ECHINOIDS

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INTRODUCTION

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Echinoids are free-living echinoderms with a test which is subspherical or modified subspherical in shape, built of interlocking calcareous plates. The test bears movable appendages (spines, pedicellariae, spheridia) externally and commonly a masticatory apparatus internally. The mouth is directed toward the substrate. The two principal groups of plates composing the test are known as the apical system and the coronal system, the former invariably including five radially situated ocular plates and five or fewer interradially situated genital plates, and the latter composed of five radial ambulacral and five interradial interambulacral areas built of contiguous meridional columns of plates. In addition, two less conspicuous plate systems, termed peristomial and periproctal, are present. The plates of the ambulacral areas are perforated for the passage of tube feet. The ambulacral plates bordering the peristome are arranged in constant manner according to a plan which has come to be known as LOVÉN's law. An anus is situated either within the apical system or in the posterior interambulacrum. The mouth is nearly always on the lower surface, but, rarely, it is anterior. The mouth and anus are each surrounded by a membrane which usually bears imbricating or dissociated plates of the peristomial and periproctal systems. The gonads are five or fewer and are interradial in position. Radial canals of the water-vascular system are internal to the test in all except a few early genera. All known types are exclusively marine. The geological range of echinoids is Ordovician to Recent.

The basic features of echinoids are so universal and distinctive that the affinity between the most varied types (*Echinus* and *Spatangus*) was recognized by ARISTOTLE, but modifications of these features are very profound. In general, the Echinoidea fall readily into two main morphological groups which formerly were assigned subclass rank (Regularia and Irregularia), each characterized by position of the anus with respect to the apical system. In recent years the so-called Irregularia have been shown to be polyphyletic and the two subclasses have been abandoned. Nevertheless, these familiar terms serve a useful descriptive purpose and are retained here as informal divisions. The term **regular** (or **endocyclic**) is applied to echinoids in which the anus is enclosed in the apical system. In this group the jaw system (Aristotle's lantern) is well developed, pentamerous radial symmetry predominates, and the equatorial (ambital) outline is more or less circular, slightly elliptical, or regularly pentagonal. **Irregular** (or **exocyclic**) echinoids are forms having the anus outside of the apical system. In this group bilateral symmetry predominates, the ambital outline is usually far from circular, and the Aristotle's lantern is absent in many.

The skeleton is composed of thousands of separate skeletal elements, more than 3,000 in *Goniocidaris,* of many different sizes and shapes. Each piece is crystallographically a single crystal. Some have elaborate microscopic detail. The plates of the test, elements of the lantern, and the external appendages account for most of the skeletal parts, but some occur in internal organs as spicules and other isolated elements. All skeletal elements except teeth and spicules have the typical echinodermal meshwork, or **stereom,** through which the living tissue or **stroma** ramifies. The principal structure (**test**) in the form of a shell is composed of ten meridional areas, each including one or more meridional columns of plates. The five alternating areas with plates perforated by pores for passage of the primary tube feet of the water-vascular system are the **ambulacra**; the other five are the **interambulacra.** In post-Paleozoic genera two columns of plates normally are present in each area, but many Paleozoic genera (e.g., *Archaeocidaris, Melonechinus*) have a larger number and are termed **pluriserial.**

The mouth is usually on the lower surface of the test but in some genera is in an anterior position. The lower surface is usually termed the **oral** surface and the opposite side, with the apical system, the **aboral** surface. The greatest circumference of the test in a horizontal sense is termed the **ambitus.** Plates on the ambitus, which are usually the largest ones of the test in regular echinoids, are termed **ambital plates.** New plates are always formed on the aboral surface, at the head of each area. In contrast to all other living echinoderms except the Holothuroidea, the radial water vessel is internal to the test in all except a few early Paleozoic genera.

The sexes are normally separate and reproduction is always sexual. The regenerative powers are strong, new spines replacing those lost by injury or predation and damaged tests being repaired or lost sections healed over.

Symmetry is normally pentameral but rare aberrant individuals may be either completely or partially abnormal (affecting only some systems), with trimerous, tetramerous, and hexamerous types known. R. T. JACKSON (1927) and others have made extensive studies of these variations.

No echinoid is known to live in fresh water or water of very low salinity. Most living species occur in the littoral and sublittoral zones, but a species of *Pourtalesia* has been dredged from a depth of 7,200 m. Various other abyssal and numerous bathyal species have been found.

ANATOMY

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The anatomy of the Echinoidea, as enterocoelous coelomate organisms with a mesodermal skeleton and several distinct organ systems, is complex. Because echinoids are readily available, of moderate size, and relatively easy to manipulate, they have been the subjects of much experimental work. Nevertheless, details and functions of some systems, such as the hemal, are still poorly known.

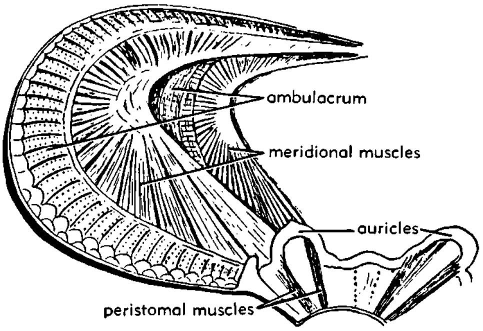

Fig. 152. Meridional muscles of *Asthenosoma* (from 4, after the Sarasins).

The anatomy of echinoids has been considered at length in the modern works of Hyman (1955) and Cuénot (1948) and in a more condensed manner by Nichols (1962) and Ailsa Clark (1962). The material presented here has been condensed largely from these publications and is intended to serve as a background for understanding and interpreting the skeletal remains found in the fossil record. Those interested in more detailed information should consult the above-cited references.

BODY WALL

The body wall of the Echinoidea consists of an external epidermis (**ectoderm**),

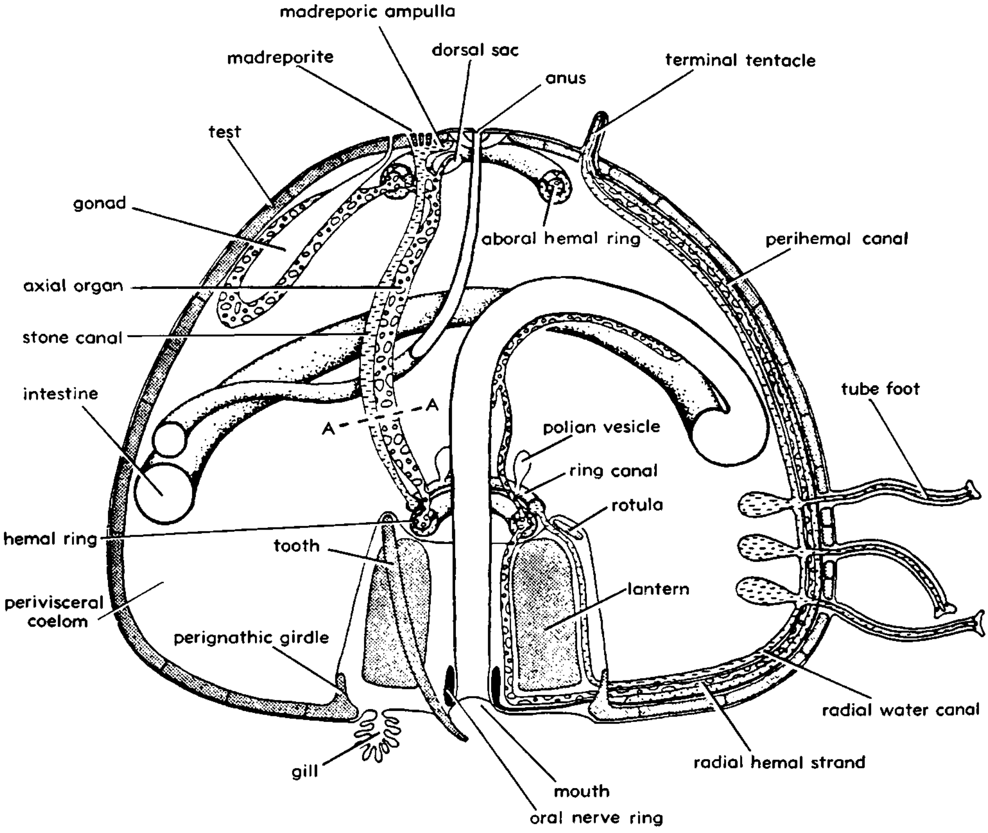

Fig. 153. Diagrammatic vertical section of regular echinoid, based on *Echinus* (5).

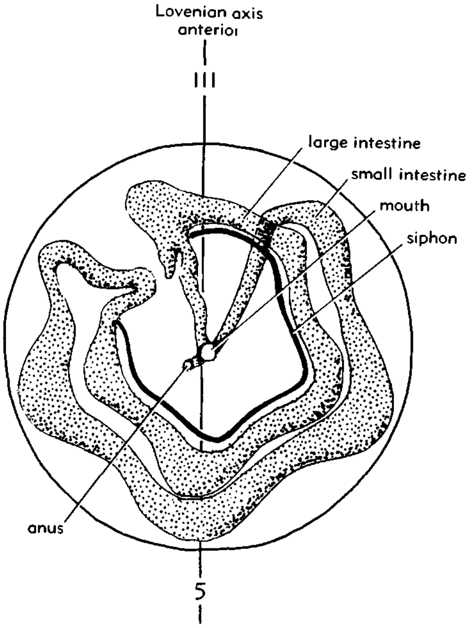

FIG. 154. Intestinal tract of *Echinus* (semischematic), oral view (modified after 3).

a middle dermis (**mesoderm**), and a coelomic lining (**endoderm**). The major portion of the various organ systems is internal to the body wall, but extensions of these systems, such as the tube feet or podia of the water-vascular system, may pass through the wall and be in contact with the external medium. Various appendages, all covered with epidermis, are attached to the body wall. These include the spines (radioles), pedicellariae, spheridia, and gills.

The epidermis is composed of a single layer of cells, and appears to be ciliated throughout, except near the outer ends of mature spines. It is usually said to be provided with a **cuticle.** Although the mesoderm is largely occupied by the calcareous plates of the test, a complex and extensive nerve plexus is present external to the plates and beneath the epidermis. Around the base of the spines and pedicellariae are two sets of muscles and a nerve ring (see Fig. 190). The outer muscle serves to manipulate movements of the spine, whereas the inner (cog muscle) holds the spine rigid if it is touched. When the tubercle supporting a spine is perforate, an elastic ligament extends from the base of the spine into the pit. The attachment of the pedicellariae is similar to that of the spines, but the muscles for the spheridia seem to be simpler in their organization. Branches from the nerve ring extend up the spines and pedicellariae.

The interstices of the plates are filled with connective tissue and stellate cells. In living echinoids no muscles are present in the body wall (the vertical muscles of the echinothurioids not forming part of the body wall proper) except for those around the base of the spines and pedicellariae. Internally, the body wall is covered by a flattened, flagellated epithelium which forms the coelomic lining. In the Echinothurioidea the imbricating plates of the test are controlled by a complex set of meridional muscles (Fig. 152) that protrude into the coelom. Peristomial muscles are also present in this group, extending along the inner surface of the peristomial plates and attaching to the auricles.

BODY CAVITY

The body cavity enclosed by the test of echinoids is divisible into several differently named spaces or hollows (coelomata). The main or **perivisceral coelom** includes most of the interior of the test (Fig. 153). The lantern and immediately adjacent organs of echinoids with external gills are enclosed within the **peripharyngeal coelom** (Fig. 155). In addition, in regular echinoids a small **perianal coelom** surrounds the anus, and is in turn enclosed in a slightly larger **periproctal coelom.** Another ring-shaped sinus, the aboral or **genital coelom,** occurs on the inner surface of the plates of the apical system and encloses the aboral hemal ring and the hemal network supplying the gonads. These aboral coelomic cavities may be fused into a single aboral sinus in irregular echinoids.

The coelomic spaces are filled with a fluid similar to sea water, the coelomic membranes being more or less permeable. The coelomic fluid contains various types of wandering coelomocytes which can move freely throughout the body tissues and organs. Experiments show that the coelomocytes originate from the mesoderm of the body wall. No special excretory organs are present in echinoderms, and it is apparent that the coelomocytes must play a major role in getting rid of waste materials.

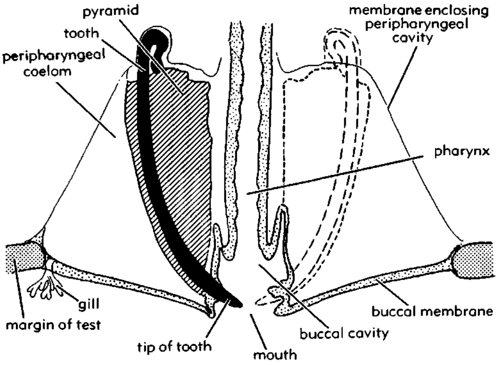

FIG. 155. Vertical section through oral area of *Paracentrotus,* showing peripharyngeal coelom and relationship of teeth to buccal cavity (modified after 3).

The **digestive tract** is prominent (Fig. 153) within the body cavity, extending from the mouth in the middle of the buccal membrane to the anus in the center of the apical system (in regular echinoids). The intestine is twisted in a loop (Fig. 154), being folded back alongside itself for part of the distance and is usually suspended by mesenteries from the interior of the test. The loop is twisted in a counterclockwise direction when viewed from the aboral side. In echinoids provided with a lantern, a small buccal cavity is present just inside the mouth and free ends of the teeth project into it (Fig. 155). A pharynx extends from the buccal cavity through the axis of Aristotle's lantern and then merges immediately into the esophagus. The esophagus then descends adorally and leads into the large intestine. This intestine continues around counterclockwise to the bend in the tract where the small intestine starts and then loops back, eventually leading to the anus. If a lantern is absent (Fig. 156), there is no buccal cavity and the esophagus connects directly to the mouth. A siphon for the passage of water to the posterior end of the large intestine branches off the main tract near the distal end of the esophagus.

The peripharyngeal cavity encloses the complex masticatory apparatus known as **Aristotle's lantern** (see "Morphology" section for description, p. *U*243) suspended within the test by a series of muscles (Fig. 157), both lantern and muscles being surrounded by a coelomic membrane. The lumen of the external gills (when present) is connected with the peripharyngeal cavity. The compasses and their muscles do not function in mastication but serve in respiration, expanding and contracting the peripharyngeal cavity and thus forcing fluid in and out of the gills. The absence of the compass in clypeasteroids is correlated with the absence of external gills. Stewart's organs, present in cidaroids and echinothurioids, are connected to the peripharyngeal cavity.

WATER-VASCULAR SYSTEM

The ring canal of the **water-vascular system** encircles (Fig. 153) the digestive tract just above the lantern and the hemal ring. The stone canal connects it to the hydropores in the madreporite and is closely associated with the axial organ. The polian vesicles arise from the ring canal in an interradial position. The radial water canals branch from the ring canal in perradial positions, run beneath the rotules and descend the sides of the lantern outside the interpyramidal muscles. The radial canal then runs between the auricles and follows up the interior of the test in perradial position to the ocular pore, passing through the latter and ending as the terminal or ocular tentacle (the so-called "eye"). The primary

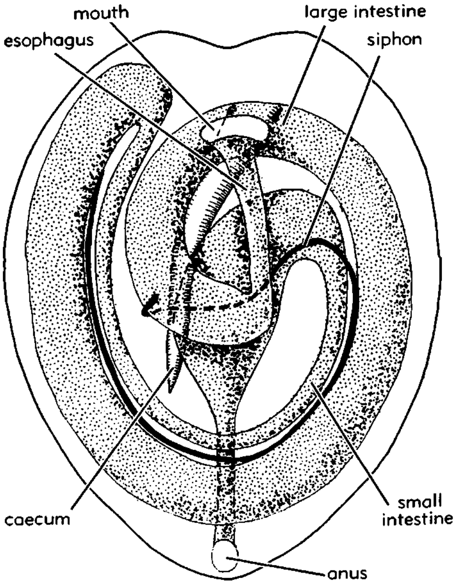

FIG. 156. Intestinal tract of *Meoma* (semischematic), oral view (modified after 4).

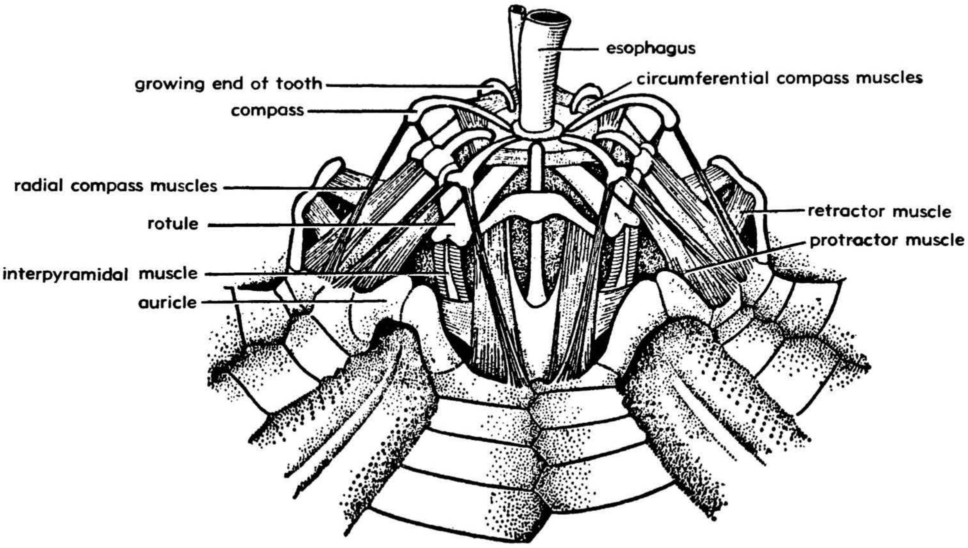

FIG. 157. Oblique view of muscles and lantern of *Echinus esculentus* (3).

podia of the late pluteus and early larval metamorphosis become the terminal tentacle of the adult. Proximally from the auricles the canal gives off an unpaired branch to the buccal tube feet and distally there are alternating branches to each tube foot and its ampulla (Fig. 158). There is a valve just in front of the ampulla. Two canals pass through the test from the ampulla and unite to form the single tube foot or podium. The relationship of the canals leading to the accessory tube feet in the clypeasteroids is uncertain, but it seems probable that they are secondary branches from the primary branches.

In regular echinoids the ambulacral tube feet are undifferentiated, being of the "suckered type," although the suckers may not be present on the younger tube feet near the apical disc. The suckered tube feet are complex (Fig. 159),. for the sucker disc bears calcareous strengthening structures, as well as muscles, a sensory ring, and mucus glands. These include a **frame** and (distal to it) the **rosette.** Calcareous spicules and other supporting structures may also be present (Fig. 160-162).

In irregular echinoids the tube feet become specialized for various functions. The primary tube feet within the petals may be bladelike or pinnate and serve for respiration (Fig. 160,*2a*; 161,*4-6*). Adoral tube feet are used for feeding and chemoreceptive purposes (Fig. 160,*2c*; 161,*1,2*), whereas tube feet within the subanal and internal fascioles (Fig. 160,*2b*; 161,*3*) are modified to serve in constructing and maintaining sanitary and respiratory tubes. These latter types, like those of some regular echinoids, may be very extensile, sometimes extending for a distance of as great as five

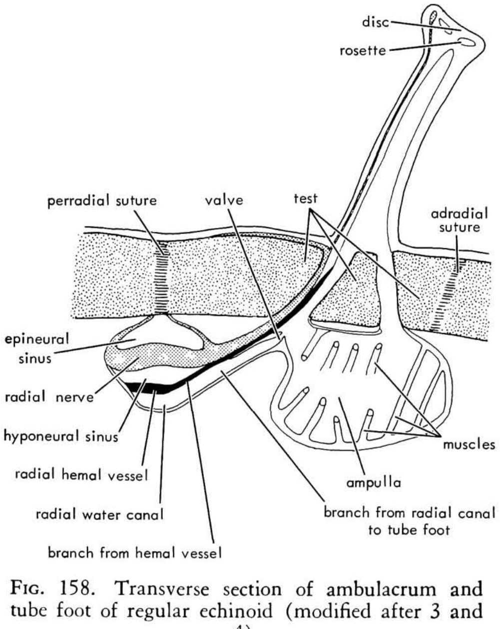

FIG. 158. Transverse section of ambulacrum and tube foot of regular echinoid (modified after 3 and 4).

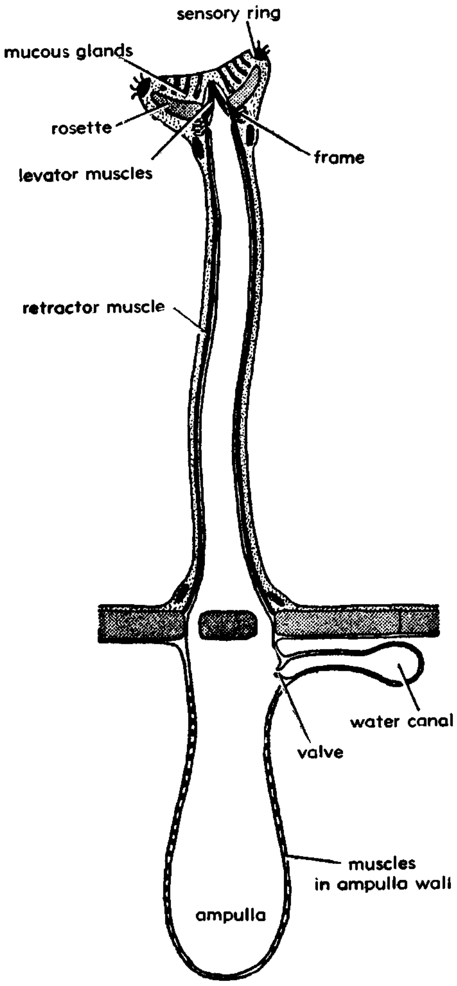

Fig. 159. Diagrammatic longitudinal section of a suckered tube foot (5).

times the diameter of the test. Still other types of tube feet of undetermined function (e.g., umbrella tube feet of *Micropyga,* Fig. 162) are known.

HEMAL SYSTEM

The hemal system of echinoids is closely associated with the water-vascular system. A hemal ring rests on top of the lantern, with the ring canal just above it (Fig. 153). A radial vessel passes down inside the lantern between it and the esophagus, then radially along the inner surface of the buccal membrane to the radial water canal, and finally accompanies it (Fig. 158) in an immediately external position with branches to the tube feet. In the interradial position a branch from the hemal ring leads to the polian vesicles. An aboral hemal ring is also present, located just under the apical system. A canal from the aboral hemal ring leads to the axial organ, where it branches into a highly anastomosing network of small vessels enclosing the organ. These rejoin at the oral end and then connect to the oral hemal ring. Branches from the aboral hemal ring connect with the gonads. A highly complex system of hemal vessels with many fine dendritic ramifications branches off the oral hemal ring and accompanies the intestinal tract. Some uncertainty exists with respect to the status of the radial hyponeural sinuses (Fig. 158). Nichols (5) and others consider it to form a separate circulatory system, the **perihemal** system. Hyman (4) interprets it as a coelomic canal that cushions the radial nerve and perhaps supplies it with nutrition.

The function of the axial organ (or axial gland) has been in dispute, but recently Boolotian & Campbell (1) have shown by time lapse photography that it pulses several times per minute and is a "primitive heart." Coelomic fluids are moved from

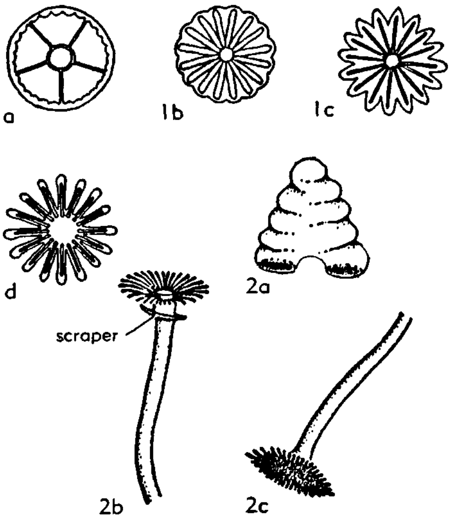

Fig. 160. Top and lateral views of tube foot.——*1.* Plan views of top of suckered tube feet, showing calcareous rosette; *1a, Echinus; 1b, Brissopsis; 1c, Schizaster*; *1d, Echinocardium.*——*2.* Lateral views of terminal disc of tube feet; *2a,* respiratory tube foot of spatangoid; *2b,* funnel-building tube foot of spatangoid; *2c,* feeding tube foot of spatangoid (5).

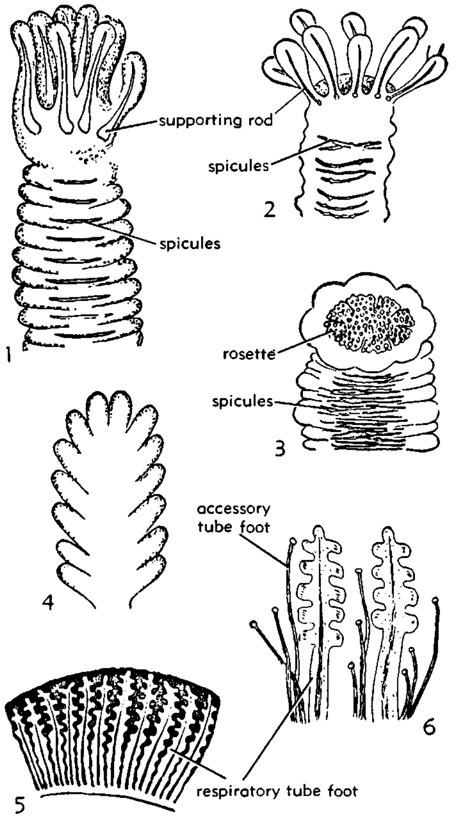

FIG. 161. Tube feet.——*1.* Frontal tube foot of *Echinocardium.*——*2.* Penicillate tube foot of *Palaeotropus.*——*3.* Subanal tube foot of *Palaeotropus.*——*4.* Respiratory tube foot from petal of *Spatangus.*——*5.* Plan view of respiratory tube feet in petal of *Clypeaster.*——*6.* Lateral view of respiratory tube feet and associated accessory tube feet in petal of *Clypeaster* (from 4, after various authors).

the perivisceral cavity into and throughout the hemal system. These authors also observed regular pulsations of the stone canal and verified a direct connection between it and the axial gland. They consider that the axial gland and pulsating stone canal are probably responsible for moving fluids throughout the water-vascular system also.

NERVOUS SYSTEM

The nervous system is external to the hemal system in position (Fig. 158), being separated from it in the radii by the hyponeural sinuses and enclosed externally by the epineural sinus and the body wall. The circumoral nerve ring surrounds the buccal cavity or lower end of the pharynx adjacent to the mouth and inside the lantern. The radial nerves follow the radial water canal and hemal vessels, separated from the latter by the hyponeural sinus. The epineural sinus, lying between the test and the radial nerve, possibly functions as a cushion. The radial nerves give off a branch to each tube foot and other branches that after passing through the pores for the tube feet connect to the extensive subepidermal nerve plexus. Another plexus of nerves from the circumoral ring ascends the digestive tract and forms a layer beneath the epithelial lining. Other branches, in radial positions, lead from the aboral surface of the ring into the muscles of the lantern. An aboral nerve ring with branches leading to the gonads has been observed in a few regular echinoids just below the apical system.

REPRODUCTIVE SYSTEM

The reproductive system consists of gonads suspended by mesenteries from the inner surface of the interambulacra, and connected by a short gonoduct to the pore in the genital plate of the apical system. In regular echinoids there are five gonads, but in irregular echinoids they may be reduced in number to as few as two. *Schizaster*

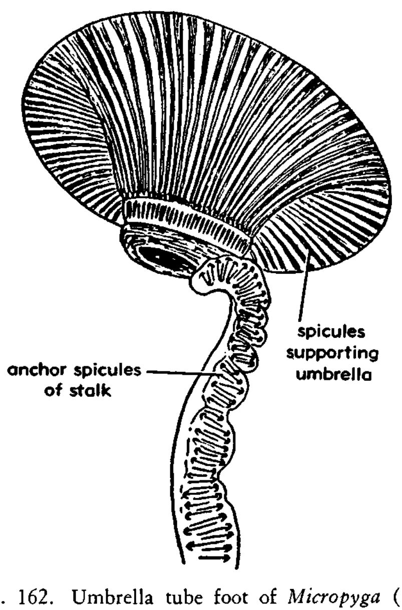

FIG. 162. Umbrella tube foot of *Micropyga* (from 4, after Döderlein).

canaliculatus has gonads in interambulacra 1 and 4 only. The gonoducts are closely associated with the aboral nerve and hemal rings, as well as the aboral coelomic sinus. When ripe, the gonads are very voluminous, but after spawning they are greatly reduced in size. Echinoids are normally dioecious but hermaphroditic individuals have been reported as abnormalities. In most echinoids the sexes cannot be distinguished externally but in some a sexual dimorphism is present. In *Psammechinus miliaris* and a number of other regular echinoids the gonoduct terminates in a short papilla in the males but not in the females. These papillae are present in both sexes of *Echinocyamus pusillus* but those of the males are longer. In some clypeasteroids the genital pore is larger in the females than in males. Eggs and sperm are discharged into the water and fertilization and development follow immediately. In temperate and boreal climates most echinoids seem to have an annual breeding cycle, but some reports indicate the probability of lunar cycles in some species in tropical areas. The spawning period may extend over several months and may take place at different times in different localities. *Lytechinus variegatus* is ripe in March and April in the West Indies, but does not spawn in the Carolinas until June and July. Some echinoids (e.g., *Lytechinus variegatus, Echinus esculentus*) are known to move inshore and aggregate prior to spawning.

Like other echinoderms, echinoids possess considerable regenerative powers. Spines, pedicellariae, and tube feet are readily replaced. Broken spines may have the lost portion replaced. At times, owing to unfavorable conditions, nearly all the spines may be shed and then with the return of a favorable environment, a complete set is regrown. Damage to the test is repaired by filling the wound with coelomocytes, followed by deposition of calcareous plates. Seemingly, however, the new plates are irregularly arranged and do not duplicate the pattern of the lost plates.

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SKELETAL MORPHOLOGY

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SHAPE

EXTERNAL

Although the external aspect of an echinoid is generally characteristic of the order to which it belongs, the geometrical form alone is not commonly of greater diagnostic value. The primitive shape, as in the order Cidaroida, is spheroidal, with slightly flattened apical and oral surfaces. In some Cidaroida and also in some Paleozoic genera (e.g., *Melonechinus*) the test may be tall, with reduced adapical and adoral surfaces, and in some genera it is vertically fluted. In most other regular echinoids the test is roughly hemispherical, but in the Echinothuriidae it is more or less depressed, as in the majority of Paleozoic forms (Lepidocentridae). In one regular order (Temnopleuroida) the test is deeply sculptured. Among irregular echinoids the test may be depressed-hemispherical or tall and conical (Holectypoida), thin and flattened (Clypeasteroida), heart-shaped or elongate oval (Spatangoida), or bottle-shaped with anterior rostrum (some Holasteroida).

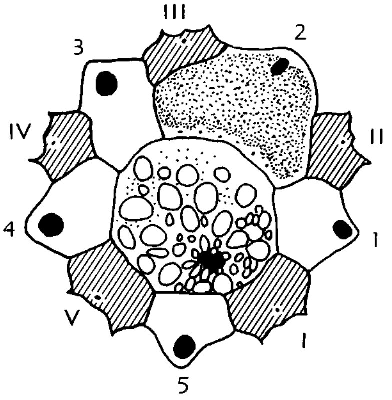

FIG. 163. Apical system of *Strongylocentrotus* showing Lovénian orientation and numerical designations of ocular plates (Roman numerals) and genital plates (Arabic numerals) (9).

INTERNAL

The inner surface of the test in regular echinoids, apart from the perignathic girdle, shows little to indicate the disposition of the soft parts. The mesenteries supporting the intestine are attached to minute projections from the inner surface of the test. In some well-preserved internal molds of fossils these may be seen as pits. In the holectypoid family Discoididae and in one clypeasteroid family (Fibulariidae) the base of the test supports ten simple internal radiating partitions. In other clypeasteroids the test is reinforced by a more or less elaborate internal skeleton of pillars and processes, from the arrangement of which it is possible to deduce the course of the intestine and associated organs and the position of the gonads.

ORIENTATION

In paleontology the Lovénian system (12) of orienting the test has been widely used, particularly because it agrees well with the anteroposterior axis of irregular forms. If an irregular echinoid is placed in the normal position of life, that is, with the apical surface uppermost, the plane of bilateral symmetry passes through the mouth, anus, and apical system. Study of living specimens shows that they move with the mouth in a forward position and with the anus posterior. Within the apical system (Fig. 163) this axis passes through the ocular plate to the left of the madreporite and through the opposite genital plate, and usually corresponds with the longest dimension of bilaterally symmetrical forms. The ocular and genital plates are numbered in relation to this axis, the former with Roman and the latter with Arabic numerals. In aboral view, the right posterior ocular is I, the right anterior II, the anterior III, the left anterior IV, and the left posterior V. The right posterior genital is 1, the right anterior (with the madreporite) 2, the left anterior 3, the left posterior 4, and the posterior 5. The anteroposterior axis thus passes through ocular III and genital 5. The ambulacral and interambulacral areas are similarly designated. Utilizing the madreporite (genital 2) as a point of reference, this same system can be applied to regular echinoids.

In the adoral view of the test, the left posterior ambulacrum is I, and the others are II, III, IV, and V in clockwise succession (Fig. 164). Left and right relationships are reversed with respect to those just noted on the aboral surface. The two columns of each area are designated by the letters *a* and *b* in the same clockwise order. Examination of the first-formed ambulacral plates (on the peristomial edge of the test) shows that five are larger than

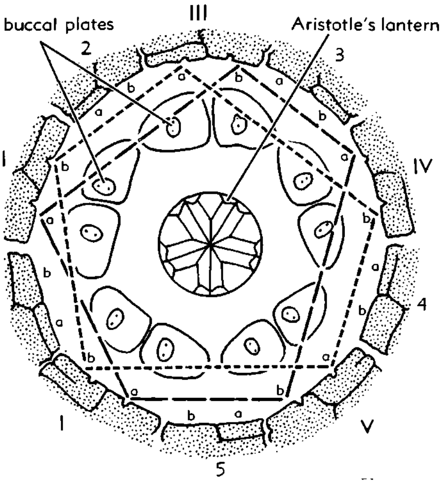

FIG. 164. Diagrammatic oral view of peristomial region of regular echinoid showing Lovénian orientation and numerical designations of ambulacral and interambulacral plates; larger plates of ambulacral tracts at peristome margin joined by long-dashed lines, and smaller plates of these tracts joined by short-dashed lines (12).

others and five smaller. The larger are (with rare inversions) those which begin the columns Ia, IIa, IIIb, IVa, and Vb, joined in Figure 2 by long-dashed lines; the smaller are Ib, IIb, IIIa, IVb, Va, joined in Figure 2 by short-dashed lines. By means of this arrangement, termed *Lovén's law,* which applies to all echinoids, it is usually possible to identify each ambulacrum and interambulacrum and thus to orient the test (Fig. 164). Partial or complete inversion of this sequence may occur in Clypeasteroida.

STRUCTURE

PLATE SYSTEMS

Plates of the echinoid test fall into four categories designated as (1) the apical sys-

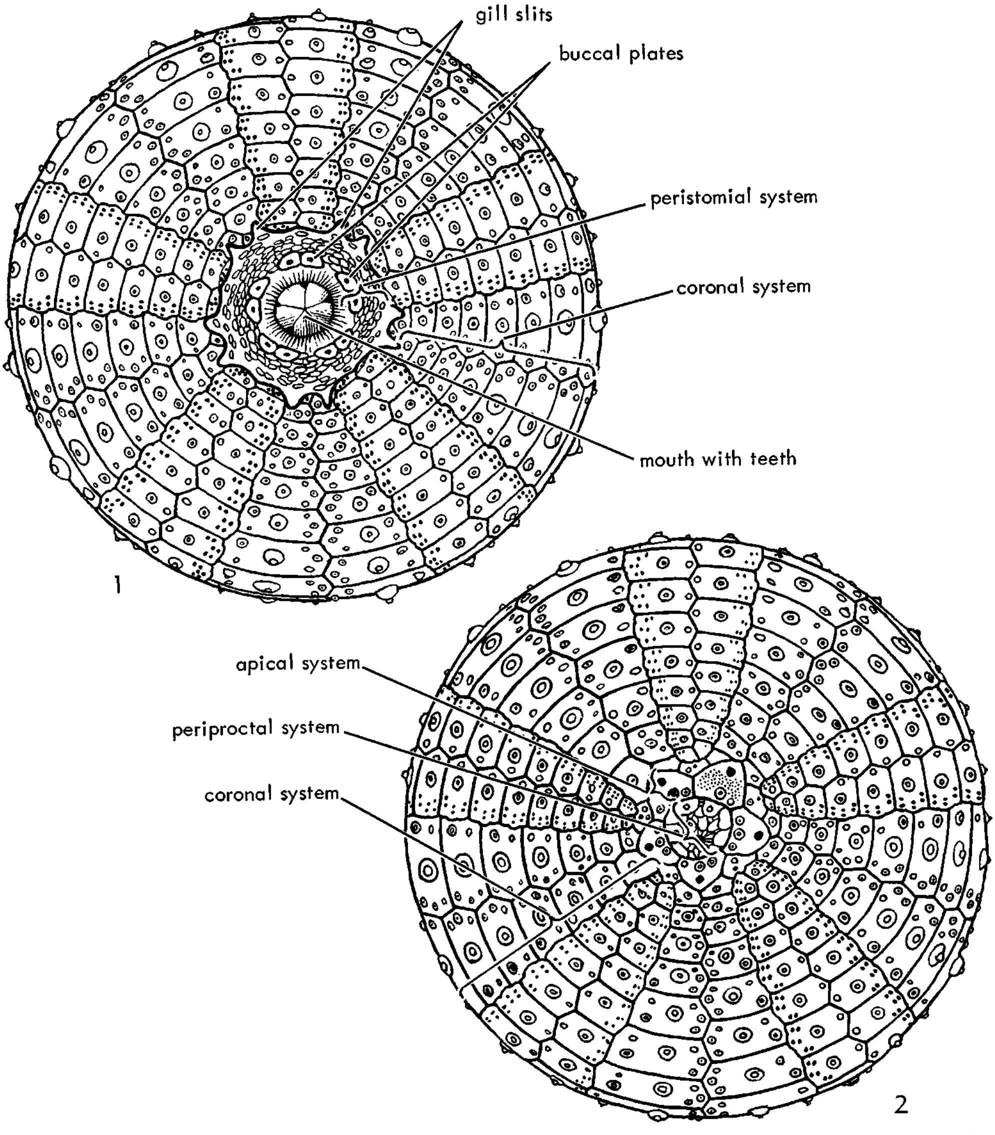

Fig. 165. Plate systems of echinoid test illustrated by *Echinus* (diagram.).——*1.* Oral surface (Durham, n).——*2.* Aboral surface (33 after MacBride).

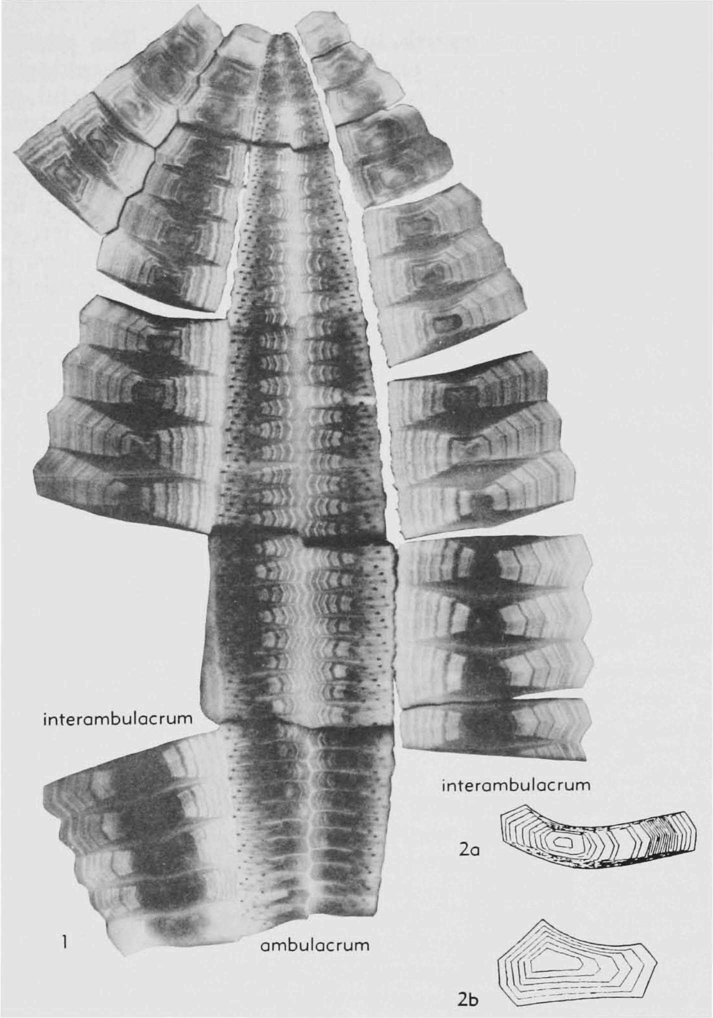

FIG. 166. Growth lines of echinoid test plates.——*1.* Protograph of thin section of ambulacral and interambulacral plate columns of *Echinus esculentus* showing clearly marked growth lines (3).——*2.* Differential peripheral growth of test plates of *Clypeaster* indicated by spacing of growth lines (35); *2a,b,* ambulacral and interambulacral plates of aboral region.

tem, (2) the coronal system, (3) the peristomial system, and (4) the periproctal system (Fig. 165). The coronal plates are formed at or near the borders of the ocular plates of the apical system, and some of the peristomial plates at least are derivative from the coronal plates.

