*, *U389-U390*).

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,*

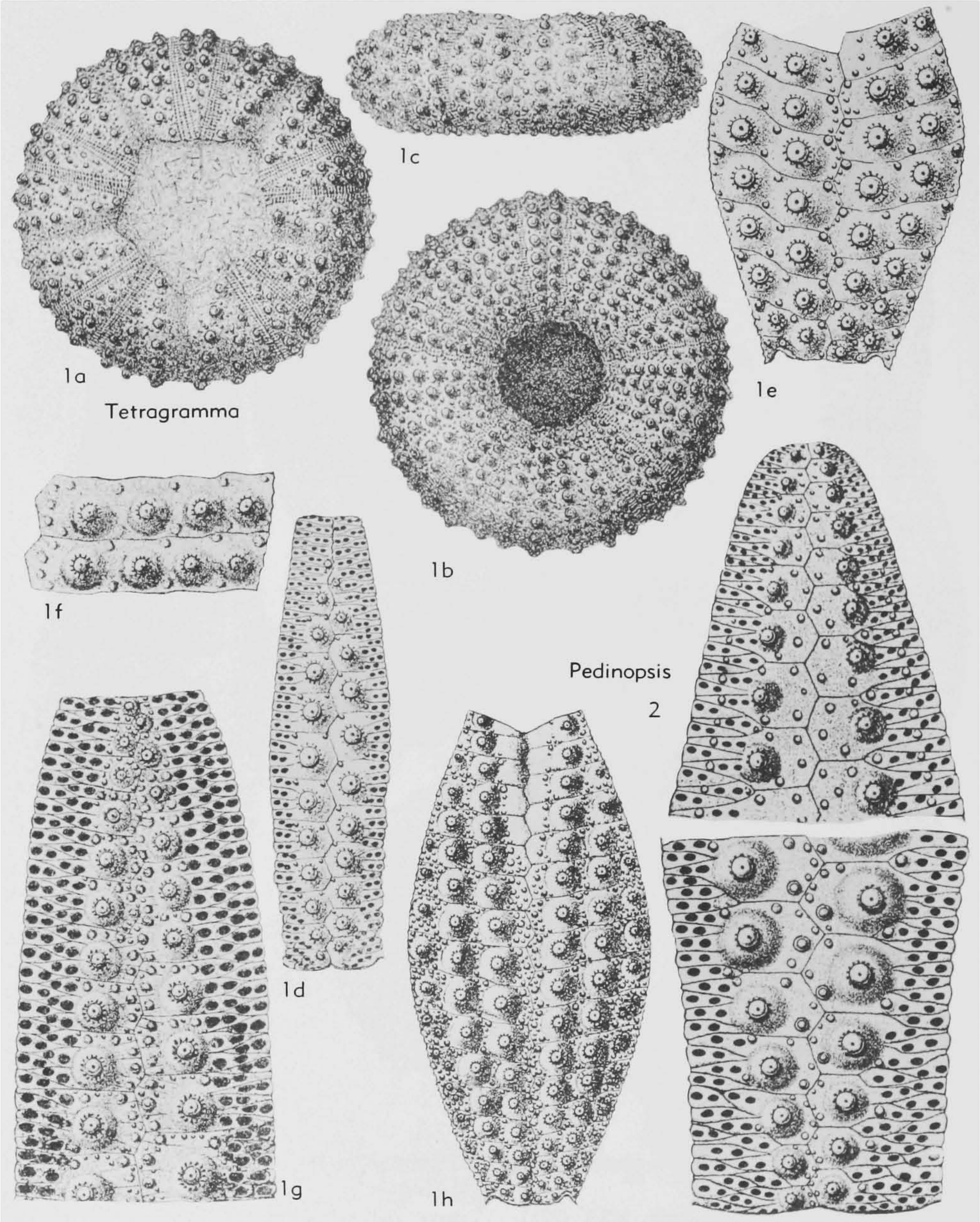

FIG. 291. Pseudodiadematidae (p. U388-U391).

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.*

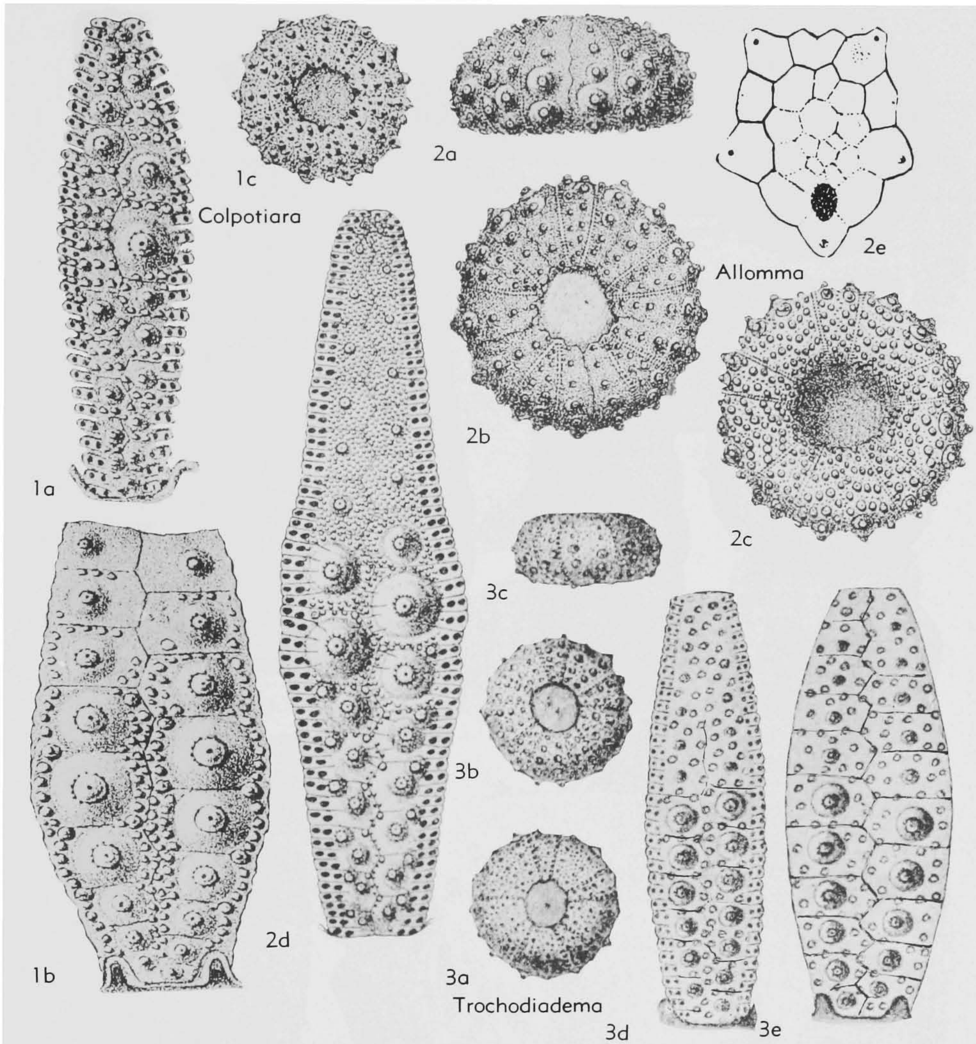

FIG. 292. Family Uncertain (p. U392-U393).

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,

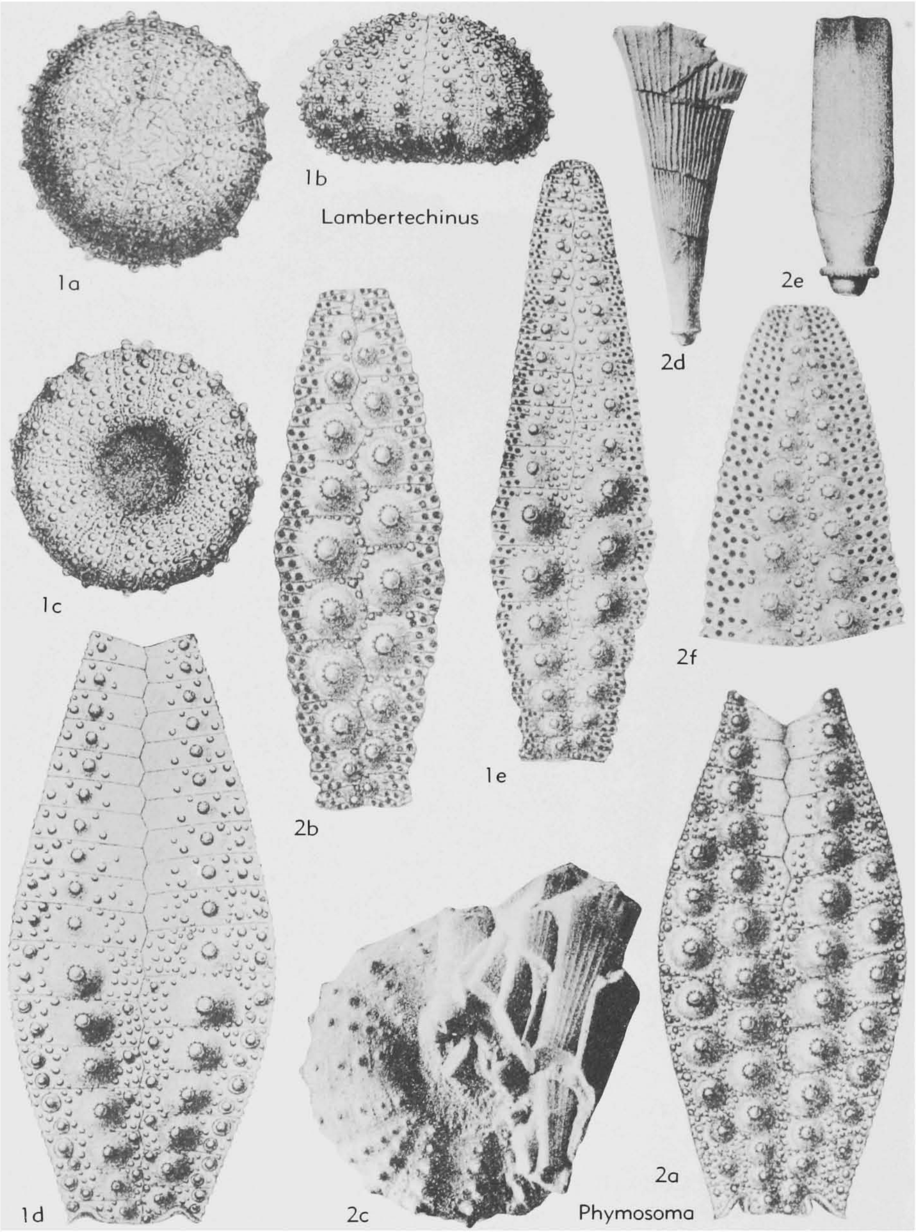

FIG. 293. Phymosomatidae (p. U395-U396, U400).

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.]

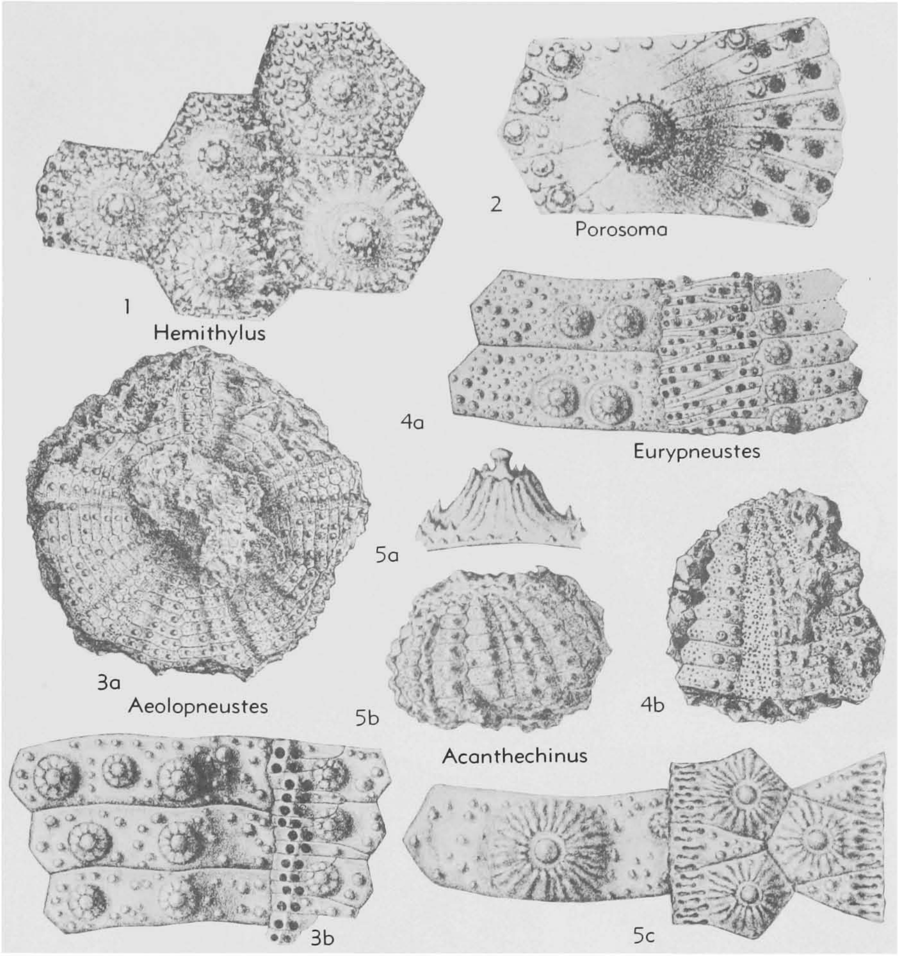

FIG. 294. Phymosomatidae (p. *U*397-*U*400, *U*402).

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.*,

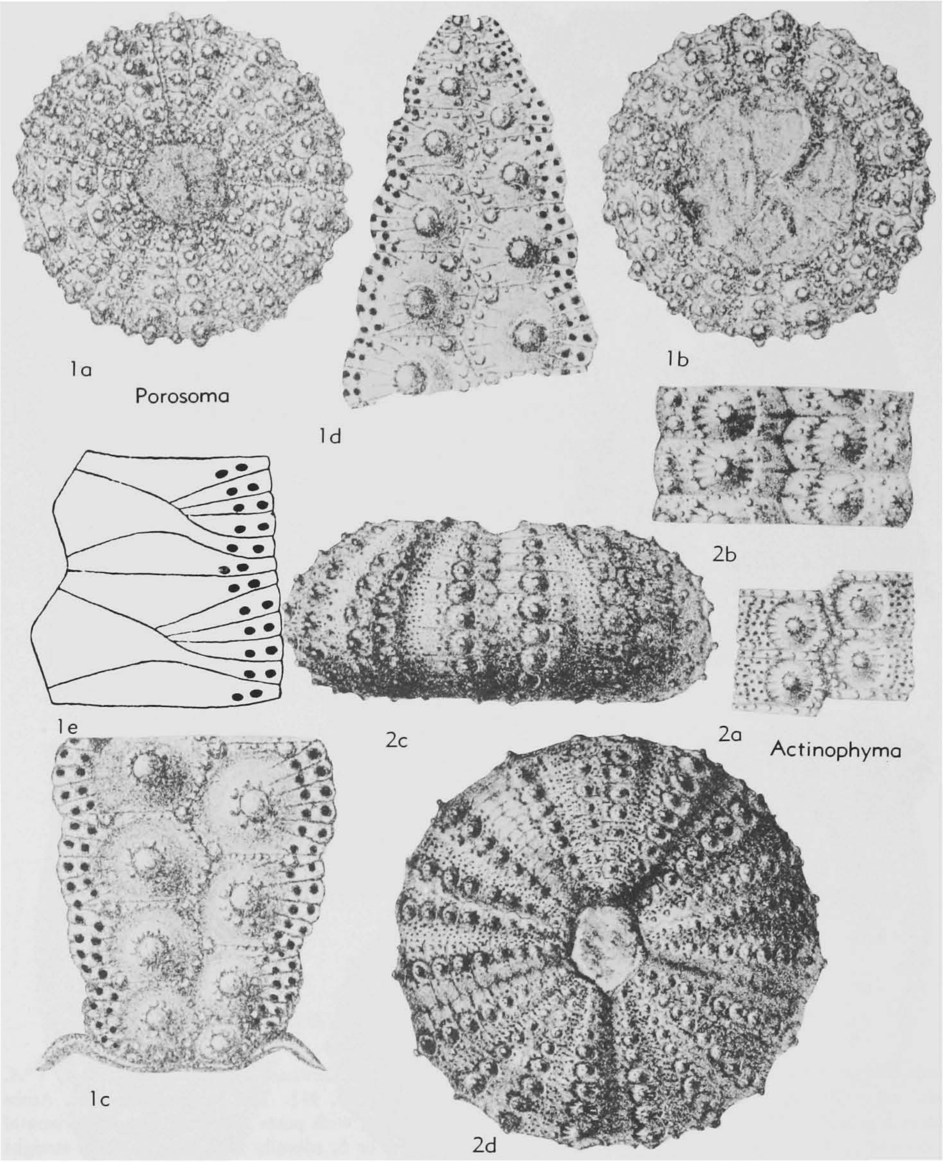

FIG. 295. Phymosomatidae (p. U397, U402).

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,

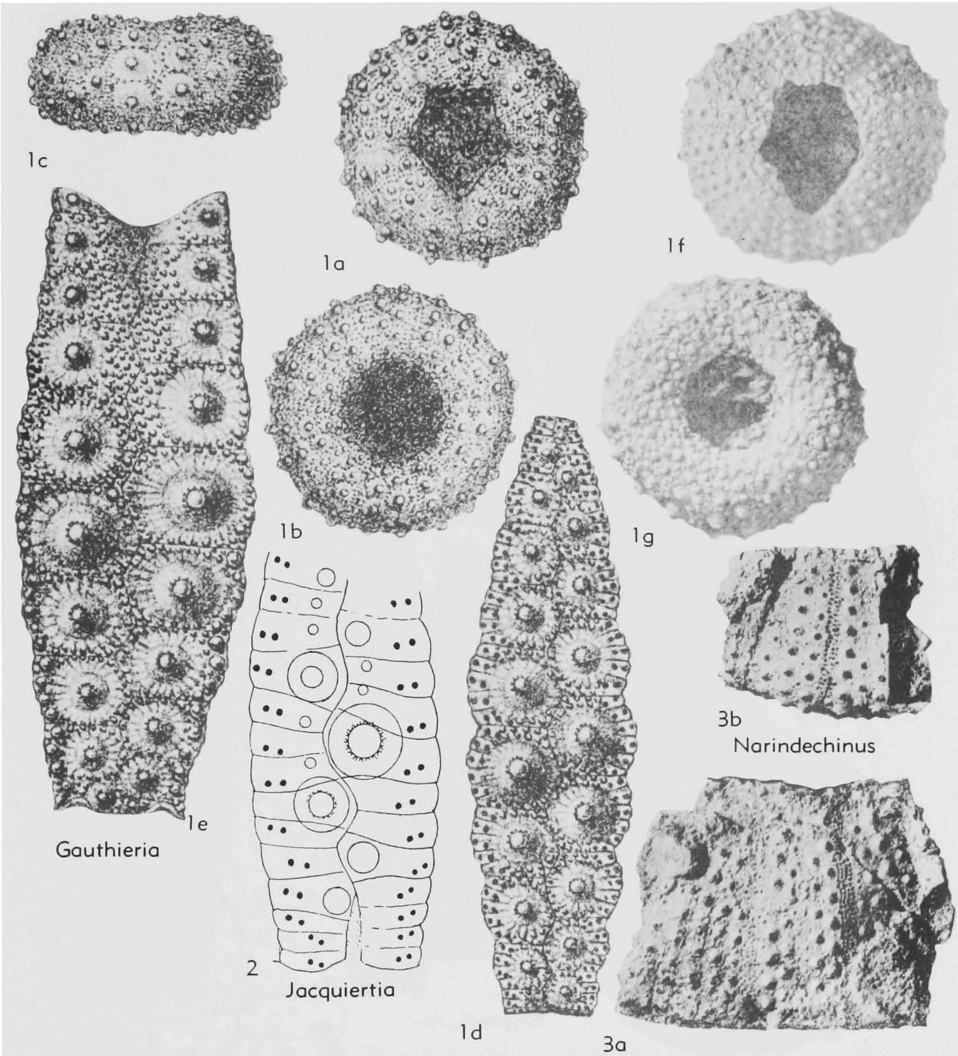

FIG. 296. Phymosomatidae (p. *U*398, *U*400-*U*401).

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-

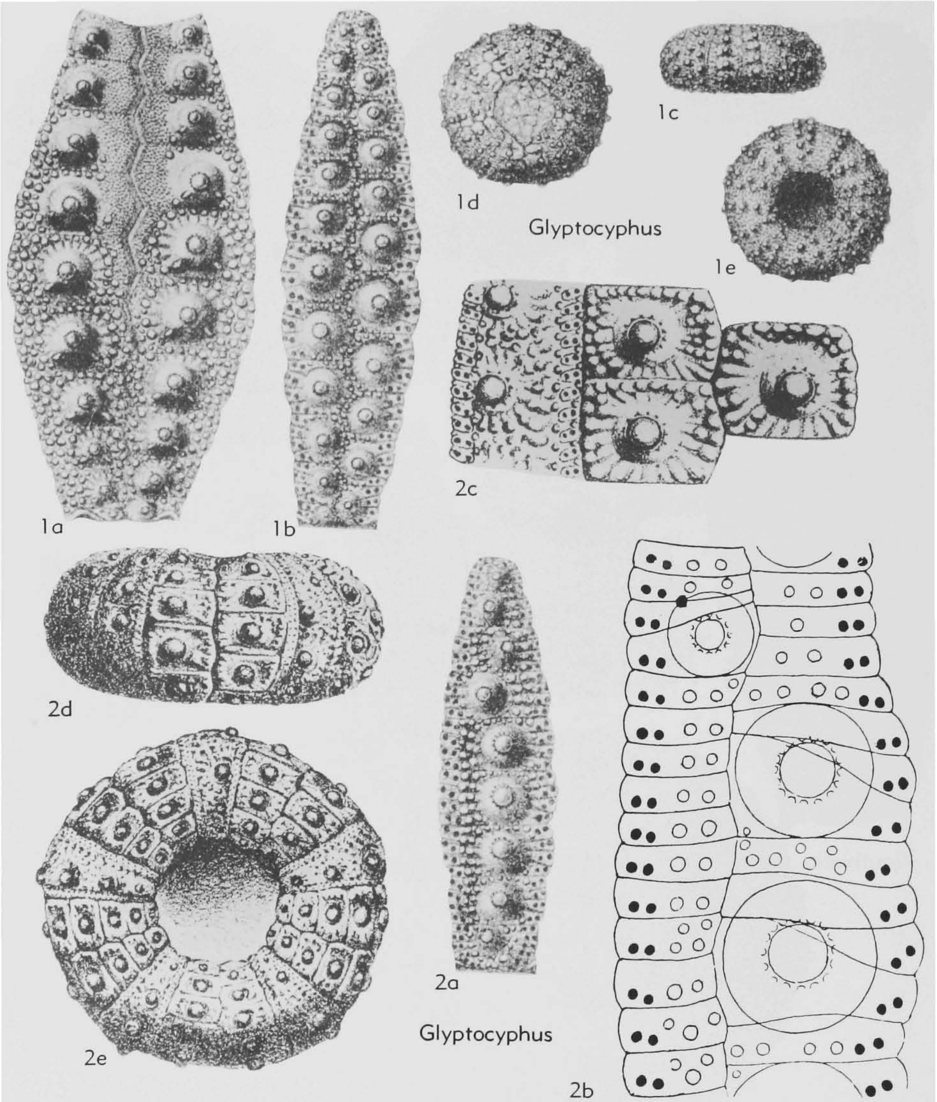

FIG. 297. Phymosomatidae (p. U399).

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-*

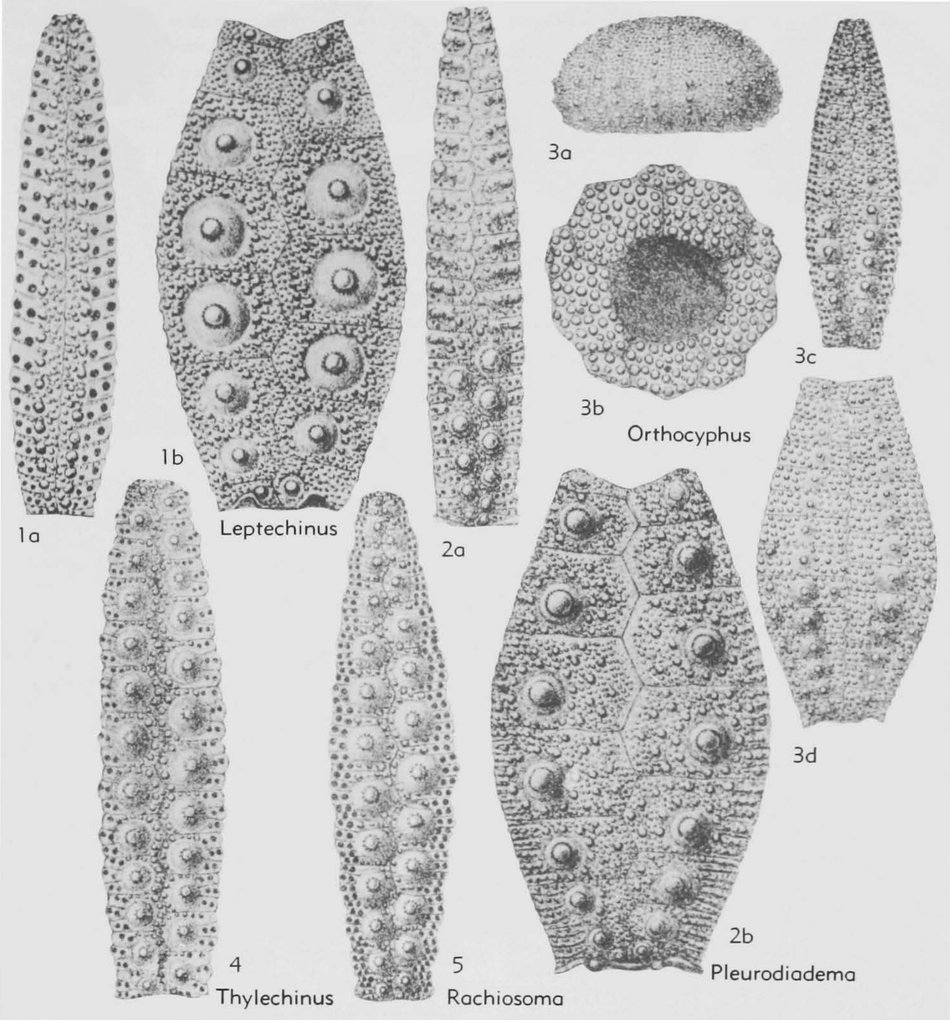

FIG. 298. Phymosomatidae (p. *U*400-*U*403).

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

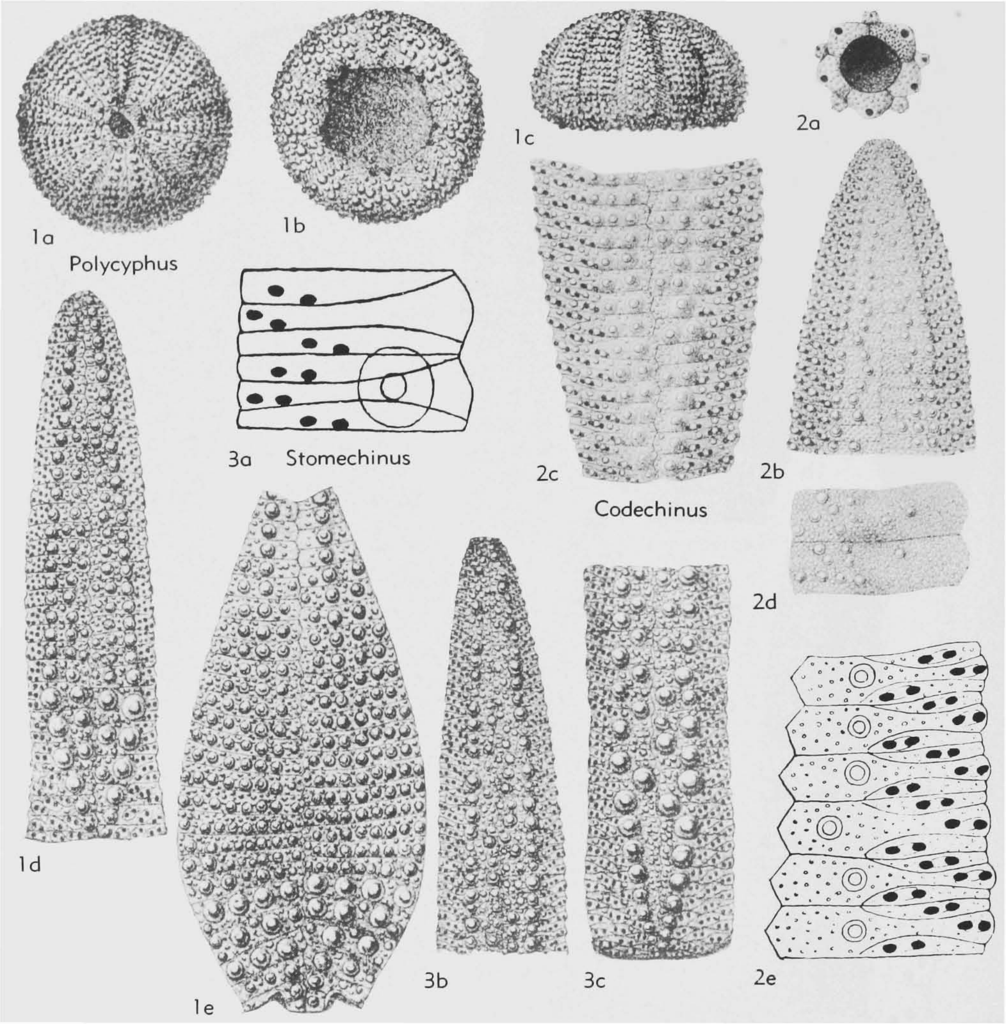

FIG. 299. Stomechinidae (p. U403, U406).

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),

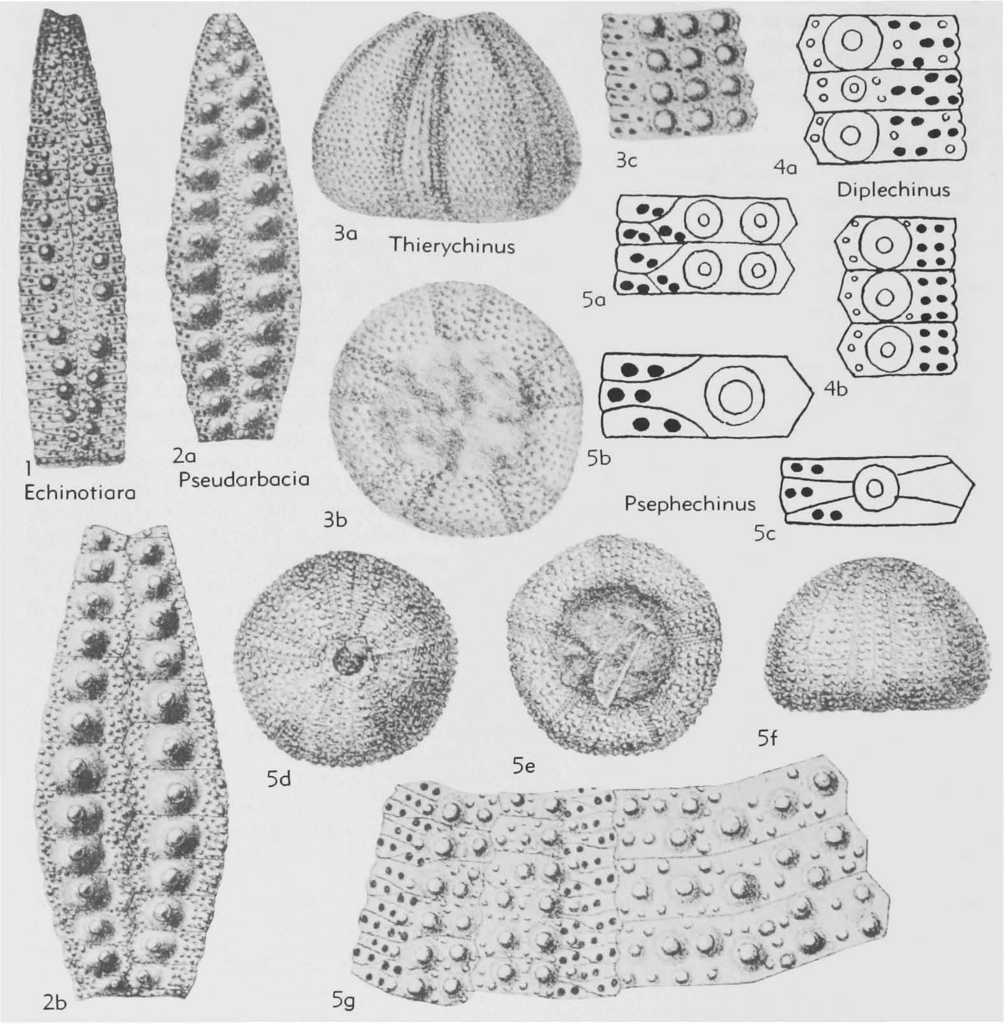

FIG. 300. Stomechinidae (p. U403-U404, U406-U407).