GROWTH AND IMBRICATION

All coronal plates are formed at the edge of the apical system, new plates being inserted between the ocular plates and those previously formed. In the adult stage, therefore, the oldest plates are adjacent to the peristomial margin, and the youngest plates are at the adapical end of each column. The adoral plates of mature individuals were adapical or ambital during earlier stages of growth, and they gradually changed in position from adapical, to ambital, to adoral as new plates were added adjacent to the oculars. As long as the test increases in size, individual plates continue to grow. Within the coronal system a plate never decreases in size during normal growth. In some genera (e.g., *Echinus*) new plates continue to be added throughout life; in others growth is by enlargement of preexisting plates after a characteristic number of plates is reached. In many echinoids, a great modification in the shape of older plates appears between their first position at the margin of the apical system and their ultimate position on the adoral surface or at the ambitus. The presence of growth lines (Fig. 166,*1*) is easily demonstrated in most echinoids by careful removal of the thin surface layer of the plates. The growth lines demonstrate, contrary to much previous speculation, that no resorption of the plates has occurred, except in a few places around pores for tube feet or in gill slits. Study of the growth lines, particularly in irregular echinoids, reveals the changes in

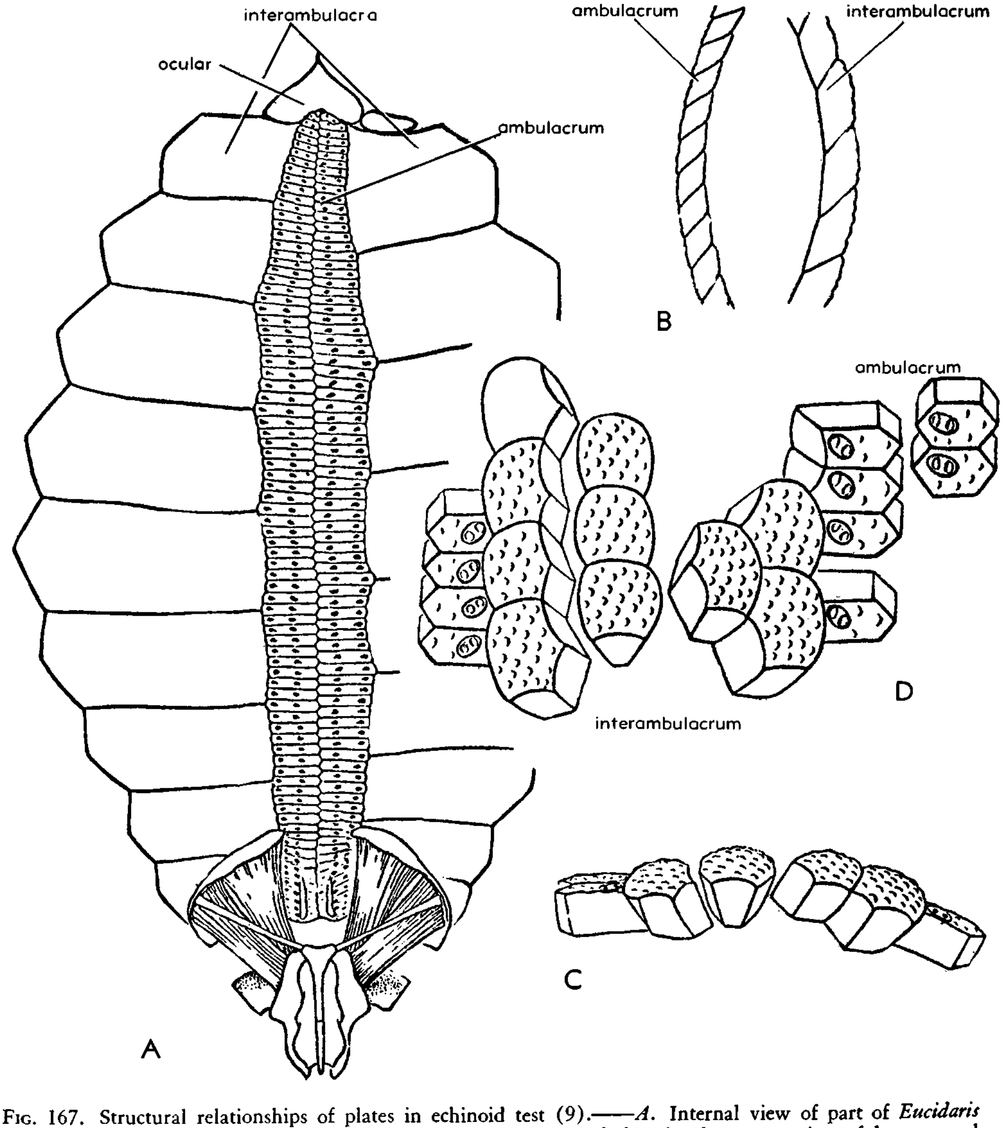

FIG. 167. Structural relationships of plates in echinoid test (9).——*A*. Internal view of part of *Eucidaris* test showing relation of ocular plate to ambulacral and interambulacral columns, portion of lantern and muscles attached to it at bottom of figure, ×2.——*B*. Meridional imbrication of ambulacral and interambulacral plates (diagram.).——*C, D*. Oblique and external views of plate columns in *Lepidesthes* showing imbrication (diagram.).

shape (Fig. 166,*2*), very marked in some species, that plates have undergone as their relative position on the test changed with growth.

Among cidaroids, characterized by narrow simple ambulacra and more or less globular tests, changes in shape with increasing age are minor. Among Paleozoic echinoids it is commonly not individual plates but entire areas that are modified by the introduction of additional columns of small unspecialized plates. In many irregulars the plates, especially of the ambulacra, are differently shaped in different parts of the same area, and the areas differ among themselves also.

Inasmuch as coronal plates originate from the ocular margins, each ocular plate stands at the head of the ambulacral columns of a single ambulacrum and the adjacent halves of the adjoining interambulacra. Thus, in echinoids having only 20 columns of plates, ocular I heads columns 5b, Ia, Ib, and 1a; ocular II heads columns 1b, IIa, IIb, and 2a, and so on (Fig. 167,*A*).

Although the test of most echinoids is rigid, with sutures usually normal to the surface, it may be flexible, with oblique sutures between overlapping plates (as in the Echinothurioida and Recent *Astropyga*). The presence of oblique sutures need not imply flexibility of the test, however. For example, in *Diadema* (Rec.), the sutures are inclined, but the test as a whole is rigid.

Imbrication may occur between plates of a single column, between one column and another, or between one area and another. When ambulacral plates overlap in meridional series, they always do so adorally, that is, each plate overlaps its neighbor toward the peristome. Meridional imbrication in interambulacral columns, on the other hand, is always adapical (Fig. 167,*B*). The adradial columns of ambulacral plates in the Palaechinidae overlap the adradial interambulacral columns. In the Echinocystitoida this is reversed (Fig. 167,*C*), with interambulacra overlapping ambulacra. In the Lepidocentridae the inner interambulacral columns from the interradial line outward bevel over outer columns toward the ambulacra (Fig. 167,*D*).

In most imbrication, the sutural face is merely an inclined plane. In *Astropyga,* however, this surface is S-shaped, which makes parting of the plates from each other possible, though movement of one plate over another is extremely restricted or impossible.

Studies of growth lines in the interambulacral plates demonstrate, despite many previous statements to the contrary, that the ambulacral plates retain a constant position with respect to the adjacent interambulacral plates and that the ambulacral columns do not migrate between the adjacent interambulacral columns.

CRYSTALLOGRAPHIC ORIENTATION

During the last few years many new data, in part unpublished, on crystallography of the echinoid test have been collected, leading to major modifications of many commonly accepted ideas about it. This section on crystallography has been supplied by David M. Raup (Johns Hopkins University) and includes previously unpublished results of his investigations.

Echinoids are typical echinoderms in that nearly all elements of the skeleton appear to be single crystals of calcite. This is true for plates of the corona, spines, spicules of the tube feet, elements of the pedicellariae, and with some exceptions (Prenant, 19), parts of the lantern. The only consistent exception is found in tubercles composed of coarse aggregates of crystals. Nissen (18) has suggested that the typical skeletal part is actually not a continuous crystal lattice but rather a bundle of submicroscopic fibers with parallel orientation. This distinction is not critical for the morphologist at present, and in the summary which follows it is assumed that individual elements are single crystallographic units.

The crystals invariably show a preferred orientation with respect to morphology, but homologous parts in different species commonly show marked differences in orientation. These differences provide a useful taxonomic tool. Laboratory determinations of crystal orientation are not difficult to make. They are most effectively obtained with a petrographic microscope and universal stage, using standard mineralogical techniques (Raup, 20). The crystal orientation is defined by position of the *c*-axis (optic axis) relative to morphology. Orientations may be studied in Recent forms, as well as in fossils in which the original calcite is preserved.

Although the literature of echinoid crystallography is relatively large (see Raup, 20, for partial review) we have systematic knowledge only for the principal plates of the corona, including ocular and genital plates.

Data for ambulacral and interambulacral plates of 120 species have been published (Raup, 23) and data for an additional 150 species await publication. In general (Fig. 168,*1*), the *c*-axes of these plates are either perpendicular or tangential to the plate surface. If tangential, they parallel the plate columns. Also, the ambulacrals usually have essentially the same crystal orientation as the interambulacrals, although precise determinations often show slight but consistent differences. In a few cidarids and arbaciids, however, the ambulacrals have perpendicular *c*-axes and the interambulacrals have tangential *c*-axes. The only known examples of truly inclined *c*-axes, rather than tangential or perpendicular ones, are found in the Conulidae and in some genera of the Arbaciidae, Toxopneustidae, and Strongylocentrotidae. In these (Fig. 168,*2*) the angle between the *c*-axis and the plate surface is ontogenetically controlled (Raup, 21). Within limits of precision that have been accepted, calcite orientation is usually stable at the family level and closely related families tend to have the same crystallography. As a taxonomic character, crystallography of ambulacrals and interambulacrals is best applied at relatively high phylogenetic levels.

The crystallographic situation in plates of the apical system is much more complicated. Comparison of work by Kirchner (11), Lucas (13), and Jesionek-Szymanska (10) reveals many contradictions and uncertainties. A few generalizations are possible, however, based on systematic study of 85 species (Raup, unpublished) as follows.

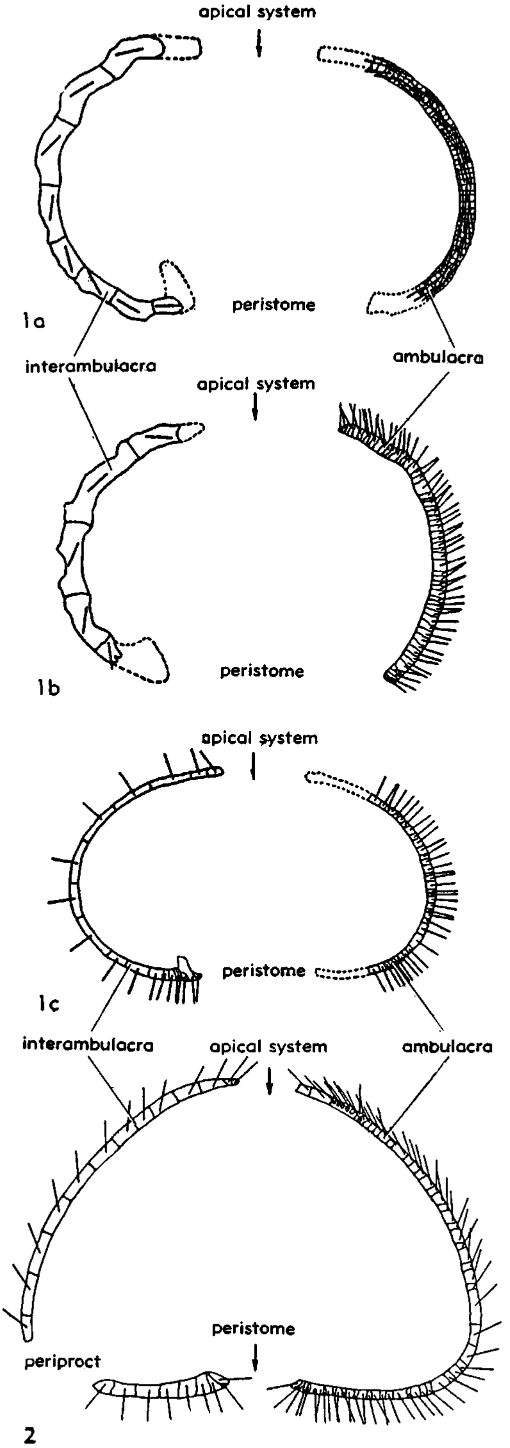

Fig. 168. Orientation of *c*-axis in coronal plates of echinoids (23).——*1*. Common patterns; *1a*, axes all tangential to surface, *Eucidaris thouarsii* (Valenciennes); *1b*, ambulacral plates with *c*-axes nearly normal to surface and interambulacral plates with axes tangent, *Plegiocidaris florigemma* (Phillips); *1c*, axes all normal to surface, *Pedina sublaevis* Agassiz.——*2*. Ontogenetic variation of *c*-axis orientation, *Conulus albogalerus* Leske.

(1) The crystal orientations in ocular plates bear no consistent relation to those in genital plates or to those in the rest of the corona, except that species which are aberrant with respect to one tend to be aberrant with respect to the others.

(2) Orientations of plates in the apical system are usually stable at the generic level, but broad spectra of variation are encountered when various genera are compared.

(3) In a given specimen, all ocular plates have similar orientations with respect to morphology. The *c*-axes have azimuths which parallel the plate columns on the corona, but the axes may be perpendicular, tangential, or inclined either toward the center of the apical system or away from it.

(4) The *c*-axes of genital plates 1, 2, and 4 are uniformly almost perpendicular to the plate surface.

(5) The *c*-axes of genital plates 3 and 5 (if present) may be perpendicular, inclined, or tangential. If they are inclined or tangential, their axes run perpendicular rather than parallel to the coronal plate columns. The *c*-axis of G-3 plunges in a counterclockwise direction and that of G-5 plunges in a clockwise direction. This pattern defines a plane of bilateral symmetry which does not coincide with any morphological symmetry axis in the adult but rather appears to reflect VON UBISCH's primordial plane of symmetry and is thus a relic of larval development.

As a tool in taxonomy and phylogeny, crystal orientation patterns in ocular and genital plates seem to have more promise than those of other plates of the corona because of the greater variation between (and to some extent within) genera. This greater variability suggests greater sensitivity to natural selection and thus may ultimately provide answers to basic and as yet unsolved questions of the functional significance of crystal orientations in echinoids. In the meantime, many more measurements on all elements of the echinoid skeleton are needed before the full potential of crystallographic approaches can be realized.

APICAL SYSTEM

The apical system is the focal point of the echinoid test, since plates comprising it are among those first formed at the time of metamorphosis and since it marks the site of origination of coronal plates. The apical system is composed of **ocular** and **genital** plates. The oculars are invariably five in number and they define the five **radii** of the test. The genitals are also originally five (except in some early Paleozoic genera) and they define the five **interradii.** The oculars generally are smaller than the genital plates and each commonly is perforated by a single small pore. The genital plates, except the madreporite, are entire in youth, but with attainment of sexual maturity they are perforated by one or more genital pores. Genital 2 is also perforated by one or more hydropores which serve as portal to the water-vascular system, and this plate is termed the **madreporite.** The madreporite commonly is larger than the other genitals. In regular echinoids the ocular and genital plates form a single or double circlet around the periproctal membrane, which is either naked or covered by periproctal plates. When the oculars are in contact with the periproct, they are described as **insert,** and if all are in contact with the periproct, the apical system is described as **monocyclic** (Fig. 169,*2*). When

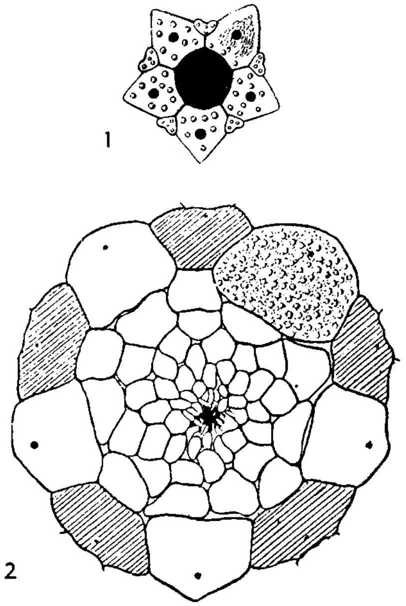

FIG. 169. Types of echinoid apical systems.——*1.* Dicyclic type, *Pseudodiadema* (27b).——*2.* Monocyclic type, *Phyllacanthus* (9).

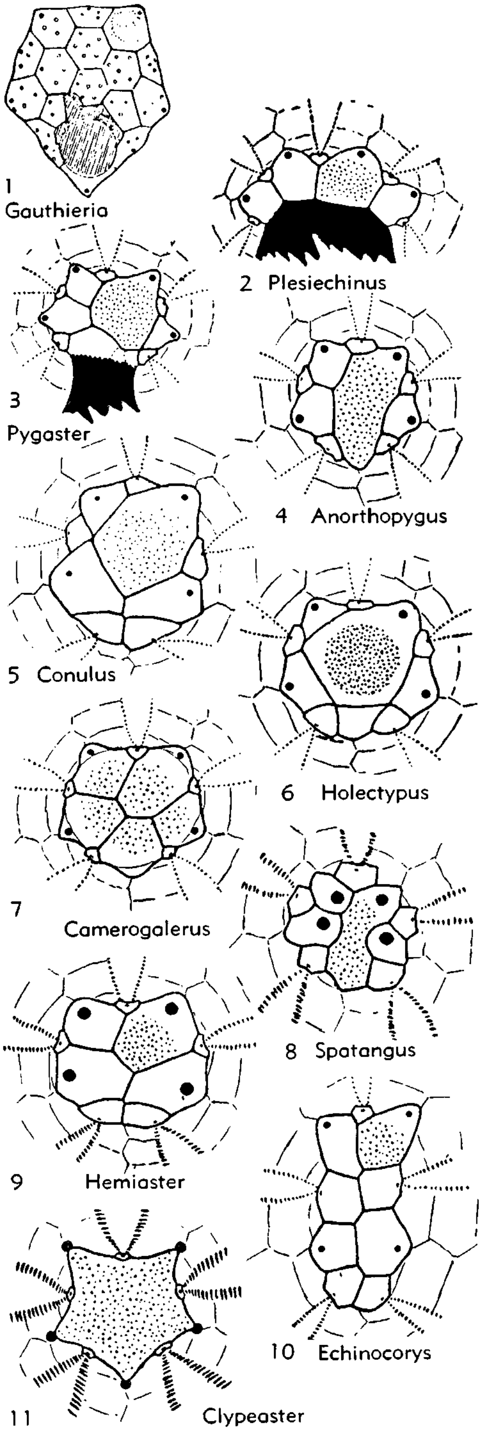

Fig. 170. Periproct and apical systems.——*1*. Posterior migration of periproct in *Gauthieria* (14). ——*2-11*. Apical systems of various genera (29b).

only genitals are in contact with the periproct, the oculars are described as **exsert.** If the oculars are all exsert (Fig. 169,*1*) the apical system is classed as **dicyclic.** If some of the oculars fail to become insert, the last to remain insert are consistently II and III. The number of exsert oculars may be a specific character of the adult, reached at an early stage of growth and, apart from slight variations, does not alter with further growth.

The order of insertion (I, V, IV, II, III), whether it affects all or only some of the oculars, emphasizes bilateral symmetry of the test about the III-5 axis already demonstrated by position of the madreporite. Oculars V and I are symmetrical about the posteror interambulacrum 5, and oculars IV and II are symmetrical about the anterior ambulacrum III.

In irregular echinoids, the posterior genital (5) may be destroyed during movement of the periproct into the posterior interambulacrum, reducing the number of genital plates to four (**tetrabasal**). Alternatively it may be retained or, as in *Echinocardium,* incorporated into the periproctal system of plates. Where genital 5 is retained in the apical system, commonly it has no genital pore and the corresponding gonad has been lost. In other instances, as among clypeasteroids, the genital plates are no longer discrete and have seemingly fused together (**monobasal**) to form a single large central plate, with hydropores present over its entire area in some forms.

Disruption of the apical system characteristic of the irregulars is not brought about abruptly but is foreshadowed in more than one regular genus (e.g., *Heterodiadema, Loriolia, Gauthieria*) (Fig. 170,*1*) which shows the system drawn out posteriorly to a point. In most irregular echinoids, the excentric periproct accompanies a marked bilateral symmetry, but in some genera (e.g., *Plesiechinus, Pygaster*) little apart from the periproct is found to distinguish them from some contemporary regular genera.

In the most primitive type of irregular apical system (*Plesiechinus,* Fig. 170,*2*), the periproct is still in contact with the five ocular and four genital plates arranged in an arc around the anterior edge of the periproct. In *Pygaster* (Fig. 170,*3*) contact with the periproct is maintained, but the oculars and genitals have come together again into a compact group, in which genital 5 is replaced by one or more imperforate plates. In *Anorthopygus* (Fig. 170,*4*) the periproct is completely removed from the apical system and the madreporite has grown backward so as to separate oculars I and V—the **ethmolysian** (ethmolytic) condition. In *Conulus* (Fig. 170,*5*) the apical system is **ethmophract**—that is, the madreporite is separated from oculars I and V, now in contact with each other, by the meeting of genitals 1 and 4, and the fifth genital is not replaced.

In *Coenholectypus* genital 5 is perforate, presumably because it was once associated with a functional gonad. In the closely related *Holectypus* the periproct is far removed, and the apical system has an imperforate plate in the position of the fifth genital (Fig. 170,*6*). In *Camerogalerus* (Fig. 170,*7*) the five genital plates are about equal in size and clearly discrete, and all are perforated by hydropores.

Other irregular echinoids have a marked longitudinal bilateral symmetry accompanied by a separation of the ambulacra into two groups, the anterior three being designated as **trivium** and the posterior two as **bivium.** Nevertheless, the apical system may remain compact and ethmolysian (Fig. 170,*8*), as in some Spatangoida; or compact and ethmophract (Fig. 170,*9*) as in other spatangoids. In other echinoids (e.g., Holasteroida) the apical system becomes elongate (Fig. 170,*10*), derived from an ethmophract condition. Genitals 1 and 4 meet in the mid-line, with oculars II and IV meeting in front of them and I and V behind them. In some (e.g., Collyritidae) the apical system is **disjunct.** The oculars of the trivium, with all four genital plates, remain together anteriorly, whereas oculars of the bivium are situated at some distance posteriorly. The intervening space is occupied by a variable number of narrow supplementary plates which separate the lateral interambulacra along the anteroposterior axis.

Where the apical system is monobasal (Fig. 170,*11*), as in the Clypeasteroida, it is composed of a single, large, central madreporite, pentagonal or stellate in outline, and five minute oculars. The genital pores may open in the angles or midway along the sides of the large central plate, or at some distance outside it in the interambulacra.

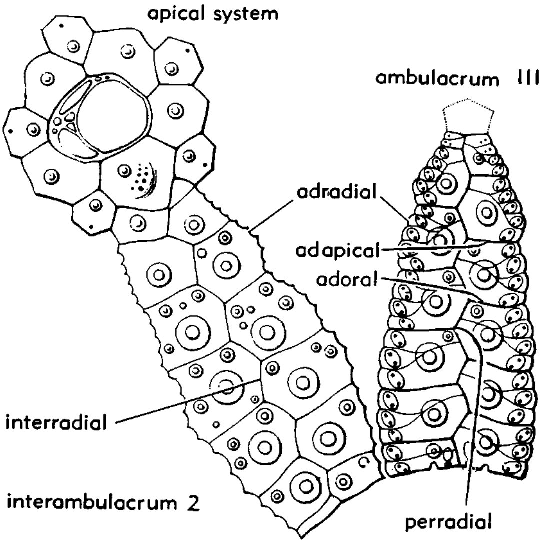

FIG. 171. Nomenclature of sutures in ambulacral and interambulacral areas, young *Strongylocentrotus,* enlarged (diagram.) (12).

CORONAL SYSTEM

General. Plates of the coronal system are arranged in ten meridional areas extending from the edge of the apical system to the edge of the peristome. Of these ten areas, the five ambulacra radiate from the ocular plates and are radial in position, whereas the five interambulacra alternate with them and are interradial in position. Except in some Paleozoic groups and a few aberrant later genera, each area is composed of two columns of alternating plates, giving 20 columns for the entire corona. Each plate is in contact with neighboring plates by means of sutures (Fig. 171). The meridional suture between the two columns of an ambulacrum is termed the **perradial** suture. The meridional suture between the two columns of an interambulacrum is the **interradial** suture. The **adradial** suture is the meridional suture separating an ambulacrum from an interambulacrum. The transverse (horizontal) sutures of the individual plates are distinguished as **adapical** (above,

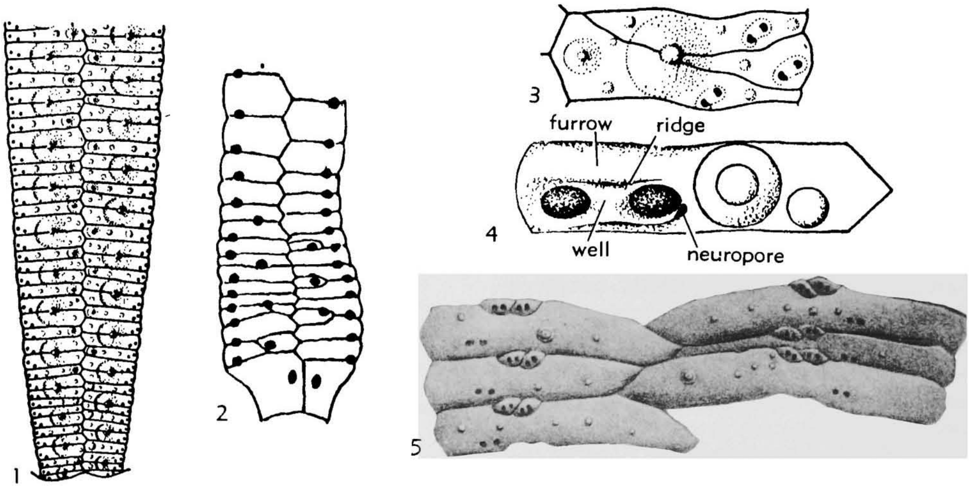

FIG. 172. Morphological features of ambulacral plates.——*1.* Adoral region of ambulacrum of *Orthopsis* showing primary plates (6).——*2.* Occluded plates in phyllode of *Echinanthus* (14).——*3.* Triads of *Echinus* with demiplate (6).——*4.* Cidarid plate with pore pair and neuropore (14).——*5.* Included plates in ambulacrum of *Echinothuria* (14 after Wright).

toward the apical system) and **adoral** (below, toward the peristome). The sutures interlocking with plates of the contiguous column are designated **adapical-transverse** and **adoral-transverse.**

All coronal plates have an external ornament of **tubercles** and **granules.** The larger tubercles support movable spines or **radioles,** and the smaller ones bear minute flexible organs termed **pedicellariae.**

The first-formed **primordial plates** of each area are situated in a row around the peristome in all later echinoids. Each ambulacrum begins with a pair of plates, and each interambulacrum with a single plate immediately followed by a pair. Thus, the initial transverse row includes 15 plates; each succeeding row contains 20 plates. However, in some regular echinoids the first-formed plates are resorbed during growth, so that 20 plates are found in the first (**basicoronal**) surviving row of coronal plates. In rotulinid genera one of the later interradial plates seems to have been inserted into the primordial circle so that it includes 20 plates. In some early Echinocystitoida only ambulacral plates are present on the peristomial margin.

Ambulacra. The ambulacra each consist of two or a larger even number of columns of plates extending from the margin of an ocular plate to the edge of the peristome. In most echinoids each mature plate is perforated by two pores forming a **pore pair.** Each pore pair gives passage to one **tube foot,** which is connected internally with the water-vascular system. The pores of a pair may be similar, round, oval, or pyriform openings, or one may be greatly elongated in comparison with the other. When first deposited, the primordium of a new plate is formed at the edge of the ocular and does not inclose its corresponding tube foot. However, the plate soon grows around the tube foot and shortly thereafter processes grow out from opposite sides of the pore, uniting in the middle and dividing the pore into the two pores characteristic of more mature plates. As the processes grow out, they penetrate the stalk of the foot and divide it into two parts at this point, corresponding to the resulting two pores of the pore pair. A third pore, called **neuropore** (Fig. 172,*4*), may occur near the pore pair. The neuropore serves for passage of the nerve supplying the tube foot. Each plate also bears one or more tubercles and a number of granules.

A **primary** ambulacral plate (Fig. 172,*1*) extends across the entire width of a column, from the perradial to the adradial suture. A **reduced** plate is one which has lost contact with either or both of these sutures. Reduced plates are of three types: **demiplates** (Fig. 172,*3*), which touch the adradial but not the perradial suture; **occluded** plates (Fig. 172,*2*), which touch the perradial but not the adradial suture; and **included** plates (Fig. 172,*5*), which touch neither the adradial nor the perradial suture (plates of the inner columns of the multicolumned Paleozoic genera not considered homologous with reduced plates).

The Cidaroida appear to have the simplest type of ambulacral structure. In them, the ambulacra are usually one-fifth to one-quarter the width of the interambulacra and are built throughout of simple, equal, primary plates. Each plate (Fig. 173) is divided into two parts, an outer **poriferous** area and an inner **interporiferous** area, the latter being about twice the width of the former and nearest to the perradial suture. In the poriferous zones the pore pairs are generally placed in a single meridional series (**uniserial**), but in *Diplocidaris* they are **biserial,** with the pore pair of every alternate plate slightly removed from the adradial suture. The pores of a pair are usually horizontal and equal, but not uncommonly they are oblique in the adapical region and in a few forms throughout the area. They are usually distinctly separated (**nonconjugate**), but in some species they are surrounded by a distinct wall or are associated with an intervening granule, or they may be joined by a groove (**conjugate**).

In interporiferous zones a **marginal tubercle** typically occurs close to the inner pore, the two resulting vertical columns of tubercles usually being conspicuous. A marginal tubercle consists of a low swelling crowned by a rounded boss, or **mamelon,** which is never crenulate and is perforate only in one genus *(Procidaris)*. The remainder of the interporiferous zone is ornamented by a variable number of smaller so-called **inner tubercles** and **granules.**

An ambulacral plate may be an independent **simple** unit with its own tubercle or tubercles (as in Cidaroida); or it may be a **compound** plate, built of a number of primary components or of primary elements combined with reduced plates, with parts bound together by a single tubercle which transgresses the transverse sutures of the component plates. Compound plates are of four basic types as follow.

(1) **Diadematoid** plates are composed of three primary plates, with the middle, larger one reduced in height medially but expanded perradially and adradially (Fig. 174,*1*). Such a group of three is termed a **triad.** In some forms two plates are thus associated and these are then termed **diads.**

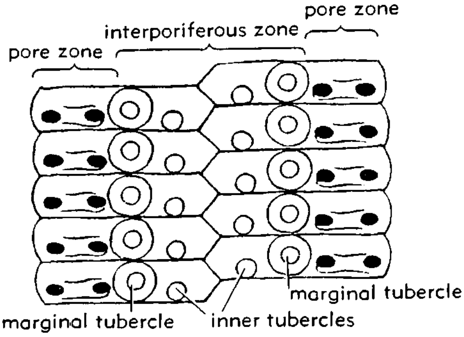

FIG. 173. Cidaroid ambulacrum (diagram.) showing zones and tubercles (14).

(2) **Arbacioid** plates are derivatives of the diadematoid type produced by further perradial expansion of the middle component, so that the adapical and adoral components are reduced to demiplates (Fig. 174,*2*). By the intercalation of additional demiplates the **phymosomatoid** type is evolved (Fig. 174,*3*).

(3) **Echinoid** plates primitively are composed of a single demiplate embraced between two primary plates of which the larger is adoral in position (Fig. 174,*4*). By the intercalation of additional demiplates this gives rise to the most advanced compound plates known (Fig. 174,*5*).

(4) **Echinothurioid** plates, known only in the Echinothuriidae and the rare *Noetlingaster,* are composed of a primary plate with two small included plates on its adoral margin. These are, apparently, derived from the outer demiplates of the arbacioid type (Fig. 174,*2*), and of each apparent pair of included plates, one belongs with the primary plate above and one with the primary plate below.

Each type of compound plate in its simplest form consists of three components, but the arbacioid and echinoid types are capable of much elaboration by incorporation of additional plates.

In many Paleozoic genera, although compound plates are not formed, the same re-

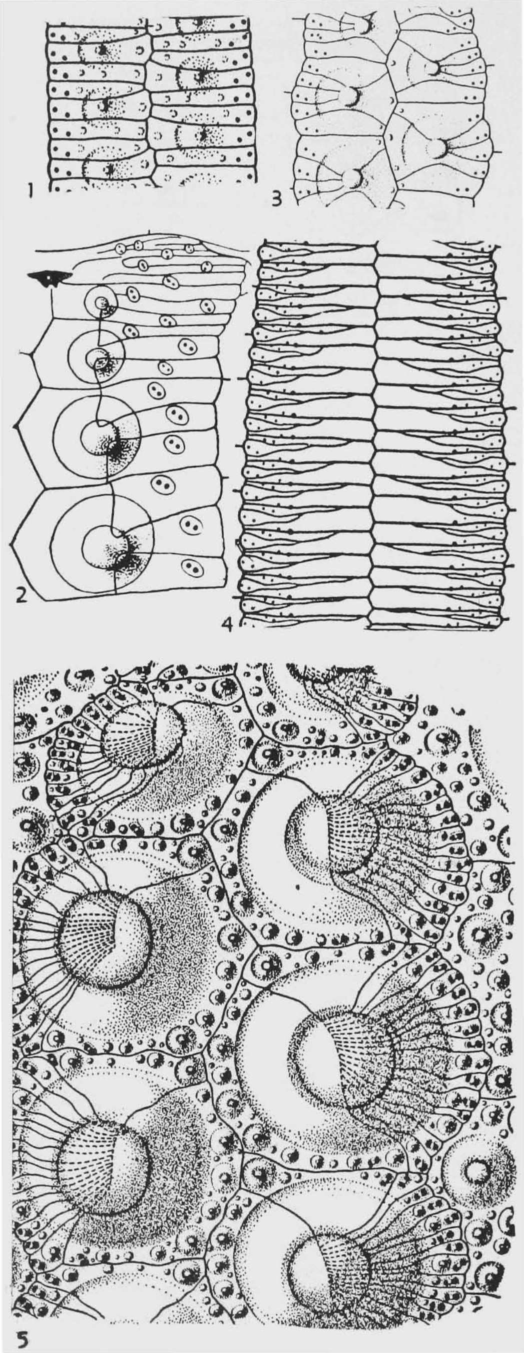

Fig. 174. Morphological features of ambulacral plates.——*1*. Diadematoid triads in *Acrosalenia* (6).——*2*. Arbacioid triads in *Arbacia* (2).——*3*. Phymosomatoid compound plates of *Phymosoma* (6).——*4*. Echinoid compound plates of *Echinus* (6).——*5*. Complex echinoid compound plates of *Heterocentrotus* (6).

sult (i.e., multiplication of tube feet, functionally advantageous to the echinoid) is attained by increasing the number of columns of plates. All plates are simple, without elaborate ornament, and each bears a single pore pair. In the Palaechinidae progressive specialization is recognized from *Palaechinus,* in which the ambulacra are built of two columns of cidaroid primary plates with uniserial pore pairs, to *Melonechinus,* which displays at the ambitus as many as 12 columns of plates with multiserial pore pairs (Fig. 175). In the Echinocystitidae the number of plate columns ranges from two to 20. In the two-columned *Lepidechinus* and *Lepidocidaris* every third plate tends to be larger than others, thus foreshadowing the development of triad groups, but the plates are all simple primaries and the pore pairs are uniserial. In all Paleozoic echinoids, the ornament of ambulacral plates consists of small, imperforate tubercles and granules.

In the many-columned types, it is only the adradial columns that are complete from the apical system to the peristomial margin. The median columns become progressively shorter as the perradius is approached. Correspondingly, it is only at the ambitus that the full complement of columns is found.

In Cidaroida the ambulacra are much narrower than the interambulacra, and as many as 20 ambulacral plates may correspond to each interambulacral plate. However, with increasing complexity and the development of compound plates the two groups tend to reach an equality in size. The mechanical structure of the corona is therewith completely transformed from the cidaroid condition, in which straight or slightly sinuous areas of small, narrow ambulacrals form long lines of weakness, to the phymosomatid or heterocentrotid condition, in which all the meridional sutures run in broad zigzags between large structural units having hexagonal outlines. The ornament of such highly specialized ambulacral compound plates is scarcely distinguishable from that of the interambulacral plates.

The irregular echinoids display ambulacral specializations no less striking than those just described, but their nature is basically different. Although reduced plates

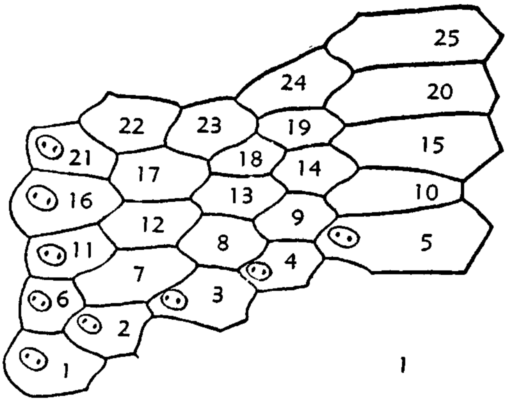

FIG. 175. Part of single ambulacral column of *Melonechinus* (pores omitted in part) [numbers on plates indicate sequence of their addition to test] (9).

occur in all groups, true compound plates are completely unknown. Within the tooth-bearing gnathostomatous irregular echinoids, **pseudocompound** groupings (Fig. 176, *1,2*) occur, but the large primary tubercle that binds the associated elements together in compound plates is lacking. In other irregular echinoids, specialization takes the form of differentiation of various parts in each area and between the areas themselves. Firstly, since the apical system, and still more the peristome, may no longer mark the polar extremities of the test, the ambulacra may not all be of the same length. The peristome is usually anterior in position, and accordingly the ambulacra of the trivium are commonly shorter than those of the bivium. The adapical, ambital, and adoral regions of each area are usually developed differently and in some spatangoids the anterior ambulacrum (III) differs from the paired ambulacra.

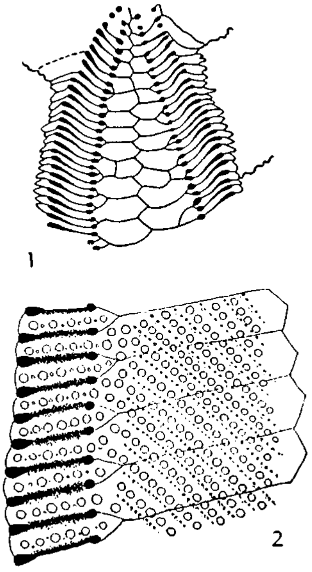

FIG. 176. Petaloid ambulacral plates.——*1.* Pseudocompound plates in petal of *Weisbordella* (26). ——*2.* Combed area in petal of *Arachnoides* (14).

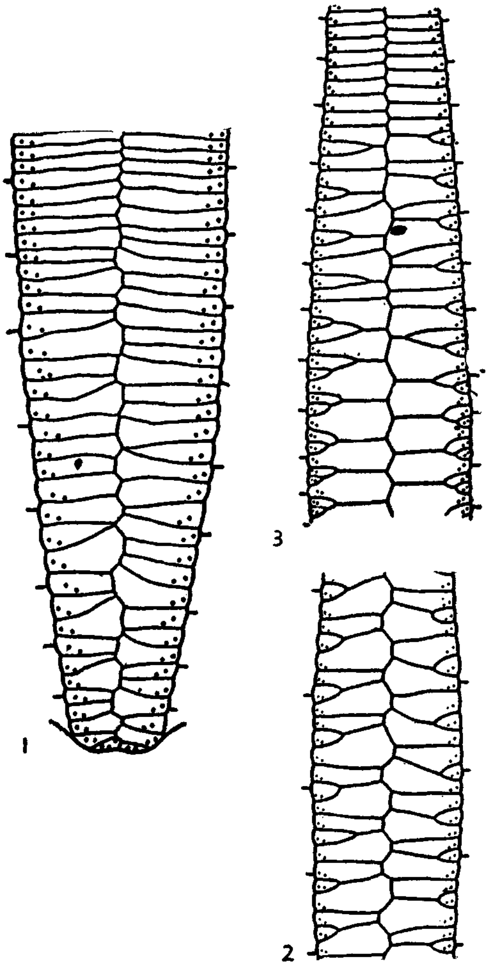

FIG. 177. Types of ambulacral structures in echinoids (6).——*1.* Plesiechinoid type in adoral half of ambulacrum of *Plesiechinus*.——*2.* Pyrinid type in medial part of ambulacrum of *Conulus*.——*3.* Discodeid type in medial part of ambulacrum of *Camerogalerus*.

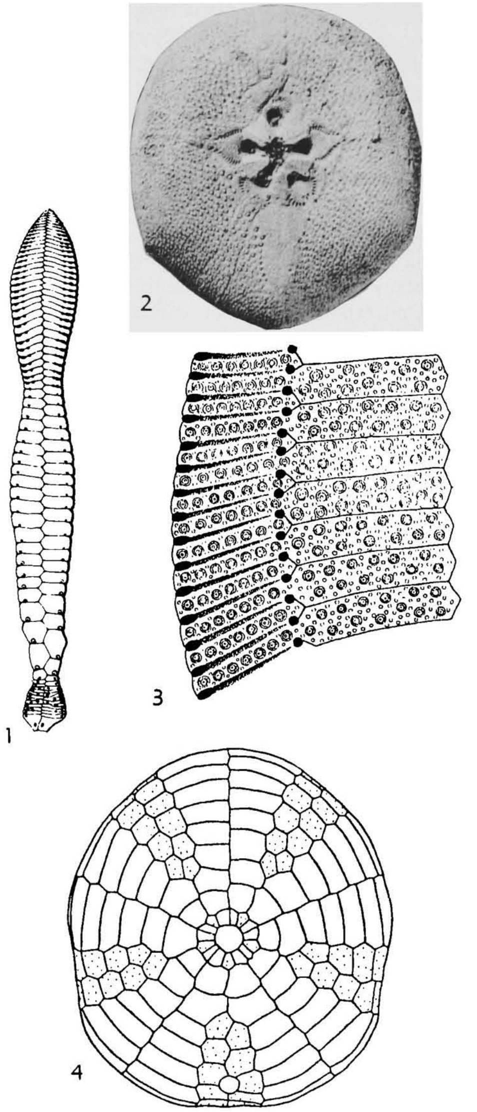

FIG. 178. Plate features of ambulacra and interambulacra in three echinoid genera.——*1.* *Cassidulus* ambulacrum IV (12).——*2.* Oral surface of *Hardouina* showing floscelle (30).——*3.* Demiplates in petal of *Clypeaster* (14).——*4.* Oral surface of *Clypeaster speciosus* VERRILL (interambulacra stippled), ×0.5 (26).

In the gnathostomous irregulars and Cassiduloida, reduced plates are mostly concentrated in the adoral region, but a few clypeasteroids and spatangoids also have reduced plates in the adapical region.

In the Pygasteroida two types of ambulacral structures are found. In the **plesiechinoid** type (Fig. 177,*1*) diademoid triad-grouping occurs adorally and simple, nearly cidaroid plating ambitally and adapically. Reduced plates are rarely developed and invariably these are demiplates. In the **pygasteroid** type the plates are simple and nearly equal throughout, but the tubercles are rhythmically arranged in triads.

Among the Holectypoida, the ambulacral plates are grouped in triads which become more prominent away from the apical system. The pore pairs tend to group in arcs of three adorally.

The **pyrinoid** type recalls the echinoid type (a demiplate inclosed between two primary plates), but the regular castellation of the perradial suture is noteworthy (Fig. 177,*2*). In the **discoidoid** type simple, nearly cidaroid plating occurs adapically, with pyrinoid triads at the ambitus; adorally, primary plates are separated by pairs of demiplates (Fig. 177,*3*), recalling the condition in *Echinus*.

In the Cassiduloida, regional differentiation of each area is developed (Fig. 178,*1*). There is also a well-marked separation of trivium and bivium. Adapically the ambulacra are **petaloid.** The plates of the petals are of cidaroid dimensions and are expanded horizontally compared with the narrow ambital region. The external pore of each pair may be elongated and the internal one minute, or both may be equal and tear-shaped. Where unequal, the pores are usually conjugate. The petals may contract more or less abruptly at their ambital extremities, being then described as **closed**; or they may be **open,** not markedly contracted. Feebly developed petaloid areas are described as **subpetaloid.** In the ambital region the ambulacral plates are simple, rather high primaries with minute pores. Adorally, a special structure known as the **phyllode** is developed. The areas are abruptly widened and they contract again just before the peristome is reached. Within the expanded phyllodal area the plates may be crowded so intensely that the structure is difficult to resolve. In some primitive and some possibly degenerate forms, it seems to be a derivative of the pyrinid triad, with a castellated median suture. In more advanced forms an alternation of primary and occluded plates is seen, and according to some authors the primary plates are themselves reduced to demiplates so that the phyllode appears to be built of four columns. Among the cassiduloids the phyllodes of earlier species have double pores, but in all Cenozoic and most post-Cenomanian species only single pores are present in ambulacra outside of the petaloid area. Adjacent to the peristome the narrow primordial ambulacrals are deeply sunken between the swollen primordial interambulacrals (**bourrelets**), the whole forming a rosette-like structure known as the **floscelle** (Fig. 178, *2*).

In the Clypeasteroida petals are highly developed, with widely separated, usually conjugate pores. In most the petals are built of primary plates, but in the Clypeasterina they are composed of alternating primaries and demiplates (Fig. 178,*3*), and in the Neolaganidae they may be very complex. At the ambital extremities the petals are usually closed, but rarely they remain open or are even divergent. The tube feet within the petals are respiratory, but minute accessory tube feet occur outside of the petals and extend even into the interambulacral areas. Outside the petals the ambulacra may widen considerably, so much so that the interambulacra may be interrupted on the adoral surface by the meeting of one or more rows of ambulacral plates in the interradial line (Fig. 178,*4*). At the ambitus and on the oral surface, the ambulacra are usually as wide or wider than the interambulacra.

In the Holasteroida and Spatangoida the peristome is always more or less excentric anteriorly. Two chief types of ambulacral structures are seen. In the holasteroids there is only rudimentary adapical subpetaloid development. The plates are high and the small pores are at most only slightly unequal. They may be arranged *en chevron*. Ambitally, the pores are minute, whereas around the mouth they are generally enlarged (Fig. 179,*2*).

In spatangoids the paired areas (I and V; II and IV) normally are markedly petaloid adapically (Fig. 179,*1*). The petals may be flush with the surface of the test or more or less deeply sunken, the plates of one column being larger in some than those of the other. The anterior ambulacrum may be similar to the others, but commonly it is nonpetaloid and less deeply sunken (Fig. 179,*3*). In *Echinocardium* this area is built of a complex series of primary and intercalated reduced plates of all three types, the resulting structure offering a curious similarity to that of the Paleozoic *Lovenechinus*. Demiplates may also be developed in the petals when these are flexuous. If an internal fasciole is present, the structure of parts inclosed by the fasciole may be more complex than that of external portions.

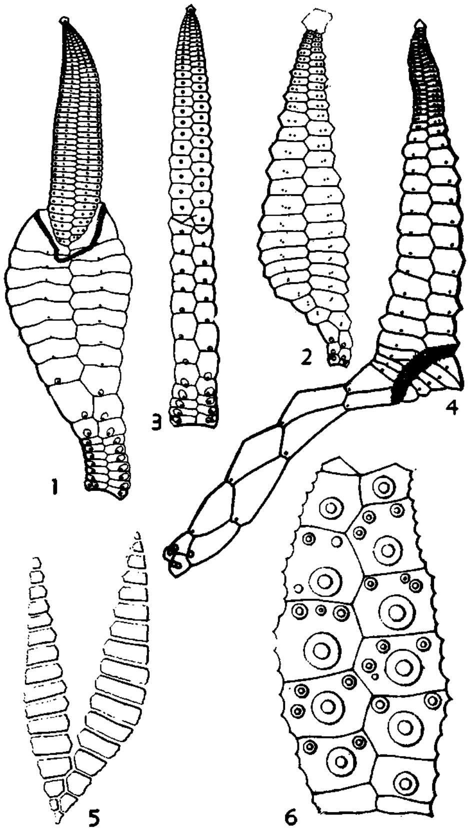

Fig. 179. Structural patterns of ambulacra and interambulacra (12).——*1*. Ambulacrum II of *Meoma* showing petaloid adapical part.——*2*. Ambulacrum II of *Echinocorys* with enlarged pores near peristome.——*3*. Ambulacrum III of *Meoma* showing nonpetaloid adapical part.——*4*. Ambulacrum V of *Micraster* with elongation of plates adorally, ×7.——*5*. Interambulacrum 3 of *Collyrites* with single primordial plate bordering peristome.——*6*. Interambulacrum 3 of *Stronglyocentrotus* with 2 postprimordial plates bordering peristome.

In holasteroids and spatangoids the ambu-

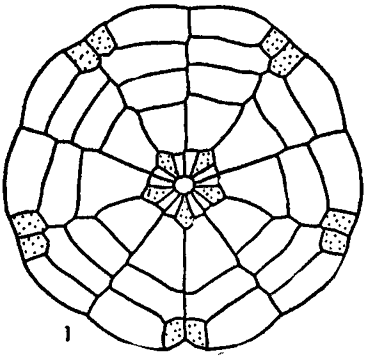

Fig. 180. Oral surface of *Arachnoides* showing discontinuous interambulacra (stippled) (26).

lacral plates of the ambital region are simple and hexagonal in form. On the adoral surface they tend to become narrow and elongate (Fig. 179,*4*). The circumoral tube feet are always large and are grouped into what has been called a phyllodal structure, though not strictly comparable with the phyllodes of Cassiduloida. The ornament of the two posterior areas tends to degenerate into a minute granulation or mammillation, without appendages.

Interambulacra. The interambulacra do not have as intimate and vital a connection with the internal organs as the ambulacra. In most echinoids they bear only the organs of defense (spines, pedicellariae), some of which also have locomotory uses. These appendages are borne on tubercles. Smaller granules without appendages also occur. In clypeasteroid echinoids, accessory tube feet may extend into interambulacral areas. In general, no fundamental difference between ambulacral and interambulacral ornamentation can be pointed out.

Typically, and always in young stages, an interambulacrum begins with a single primordial plate at the peristomial margin (Fig. 179,*5*), though in the adult stage of many regular echinoids this plate has been lost by resorption (Fig. 179,*6*). As with the ambulacra, new plates are formed at margins of the ocular plates. The interambulacra may consist of as many as 14 columns each, but in all post-Paleozoic forms (except a few aberrant genera and some Clypeasteroida) they are built of two columns of alternating plates which usually are continuous from apical system to peristome. In many-columned Paleozoic genera it is only the adradial columns which are continuous. In these, each column approaching the interradial line is progressively shorter. The maximum number of columns is found only at the ambitus.

In all noncidaroid post-Paleozoic regulars and in primitive irregular types each interambulacral plate bordering the peristome is notched at or near each adradial margin by **gill slits** (Fig. 188,*3*), which are smooth incised grooves, each outlined by a raised lip; they serve for accommodation of the external gills or branchiae.

In the Cidaroida and in post-Paleozoic regular echinoids with primitive ambulacral structure, the interambulacra are much broader than the ambulacra, while, in the meridional sense, each interambulacral plate corresponds with a number of ambulacrals. In regular echinoids with compound ambulacral plates, these approach equality in size with the interambulacral plates. In the Holectypoida and Cassiduloida, one interambulacral plate generally corresponds to two or three ambulacral plates adorally and ambitally, and to five or more lathlike plates adapically. In Clypeasteroida, when the interambulacra are broken by adoral expansion of the ambulacra (Figs. 178,*4*; 180) it is always the primordial interambulacral plates which are isolated from the following plates.

In the Holasteroida and Spatangoida, every interambulacral plate is more or less specialized in form. The adoral surface is largely taken up by the posterior interambulacrum and ambulacra I and V (the peristome being always excentric anteriorly). The primordial plate of interambulacrum 5 in primitive forms is narrow and elongate and only just reaches the peristome. In more advanced echinoids it becomes hammer-shaped and expanded into a lip, or **labrum,** which may overhang so as to shield the peristome almost completely. The succeeding plates of this interambulacrum form the **plastron (sternum)**, bordered on each side by the **periplastronal** areas of ambulacra I and V. In more primitive types, the labrum and sternum are scarcely differentiated. In the Collyritidae, the sternum is built of alternating large pentagonal

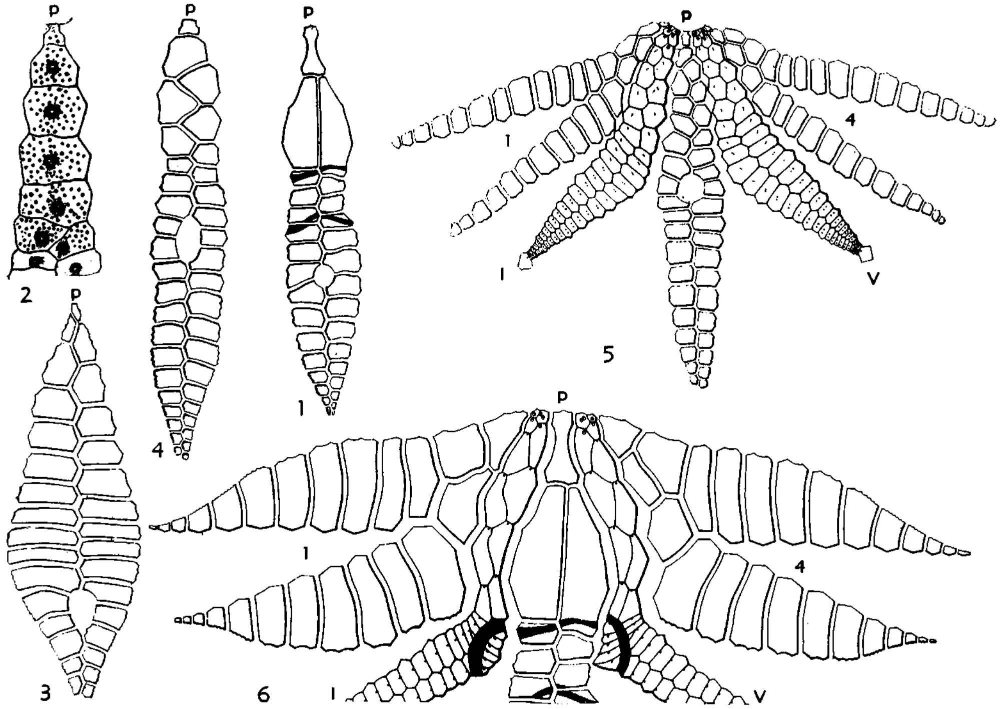

FIG. 181. Interambulacra of sternal region (*p*, peristome).——*1*. Amphisternous plastron of *Brissus* followed by episternous plates (12).——*2*. Meridosternous (and metasternous) plastron of *Cardiotaxis* (31).——*3*. Protosternous interambulacrum 5 of *Collyrites* (12).——*4*. Meridosternous (and orthosternous) interambulacrum 5 of *Holaster* (12).——*5*. Heteronomy between interambulacra 1 and 4 in *Echinocorys* as interpreted by LOVÉN (12).——*6*. Heteronomy between interambulacra 1 and 4 in *Micraster* as interpreted by LOVÉN (12).

plates (**protosternous,** Fig. 181,*3*), which in the Holasteridae (Fig. 181,*4*) come to overlap one another more and more until finally the plastron is built of a single column of large, hexagonal plates (**meridosternous,** Fig. 181,*2*).

In the Spatangoida the labrum is usually prominent. The sternum is built of the first pair of plates behind the labrum (**amphisternous**). These become very large and are separated by a straight, median interradial suture (Fig. 181,*1*). They bear an ornament of closely packed tubercles arranged *en chevron*. The next succeeding plates are termed **episternal** plates.

In the paired inferoambulacra of Spatangoida, the primordial plates are narrow and only just reach the peristome. In advanced forms these become excluded altogether from the peristome, which is thus bounded by the labrum and ten primordial ambulacral plates.

The posterolateral interambulacra of Spatangoida and some Holasteroida are not symmetrical, but area 1 has always one plate less than its vis-à-vis, area 4. This heteronomy differs in pattern between the holasteroids and spatangoids. In the Holasteridae it was interpreted by LOVÉN (1874) as being due to fusion of the first pair of plates in area 1 into a single plate (Fig. 181,*5*), and in the Spatangoida as due to the fusion of the second and third plates of column 1a (Fig. 181,*6*). However, study of the ontogeny of *Echinocardium cordatum* (GORDON, 4) shows that no fusion, but only displacement of plates, takes place in this species.

The character of the interambulacral ornamentation is of great systematic value in groups where the spines are few and differentiated into various kinds. The basic arrangement is best understood in terms of the Cidaroida.

Each interambulacral plate (Fig. 182,*2*)

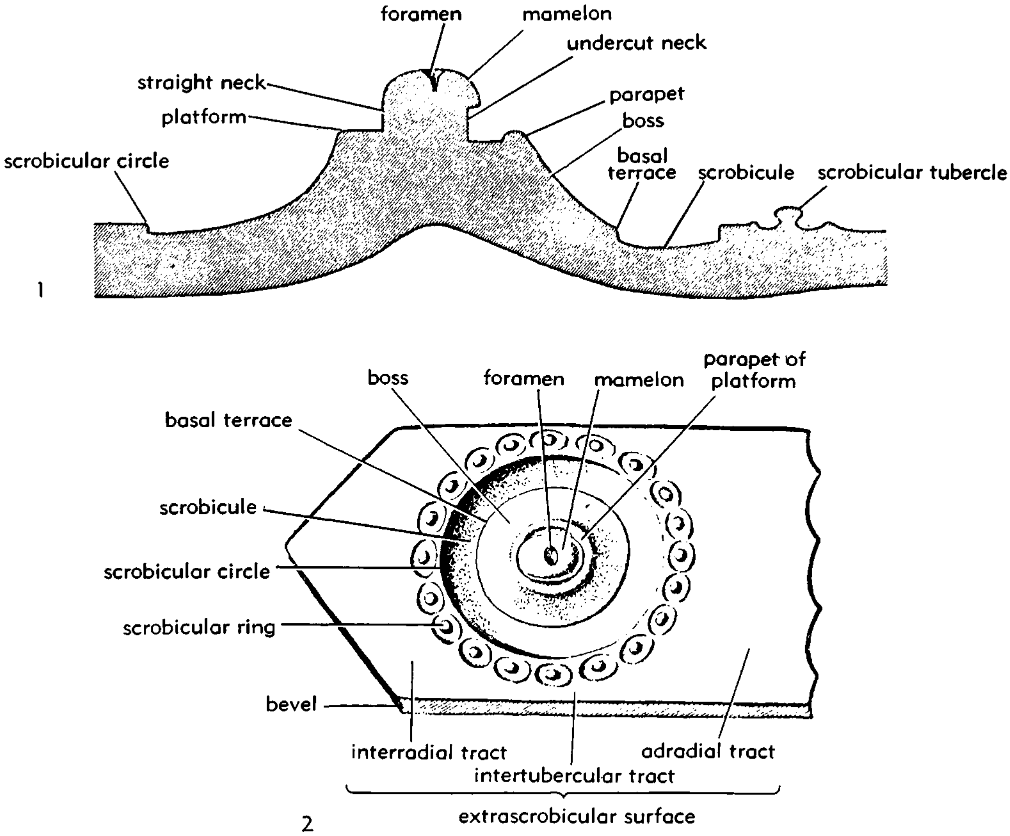

FIG. 182. External morphology of interambulacral plates (12).——*1,2*. Vertical section and surface of cidaroid interambulacral plate, enl. (1 is composite showing more than one type of tubercle).

of a cidaroid bears one prominent, more or less central **primary tubercle** with which the large primary spine (**radiole**) is articulated. The tubercle is situated in a smooth area termed **scrobicule** or **areole** which serves for attachment of the muscles that move the spine. The scrobicule is surrounded by a **scrobicular circle** of smaller **secondary tubercles.** The remaining area of the plate is termed the **extrascrobicular** surface. It is covered by very small **miliary tubercles** for the attachment of pedicellariae or very small spines.

The primary tubercle consists of a hemispherical **mamelon** which may be **perforate,** with a circular or elliptical pit, or **imperforate.** In plan the mamelon may be circular or transversely elliptical. The mamelon is set upon a **neck** which may be straight or undercut. The neck rises from the **boss** and stands on a **platform,** which may be either flush or impressed and surrounded by a **parapet.** The parapet (or margin of the flush platform) may be **smooth** (**noncrenulate**) or **crenulate.** The boss may pass down imperceptibly into the scrobicule or it may be limited by a vertical wall, the **basal terrace** (Fig. 182,*1*).

The scrobicule is generally impressed below the level of the extrascrobicular surface. The secondary tubercles of the scrobicular circle are mamelonate and may be perforate or imperforate, smooth or crenulate, and each of them usually has a miniature areole. The scrobicular circle of one plate may be in contact with those of adjoining plates in the same column, so that only a single row of tubercles separates the scrobicules, which are then indicated to be **contiguous**; or the intervening row of secondary tubercles may disappear causing the scrobicules to become **confluent**; or adjacent scrobicular circles may be complete and independent.

The extrascrobicular surface is covered by smaller tubercles and granules. Tubercles, which are mamelonate, may not be easily distinguished from those of the scrobicular circle. They generally diminish in size toward edges and corners of the plate and are interspersed with minute, wartlike granules which bear no appendages.

In primitive euechinoids the interambulacral ornamentation resembles that of Cidaroida, with a single large primary tubercle in a scrobicular circle. Some specialized types (e.g., *Echinus*) possess a larger number of tubercles which are more or less equal in size and arranged in regular horizontal and vertical series. The primary tubercles are usually a little larger than the others, but they can be recognized in any case by the fact that they alone form a complete meridional series, whereas the others (termed also secondary tubercles) are not present on the adapical and adoral plates. With multiplication in number and decrease in size of the tubercles, the finer structures, such as crenulation and scrobiculation, tend to disappear.

In Temnopleuroida the plates of both ambulacra and interambulacra are sculptured and pitted. In the Glyphocyphidae, these pits take the form of rounded depressions along the sutures, while a pattern of raised ridges connects the primary tubercles and may form an intricate network. In the Temnopleuridae the general surface of the plates exhibits sutural grooves and pores, as well as deeper pits and depressions, and the plates are united by dowel-like structures on the sutural faces.

In the majority of Paleozoic echinoids (except genera such as *Miocidaris* and *Archaeocidaris*), the interambulacra bear only small, simple, imperforate tubercles.

In most irregular echinoids the tubercles are numerous, usually about even in size and nearly always perforate. Only in the Holectypoida and Pygasteroida can a regular, serial arrangement be recognized.

In most Holectypoida a continuous meridional series of primary tubercles can be traced, situated a little adoral to the center of each plate. A number of plates (varying with the genus) at each extremity of the area carry only the primary tubercle, but as the ambitus is approached, the interradial tract of each plate comes to bear a horizontal row of tubercles set adapically just above the primary tubercle; in the adradial tract two such rows appear, one adapical and one adoral in position, and related to each other *en échelon* (Fig. 183,*1*). In some Holectypoida both interradial and adradial tracts bear two rows of tubercles arranged *en échelon* (Fig. 183,*2*). The number of plates at the extremities which bear only the primary tubercle is progressively reduced and number and size of the tubercles tend to increase on the adoral surface while tubercles on the adapical surface are reduced. In the Discoididae and Conulidae a number of minute, sunken tubercles are scattered over the plates of the adoral region. These bear minute, club-shaped glassy radioles of uncertain homology and function.

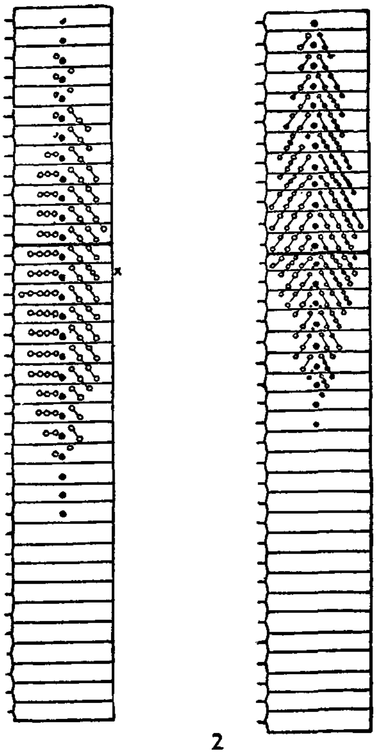

FIG. 183. Interambulacral tubercle patterns in single plate columns (diagram.) (29a).——*1. Holectypus.* ——*2. Conulus.*

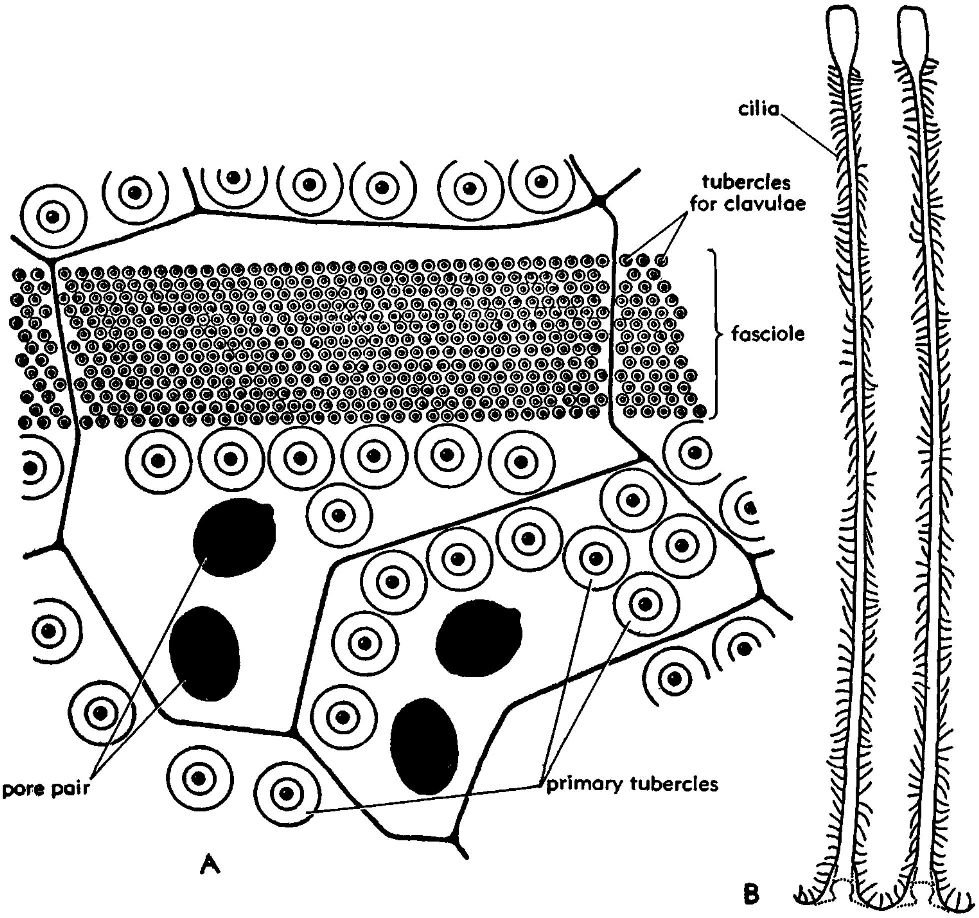

FIG. 184. Fasciole passing across ambulacrum II outside petal of *Echinocardium cordatum* (PENNANT) (16).——*A*. Detail of fasciole, surface view, enl.——*B*. Side view of 2 clavulae, enl.

In the Cassiduloida, the tubercles are closely crowded and commonly arranged in linear patterns, though no regularity of arrangement has been recognized in some. The primordial interambulacral plates in varying degree are swollen, forming bourrelets covered with equal-sized tubercles. On the adoral surface the interambulacra are commonly somewhat swollen above the sunken ambulacra, giving a cushion-like or **pulvinate** appearance.

In the Clypeasteroida the tubercles are small and closely crowded, usually without apparent pattern. In the Holasteridae the tubercles tend to be small and generally well separated. In the Spatangoida they are small and densely crowded, with notable specializations. In some, adapical parts of the interambulacra bear a few enlarged adradially placed tubercles surrounded by smaller ones. The bilateral symmetry in this group is accompanied by a differentiation of the ornament of the adapical and adoral surfaces. On the adapical surface the tubercles may be arranged in oblique lines streaming forward and downward. On the adoral surface the base of each tubercle may be canted up so as to tilt the boss posteriorly.

Many Spatangoida and some Holasteroida bear one or more bands of small strongly ciliated and modified spines called **clavulae** which serve to create water currents. The bands of fine and dense tuberculation on these areas are termed **fascioles** (Fig. 184). These, when fully developed, are conspicuous narrow bands with fine,

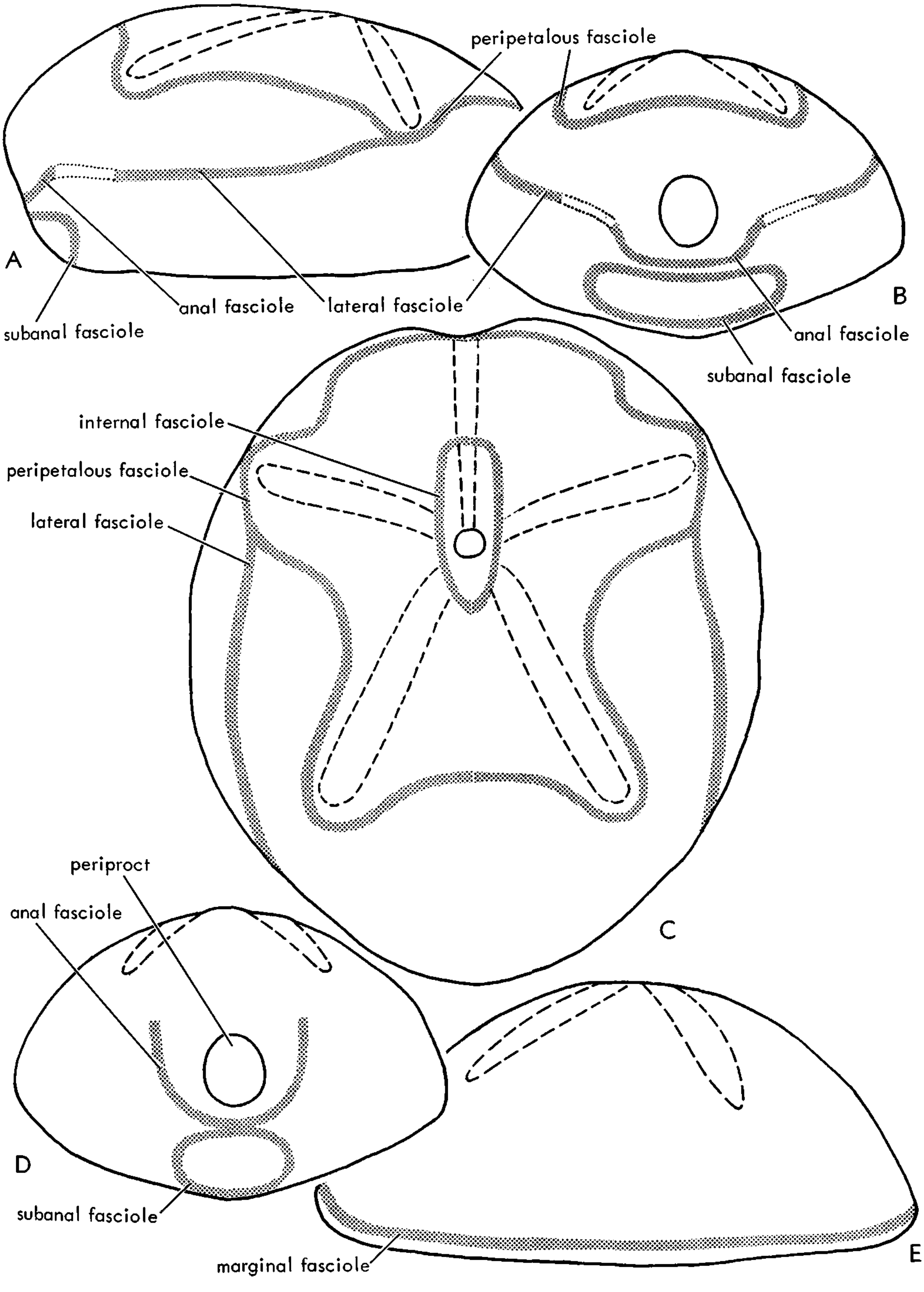

FIG. 185. Fascioles of spatangoid tests (diagram.) (Durham, n).——*A*. Side view of test showing lateral and other fascioles (termed lateroanal fasciole if lateral and anal fascioles are continuous).——*B*. Posterior view of test showing subanal and other fascioles.——*C*. Aboral view of test showing peripetalous and other fascioles.——*D*. Posterior view of test showing anal and subanal fascioles.——*E*. Side view of test showing marginal fasciole.

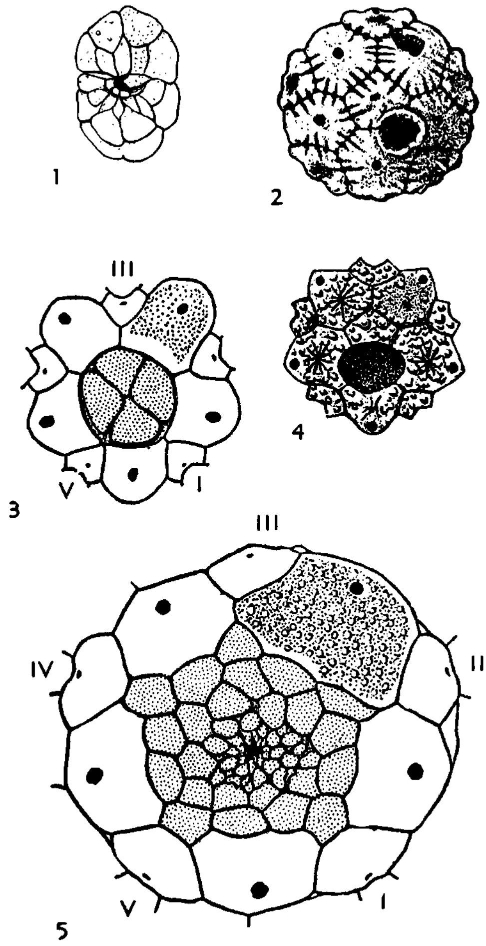

FIG. 186. Plates of periproct and apical system.——*1.* Periproctal plates of *Offaster* (27a).——*2.* Apical system of *Salenia scutigera* GRAY showing large suranal plate and periproct displaced toward ambulacrum I (14).——*3.* Apical system and periproctal plates of *Arbacia punctulata* (LAMARCK) (9).——*4.* Apical system of *Acrosalenia marcoui* COTTEAU showing large suranal plate and posteriorly displaced periproct (14).——*5.* Apical system and periproctal plates of *Eucidaris tribuloides* (LAMARCK) (9).

uniform tubercles passing across both ambulacra and interambulacra. Fascioles vary in position, but, except for a part of the subanal fasciole, are not found on the adoral surface. They inclose various parts of the remaining area of the test and are described according to position as follows.

(1) **Subanal** fasciole, encloses a roughly elliptical area beneath the periproct on the posterior face of the test (e.g., *Micraster*) (Fig. 185,*A,B,D*).
(2) **Marginal** fasciole, encircles the ambitus just above the adoral surface (e.g., *Cardiaster*) (Fig. 185,*E*).
(3) **Peripetalous** fasciole, encloses the petals and apical system (e.g., *Hemiaster*) (Fig. 185,*C*).
(4) **Internal** fasciole, encloses the inner portion of the adapical region, the petals continuing outside of it (e.g., *Echinocardium*) (Fig. 185,*C*).
(5) Paired **lateral** fascioles, run from the peripetalous fasciole to meet beneath the periproct (Fig. 185,*B,C*).

More than one type of fasciole may be found in a single species, but all five types are never found together.

PERIPROCTAL SYSTEM

The flexible membrane through which the anus opens is naked in a few echinoids, but usually it is covered by overlapping or dissociated plates. These tend to be disposed in irregular circlets or a spiral and to diminish in size toward the center (Fig. 186,*5*), but they may exhibit no recognizable pattern. In the Arbaciidae, however, the periproctal plates are nearly always four in number (Fig. 186,*3*). In Acrosaleniidae, Saleniidae, and the young of some other groups a single prominent **suranal plate** pushes the anal opening away from the center of the periproct, in Acrosaleniidae toward interambulacrum 5 and in Salenii-

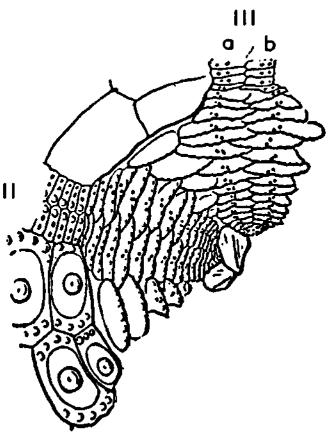

FIG. 187. Peristomial plates of *Eucidaris* (9).

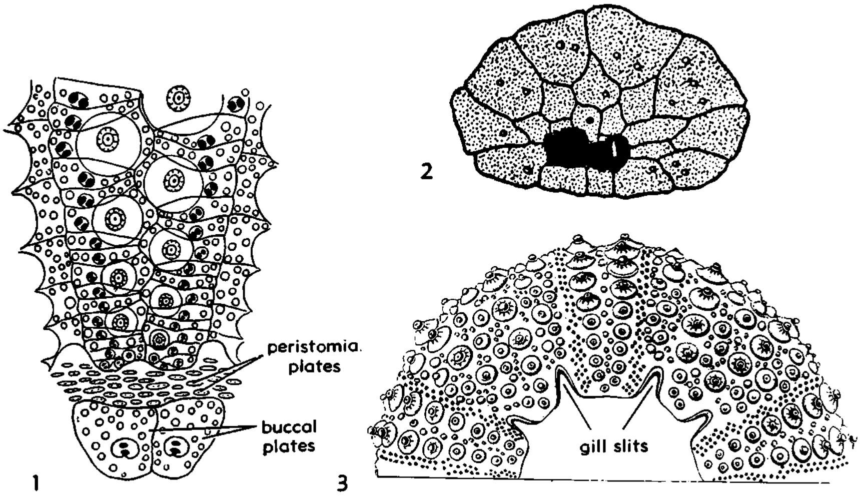

FIG. 188. Morphological features of peristomial region.——*1.* Segment of buccal membrane (toward bottom of figure) of noncidaroid regular echinoid bearing large buccal plates and diminutive peristomial plates, ×4.3 (14).——*2.* Irregular plates of buccal membrane in *Echinocorys* (29b).——*3.* Gill slits around peristome of *Pseudodiadema* (27b).

dae toward ambulacrum I (Figs. 186,*2,4*). In irregular echinoids the periproctal plates are usually small and arranged in indefinite circlets (Fig. 186,*1*). It has been demonstrated in *Echinocardium* that genital 5 becomes part of the periproctal complex of plates. Except in Acrosaleniidae and Saleniidae, however, periproctal plates are rarely preserved in fossils.

PERISTOMIAL SYSTEM

The peristome, or area between the adoral margin of the corona and the mouth opening, is covered by a membrane which usually is more or less completely covered by plates having different origin and arrangement in various groups.

In echinoids such as the Cidaroida, the peristome is covered with regular series of plates corresponding to each area of the corona (Fig. 187). Those corresponding to the ambulacra are ambulacral plates which became incorporated on the membrane as the peristome enlarged; those nearest to the corona each bear a pore pair, the pores of which are situated, not side-by-side as usual in the corona, but one above the other as the mouth is approached. The outer pore comes to lie above the inner and is gradually reduced in size until it disappears altogether, while the inner pore is correspondingly enlarged. The plates corresponding to the interambulacra, usually in single series, have been termed interradial or nonambulacral plates. The latter term should be abandoned, since evidence now available indicates that they must be of interradial origin. They are usually excluded from the mouth opening by the meeting of peristomial ambulacral plates. All peristomial plates are strongly imbricate toward the mouth. Where peristomial ambulacral (but no interradial) plates are present, it seems that the interradials must have been resorbed.

In some echinoids the ambulacral areas are represented on the buccal membrane only by ten large **buccal plates** with radially oriented pores (Fig. 188,*1*). The remaining area is covered by minute plates of uncertain origin. In many irregular types no plates or only small irregular plates occur on the buccal membrane (Fig. 188,*2*).

LANTERN AND GIRDLE

Most Echinoidea possess a complex jaw-apparatus (Fig. 189,*A,E*) consisting of (1) five teeth and their associated structures forming an **Aristotle's lantern,** and (2) outgrowths inside the test of plates at the base of the corona forming the **perignathic girdle** (Fig. 189,*D,F,G*). The lantern is poised within the body of the sea urchin so that

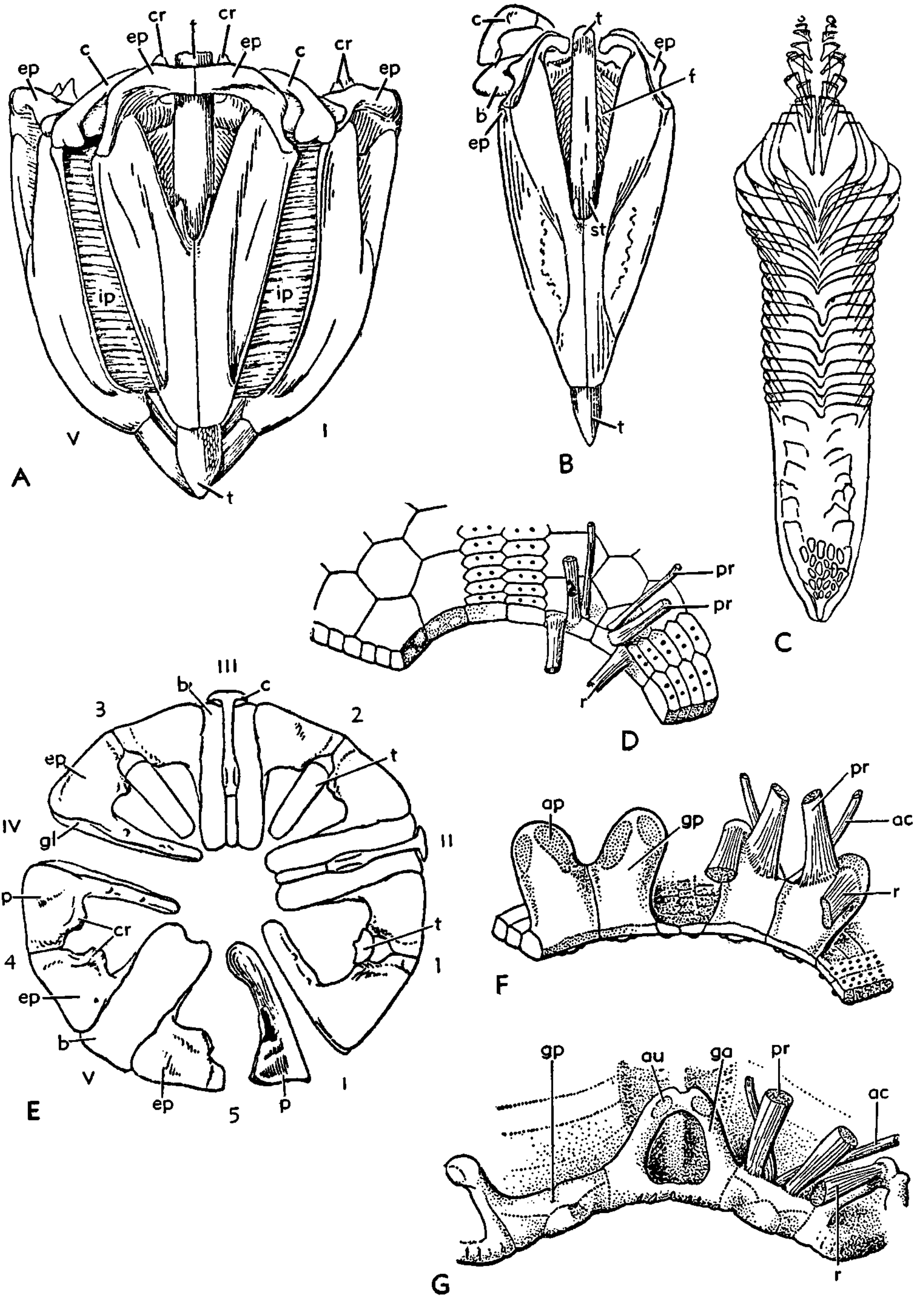

FIG. 189. Morphological features of Aristotle's lantern and adjacent peristome border.——*A*. Lantern of *Strongylocentrotus* viewed from side of interambulacrum 5 (9).——*B*. Pyramid of *Diadema* (9).——*C*. Structure of tooth showing varied form of cones in different parts (8 after Devanese).——*D*. Oblique internal view of peristome border of Paleozoic echinoid showing lantern muscles attached to inner surface of

(Continued on facing page.)

points of the teeth protrude through the mouth. The girdle serves for attachment of the muscles which hold the lantern in position and control certain of its movements.

The lantern is made up of 40 calcareous ossicles held together partly by sutures and partly by muscles, as follows: five **teeth** consisting of long, gently curved blades, curled over at the top in a soft, pulpy growing portion and, unlike most of the test, composed of a series of cones, one inside the other (Fig. 189,*C*). Each tooth is enclosed for the greater part of its length in a pyramid which is built of two **demipyramids** joined by a suture (Fig. 189,*B*). The movement of the tooth is guided by a **dental slide** formed by a pair of crests close to the suture. Neighboring pyramids are joined by interpyramidal muscles attached to horizontal corrugations on the external face of each pyramid. The teeth and pyramids are **interradial** in position. The teeth are either grooved or keeled longitudinally.

Each demipyramid is capped by an **epiphysis**, which is united to the demipyramid by suture. The pyramidal suture does not extend to the full height of each pyramid, so that a gape called the **foramen magnum** occurs between the tops of each pair of demipyramids. The epiphyses may or may not meet over the foramen magnum. The top surface of the demipyramids may be smooth or pitted.

The epiphyses of neighboring pyramids are joined by and interlock with a **brace** or **rotula** after the fashion of the shoulder-joint of vertebrates—that is, by the articulalation of condyles on the rotula with glenoid cavities on the epiphysis.

The five **compasses** each consist of a slender, curved rod above the rotulae, to which they are attached by ligaments. Each compass consists of two portions, the outer of which is usually bilobed at the end. The rotulae and compasses are radial in position.

These 40 pieces (five teeth, ten demipyramids, ten epiphyses, five rotulae, and five compasses of two parts each) are operated by 60 muscles. These are (1) the ten **protractors,** which push the teeth downward through the mouth; (2) ten **retractors,** which withdraw the teeth and separate their points; (3) ten **radial compass muscles,** which maintain the vertical position of the pyramids and control inclined motion of the whole structure; (4) five powerful **interpyramidal muscles,** which bring the points of the teeth together for biting; (5) 20 **rotula muscles**, which accommodate the rotulae to the movements of the pyramids; and (6) five **circumferential compass muscles** of uncertain function. Some of these muscles work between one lantern piece and another. The others are attached to the perignathic girdle or to the inner surface of the test when no girdle is present. Since the lantern is attached to the test only by these muscles, it is freely suspended and can be moved in various oblique directions.