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,

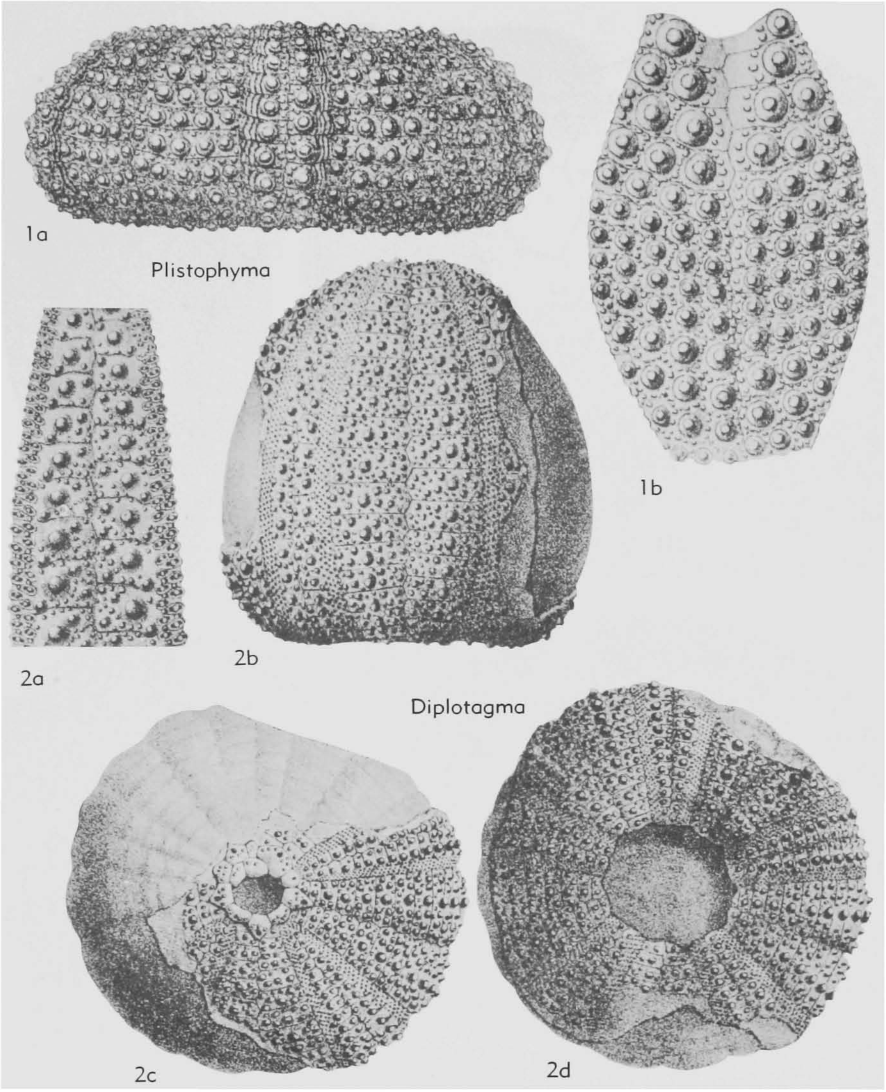

FIG. 301. Stomechinidae (p. *U*403, *U*408).

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.*-

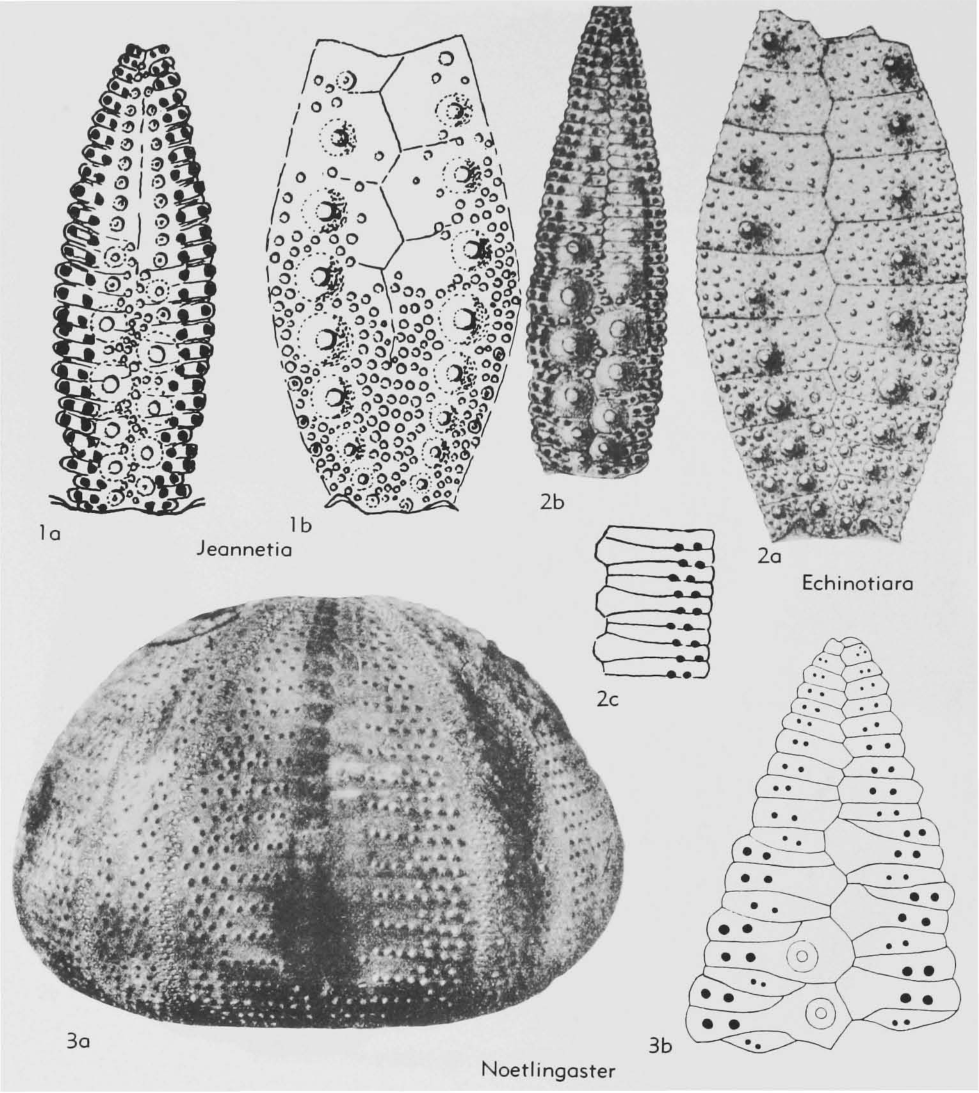

FIG. 302. Stomechinidae (p. U403-U405).

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-

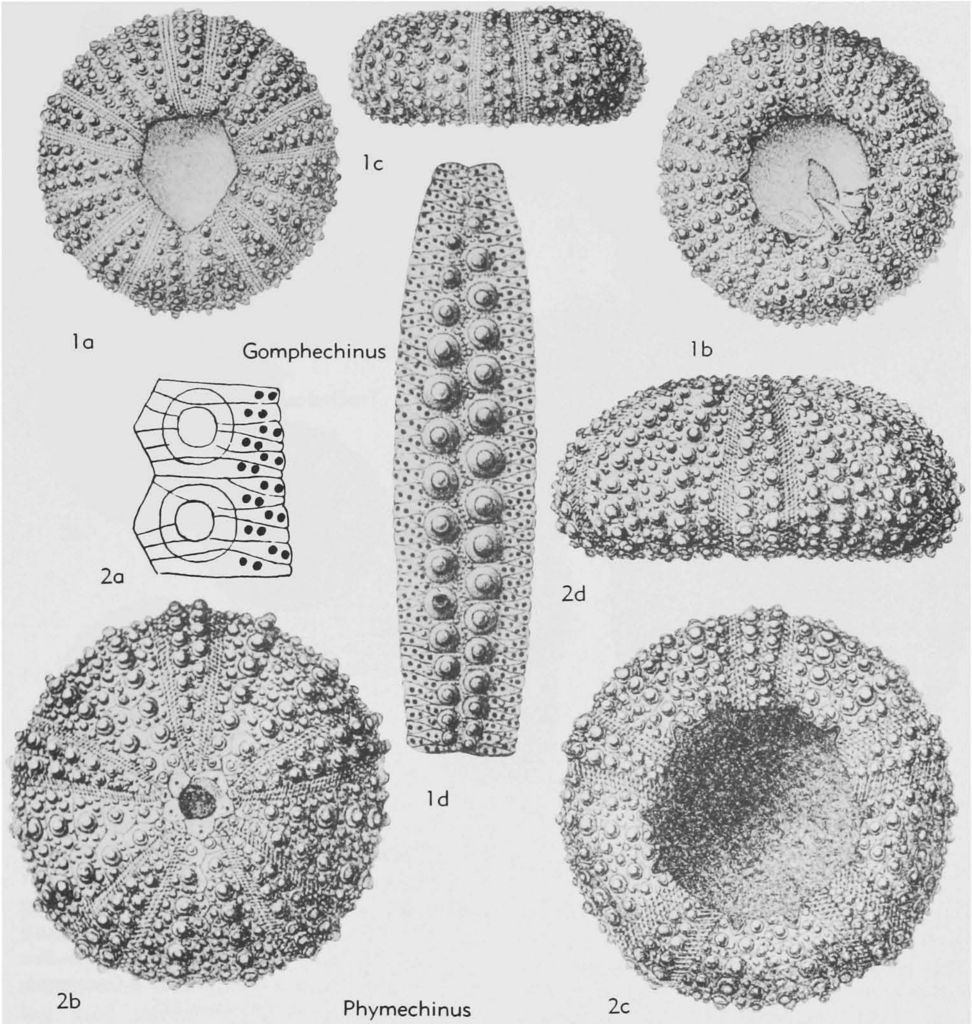

FIG. 303. Stomechinidae (p. U404-U405).

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.

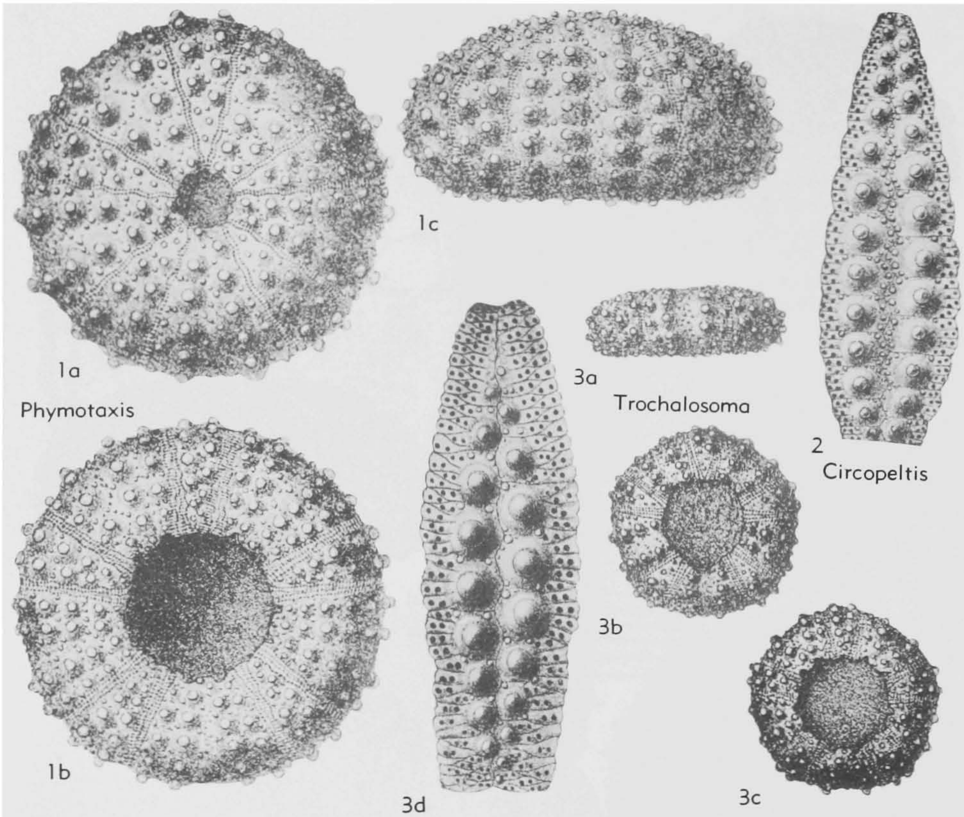

FIG. 304. Stomechinidae (p. U403, U405-U406, U408).

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

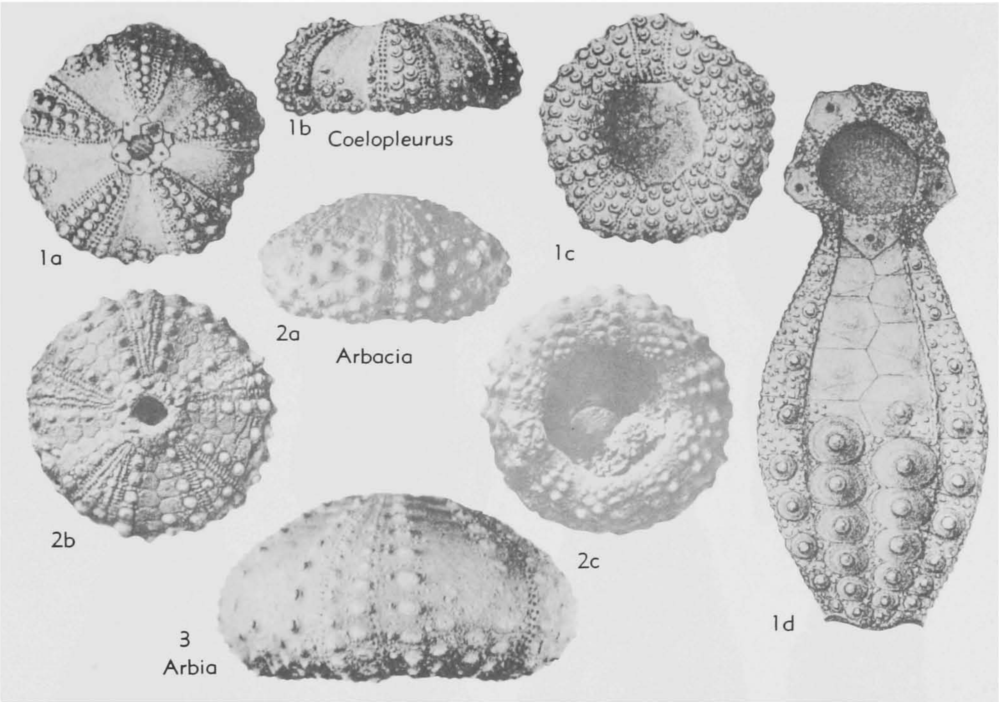

FIG. 305. Arbaciidae (p. *U*409-*U*410, *U*412).

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

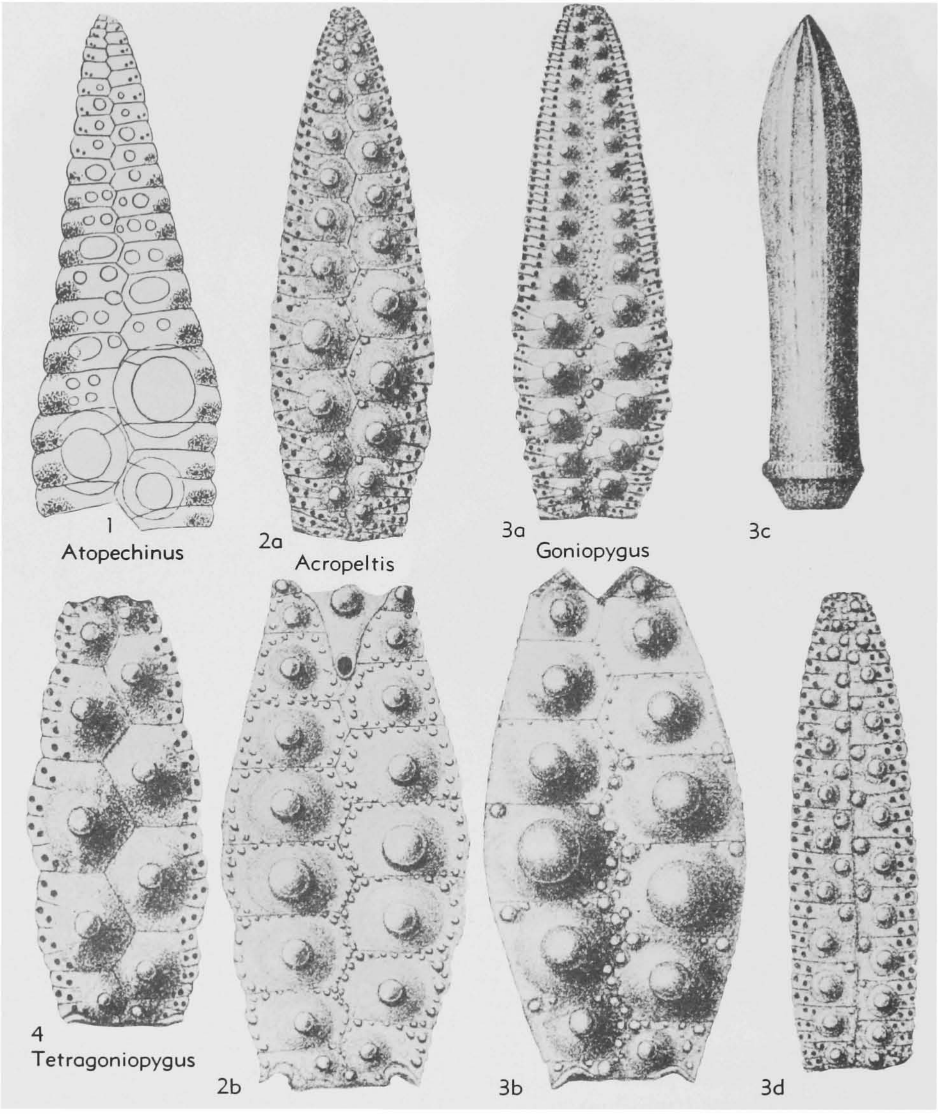

FIG. 306. Arbaciidae (p. U409-U412).

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.

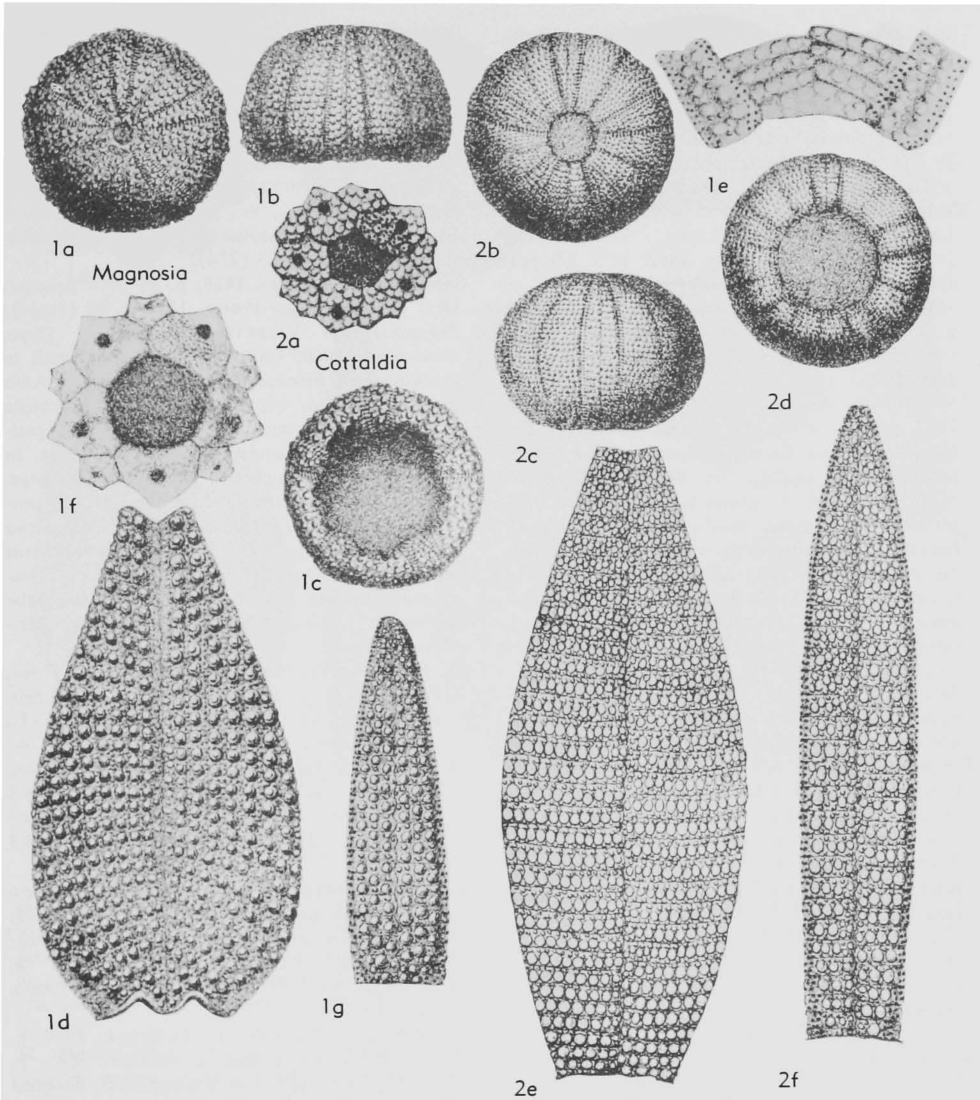

FIG. 307. Arbaciidae (p. *U*412-*U*413).

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

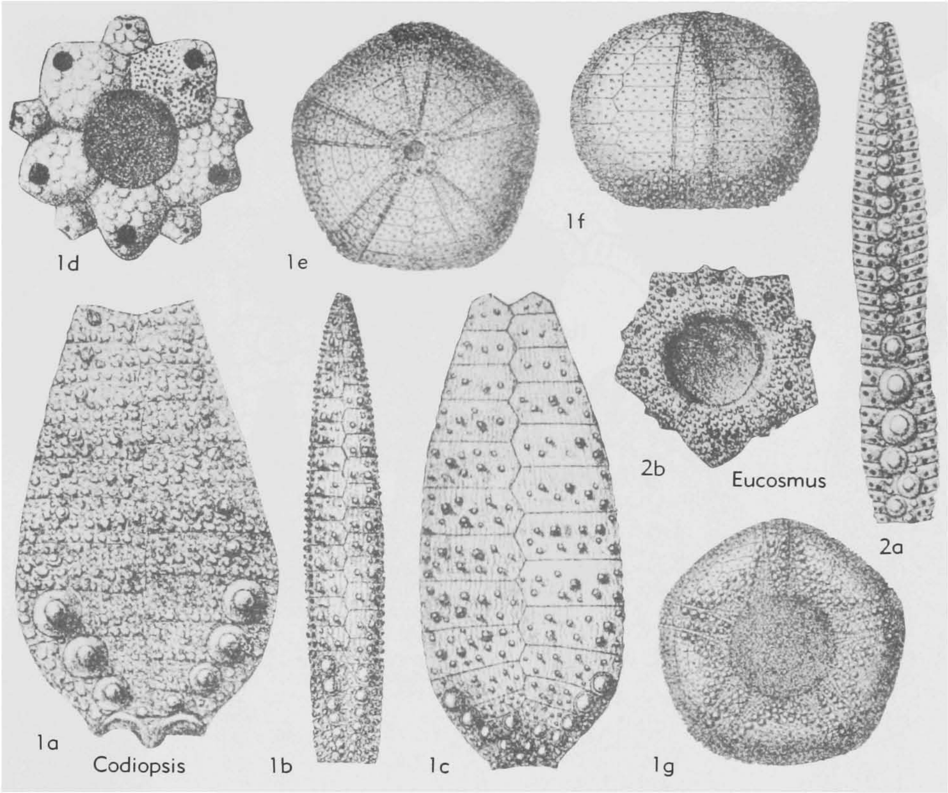

FIG. 308. Arbaciidae (p. *U*411-*U*413).

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*

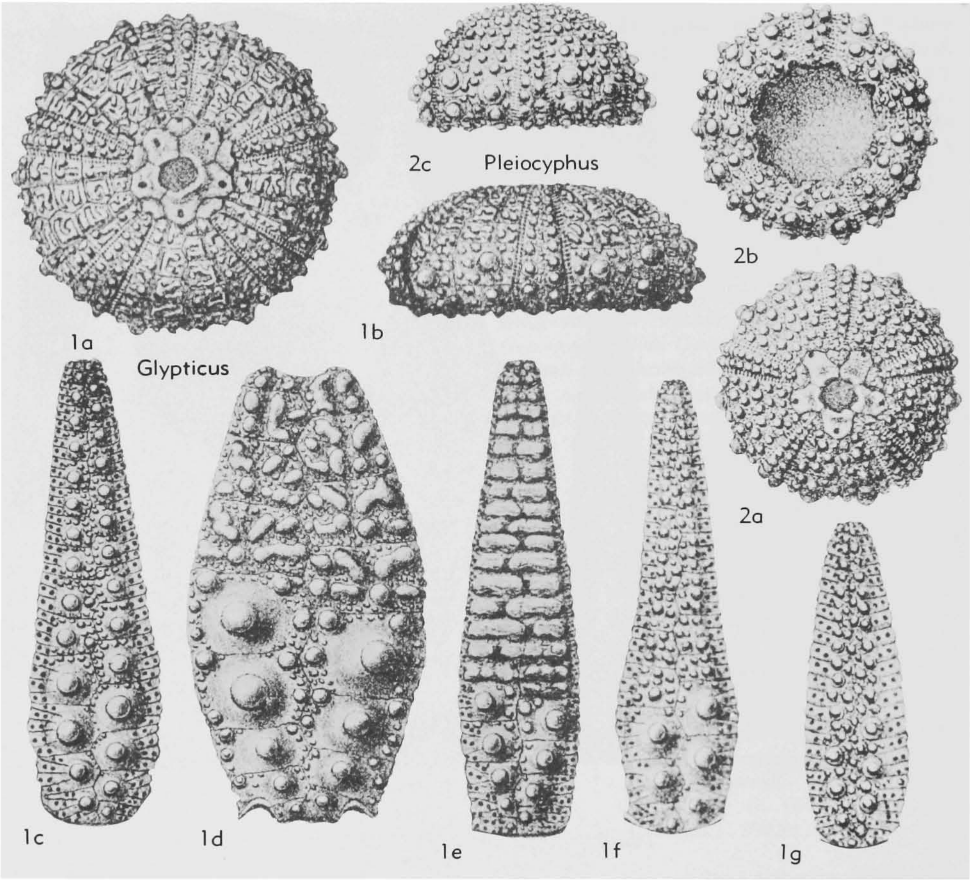

FIG. 309. Arbaciidae (p. U412-U413).

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.

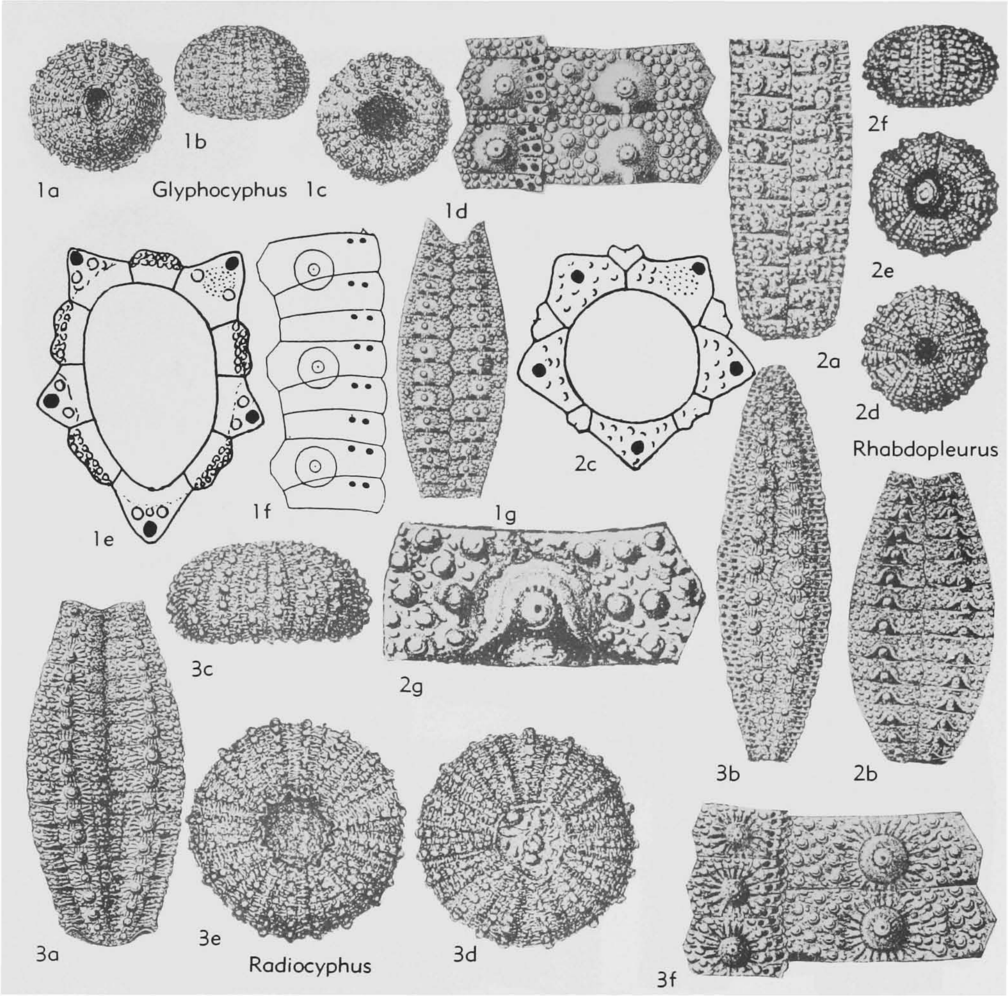

FIG. 310. Glyphocyphidae (p. U414-U415, U417-U418).

(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).