The perignathic girdle is not developed in a majority of Paleozoic genera (Fig. 189,*D*) nor in the very young stages of Cidaroida. In these forms, the lantern muscles are attached simply to the inner surface of the primordial interambulacral plates. In adult Cidaroida (Fig. 189,*E*) there are prominent, vertical, wing-shaped outgrowths from these plates, the **apophyses,** to which the radial compass muscles, the protractors and retractors are attached. In all other jaw-bearing forms there are also outgrowths from the ambulacral plates at the peristomial margin, termed **auricles** (Diadematoida, Fig. 189,*G*; Pygasteroida, Fig. 190,*2*; Clypeasteroida, Fig. 190,*3*). The auricles are like flattened pillars in shape and are taller than the apophyses. They are joined to the coronal plates and to the apophyses by suture and are usually separated from each other by a space, which may be arched over by supplementary pieces attached to the pillars. In some forms (e.g., Clypeasteroida) they may be joined to each other by suture. When auricles are present,

plates (2).——*E.* Apical view of lantern of *Strongylocentrotus,* areas 2, 3, and III complete, others with various structures removed (9).——*F.* Oblique internal view of peristome edge and girdle of *Cidaris* showing apophyses and attachment of lantern muscles (2).——*G.* Internal view of peristome edge and girdle of *Paracentrotus* (2). [Explanation: *ac,* radial compass muscle; *ap,* protractor muscle attachment scar; *au,* retractor muscle attachment scar; *b,* brace; *c,* compass; *cr,* crest of epiphysis; *ep,* epiphysis; *f,* foramen magnum; *ga,* auricle; *gl,* glenoid cavity; *gp,* apophysis; *ip,* interpyramidal muscle; *p,* top of pyramid; *pr,* protractor muscle; *r,* retractor muscle; *st,* styloid process; *t,* tooth.]

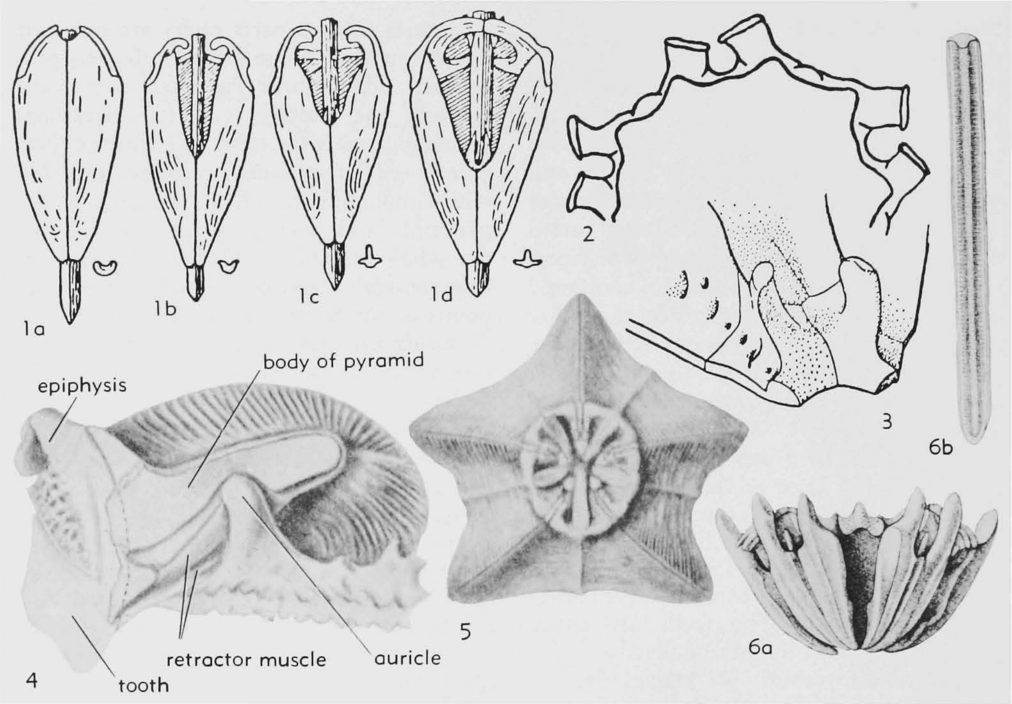

FIG. 190. Morphology of lantern and girdle.——*1.* External view of regular pyramids and cross sections of teeth (7 after Jackson); *1a,* cidaroid; *1b,* aulodont; *1c,* stirodont; *1d,* camarodont.——*2.* Girdle of *Pygaster* (7).——*3.* Auricles of *Clypeaster* (26).——*4.* Side view of pyramid of *Clypeaster* in position adjacent to auricles and tooth (14).——*5.* Lantern of *Clypeaster* viewed from above (14).——*6.* Lantern and tooth of *Echinoneus* (34); *6a,* lantern, ×29; *6b,* tooth, ×87.

the protractor muscles are attached to them and the retractor and radial compass muscles to the apophyses.

Among echinoids the structure of the pyramid (Fig. 190,*1*) and teeth provides useful criteria for separating various higher categories. In Cidaroida the teeth are grooved longitudinally, the foramen magnum is shallow, the epiphyses are narrow and not fused together. The tops of the pyramids are not pitted, and the girdle consists of apophyses only. In the condition termed **aulodont,** the teeth are longitudinally grooved, the foramen magnum is shallow and the epiphyses separate, as in Cidaroida, but the tops of the pyramids are pitted and auricles are developed in the girdle. **Stirodont** is the term applied when the teeth are keeled longitudinally and the foramen magnum is deep. The epiphyses are separate, the tops of the pyramids are pitted, and auricles are present in the girdle. In the **camarodont** condition the teeth are keeled, and the epiphyses meet in a suture over the deep foramen magnum. The tops of the pyramids are pitted and auricles are present in the girdle.

In the Holectypoida the apophyses are feebly developed or absent, and the auricles commonly are supported from behind by buttresses which develop into the massive partition-walls of *Discoides*. In *Echinoneus,* one of the two living holectypoids (Fig. 190,*6*), a complete lantern is formed, but it is never functional, being resorbed before the mouth is opened. It is clearly of the stirodont type, however, as in the fossil *Holectypus* and *Discoides,* with keeled teeth and separate epiphyses. The girdle of *Conoclypus* is supported by a peristomial invagination, so that the auricles are raised well above the floor of the test. The auricles are interradial in position, although their ambulacral origin can be traced. In the Oligopygidae the auricles are likewise interradial but are recumbent on the floor of the test.

A well-developed lantern is present in Clypeasteroida (Fig. 190,*4*,*5*). It is low, flaring, and somewhat asymmetrical, and compasses are never present. The anterior pair of pyramids and the posterior tooth may be larger than the rest, as in Clypeasteridae, or the reverse may be the case, as in Fibulariidae. The rotulae lie, not above, but impressed between the epiphyses. The auricles are generally fused into a single interradial structure in the more specialized clypeasteroids.

In the Cassiduloida, no trace of lantern or girdle is known in any adult form, though both have been observed in the young of *Echinolampas* and *Conolampas*. Neither lantern nor girdle has been observed in any of the Holasteroida or Spatangoida.

APPENDAGES

GENERAL

The tubercles of the coronal plates bear movable appendages (Fig. 191), each of which articulates with its tubercle by a ball-and-socket joint and is moved by muscles. The three principal types of appendage are **spines** or **radioles, pedicellariae,** and **spheridia.** The spines, like the tubercles on which they rest, may be ranked as **primary, secondary,** and **miliary.**

SPINES

Although the spines are extremely varied in form, from the massive thorny primary spines of Cidaroida to the tessellate spines of *Colobocentrotus* and the short hairlike spines of Spatangoida, they all have a common, basic gross structure which is most easily explained in terms of the cidaroid type.

In the cidaroids each primary spine (Fig. 192,*1*) consists of a distal **shaft,** which may be straight or curved, cylindrical or flattened, stout or slender, club-shaped or bladed, smooth or variously ornamented with secondary spines or thorns which may be arranged in longitudinal rows or in well-spaced whorls (**verticillate**). At the base of the shaft is a smooth **neck** that varies in length relative to the length of the shaft. Below the neck is the **collar,** marked with fine longitudinal striations and flaring out into the **milled ring,** to which are attached the ligaments and muscles which anchor the spine and control its movements. Below the milled ring is the smooth **base,** hollowed proximally by the **socket** or **acetabulum** which articulates with the mamelon of the tubercle. When the tubercle is perforate, a strand of connective ligament runs to a similar feature in the socket. Spines mounted on crenulate tubercles are correspondingly crenulate around the margin of the socket.

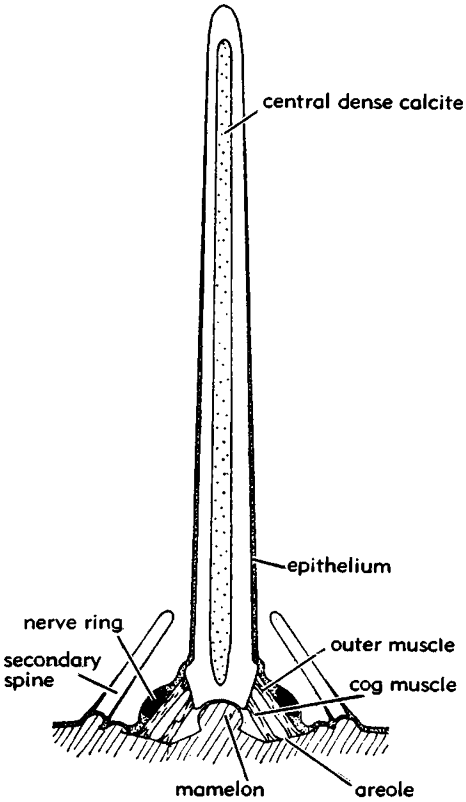

Fig. 191. Diagrammatic section of spine and tubercle of living echinoid (17).

The microscopic structure of the primary interambulacral spines is of great systematic importance in regular echinoids. As seen in transverse section (Fig. 192,*2*) the **central core** or **medulla** consists of an irregular calcareous mesh. Outside the core is a **radiating layer,** built of septa connected by trabeculae. The outer or **cortex** layer is compact but perforated by longitudinal channels (appearing as pores in transverse section), one

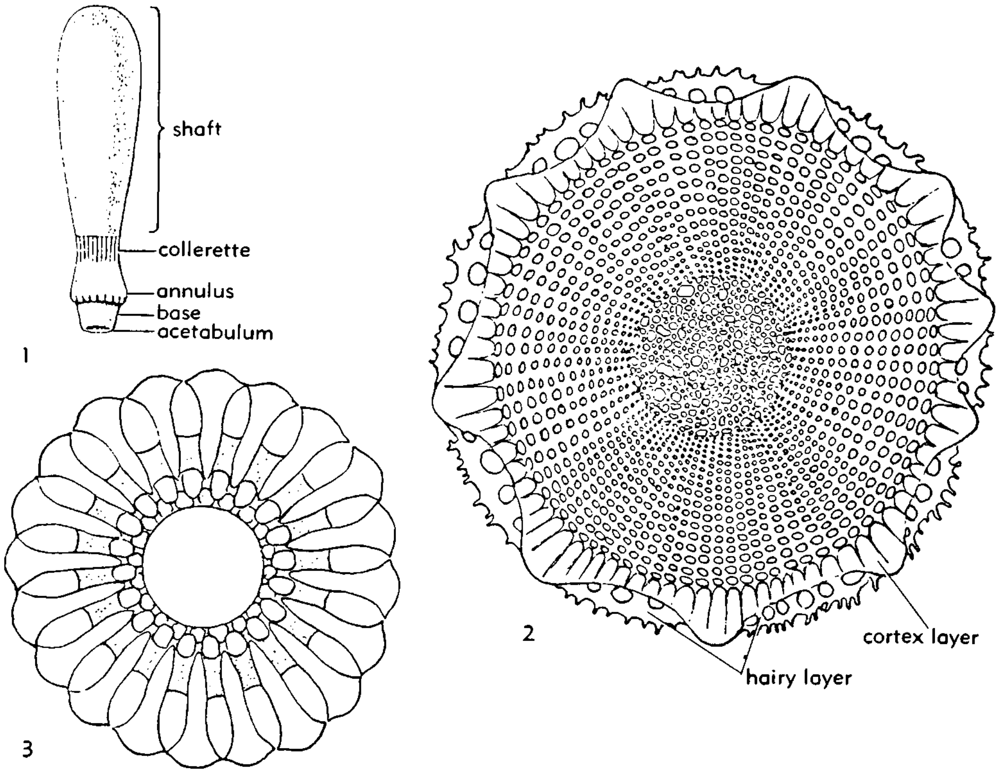

FIG. 192. Morphology of primary echinoid spines.——*1.* Side view of cidaroid spine showing named parts (25).——*2,3.* Cross sections of primary spines of *Stereocidaris,* ×40 (14), and *Centrostephanus,* ×55 (14).

opposite the end of each septum. The cortex does not extend below the neck. From the outer surface of the cortex a great number of fine **hairs** extend; these may be short and thin or long and fluffy, or branching and anastomosing so as to conceal the cortex layer. The tips of the hairs may be plain, singly or doubly hooked, or minutely tuberculate. The septa are bladelike and run the full length of the spine, and it is their exposed edges that give the collar its striated appearance. The hair coat is very rarely preserved in fossils, and even in living forms it is frequently worn off by abrasion.

The secondary (scrobicular) and ambulacral spines differ from the primaries in lacking both the central core and the cortex layer.

In the Echinothuriidae the spines are hollow tubes, the wall of which consists of a single, compact layer perforated by regularly spaced longitudinal canals. Between the canals the wall is raised into longitudinal ridges. The central axial core of larger radioles may be partly filled with an irregular calcareous mesh.

In most other echinoids the spines lack the cortex layer and consist only of the wedge-shaped septa set around an axial cavity (Fig. 192,*3*) which may be partly or wholly filled with a loose calcareous mesh or solid.

The spines of many irregular echinoids are short (except in specialized areas of some spatangoids), thin and longitudinally striate. Many of these forms have a burrowing mode of life, and the spines of the oral surface, especially those of the plastron of Spatangoida, are paddle-shaped and serve for burrowing and locomotion. The spines of some spatangoids are longitudinally fluted and of minaret-like form.

In systematic work, the size, form, and ornamentation of the spines, their general microscopic structure and detailed form and

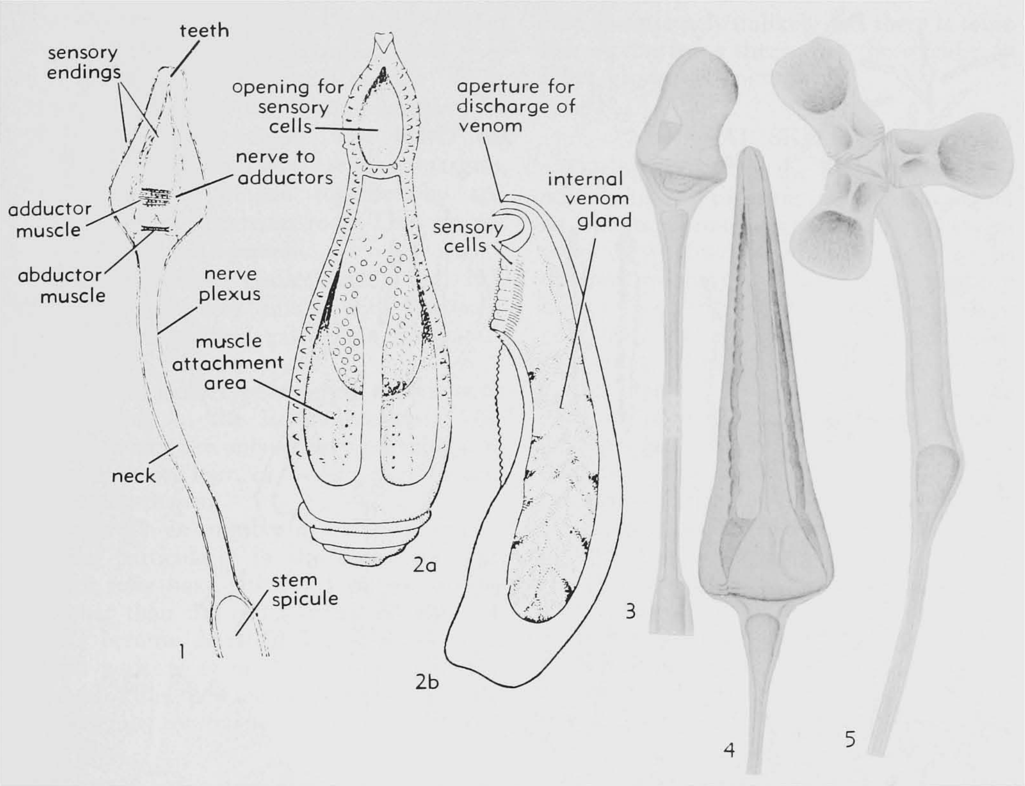

FIG. 193. Morphology of pedicellariae.——*1.* Diagrammatic section of typical pedicellaria of living echinoid (17).——*2.* Valve of globiferous pedicellaria of cidaroid; *2a,b,* internal view and longitudinal section (2 after Mortensen & Prouho).——*3.* Ophicephalous pedicellaria with stalk, ×50 (14).——*4.* Blades of tridentate pedicellaria, ×28 (14).——*5.* Triphyllous pedicellaria with open jaws, ×55 (14).

number of their septa (as well as details of the hair coat in Cidaroida) are all of importance. Unfortunately, fossil spines can rarely be related to particular tests, and in some the internal structure has been obliterated by recrystallization.

PEDICELLARIAE

The minute, grasping, defensive, and scavenging organs known as pedicellariae are attached to small tubercles on the test of echinoids. Each (Fig. 193,*1*) consists of a muscular **stem** stiffened by a calcareous rod and a movable head, usually built of three jawlike **valves.** The whole is enveloped in a muscular sheath and in life is constantly in motion. Four principal types of pedicellariae are recognized.

(1) **Globiferous** pedicellariae (Fig. 193, *2*) possess elongated valves, commonly terminating in a sharp tooth. In Cidaroida and some Spatangoida the valves are hollow and contain poison-secreting glands. In other groups the glands, which may be double, are external to the valves.

(2) **Tridentate** pedicellariae (Fig. 193,*4*) are usually the largest and possess

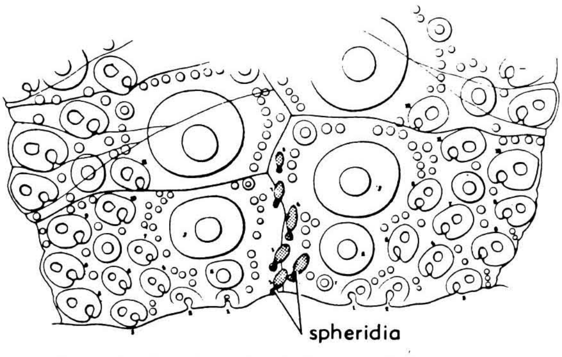

FIG. 194. Adoral region of ambulacrum of *Strongylocentrotus* showing spheridia (12).

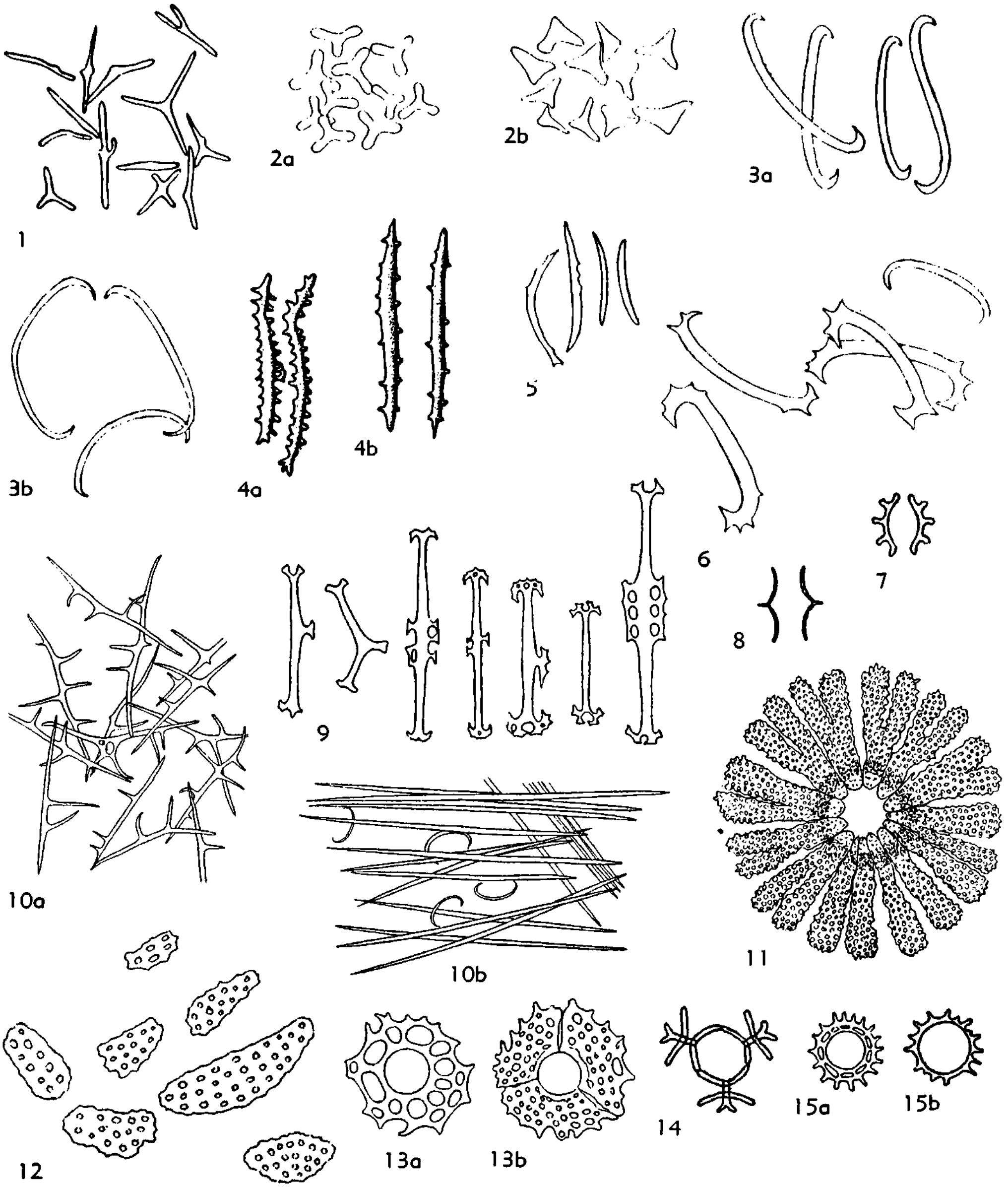

Fig. 195. Calcareous spicules and plates from echinoid tissues.——*1. Aporocidaris milleri* (Agassiz), from intestinal wall, ×80 (14).——*2. Goniocidaris* (14); *2a, G. tubaria* (Lamarck), from intestinal wall, ×80; *2b, G. umbraculum* Hutton, from intestinal wall, ×80.——*3. Polyechinus agulhensis* (Döderlein) (14); *3a,b,* from tube foot and buccal membrane, ×200.——*4. Brissopsis* (32a); *4a, B. elongata* Mortensen, from tube foot, ×110; *4b, B. lyrifera* Forbes, from tube foot, ×110.——*5. Schizocidaris assimilis* Mortensen, from tube foot, ×75 (14).——*6. Selenechinus armatus* (de Meijere), from tube foot, ×180 (14).——*7. Echinodiscus auritus* Leske, from sucking disc of tube foot, ×250 (14).——*8. Mellitella stokesii* (Agassiz), from sucking disc of tube foot, ×280 (14).——*9. Micropyga tuberculata* Agassiz, from tube foot, ×120 (14).——*10. Echinometra mathaei* (de Blainville) (14); *10a,b,* from water vessel and gonads, ×80, ×100.——*11. Pericosmus melanostomus* Mortensen, from sucking disc of tube foot, ×8 (32d).——*12. Arachnoides placenta* (Linné), from buccal membrane, ×80 (14).——*13. Diadema setosum* (Leske) (32c); *13a,b,* from sucking discs of primordial tube foot and second tube foot, ×200.——*14. Heliophora orbiculus* (Linné), from sucking disc of tube foot, ×300 (14).——*15. Clypeaster* (14); *15a, C. rarispinus* de Meijere, from sucking disc of tube foot, ×175; *15b, C. latissimus* (Lamarck), from sucking disc of tube foot, ×210.

three long, pointed valves without poison glands or terminal teeth.

(3) **Ophicephalous** pedicellariae (Fig. 193,*3*) are most abundant in the circumoral region. The valves are blunt-ended, with serrate margins, and are hinged together by arc-shaped calcareous rods. They do not occur in Cidaroida.

(4) **Triphyllous** pedicellariae (Fig. 193, *5*) are very small, with flattened, finely-toothed valves not hinged to each other.

An additional type, termed **dactylous,** is found only in the Echinothuriidae. The valves, which are only slightly movable if at all, are three, four, or five in number and are spoon-shaped.

Variation in number of valves is considerable, particularly in the tridentate type, which may have either a lesser or greater number than the usual three. Pedicellariae easily become detached from the test after death with decay of their muscular attachments. Thus they are rarely reported in the fossil state, especially in association with the tests.

SPHERIDIA

The **spheridia** (Fig. 194) are minute, club-shaped calcareous bodies of uncertain function movably attached to minute tubercles. They are confined to the ambulacral areas in the adoral region. They occur in all living groups of Echinoidea except the Cidaroida. They vary greatly in number, from one per ambulacrum (close to the peristomial margin) in *Arbacia* and various clypeasteroids to several on each of the adoral ambulacral plates. They may hang freely down from the surface of the test or may be lodged in grooves or pits or in closed chambers, when they cannot be seen from the exterior.

SPICULES

In addition to skeletal features already described, many echinoids possess calcareous spicules and plates (Fig. 195) imbedded in the soft tissues, for example, in the tube feet, peristomial membrane, and wall of the gut. They are much used in the systematics of Recent forms but have not been identified in the fossil state. Their association with particular fossil tests would in any case be extremely unlikely and there is some risk of confusing them with the spicules of other groups of animals.

LARVAL SKELETON

During larval life the developing young echinoid is very different in appearance from its parents, so much so that the larval stages when first observed were thought to be different animals and were given separate names. In echinoids with a planktonic stage (the majority) after the egg is fertilized, the young echinoid passes through the so-called dipleurula stage before developing into the **pluteus** (or **echinopluteus**) larva. The pluteus (Fig. 196,*A,D*) is strikingly dissimilar to an adult echinoid and has a calcareous skeleton, which, at the time of metamorphosis into the **imago** (Fig. 196,*F*) or immature adult, in part forms the nucleus for some of the adult plates and in part is resorbed.

At first the body of the pluteus has two pairs of upward-projecting **arms** and then an additional four pairs develop. In the irregular echinoids a downward-projecting arm, the **spike,** usually appears also. The body is supported by a more or less complex calcareous basketwork (Fig. 196,*C*), and each of the arms has an axial calcareous rod. In some, the skeleton becomes very complex and ornate (Fig. 196,*E*); in others it is quite simple (Fig. 196,*B*).

No pluteus larvae have yet been reported from the fossil record, but it seems highly probable that they should be present in microfossil assemblages.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO ECHINOIDS

By J. Wyatt Durham and C. D. Wagner

This glossary has been compiled from the text of the section on echinoids. The definitions have benefited from the criticism and suggestions of H. B. Fell, A. G. Fischer, P. M. Kier, R. V. Melville, D. L. Pawson, authors of other parts of this section, and of R. C. Moore, Editor. Suggestions from Leigh W. Mintz have led to clarification of numerous definitions.

abactinal. Aboral or apical aspect; side opposite mouth.

aboral. Side opposite mouth; direction away from mouth.

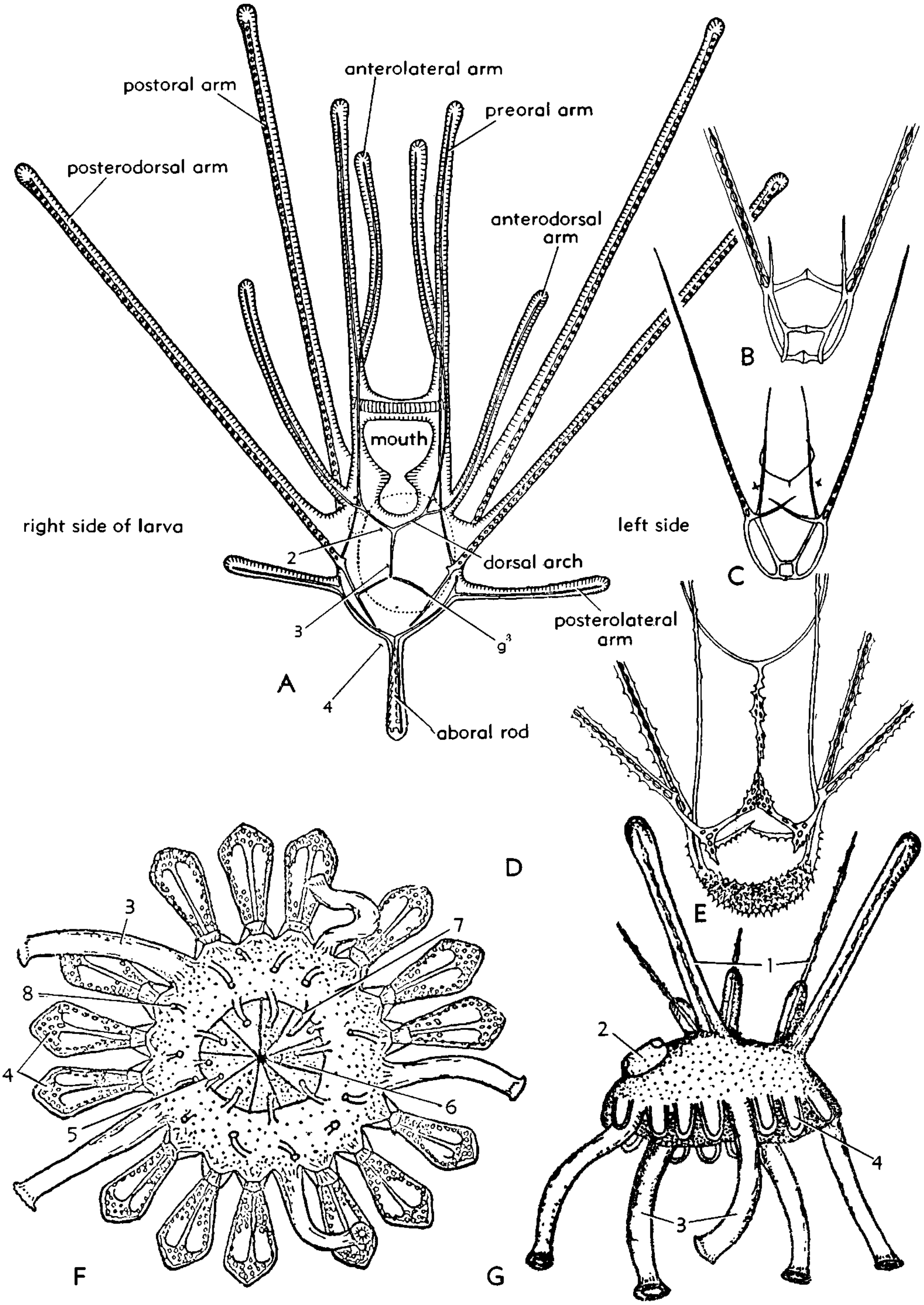

FIG. 196. Morphological features of echinoid larvae.——*A*. Pluteus of *Echinocardium cordatum* (PENNANT), dorsal view showing spicular skeleton; numerals 2-4 indicate positions of apical plates of inter-

(Continued on facing page.)

acetabulum. Concave proximal or articulating end of spine.

actinal. Oral aspect; side on which peristome is situated.

adapical. Toward apical system.

adapical suture. Suture along apical side of coronal plate.

adoral. Toward mouth.

adoral suture. Suture along side of coronal plate nearest mouth.

adradial. Position corresponding to boundary between ambulacral and interambulacral areas.

amb. Abbreviated designation of ambulacrum.

ambitus. Greatest horizontal circumference of test.

ambulacra (sing., **ambulacrum**). Five segments of test extending from apical system to peristome, each underlain by radial water vessel, and alternating with 5 interambulacra; designated by Roman numerals in Lovénian system.

ambulacral. Corresponding in position or pertaining to ambulacra.

ambulacral furrow. Food groove.

ambulacral pore. Opening through ambulacral plate for passage of tube foot.

amphiplacous. With basicoronal interambulacral plate abutting against 2 plates adapically.

amphisternous. With labrum followed by 2 large, more or less equal sternal plates opposite one another.

ampulla (pl., **ampullae**). Contractile chamber of water-vascular system internal to test, forming part of each tube foot complex; of skeleton, *see* camella.

anal fasciole. Fasciole adoral and lateral to periproct; if connecting with lateral fascioles, termed latero-anal fasciole.

anal plates. Paired interambulacral plates in contact with periproct of irregular echinoids; plates of periproctal system.

apex. Highest part of test.

apical system. Plates at aboral terminus of ambulacra and interambulacra including ocular and genital plates (when present); may include one or more complemental plates.

apophysis (pl., **apophyses**). Internal projection from interambulacral basicoronal plates for attachment of muscles supporting lantern.

arbacioid compound plate. Plate with 3 elements, of which adapical and adoral ones are demiplates.

areole. Scrobicule or depression around boss for attachment of muscles controlling movement of spines.

Aristotle's lantern. Structure of 40 or fewer skeletal elements serving for mastication.

aulodont. Descriptive term for lantern with open foramen magnum and with cross section of teeth broadly U-shaped.

auricle. Internal process arising from basicoronal ambulacral plates for attachment of muscles supporting lantern.

base. Portion of spine below milled ring.

basicoronal. Referring to corona at edge of peristome.

bidentate. Type of pedicellaria with head consisting of 2 long pointed valves.

bigeminate. Having 2 pore pairs.

bivium. Two posterior ambulacra.

boss. Part of tubercle below mamelon shaped like truncated cone.

bourrelet. Externally inflated adoral part of interambulacral areas.

brace. Rotula.

branchial slit. Gill slit.

buccal membrane. Tissue between peristomial margin and mouth.

buccal plates. Ten large primordial plates on buccal membrane with pores for buccal tube feet.

buccal system. Peristomial system of plates.

buttress. Ridge of skeletal material extending adapically from auricle on inner surface of test.

camarodont. Descriptive term for lantern with keeled teeth and closed foramen magnum.

camella (pl., **camellae**). Pouchlike ampulla forming bulge on inner wall of the test.

Carpenter system. Ambulacral areas of test designated by capital letters (*A* to *E*) and interambulacral areas by letters of adjacent ambulacra.

catenal plate. Supplementary plate (or plates) along III-5 axis between anterior and posterior portions of apical system where these are disjunct.

clavulae (sing., **clavula**). Small ciliated spines in fascioles.

collar. Smooth tapering portion of spine located above milled ring.

compact. Type of apical system with no separation between anterior and posterior elements.

compass. Slender arched radial rod in ambulacral position at top of lantern.

complemental plate. Supplementary plate (or plates) in apical system.

compound plate. Ambulacral plate unit composed of 2 or more individual plates, each with pore for tube foot, bound together by single large primary tubercle.

ambulacra 2, 3, and 4, respectively, in late larva; g^3 marks posterior extension of right posterodorsal rod, part of which later gives rise to genital 3; outlines of stomach and small "echinus rudiment" indicated by broken lines; enl. (4).——*B*. Spicular skeleton of early pluteus of *Echinothrix diadema* (LINNÉ), full length of arms not shown, ×175 (32b).——*C*. Spicular skeleton of pluteus of *Cyrtechinus verruculatus* (LÜTKEN), ×100 (32b).——*D*. Pluteus of *Diadema setosum* (LESKE), ×60 (32b).——*E*. Spicular skeleton of pluteus of *Echinodiscus auritus* (LESKE), full length of arms not shown, ×225 (32b).——*F,G*. Lateral and oral views of imago of *Arbacia punctulata* (LAMARCK), enl. (1, remnant of pluteal arms; 2, oral lobe of pluteus; 3, primary tube feet; 4, juvenile spines; 5, peristome; 6, teeth; 7, buccal tube feet; 8, postbuccal adult tube feet) (8).

conjugate pores. Pores of pair connected by groove in external surface of test.

corona. Principal skeletal structure excluding apical, periproctal, and peristomial systems, lantern, and appendages; all ambulacra plus interambulacra.

cortex. Differentiated dense outer layer of spine usually bearing ornamentation; nonliving on mature spine.

crenate. Crenulate.

crenulate. Descriptive term for tubercle or acetabulum of spine with ribbed periphery.

dactylous. Type of pedicellaria with spoon-shaped jaws mounted on individual stalks.

demiplate. Ambulacral plate which touches adradial suture but not perradial suture.

demipyramid. One of 10 elements which support teeth in Aristotle's lantern.

diadematoid compound plate. Plate with 3 primary elements, of which the middle one is largest.

dicyclic. Type of apical system with ocular and genital plates in 2 concentric circles, genitals alone in contact with periproctal margin.

disjunct. Type of apical system with anterior part (usually genital plates 1, 2, 3, and 4 and ocular plates II, III, and IV) separated from posterior part (ocular plates I and V, forms with disjunct apical system lacking genital 5).

echinoid compound plate. Plate with 3 or more elements of which adoral and adapical ones are primaries and adoral one is largest.

echinothurioid compound plate. Plate of 3 elements (primary with 2 small included plates on its adoral margin).

endocyclic. With periproct located within oculogenital ring.

endopetalous fasciole. *See* internal fasciole.

epiphysis. Element at top of Aristotle's lantern in interambulacral position.

episternal plates. Second pair of postlabral plates in amphisternous spatangoids.

epistroma. Adventitious skeletal material on outer surface of test plates.

ethmolysian. See ethmolytic.

ethmolytic. Type of apical system in which genital plate 2 extends posteriorly between oculars I and II and genital 1 on one side and oculars III, IV, and V and genitals 3 and 4 on other; genital plate 5 may or may not be present.

ethmophract. Type of apical system in which genital plates 1, 2, 3, and 4 mutually adjoin; genital plate 5 may or may not be present.

exocyclic. With periproct located outside of oculogenital ring.

exsert. With ocular plates not in contact with periproctal margin.

fasciole. Narrow band of small densely ciliated spines (clavulae) in which cilia beat to create currents; on denuded test narrow band of small tubercles which bears such spines.

floscelle. Star-shaped area around peristome formed by phyllodes and bourrelets.

food groove. Narrow grooves leading to peristome in adoral ambulacral areas supplied with specialized tube feet for food gathering and transport; may extend into interambulacral areas and onto aboral surface.

foramen magnum. Space between upper ends of paired demipyramids of lantern.

genital plate. Primordial interradial apical plate usually with one or more pores for discharge of genital products.

genital pore. Opening in genital plate for discharge of reproductive products.

gill slit. Indentation of peristomial margin of interambulacra for passage of stem of external branchia.

globiferous. Type of pedicellaria with 3 valves containing poison glands.

gonopore. See genital pore.

holamphisternous. Type of plastron having symmetrical pair of sternal plates followed by symmetrically paired but otherwise undifferentiated plates.

hypophyllode. Primitive or feebly developed phyllode.

included plate. Ambulacral plate which touches neither perradial nor adradial suture.

insert. With ocular plates in contact with periproctal margin.

interamb. Abbreviated designation of interambulacrum.

interambulacra (sing., **interambulacrum**). Five segments of test extending from apical system to peristome, alternating with ambulacra; designated by Arabic numerals in Lovénian system.

intercalary. Type of apical system in which ocular plates II and IV meet at mid-line so as to separate anterior and posterior portions.

internal fasciole. Fasciole surrounding apical system and crossing all petals.

internal support. Rod- or pillar-like structure between inner oral and inner aboral surfaces of test.

interporiferous zone. Area between 2 inner pore rows of ambulacrum.

interradial suture. Suture between 2 columns of plates in interambulacrum; in forms with more than 2 columns in interambulacral area, suture between 2 middle columns.

interradius. Interambulacrum.

irregular. With periproct located outside oculogenital ring.

keel. Raised or ridged section of corona; also longitudinal ridge on internal side of tooth.

labrum. More or less enlarged and modified liplike primordial plate bordering peristome in interambulacrum 5.

lantern. Structure of 40 or fewer skeletal elements which serves for mastication (same as Aristotle's lantern).

lateral fasciole. Fasciole extending posteriorly from peripetalous fasciole; termed lateroanal fasciole if connected with anal fasciole.

lateroanal fasciole. Fasciole formed by union of lateral and anal fascioles.

Lovénian symmetry. Bilateral symmetry with respect to plane passing through apical system, peristome, and periproct in irregular echinoids; recognized in regular echinoids chiefly by position of madreporite.

Lovénian system. Numbering system in which ambulacral and interambulacral areas of test are designated by Roman (I-V) and Arabic (1-5) numerals, respectively.

lunule. Opening from aboral surface through oral surface of test at perradial or interradial suture.

madreporite. Plate (or plates) of apical system perforated to provide access to water-vascular system from exterior.

mamelon. Raised, rounded top of tubercle on which spine articulates.

margin. Ambitus of corona in flattened echinoids.

marginal fasciole. Fasciole extending around ambitus.

masticatory apparatus. See Aristotle's lantern.

medulla. Meshlike central core of spines.

meridoplacous. With first adoral interambulacral plate abutting adapically against single plate.

meridosternous. Type of plastron with labrum followed by single large plate.

mesamphisternous. Type of plastron having symmetrical pair of sternal plates followed by alternating plates.

metasternous. Meridosternous plastron with sternal followed by several large plates in single column.

mid-zone. Region of corona midway between the apical system and peristome.

microcanal system. System of canals within plates of corona for passage of secondary branches of water-vascular system leading to accessory tube feet, apparently found only in clypeasteroid echinoids.

miliary. Very small, nonprimary spine.

miliary tubercle. Tubercle supporting miliary spine.

milled ring. Flange near base of spine for attachment of muscles that move spine.

monobasal. Type of apical system with genital plates apparently fused, suture lines being obliterated.

monocyclic. Type of apical system with genital and ocular plates arranged in single ring around periproct.

multiserial. Type of ambulacrum with pore pairs arranged in more than 2 longitudinal series.

neck. Smooth cylindrical portion of primary spine between collar and shaft.

neuropore. Single pore in ambulacral plate for passage of branch of radial nerve to exterior of test.

notch. Indentation of margin of test, usually at perradial suture.

occluded plate. Ambulacral plate which touches perradial but not adradial suture.

ocular plate. Primordial plate of apical system at terminus of ambulacrum, perforated by ocular pore.

ocular pore. Perforation in ocular plate for passage of terminal tentacle.

oculogenital ring. System of ocular and genital plates at apical end of ambulacral and interambulacral areas, surrounding periproct in regular echinoids.

oligoporous. Referring to compound or pseudocompound ambulacral plate with few pore pairs, usually 3.

ophicephalous. Type of pedicellaria with jaws which lock together.

oral. Side of test on which the peristome is located, usually directed toward substrate.

orthosternous. Meridosternous plastron with sternal followed by more or less equal-sized plates in 2 columns.

pedicel. See tube foot.

pedicellariae (sing., **pedicellaria**). Minute stalked specialized grasping or defensive organs articulated on granules.

perforate tubercle. Tubercle with small depression in top for ligament connecting spine with tubercle.

perignathic girdle. Continuous or discontinuous ring of internal processes around peristomial opening for attachment of muscles supporting and controlling lantern.

peripetalous fasciole. Fasciole passing around petals of ambulacra I, II, IV, and V and around or across ambulacral petal III.

peripodium. Raised rim around pore pair on external surface of test.

periproct. Opening in test for anus, covered in life by periproctal membrane, commonly plated.

periproctal system. Collective term for plates on periproctal membrane.

peristome. Opening in test for mouth, covered in life by peristomial membrane, commonly plated.

peristomial system. Collective term for plates on buccal membrane.

perradial. Having meridional position at mid-line of ambulacrum.

perradial suture. Suture between 2 columns of ambulacrum; in forms with more than 2 columns in ambulacrum, suture between 2 middle columns.

petal. Differentiated adapical segment of ambulacrum with tube feet more or less specialized for respiration; pores of pair in petal typically unequal or enlarged.

phyllode. Area of enlarged pores in adoral portion of ambulacra.

pillar. Internal supporting columns between aboral and oral sides of test.

plastron. More or less inflated and enlarged adoral segment of interambulacrum 5.

plate. Individual more or less flattened skeletal element composed of single calcite crystal.

polyporous. Referring to compound or pseudocompound ambulacral plate with many pore pairs, usually 5 or more.

pore pair. Ambulacral pore divided by wall of stereom through which single tube foot passes.

preanal plates. Paired interambulacral plates between episternal and anal plates in echinoids with plastron.

primary plate. Ambulacral plate that extends from perradial to adradial suture.

primary spine. First-formed and usually largest spine of coronal plates, situated over growth center of plate except on compound ambulacral plates.

primary tubercle. Tubercle articulating with primary spine.

primordial plates. First plates formed following metamorphosis in each plate system.

protamphisternous. Type of plastron with asymmetrical pair of sternal plates followed by alternating plates.

protosternous. Type of plastron with labrum followed by 2 simply alternating, slightly enlarged plates.

pseudocompound. Referring to group of 2 or more associated primary or reduced plates not bound together by primary tubercle.

pyramid. Large beaklike or winglike element of lantern in interambulacral position.

radial. Ambulacral.

radiole. Spine.

reduced plate. Ambulacral plate excluded from perradial suture or adradial suture, or both.

regular. Type of test having periproct within oculogenital ring of apical system.

rostrum. Raised or attenuated area of interambulacrum 5.

rotula (pl., **rotulae**). Massive radial element at top of lantern in ambulacral position.

scrobicule. Depressed ring around base of tubercle for attachment of muscles of spine.

secondary spine. Intermediate-sized spine, later in appearance than primary spine.

secondary tubercle. Tubercle with which secondary spine articulates.

septa. Radial structures external to medulla in spines.

shaft. Main part of spine.

sieve plate. See madreporite.

spheridia. Minute spherically modified spines on short stalks commonly situated adorally in pits near perradial suture.

spicules. Minute calcareous discs or diversely shaped rods imbedded in various tissues of body.

spine. Movable elongated calcareous shaft mounted on tubercle and articulating with it.

stereom. Calcareous mesh of which skeletal elements are composed.

sternal plates. First pair of postlabral plates in echinoids with plastron.

sternum. See plastron.

stirodont. Descriptive term for lantern with keeled teeth and open foramen magnum.

subanal fasciole. Fasciole enclosing more or less elliptical area on posterior face of test below periproct.

subpetaloid. Type of ambulacrum showing tendency toward petaloid development.

suranal plate. First-formed and largest plate of periproctal system; not recognizable in many echinoids.

suture. Narrow zone marking contact between adjacent plates; usually represented by line on surface of test.

terminal tentacle. Terminal podium of radial vessel of water-vascular system extending through ocular pore.

test. Collective term for plates of coronal, apical, periproctal and peristomial systems.

tetrabasal. Type of apical system with 4 separate genital plates (genital 5 not present).

tooth. Calcareous rod located in pyramid in interambulacral position in lantern (upper end of tooth uncalcified).

tridentate. Type of pedicellaria with 3 long, pointed, jawlike valves.

trigeminate. Having 3 pore pairs.

triphyllous. Type of minute pedicellaria with 3 leaflike jaws not hinged to one another.

trivium. Three anterior ambulacra.

tube foot. End of branch of water-vascular system serving for grasping, adhesion, locomotion, respiration, or combination of these.

tubercle. Knoblike structure on outer surface of test plates with which spine articulates.

ultramphisternous. Type of plastron with sternal and succeeding plates symmetrically paired, latter differentiated into episternal, preanal, and anal plates.

uniserial. Referring to ambulacrum with pore pairs in single longitudinal row.

zygopore. Pore pair.

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ECOLOGY AND PALEOECOLOGY

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Few detailed studies of the ecology of echinoids have been made. Cooke (3) has given an annotated bibliography of some pertinent papers subsequent to 1930. Brattström (1) has studied factors limiting the distribution of echinoderms at the entrance to the Baltic. Nichols (4) has presented an outstanding study of the burrowing habits of *Echinocardium cordatum* and other British spatangoids. Many specific details are available in Mortensen's monograph (5) in his discussions of individual species. Some details of ecology are presented in the individual parts of this *Treatise* volume. Other details and broad generalities are given here.

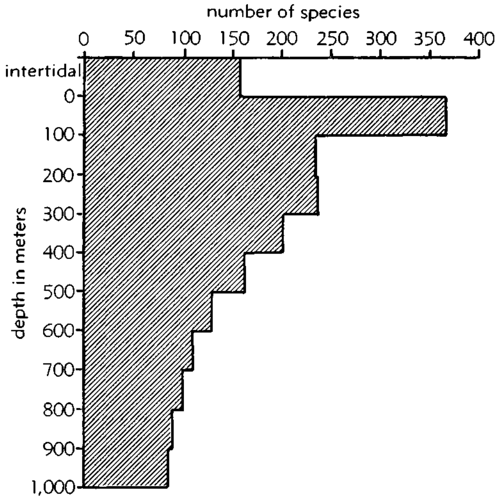

FIG. 197. Distribution of living species of echinoids in upper 1,000 m. of the sea (data from Mortensen, 5).

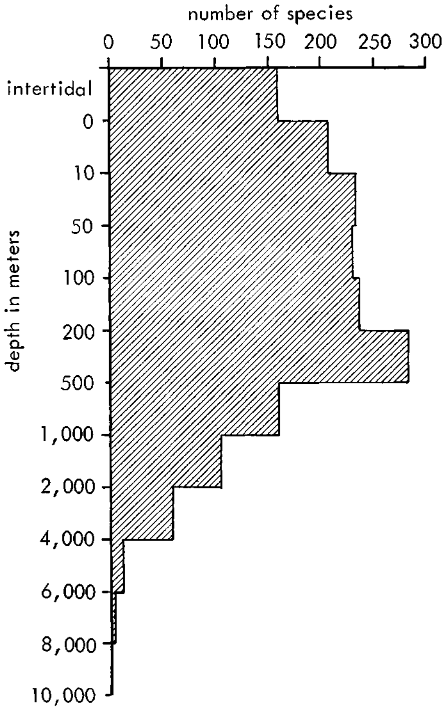

FIG. 198. Distribution of living species of echinoids in the sea (data from Mortensen, 5, and Brun, 1957).

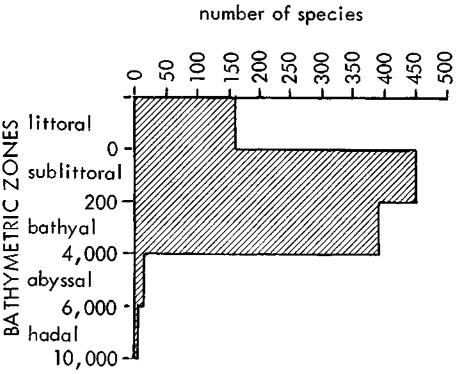

FIG. 199. Distribution of living species of echinoids in the sea according to bathymetric zones (sources as for Fig. 198).

The Echinoidea are aquatic organisms represented by about 800 living species, primarily inhabitants of waters of normal marine salinity. However, a few (e.g., *Mellita quinquiesperforata*) may live in waters with a salinity as low as about 20 per cent (Aransas Bay, Texas). The studies of BRATTSTRÖM (1) show that in the Öresund (at the entrance to the Baltic) *Echinocyamus pusillus* likewise may live in water of about this same low salinity. Others occasionally live where the salinity possibly may range above 40 per cent (e.g., *Lytechinus*, in Laguna Madre, Texas).

Most echinoids live in subtropical and tropical regions where the shallow-water types are highly diversified and abundant. The diversity decreases away from the warmer areas, but *Psammechinus miliaris, Echinus esculentus, E. acutus norvegicus, Echinocyamus pusillus, Echinocardium cordatum, Echinarachnius parma, Schizaster fragilis, Spatangus purpureus,* and *Strongylocentrotus droebachiensis* are known from 70°N. latitude or farther north. An even larger number of echinoids is known from the Antarctic region, where the fauna is characterized by a diversity of cidarids and by the presence of many species that brood their young.

Bathymetrically, living echinoids are distributed (Fig. 197-199) from the littoral[1] to the hadal zones. More than 150 species are known to occur between high and low tides, that is, in the littoral zone. More than 360 species are found in the first 100 m.

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[1] Bathymetrical zones referred to are those proposed in the *Treatise on Marine Ecology and Paleocology* (Geol. Soc. America, Mem. 68, 1957).

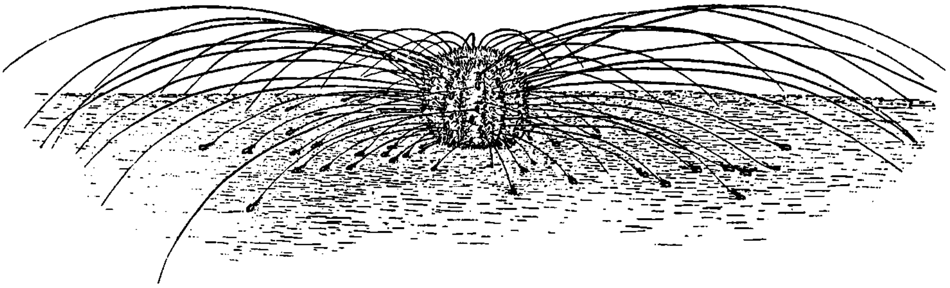

Fig. 200. Diadematoid echinoid *Plesiodiadema indicum* (Döderlein), showing exceptionally long curved slender spines, ×0.35 (Mortensen, 1923).

below the littoral zone, numbers of species gradually decreasing thereafter with increasing depth. At least two species, members of the genus *Pourtalesia,* are known to occur in the hadal zone, below 6,000 m. One family of regular echinoids (Echinothuriidae) and five families of irregular echinoids (Aeropsidae, Hemiasteridae, Asterostomatidae, Pourtalesiidae, Urechinidae) are represented in the abyssal and hadal zones, that is at depths below 4,000 m. The genera of these families known to occur in these depths are *Aceste, Aeropsis, Ceratophysa, Delopatagus, Helgocystis, Hemiaster, Homolampas, Kamptosoma,* and *Pourtalesia.* Many shallow-water species have a limited bathymetric range.

All known echinoids are benthonic. Many regular types live free on the sea floor, moving about by use of their spines and to some extent their tube feet. Where the substrate is rocky they may utilize cavities and crevices for protection and some (e.g., *Strongylocentrotus purpuratus, Echinostrephus aciculatus*) excavate cavities in rocks. The holes seem to be created by a rotary action of the spines, sometimes aided by gnawing action of the teeth. *S. purpuratus* is even known to bore into steel piling. The burrows of *Echinostrephus* may be as much as 4 inches deep. As the echinoid grows, it enlarges its burrow and in some instances appears to become imprisoned because the aperture is no longer large enough for egress. Some investigations indicate that the formation and utilization of burrows is a protection against wave action and thus is limited to areas of excessive wave action.

Other rocky-shore echinoids (e.g., *Podophora, Colobocentrotus*) protect themselves against wave action by the development of short flat-topped spines on the aboral surface and powerful sucker-like tube feet on the oral surface, enabling them to adhere like limpets to the rocks. The broad, flat shield-shaped spines of the fossil *Anaulocidaris* may indicate a similar habitat.

The aspidodiadematid *Plesiodiadema indicum* (Fig. 200) has very long, downwardly curved primary spines with enlarged tips that seemingly serve to keep it from sinking into the soft substrate on which it dwells. Many echinothuriids have similar hooflike structures on the end of the primary spines of the oral surface. Presumably, these serve the same purpose as those of *Plesiodiadema.*

Many present-day irregular types of echinoids live more or less buried in sand or muddy substrates. Some species of *Clypeaster* and *Encope* may live as much as 5 or 6 inches below the surface in sandy sediments. The minute *Echinocyamus* nestles among particles of sand and gravel. In quiet water *Dendraster excentricus* and rotulinid species assume a steeply inclined position with only the anterior third or fourth of the test buried in sediment, while the rest of the test extends up above the sea floor. Such species may have the food grooves leading to the mouth poorly developed in the anterior portion of the test. However, the same individuals, when disturbed by strong wave action, burrow beneath the surface of the sand. *D. laevis,* which lacks the marked eccentricity of *D. excentricus,* is not known to assume the inclined position.

The deep-water pourtalesiids (e.g., *Echinosigra*), with a funnel-like structure surrounding the peristome and a subanal

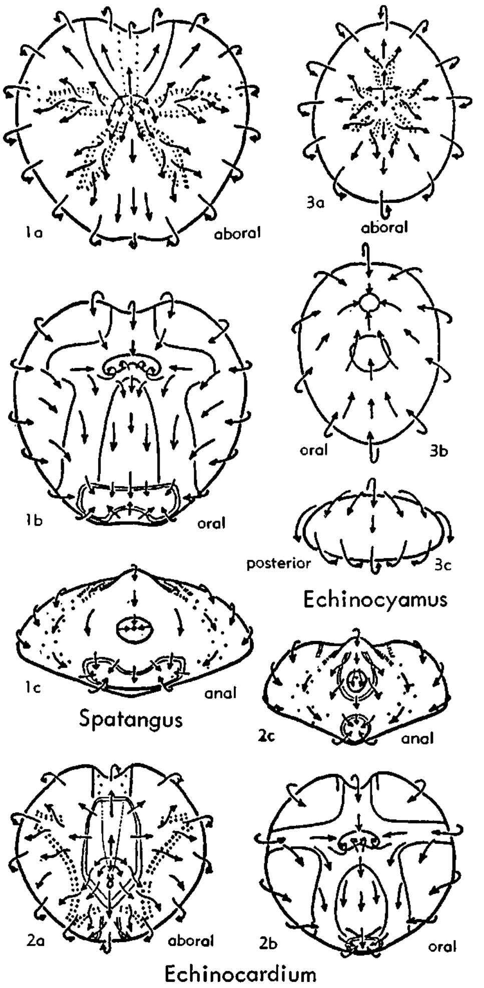

Fig. 201. Courses of ciliary currents (diagram.) on surface of test *(1,2)*, two spatangoids, and *(3)* clypeasteroid (4).——*1a-c. Spatangus purpureus.*——*2a-c. Echinocardium cordatum.*——*3a-c. Echinocyamus pusillus.*

fasciole, presumably dwell partially submerged in the substrate, with only the upper surface exposed. The extinct holasterid *Hagenowia,* which in shape is suggestive of some pourtalesiids, presumably plowed through the fine calcareous substrate in which it dwelt with only the top of its long "neck," bearing the apical system, exposed.

The development of fascioles in the spatangoids is closely correlated with their burrowing habits and the kind of substrate inhabited. Nichols' recent study (4) has greatly clarified the functions of the fascioles, the different types of tube feet, and the various kinds of spines found in this group. The cilia on the clavulae of the fascioles, the bases of the spines, and the intervening epithelium work to create ciliary currents over the surface of the test (Fig. 201). On *Echinocardium, Spatangus,* and *Brissopsis* currents pass outward from the apical system along the ambulacra and over the ambitus (Fig. 202). On the oral surface some currents lead to the mouth, but most run posteriorly to the subanal fasciole, thence away from the test out through the sanitary tube. Presumably, somewhat similar currents are present on most irregular echinoids, varying in pattern according to their habits. Possibly the presence of fascioles indicates active burrowing of one type or another, inasmuch as *Echinocyamus pusillus* (Fig. 201), a nestler, has no fascioles.

Among the burrowing spatangoids studied by Nichols (4) the presence of respiratory funnels and sanitary tubes is apparently correlated with kind of substrate and depth

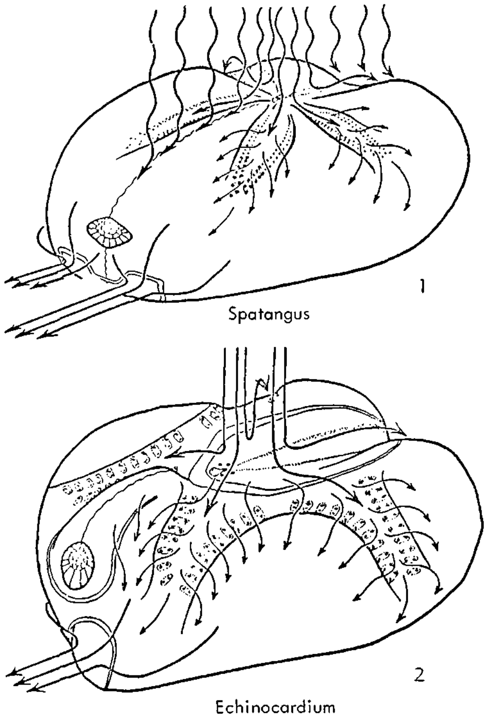

Fig. 202. Principal currents to and from test (diagram.) in two spatangoids (4).——*1. Spatangus purpureus.*——*2. Echinocardium cordatum.*

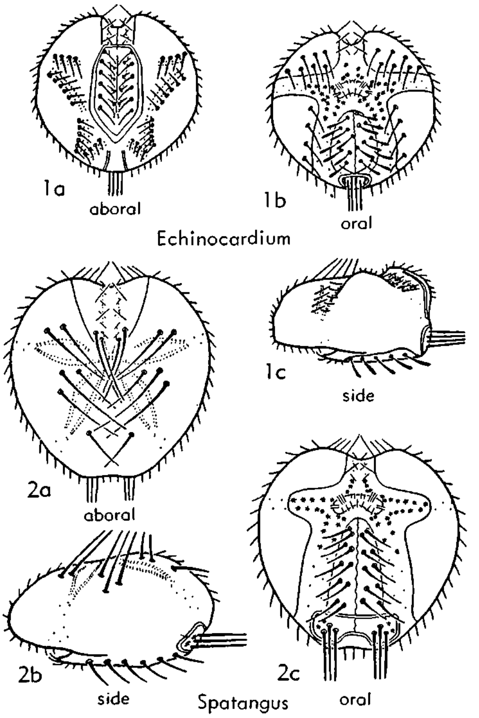

FIG. 203. Arrangement of spines (diagrammatic) in irregular echinoids (only a few of each series of spines shown) (4).——*1. Echinocardium cordatum; 1a-c,* aboral, oral, and lateral views.——*2. Spatangus purpureus; 2a-c,* aboral, lateral, and oral views (4).

of burial. *Echinocardium cordatum,* which burrows to a depth of 18 cm., usually in a sandy substrate, has both a respiratory funnel and a sanitary tube. *Spatangus purpureus,* normally a shell-gravel inhabitant that burrows to a depth of 2 cm. (to top of test), does not maintain a respiratory funnel at all times but regularly has a sanitary tube. *S. raschi,* which plows along the surface of a sandy mud substrate, has the apical surface exposed but utilizes a sanitary tube. NICHOLS considers that inasmuch as *S. purpureus* inhabits only clean shell gravel, enough water is drawn through the interstices of the gravel for respiratory purposes. This species is not equipped with dorsal burrow-building tube feet and could only maintain a respiratory funnel, if at all, by activity of the apical spines. In the species studied, the respiratory funnels and sanitary tubes are built by the combined action of the tube feet and the spines. The spines establish the tubes and funnels by a rotary action, mucus exuded by the tube feet being wiped onto the spines and the spines in turn plastering it onto the wall of the tubes and thereby strengthening them. In *Echinocardium cordatum,* after the animal has burrowed to a depth such that the spines can no longer reach the surface, the upper part of the respiratory funnel is maintained by the tube feet alone.

The clypeasteroid *Echinocyamus pusillus* (Fig. 201,*3*), also studied by NICHOLS, is a minute form which usually is a nestler in shell gravel. It never has been observed to push itself actively into the substrate, but is known to succeed in covering itself by pass-

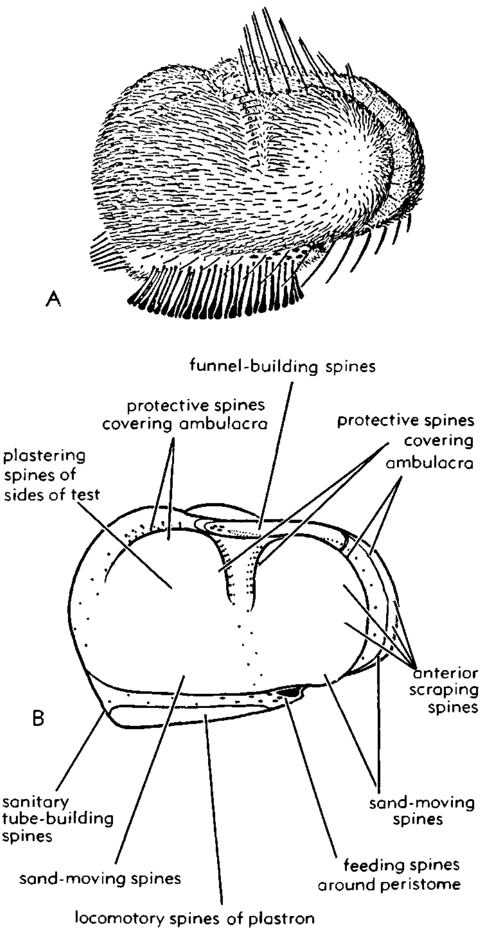

FIG. 204. Diagrammatic side views of spatangoid *Echinocardium cordatum* showing types of spines, their distribution and function *(A),* with tube feet and spines intact, and *(B)* denuded test showing areas of origin of different types of spines (4).

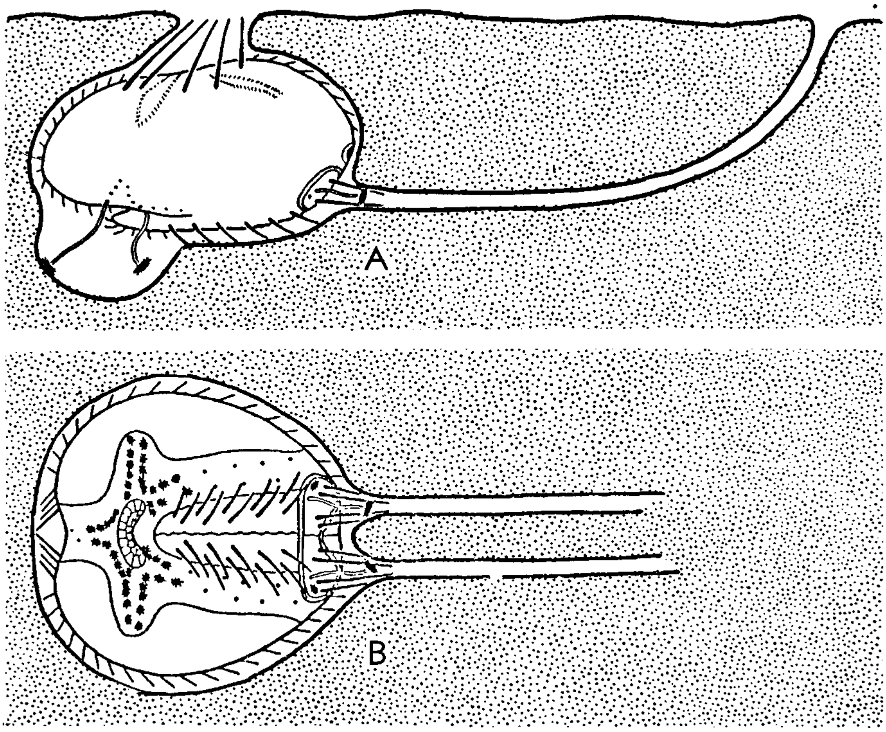

FIG. 205. Spatangoid echinoid *Spatangus purpureus* in newly made burrow, *(A,B)* side and bottom views; respiratory canal maintained by funnel-building spines, feeding excavation with 2 penicillate oral tube feet shown, and double sanitary canal built by sanitary-tube-building spines and penicillate tube feet; respiratory and sanitary canals lose direct communication with surface as animal burrows deeper (4).

ing small particles up onto its upper surface by means of the accessory tube feet. In this animal there are seemingly no feeding or burrow-building tube feet (the function of the accessory tube feet is little known, but they may also serve in food gathering), although there are 10 large sensory tube feet around the peristome.

The function and arrangement of the various kinds of spines have been studied by NICHOLS in *Echinocardium* and *Spatangus* (Fig. 203, 204). (1) The flattened spines on the plastron serve for locomotion, (2) the medium-length lateral spines adjacent to and outside the posterior ambulacra operate to move sand, (3) the short spines around the mouth assist in feeding, (4) the short lateral spines on the sides of the test help in maintaining the walls of the burrow and in passing sand posteriorly, (5) the short spines on the anterior margin of the test scrape material from the front wall of the burrow, (6) the spines adjacent to the sides of the petals form a protective arch over the petals, (7) the long dorsal spines aid in building the respiratory funnel, and (8) the tufts of longer spines within the subanal fasciole build the sanitary tube. The tubercles to which the different kinds of spines are attached are differentiated morphologically, and it seems very possible that the function of the spines and habits of many fossil echinoids can be inferred by comparing them to those living species that have been studied in this manner.

The division of labor among tube feet has also been studied by NICHOLS (Fig. 205, 206). Contrary to the interpretation of previous investigators, he has shown that the very extensile penicillate tube feet of the dorsal region of the anterior ambulacrum of *Echinocardium cordatum,* that often are observed extending out of the respiratory funnel, are not engaged in food gathering but are primarily used in building and maintaining the respiratory funnel. The penicillate tube feet of the phyllodes around the mouth serve for food gathering, while the penicillate tube feet within the subanal fasciole help to build and maintain the sanitary tube that carries waste products away. The tube feet of the petaloid parts of the ambulacra serve for respiration, while the nonspecialized tube feet of the remaining areas apparently serve for sensory purposes only. Nichols also has indicated that *Echinocardium cordatum,* which burrows much deeper than the other species studied, has a much greater number of penicillate respiratory funnel and sanitary tube-building tube feet than other species (Table 1). The numbers of tube-building tube feet seemingly also vary according to the kind of substrate in which the echinoid commonly dwells. The pores for the tube feet also vary (Fig. 207) in character according to function of the tube feet. Comparative study of the pores of fossil forms should enable similar inferences regarding the kinds, functions, and numbers of tube feet.

Among extinct echinoids it seems probable that those with elongated flexible tests and short spines (e.g., *Aulechinus*) may not have maintained a regular orientation with respect to the substrate and even may have lain on their sides like holothurians. Types with rigid tests and short spines (e.g., *Bothriocidaris, Melonechinus*) probably were oriented normally with the oral surface adjacent to the substratum but not buried within it. The more flexible lepidocentroids with flattened oral surface (e.g., *Proterocidaris*) probably lived with the oral surface submerged in the substrate and the apical surface projecting above the sea floor.

Like other echinoderms, echinoids tend to be gregarious, or at least to occur in very large numbers in local areas where conditions are favorable. More than 400 individuals of the sand dollar *Dendraster excentricus* were counted in an area of nine square feet in Puget Sound. Similarly Swan (6) has recorded more than 1,300 specimens of the urchin *Stronglyocentrotus droebachiensis* from an area of three square meters along a rocky shore in Maine. Fossil sand dollars closely related to the living *D. excentricus* in some places form a major constituent of individual beds in the upper Cenozoic of California, but there concentrations do not persist laterally. Concentrations such as those referred to are not always present, however, and in some areas no echinoids, or only scattered individuals, occur.

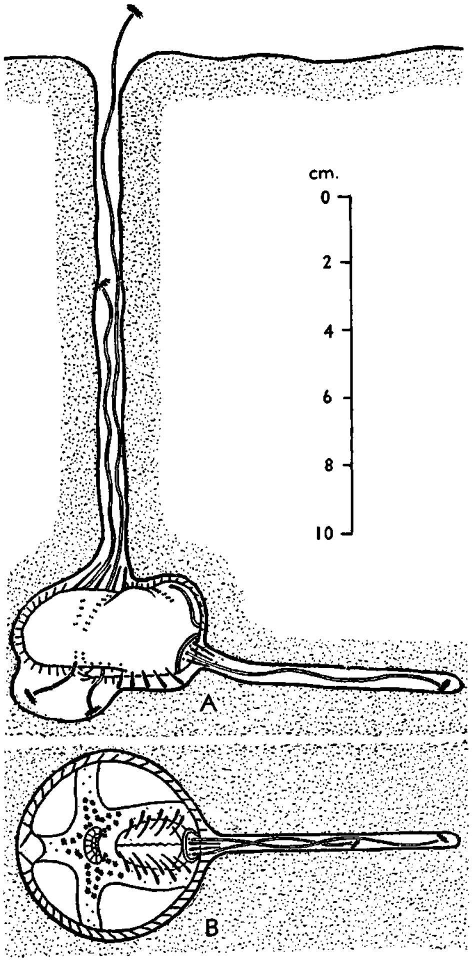

Fig. 206. Spatangoid echinoid *Echinocardium cordatum* in burrow with long open respiratory canal and blind sanitary canal, showing expanded dorsal penicillate tube feet, oral feeding tube feet, and subanal burrow-building tube feet; *(A)* side view, *(B)* bottom view (4).

Regular echinoids often seem to show no preferred direction of locomotion but at times a weak preference for movement with ambulacrum III anterior is apparent. Irregular echinoids have a strong preference for movement with ambulacrum III anterior. Some spatangoids seemingly can move in

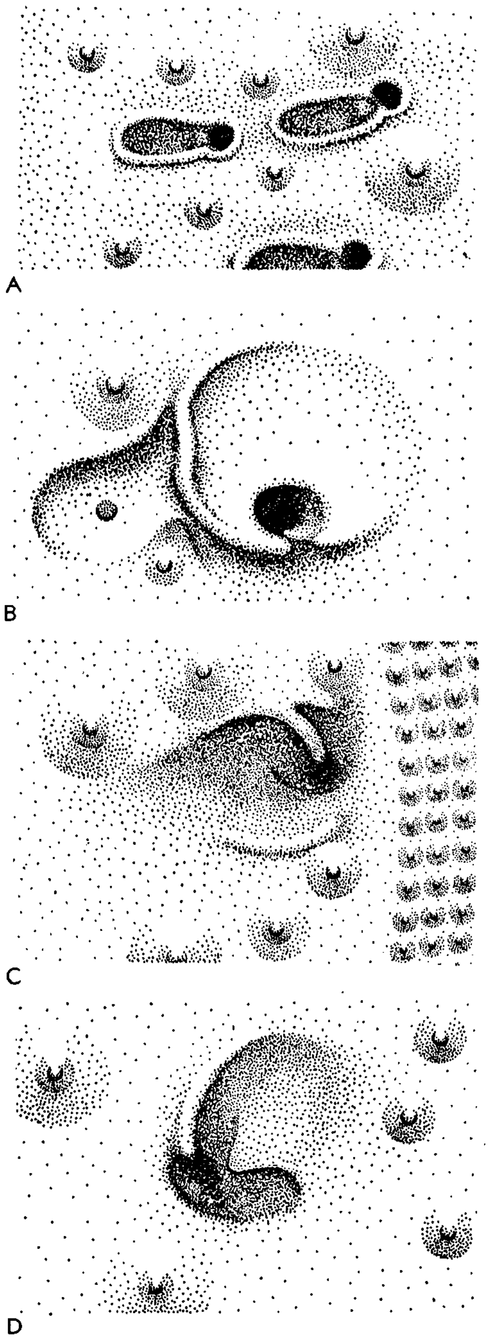

FIG. 207. Pores in test of *Echinocardium cordatum* for various types of tube feet (4).——*A*. Pores for funnel-building tube feet in ambulacrum III, within inner fasciole.——*B*. Pores for oral food-gather-

(Continued at right.)

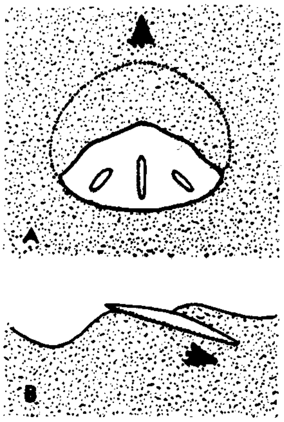

FIG. 208. Sand dollar *Mellita lata* burrowing, *(A)* seen from above, *(B)* side view (2, courtesy Trustees, British Museum, Natural History).

no other direction, but a few clypeasteroids have a limited capacity for movement in other directions. Movement is primarily accomplished by use of the spines but regular echinoids use their tube feet to ascend steeply inclined or vertical surfaces. In sand dollars the tube feet aid in burial by moving sand grains onto the aboral surface. *Lytechinus variegatus,* using its spines, can move along a horizontal sandy surface at a rate of 3 to 5.5 inches per minute. *Mellita quinquiesperforata* may assume a slightly inclined position (Fig. 208) near the surface of a sandy substrate, with the anterior margin buried and the posterior slightly exposed. In this position it may move continuously through the sand at a rate of 0.5 to 1 inch per minute.

Many regular echinoids react negatively to strong light, retreating into shaded areas or cavities during daylight. Others cover the aboral surface with fragments of plants, shells, and pebbles, holding them in place with their tube feet. In some echinoids (e.g., *Diadema*) the spines will quickly cluster and point toward the source of a shadow suddenly cast upon them. Mechanical irritation causes a similar reaction.

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ing tube foot in adoral plate of ambulacrum II (column b), two tubercles and pit (with stalk) for spheridia to left of wall.——*C*. Pores for subanal burrow-building tube foot in ambulacrum I (column b) within subanal fasciole.——*D*. Pore for sensory tube foot in ambital area of ambulacrum III.

TABLE 1. *Number and Kind of Tube Feet in Some British Echinoids (Nichols, 1959)*

	Tube feet, approximate number per animal							
	Respiratory	Feeding	Burrow-building		Sensory only		Depth to top of burrow	Kind of substrate
Spatangus purpureus	200	50	subanal	4	anterior ambulacral	32	2 cm.	shell gravel
					lateral	50		
					periplastronal	12		
S. raschi	200	40	subanal	4	anterior ambulacral	54		sandy mud
					lateral	73		
					periplastronal	14		
Echinocardium cordatum	70	40	subanal		anterior ambulacral	8	18 cm.	
			anterior ambulacral	70	lateral	40		sand
					periplastronal	16		
E. pannatifidum	95	45	subanal	4	anterior ambulacral	24	3 cm.?	shell gravel
			anterior ambulacral	6	lateral	22		
					periplastronal	16		
E. flavescens	55	32	subanal	4	anterior ambulacral	14	3 cm.?	shell gravel
			anterior ambulacral	5	lateral	45		
					periplastronal	12		
Brissopsis lyrifera	120	35	subanal	6	anterior ambulacral	7	6-8 cm.	
			anterior ambulacral	30	lateral	45		mud
					periplastronal	22		
Echinocyamus pusillus	45	none	none		buccal	10	nestler	shell gravel

A few urchins (e.g., *Psammechinus miliaris*) are known to react negatively to gravity, constantly ascending even steeply inclined surfaces if given the opportunity. The purpose of this reaction in nature is uncertain.

Most regular urchins will eat almost any organic material if given the opportunity and the need. However, some (e.g., *Echinus esculentus*) tend to be carnivorous and others (e.g., *Strongylocentrotus*) herbivorous. *Arbacia* has even been known to capture live specimens of the fish *Fundulus* at night. It is believed, however, that the fish were in a weakened condition. Clypeasteroids with well-developed food grooves and small mouths seem to live largely on small organic particles and organisms trapped by mucous strands and carried by ciliary currents or accessory tube feet or both along food grooves to the mouth. The spatangoids seemingly may either ingest large quantities of the substrate and digest the organic material from it, or where the oral food-gathering tube feet are well developed, organic material may be more or less sorted from the nonorganic components before ingestion.

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PHYLOGENY AND EVOLUTION

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The presence of a lantern, articulated spines, an internal radial water vessel, and presence of the Lovénian formula in the plates around the peristome place the Ordovician echinoderm *Bothriocidaris* among the echinoids.[1] *Eothuria,* considered by MacBride and Spencer to be a plated holothurian, has the same characters and likewise appears to be an echinoid. Accordingly, the oldest known echinoids (all Ordovician) include *Bothriocidaris* and *Eothuria,* as well as two other genera of undisputed echinoidean character, *Aulechinus* and *Ectinechinus.* The important common characters that stand out from a consideration of these genera are:

1. Both rigid (*Bothriocidaris*) and flexible tests are present, with differentiated ambulacra and interambulacra.
2. The apical system includes a full complement of oculars (except in *Eothuria*), but there is only one genital (none in *Bothriocidaris*).
3. The anus is within the apical system, a periproctal system of plates is present, and the mouth is at the opposite pole.
4. The ambulacra extend from the apical system to the mouth, with ambulacral plates always reaching the peristomial margin. Interambulacral plates may not extend to the margin.
5. The radial water vessel is internal in *Bothriocidaris* and *Eothuria*[2] but rests in a groove open to the exterior (although with internal ampullae) in *Aulechinus* and *Ectinechinus.*
6. The pores for the tube feet are close to the perradial suture in *Aulechinus, Ectinechinus* and *Eothuria,* but nearly medial in *Bothriocidaris.*
7. The ambulacral pores are variable in number, single in *Aulechinus,* double in *Ectinechinus* and *Bothriocidaris,* and multiple in *Eothuria.*
8. *Bothriocidaris* and *Eothuria* each have distinctive types of lanterns differing from that present in *Aulechinus* and *Ectechinus.*
9. All of these genera except *Bothriocidaris* have small apparently undifferentiated spines articulating in pits rather than on tubercles. In *Bothriocidaris* they rest on tubercles.

Review of the above-cited characters makes it seem evident, as it did to MacBride & Spencer, that the echinoid ancestry must extend considerably farther back in geologic time than the Ordovician. Further, the ancestral echinoid must have had the potential to give rise to these distinctive types as well as to all subsequent diverse morphologies present among the Echinoidea. It would seem that this ancestor must have had differentiated ambulacral and interambulacral areas; periproct and peristome at opposite poles; a full complement of ocular plates, but only a single genital plate and thus a single genital gland; articulating spines; internal ampullae for the tube feet; and masticatory apparatus either very simple or lacking. The clearly internal radial water vessel of *Bothriocidaris* casts doubt on the common inference that it was external in the ancestor.

The Lower to Middle Cambrian free-living edrioasteroid *Stromatocystites* has often been suggested as representing the stock from which the echinoids arose. This seems quite improbable inasmuch as the anus is already on the oral surface (i.e., irregular), and the ambulacra are restricted to this surface. In view of the fact that the highly differentiated Edrioasteroidea, Eocrinoidea, and Helicoplacoidea are already present in the lower part of the *Olenellus* Zone of the Lower Cambrian, it may well be that the ancestral echinoid had appeared before Cambrian time. Certainly, the diverse types present in the Ordovician indicate a pre-Ordovician ancestry.

The Early Cambrian Helicoplacoidea had well-differentiated ambulacra and interambulacra, seemingly had the mouth and anus at opposite poles, and thus are marked-

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[1] Myannil (7) has recently published a description of new and important specimens of *Bothriocidaris* with all new data confirming its place among echinoids.

[2] Erroneously stated to be in an open external furrow by Durham & Melville (1, p. 262) (see MacBride & Spencer, 1938, p. 130, and fig. 8C).

ly different from the contemporaneous Eocrinoidea. This suggests that the echinozoan lineage (2), to which the Helicoplacoidea would seem to belong, had already arisen and that the common ancestor for the Echinodermata is not to be found in the Eocrinoidea, but in some unknown pre-Cambrian type.

Post-Ordovician evolution among the Echinoidea has moved along various paths, often independent of one another. The result has been the diversity of types presented in this volume, as well as others as yet unrecorded. The principal pathways followed seem to have included the following:

1. Adoption of a rigid test by most.
2. Development of anteroposterior orientation and preferred direction of locomotion.
3. Improvement of the water-vascular system by modification and specialization.
4. Modification of appendages for special functions.
5. Increased efficiency of reproduction and protection of young.
6. Specializations for feeding purposes.

Although all known Ordovician echinoids except *Bothriocidaris* had flexible tests, by the end of the Devonian, types with rigid tests (Palaechinoida) were well established, competing with their contemporaries with flexible tests (Echinocystitoida, Archaeocidaridae). The Miocidaridae, with imbricating plates, are the only echinoids reported to have persisted from the Paleo zoic into later geologic time. By the end of the Triassic the derivative Cidaridae with rigidly sutured plates were in full sway. The Cidaroida gave rise to all the subsequent diversity, with most forms characterized by a rigid test. The most notable exception to the generally rigid tests of post-Triassic echinoids occurs among the Echinothurioida, where seemingly, accompanying their exploration of deeper water habitats, calcification was reduced, resulting in a flexible test. In this group, however, imbrication of plates, even though of the same general type as in the Echinocystitoida, is rarely as complete. Commonly gaps of considerable size are present between adjacent plates along the sutural area and they imbricate only near the ends. A very few other living echinoids (e.g., *Astropyga*) have more or less flexible tests, but the rigid test seems to be the most successful, judging by its prevalence among modern echinoids.

Most regular echinoids do not seem to have a preferred direction of locomotion, and movement may begin in any direction, although observations suggest that there is a preferred direction for some. FELL has shown that there is a persistent tendency for the anus to move out of the apical system, ultimately resulting in its localization in interambulacrum 5 and the resultant development of an anteroposterior orientation. Soon after the development of this axis, the test elongated in this same direction. At the same time preferred locomotion along the direction of this axis appeared and with this major step some echinoids began to burrow in the substrate, and a whole new habitat was opened for exploration.

Improvement and modification of the water-vascular system has occurred in many different ways. Seemingly, the first step was migration of the tube feet from perradial to adradial areas of the ambulacra during the lower and middle Paleozoic. At nearly the same time, the Palaechinoida initiated multiplication of the functionally advantageous tube feet by increasing the number of ambulacral columns, along with retention of small plates, while the main stock retained the single column of small ambulacral plates. Subsequently, in the Mesozoic, the formation of compound ambulacral plates permitted strengthening of the test and at the same time ultimately led to multiplication of tube feet to a degree comparable with that of the palaechinoids—compare the ambulacra of *Heterocentrotus* with those of a genus such as *Proterocidaris*.

Accompanying the invasion of substrates permitted by oriented locomotion came a division of responsibilities among the tube feet. On the apical surface some of the tube feet were modified to serve as respiratory organs, and petals developed for accommodation of the elongated bladelike respiratory tube feet. At the same time the external gills present in the regular Euechinoidea and more primitive irregular types were lost. Adorally the tube feet were modified to serve primarily as food-gathering or food-sensing organs, ultimately resulting, in more specialized types, in the formation of phyllodes or pseudophyllodes. Adapically in burrowing types, the tube feet of the anterior interambulacrum adjacent to the apical system became elongated and modified to aid in building a respiratory funnel to the surface, while posteriorly a few tube feet of ambulacra I and V adjacent to the periproct became similarly modified to help in building and maintaining a sanitary tube (8).