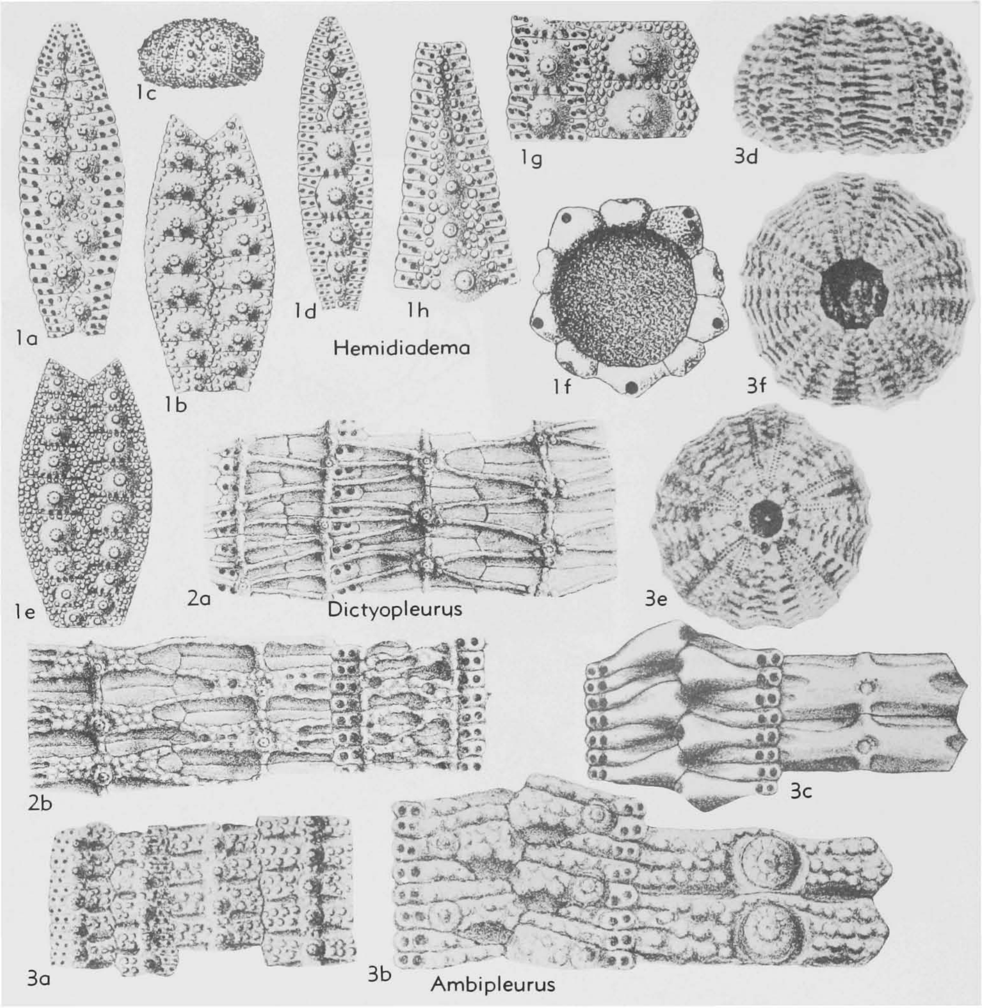

FIG. 311. Glyphocyphidae (p. U415-U417).

——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

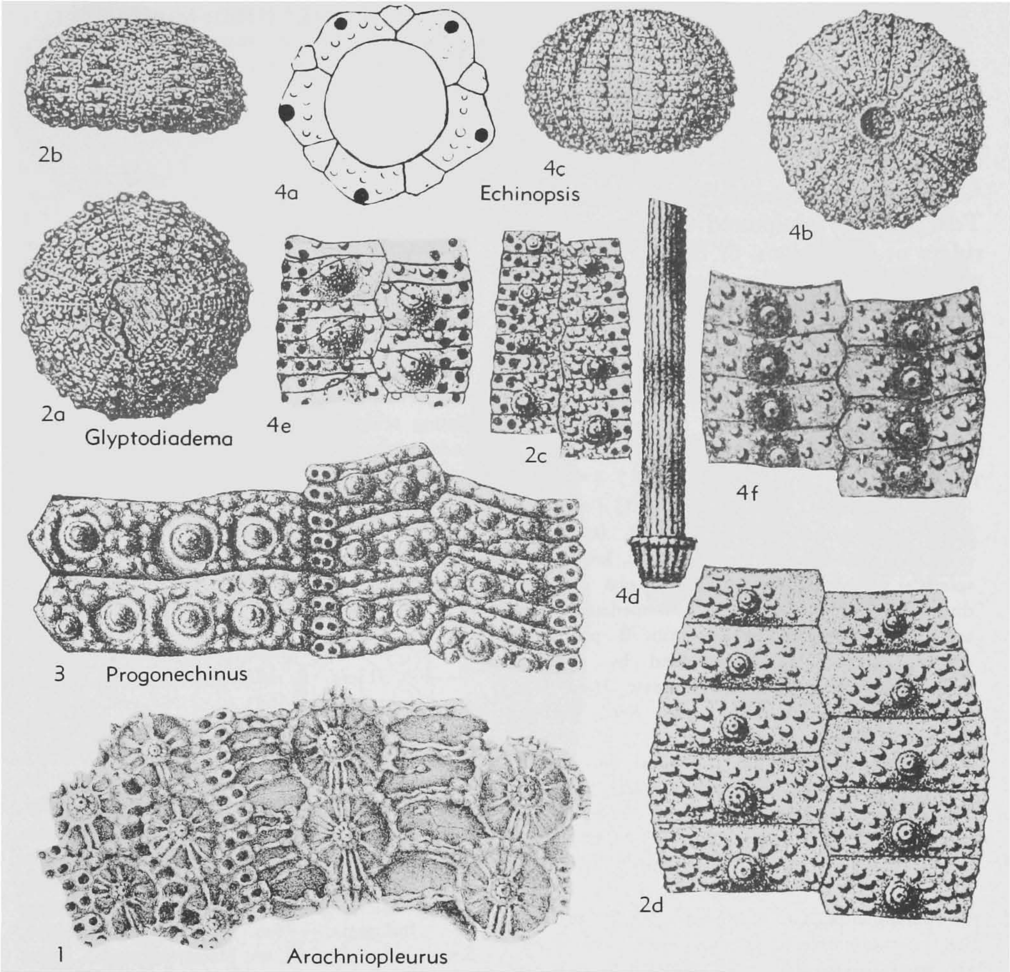

FIG. 312. Glyphocyphidae (p. *U*415-*U*417).

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).

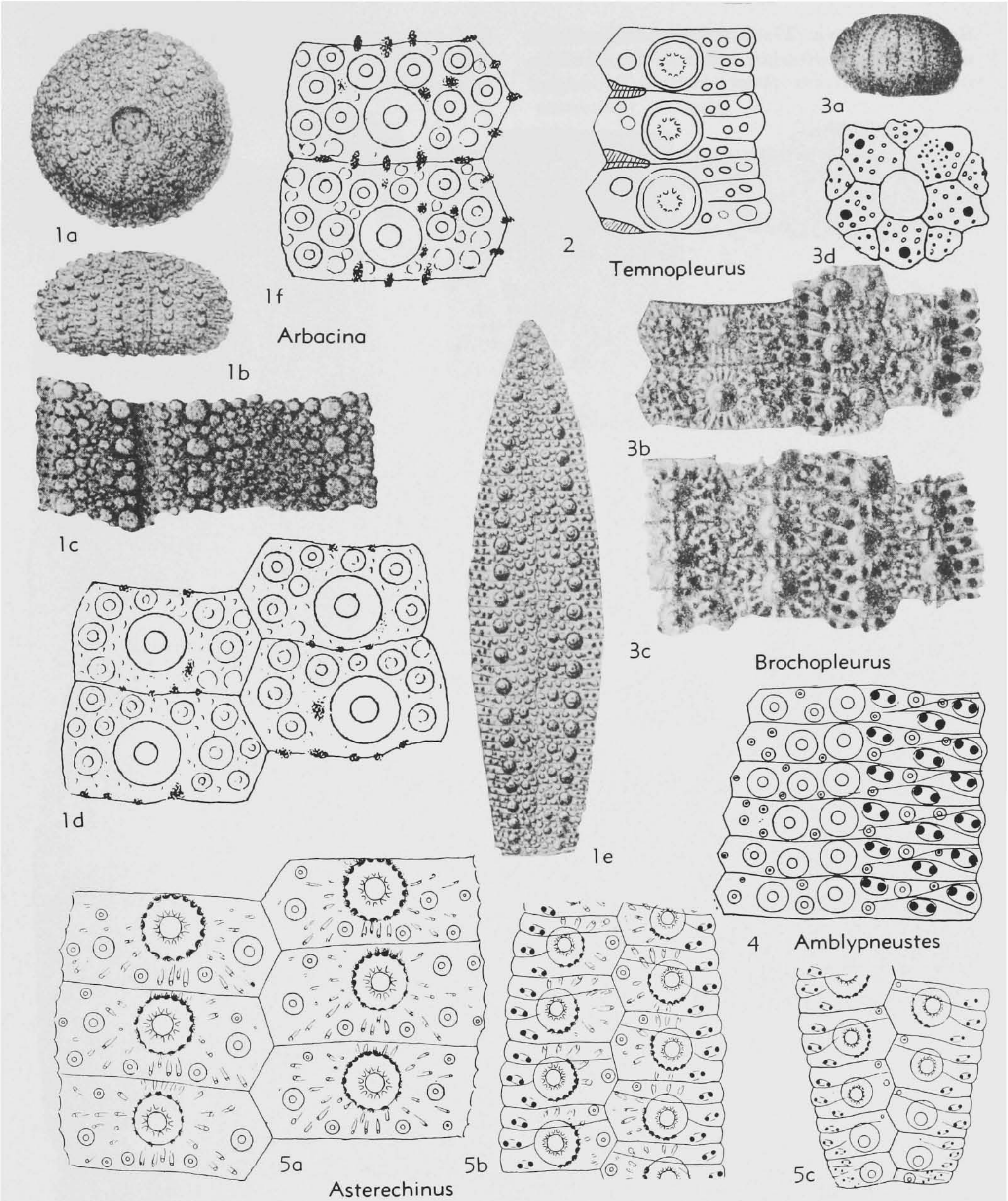

FIG. 313. Temnopleuridae (p. U418).

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

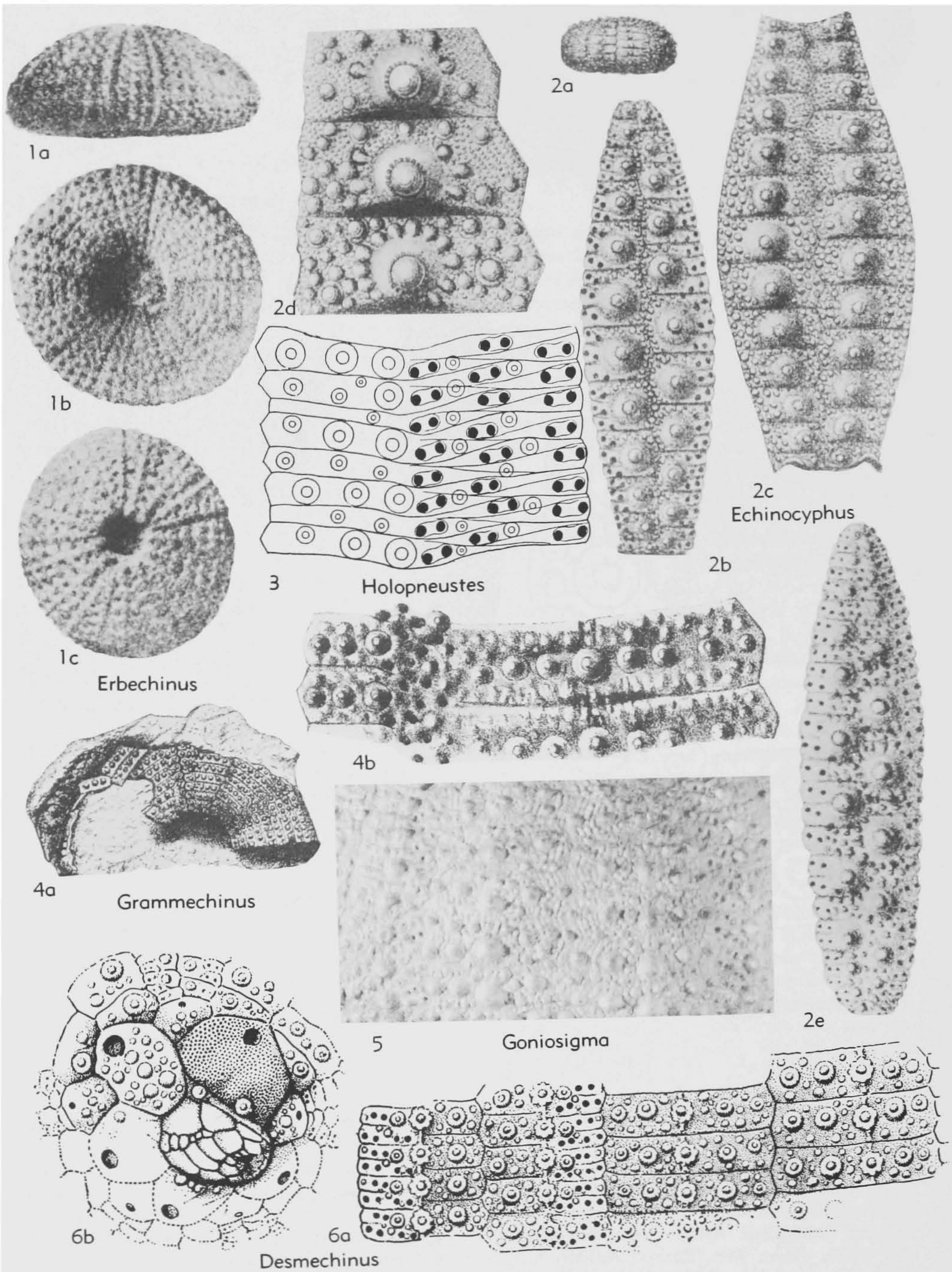

FIG. 314. Temnopleuridae (p. U418-U423).

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

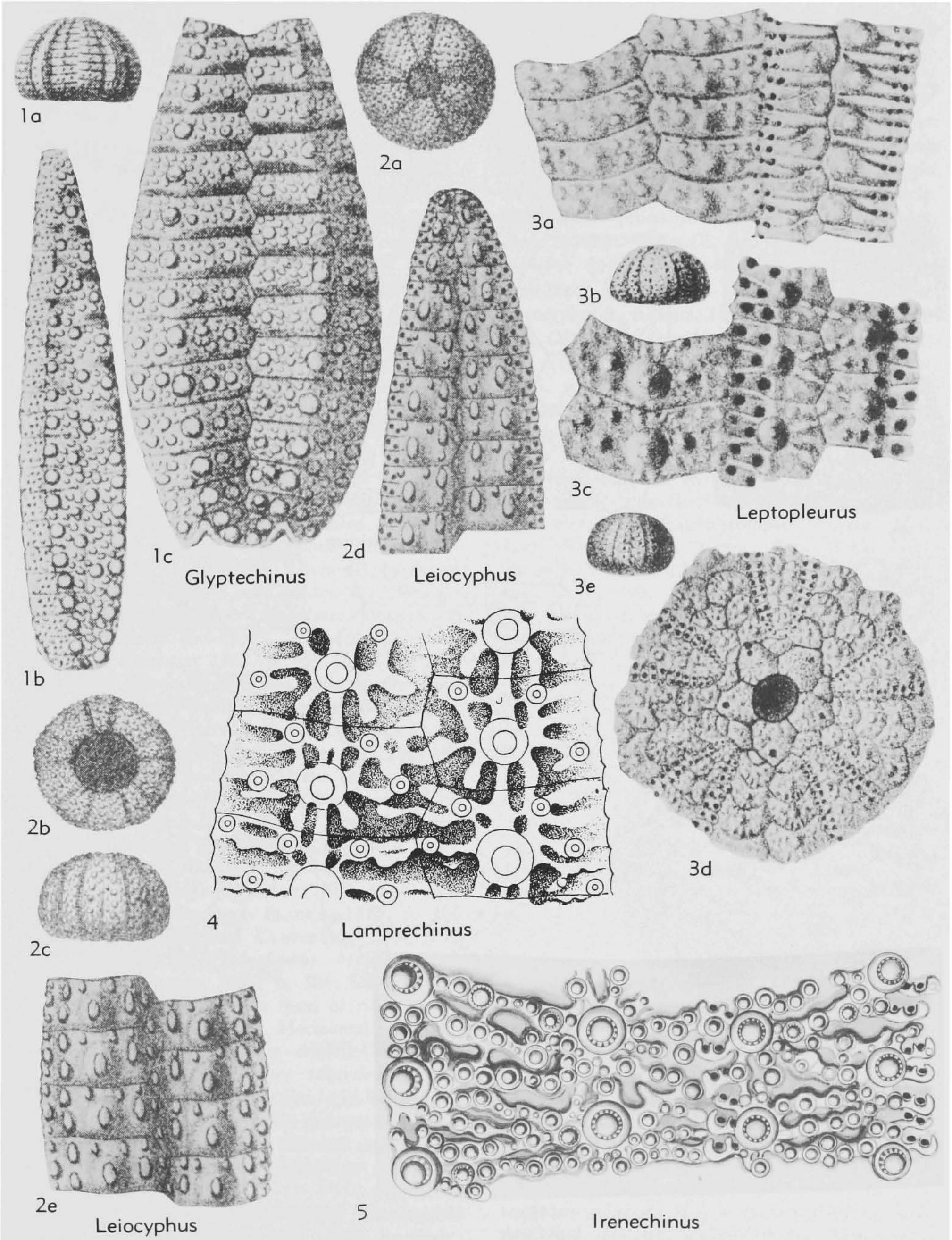

FIG. 315. Temnopleuridae (p. *U*419, *U*423).

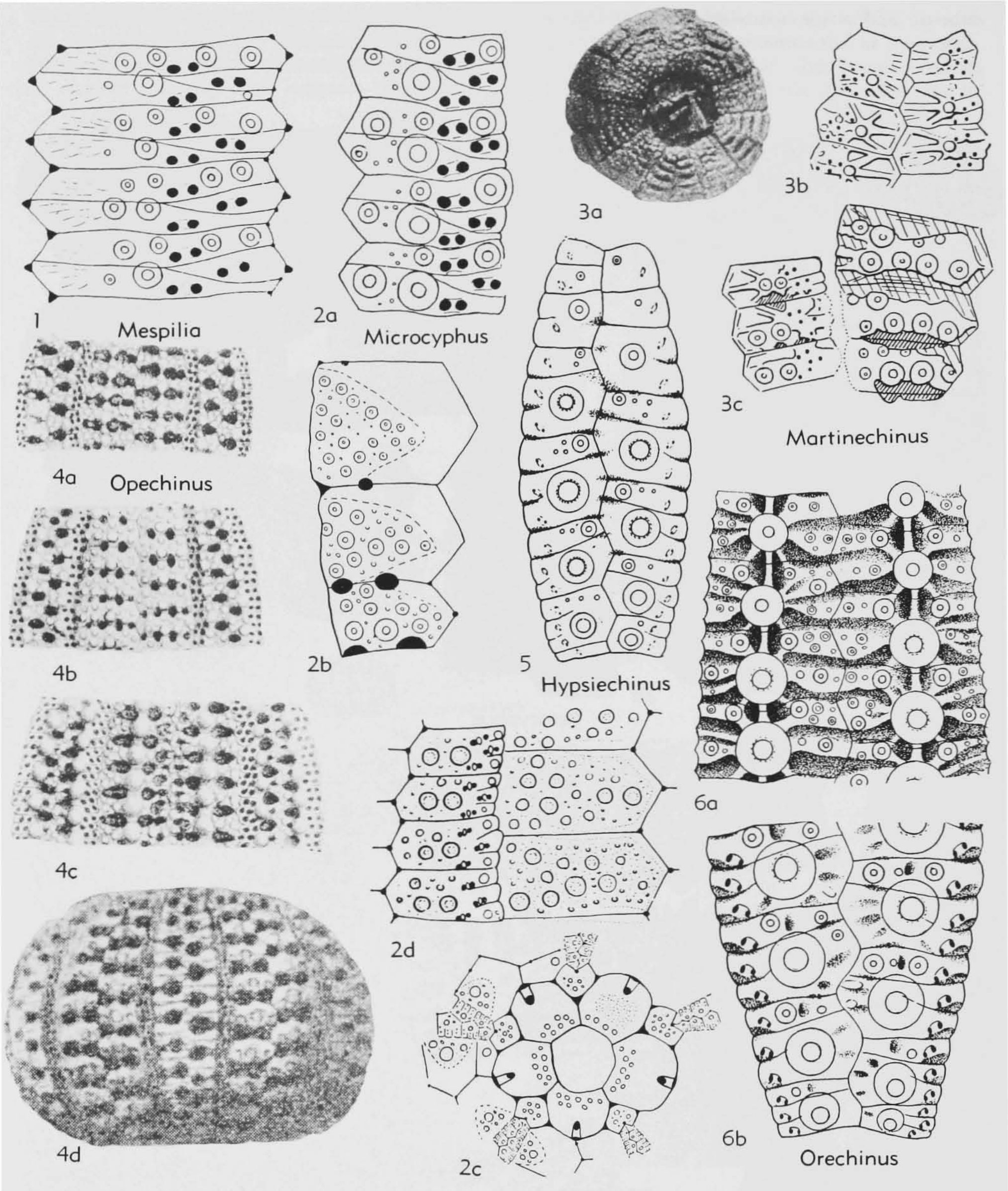

FIG. 316. Temnopleuridae (p. U423-U424).

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.

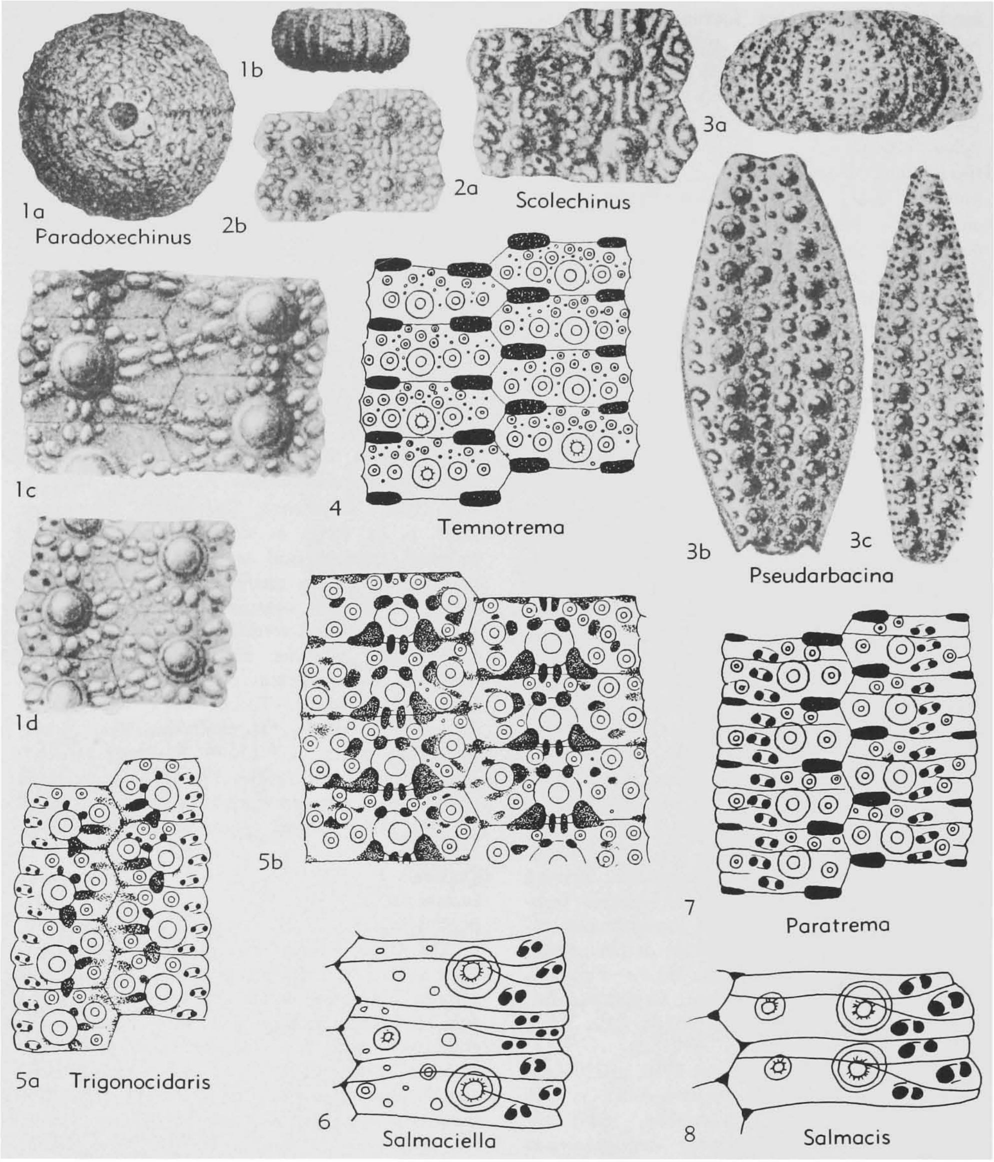

FIG. 317. Temnopleuridae (p. U424-U425).

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.*

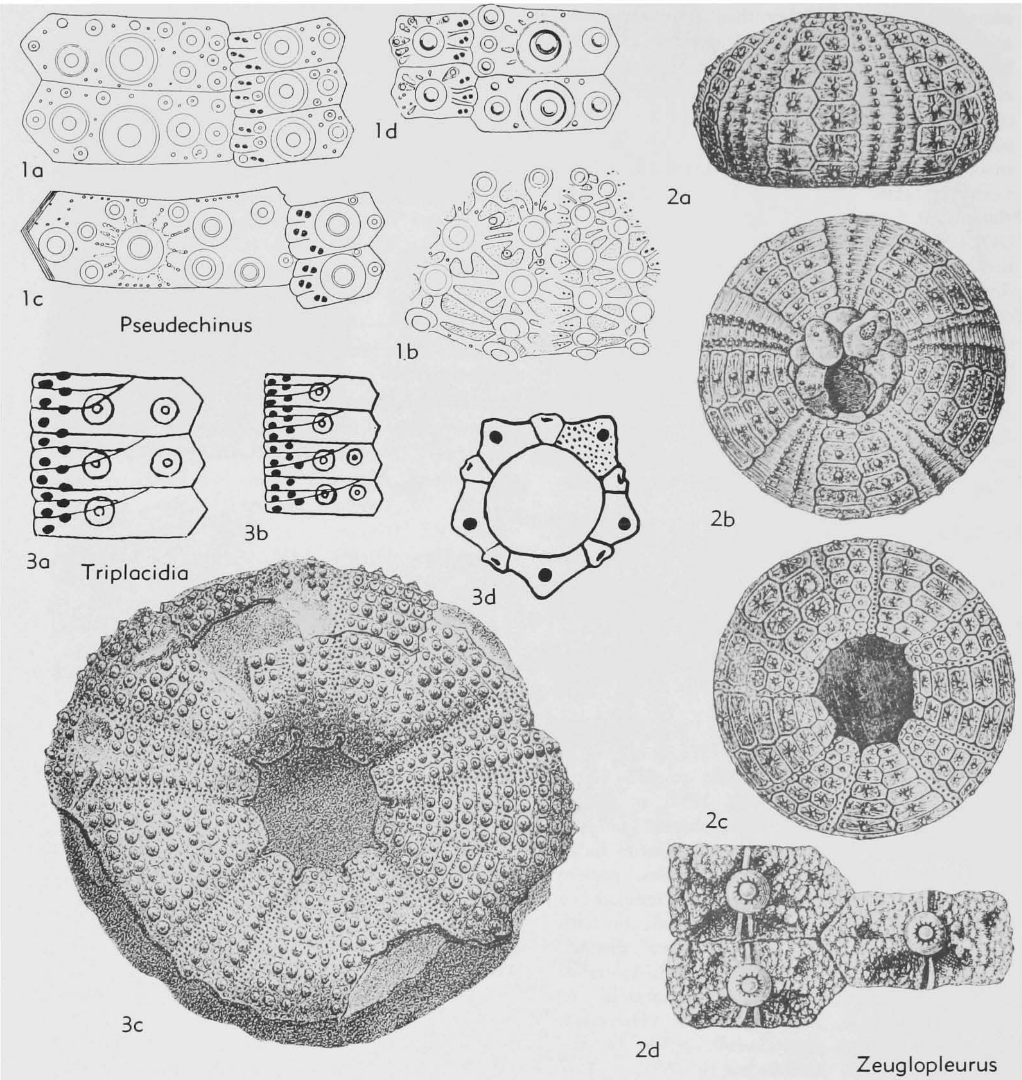

FIG. 318. Temnopleuridae (p. U425-U426).

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.*

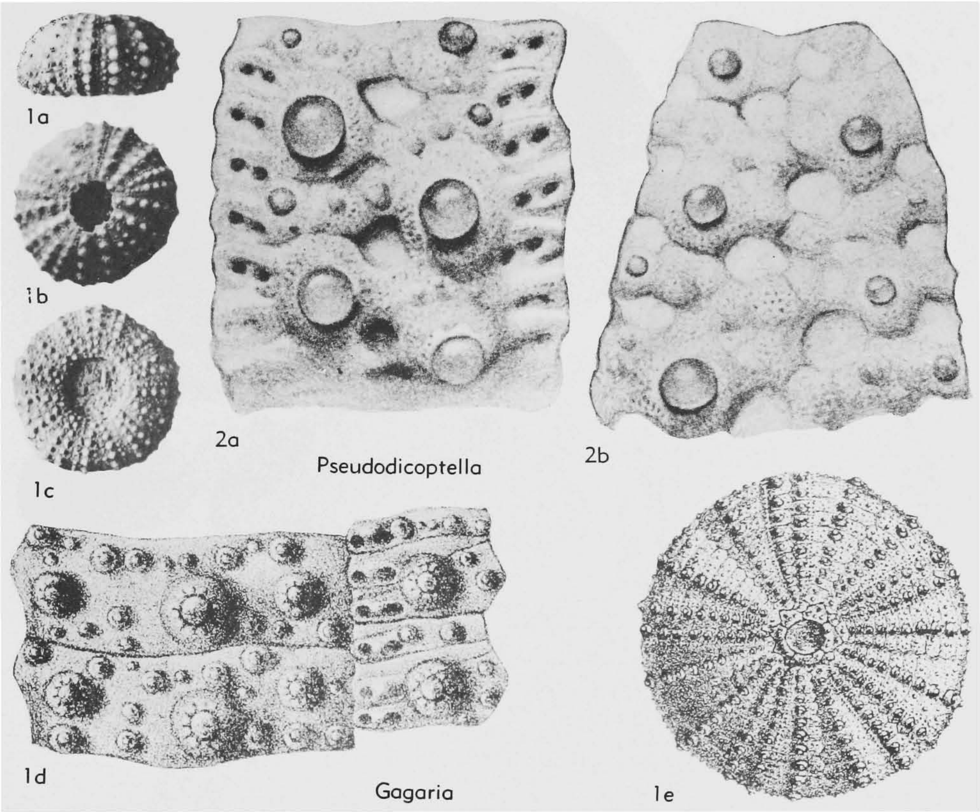

FIG. 319. Temnopleuridae *(2)*; Family Uncertain *(1)* (p. *U*425, *U*430-*U*431).