Among the clypeasteroids still another modification of the water-vascular system, primarily to aid in food gathering, has occurred. In addition to the regular respiratory tube feet in the petals, minute accessory tube feet are present over much of the surface of the test, even extending into large areas of the interambulacra in some species. An accessory canal system (microcanal system) developed within the calcareous plates of the test in order to accommodate the vessels connecting the accessory tube feet to the radial canals. In some forms these accessory tube feet are exceedingly numerous, several of them occurring around the base of each spine. Possibly interruption of the interambulacral areas on the oral surface of many clypeasteroids is a corollary to the extensive development of accessory tube feet, as is the general narrowing of the interambulacral areas on the oral surface. Although poorly known and little studied as yet, the accessory tube feet seem to function primarily to gather minute organic particles on which these echinoids feed. They become more abundant and usually larger in diameter as the food grooves leading to the mouth are approached.

The earliest echinoids seemingly had small unspecialized spines. No pedicellariae have yet been recognized in association with them. However, the presence of granules, in addition to tubercles, on some of the later Paleozoic genera suggests that pedicellariae, as well as differentiated spines, were present. Pedicellariae have been reported from Mississippian and Pennsylvanian strata by GEIS (3) and have been observed on a number of Jurassic echinoids, and it seems that these appendages were well developed and highly specialized by that time. By the Silurian some echinoids already had highly specialized spines (e.g., *Silurocidaris*), and diversification of spines in size and shape for locomotory and protective purposes proceeded rapidly among the Cidaroida. Among the regular echinoids, specialization of the spines on the apical surface for protection took many directions, from the large flat, shield-shaped spines of *Anaulocidaris* to the flat-topped pavement-forming spines of *Colobocentrotus*. In some, as among the Echinothurioida, poison glands are present on the tips of the spines. The primary spines may be greatly elongated (as in the Cidaroida) to aid in locomotion. With the development of the anteroposterior axis in the irregular echinoids came a specialization of spines, especially in spatangoids, according to position on the test. Some became short and paddle-shaped for locomotion through the substrate, others elongated to aid in tube building for respiratory and sanitary purposes, while still others were modified into the highly ciliated clavulae of the fascioles, serving to create water currents over the surface of the test.

Reproduction in most echinoderms takes place by discharge of eggs and sperm into the sea, fertilization and subsequent development taking place by chance outside of the test. Inasmuch as planktonic larval stages occur among all groups of living echinoderms, it seems probable that this was an early development in the common ancestral lineage. Enormous wastage, consequent on utilization of very large numbers of eggs and sperm, occurs in this method of reproduction and a number of echinoids have improved upon it. Most planktonic larvae are planktotrophic, that is, they feed on other smaller organisms. Others, however, depend on yolk stored in the egg (lecithotrophic). In this latter group, fewer and larger eggs are utilized. Direct development, with omission of the planktonic larval stage, occurs in a number of genera. Consequent on this, various means of protecting the young have appeared. In some cidaroids (e.g., *Ctenocidaris*) the young remain on the surface of the test, either around the apical system or around the mouth. The corresponding portion of the test is commonly depressed and the adjacent primary spines arch over the brood.

Among spatangoids such as *Abatus*, the

paired petals of the females may be greatly depressed to serve as brood pouches. In clypeasteroids such as *Echinocyamus,* a brood pouch may develop on the aboral surface of females of some species, while in the fossil *Fossulaster* it is on the oral surface. How the eggs or young get into these protective devices is unknown. As a consequence of these structures, a marked sexual dimorphism is developed in these genera.

All known Ordovician echinoids have relatively small peristomial areas, and it would appear that they must have fed on relatively small organic particles, perhaps obtained by rasping of the teeth of the lantern. Soon, however, a relatively larger peristome appeared in the Cidaroida and it is present in many of their regular descendants. This enabled the ingestion of larger particles and presumably adoption of a more omnivorous diet, as well as protrusion and utilization of the tips of the teeth and lantern for locomotion.

With the development of the anteroposterior axis, oriented locomotion, and invasion of the substrate, a whole new food supply became available. Burrowers like the spatangoids lost the lantern, the mouth remained moderate in size, moved to an anterior position, and food was obtained by ingestion of sediment along with masses of small organic particles gathered together by the specialized tube feet around the mouth. The Clypeasteroida developed accessory tube feet for gathering small organic particles and the food-groove system for conveying it to the central mouth. With increasing efficiency of this system, the mouth decreased in size, and the lantern seemingly was used only for mastication and not for food gathering. Sand dollars such as *Dendraster excentricus* have retained the centrally located mouth but have concentrated the food-gathering apparatus in the posterior portion of the test and assumed a semi-upright position on the sea floor, gathering food from the organic material suspended in the water above the sea floor.

At present the echinoids seem to be quite successful inhabitants of the marine realm, best suited to and as a result most diversified in tropical and warm temperate regions. In view of the present restriction of the tropics as compared to intervals in the late Mesozoic and early Cenozoic, it appears that they are probably more successful now (nearly 800 living species) than at any time in the past. At present they are known from all depths except the hadal trenches and include such forms as the armored *Colobocentrotus,* an inhabitant of the breaker zone, and the bizarre pourtalesiids, that largely live in bathyal depths. Included too are rock-borers (e.g., *Echinostrephus*) and burrowers beneath the sea floor (e.g., *Echinocardium*). The small *Echinocyamus* merely nestles down into the substrate, where its components are large enough to permit such action. However, the majority of echinoids merely move about on the sea floor or nestle in crooks and crannies.

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CLASSIFICATION

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INTRODUCTION

The history of the classification of echinoids has been reviewed by numerous previous investigators. Most useful are the works of AGASSIZ & DESOR (1846-47), DESOR (1855-58), DUJARDIN & HUPÉ (1862), A. AGASSIZ (1872-74), POMEL (1869; 1883), MORTENSEN (1904), LAMBERT & THIÉRY (1909-25, including a very extensive bibliography, albeit occasionally the citations are inaccurate or too incomplete for easy utilization), COULON (1933), and GIGNOUX (1933). The historical review presented here covers material published through 1965. It deals only with names and concepts of classification that ultimately were used or elevated in rank for use at the ordinal and higher levels. Our legal nomenclature dates from the tenth edition (1758) of *Systema Naturae* in which LINNÉ assigned all recognized echinoids to the genus *Echinus*. Early post-Linnean development of classificatory schemes was characterized by proposal of concepts and names at low-ranking levels, and their subsequent elevation to higher ranks. For example, the subclasses Regularia and Irregularia of many modern works were formally proposed at the family level (LATREILLE, 1825).

The section on the classification used in the *Treatise* is likewise concerned only with classification at the higher levels. Nomenclature and classification used by the individual authors within their various areas of responsibilities is mostly considered in the introductory material to their sections. At the 1953 International Congress of Zoology at Copenhagen proposals were made (ICZN, 1953) to extend the rules of nomenclature to include all higher category names. It proved difficult to obtain agreement on the application of the rules at these levels and in consequence the *Code* does not yet contain these provisions. However, in response to the requests in the *"Copenhagen Decisions"* (ICZN, 1953) DURHAM & MELVILLE (1957) included a list of all higher category names that had come to their attention at that time and designated type genera for them. In order to establish a reference standard to which the higher categories and their names can be unequivocally related it appears highly desirable to have designated types and this practice is continued in this section on classification for all higher categories that are used in this volume.

HISTORICAL REVIEW

In 1758 LINNÉ assigned all living echinoids to the genus *Echinus* (recognizing 17 species), although 24 years earlier (1734), JACOBEUS THEODORUS KLEIN had published the *Naturalis Dispositio Echinodermatum,* a much more advanced classification in which he recognized 22 genera and 12 suprageneric taxa of two ranks. KLEIN's work was so far superior to that of LINNÉ that many Continental authors, led by the French echinologists, have continued to use his names and attribute them to him, even though they antedated the tenth edition of the *Systema Naturae*. This practice was followed by MORTENSEN in parts of his monograph (1928-51), even though at times he appealed to the International Commission on Zoological Nomenclature to establish or maintain other nomenclature that he favored.

It was not until LESKE's (1778) *Additamenta ad Kleinii* that many of KLEIN's names were validated for nomenclatorial purposes. Those of KLEIN's names which were accepted by LESKE in this work legally must be attributed to LESKE as the first post-Linnean author to use them. LESKE did not accept all of KLEIN's nomenclature and systematics, and as a result some of KLEIN's names do not validly appear until later, in the works of others.

KLEIN recognized three major categories among the echinoids, based upon the position of the anus: Anocysti, with anus on the upper surface; Catocysti, with anus on the lower surface; and Pleurocysti, with anus on the side. Also KLEIN proposed the term Echinodermata for the echinoids alone, in recognition of their "spiny skin." It was not until later (beginning with BRUGUIÈRE in 1791) that it was extended to include the other members of the phylum.

After Leske's work, the first significant additions were those of Lamarck (1801, 1816), who proposed a number of new genera. Parkinson (1811) repeated Klein's classification and validated more of his pre-Linnaean names. De Blainville in 1822 used "Ceratodermaires" as a class for the Echinodermata in the modern sense, and "Cycloides" for the Echinoidea, and divided them into "reguliers" and "irreguliers."

Gray, in 1825, recognized the difference between regular (families Cidaridae and Echinidae) and irregular types. He placed the latter in his "annectant group," which included the families Scutellidae, Galeritidae, and Spatangidae.

Latreille (1825) formally proposed, at the family level, the terms Regularia and Irregularia, although the concepts of these two groups date from Cuvier (1817) who did not formally recognize them in his classification. De Blainville (1834) recognized two major groups of echinoids, Echinides excentrostomes and Echinides centrostomes, basing his divisions on the position of the peristome, whether eccentric or central.

The appearance (1835) of L. Agassiz's *Prodrome d'une monographie des radiares ou èchinodermes* marked the beginning of a new epoch in the study of echinoids. This vigorous and influential naturalist continued his studies on the group until the publication of the *Catalogue raisonné des Échinides* (with Desor, in 1847). He left a marked impress on "echinology" and his influence, through his son Alexander, continued into the present century. In the *Prodrome* Agassiz recognized three families in his order Echinides, the Spatangues, Clypeástres, and Cidarites. In the *Catalogus Systematicus Ectyporum Echinodermatum* (1840) these names were formally latinized to Spatangoidea, Clypeastroidea and Cidaroidea, but still assigned family rank. This classification was less refined than that of Gray but did not suffer from the obvious errors of presentation present in the latter's work and was thus more widely accepted.

The series of papers by Agassiz and his disciples opened the way to marked and rapid advances in the knowledge and classification of echinoids. Agassiz's classification of 1840 was further elaborated in the *Catalogue raisonné des Échinides* by Agassiz & Desor (1846-47). It was modified in this work by the addition of the family "des Cassidulides," the recognition of four "groups" ("Cidarides proprement dit"; "Salenies"; "Echinides"; and "Echinometres") within the cidarids, and the recognition of two additional "groups" ("Echinoneides" and "Nucleolides") within the cassidulids. Agassiz & Desor recognized 101 genera and subgenera and slightly more than 1,000 species, a far cry from the single genus and 17 species of Linné 90 years previously. These authors, like many subsequent French echinologists, failed to latinize their suprageneric taxa, and as a result one can only attribute higher category names to them by invoking Article 11, e, iii of the present Code of Nomenclature (1961). D'Orbigny (1851) fully latinized his nomenclature and recognized seven families (Ananchytidae, Spatangidae, Nucleolitidae, Galeritidae, Clypeasteridae, Echinidae, and Cidaritidae) within his order Echinoidea.

F. M'Coy was apparently far ahead of most of his contemporaries in his evaluation of the rank to be assigned to higher categories, for in 1849 he proposed the order Perischoechinida for the reception of *Archaeocidaris, Palaechinus,* and *Melonites* [*Melonechinus*], noting that these Paleozoic echinoderms differed from members of the order Echinida by having a great number of rows [columns] of plates in the test.

In 1855 Gray recognized the Irregularia as a "subdivision" (corresponding to his "annectant group" of 1825) of the Echinida, dividing them into two "sections," Mesostoma (with mouth subcentral) and Apomesostomi (with mouth excentric) on the basis of characters used by Klein. He formally recognized the families Scutellidae, Galeritidae, and Echinolampasidae in the first section and Spatangidae and Leskiadae in the second section. In addition, in his "systematic index" (*op. cit.,* p. 65-66) he recognized uncategorized (latinized) subdivisions under each of his families. These (Clypeasterina, Rotulina, Fibularina, Echinoneina, Cassidulina, Echinobrissina, Spatangina, and Brissina) have subsequently formed the basis for additional families and higher-ranking taxa.

DESOR, in his *Synopsis des Echinides fossiles* (1855-58), recognized the "Echinides reguliers ou endocyclique" with two families (Tessellés and Cidarides) and "Echinides irréguliers ou exocycliques" with five families (Galéridées, Dysastéridées, Clypéastroïdes, Cassidulides, and Spatangoides). He based his classification on a totality of characters including the endocyclic or exocyclic character of the periproct, the character of the ambulacra, the position and character of the mouth and the masticatory apparatus, the structure of the apical system, the position of the periproct, the shape and structure of the tubercles and spines, and the kinds of fascioles. DESOR also recognized two or more "tribes" within most of his families.

Although LATREILLE (1825) had formally recognized the distinction between regular and irregular echinoids in 1825, it was not until the time of ALBIN GRAS (1848) that this concept began to be consistently recognized in the classificatory schemes. Authors such as WRIGHT (1855-60), DESOR (1855-58), and DUJARDIN & HUPÉ (1862) followed the lead of GRAS in accepting the significance of this character.

In 1853 ALCIDE D'ORBIGNY prepared the first part of the Cretaceous echinoids for the many-volumed *Paléontologie Française*. On his death (1857) the description of the remaining Cretaceous, Jurassic, and Eocene echinoids was continued by G. COTTEAU and terminated in 1894. This work was largely descriptive and accompanied by numerous illustrations. Because of the seeming excellence of the descriptions and illustrations, the figures have been copied widely and disseminated in systematic literature and have greatly influenced echinoid systematics. Unfortunately, comparison of illustrations with the specimens upon which they were supposed to have been based has shown that there may be but slight resemblance between the two. Characters shown on these illustrations may or may not be present on the specimens. No illustration from this work or other contemporary studies illustrated by the same group of artists should be accepted as valid unless it has been favorably compared with the original (or a photograph of it) or undoubted specimens of the same species.

In England, T. WRIGHT (1855-60), almost as early as D'ORBIGNY, began his extensive studies on British echinoids and other echinoderms with his *Oolitic Echinodermata*. The volume on the Cretaceous was completed in 1871. WRIGHT's illustrations were not as impressive as those in the *Paléontologie Française* and consequently they have not been as extensively copied, but they are more reliable. He recognized 5 families in the suborder Endocyclica and 8 families in the suborder Exocyclica.

ALEXANDER AGASSIZ followed his father's footsteps in the study of echinoids. In 1872-74 he published the important work *Revision of the Echini,* which gathered together an immense amount of information about the morphology and distribution of living echinoids. Included also are exceedingly valuable chronologic lists, a bibliography and a synonymic index. The classification used was basically an updated version of AGASSIZ & DESOR, with the addition of subfamilies, a modernization of the nomenclature, and the utilization of the suborders (of the order Echini) Desmosticha (ambulacra equal and bandlike) and Petalosticha (petaloid ambulacra) of HAECKEL (1866). He also studied the Paleozoic groups for which M'COY had proposed the order Perischoechinida, and which had variously been considered as a group coordinate with the echinoids (M'COY) or referred to the crinoids (L. AGASSIZ), and concluded that they should form a third suborder of the Echini.

The first volume of ZITTEL's influential and impressive *Handbuch der Paläontologie* appeared during the years 1876-80. In this work he recognized the subclasses Palechinidea, and Euechinoidea of the class Echinoidea. He separated the Palechinidea on the basis of their age and the fact that the test was usually composed of more than 20 columns of plates, and recognized the orders Cystocidaridae, Bothriocidaridae, and Perischoechinidae. The subclass Euechinoidea was divided into the orders Regulares and Irregulares (referring to the position of the anus), with 4 families under the first and 2 suborders (Gnathostomata, with jaw apparatus; and Atelostomata, without jaw apparatus) with 6 families under the latter.

In 1869 Pomel recognized two suborders, "Tesselés" and "Échinides non Tesselés," and proposed a twofold classification of the "Échinides Tesselés" or suborder of "true echinoids." On one hand he divided them into three superfamilies: Globiformes, with anus opposite the mouth and orientation indicated by the madreporite; Lampadiformes, with mouth central and anus more or less independent of apical system and indicating orientation but otherwise regular in shape; Spatiformes, with mouth anterior and anus posterior, marking a distinct bilateral symmetry. On the other hand Pomel also noted that the "true echinoids" could be divided into two groups (Atelostomes and Gnathostomes) according to the absence or presence of a dental apparatus and finally concluded that this classification was "more natural" than the other. He noted that the suborder of the Tesselés or Périschéchinides (of M'Coy) was characterized by the numerous columns of plates, with the central ones of each area having a hexagonal shape, and recognized two families (Paléchinides and Mélonéchinides) within it.

Later Pomel (1883), still considering the echinoids as an order, combined the two methods and made the Spatiformes and Lampadiformes families under the Atelostomes; and the Globiformes along with the new group Clypeiformes (removed from the Lampadiformes because of the presence of a masticatory apparatus), families of the Gnathostomes.

A few years later, Duncan (1889) reviewed the classification of the echinoids, ranking them as a class, and presented a classificatory scheme that actually regressed from that of Zittel in that he did not differentiate the regular and irregular echinoids, recognizing 5 coordinate orders (Cidaroida, Diadematoida, Holectypoida, Clypeastroida, and Spatangoida) within the subclass Euechinoidea, and the new order Plesiocidaroida (for *Tiarechinus*) within the subclass Perischoechinoida, in addition to the three present in Zittel's scheme.

In 1895, Munier-Chalmas in Bernard (1895) presented a classification markedly different from those of his contemporaries. He based it upon the position and character of the dental apparatus, the character of the peristome, the number of columns of interambulacral plates and the character of the apical system. The higher categories of his classification are as follows:

Classification of Echinoids by Munier-Chalmas, 1895

- Class Échinides
  - Subclass Homognathes, pyramids similar, erect
    - Order Holostomes, peristome entire
      - Suborder Monoplacidés, a single column of interambulacral plates
      - Suborder Polyplacidés, numerous columns of interambulacral plates
      - Suborder Tétraplacidés, 4 columns of interambulacral plates
      - Suborder Diplacidés, 2 columns of interambulacral plates
    - Order Glyphostomes, peristome with gill slits
      - Suborder Glyphostomes Endocycles, regular echinoids
      - Suborder Glyphostomes Exocycles, periproct outside apical system
  - Subclass Hétérognathes, pyramids not equal, depressed, apical system fused
  - Subclass Atélostomes, no jaw apparatus, periproct outside apical system
    - Order Dysastéridés, apical system disjunct
    - Order Synastérides, apical system not disjunct
      - Group 1, apical system monobasal
      - Group 2, apical system tetrabasal
    - Appended to Échinides:
      - I. Cystoéchinides (for *Cystocidaris*), a transition group between cystoids and echinoids
      - II. Blastoéchinides (for *Tiarechinus*), a group converging toward the blastoids.

Haeckel (1896, p. 481-489) in his *Systematische Phylogenie der Wirbellosen Thiere (Invertebrata)* presented a classification notable for the introduction of new, as well as a dual, nomenclature. It is as follows:

Classification of Echinoids by Haeckel, 1896

- Class Echinoidea
  - Subclass Cystechinida
    - Order Promelonaria
    - Order Eumelonaria
  - Subclass Palechinida (or Palaeoechinoidea)
    - Order Stenopalmaria
    - Order Eurypalmaria
  - Subclass Autechinida (or Euechinoidea)
    - Order Desmosticha (=Cidaronia)
      - Suborder Cidaridaria
      - Suborder Diademaria
    - Order Anthosticha (=Clypeastronia)
      - Suborder Conoclyparia (=Holectypida)
      - Suborder Scutellaria

- Order Petalosticha (=Spatangonia)
  - Suborder Cassidularia
  - Suborder Spatangaria

J. W. GREGORY (1900) presented a classification that recognized three subclasses of echinoids, with the first two based primarily on the internal versus external position of the gills and the third with the periproct outside of the apical system. The major elements of his classification are as follows:

Classification of Echinoids by Gregory, 1900

- Class Echinoidea
  - Subclass 1, Regularia Endobranchiata
    - Order 1, Bothriocidaroida
    - Order 2, Cystocidaroida
    - Order 3, Cidaroida
    - Order 4, Melonitida
    - Order 5, Plesiocidaroida
  - Subclass 2, Regularia Ectobranchiata
    - Order 1, Diademoida
      - Suborder 1, Calycina
      - Suborder 2, Arbacina
      - Suborder 3, Diademina
      - Suborder 4, Echinina
  - Subclass 3, Irregularia
    - Order 1, Gnathostomata
      - Suborder 1, Holectypina
      - Suborder 2, Clypeastrina
    - Order 2, Atelostomata
      - Suborder 1, Asternata
      - Suborder 2, Sternata

In 1903 DELAGE & HÉROUARD, in their detailed treatment of morphology and anatomy, used a classification in which the primary separation was into the subclasses Reguliers and Irreguliers, based on the position of the periproct with respect to the apical system.

DÖDERLEIN (1906), studying the material collected on the "Deutsches Tiefsee-Expedition," was greatly impressed by the differentiation of the pedicellariae and the light they cast upon relationships. As a result of his studies, he proposed the following classification of Recent echinoids, with characters of the pedicellariae playing an important role in the assemblage of characters used.

Classification of Echinoids by Döderlein, 1906

- Subclass Cidariformia
- Subclass Diadematiformia
  - Order Regularia
    - Suborder Diadematina
      - Tribe Streptosomata
      - Tribe Stereosomata
    - Suborder Saleniina
    - Suborder Arbaciina
    - Suborder Echinina
  - Order Irregularia
    - Suborder Clypeastroidea
    - Suborder Spatangoidea

LAMBERT & THIÉRY published the first part of their compendium *Essai de nomenclature raisonée des Échinides* in 1909, the last part being issued in February 1925. They attempted to list, evaluate, and assign an age to every known species and give a reference to an adequate description of each. The work suffers from contradictions, sometimes from one page to next, and like many similarly long-extended works, the refinement of the systematics varies from part to part. Likewise, the work was not carefully edited and little attention was given to the Code of Nomenclature. However, despite all its faults, it is an invaluable reference and sourcebook, and very influential because of its completeness. The classification used embodies many new names for all categories above species rank and it contains a number of new concepts. The higher categories and their arrangement are as follows:

Classification of Echinoids by Lambert & Thiéry, 1909-1925

- Class Echinoidea
  - Subclass Gnathostomata
    - Order Plagiocysta
        - Suborder Cystocidaroida
    - Order Endocysta
      - Section Homalostomata
        - Suborder Bothriocidaroida
        - Suborder Perischoechinoidea
        - Suborder Cidaroida
      - Section Glyphostomata
        - Suborder Streptosomata
        - Suborder Stereosomata
    - Order Exocysta
        - Suborder Pileatoida
        - Suborder Clypeastroida
  - Subclass Atelostomata
    - Order Brachygnata
        - Suborder Globatoroida
    - Order Nodostomata
        - Suborder Procassiduloida
        - Suborder Spatangoida

In 1896 JACKSON published the first of his detailed morphological studies on echinoids. This work dealt with the Palaechinoida and included a partial classification showing the relationships of Paleozoic echinoids to the cidarids. This classification was essentially that of ZITTEL. Later JACKSON (1912) elaborated and slightly modified his earlier scheme, including all echinoids within it. In this later scheme he eliminated the subclasses Palaechinoida and Euechinoida and recognized seven coordinate orders under the Class Echinoida. The Exocycloida were ranked as an order with 3 suborders (Holectypina, Clypeastrina, and Spatangina). The most notable advance was the recognition within the order Centrechinoida [Diademoida auctores] of three suborders (Aulodonta, Stirodonta, and Camarodonta) based upon the characters of the lantern and teeth.

JACKSON (40, p. 208) considered that *Bothriocidaris* represented the most "primitive type" of echinoid, an interpretation that was followed by many students of the group. Later, MORTENSEN (1928) raised doubts about the interpretation of *Bothriocidaris* and concluded that it was a cystoid. This precipitated a series of papers (espec. BATHER, 1931; CLARK, 1932; HAWKINS, 1931; JACKSON, 1931) defending its position among the Echinoidea, and a reply by MORTENSEN (1931; see also his Monograph, v. 5, p. 565-567, 1951) maintaining his position. DURHAM & MELVILLE (1957) considered that *Bothriocidaris* was a "true echinoid," though not on the direct line to later groups. This view was also held by CUÉNOT (1948), while TERMIER & TERMIER (1953) considered the genus to be of uncertain affinities. Fortunately MYANNIL (1962) has collected additional and well-preserved material demonstrating unequivocally the presence of a system of peristomial plates and a lantern, although the latter is of a somewhat different and more primitive type than that in the main line of echinoid development. Spines that are typically echinoid-like in appearance (59, pl. 4, fig. 2) adhere to at least one specimen. As BATHER noted, an internal radial water vessel must have also been present. The lantern and spines, as well as the characters of the plating of the test, indicate that *Bothriocidaris* is unequivocally an echinoid in terms of current concepts. MYANNIL considered that the Bothriocidaroida, Echinocystitoida, Palaechinoida, and Cidaroida each represent a separate line of descent from the ancestral echinoid.

The first volume of MORTENSEN's monumental *Monograph of the Echinoidea* (5 4to vols., 16 pts.) appeared in 1928, the last being completed in 1951. MORTENSEN thoroughly described every Recent species known to him and reviewed every recorded genus, fossil or living. The systematic position of every genus was analyzed, relationships and suggested derivations were indicated, and the limits and affinities of each family were considered. His major classification of the Echinoidea (restricted) (as summarized in v. 5, pt. 2, p. 565-574, 1951) is as follows:

Classification of Echinoids by Mortensen, 1951

- Class Echinoidea
  - Subclass Regularia
    - Order Melonechinoida
    - Order Megalopoda (referred to echinoids with some uncertainty)
    - Order Lepidocentroida
    - Order Cidaroida
    - Order Aulodonta
    - Order Stirodonta
    - Order Camarodonta
  - Subclass Irregularia
    - Order Holectypoida
    - Order Clypeastroida
    - Order Cassiduloida
    - Order Spatangoida

Suborders were recognized in many of these orders and as indicated in the summary section, as well as in numerous other places in the work, many of the orders were considered to be polyphyletic and merely families grouped together for convenience. Most significant of these conclusions was that the Irregularia had originated from more than one source among the Regularia. Notably he considered: *Pygaster* and its close allies to be derived from the pedinids; *Holectypus* and its close allies to be descendants of the diadematids, probably *Eodiadema*; the conulids and discoidids as derived from "some primitive stirodonts"; and the galeropygids as of probably diadematid origin, perhaps from the genus *Mesodiadema*. MORTENSEN, like BEURLEN (1934), derived his spatangoid suborders Meridosternata and Amphisternata from the collyritid-disasterid stem.

Another noteworthy conclusion of MORTENSEN was derivation of the Echinothuriidae from Paleozoic Lepidocentridae, rather

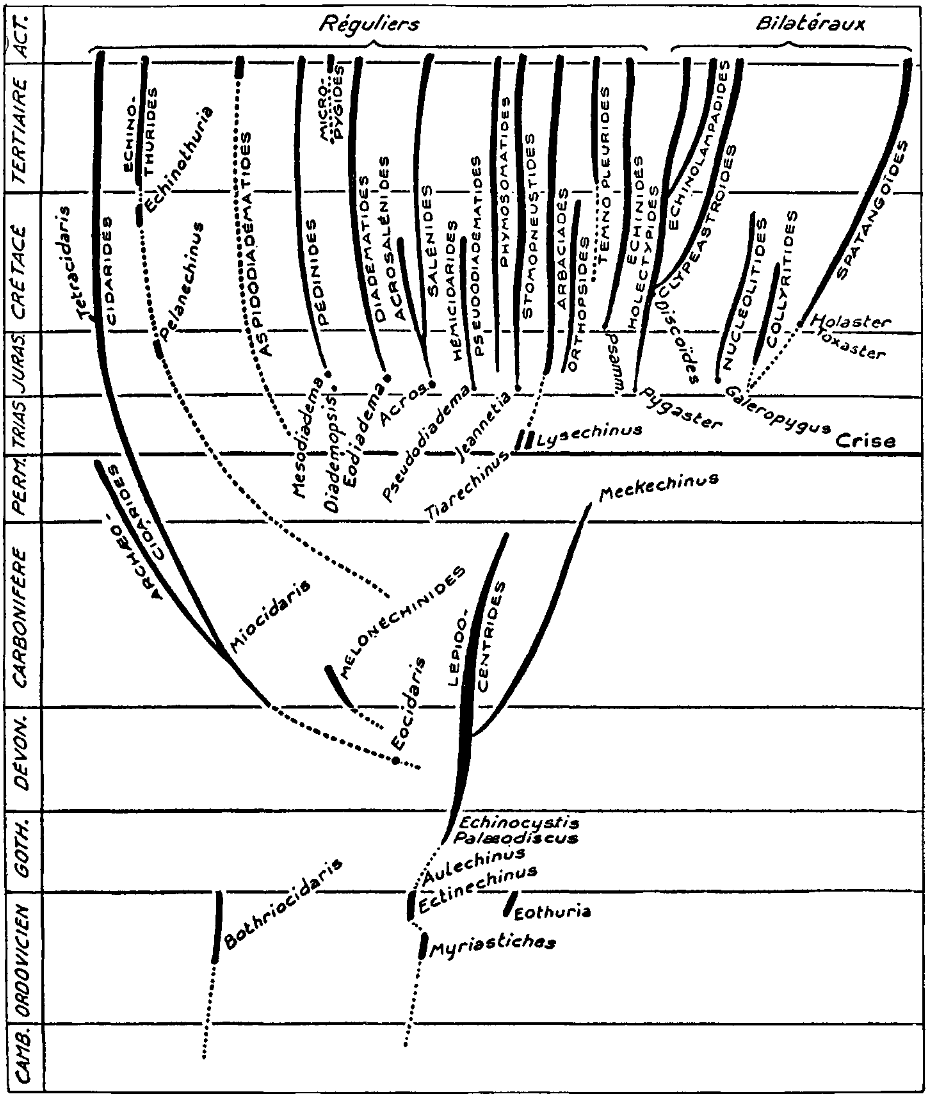


FIG. 209. CUÉNOT's phylogenetic tree of the Echinoidea (20).

than from a diadematid ancestry. He based this conclusion primarily on the occurrence of imbricating coronal plates in each, "many plated" ambulacra in some echinothurids, the numerous peristomial plates in both families, and the seeming absence of external gills in some echinothurids. He overlooked (or discounted) the fact that if such a derivation is accepted, the complex perignathic girdle of the echinothurids, as well as their external gills, would then have to be of independent origin from the similar structures in the other noncidaroid regular echinoids.

MORTENSEN did not present any graphic scheme showing his interpretation of the genetic relationships among the families and higher categories of the echinoids. It is difficult to construct a phylogeny on the basis of his work, because at times he made no choice between possible alternatives and in some cases he presented conflicting conclusions in different parts of the work. It is unfortunate that he was not able to summarize his views in a more complete form before his death.

In 1933 Gignoux published his *Les oursins réguliers fossiles, evolution et classification.* This excellent descriptive study was primarily concerned with descriptions of morphologic features and their evolutionary development and not with a synthesis of the resultant data into a classificatory hierarchy. He noted that our knowledge of echinoid evolution as documented by the fossil record is very incomplete, and for that reason did not care to propose a "rigid classification." He recognized *Bothriocidaris* as the ancestral echinoid and grouped the regular echinoids in three major categories: Paléchinidés, Cidaridés, and Glyphostomés.

The suborder Urechinina was proposed by H. L. Clark (1946) for irregular echinoids with a sternum in which the "labrum [is] followed by a single plate." As defined, this suborder includes some but not all of the Holasteroida as proposed subsequently by Durham & Melville (1957).

The section on echinoids in the *Traité de Zoologie* (ed. P.-P. Grassé) was prepared by L. Cuénot (1948). It is a very clear and careful presentation, emphasizing anatomy and morphology, but includes only representative genera in each group. His phylogenetic tree (Fig. 209) expresses his ideas on relationships clearly, although he did not formally recognize any categories except subclasses (Reguliérs, Bilatéraux) above the family level. Notable is his representation of both the echinothurids and cidarids as representing distinct lineages from the other regular echinoids, deriving each from a Paleozoic ancestry. Although not as positive in his conclusions as Mortensen, he noted that two very distinct irregular types (*Pygaster, Galeropygus*) appear early in the Jurassic and suggests that they were derived from different sources. He likewise noted that in several groups of regular echinoids at different times the periproct started to move out of the apical system into interambulacrum 5 (citing the genera *Palaeopedina, Acrosalenia, Pseudosalenia, Hyposalenia, Goniophorus, Gauthieria,* and *Heterodiadema*), thus suggesting that there have been repeated attempts at the development of the irregular condition.

In the *Traité de Paléontologie* (ed. J. Piveteau), the section on the Echinoidea was prepared by Termier & Termier (1953). They were impressed with the plasticity of the echinoid branch of the echinoderms and noted that in consequence there are many obstacles to the establishment of a "rigorous" classification and a clear delineation of affinities. As a result many of their suprafamilial taxa are polyphyletic in origin (Fig. 210). Their order-subclass classification is a but slightly modified version of that used by Mortensen. *Bothriocidaris* they considered to be derived from a protocrinid ancestry, while the remaining echinoids were derived from the stromatocystitids. Their phylogeny shows the diadematid, echinothurid and cidarid stocks as directly derived from Paleozoic ancestors among the Lepidocentroida. The Aulodonta include descendants from both cidaroid and lepidocentrid ancestries. The cidarids gave rise to stirodonts twice and to the diadematids once. The Camarodonta are derived from 3 separate ancestries among the Stirodonta. The Irregularia are derived from pseudodiadematid, diadematid, and pedinid ancestors. The Protosternata were derived from cassiduloid and galeropygid stocks, as were the Meridosternata. Only the Cidaroida, Cassiduloidea, and Amphisternata, among post-Paleozoic echinoids, are shown as monophyletic in origin.

In 1960, André Devriès, as a result of his detailed morphologic studies on the phymosomatids and the genera *Heteraster* and *Toxaster,* presented an evolutionary scheme (Fig. 211) for these groups and their relatives. He considered the cidarids and diadematids to be derived from a Paleozoic lepidocentroid source. The irregulars are likewise polyphyletic: the pygasterids and *Loriolella* arising from a pedinid ancestry; the holectypids and the part of the galeropygids which gave rise to the Cassiduloida being derived from the diadematids; the remaining galeropygids possibly arose directly from a lepidocentroid source, and, in turn, through the collyritids gave rise to the other spatangoids.

Durham & Melville (1957) presented a classification (Fig. 212) that conformed to the phylogeny they accepted and that

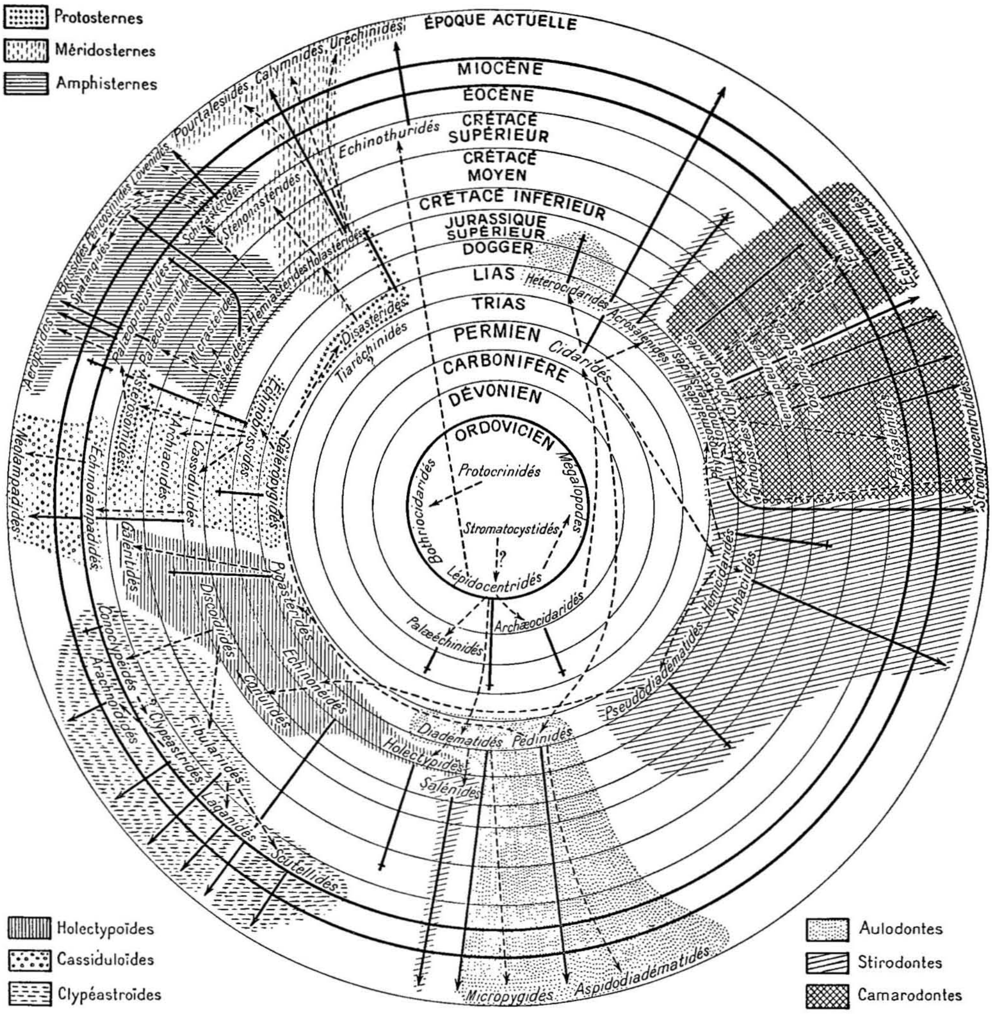


FIG. 210. The TERMIER & TERMIER phylogenetic chart of the Echinoidea (68).

was intended for use in the *Treatise*. In large part, but not completely, their phylogenetic tree agreed with relationships suggested by MORTENSEN in his monograph. As a result, they recognized 18 orders, in contrast to the 11 present in MORTENSEN's classification. They considered that the irregular condition had arisen in at least three different lineages and thus they abandoned this character (recommending usage of "regular" and "irregular" as morphologic terms only) as a basis for differentiating subclasses. Instead, they recognized the Perischoechinoidea and Euechinoidea as subclasses, differentiating them primarily on the lack of a perignathic girdle or of auricles in it, and the absence of gill slits in the Perischoechinoidea; and the presence of a complete girdle and gill slits (or descent from such forms) in the Euechinoidea. The presence or absence of branchial slits was considered (although not so stated) to correspond to the presence or absence of external gills.

DURHAM & MELVILLE considered that the echinothurids were derived from some pedinid stock and that their resemblance to the lepidocentrids was purely a product of adaptive convergence. Thus, contrary to the earlier opinions of MORTENSEN, TERMIER &

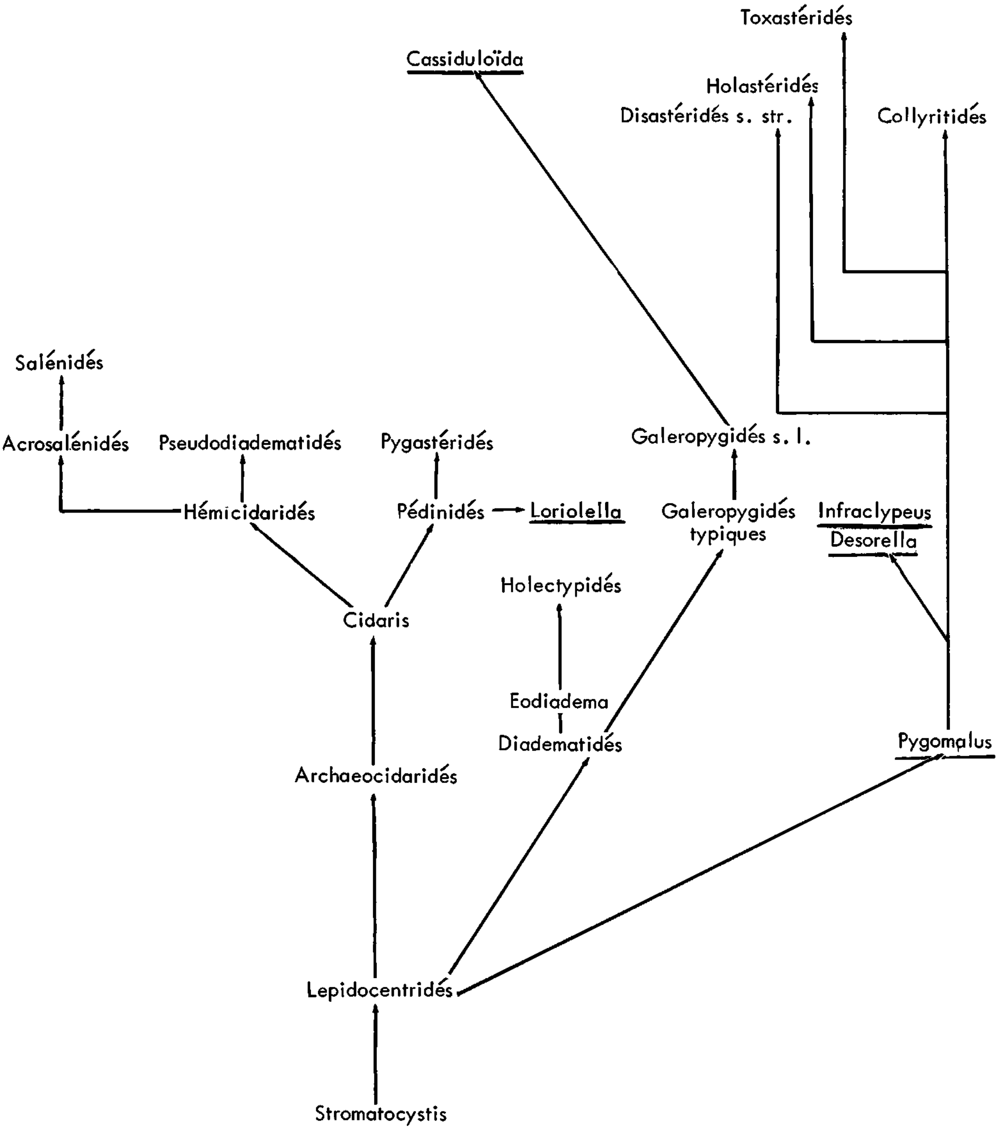


FIG. 211. Evolutionary relationships of certain groups of echinoids as interpreted by DEVRIÈS (24).

TERMIER, CUÉNOT, and the subsequent works of DEVRIÈS and PHILIP, they concluded that the cidarids were the only stock that continued from the Paleozoic into the Mesozoic. They also considered both *Bothriocidaris* and *Eothuria* to be echinoids. Among the euechinoids they recognized four superorders (Diadematacea, Echinacea, Gnathostomata, and Atelostomata), each representing a major branch of the subclass and composed of phylogenetically closely related orders. Subsequent developments have caused some modification of their classification, but for the most part it forms the basis of the scheme used in the present work.

While this volume was in press, PHILIP (1965) published a criticism of the classification proposed by DURHAM & MELVILLE and presented a classification which in his view (p. 44) "approaches that presented by Mortensen in his monograph." PHILIP also

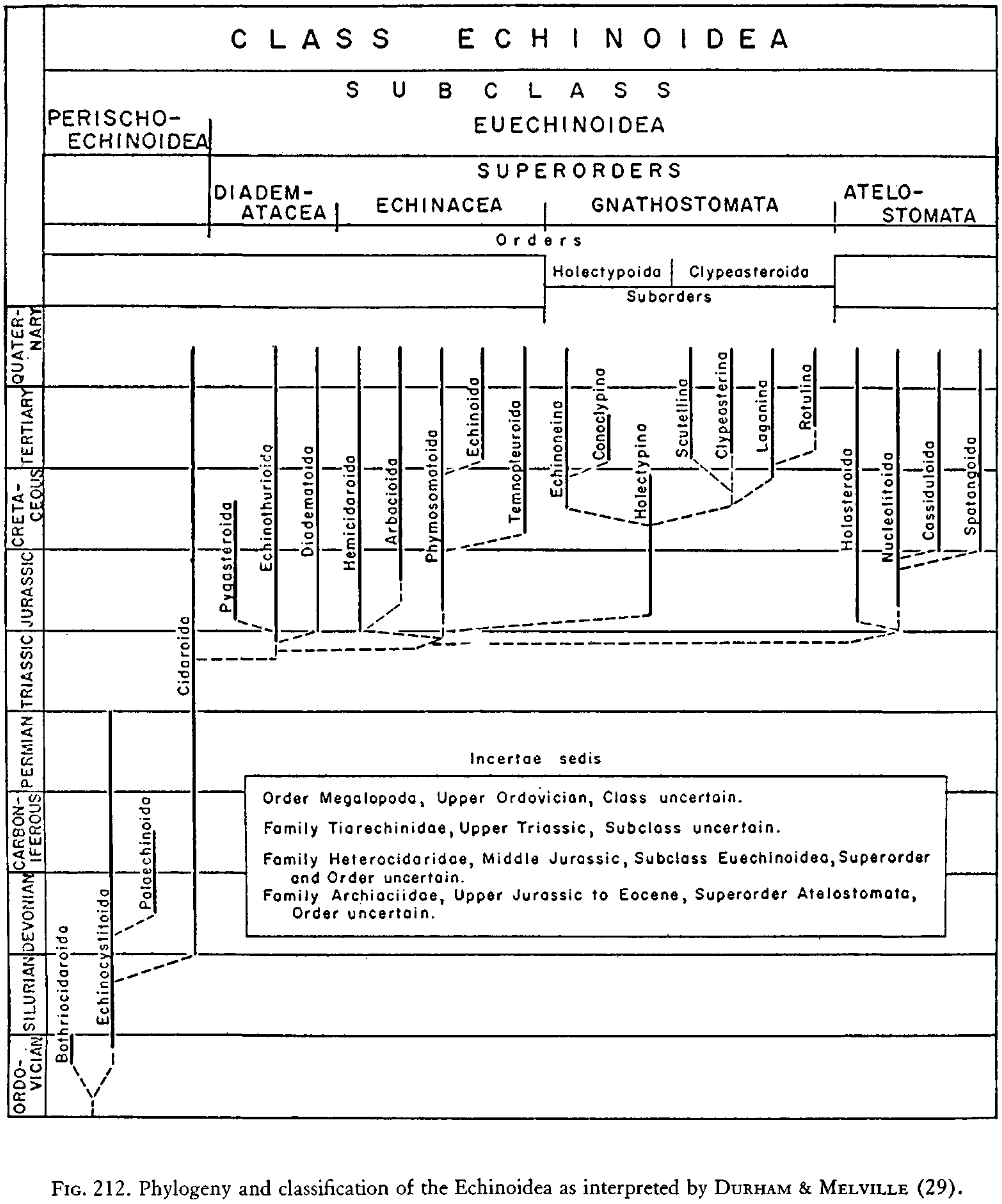


Fig. 212. Phylogeny and classification of the Echinoidea as interpreted by Durham & Melville (29).

noted (p. 56) that "these collocations [his] cannot be claimed as more than grades (in the sense of Huxley, 1958)" and (p. 45, *abstract*) that "—the superorders Gnathostomata and Atelostomata are recognized as broad morphological grades probably uniting stocks of different ancestry." Philip's classification is thus one of grades and is based on a different philosophy than that used by Durham & Melville. The classification of Echinoidea adopted in this volume, like that of Durham & Melville, is based on the philosophy that a classification should reflect phylogeny, and thus is largely at variance with that of Philip. One of his proposals, the elevation to higher than ordinal rank of a taxon (Philip adopted Pseudoechinacea Mortensen at superordinal rank) for *Bothriocidaris*, deserves serious consideration, but because of the time of appearance of his paper, this could not be incorporated into the classification used herein.

As an appendix to their paper, DURHAM & MELVILLE (29, p. 262-272), in response to the recommendations of the *Copenhagen Decisions on Zoological Nomenclature* (ICZN, 1953), included a section on "Echinoid Order-Class Group Nomenclature." In compiling their lists of names, they decided to accept authorship and priority as of the first appearance of a name in latinized form, rather than from its first appearance in the vernacular. However, the new zoological Code (1961) contains a proviso (Article 11, e, iii) for names in the family-group category, which grants authorship and priority to the first appearance in the vernacular prior to 1900, providing that it has been so recognized by subsequent authors. If rules are eventually adopted for the higher-ranking groups it appears probable that the same rule would be adopted for them. Under this proviso, many of the authorships and dates credited to names in the DURHAM & MELVILLE list would be superseded.

At the same time DURHAM & MELVILLE designated type genera for all named groups that had come to their attention. Strict application of Article 11,e,iii would invalidate those of their type designations that applied to names which first appeared in the vernacular, so, in continuation of the spirit in which the list was prepared, all such type designations in their list are here designated as likewise applying to the first appearances of those names in the vernacular. DURHAM & MELVILLE, as a result of their compilation also prepared a list of names that they recommended for use in order-class group nomenclature, as follows:

Order-class Group Names Recommended for Use in Echinoid Classification by Durham & Melville, 1957

CLASS NAME
- Echinoidea LESKE, 1778

SUBCLASS NAME
- Endocyclica BRONN, 1860
- Euechinoidea BRONN, 1860
- Exocyclica BRONN, 1860
- Perischoechinoidea M'COY, 1849
- Pseudoechinoidea MORTENSEN, 1935

SUPERORDER NAMES
- Atelostomata ZITTEL, 1879
- Diadematacea DUNCAN, 1889
- Echinacea CLAUS, 1876
- Gnathostomata ZITTEL, 1879

ORDER NAMES
- Arbacioida GREGORY, 1900
- Bothriocidaroida ZITTEL, 1879
- Brachygnata LAMBERT, 1915
- Cassiduloida CLAUS, 1880
- Cidaroida CLAUS, 1880
- Clypeasteroida A. AGASSIZ, 1873
- Diadematoida DUNCAN, 1889
- Echinoida CLAUS, 1876
- Echinocystitoida JACKSON, 1912
- Echinothurioida CLAUS, 1880
- Hemicidaroida BUERLEN, 1937
- Holasteroida DURHAM & MELVILLE, 1957
- Holectypoida DUNCAN, 1889
- Megalopoda MACBRIDE & SPENCER, 1938
- Nucleolitoida HAWKINS, 1920
- Palaechinoida HAECKEL, 1866
- Phymosomatoida MORTENSEN, 1904
- Plesiocidaroida DUNCAN, 1889
- Pygasteroida DURHAM & MELVILLE, 1957
- Spatangoida CLAUS, 1876
- Stereosomata DUNCAN, 1889
- Temnopleuroida MORTENSEN, 1942

SUBORDER NAMES
- Amphisternata MORTENSEN, 1907
- Aspidodiademina MORTENSEN, 1939
- Calycina GREGORY, 1900
- Cassidulina CLAUS, 1880
- Clypeasterina A. AGASSIZ, 1873
- Conoclypina HAECKEL, 1896
- Diademina DUNCAN, 1889
- Echinina CLAUS, 1876
- Echinoneina H. L. CLARK, 1925
- Holectypina DUNCAN, 1889
- Laganina MORTENSEN, 1948
- Meridosternata MORTENSEN, 1907
- Orthopsina MORTENSEN, 1942
- Pedinina MORTENSEN, 1939
- Protosternata MORTENSEN, 1907
- Rotulina DURHAM, 1955
- Scutellina HAECKEL, 1896

TREATISE CLASSIFICATION

The classification used herein (Fig. 213), although based upon that proposed by DURHAM & MELVILLE (29), is a composite of the views and opinions of the authors (J. W. DURHAM, H. B. FELL, A. G. FISCHER, P. M. KIER, R. V. MELVILLE, D. L. PAWSON, and C. D. WAGNER) of the individual parts of the systematic section on the Echinoidea. As a result, some particulars of the expressed classification and relationships are not unanimously agreed upon.

Some of the suggested timings of events expressed on the chart (Fig. 213) and in this section have been modified by DURHAM from those indicated in the individual systematic parts on the basis of the overall perspective of the classification.

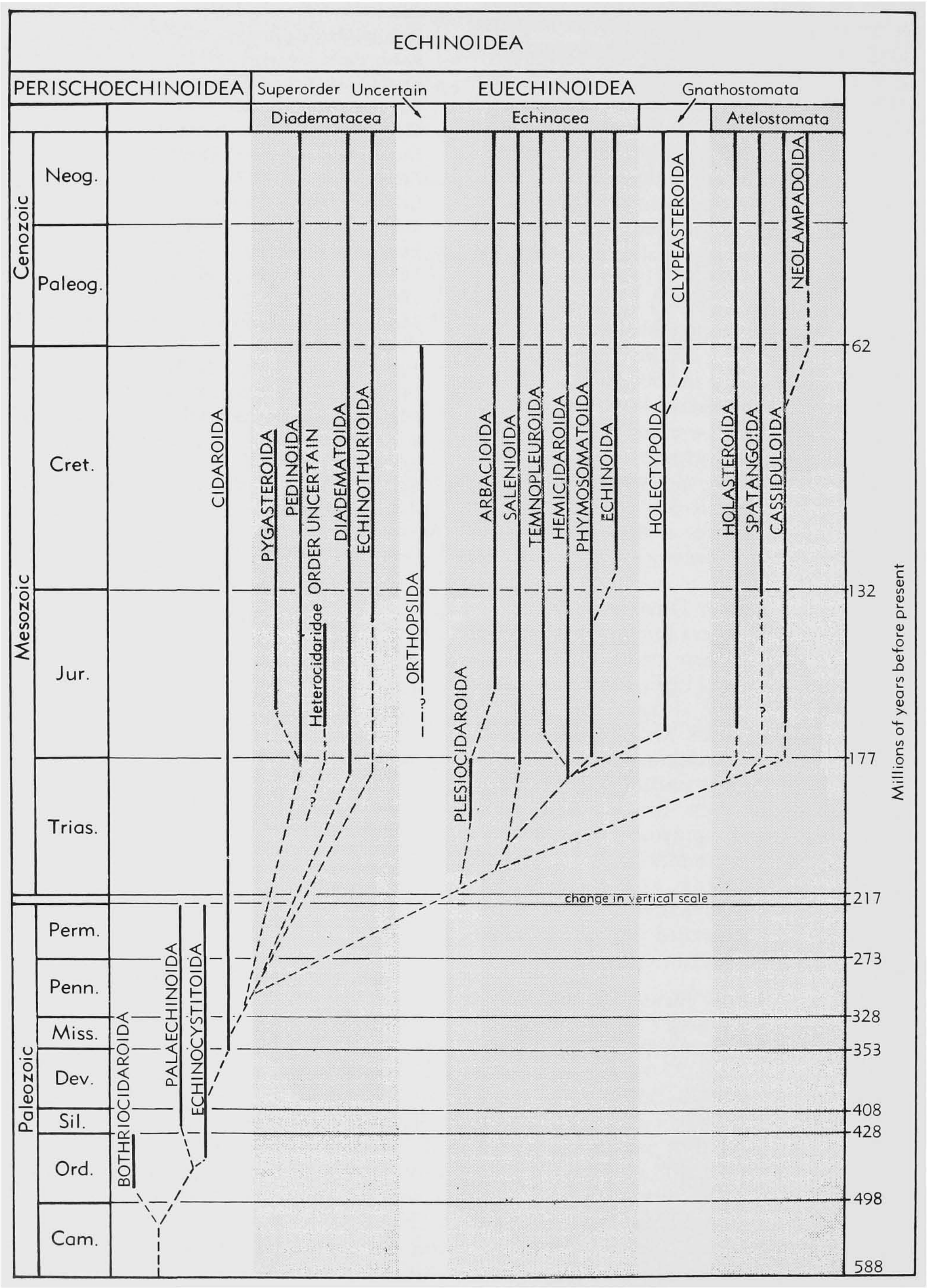


FIG. 213. Phylogeny of the Echinoidea (Durham, n).

Evolution is a branching and diversifying continuum and our classifications are artifacts superimposed upon this continuum as a shorthand for the purposes of communication. The principle that classification must reflect phylogeny is here accepted as an overriding precept. Therefore, every taxon must be monophyletic, and the classification used herein is an attempt to express the genetic relationships within the class as they are now understood or inferred.

It has been stated that a phylogeny must always show derivation of a higher-ranking taxon from one of lower rank. Acceptance of this precept leads ultimately to a single species (or subspecies) as the lowest conceptual taxon as the source of a new stock. Because of incomplete knowledge of the fossil record, it is often difficult or impossible to pinpoint this source, but this does not invalidate the conclusion. Furthermore, although the stated precept is correct in theory, the practical exigencies of graphically presenting the phylogeny of a large and complex group in limited space usually precludes its expression.

One of the major events in the evolution of the echinoids was the acquisition of external gills by some. This event occurred near the end of the Paleozoic, about midway in the course of their history, and apparently it was accomplished at about the same time as auricles appeared in the perignathic girdle. The development of these structures seemingly permitted the deployment of this stock into all the subsequent diversity of Mesozoic and Cenozoic noncidaroid echinoids. Meanwhile the parent stock continued on as the modern Cidaroida. It therefore seems appropriate to recognize two subclasses, the Perischoechinoidea and Euechinoidea, on the basis of these characters.

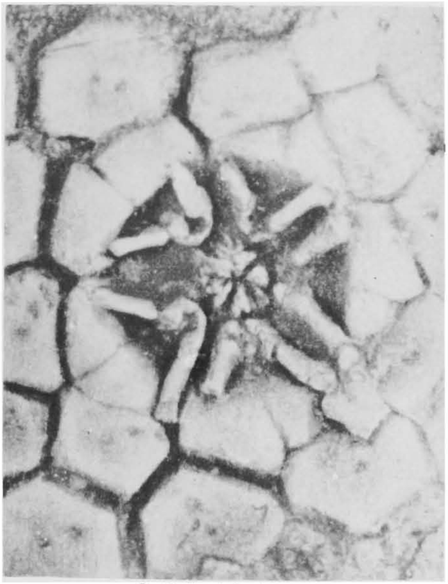


Fig. 214. Internal view of lantern of *Bothriocidaris*, ×6.8 (59, pl. 3, fig. 2).

The **Perischoechinoidea**, as thus conceived, are characterized by absence of external gills (or lack of descent from such forms); corona with ambulacra composed of two to many columns, and interambulacra with one to many columns of plates; apical system endocyclic; ambulacral plates not compound; perignathic girdle absent or composed of apophyses only; lantern present, with grooved teeth. Presumably there were no spheridia or ophicephalous pedicellariae. The name was originally proposed by M'Coy (1849), as the order Perischoechinida, for Paleozoic echinoids, which, as then known, were characterized by having an odd number (3 or more) of columns of plates in the interambulacra. M'Coy regarded them as a group of equal rank with the Echinoidea, which were characterized by an even number of columns in the interambulacra. The concept was ultimately expanded to include the Bothriocidaroida, as well as the Cidaroida, by Durham & Melville (29). As here accepted, it includes the orders Bothriocidaroida, Palaechinoida, Echinocystitoida, and Cidaroida. Durham & Melville (29) designated *Palaechinus* M'Coy as the type-genus.

The **Bothriocidaroida** are characterized by a rigid test, sutures normal to the surface; interambulacra composed of a single column of plates, not reaching peristome; lantern with primitive pyramids and teeth; peristome plated; madreporite radial in position; with imperforate tubercles. The lantern (Fig. 214, 215) and spines clearly indicate that *Bothriocidaris* is an echinoid, while the character of the plates around and on the peristome (Fig. 216, 217), as well as the apparent lack of a differentiated set of genital plates in the apical system, raises doubts as to whether ranking the taxon

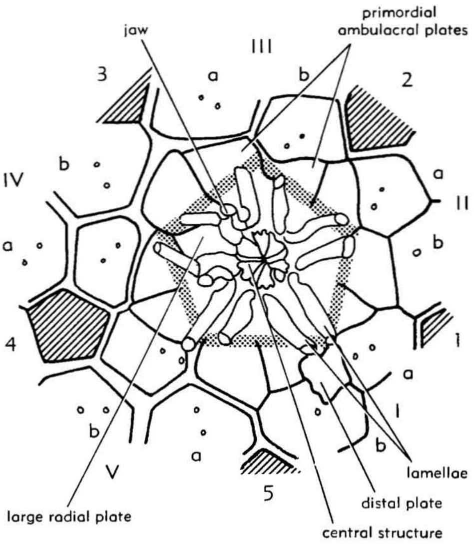


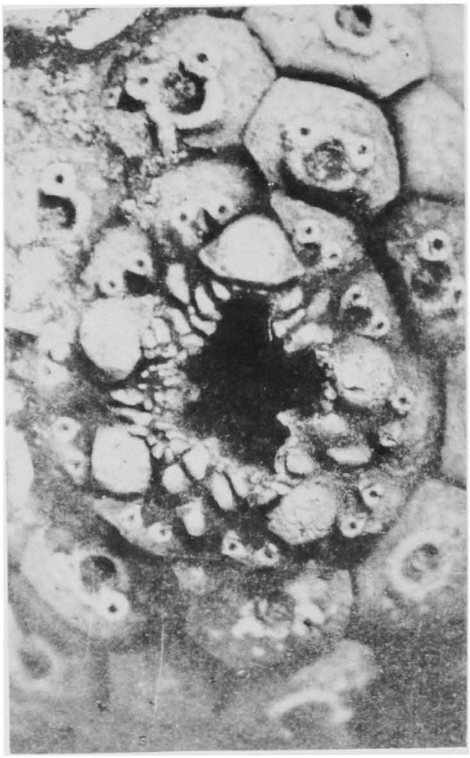
Fig. 215. Diagram of lantern of *Bothriocidaris*, ×6.8 (after 59, fig. 16).

based on it as an order adequately emphasizes its distinctiveness. The group was raised to ordinal rank by Zittel in 1879. The order is monotypic, including only the genus *Bothriocidaris* Eichwald.

The rigid test and characters of the peristome and apical system of the Mid-to-Late Ordovician Bothriocidaroida, when contrasted with the flexible test of the Late Ordovician Echinocystitoida, indicate that the two orders had already greatly diverged from their common ancestor. It appears probable that this separation may have occurred in the Cambrian and that we should look for the ancestral echinoid stock in that interval.

The **Palaechinoida** have a rigid test, ambulacral plates beveling over adjacent interambulacral plates; no perignathic girdle; perforate or imperforate tubercles; and an apical system with both ocular and genital plates. The peristome is covered with ambulacral and interambulacral plates. Members of this group are easily differentiated from their contemporaries by the rigid test. The name was first proposed by Haeckel (1866); Durham & Melville (1957) designated *Palaechinus* M'Coy as the type-genus.

The **Echinocystitoida** are characterized by strongly imbricating and flexible tests; ambulacral plates beveling under adjacent interambulacra; ambulacral plates imbricating adorally, interambulacral plates imbricating adapically; apical system with genital plates; absence of perignathic girdle. Most genera have perforate primary tubercles, but in others their character is uncertain. The flexibility of the test and the method of imbrication readily distinguish this Paleozoic group from contemporary palaechinoids. No resorption has been recognized around the peristome and the primordial plates are retained in the test. Zittel (1879) proposed the order Cystocidaridae for this group, basing it on his genus *Cystocidaris,* a synonym of *Echinocystites.* Jackson (1912) proposed Echinocystoida as a substitute name for Cystocidaridae, basing it on the genus *Echinocystites* Wyville-Thomson. Durham & Melville (1957) formally designated Wyville-Thomson's genus as the type. They preferred to retain the ordinal name based on the earlier genus, even though it was originally founded on the



Bothriocidaris

Fig. 216. Peristome and peristomial plates of *Bothriocidaris,* ×10 (59, pl. 5, fig. 1).

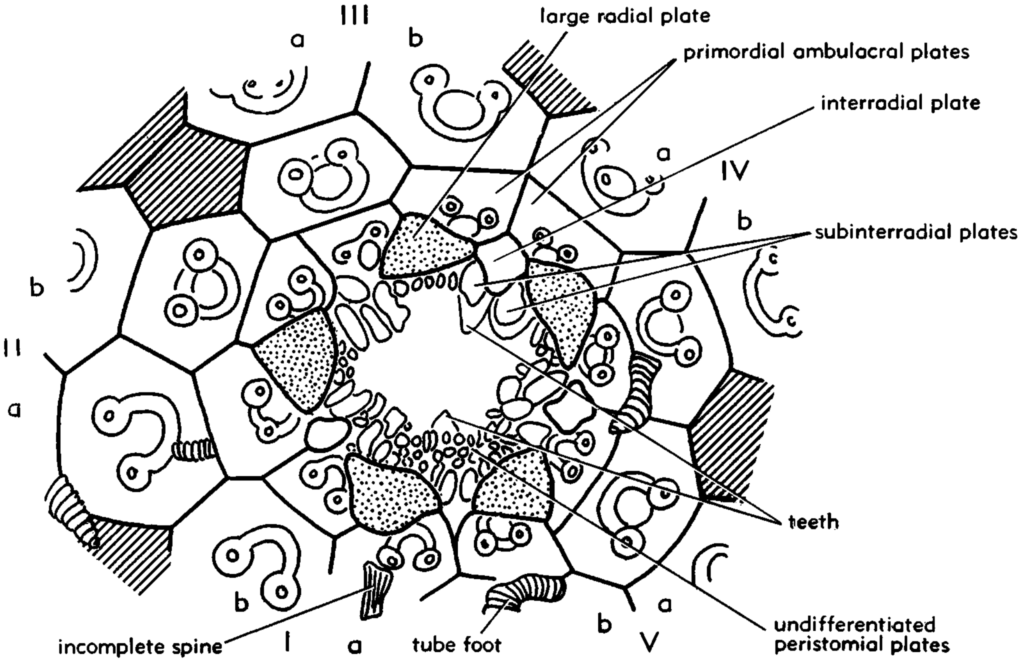


FIG. 217. Diagram of peristome and peristomial plates of *Bothriocidaris,* ×10 (after 59, fig. 12).

erroneous interpretation that the periproct was exocyclic.

The order Megalopoda was established by MACBRIDE & SPENCER (1938) for their genus *Eothuria* on the premise that it was a plated holothurian. MORTENSEN, as well as DURHAM & MELVILLE, considered that *Eothuria* was probably an echinoid. Accepting this conclusion, KIER (this volume) has referred *Eothuria* to the family Lepidocentridae. Thus, Megalopoda becomes a junior synonym of Echinocystitoida.

The order **Cidaroida** is the one group that can unequivocally be shown to cross the boundary from the Paleozoic into the Mesozoic. This conservative group is characterized by rigid or flexible test; endocyclic periproct; apical system with genital plates; ambulacra of two columns, conspicuously narrower than interambulacra; primary interambulacral tubercles conspicuous, with well-defined areole; primordial interambulacral plates resorbed round peristome; peristomial membrane covered with imbricating plates; perignathic girdle absent or composed of apophyses only; spheridia absent; globiferous and tridentate pedicellariae only; primary spines with a cortex layer. The primary interambulacral tubercles of all Paleozoic members of the order, as well as all post-Paleozoic members, except those of the small family Psychocidaridae, are perforate. All post-Paleozoic cidarids have interambulacra with two (except for the genus *Tetracidaris*) columns of plates and all post-Triassic members have rigid tests. CLAUS (1880) first used the name (as Cidarideae) at the ordinal level. DURHAM & MELVILLE formally designated *Cidaris* LESKE as the type-genus.

The subclass **Euechinoidea,** as here interpreted, is characterized by presence of external gills or descent from such forms; corona composed of bicolumnar ambulacra and interambulacra, usually rigid; presence of auricles in perignathic girdle, or descent from such forms; lantern with grooved or keeled teeth, or absent; apical system of genital and ocular plates; presence of spheridia and ophicephalous pedicellariae. All unequivocal known members of this subclass are of post-Paleozoic age and most are post-Triassic. The majority, by far, of post-Paleozoic echinoids are referable to this subclass. A few inadequately known Mississippian and Pennsylvanian fossils (GEIS,

1936) suggest the possibility that the taxon may have originated as early as mid-Paleozoic, and inferences as to the amount of time necessary for the four superorders to differentiate from one another by the Late Triassic and Liassic lend some support to this suggestion. The subclass Euechinoidea was formalized by Bronn (1860). Durham & Melville (1957) designated *Echinus* Linné as the type.

The genera *Tiarechinus* and *Lysechinus* (family Tiarechinidae), from the Late Triassic, appear to lack gill slits (and presumably, therefore, external gills) and thus are not easily referable to the Euechinoidea. However, in many features they are closely similar to some of the modern deep-sea arbaciids. The arbaciids resemble the tiarechinids more than any other group and thus may well be derived from them. Inasmuch as the arbaciids are unequivocal euechinoids, the tiarechinids are referred to the same subclass and superorder, utilizing Duncan's order Plesiocidaroida for them.

Within the Euechinoidea 18 orders and one ordinally unassigned family are recognized. On the basis of evolutionary relationships and common possession of morphological features deemed of major significance, all these orders except one (Orthopsida) may be readily grouped in four superorders: Diadematacea, Echinacea, Gnathostomata, and Atelostomata. The Orthopsida are not clearly referable to either the Diadematacea or Echinacea because of inadequate knowledge of their morphology and evolutionary relationships.

The superorders Diadematacea and Echinacea include predominantly radially symmetrical echinoids, many being characterized by compound ambulacral plates. The **Diadematacea** are characterized by perforate tubercles; presence of lantern with open foramen magnum and most with simple grooved teeth; a complete perignathic girdle; presence of gill slits; and ambulacra tending to have compound plates of diadematoid type. The lantern and teeth (except Pygasteroida) are of cidaroid type, suggesting that they originated from the latter group, perhaps in the mid-Paleozoic if the pedicellariae and plates described by Geis (30) are not referable to some poorly known perischoechinoid. All orders, except the small group of Pygasteroida, are characterized by simple grooved teeth. The pygasteroids have an unusual type of keeled tooth (53) but are otherwise so closely similar to the pedinoids that they are included here.

Of the four orders referred to the Diadematacea, the **Echinothurioida** have been the object of most controversy. They are characterized by a flexible test; spines with hollow axis; noncrenulate tubercles; simple ambulacral plates on peristomial membrane; ambulacral plates compounded on a modified diadematoid plan; grooved teeth; endocyclic periproct. The external gills commonly are inconspicuous and may have been secondarily lost in some, and correspondingly, the gill slits may be poorly defined and difficult to recognize. However, a well-developed perignathic girdle is present. The presence of external gills, a perignathic girdle, and hollow spines indicates strongly that echinothurioids, contrary to the opinion of Mortensen and others, are not direct descendants of the Paleozoic echinocystitoids characterized by a flexible test but without perignathic girdle and external gills. The ordinal name was first proposed by Claus (1880) as Echinothurideae. Durham & Melville (1957) designated *Echinothuria* Woodward as the type-genus. Not unexpectedly, considering the fragile test and usual deep-water habitat, the fossil record of the order is poor and the earliest known genus is *Pelanechinus,* from the late Jurassic of England.

The order **Diadematoida** is characterized by a rigid or flexible test; spines with hollow axis; tubercles crenulate or noncrenulate; peristomial membrane without ambulacral or interambulacral plates but with ten buccal plates; ambulacral plates simple or with diadematoid compounding; endocyclic periproct; grooved teeth; external gills and well-developed gill slits. No member of the order is certainly known from the pre-Jurassic, although Mortensen has suggested that a spine from the Lower Carboniferous of Germany may belong to a diadematoid. The hollow spines, flexible test of some, and type of ambulacral plating, suggest that the Diadematoida and Echinothurioida are closely related. Duncan (1889) first accorded the group ordinal rank. The substitute name Centrechinoida

JACKSON (1912) is unnecessary, inasmuch as the generic name *Diadema* GRAY, 1825, was validated under the Plenary Powers of the International Commission on Zoological Nomenclature (Opinion 206, 1954). DURHAM & MELVILLE (1957) designated *Diadema* GRAY as the type-genus.

The **Pedinoida** have a rigid test; solid spines; noncrenulate tubercles; endocyclic periproct; ambulacra with simple to compound plates; peristomial membrane with 10 buccal plates; shallow gill slits; and grooved teeth. The Late Jurassic echinothurioid genus *Pelanechinus* has many characters in common with some pedinoids, suggesting close relationships between the two orders. The diadematoid type of compound plating and the grooved teeth also indicate its close relationship to the Diadematoida. MORTENSEN (1939) proposed Pedinina as a suborder, whereas FELL (this volume) has elevated it to the rank of an order. DURHAM & MELVILLE (1957) designated *Pedina* L. AGASSIZ as the type-genus. The genus *Diademopsis* occurs in the Late Triassic of western Europe; the order is most diversified in the Jurassic and Cretaceous and at present is represented only by the living *Caenopedina.*

The small extinct order **Pygasteroida** differs from the Pedinoida in having an exocyclic periproct; teeth triangular in cross section, with an unusual buttressed keel; and consistently simple ambulacra. The order ranges through the Jurassic into the Cretaceous (Cenomanian). Immature specimens of *Plesiechinus ornatus* (J. BUCKMAN) are so similar to members of the pedinoid genus *Palaeopedina* that they were assigned to it by LAMBERT & THIÉRY (1910, p. 196), but a series of growth stages shows that they are undeniable pygasteroids. This short-lived group experimented with the irregular condition but for some reason were unsuccessful. Despite their general similarity, the hollow spines, crenulate tubercles, and simple keeled stirodont teeth of *Holectypus* demonstrate that the pygasterids and holectypids are not closely related. The group was given ordinal rank by DURHAM & MELVILLE (1957). *Pygaster* L. AGASSIZ is here designated as the type-genus.

The common possession of external gills, a diadematoid type of ambulacra, and auricles in the perignathic girdle indicate that the Diadematoida, Echinothurioida, and Pedinoida are derived from a common ancestor, which is linked to the Cidaroida by the possession of apophyses in the perignathic girdle and general similarity of the spines and tubercles, as well as the lantern. The Pedinoida (and their derivative, the Pygasteroida) have solid spines and a rigid test, like the Cidaroida, and are thus judged to have departed from the ancestral euechinoid stem earlier than the remaining Diadematacea with hollow spines.

The Jurassic family Heterocidaridae, based on the genus *Heterocidaris* COTTEAU, is characterized by diadematoid ambulacral plating, interambulacra overlapping ambulacra, perforate and crenulate tubercles, indistinct gill slits, and solid spines with a granulated cortex. The lantern is unknown. The general aspect suggests the Diadematoida but the solid spines preclude reference to this order. At present the order is left uncertain, but its assignment to the Diadematacea appears reasonably secure.

Simple keeled teeth differentiate members of the superorder Echinacea from those of the Diadematacea. The **Echinacea** are characterized by a rigid test; endocyclic periproct; solid spines; well-developed external gills and gill slits; peristomial membrane with 10 buccal plates; ambulacra simple or with various types of compound plating; lantern present, with simple keeled teeth; and girdle with well-developed auricles. The simple keeled teeth characteristic of the order differ markedly from those of pygasteroids with the keel bolstered by lateral buttresses.

The genus *Tiarechinus,* here assigned to the order Plesiocidaroida, appears in the Late Triassic (Carnian) and thus, if its relationship to the Arbacioida is correctly inferred, is the oldest undoubted euechinoid, as well as the oldest member of the superorder Echinacea. The genus *Acrosalenia* appears to be represented in the latest Triassic (Rhaetic) and is thus the earliest undoubted member of the Echinacea that can be assigned to an order (Salenioida). By the end of the Jurassic four more echinacean orders (Arbacioida, Hemicidaroida, Temnopleuroida, Phymosomatoida) had appeared and the last, the Echinoida, appeared within the Cretaceous. CLAUS (1876) used Echinideae as a taxon at the subordinal level. Durham & Melville (1957) emended it to Echinacea and designated *Echinus* Linné as the type-genus.

The enigmatic small group of the Tiarechinidae are characterized by a rigid small test; imperforate tubercles, noncrenulate; primordial interambulacral plate persistent, followed by three plates; apical system very large; peristome large; gill slits absent (or indistinct?). Although not used by Mortensen or Durham & Melville, Duncan's (1889) order **Plesiocidaroida** is here employed for this family. The peculiar arrangement of plates in the interambulacra is like that in the newly metamorphosed imago of *Arbacia* and the general morphology is suggestive of the arbacioids. They are known only from the Triassic. On this basis it is considered that the arbacioids may have been derived from the Triassic tiarechinids.

The **Arbacioida** are characterized by a rigid test, ambulacral plating simple to compound, when compound of the arbacioid type; primary tubercles imperforate, noncrenulate; spines smooth, with some development of cortex; periproct with 4 or 5 plates; lantern stirodont; primordial plates persistent; epistroma usually present. The group first appeared in the mid-Jurassic and has continued on to the Recent. Gregory (1900) first ranked the group as a suborder (Arbacina). *Arbacia* Gray was designated as the type by Durham & Melville (1957).

The suborder Calycina Gregory (1900) has priority over Salenina Delage & Hérouard (1903) and was recommended by Durham & Melville (1957), but Salenioida is preferred by Fell & Pawson for use in the *Treatise* because Gregory's name was not based on any included taxon. The **Salenioida** are characterized by a rigid test of cidaroid aspect; stirodont lantern; ambulacra simple or with diadematoid compounding of plates; apical system with one or more large suranal plates; primary tubercles usually crenulate; and spines with collar and cortex. The apical system with suranal plates and posteriorly positioned periproct are easily recognized and distinctive features. The genus *Acrosalenia* is uncertainly identified in the Late Triassic, the group continuing on to the Recent. The group is elevated to ordinal rank by Fell & Pawson (this volume). *Salenia* Gray was designated by Durham & Melville (1957) as the type-genus.

The **Hemicidaroida** are characterized by a stirodont lantern; apical system without large suranal plates; ambulacral plates diadematoid, simple adapically in some; primary tubercles perforate, mostly crenulate; and peristome large, with conspicuous gill slits. Two genera (*Hessotiara* and *Pseudodiadema*) representing two families are present in the basal Jurassic (Hettangian), while the genus *Diplopodia* is reported from the Rhaetic, indicating that the order must have had a prior origin. No members are known in the post-Cretaceous. Hemicidarina was proposed by Beurlen (1937) as a suborder. Durham & Melville (1957) designated *Hemicidaris* L. Agassiz as the type-genus and ranked the assemblage as an order. The family Pseudodiadematidae is assigned to the order by Fell & Pawson (this volume), although Durham & Melville had included it in the Phymosomatoida.

The lack of large suranal plates and imperforate primary tubercles distinguish the **Phymosomatoida** from the Hemicidaroida. The order is characterized by a stirodont lantern; apical system without large suranal plates; primary tubercles imperforate; ambulacral plates simple or diadematoid. The genus *Jeannetia* appears in the Hettangian of France. The genera *Glyptocidaris* (Phymosomatidae) and *Stomopneustes* (Stomechinidae) are the only two representatives in the Recent; the order was most diversified in the Cretaceous. The order is presumably derived from the Hemicidaroida by loss of the perforate condition of the primary tubercles. The Phymosomina were proposed as a "tribe" by Mortensen (1904), later considered as a suborder in his monograph, and elevated to an order by Durham & Melville (1957), who designated *Phymosoma* Haime as the type-genus.

The Temnopleuroida and Echinoida, in contrast to the other Echinacea, have a closed foramen magnum in the lantern. The **Temnopleuroida** are characterized by a camarodont lantern; test usually sculptured, if not, gill slits sharp and deep; ambulacral plates compound, diadematoid or echinoid in character. *Glyptodiadema* appears in the

Pliensbachian, but the order is most diversified in the Recent. It seems possible that the order may have had its origin in the Pseudodiadematidae (order Hemicidaroida). The group was given subordinal rank (as Temnopleurina) by MORTENSEN in his monograph (1942) and was elevated to ordinal rank by DURHAM & MELVILLE (1957) who designated *Temnopleurus* DUNCAN as the type.

The order **Echinoida** is characterized by a camarodont lantern; nonsculptured test; shallow gill slits; imperforate and noncrenulate tubercles; and compound ambulacral plates of echinoid type. The genus *Spaniocyphus,* referred to the order by FELL & PAWSON (this volume) occurs in the Valanginian of Europe, while *Trochoechinus* is found in the Upper Cretaceous, and *Psammechinus* may occur in the Upper Cretaceous. The genus *Echinometra* is first recorded in the Paleocene. The maximum diversity is in the Recent. MORTENSEN (1951) suggested that the order may have been derived from the Stomechinidae. CLAUS (1876) ranked the group as a suborder, MORTENSEN in his monograph considered it as a suborder. DURHAM & MELVILLE elevated it to ordinal rank and designated *Echinus* LINNÉ as the type-genus.

The small order **Orthopsida** is of uncertain superordinal assignment. It is characterized by a camarodont lantern; rigid test; ambulacral plates simple or with a few triads (29, p. 254, text-fig. 1-c); tubercles perforate, noncrenulate. The genus *Dubarechinus* occurs in the Domerian of Morocco, while the order becomes extinct by the end of the Cretaceous. FELL & PAWSON (this volume) suggest that the group may be independently derived from some aulodont ancestry, although DURHAM & MELVILLE had suggested a possible hemicidarid derivation. Orthopsina was proposed as a suborder by MORTENSEN (1942) and is elevated to ordinal rank by FELL & PAWSON (this volume). DURHAM & MELVILLE designated *Orthopsis* COTTEAU as the type-genus.

The two remaining superorders, Gnathostomata and Atelostomata, in contrast to the preceding euechinoids (except the order Pygasteroida), are characterized by an exocyclic periproct and a lack of truly compound plates in the ambulacra. A posteriorly eccentric but still endocyclic position of the periproct is found in several distinct groups of the Euechinoida, such as *Palaeopedina* of the Pedinoida, *Heterodiadema* and *Pseudodiadema* of the Hemicidaroida, and *Phymosoma* of the Phymosomatoida. As far as can be recognized, this exocyclic tendency was not very successful in the Diadematacea, resulting only in the short-lived Pygasteroida, but in the Echinacea it was very advantageous, resulting in the gnathostomous order Holectypoida and ultimately the very successful, mainly Cenozoic, Clypeasteroida or sand dollars.

The origins of the **Atelostomata** are less clearly evident but the fact that young *Apatopygus recens, Echinolampas depressa,* and *Conolampas sigsbei* possess lanterns (MORTENSEN, 1948, p. 266, 305) and auricles is evidence that they must be descended from a euechinoid ancestry. The teeth in young *Apatopygus* are keeled, indicating that they are probably derived from an echinacean ancestry or the Echinacea themselves. However, the common occurrence of hollow spines, as well as perforate and crenulate tubercles in both the Atelostomata and Gnathostomata, likewise suggests a close affinity to the Diadematoida. An alternative possibility to derivation from the echinacean stem (as shown in Fig. 213) is to postulate that the stirodont type of lantern and teeth has arisen more than once and that the Holectypoida were derived from a diadematoid ancestor. However, the general morphology of the test is more suggestive of a pseudodiadematid origin and this source is here accepted.

The **Gnathostomata** are characterized by a rigid corona; exocyclic apical system; adults mostly with lantern and keeled teeth; apical system and peristome approximately opposite; spines hollow; primary tubercles usually perforate and crenulate. The genus *Holectypus* appears in the Domerian and in the position of the periproct is already well removed from a regular echinoid ancestor, suggesting that intermediates may well be searched for in the Triassic. Gnathostomata was proposed by ZITTEL (1879) as a suborder. DURHAM & MELVILLE (1957) employed it as a superorder, designating *Clypeaster* LAMARCK as the type.

The Gnathostomata are easily separated

into two groups, the Holectypoida and Clypeasteroida, here accepted as of ordinal rank. The **Holectypoida** are characterized by interambulacra wider than ambulacra; apical system monobasal or not; absence of a microcanal system in walls of test; teeth keeled and with lateral flanges when present. The morphologic diversity is very great and wide morphologic gaps exist between known taxa, suggesting that knowledge of their fossil record is very uneven. The obvious gaps in the record of morphologic types make interpretation of evolutionary relationships hazardous, but WAGNER & DURHAM (this volume) have recognized the same three suborders as DURHAM & MELVILLE (1957), albeit with a differing content of families. The suborder Holectypina has orderly ornament, distinct gill slits, and radially positioned auricles. The suborder Echinoneina (H. L. CLARK, 1925; type-genus *Echinoneus* LESKE, 1778, SD DURHAM & MELVILLE, 1957) lacks orderly ornament, has lantern and girdle rudimentary or lacking in adults, and no gill slits. The suborder Conoclypina (ZITTEL, 1879; type-genus *Conoclypus* L. AGASSIZ, here designated) is characterized by petaloid or subpetaloid ambulacra, interradially positioned auricles, monobasal apical system, and lack of orderly ornament.

The suborder Conoclypina (families Oligopygidae and Conoclypidae) and the members here referred to it was assigned to the Cassiduloida (and thus by inference to the superorder Atelostomata of the present classification) by MORTENSEN and PHILIP (1963). The monobasal apical system and petaloid ambulacra support such an assignment but the well-developed lantern and interradial auricles (in genera where the internal structures have been studied, *Conoclypus, Oligopygus, Bonaireaster*) are here considered to be more important indicators of affinities. Petals and the monobasal apical system are known to have developed independently in the Clypeasteroida and Cassiduloida and thus cannot be considered as indicative of affinities. All known unequivocal cassiduloids, from the earliest *(Galeropygus)* on, lack a lantern in the adult and thus unless paedogenesis or some similar process is invoked, the presence of a lantern in the Conoclypina could not be explained if they were assigned to the Cassiduloida.

As here interpreted, the Holectypoida appeared in the Liassic, had their heyday in the Cretaceous, decreased rapidly by the Eocene, and are represented in the Recent only by two closely related genera. DUNCAN (1889) proposed the Holectypoida as an order and DURHAM & MELVILLE (1957) designated *Holectypus* DESOR as its type.