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

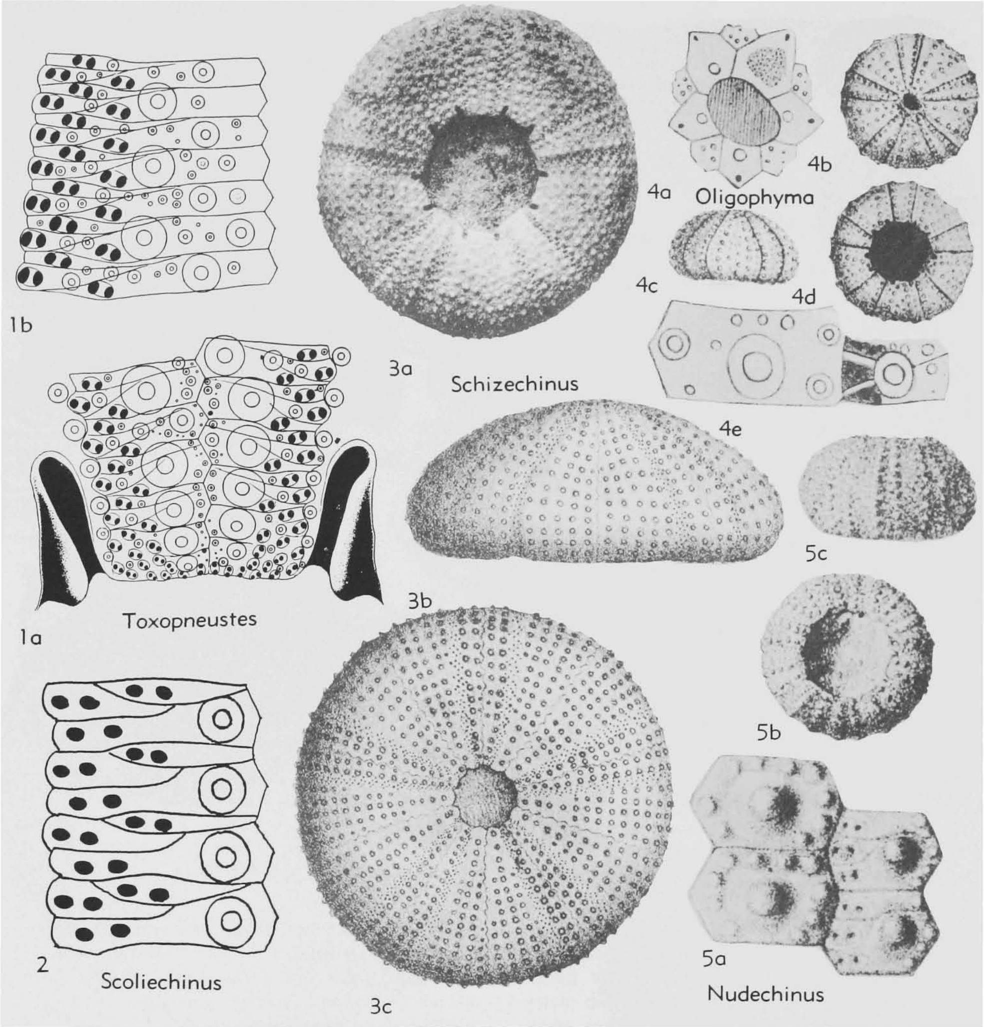

FIG. 320. Toxopneustidae (p. *U*427-*U*429).

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.

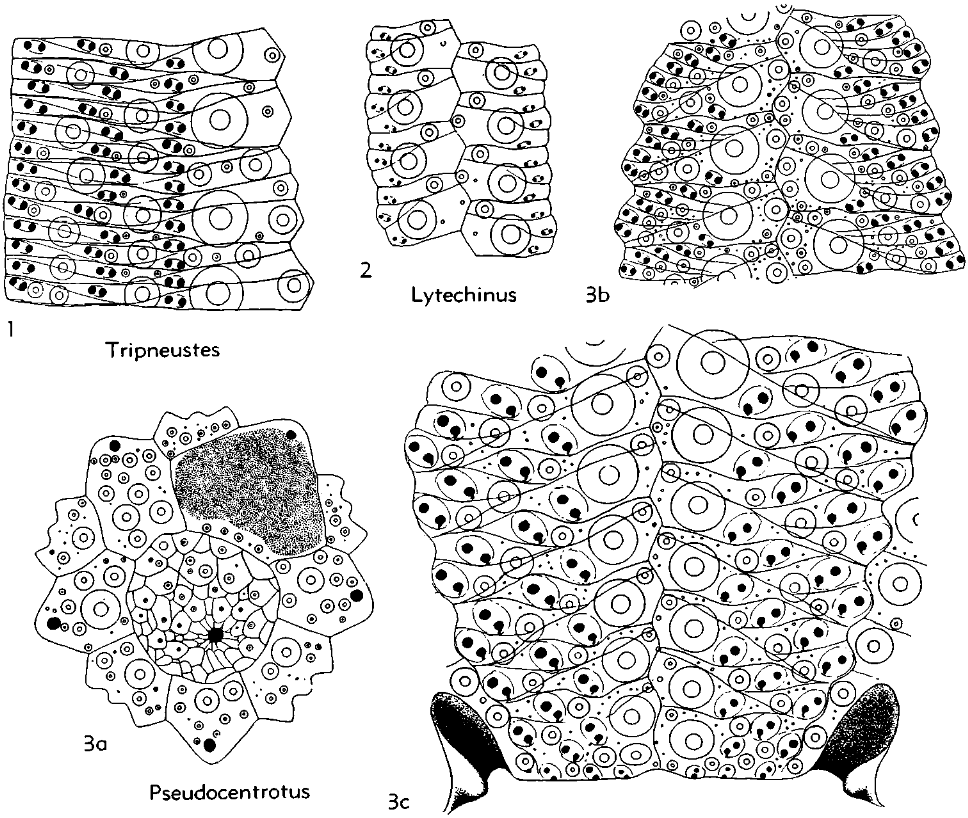

FIG. 321. Toxopneustidae (p. *U*427-*U*429).

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

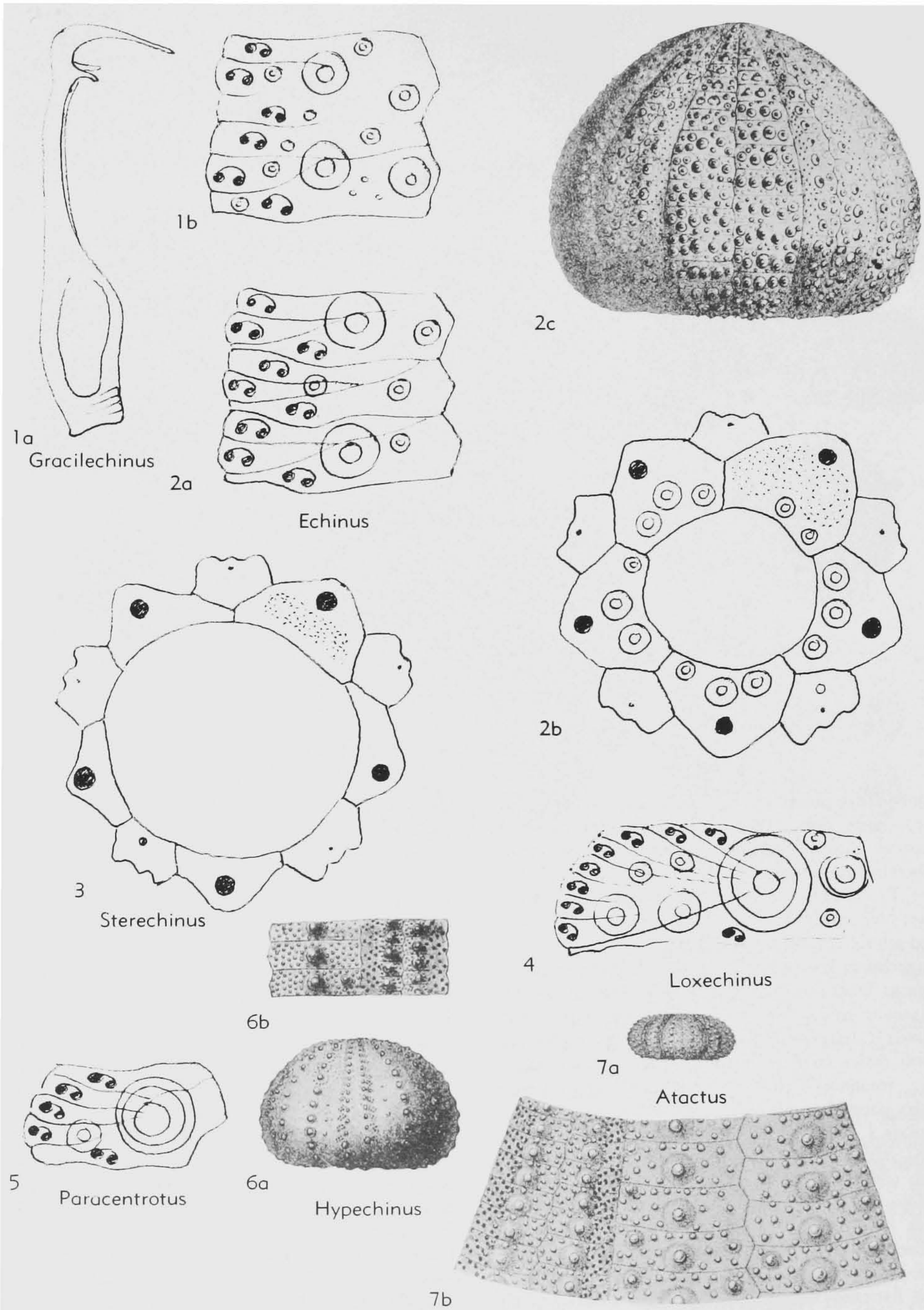

FIG. 322. Echinidae (p. *U*431, *U*433).

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.

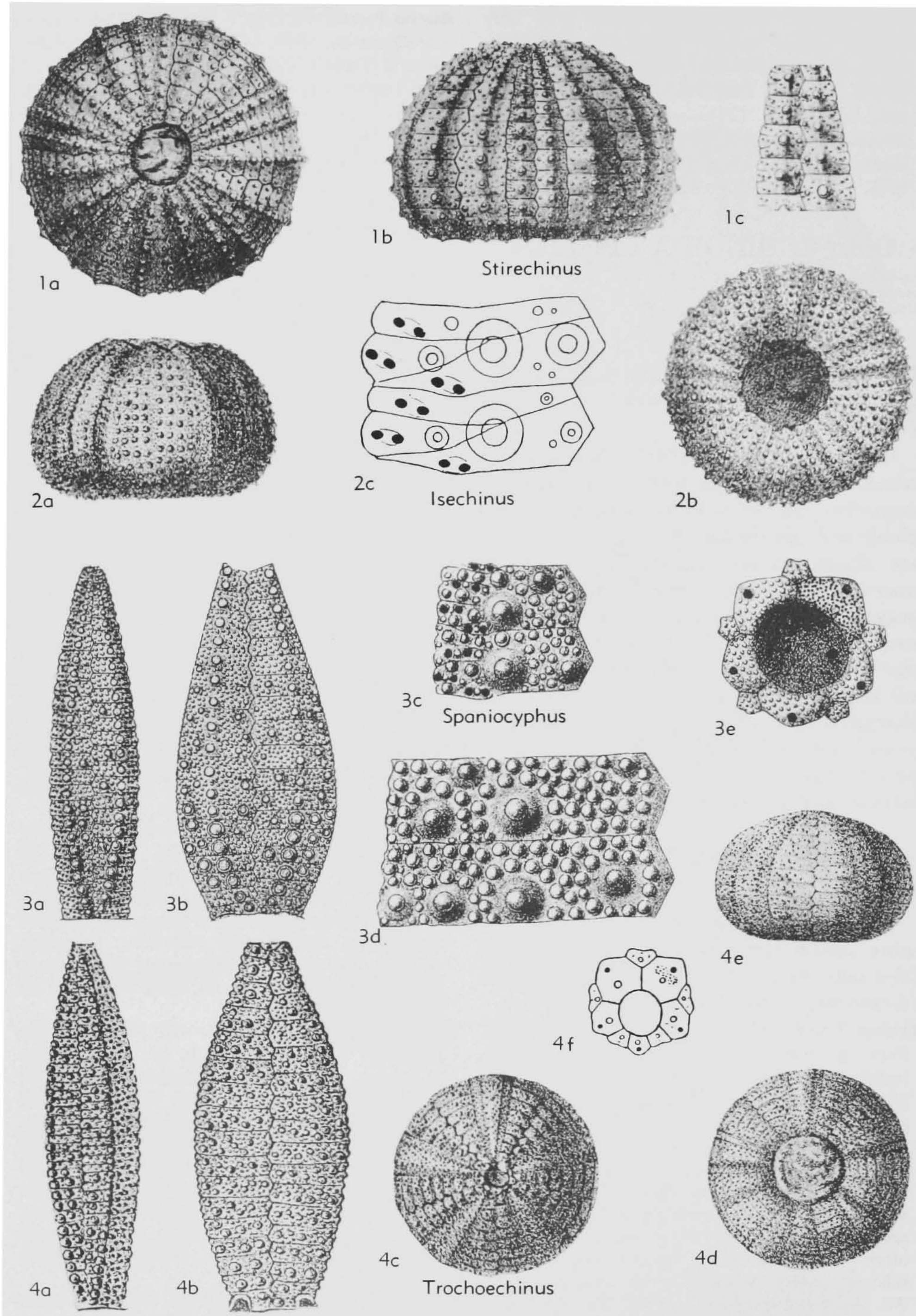

FIG. 323. Echinidae *(1-2)*; Family Uncertain *(3-4)* (p. *U*431, *U*433, *U*436).

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

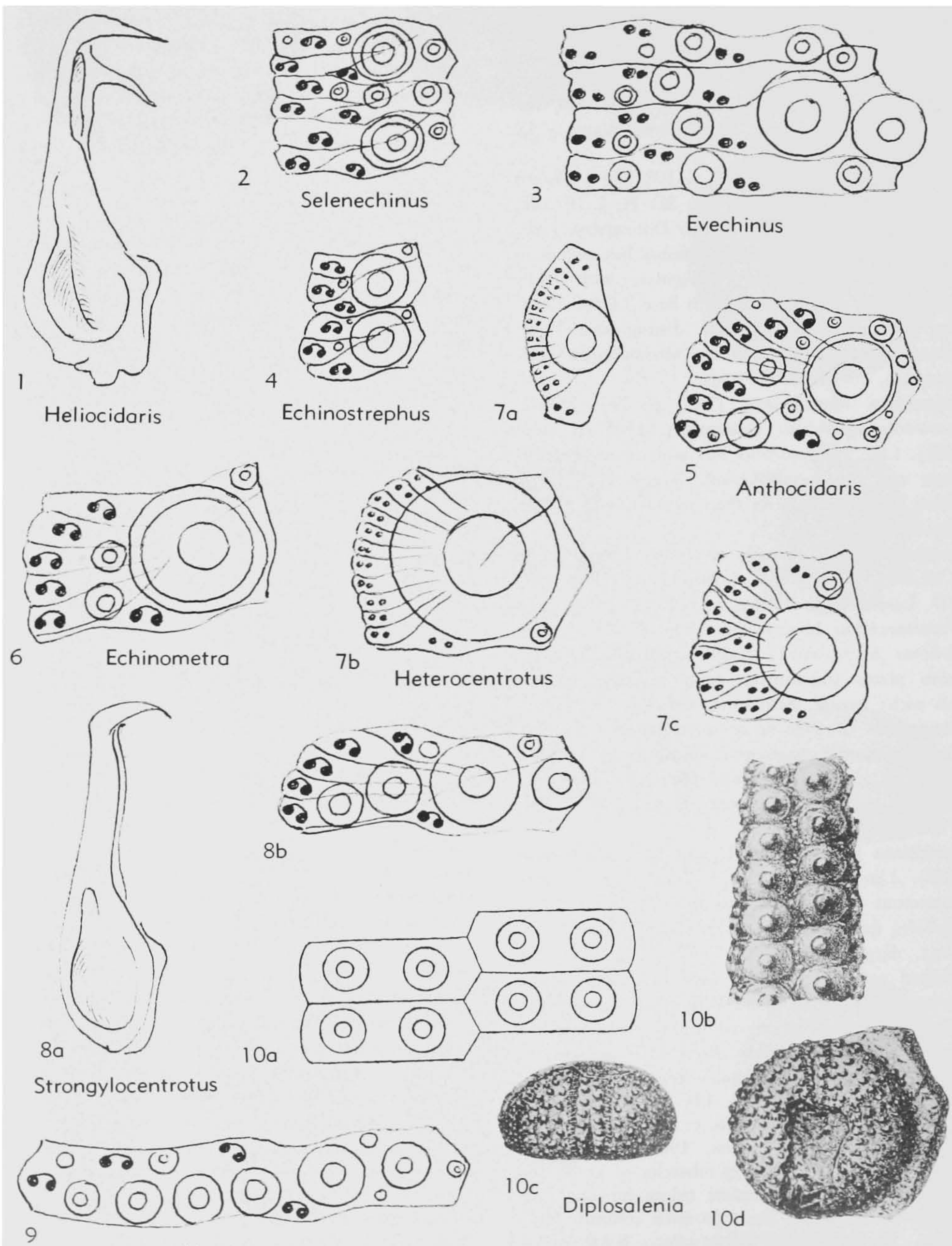

FIG. 324. Echinometridae *(1-7)*; Strongylocentrotidae *(8-9)*; Parasaleniidae *(10)* (p. *U*433-*U*436).

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]

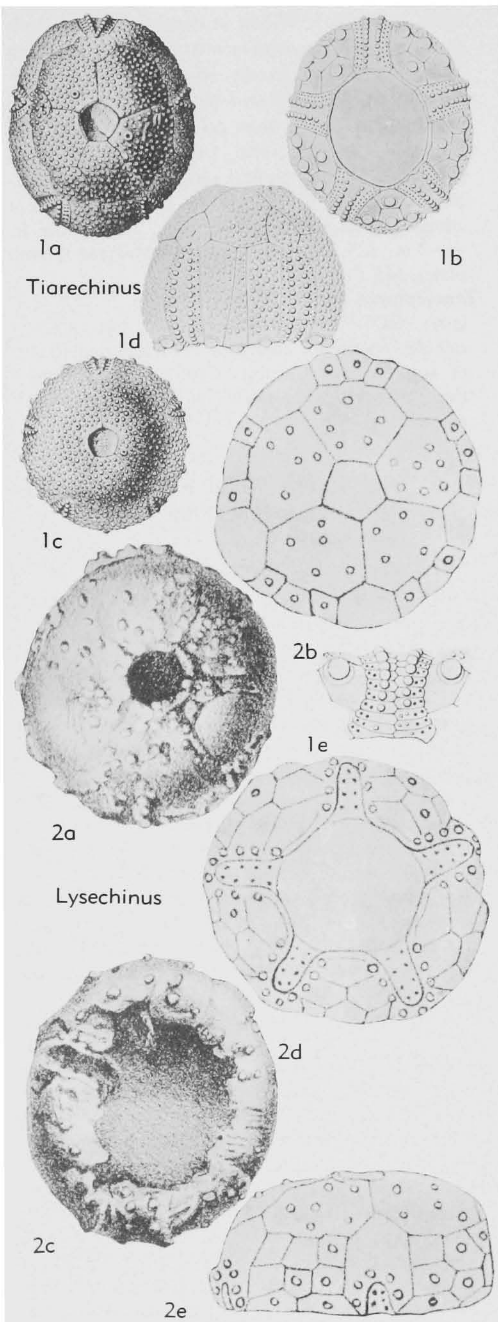

FIG. 325. Tiarechinidae (p. *U*437).

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*,

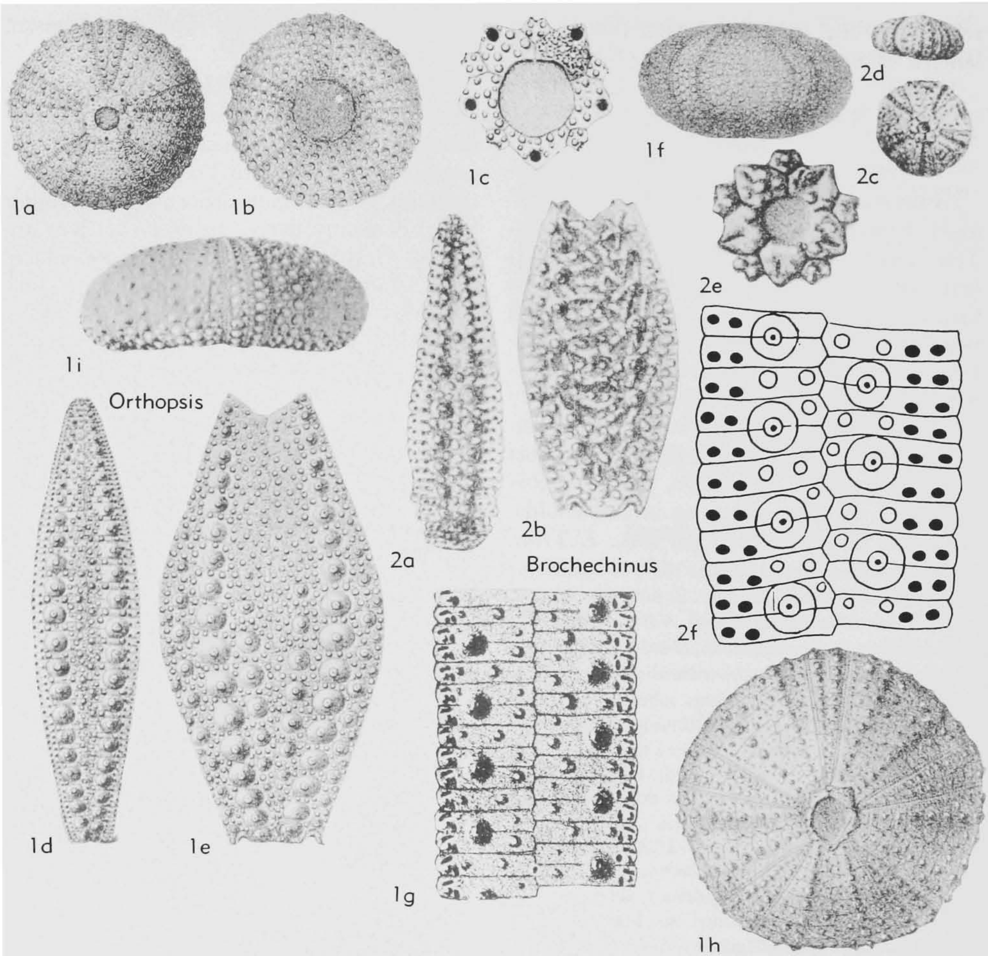

FIG. 326. Orthopsidae (p. U437-U438).

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).

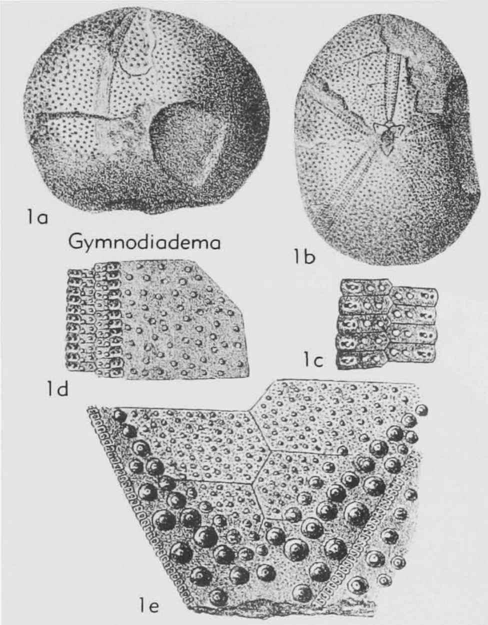

FIG. 327. Orthopsidae (p. *U*438).

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.

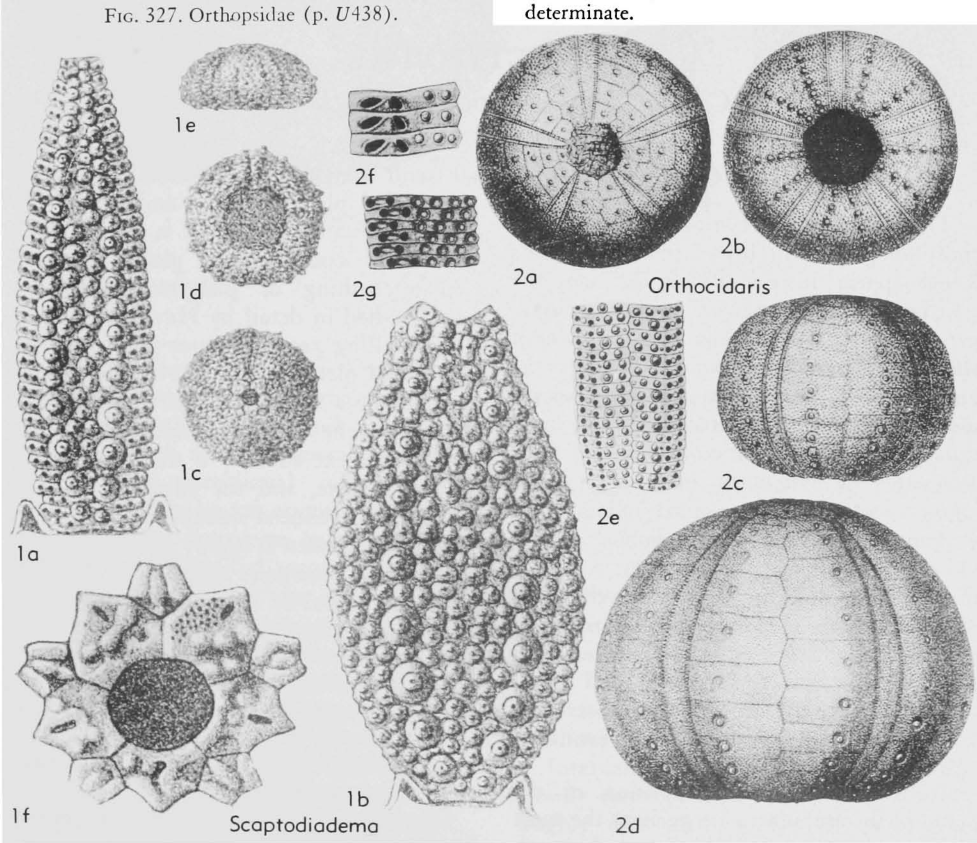

FIG. 328. Orthopsidae (p. *U*438).

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-

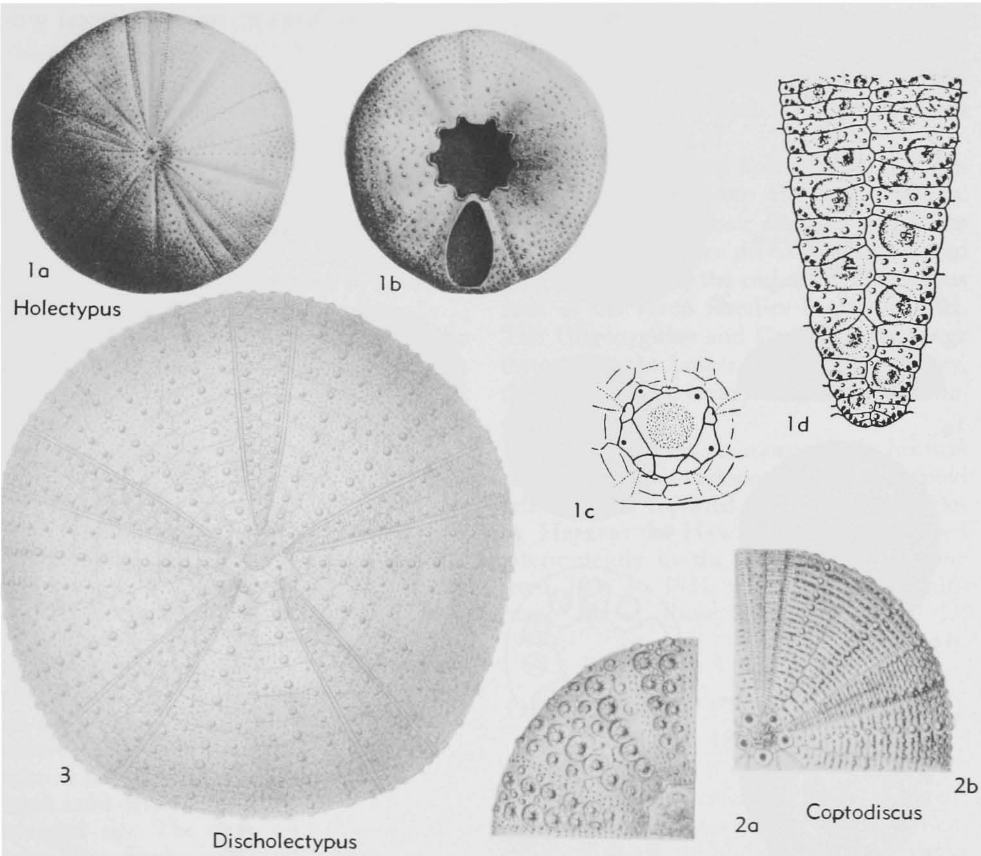

FIG. 329. Holectypidae (p. U444).

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.

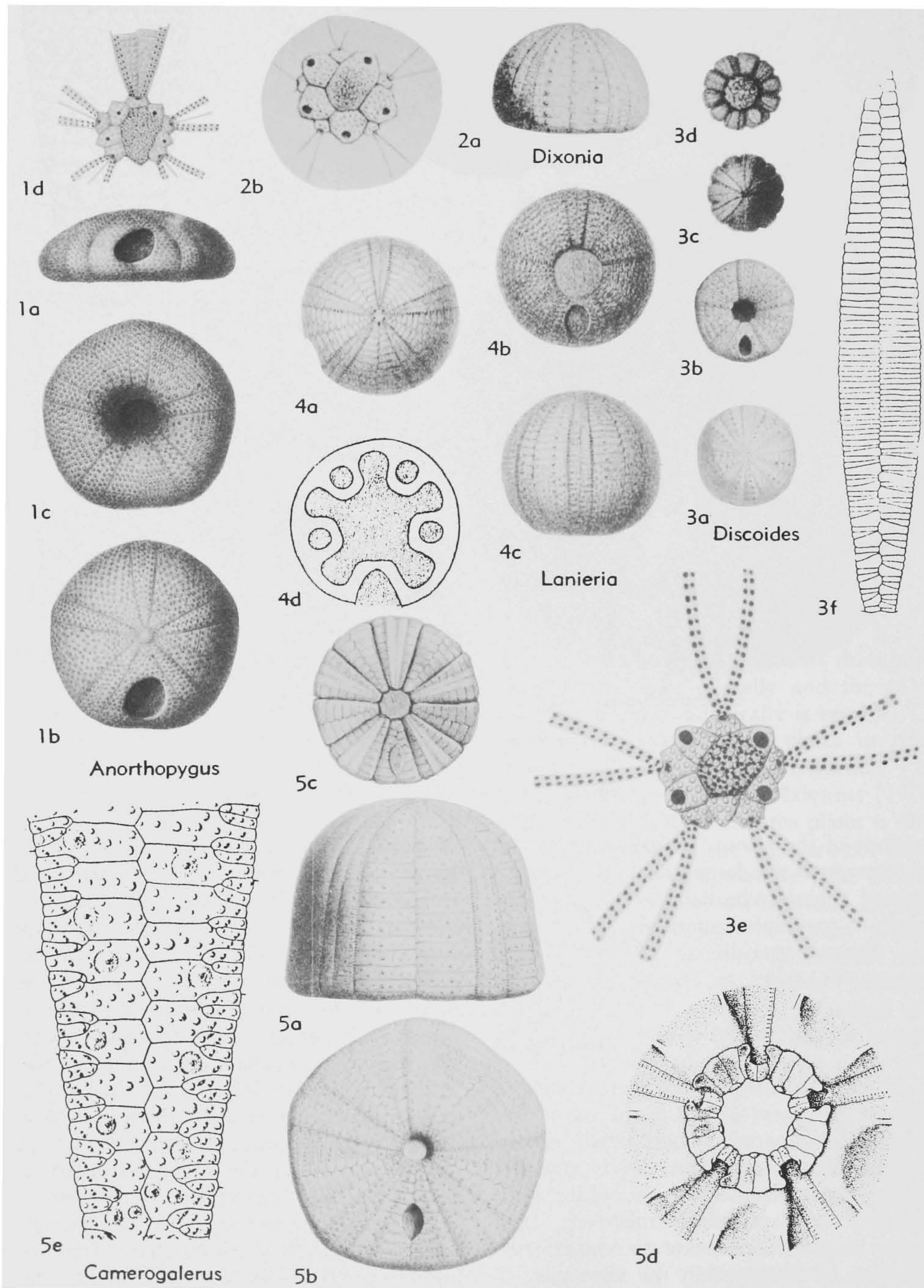

FIG. 330. Anorthopygidae *(1)*; Discodeidae *(2-5)* (p. *U*444-*U*445).

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.)*.

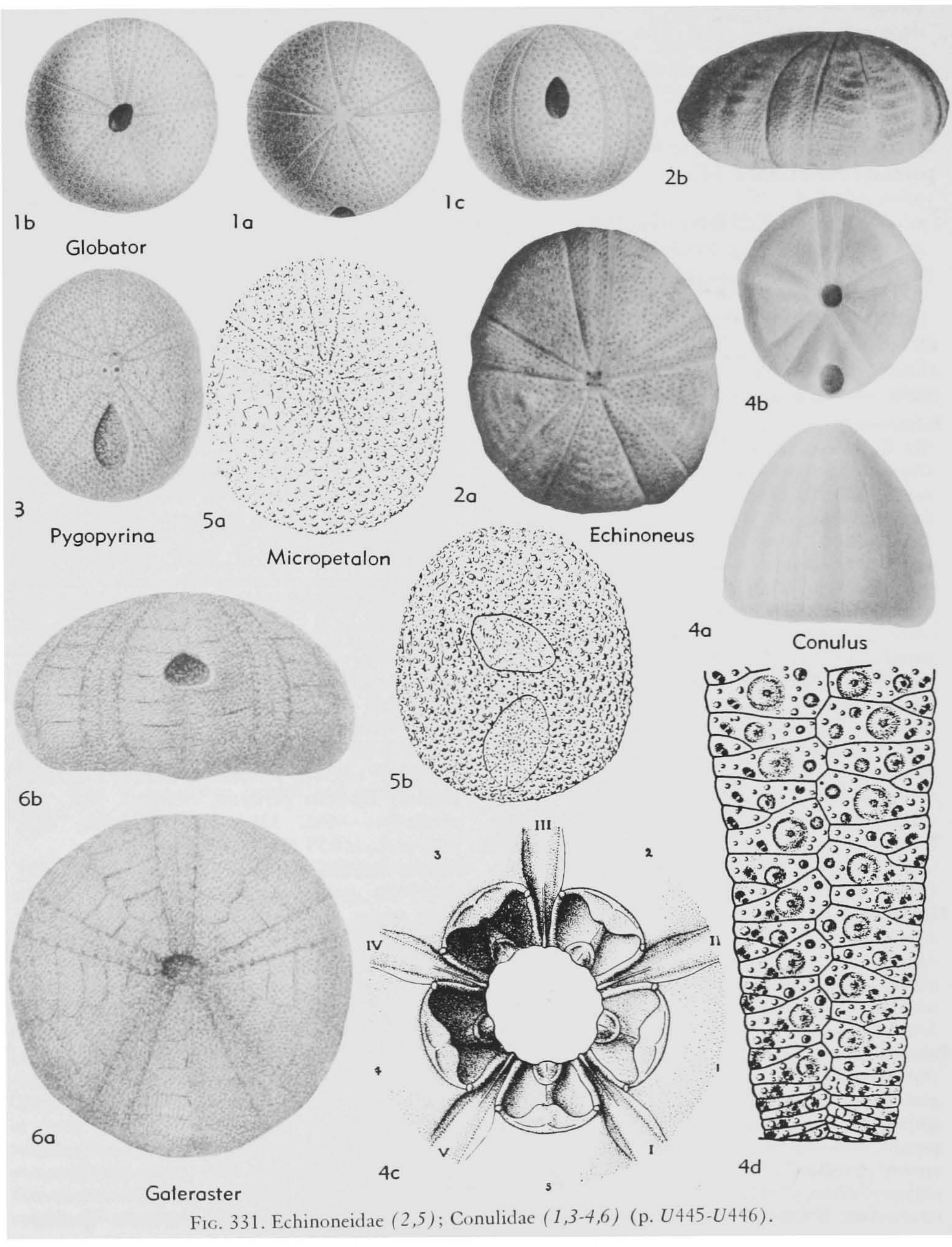

FIG. 331. Echinoneidae *(2,5)*; Conulidae *(1,3-4,6)* (p. *U*445-*U*446).

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,

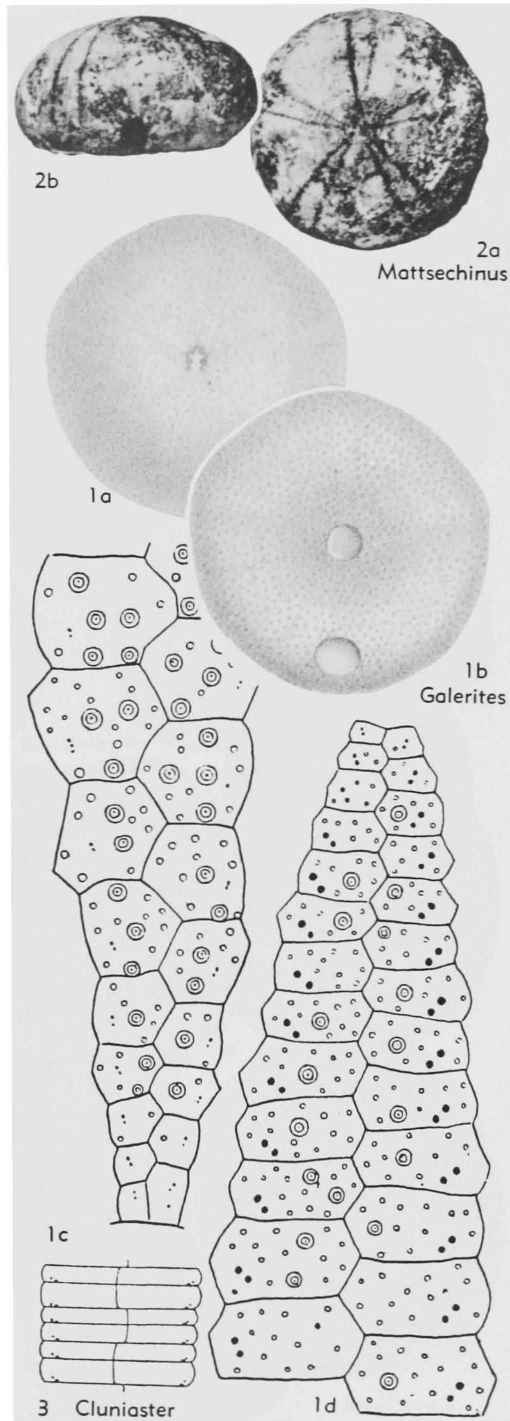

FIG. 332. Galeritidae *(1)*; Family Uncertain *(2-3)* (p. *U*447).

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).

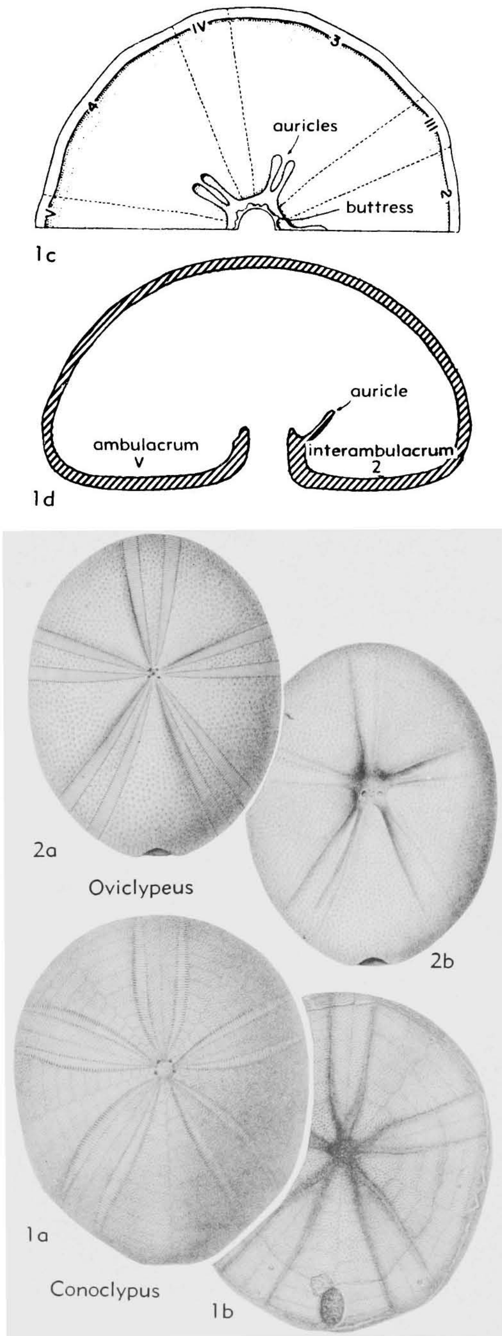

FIG. 333. Conoclypidae (p. U447-U448).

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. U523.]

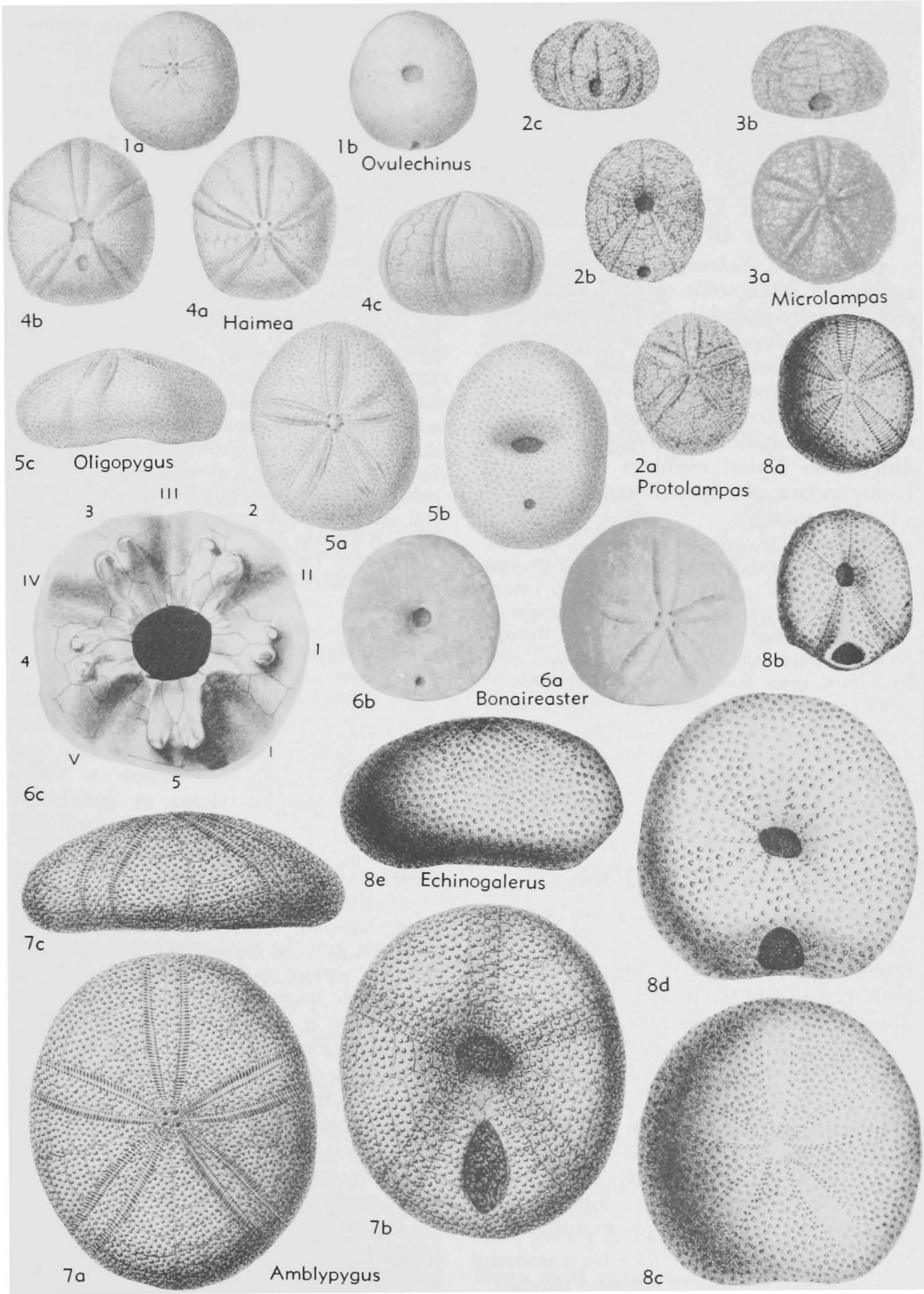

FIG. 334. Oligopygidae *(1-6)*; Family Uncertain *(7-8)* (p. *U*448, *U*450).

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

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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.

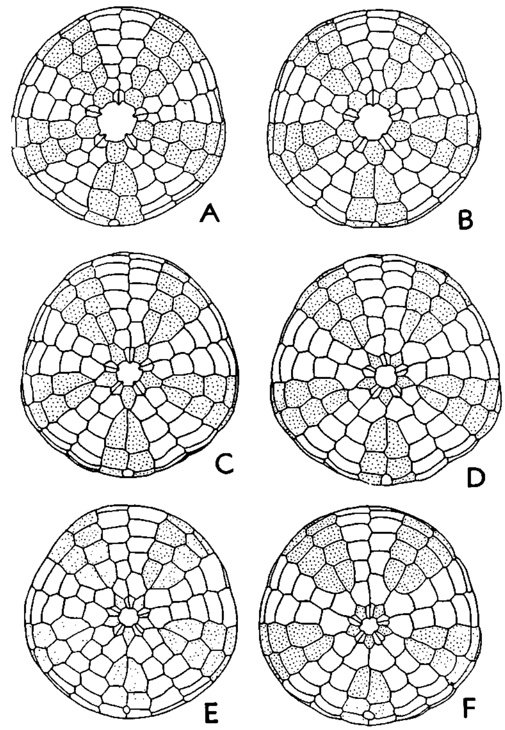

Fig. 335. *Dendraster excentricus* (Eschscholtz). Ontogeny of oral surface. Growth series from diameter of 4 mm. (*A*) to 21 mm. (*F*) enlarged to standard size to show changes in shape and relationships of plates produced by differential peripheral growth of plates (51).

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.

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-

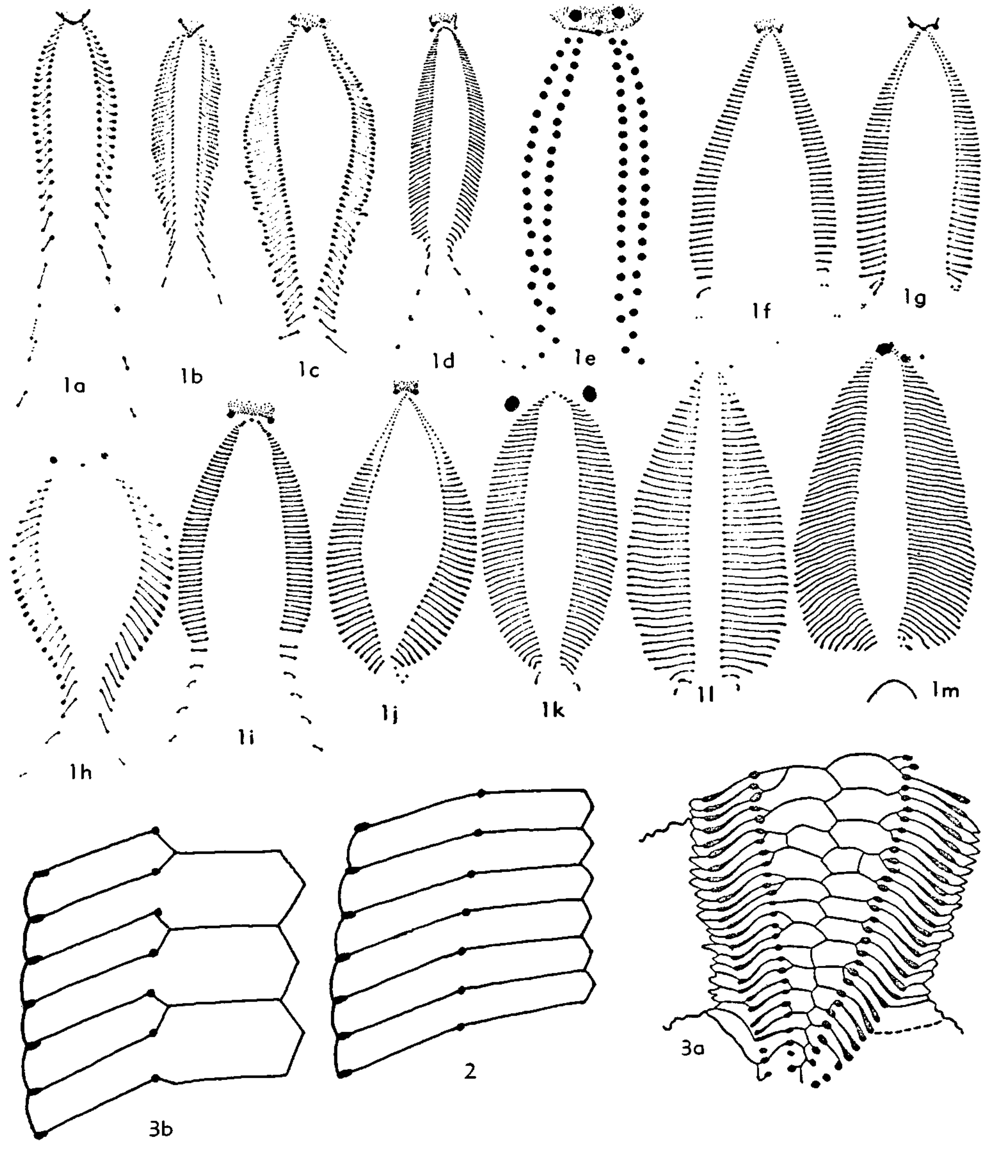

FIG. 336.——*1.* Morphology of clypeasteroid petals: *1a, Heliophora orbiculus* (LINNÉ), amb III (×2.8); *1b, Rotula deciesdigitata* (LESKE), amb V (×1.8); *1c, Laganum laganum* (LESKE), amb II (×2.4); *1d, Dendraster excentricus* (ESCHSCHOLTZ), amb IV (×0.9); *1e, Mortonia australis* (DESMOULINS), amb 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).

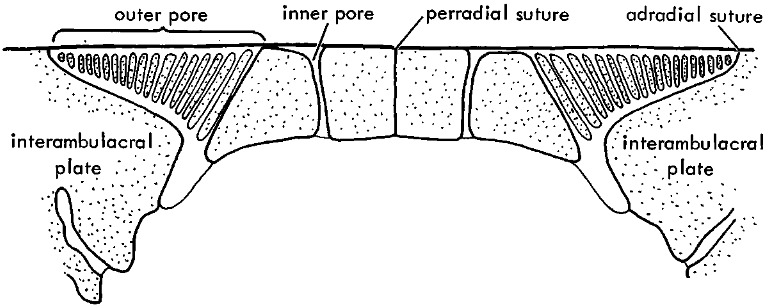

FIG. 337. Cross section of pores for respiratory tube feet in *Scutella* (after SCHAFFER, 217).

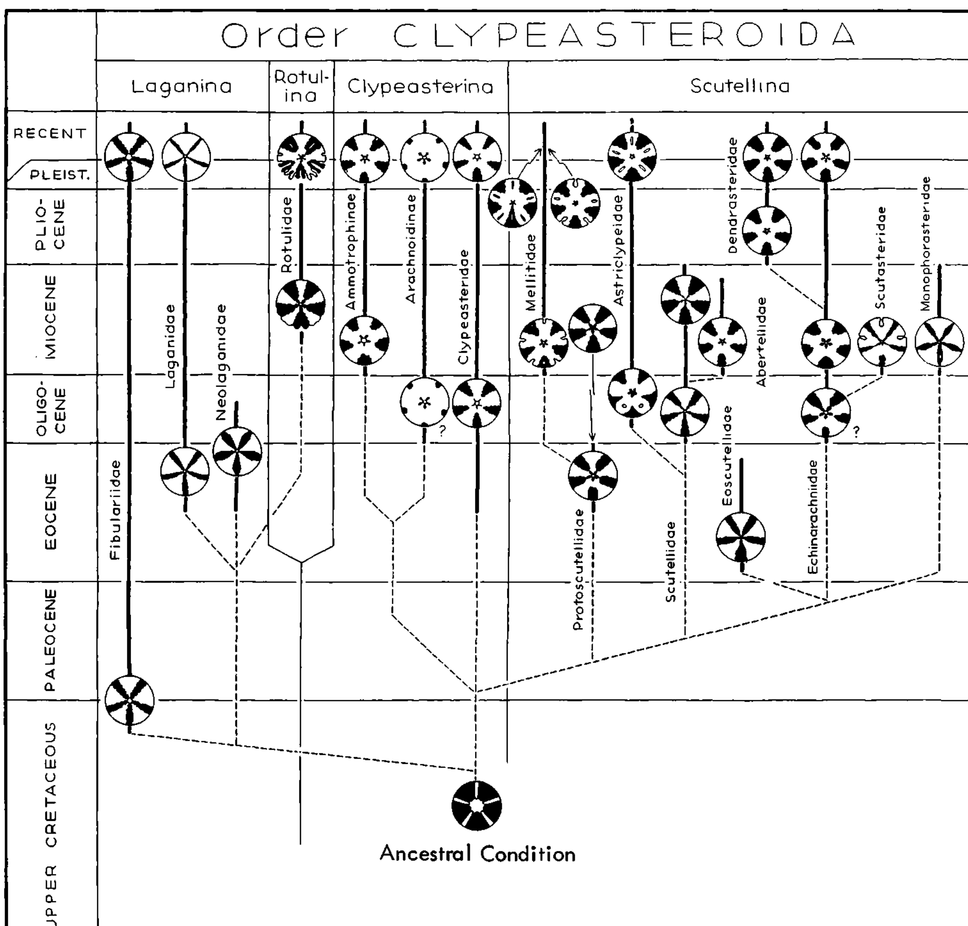

FIG. 338. Evolution of interambulacra on oral surface of Clypeasteroida. Interambulacra in black; vertical spacing proportional to time except for Pleistocene (Durham, n).

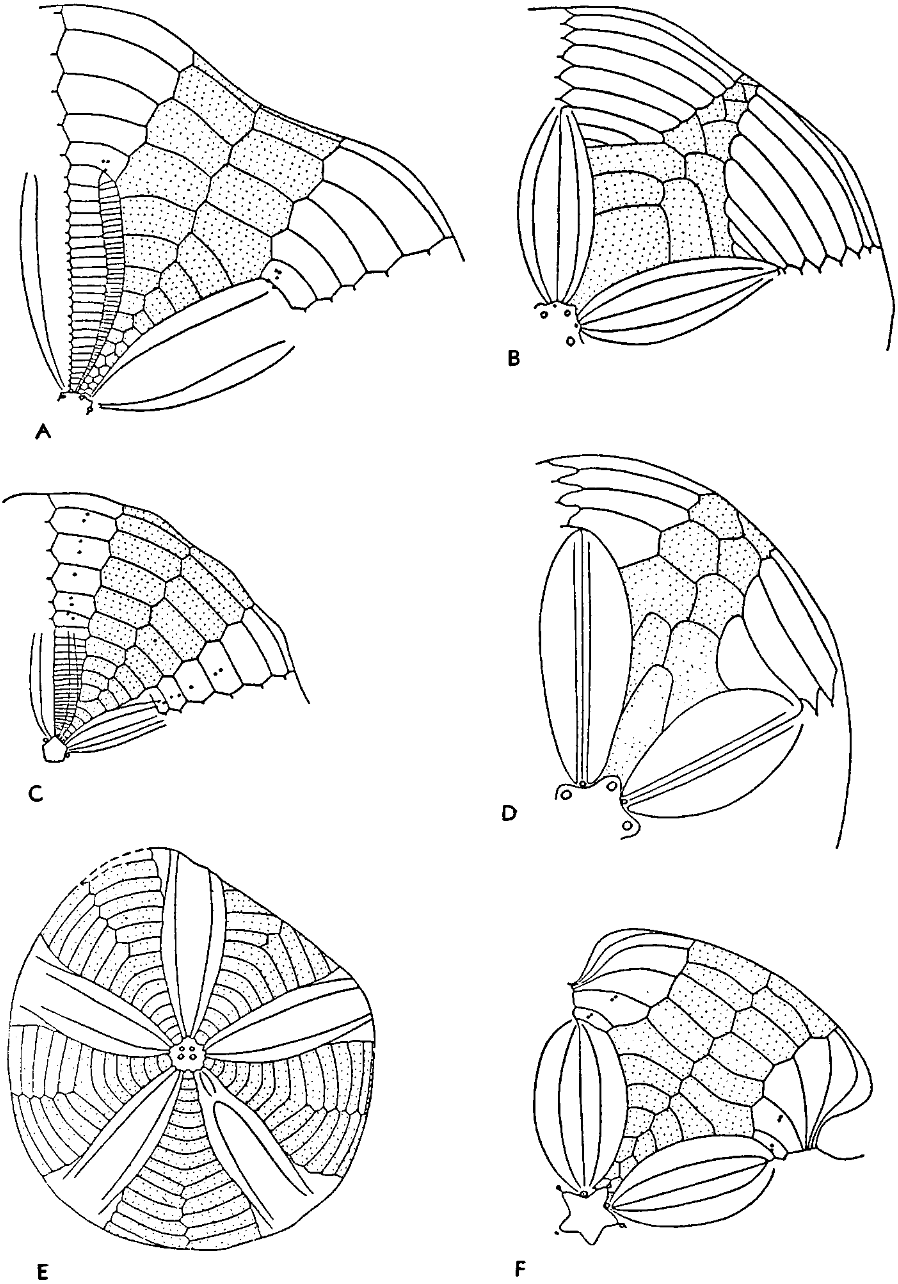

FIG. 339. Apical termination of clypeasteroid interambulacra (enlarged): *A, Clypeaster ravenelii* (A. AGASSIZ), Recent, Gulf of Mexico; *B, Laganum laganum* (LESKE), Recent, New Hebrides; *C, Heliophora orbiculus* (LINNÉ), Recent, Loanda, Angola; *D, Sanchezella sanchezi* (LAMBERT), upper Eocene, Cuba; *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-*

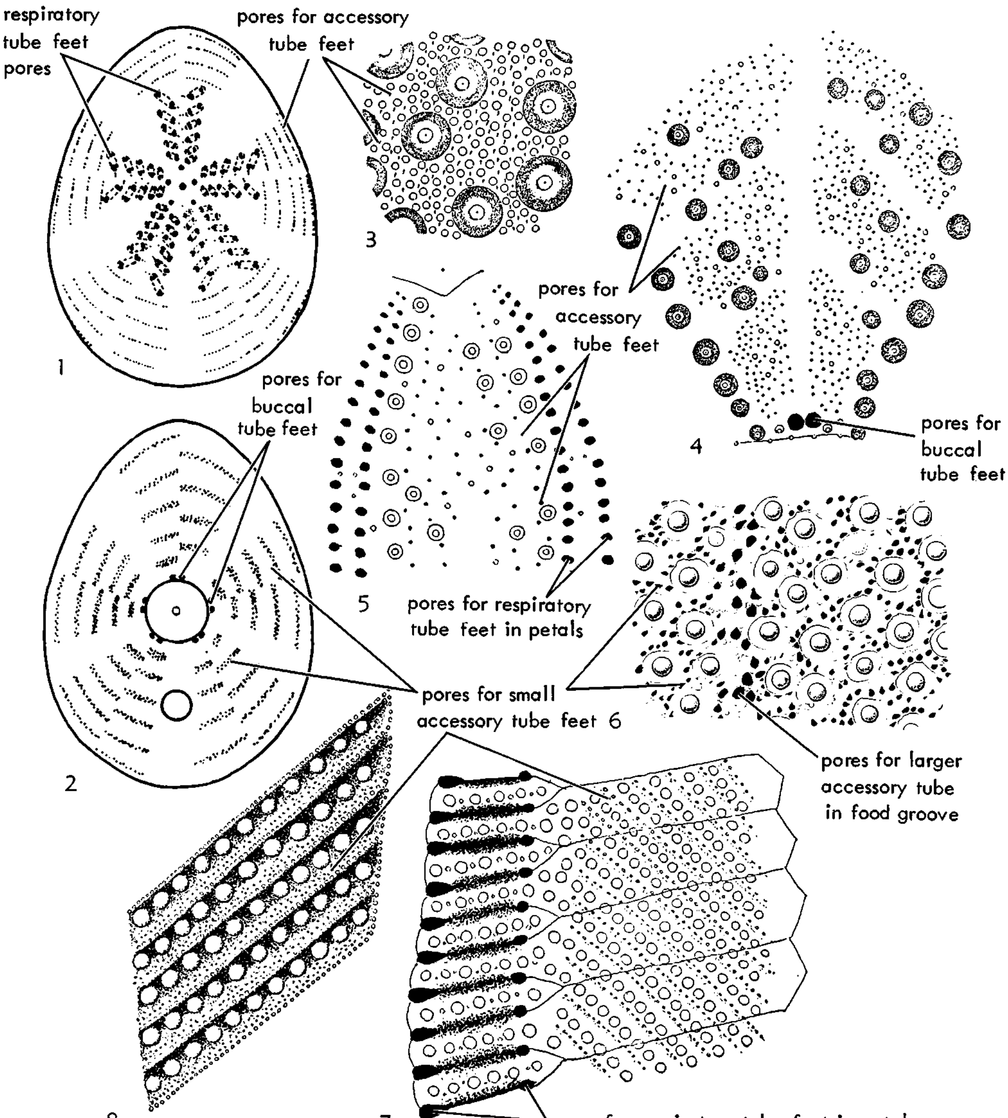

FIG. 340. Pores for accessory tube feet in Clypeasteroida (pores in black): *1,2, Echinocyamus pusillus* (MÜLLER), aboral, oral, ×9 (211a); *3, Clypeaster ochrus* CLARK, adorally, interambulacrum 5, ×18 (136g); *4,5, Laganum laganum* (LESKE), adapical and adoral ends of ambulacrum, ×15 (136g); *6, Leodia 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).

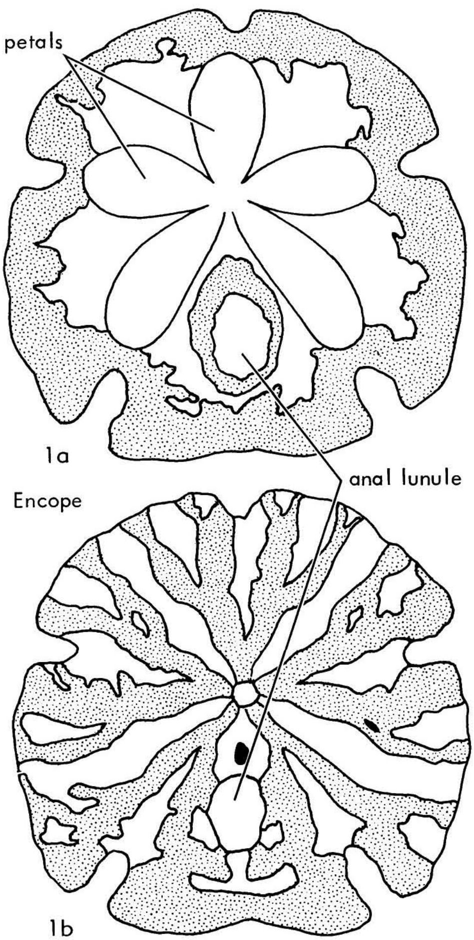

FIG. 341. *1a,b, Encope grandis* AGASSIZ, aboral and oral surfaces, showing distribution (stippled areas) of accessory tube feet, ×0.67 (Wagner, n).

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 post-primordial 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.

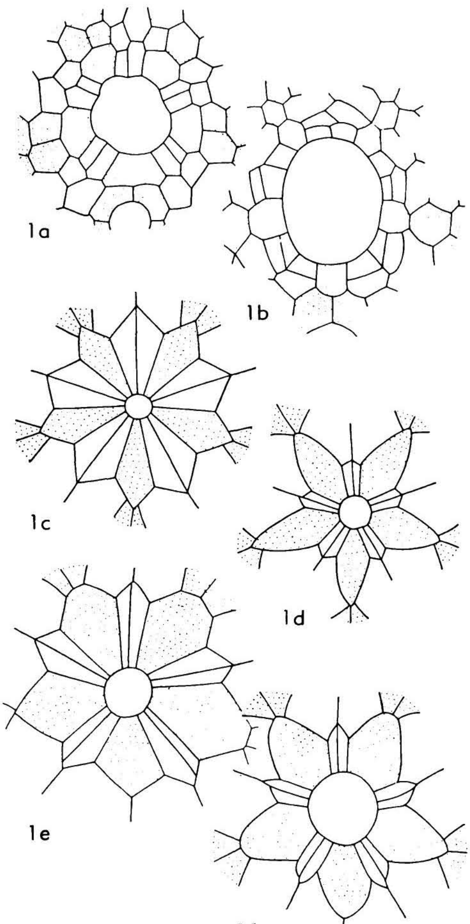

FIG. 343. Clypeasteroid basicoronal plates (enlarged): *1a, Echinocyamus pusillus* (MÜLLER), Recent, Europe; *1b, Tarphypygus clarki* (LAMBERT), upper Eocene, Cuba; *1c, Scutella subrotunda* (LESKE), "Oligo-Miocene," Malta; *1d, Periarchus lyelli pileussinensis* (RAVENEL), upper Eocene, Georgia; *1e,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

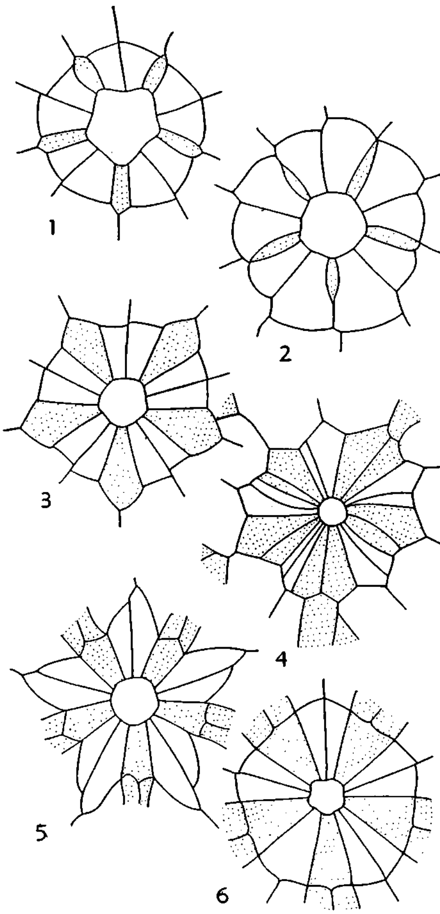

FIG. 344. Clypeasteroid basicoronal plates (enlarged): *1, Clypeaster rosaceus* (LINNÉ), Recent, Florida; *2, Clypeaster reticulatus* (LINNÉ), Recent, Philippine Islands; *3, Arachnoides placenta* (LINNÉ), Recent, east coast of Sumatra; *4, Heliophora orbiculus* (LINNÉ), Recent, Loanda, Angola; *5, Laganum 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.

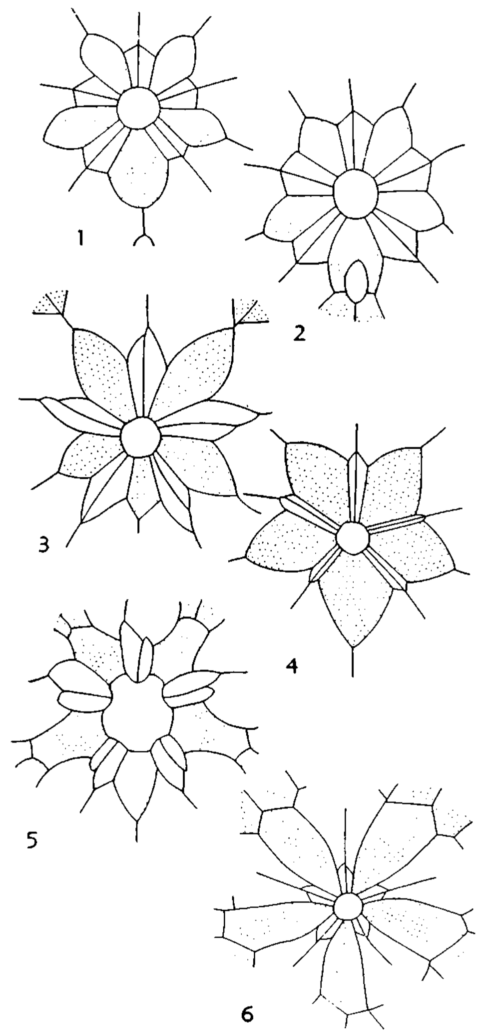

FIG. 345. Clypeasteroid basicoronal plates (enlarged): *1, Encope emarginata* (LESKE), Recent, Gulf of Mexico; *2, Mellita quinquiesperforata* (LESKE), Recent, Gulf of Mexico; *3, Vaquerosella vaquerosensis* (KEW), lower Miocene, California; *4, Amphiope bioculata* (DESMOULINS), Miocene, Europe; *5,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

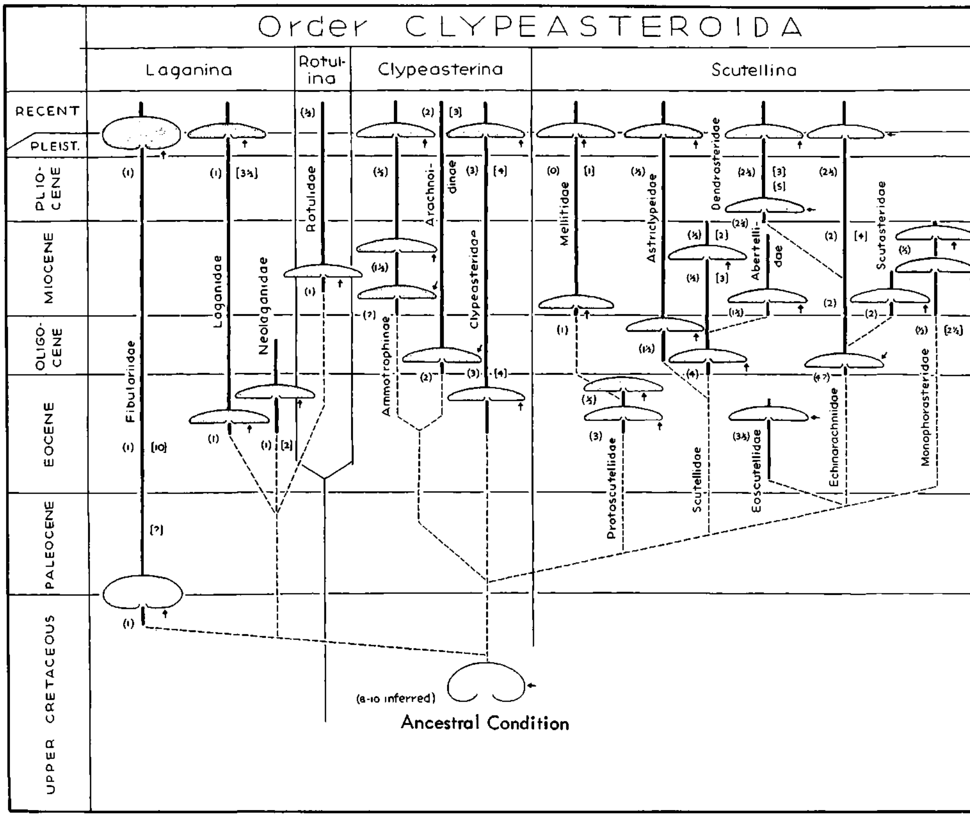

FIG. 346. Evolution of periproct position in Clypeasteroida. Diagrammatic profiles with position of periproct indicated by arrow. Minimum (in parentheses) and maximum (in brackets) numbers of plates between periproct and primordial plates indicated for each; vertical spacing proportional to time except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

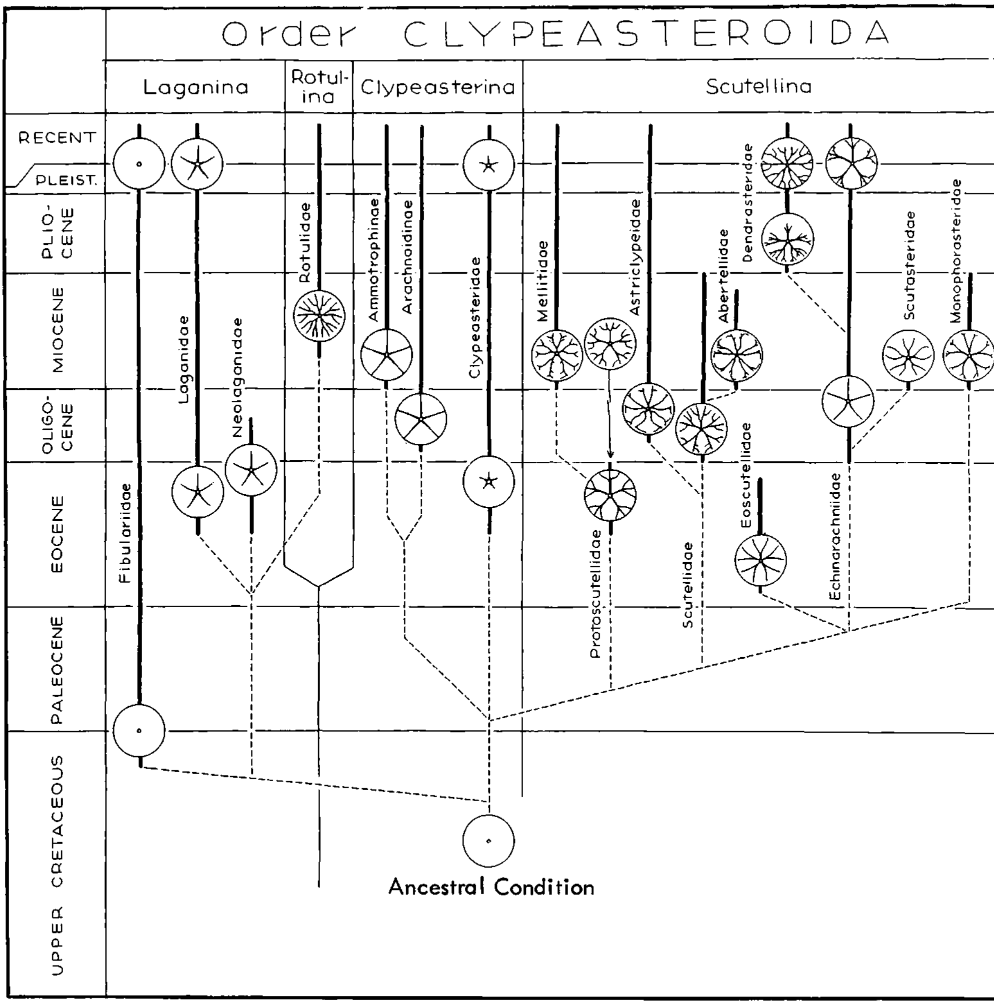

FIG. 347. Development and evolution of food grooves on oral surface in Clypeasteroida. Vertical spacing proportional to time except for Pleistocene (Durham, n).

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).

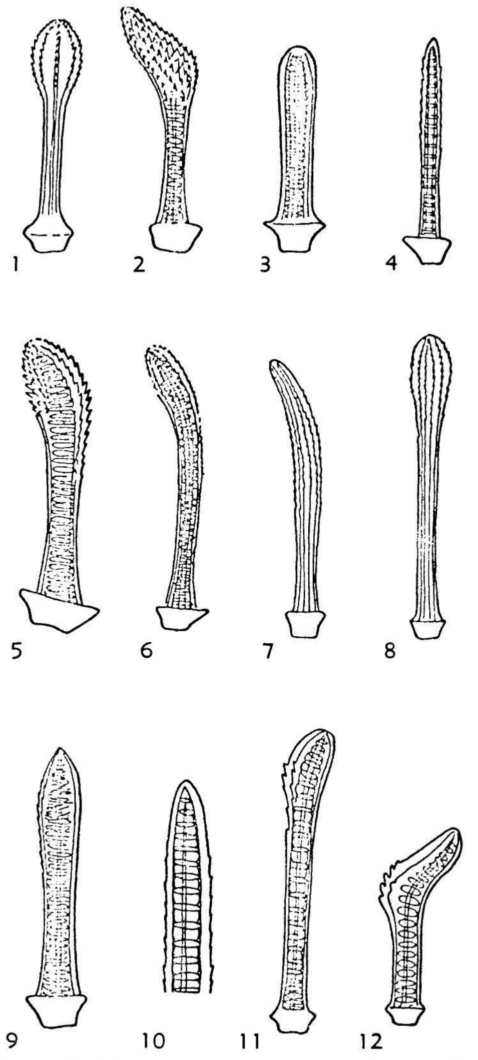

FIG. 348. Primary spines of clypeasteroid echinoids. ——*1. Scaphechinus mirabilis* A. AGASSIZ, ×45, aboral.——*2. Dendraster excentricus* (ESCHSCHOLTZ), ×55, aboral.——*3. Mortonia australis* (DESMOULINS), ×25.——*4. Fibularia ovulum* LAMARCK, ×45.——*5. Echinodiscus bisperforatus* LESKE, ×80, aboral.——*6. 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).

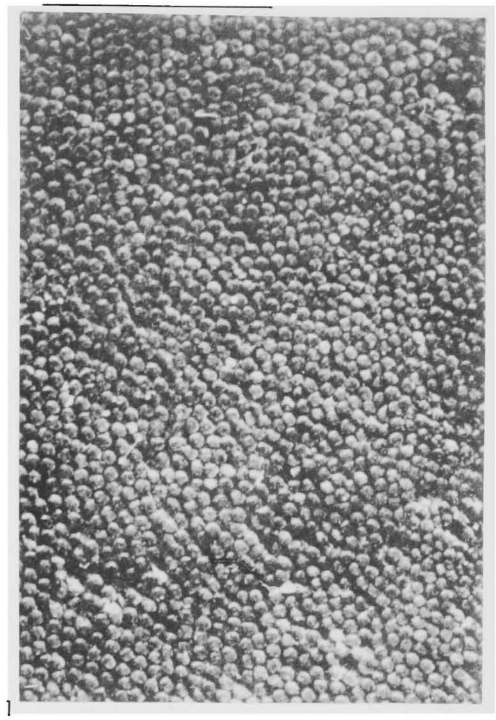

FIG. 349. Mosaic pavement effect produced by enlargement of tip of spines in *Encope wetmorei* CLARK (180).

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

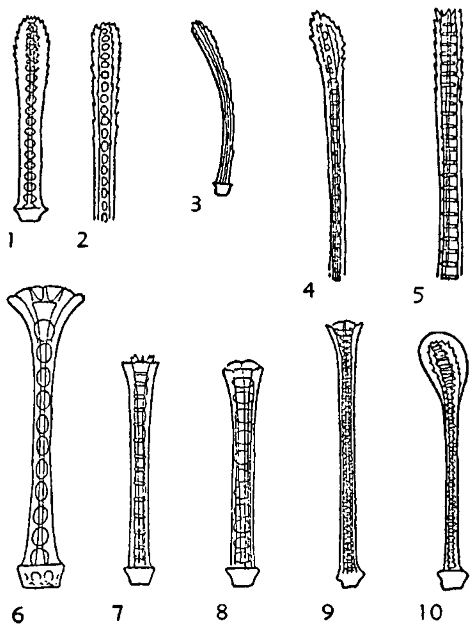

FIG. 350. Miliary spines of clypeasteroids (51, after 136g).——*1,2. Clypeaster*; *1, C. japonicus* DÖDERLEIN, ×55; *2, C. rotundus* (A. AGASSIZ), ×65.——*3. Arachnoides placenta* (LINNÉ), ×55.——*4. Scaphechinus mirabilis* A. AGASSIZ, ×100, aboral.——*5. Echinarachnius parma* (LAMARCK), ×100, aboral.——*6. 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.

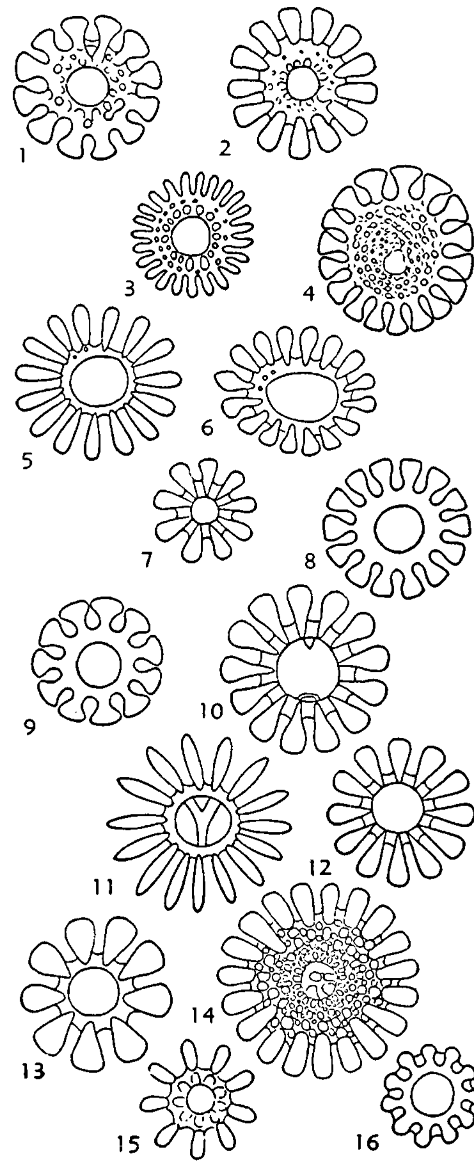

FIG. 351. Primary spines of clypeasteroid echinoids in cross section.——*1-4. Clypeaster reticulatus* (LINNÉ), ×150; *C. humilis* (LESKE), ×105; *C. annandalei* KOEHLER, ×90; *C. lamprus* H. L. CLARK, ×80.——*5. Arachnoides placenta* (LINNÉ), ×135.——*6. Fellaster zelandiae* (GRAY), ×135.——*7. Mortonia 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.

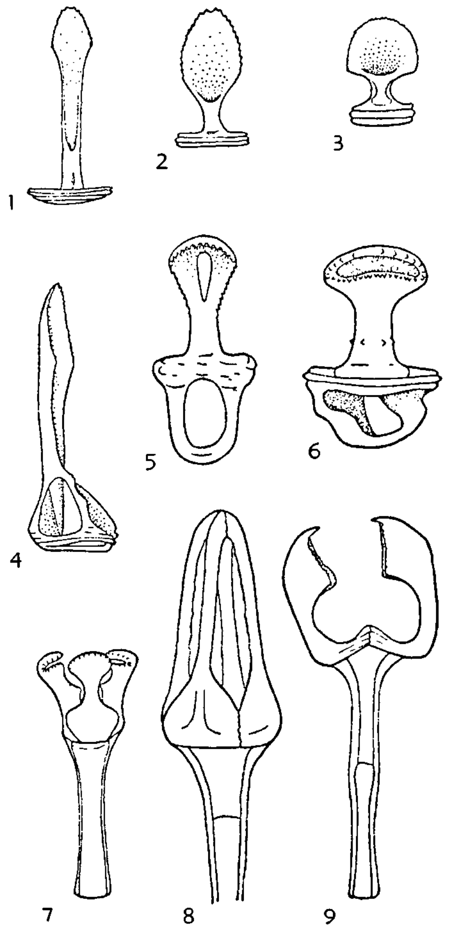

FIG. 352. Pedicellariae of clypeasteroid echinoids (51, after 136g).——*1. Jacksonaster depressum* (LESSON), ×80.——*2. Laganum fudsiyama* DÖDERLEIN, ×125.——*3,4. Clypeaster australasiae* (GRAY), ×180; *C. fervens* KOEHLER, ×42.——*5. Laganum dickersoni keiense* MORTENSEN, ×125.——*6-8. Clypeaster australasiae* (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-*

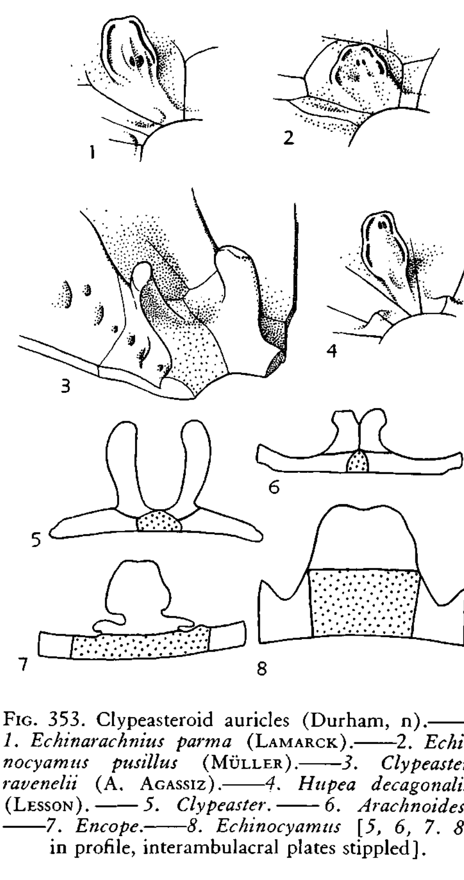

FIG. 353. Clypeasteroid auricles (Durham, n).——*1. Echinarachnius parma* (LAMARCK).——*2. Echinocyamus pusillus* (MÜLLER).——*3. Clypeaster ravenelii* (A. AGASSIZ).——*4. Hupea decagonalis* (LESSON).——*5. Clypeaster.*——*6. Arachnoides.*——*7. Encope.*——*8. Echinocyamus* [*5, 6, 7. 8,* in profile, interambulacral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

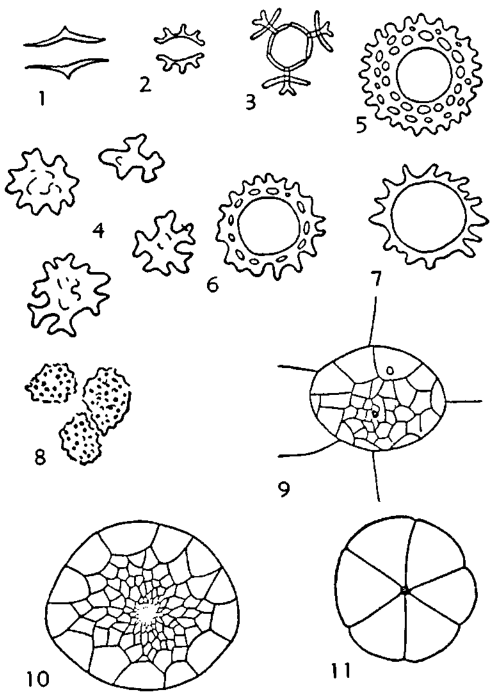

FIG. 354. Spicules, buccal plates, and periproctal plates of clypeasteroid echinoids (51, after 136g). *1. Echinarachnius parma* (LAMARCK), ×180, spicules from sucking disc of tube foot.——*2. Echinodiscus auritus* LESKE, ×210, spicules from sucking disc of tube foot.——*3. Heliophora orbiculus* (LINNÉ), ×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

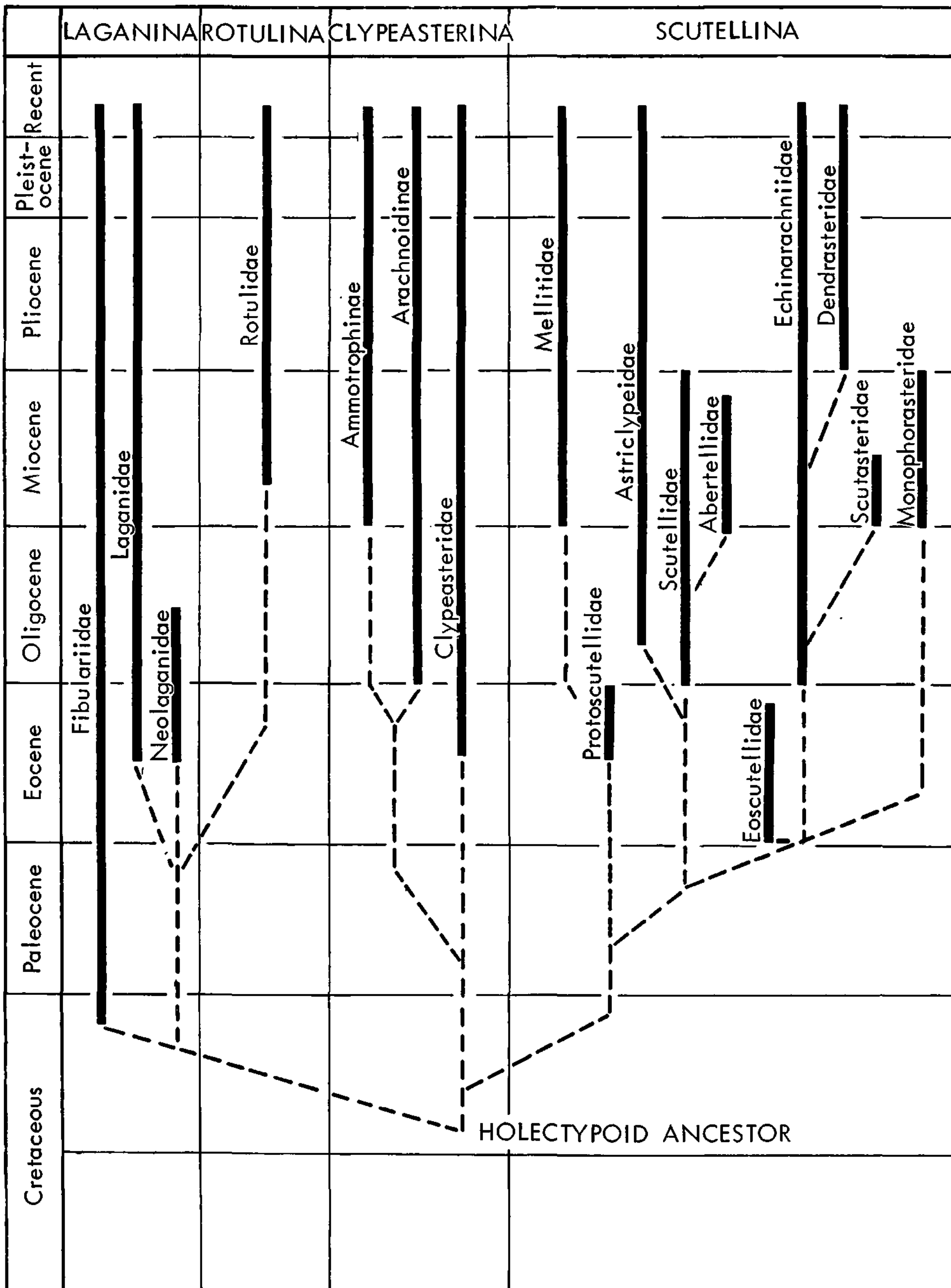

FIG. 356. Inferred phylogeny of the families of clypeasteroid echinoids (Durham, n).

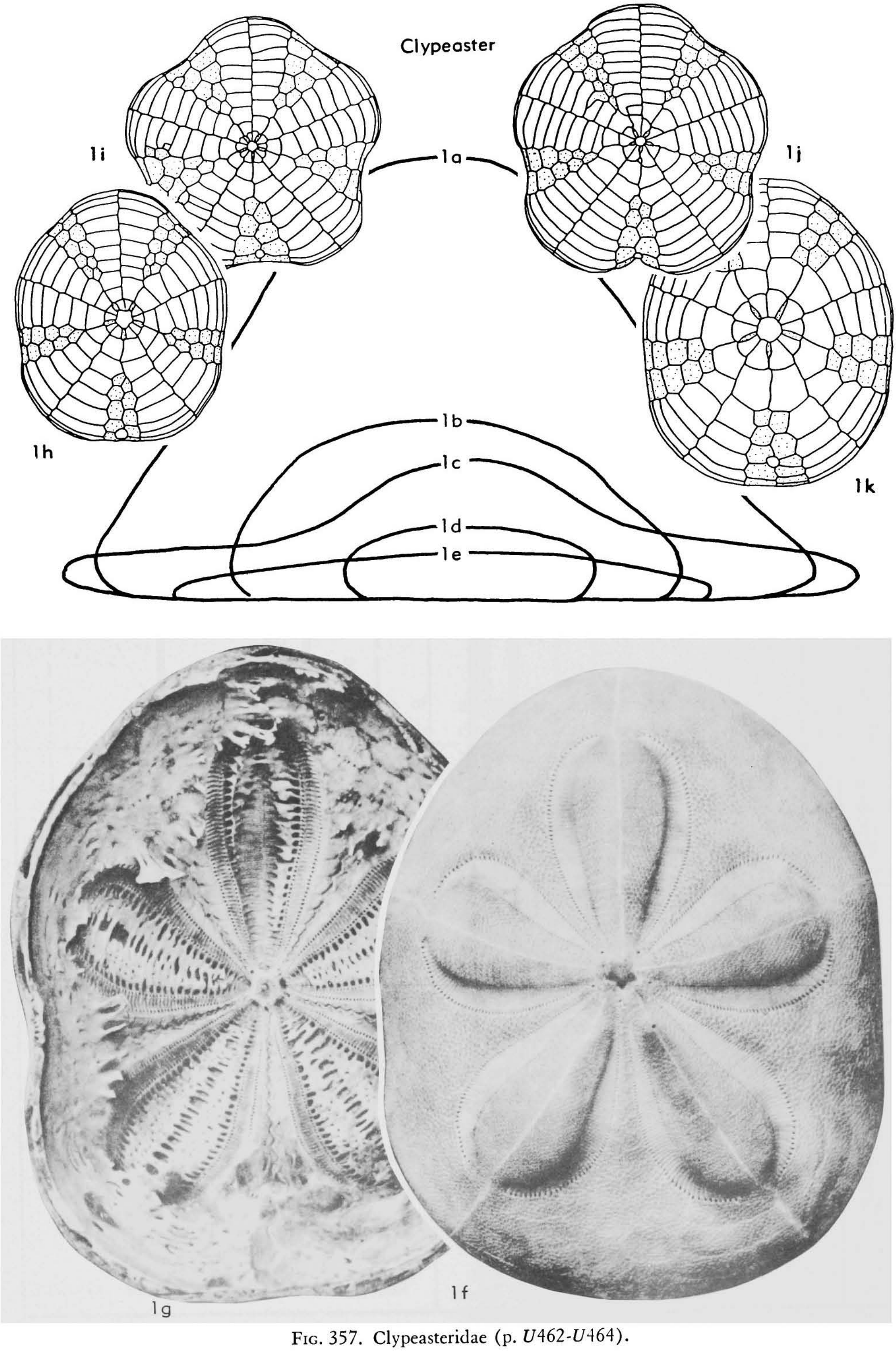

FIG. 357. Clypeasteridae (p. U462-U464).

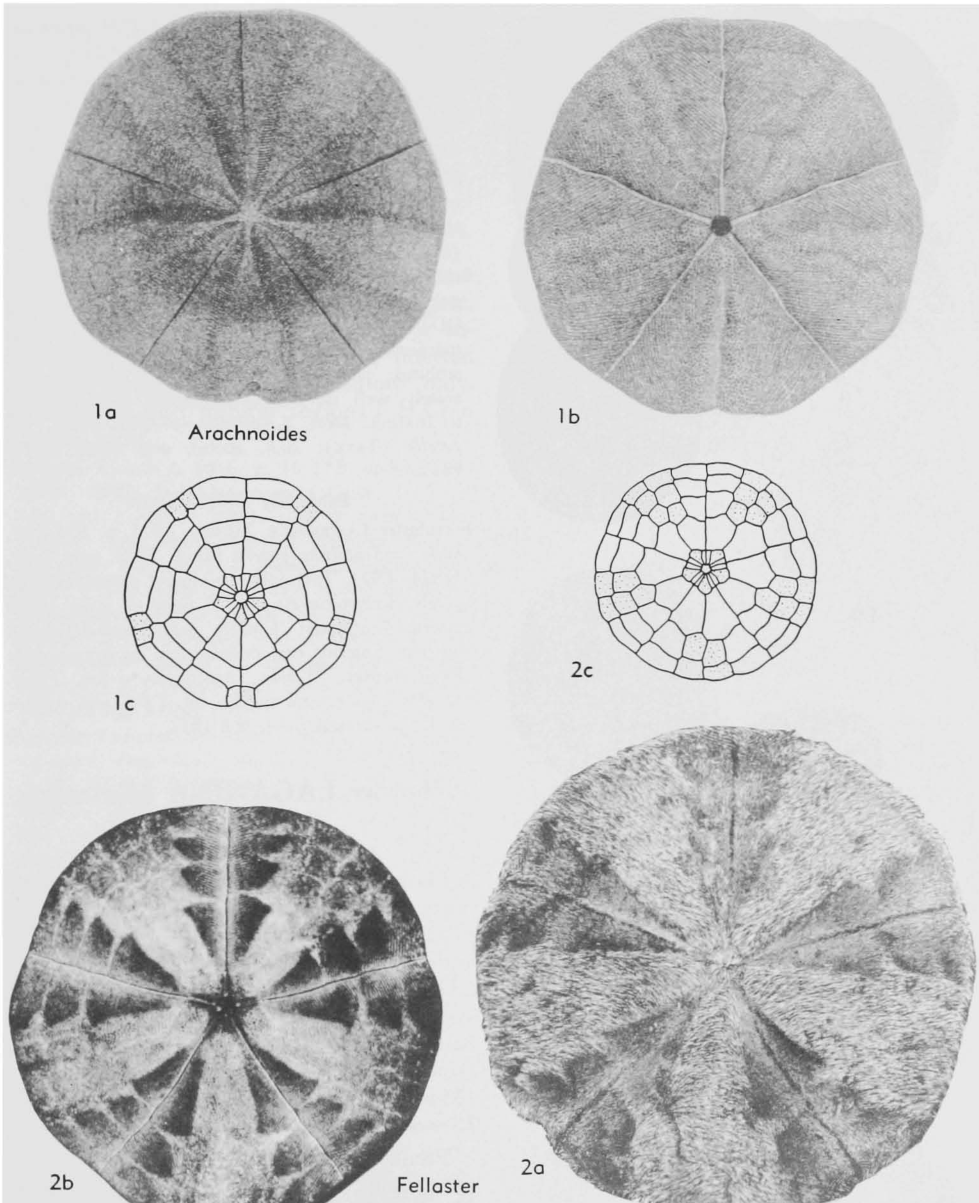

FIG. 358. Arachnoididae (Arachnoidinae) (p. *U*464).

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).

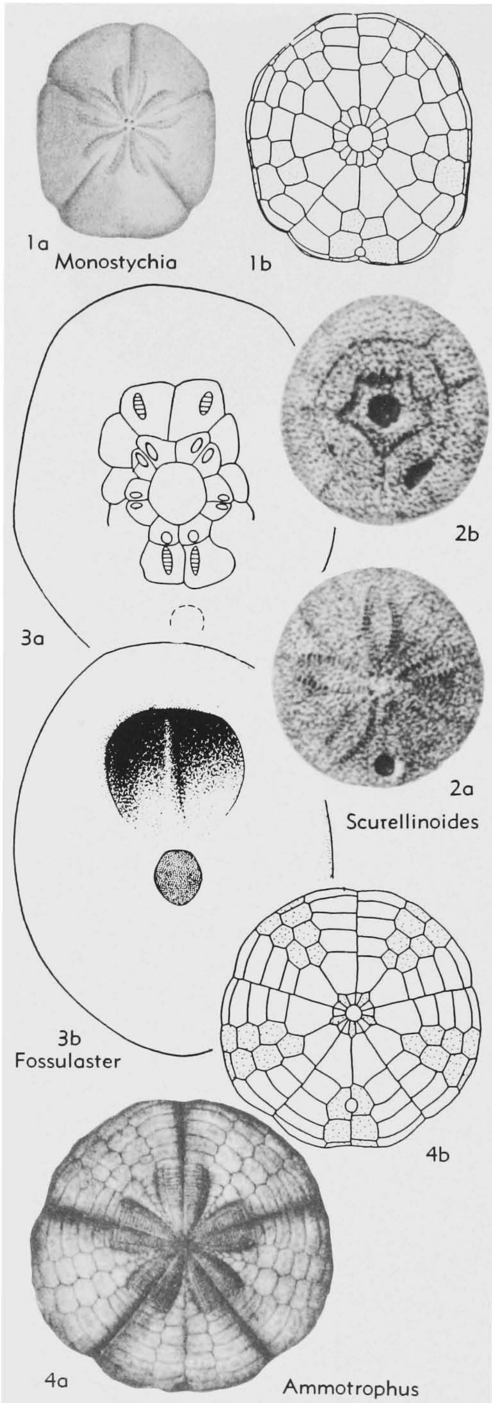

FIG. 359. Arachnoididae (Ammotrophinae) *(1-2,4)*, (Subfamily Uncertain) *(3)* (p. *U*467-*U*468).

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*.

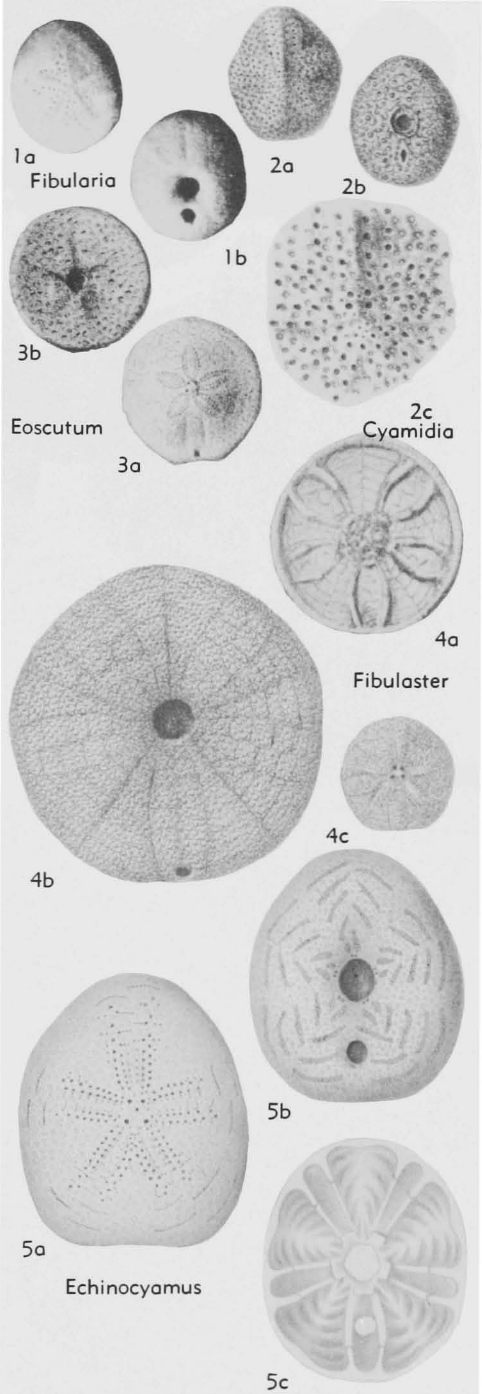

FIG. 360. Fibulariidae (p. U469, U471).

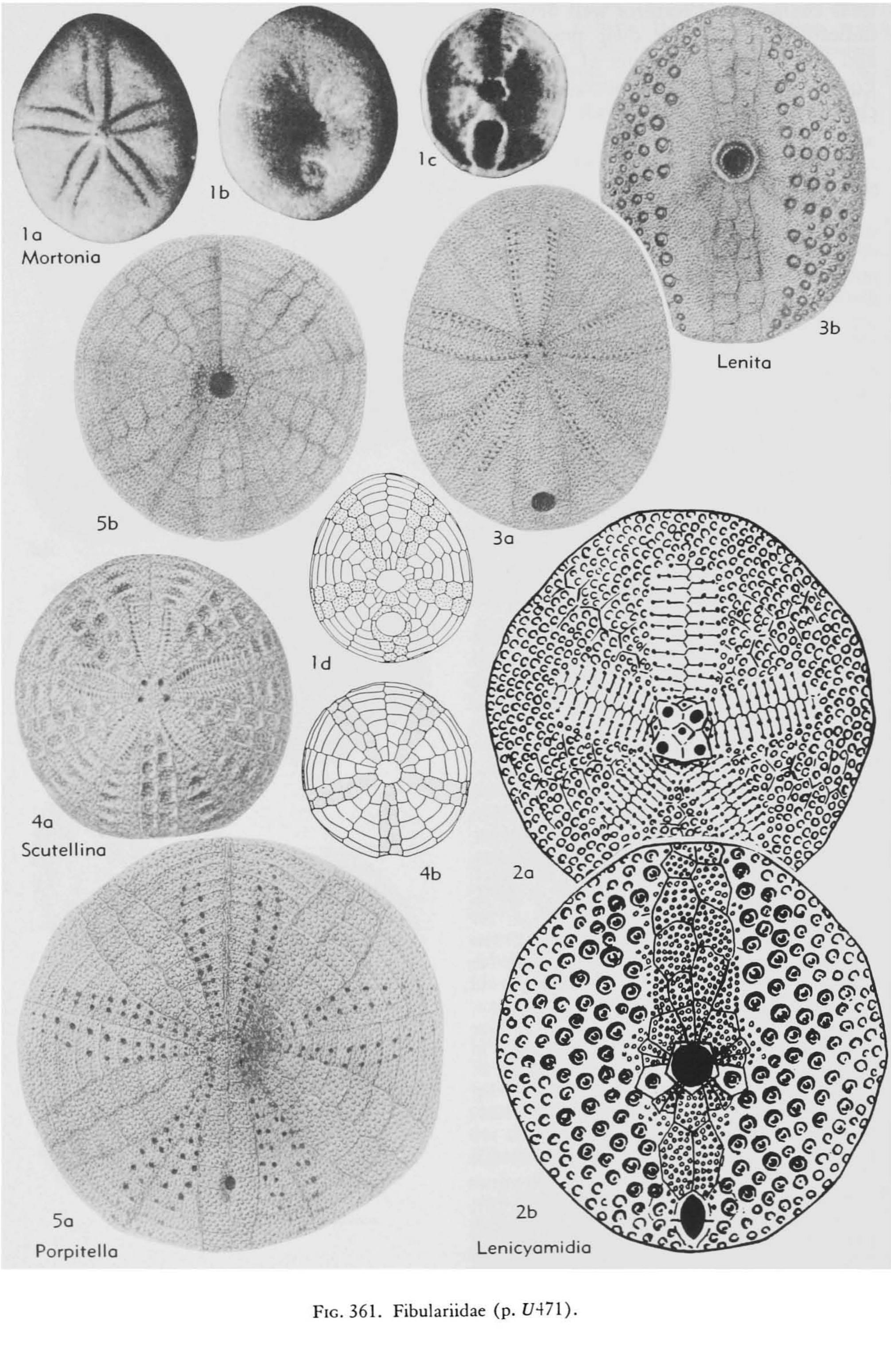

FIG. 361. Fibulariidae (p. U471).

**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;

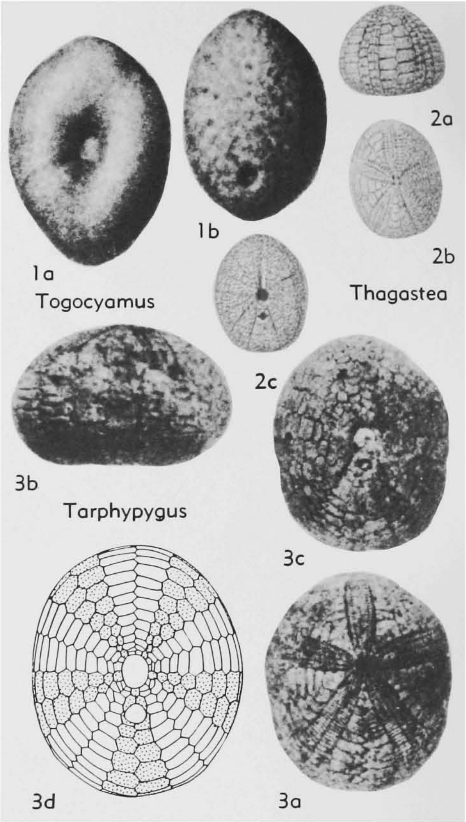

FIG. 362. Fibulariidae (p. U471-U472).

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).

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

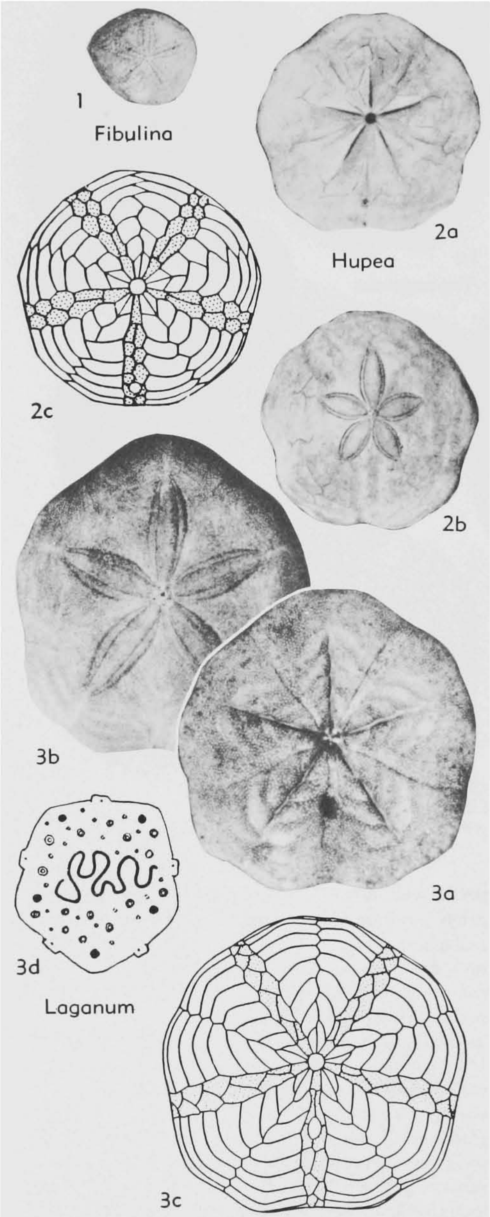

FIG. 363. Laganidae (p. U472-U473).

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

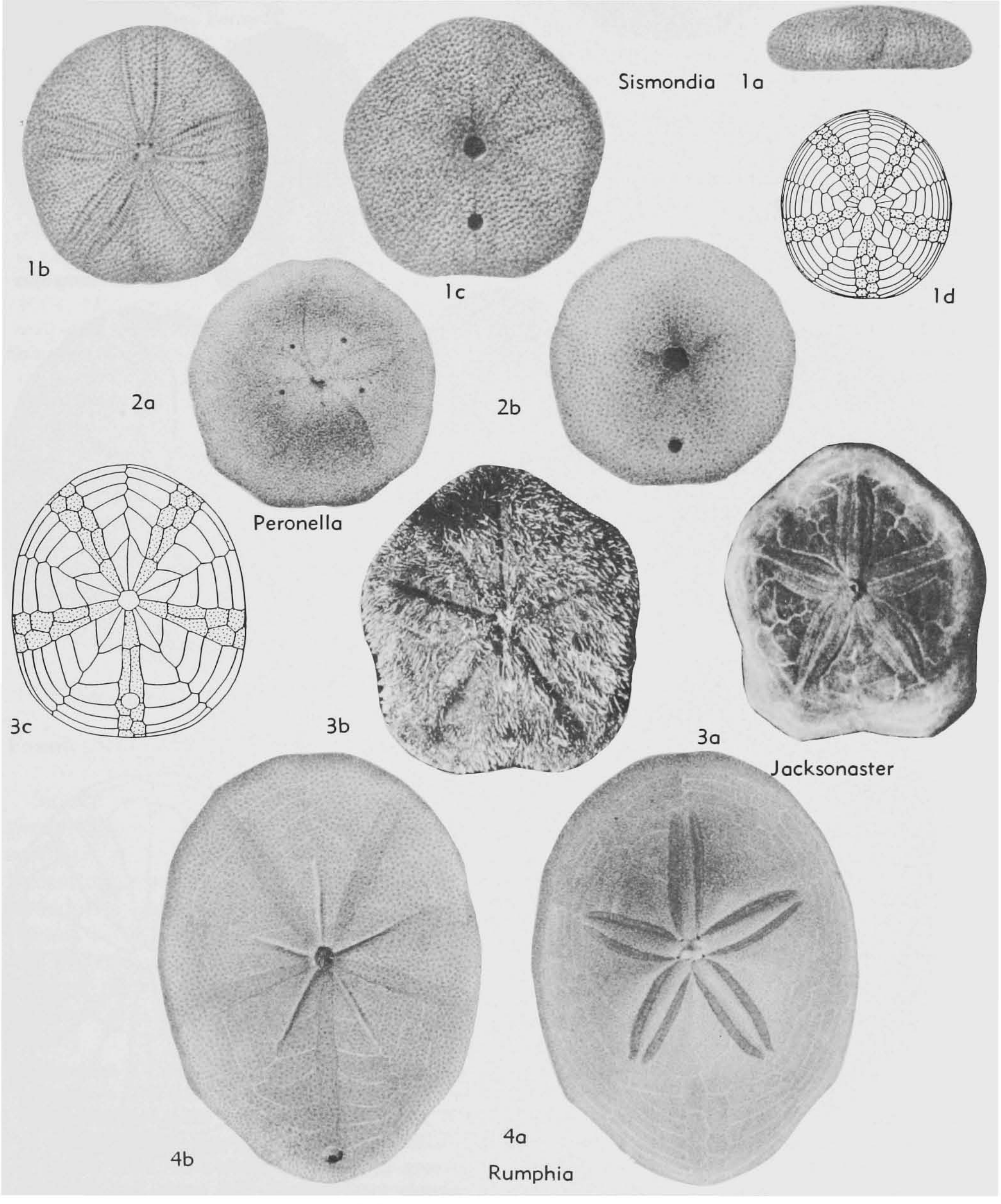

Fig. 364. Laganidae (p. *U*473, *U*475).

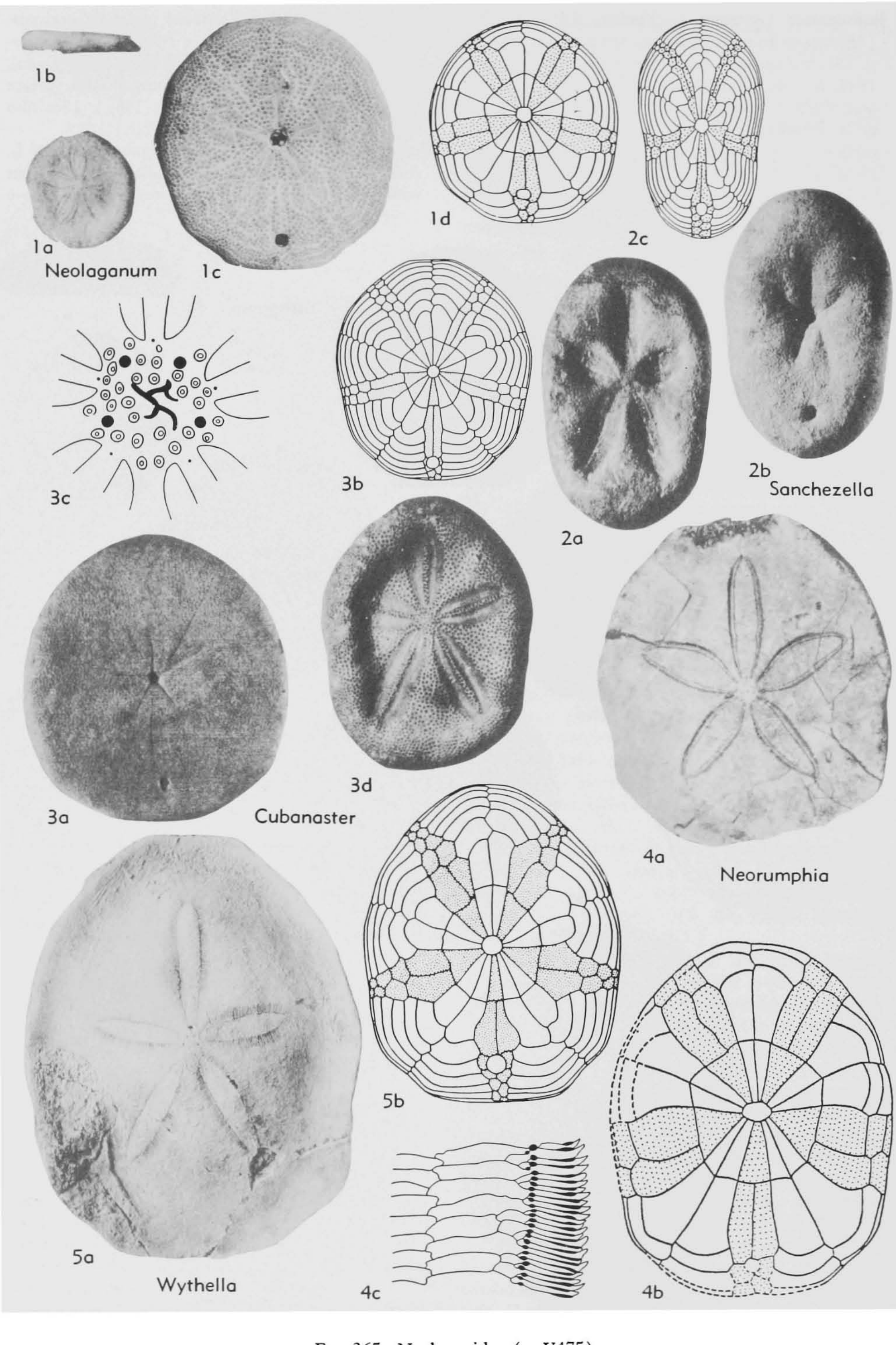

FIG. 365. Neolaganidae (p. U475).

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).

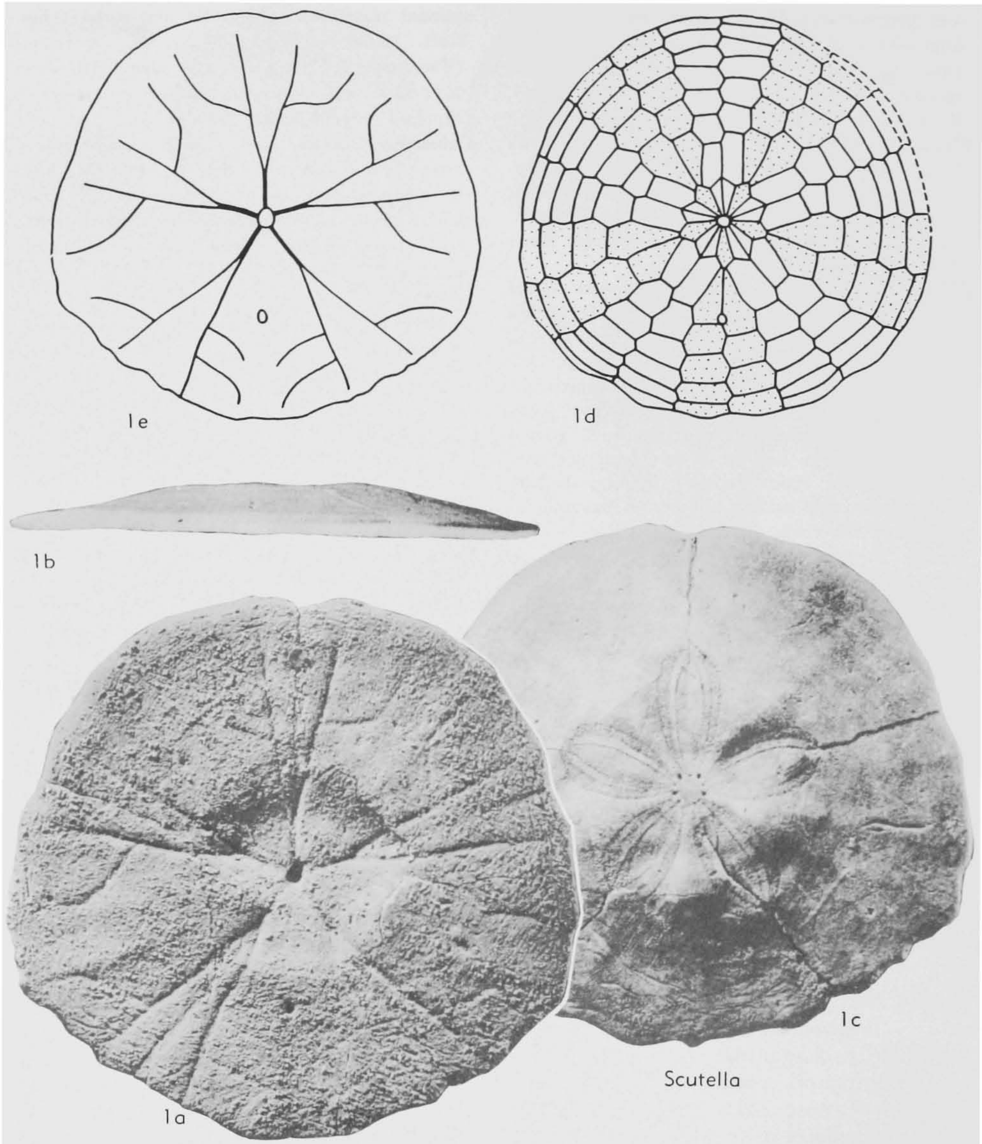

FIG. 366. Scutellidae (p. U477).

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).

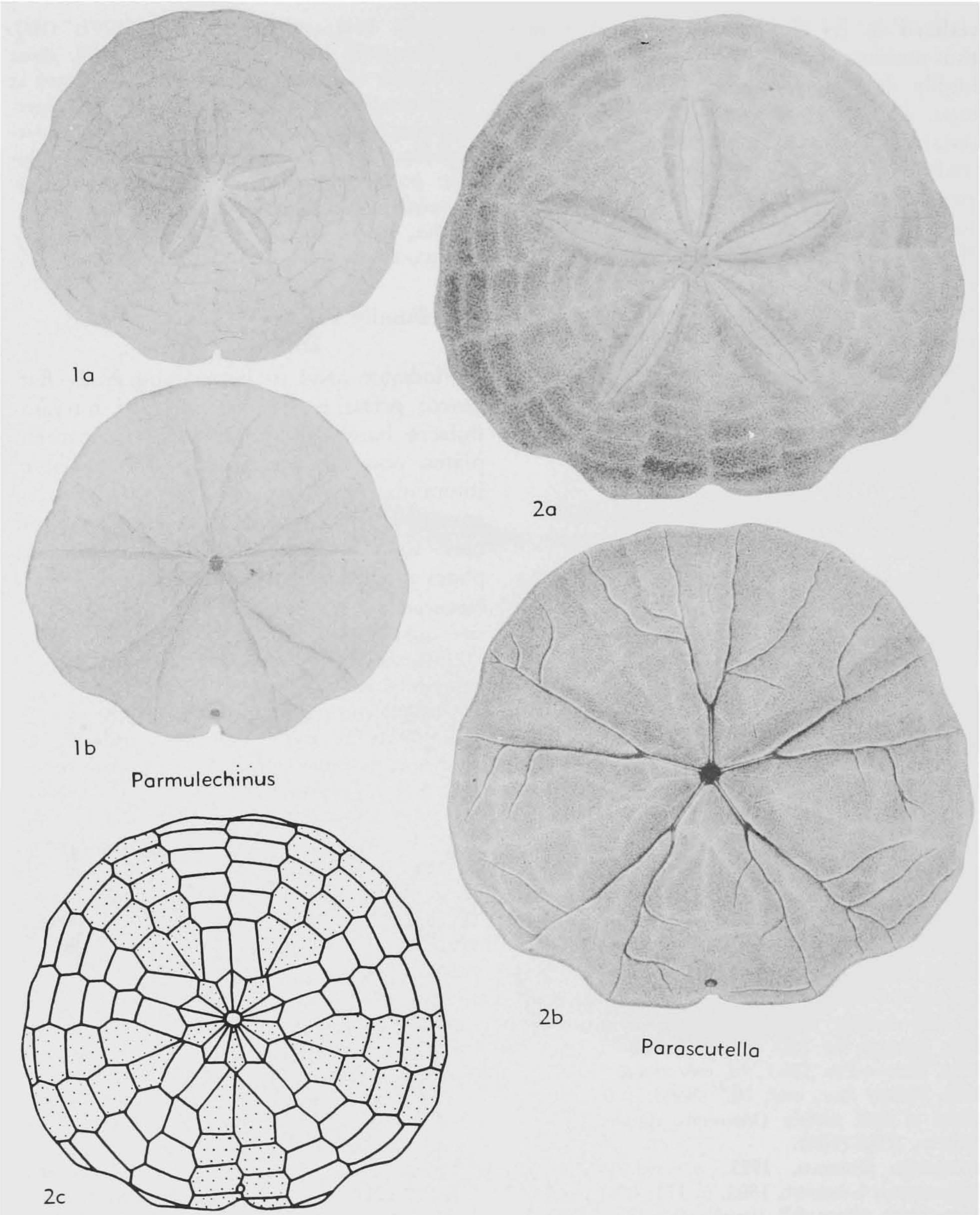

FIG. 367. Scutellidae (p. U477).

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-

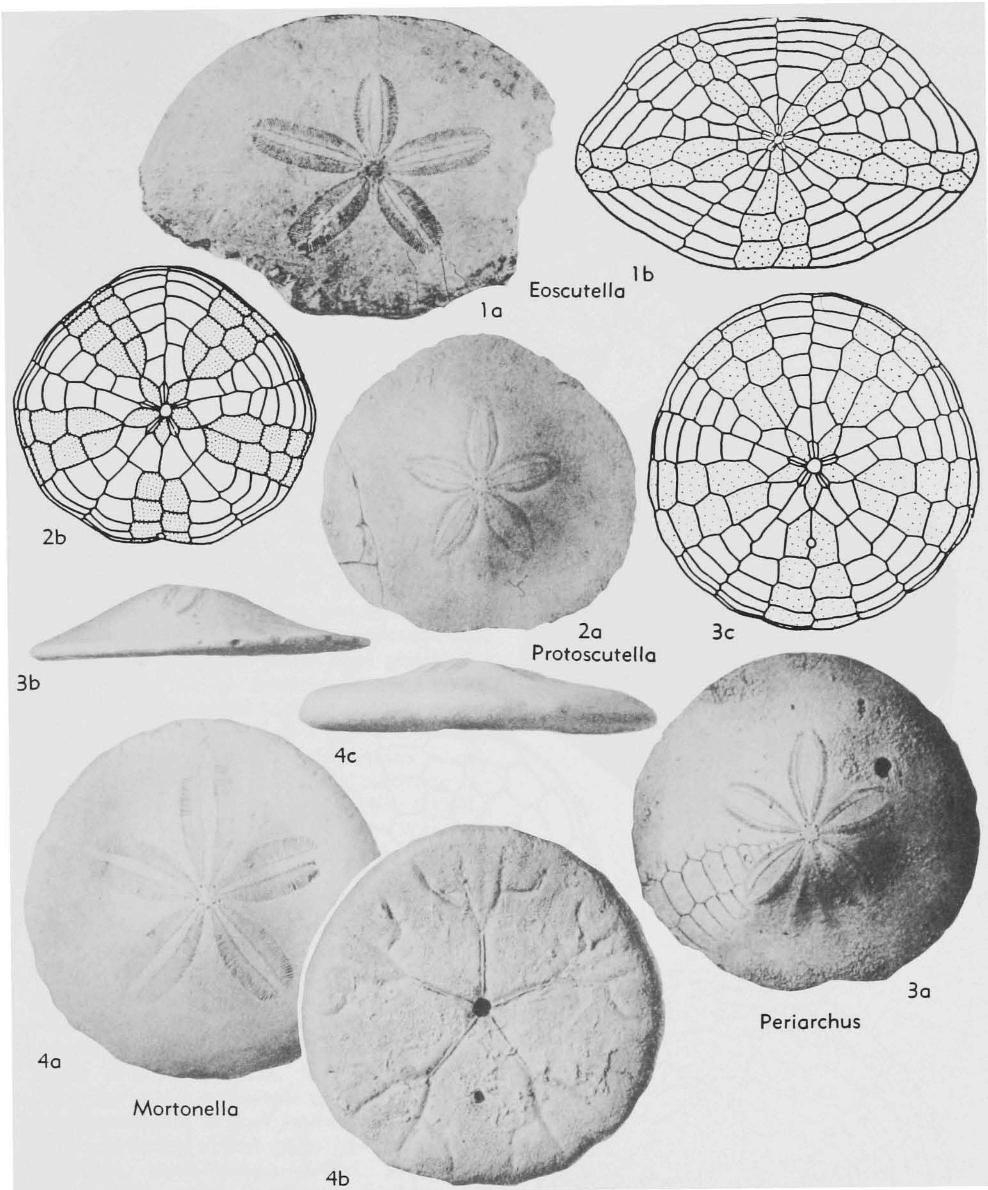

FIG. 368. Protoscutellidae *(2-4)*; Eoscutellidae *(1)* (p. *U*477-*U*479).

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.*

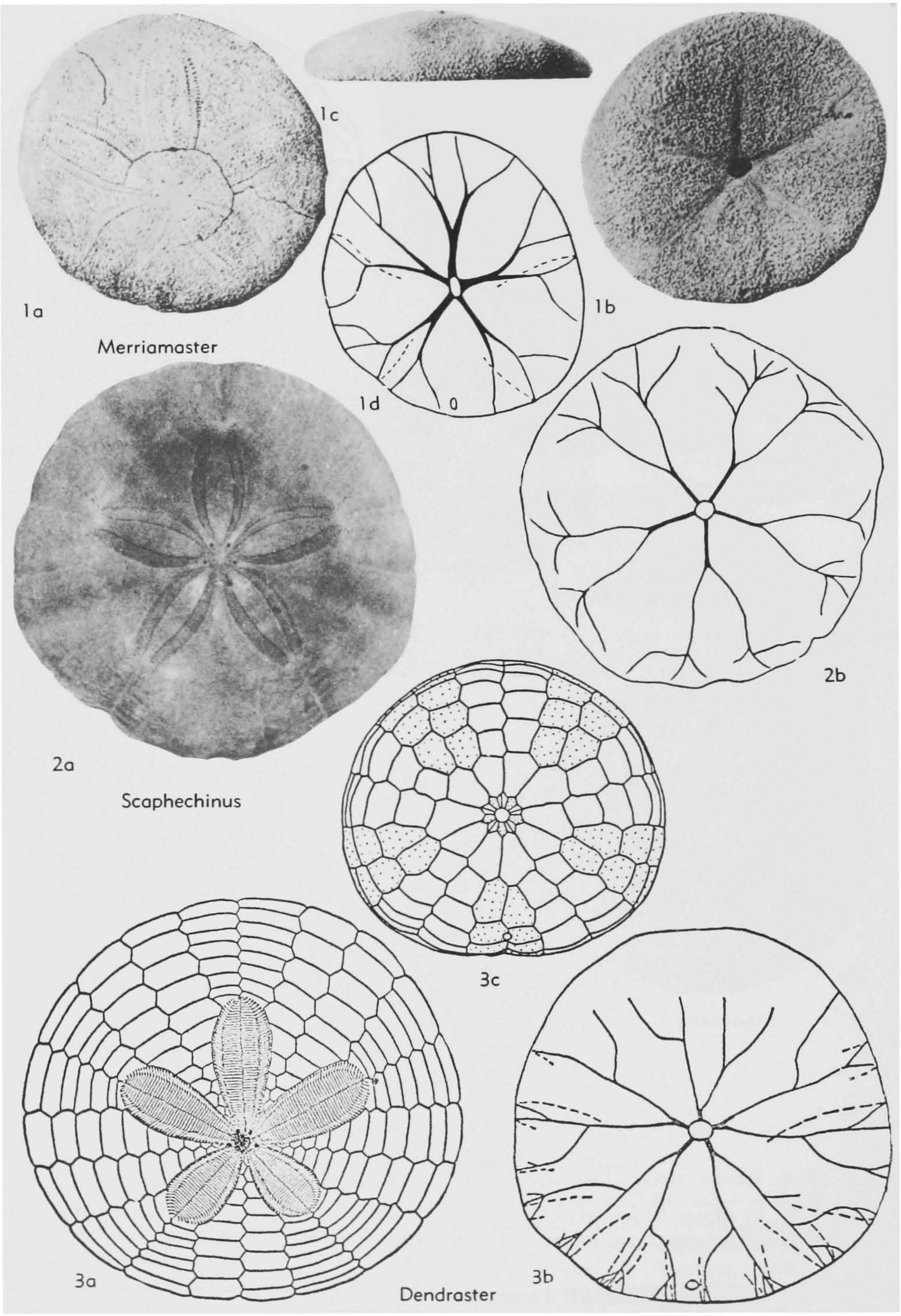

Fig. 369. Dendrasteridae (p. U481).

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;

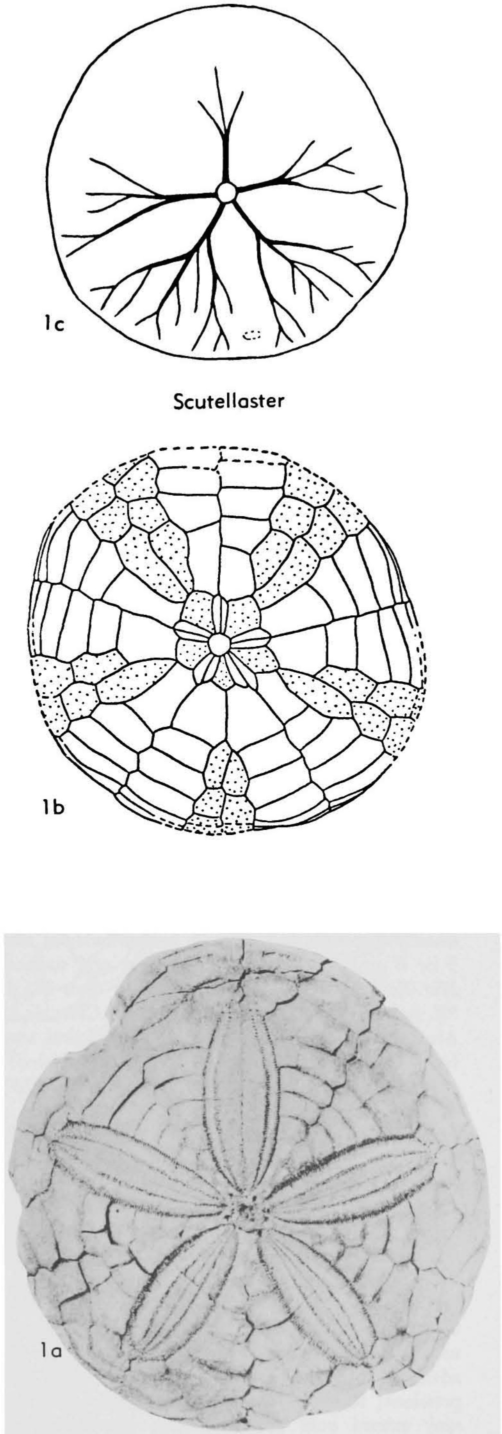

Fig. 370. Dendrasteridae (p. *U*481-*U*482).

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

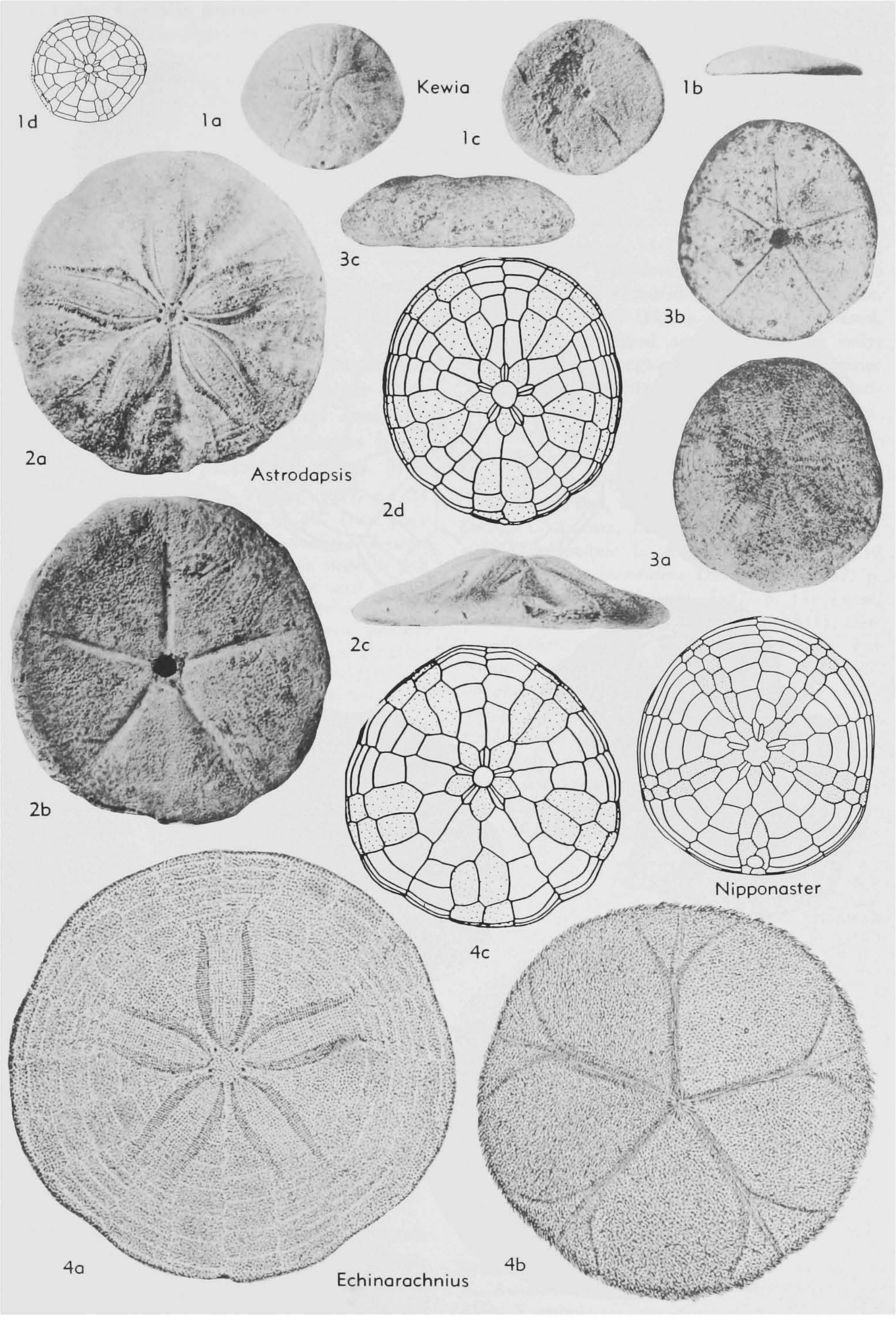

FIG. 371. Echinarachniidae (p. U482).

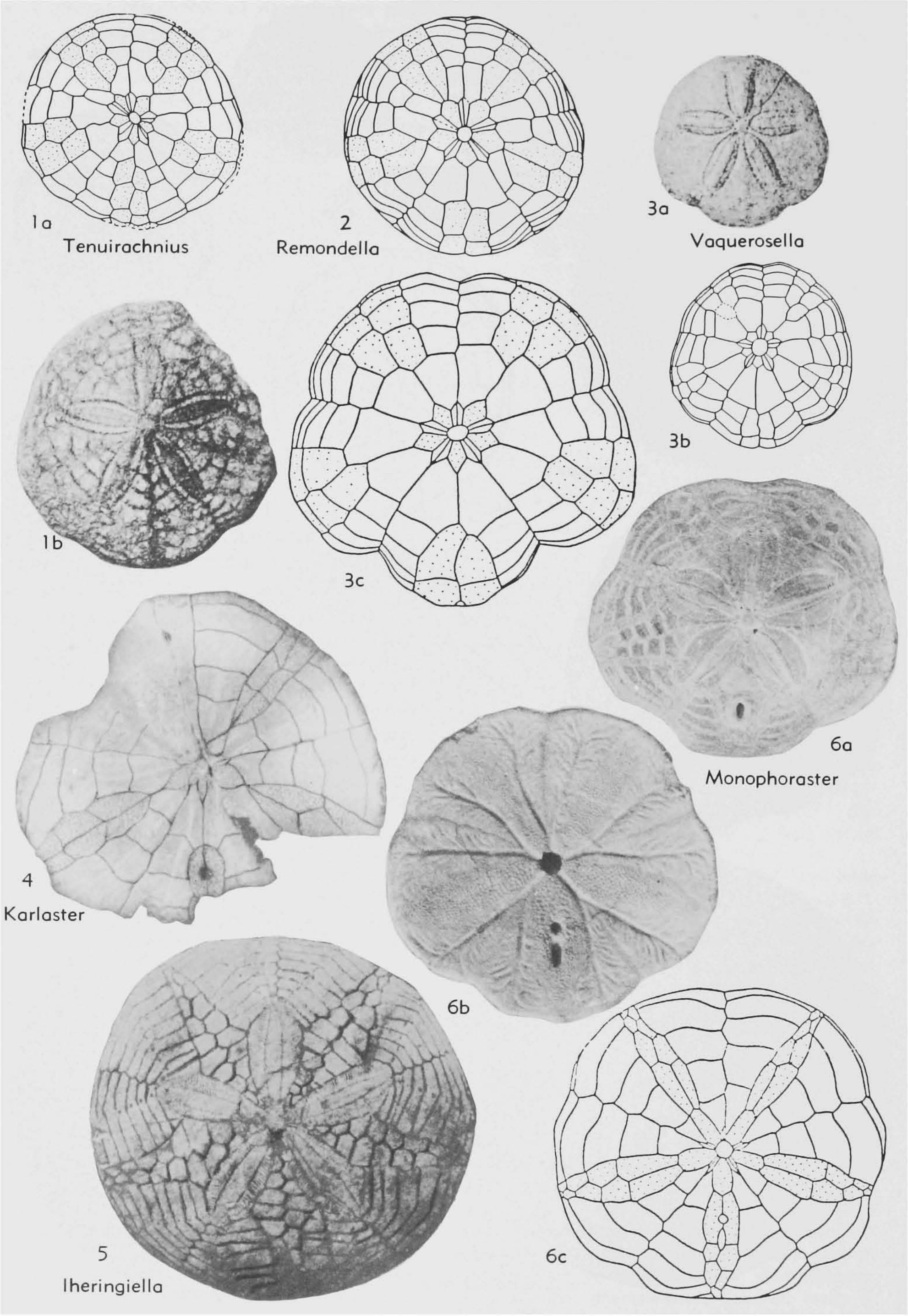

FIG. 372. Echinarachniidae *(1-3)*; Monophorasteridae *(4-6)* (p. *U*482, *U*485).

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

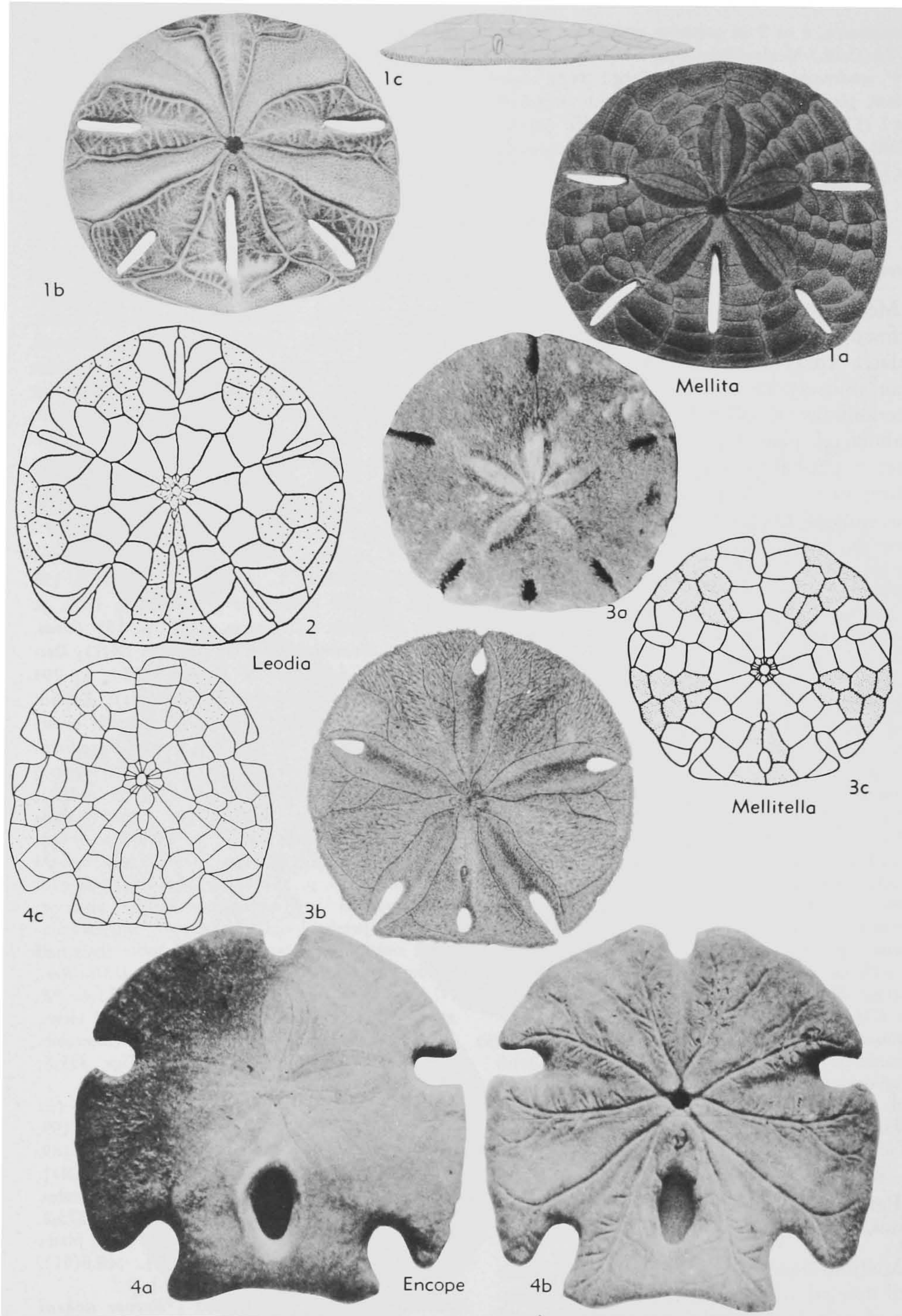

Fig. 373. Mellitidae (p. U485, U488).

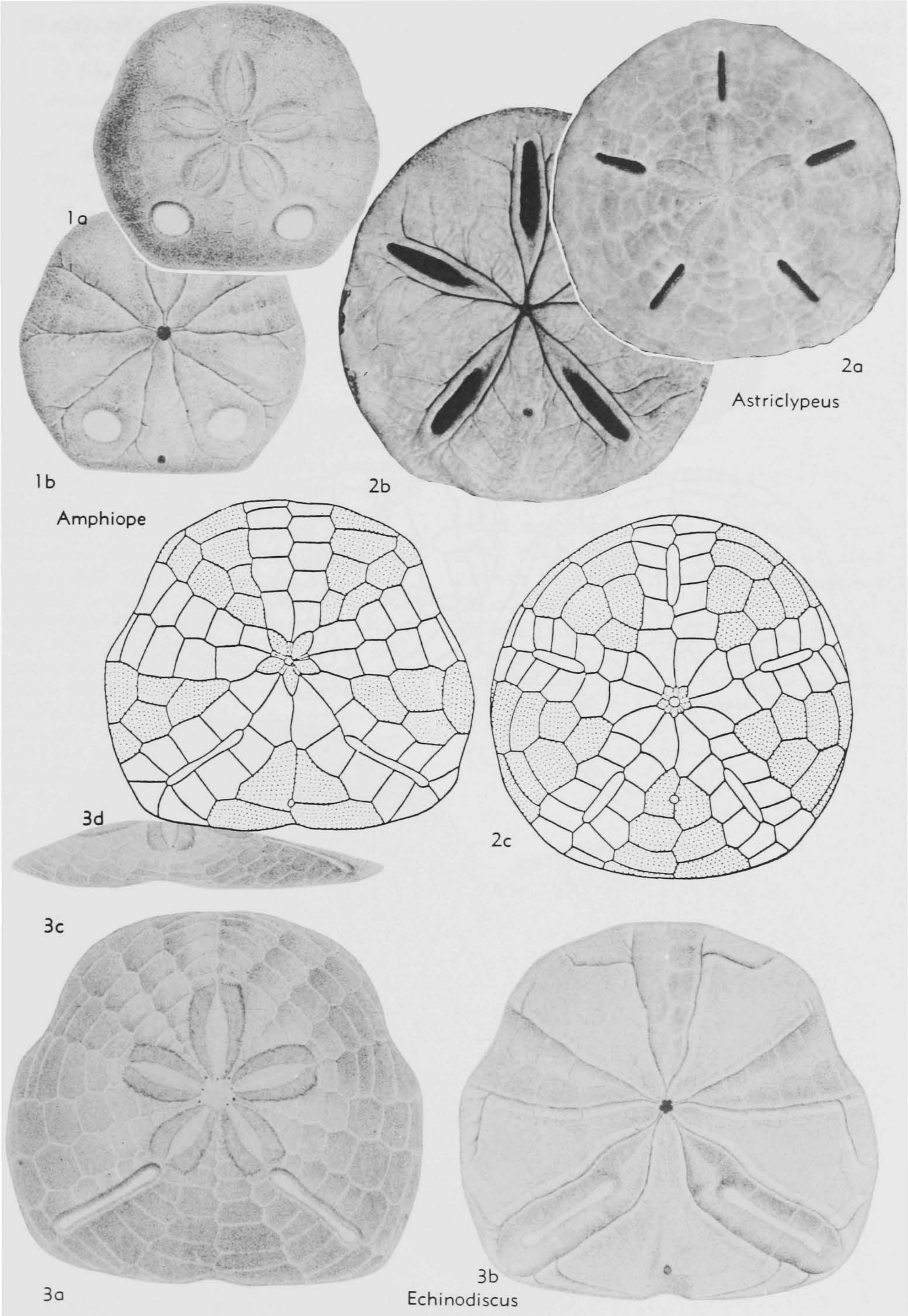

FIG. 374. Astriclypeidae (p. *U*489).

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).

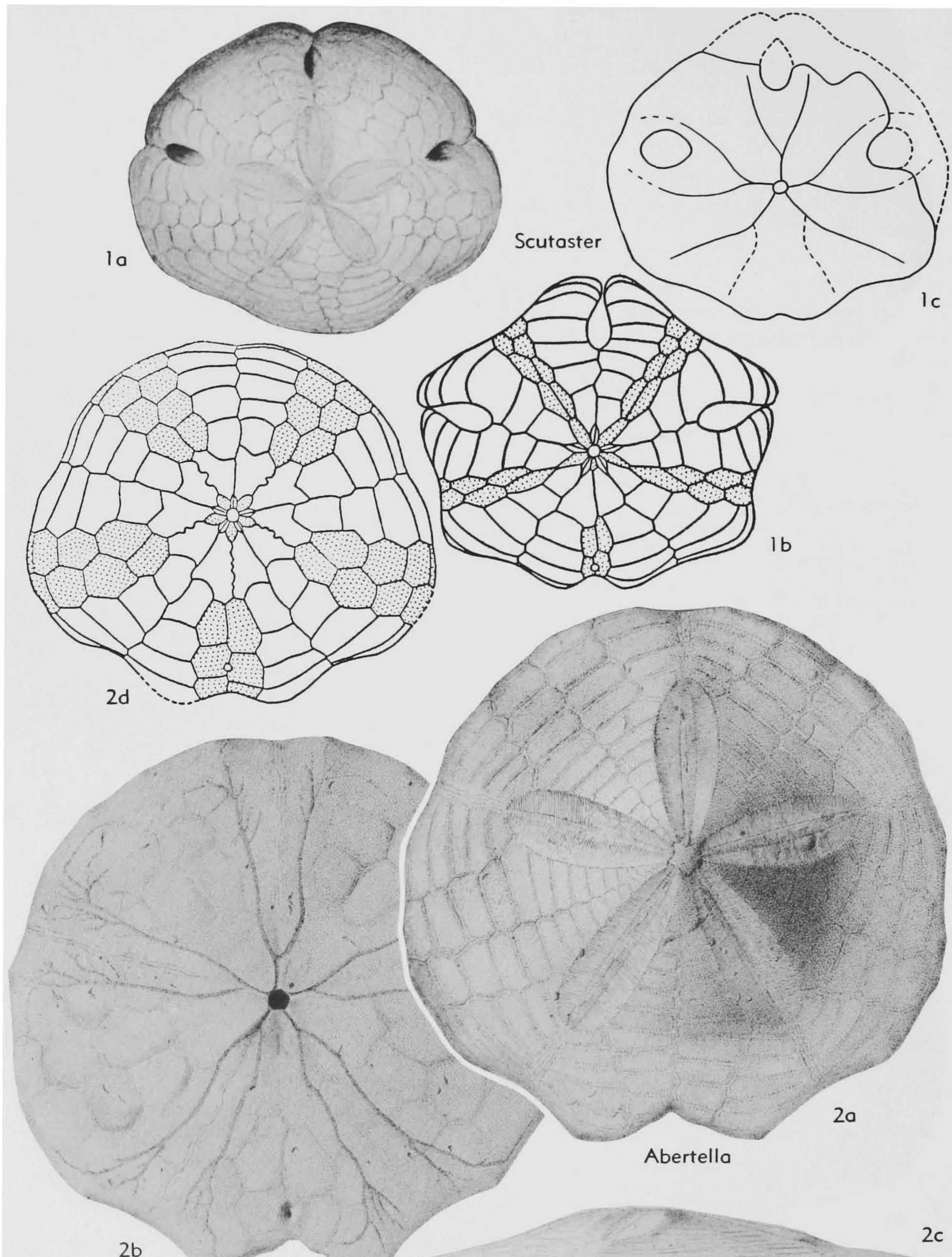

FIG. 375. Abertellidae *(2)*; Scutasteridae *(1)* (p. *U*489).

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

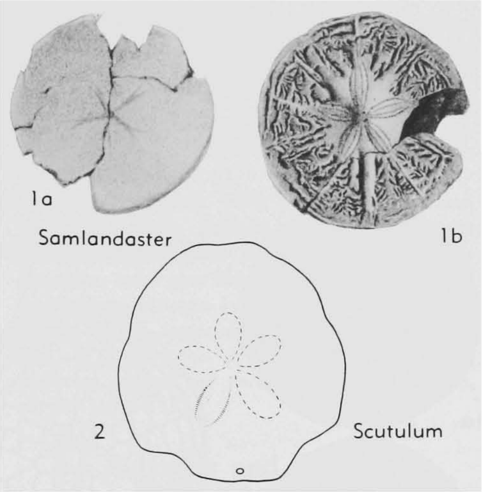

FIG. 376. Family Uncertain (p. *U*489-*U*491).

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 post-basicoronal 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).

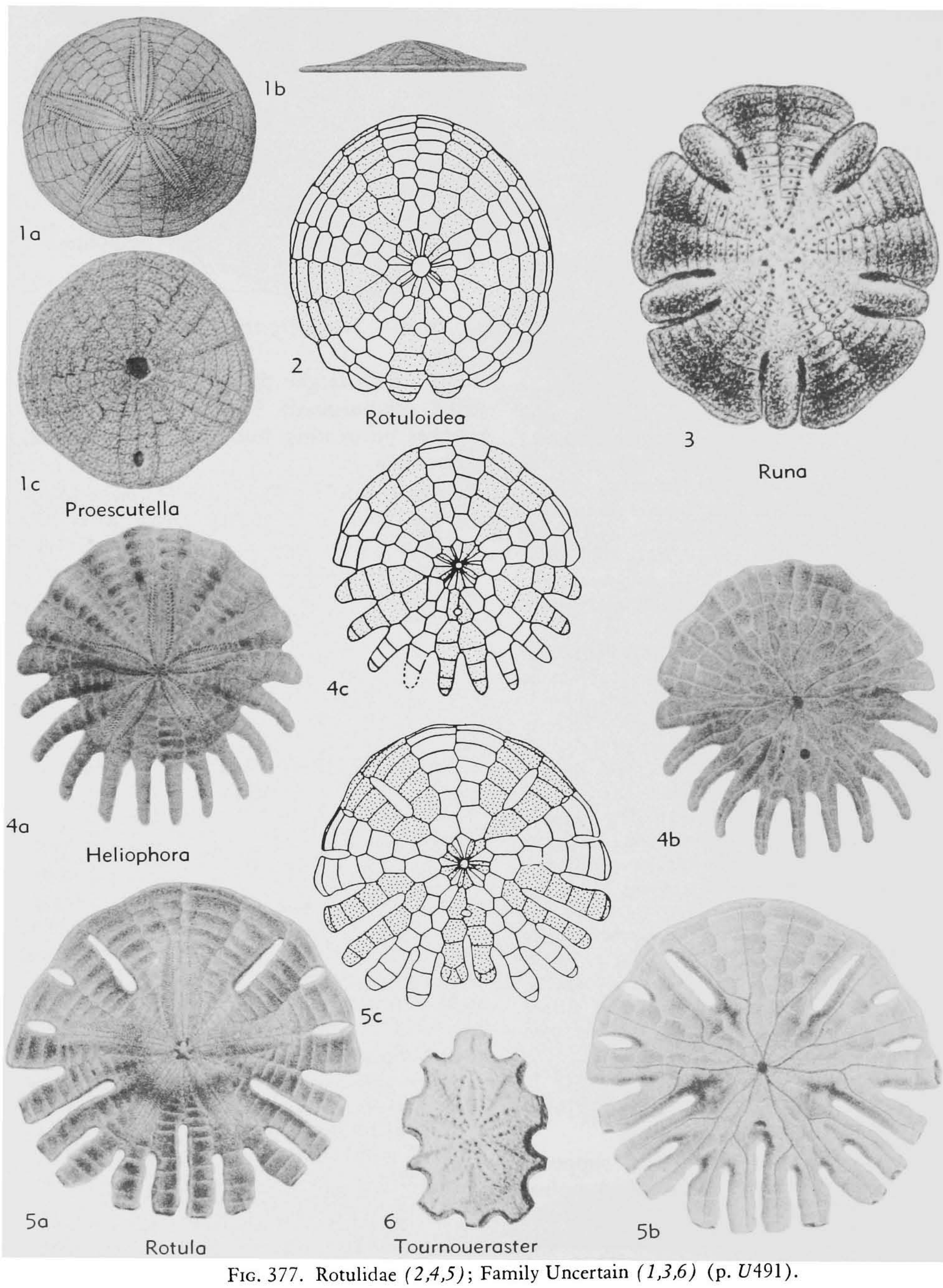

FIG. 377. Rotulidae *(2,4,5)*; Family Uncertain *(1,3,6)* (p. *U*491).

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.*