The order **Clypeasteroida** is characterized by petaloid ambulacra; ambulacra never narrower than interambulacra on oral surface; monobasal apical system; lantern without compass; peristome small, without gill slits; teeth keeled, without lateral flanges; presence of small accessory tube feet occurring outside of petals. Four suborders can be recognized. The suborder Clypeasterina has demiplates in petals, discontinuous interambulacra terminated adapically by a pair of plates, and separate auricles. The suborder Laganina MORTENSEN (1948) with *Laganum* LINK designated by DURHAM & MELVILLE (1957) as type, has narrow, continuous interambulacra on the oral surface, terminated adapically by a single plate, and fused auricles in an interradial position. The suborder Scutellina HAECKEL (1896) (as suborder Scutellaria), with *Scutella* LAMARCK designated by DURHAM & MELVILLE (1957) as type, is characterized by fused interradial auricles, interambulacra terminating adapically in a pair of plates, and absence of demiplates in petals. The suborder Rotulina DURHAM (1955), with *Rotula* SCHUMACHER designated by DURHAM & MELVILLE (1957) as type, has interambulacra terminating adapically in a series of single plates, fused auricles, no demiplates in petals, and posterior of test dentate or digitate.

The genera *Fibularia* and *Echinocyamus* have been reported in the late Senonian. The order is abundantly represented in the Cenozoic, with a maximum in the Miocene and a slight decrease to the Recent. The order appears to have been derived from some member of the Holectypina in the Upper Cretaceous. A. AGASSIZ (1873) proposed the Clypeastridae as a suborder, whereas CLAUS (1876) considered the taxon as an order (named Clypeastridea). DUR-

HAM & MELVILLE (1957) designated *Clypeaster* LAMARCK as the type-genus.

The superorder **Atelostomata** is characterized by rigid (albeit in some species very fragile) test; exocyclic periproct; absence of lantern, girdle, and branchial slits in adult; interambulacra wider than amulacra on oral surface; peristome small; primary spines hollow; and tubercles usually perforate and crenulate. Although DURHAM & MELVILLE (1957) recognized four orders (Cassiduloida, Nucleolitoida, Holasteroida, Spatangoida) subsequent studies by KIER have resulted in the union of two (Nucleolitoida, Cassiduloida). PHILIP (1963) has proposed the suborder Neolampadina (here elevated to ordinal rank) for the family Neolampadidae; thus four orders of Atelostomata are recognized in the *Treatise*.

The genus *Pygomalus* is known from the Sinemurian and *Galeropygus* from the Domerian. These two genera were already widely separated in their detailed morphology and respectively they represent the orders Holasteroida and Cassiduloida. They are so divergent from contemporary Euechinoida and Gnathostomata that it is difficult to suggest a possible ancestor. The distinctiveness of their morphology (small peristome, no lantern, and lack of large primary tubercles on interambulacral plates) suggests that their ancestry has long previously branched off the euechinoid line. The divergent apical systems and character of the ambulacra likewise suggest that the separation of the two orders had occurred at some time prior to the Early Jurassic.

The source of the third order, the Spatangoida, is uncertain but it seems to lie in one of the other two orders. As a corollary to these postulated prior ancestries the occurrence of atelostomate echinoids is to be expected in the Triassic and perhaps even in the latest Paleozoic.

The genus *Loriolella* FUCINI, which has been considered by some as a type intermediate between *Galeropygus* and its endocyclic ancestor is excluded from the Cassiduloida (which includes *Galeropygus*) by KIER because it lacks phyllodes, bourrelets, and petaloid ambulacra. *Loriolella* occurs in the Domerian, contemporaneous with the earliest known *Galeropygus*. It is here retained in the superorder but left unassigned to family or order. There seem to be traces of faint gill slits around the small peristome on some specimens. If correctly interpreted, this indicates that the genus retained external gills and would strongly support the interpretation that it was a persistent representative of the intermediates between the euechinoids and the atelostomates.

The **Cassiduloida,** as interpreted by KIER, are characterized by a compact apical system, adapically petaloid ambulacra, presence of phyllodes and bourrelets, and absence of fascioles. They are first known in the Liassic, are very abundant in the Early Tertiary and have since declined to a few living species. The name Cassidulideae was proposed by CLAUS (1880). DURHAM & MELVILLE designated *Cassidulus* LAMARCK as the type-genus. KIER (1962) showed that the change from a tetrabasal to monobasal apical system occurred in more than one stock and negated the principal basis used by DURHAM & MELVILLE to separate their orders Cassiduloida and Nucleolitoida.

The family Neolampadidae was considered by MORTENSEN to be closely allied to the cassiduloids. However, the restricted concept of the latter order employed by KIER excludes them from that taxon. PHILIP (1963) established the suborder Neolampadina for the family and at the same time showed that it was represented in the Paleogene, describing two new genera *(Pisolampas, Notolampas)* that occur as fossils. PHILIP's suborder is here elevated to ordinal rank as **Neolampadoida.** It is characterized by simple ambulacral pores, nonpetaloid ambulacra, and floscelle absent or weakly developed.

The order **Holasteroida** is characterized by absence of floscelle; no fifth genital plate; apical system typically elongate or disjunct; plastron lacking to meridosternous; paired petals not impressed. The elongate to disjunct apical system is the most notable feature of the order, readily separating it from the Cassiduloida and Spatangoida. As conceived by DURHAM & MELVILLE (1957), this assemblage includes the suborders Protosternata and Meridosternata of MORTENSEN's usage. The oldest known atelostomate echinoid, the Liassic *Pygomaulus,* is referable to this order. Members are common in the Jurassic and Cretaceous but are less abundant in the known Tertiary faunas. Living representatives are deep-water inhabitants with thin and fragile tests, types that are not ordinarily found or recognized in the fossil record. It is here considered, as noted above, that the Holasteroida and Cassiduloida are derived from a common pre-Liassic ancestor. The order was established by DURHAM & MELVILLE (1957) and *Holaster* L. AGASSIZ is here designated as the type.

The order **Spatangoida** is characterized by amphisternous plastron; compact apical system; posterior periproct; presence of phyllodes; and absence of bourrelets. The Spatangoida, as restricted by DURHAM & MELVILLE (1957) and here accepted, include only the Amphisternata of MORTENSEN and are thus a much more limited assemblage than that of other classifications. They appeared at the beginning of the Cretaceous, attained their greatest diversity during the Eocene, and have steadily declined since then. The Spatangoida were first elevated (as Spatangoidea) to a suprafamilial rank by CLAUS (1876). DURHAM & MELVILLE designated *Spatangus* GRAY as the type.

The source of the Spatangoida as here understood is obscure. MORTENSEN (1951, v. 5, pt. 2, p. 571) sought their origins, in part, among his Disasteridae (Collyritidae +Disasteridae of this volume) by "a kind of retrograde development" and, in part, among the Conoclypidae (which he derived from the Echinobrissidae). TERMIER & TERMIER (1953, p. 881) seemingly thought that the source was among their "Echinobrissides" (Nucleolitidae of this volume). DEVRIÈS (1960), on the basis of his studies of the toxasterids, considered that they arose from the collyritids. In particular, he (*op. cit.*, p. 177) would derive the genus *Holaster* and the toxasterids from a common source in the collyritids, seemingly from some form such as *Acrolusia*. These interpretations are primarily based on the ease of progression from the simple protosternous plastron of the collyritids to the more specialized amphisternous plastron, and they overlook the difficulties in deriving the compact apical system from the disjunct apical system of the collyritids. It is difficult to postulate an appropriate genetic mechanism to account for the necessary reversal of the collyritine trend to disassociation of the apical system, and in the absence of undoubted intermediates between the two types, it seems preferable to appeal to the inadequacy of our knowledge of the fossil record and suggest that the source lay somewhere in the more primitive members of the atelostomate stock. DEVRIÈS suggested that his *Toxaster lafittei,* from the Berriasian, represents the "connecting link" between the toxasterids, *Holaster*, and the collyritids. However, the height of the plates in the ambulacra and the position of the pores in the plates, in combination with the elongate apical system, suggest that his species is incorrectly assigned to *Toxaster* and is not the long sought-for intermediate.

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OUTLINE OF CLASSIFICATION

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The following outline of the classification of the Echinoidea summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each family group and higher-rank taxon. Where a single number is given, it refers to genera; where two numbers are given, the second indicates subgenera. Authorship of the systematic descriptions is indicated by recording with each division the initial letters of the author's name as shown by the tabulation below:

Authorship of Systematic Descriptions

Durham, J. W.	D
Fell, H. B.	FE
Fischer, A. G.	FI
Kier, P. M.	K
Melville, R. V.	M
Pawson, D. L.	P
Wagner, C. D.	W

Main Divisions of Echinoidea

- Echinoidea *(class)* (768;78; excludes doubtful genera). *Ord.-Rec.*
  - Perischoechinoidea *(subclass)* (99;5). *Ord.-Rec.* (D-FE-K)
    - Bothriocidaroida *(order)* (1). *Ord.* (K)
      - Bothriocidaridae (1). *Ord.* (K)
    - Echinocystitoida *(order)* (24). *Ord.-Perm.* (K)
      - Echinocystitidae (5). *Sil.-Perm.* (K)
      - Lepidesthidae (2). *Dev.-Perm.* (K)
      - Lepidocentridae (15). *Ord.-Miss.* (K)
      - Family Uncertain (2). *Dev.* (K)
    - Palaechinoida *(order)* (10). *Sil.-Perm.* (K)
      - Palaechinidae (5). *Miss.* (K)
      - Cravenechinidae (3). *Sil.-Perm.* (K)
      - Family Uncertain (2). *?Sil., L.Carb.* (K)
    - Cidaroida *(order)* (63;5). *U.Sil.-Rec.* (FE)
      - Archaeocidaridae (6). *?U.Sil., Dev.-Perm.* (FE)
      - Miocidaridae (7). *L.Carb.-L.Jur.* (FE)
      - Cidaridae (42;5). *U.Trias.-Rec.* (FE)
        - Histocidarinae (4). *Jur.-Rec.* (FE)
        - Ctenocidarinae (8). *?Eoc., Rec.* (FE)
        - Goniocidarinae (4;5). *Eoc.-Rec.* (FE)
        - Stereocidarinae (4). *U.Jur.-Rec.* (FE)
        - Rhabdocidarinae (9). *L.Jur.-Rec.* (FE)
        - Cidarinae (13). *U.Trias.(Rhaet.)-Rec.* (FE)
      - Psychocidaridae (6). *U.Jur.-Rec.* (FE)
      - Diplocidaridae (2). *Jur.-Cret.* (FE)
    - Order and Family Uncertain (1). *Sil.* (K)
  - Euechinoidea *(subclass)* (669;73). *?Carb., U.Trias.-Rec.* (D-FE-FI-K-M-P-W)
    - Diadematacea *(superorder)* (56;2). *?L.Carb., U.Trias.-Rec.* (FE-M)
      - Echinothurioida *(order)* (12). *U.Jur.-Rec.* (FE)
        - Echinothuriidae (12). *U.Jur.(Oxford.)-Rec.* (FE)
          - Echinothuriinae (8). *U.Cret.(Senon.)-Rec.* (FE)
          - Phormosomatinae (3). *Rec.* (FE)
          - Pelanechininae (1). *U.Jur.* (FE)
      - Diadematoida *(order)* (23). *?L.Carb., U.Trias.-Rec.* (FE)
        - Diadematidae (11). *L.Jur.-Rec.* (FE)
        - Lissodiadematidae (1). *Rec.* (FE)
        - Micropygidae (1). *Rec.* (FE)
        - Aspidodiadematidae (4). *?U.Jur., Rec.* (FE)
        - Family Uncertain (6). *?L.Carb., Jur.-Cret.* (FE)
      - Pedinoida *(order)* (16;2). *U.Trias.-Rec.* (FE)
        - Pedinidae (15;2). *U.Trias.(Rhaet.)-Rec.* (FE)
        - Family Uncertain (1). *U.Jur.(Oxford.).* (FE)
      - Pygasteroida *(order)* (3). *L.Jur.-U.Cret.* (M)
        - Pygasteridae (3). *L.Jur.-U.Cret.* (M)
      - Order Uncertain (1). *Jur.(Domer.-Oxford.).* (FE)
        - Heterocidaridae (1). *Jur.(Domer.-Oxford.).* (FE)

  - Order and Family Uncertain (1). *Trias.* (FE)
- Echinacea *(superorder)* (195;14). *U.Trias., L. Jur.-Rec.* (D-FE-P)
  - Salenioida *(order)* (16). *?U.Trias., L.Jur.-Rec.* (FE)
    - Acrosaleniidae (6). *?U.Trias., L.Jur.-U.Cret.* (FE)
    - Saleniidae (10). *U.Jur.-Rec.* (FE)
      - Saleniinae (5). *L.Cret.-Rec.* (FE)
      - Hyposaleniinae (5). *U.Jur.-U.Cret.* (FE)
  - Hemicidaroida *(order)* (25). *U.Trias.-U.Cret.* (FE)
    - Hemicidaridae (10). *L.Jur.-U.Cret. (Cenoman.).* (FE)
    - Pseudodiadematidae (12). *U.Trias.-U.Cret.* (FE)
    - Family Uncertain (3). *U.Jur.-U.Cret.* (FE)
  - Phymosomatoida *(order)* (38;6). *L.Jur.-Rec.* (FE)
    - Phymosomatidae (18;4). *L.Jur.-Rec.* (FE)
    - Stomechinidae (19;2). *L.Jur.-Rec.* (FE)
    - Family Uncertain (1). *U.Cret.(Maastricht.).* (FE)
  - Arbacioida *(order)* (20;4). *M.Jur.(Bathon.)-Rec.* (FE)
    - Arbaciidae (20;4). *M.Jur.-Rec.* (FE)
  - Temnopleuroida *(order)* (62;4). *L.Jur.-Rec.* (FE)
    - Glyphocyphidae (9;2). *L.Jur.-Eoc.* (FE)
    - Temnopleuridae (39;2). *U.Cret.(Cenoman.)-Rec.* (FE)
    - Toxopneustidae (13). *?Cret.-?Oligo., Mio.-Rec.* (FE)
    - Family Uncertain (1). *?Paleoc., Eoc.-U. Oligo.* (FE)
  - Echinoida *(order)* (32). *?U.Cret.(Cenoman.), Paleoc.-Rec.* (FE-P)
    - Echinidae (13). *?U.Cret.(Cenoman.), Mio.-Rec.* (FE-P)
    - Echinometridae (12). *Paleoc.-Rec.* (FE-P)
    - Strongylocentrotidae (3). *Mio.-Rec.* (FE-P)
    - Parasaleniidae (2). *Eoc.-Rec.* (FE-P)
    - Family Uncertain (2). *L.Cret.-Mio.* (FE-P)
  - Plesiocidaroida *(order)* (2). *U.Trias.(Carn.).* (D-FE)
    - Tiarechinidae (2). *U.Trias.* (FE)
- Superorder Uncertain (Echinacea or Diadematacea) (6). *L.Jur.-U.Cret.* (FE)
  - Orthopsida *(order)* (6). *L.Jur.-U.Cret.* (FE)
    - Orthopsidae (6). *L.Jur.-U.Cret.* (FE)
- Gnathostomata *(superorder)* (103). *Jur.-Rec.* (D-W)
  - Holectypoida *(order)* (30). *L.Jur.(Pliensbach.)-Rec.* (W-D)
    - Holectypina *(suborder)* (10). *L.Jur. (Pliensbach.)-U.Cret.(Senon.).* (D-W)
      - Holectypidae (5). *L.Jur.(Pleinsbach.)-U. Cret.(Senon.).* (D-W)
      - Anorthopygidae (1). *Cret.(Alb.-Cenoman.).* (D-W)
      - Discoididae (4). *Cret.* (D-W)
    - Echinoneina *(suborder)* (10). *M.Jur.(Callov.)-Rec.* (D-W)
      - Echinoneidae (3). *U.Cret.-Rec.* (D-W)
      - Conulidae (4). *M.Jur.(Callov.)-Eoc.* (D-W)
      - Galeritidae (1). *U.Cret.(Senon.).* (D-W)
      - Family Uncertain (2). *L.Cret.(Hauteriv.)-U. Cret.(Senon.).* (D-W)
    - Conoclypina *(suborder)* (8). *U.Cret.(Senon.)-Mio.* (D-W)
      - Conoclypidae (2). *Eoc.-Mio.* (D-W)
      - Oligopygidae (6). *U.Cret.(Senon.)-Oligo.* (D-W)
    - Suborder and Family Uncertain (2). *U.Cret.-Oligo.* (D-W)
  - Clypeasteroida *(order)* (73). *U.Cret. (Maastricht.)-Rec.* (D)
    - Clypeasterina *(suborder)* (7). *U.Eoc.-Rec.* (D)
      - Clypeasteridae (1). *U.Eoc.(Auvers.)-Rec.* (D)
      - Arachnoididae (6). *Oligo.-Rec.* (D)
        - Arachnoidinae (2). *Oligo.-Rec.* (D)
        - Ammotrophinae (3). *Mio.-Rec.* (D)
        - Subfamily Uncertain (1). *?L.Mio.* (D)
    - Laganina *(suborder)* (28). *U.Cret.(Senon.)-Rec.* (D)
      - Fibulariidae (14). *U.Cret.(Senon.)-Rec.* (D)
      - Laganidae (8). *Eoc.-Rec.* (D)
      - Neolaganidae (6). *Eoc.-Oligo.* (D)
    - Scutellina *(suborder)* (32). *Eoc.-Rec.* (D)
      - Scutellidae (3). *Oligo-Mio.* (D)
      - Protoscutellidae (3). *Eoc.* (D)
      - Eoscutellidae (1). *Eoc.* (D)
      - Dendrasteridae (4). *Plio-Rec.* (D)
      - Echinarachniidae (7). *Oligo-Rec.* (D)
      - Monophorasteridae (3). *Mio.* (D)
      - Mellitidae (4). *L.Mio.-Rec.* (D)
      - Astriclypeidae (3). *Oligo-Rec.* (D)
      - Abertellidae (1). *Mio.* (D)
      - Scutasteridae (1). *L.Mio.* (D)
      - Family Uncertain (2). *U.Eoc.-Oligo.* (D)
    - Rotulina *(suborder)* (3). *Mio.-Rec.* (D)
      - Rotulidae (3). *Mio.-Rec.* (D)
    - Suborder and Family Uncertain (3). *M.Eoc.-Mio.* (D)
- Atelostomata *(superorder)* (304;57). *Jur.-Rec.* (D-FI-K-W)
  - Cassiduloida *(order)* (69;3). *Jur.-Rec.* (K)
    - Galeropygidae (2). *Jur.* (K)
    - Clypeidae (5;3). *Jur.-U.Cret.* (K)
    - Nucleolitidae (12). *M.Jur.-U.Cret.* (K)
    - Echinolampadidae (6). *Cret.(Cenoman.)-Rec.* (K)
    - Faujasiidae (12). *U.Cret.-Eoc.* (K)
    - Archiaciidae (2). *Cret.* (K)
    - Cassidulidae (6). *L.Cret.-Rec.* (K)
    - Clypeolampadidae (2). *U.Cret.(Cenoman.-Maastricht.).* (K)
    - Pliolampadidae (12). *U.Cret.(Senon.)-Rec.* (K)
    - Apatopygidae (1). *Neog.* (K)
    - Family Uncertain (9). *Jur.-Rec.* (K)

- Holasteroida *(order)* (81). *L.Jur.-Rec.* (D-W)
  - Collyritidae (8). *L.Jur.-L.Cret.* (D-W)
  - Disasteridae (9). *M.Jur.-L.Cret.* (D-W)
  - Holasteridae (38). *L.Cret.-Rec.* (D-W)
  - Urechinidae (6). *?U.Eoc., Mio.-Rec.* (D-W)
  - Calymnidae (1). *Rec.* (D-W)
  - Pourtalesiidae (7). *Rec.* (D-W)
  - Stenonasteridae (1). *U.Cret.* (D-W)
  - Somaliasteridae (4). *U.Cret.(Senon.)-Paleoc.* (D-W)
  - Family Uncertain (7). *Cret.-Eoc.* (D-W)
- Spatangoida *(order)* (147;54). *L.Cret.(Berrias.)-Rec.* (FI)
  - Toxasterina *(suborder)* (13). *L.Cret.(Berrias.)-Rec.* (FI)
    - Toxasteridae (13). *L.Cret.(Berrias.)-Rec.* (FI)
  - Hemiasterina *(suborder)* (42;26). *L.Cret.(Apt.)-Rec.* (FI)
    - Hemiasteridae (15;9). *L.Cret.(Apt.)-Rec.* (FI)
    - Palaeostomatidae (5). *U.Cret.-Rec.* (FI)
    - Pericosmidae (1;3). *Eoc.Rec.* (FI)
    - Schizasteridae (19;14). *U.Cret.(Cenoman.)-Rec.* (FI)
    - Aeropsidae (2). *Rec.* (FI)
  - Micrasterina *(suborder)* (59;26). *Cret.(Cenoman.)-Rec.* (FI)
    - Micrasteridae (4;2). *U.Cret.(Cenoman.)-Eoc.* (FI)
    - Brissidae (40;16). *U.Cret.(Santon.)-Rec.* (FI)
    - Spatangidae (8;6). *Eoc.-Rec.* (FI)
    - Loveniidae (7;2). *Eoc-Rec.* (FI)
  - Asterostomatina *(suborder)* (23;2). *Eoc.-Rec.* (FI)
    - Asterostomatidae (23;2). *Eoc.-Rec.* (FI)
  - Suborder and Family Uncertain (10). *Cret.-Mio.* (FI)
- Neolampadoida *(order)* (7). *U.Eoc.-Rec.* (D-W)
  - Neolampadidae (7). *U.Eoc.-Rec.* (D-W)
- Gnathostomata or Atelostomata, Order Uncertain (5). *Jur.* (D-W)
- Doubtful genera of regular echinoids (14). *Perm.-Jur.* (FE)

[Numerical tabulations do not include 4 genera added late.]

SYSTEMATIC DESCRIPTIONS

By J. W. Durham, H. B. Fell, A. G. Fischer, P. M. Kier, R. V. Melville, D. L. Pawson, and C. D. Wagner

Class ECHINOIDEA Leske, 1778

[*nom. transl.* Bronn, 1860, p. 295 (*ex* order Echinoidea d'Orbigny, 1852, p. 114, *nom. correct. pro* ordo Echinus Leske, 1778, p. xvi)] [=Echinides Lamarck, 1801; order Echini Goldfuss, 1820; order Cycloïdes de Blainville, 1822; Echinida Fleming, 1822; order Echinata Fischer de Waldheim, 1823; order Echinoida Latreille, 1825; order Echinidea de Blainville, 1834; order Pedicellata Griffith & Pidgeon, 1834; order Cirrhi-Spinigrada Forbes, 1841; order Adostella Austin & Austin, 1842; Echinodea Düben & Koren, 1846] [Diagnosis prepared by J. Wyatt Durham. Research on authorship and synonymy by J. W. Durham, R. V. Melville, & H. B. Fell]

Free-living Echinodermata with subspherical or modified subspherical test, built of interlocking calcareous plates and bearing movable appendages (spines, pedicellariae, spheridia) externally; equipped with masticatory apparatus or descended from forms having one; mouth directed toward substrate; two principal groups of plates comprising apical and coronal systems, apical system invariably including five radially situated ocular plates and five or fewer interradially situated genital plates, and coronal system being composed of five radial ambulacral and five interradial interambulacral areas built of contiguous meridional columns of plates; in addition, two less conspicuous plate systems, termed peristomial and periproctal, are present. Plates of ambulacral areas perforated for passage of tube feet. Primordial ambulacral plates bordering peristome conforming to Lovén's law. Mouth nearly always on lower surface, rarely anterior; anus present in all individuals, situated entirely or partly within apical system, or outside of it in posterior interambulacrum; mouth and anus each surrounded by membrane which usually bears imbricating or dissociated plates of peristomial and periproctal systems. Gonads five or fewer, interradial in position. Radial canals of water-vascular system internal to test. [All known types are exclusively marine in habitat.] *Ord.-Rec.*

Subclass PERISCHOECHINOIDEA M'Coy, 1849

[*nom. transl.* Durham & Melville, 1957 (*ex nom. correct.* Bronn, 1860, *pro* order Perischoechinida M'Coy, 1949)] [Diagnosis prepared by J. W. Durham]

Regular (endocyclic) echinoids with interambulacra of one to many columns; ambulacra of two to 20 columns, without compound plates; perignathic girdle of apophyses only or none; teeth grooved; no gill slits, spheridia, or ophiocephalous pedicellariae. *Ord.-Rec.*

NONCIDAROID PALEOZOIC ECHINOIDS

By Porter M. Kier
[Smithsonian Institution, U.S. National Museum]

INTRODUCTION

This section includes all noncidaroid regular Paleozoic echinoids which are grouped in the three orders designated as Bothriocidaroida, Echinocystitoida, and Palaechinoida. The Bothriocidaroida is an aberrant order known only from the Ordovician. It consists of a single genus characterized by nonimbricating plates, lack of genital plates, and single-columned interambulacra. The Echinocystitoida, which range from Ordovician to Permian, have strongly imbricate plates, ambulacral plates that bevel under the interambulacra, and genital plates. The Palaechinoida, known from the Silurian to the Pennsylvanian, have slightly imbricating plates with ambulacra beveling over the interambulacra. The latter two orders reached their maximum in numbers during the Mississippian and became extinct before the end of the Permian. Most echinoid workers believe that they were not the ancestors of any post-Paleozoic echinoids.

EVOLUTIONARY TRENDS

Many evolutionary trends are apparent in the Palaechinoida and Echinocystitoida. Because only one genus of one age is known in the Bothriocidaroida, no trends are known in this order.

ADORAL EXPANSION OF AMBULACRA

The adoral ambulacra are enlarged in later genera of the Echinocystitoida. In Ordovician, Silurian, and Devonian genera (e.g., *Aulechinus,* Fig. 218,*1*), the adoral ambulacral plates are similar in size and arrangement to the adapical, whereas in most Mississippian and later genera the adoral ambulacra are greatly expanded, with far larger plates, larger and more widely spaced pores, and in many species more columns (e.g., *Proterocidaris,* Fig. 218,*2*; *Pronechinus*, Fig. 218,*3*). The expansion of the adoral ambulacra and increase in size of the pores would increase the locomotory and food-gathering capabilities of the echinoid.

SHIFT OF AMBULACRAL PORES

In earlier echinoids (e.g., *Ectinechinus,* Fig. 219,*1*) the pores are adjacent to the perradial suture, but by the Late Silurian, the pores shifted somewhat away from the perradial suture (e.g., *Palaeodiscus,* Fig. 219,*2*). By the Early Devonian the pores were midway between the perradial and adradial sutures (e.g., *Porechinus,* Fig. 219, *3*) and by the Middle Devonian (e.g., *Lepidocentrus,* Fig. 219,*4*) the pores were nearer to the adradial suture. In all Mississippian genera with two columns in each ambula-

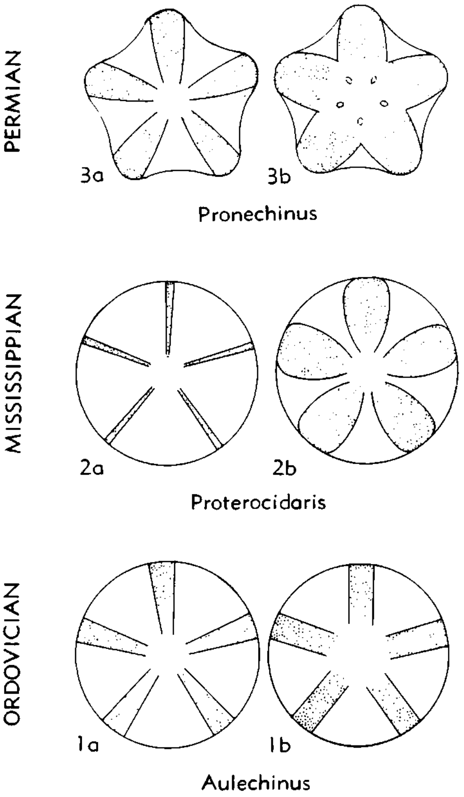


Fig. 218. Aboral (*1a,2a,3a*) and oral (*1b,2b,3b*) views showing increase in area of adapical ambulacra (shaded) in the Echinocystitoida (Kier, n).

crum, the pore pairs are adjacent to the adradial suture (e.g., *Pholidoechinus,* Fig. 219,5). This shift of the pores away from the perradial suture would decrease the amount of strain on a particular area of the test when the tube feet were contracted while attached to an object, for instead of all strain being concentrated along the perradial suture, it shifted to two areas as far distant as possible. When the tube feet were used for respiration, this separation would increase the area from which oxygen could be extracted.

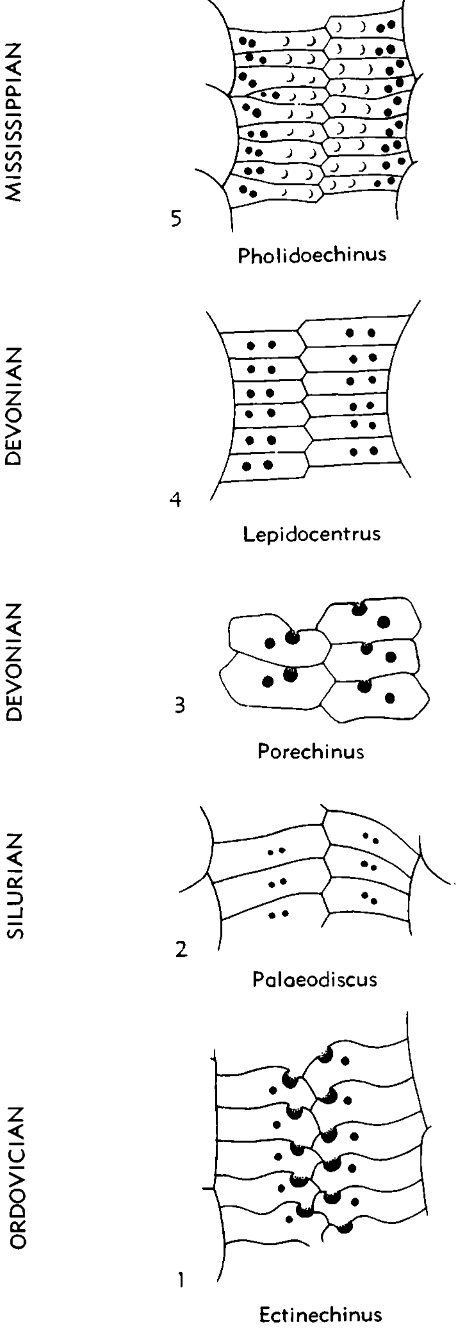


FIG. 219. View of portion of ambulacral areas showing shift of pores toward adradial suture (Kier, n).

WATER-VASCULAR SYSTEM

In Ordovician echinoids the radial water vessel is usually completely enclosed but in Silurian echinoids only the lower parts of the enclosure are still present. These remnants of the enclosures are absent in post-Mississippian species. Accordingly, loss of internal enclosure for the water-vascular system may be noted as an evolutionary trend in the noncidaroid Paleozoic echinoids.

PLATE COLUMNS IN AMBULACRA

The evolution of noncidaroid echinoids is marked by an increase in the number of ambulacral plate columns in all families having more than two columns in each ambulacrum. All Ordovician species have only two columns, but the Late Silurian *Echinocystites* and Early Devonian *Rhenechinus* have four. Among the Mississippian echinocystitids no species has fewer than six columns. In the Palaechinidae, the number of columns increased from two in *Palaechinus* to more than ten in *Melonechinus.* The increase in number of ambulacral columns enlarged the number of tube feet, and presumably it was advantageous to have more tube feet to aid in locomotion, food gathering, and respiration.

INTERAMBULACRAL PLATES

Earliest echinoids (e.g., *Aulechinus*) had irregularly arranged interambulacral plates, with no perceptible disposition in columns. Also, each plate was irregular in outline. By Late Silurian time the plates had become regularly arranged in some genera (e.g., *Myriastiches*), though they remained irregular in others (e.g., *Echinocystites*). All Devonian genera, except *Albertechinus,* have regular columns, and after the Devonian all genera have regular columns.

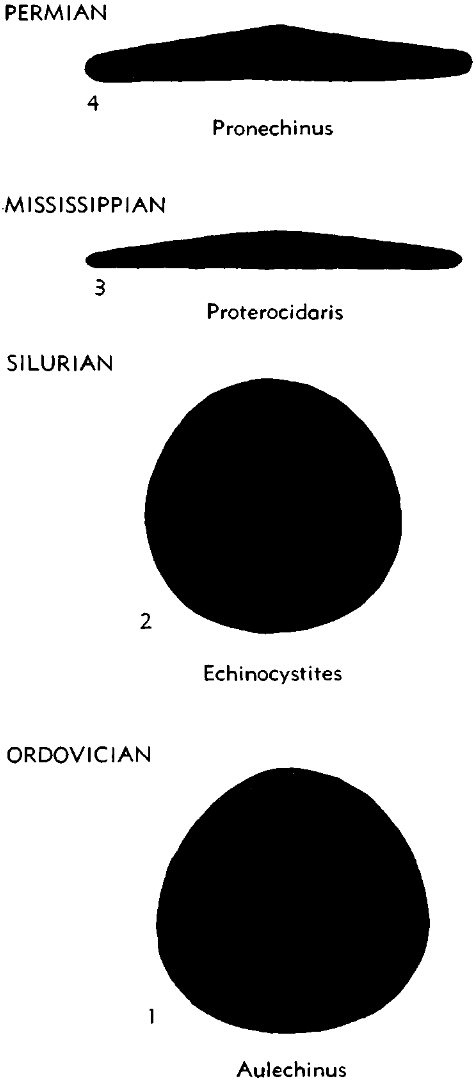


Fig. 220. Lateral profiles of four representative genera of the Echinocystitoida showing trend toward flattening of test (Kier, n).

FLATTENING OF TEST IN ECHINOCYSTITOIDA

In earliest genera (e.g., *Aulechinus,* Fig. 220,*1*; *Echinocystites,* Fig. 220,*2*) the test was high, but by the Mississippian it was low in some genera (e.g., *Proterocidaris,* Fig. 220,*3*). In both genera introduced in the Permian (*Pronechinus*, Fig. 220,*4*, and *Meekechinus*), the test was very flattened.

NUMBER OF THECAL PLATES

The number of plates in echinoid tests increased during geologic time. Ordovician genera have relatively few plates, not more than 1,000 in a single specimen, but by Silurian time 1,500 plates were present in *Echinocystites,* and by the Mississippian some specimens had as many as 3,650 plates.

SIZE OF THECA

The noncidaroid echinoids increased in size throughout Paleozoic time. Ordovician genera are all small, Silurian and Devonian genera larger, and finally in the Mississippian, echinoids reached their maximum size.

COMPLEXITY OF LANTERN

Braces, compasses, and epiphyses are absent in Ordovician echinoid genera, but by

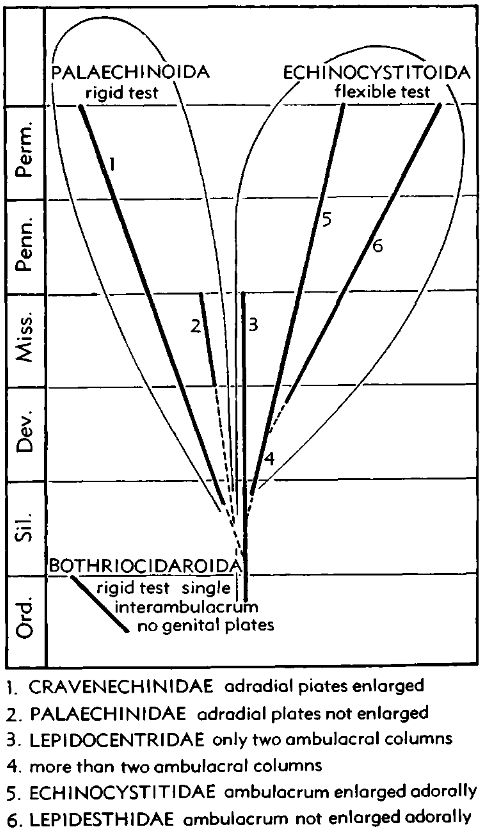


Fig. 221. Phylogeny of noncidaroid Paleozic echinoids (Kier, n).

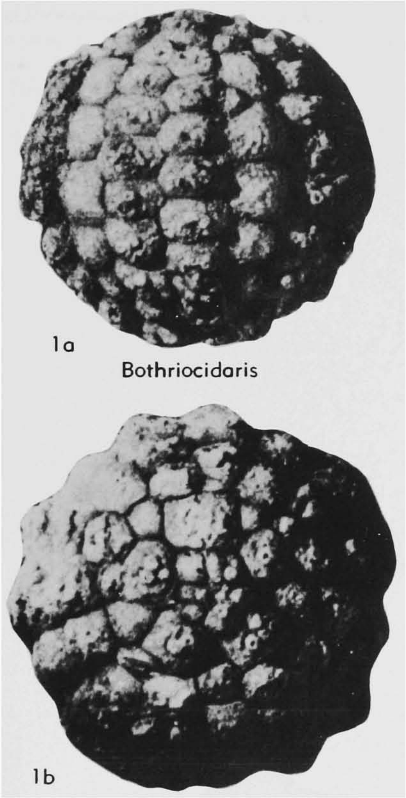


Fig. 222. Bothriocidaridae (p. *U*301).

Silurian time they were present in some species. Thus, complexity in structure of the lantern increased in the course of evolution.

COMPLEXITY OF SPINES

Among Ordovician echinoids the spines were small, undifferentiated, and situated in pits with no tubercles. By the Late Silurian, the spines were differentiated in types, and tubercles usually were present.

PHYLOGENY

The phylogeny of the noncidaroid Paleozoic echinoids (Fig. 221) has been described at the generic level by Kier (99).

Order BOTHRIOCIDAROIDA
Zittel, 1879

Plates of test thick, not imbricating; ambulacrum with 2 columns, terminating in single nonporiferous plate; interambulacrum with single column not reaching margin of peristome; no genital plates, 5 oculars, one being madreporite. *Ord.*

Family BOTHRIOCIDARIDAE Klem, 1904

Characters of order. *Ord.*

Bothriocidaris Eichwald, 1859, p. 654 [**B. globulus*; SD Lambert & Thiéry, 1910]. Characters of order. *Ord.*, Eng.——Fig. 222,*1*. **B. globulus*; *1a,b,* lat. and oral views, ×3, ×3.5 (138).

Order ECHINOCYSTITOIDA
Jackson, 1912

Plates strongly imbricate, ambulacral plates bevel under interambulacra, imbricate adorally, interambulacral plates imbricate adapically; interambulacra reaching peristome; genital plates; no perignathic girdle. *Ord.-Perm.*

Family ECHINOCYSTITIDAE Gregory, 1897

[Echinocystitidae Gregory, 1897, p. 133]

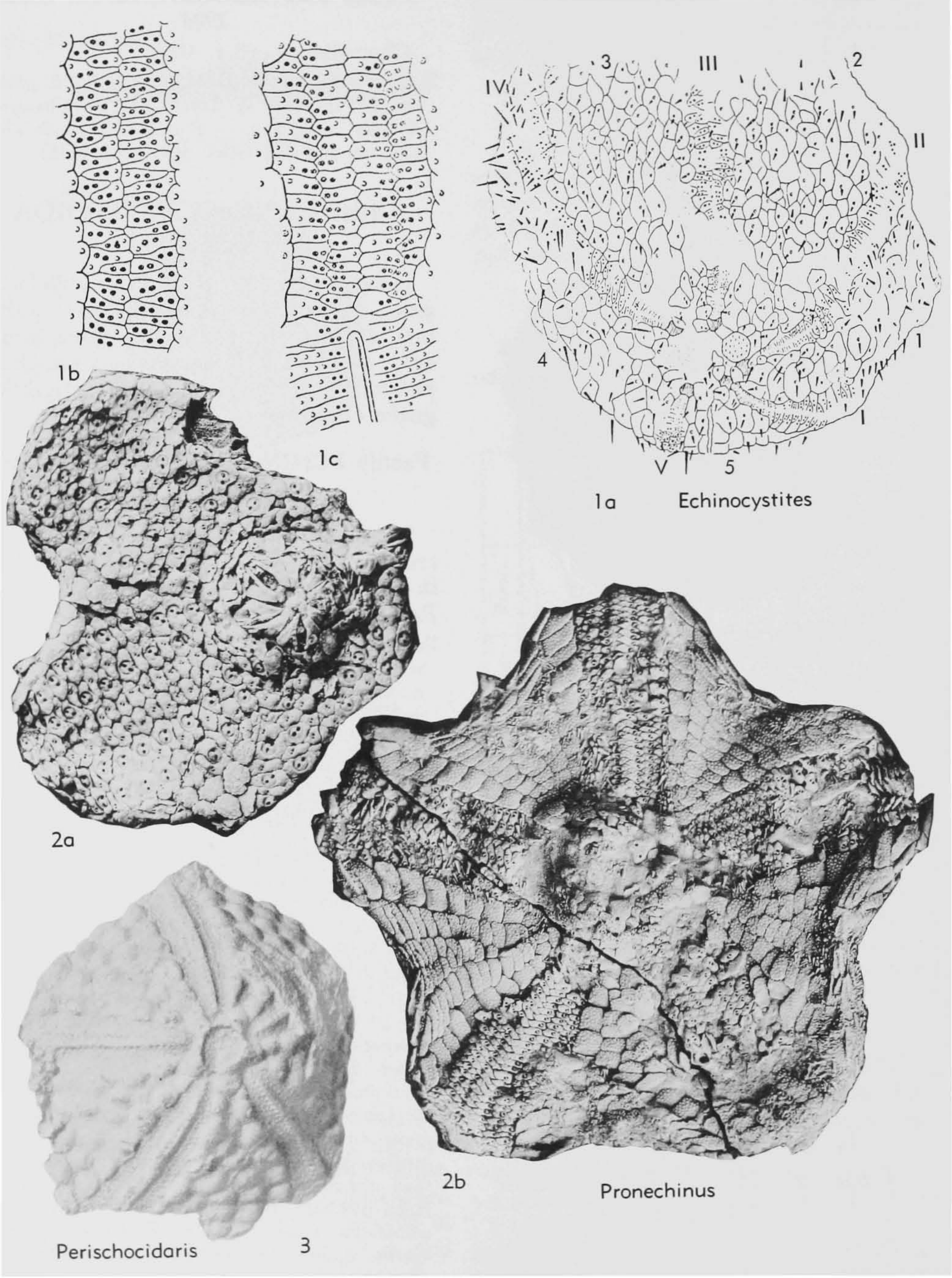
More than two columns in each ambulacrum, ambulacral plates enlarged adorally in all Mississippian and later genera. *Sil.-Perm.*

Echinocystites Thomson, 1861, p. 106 [**E. pomum*; SD Gregory, 1897, p. 133] [=*Cystocidaris* Zittel, 1879, p. 480 (obj.)]. Plates very imbricate; ambulacrum adorally with 4 columns, adapically occluded plates alternate with primaries; interambulacrum with many irregular columns, small perforate primary tubercle on each plate. *Sil.*, Eng. ——Fig. 223,*1*. **E. pomum*; *1a,* apical part of test, ×2; *1b,c,* ambs, ×4 (83). [=*Echinocystis* Gregory, 1897, p. 124 *(nom. van.)*.]

Pronechinus Kier, 1965, p. 00 [**P. anatoliensis*; OD]. Outer columns of adoral ambulacra with large plates with peripodia alternating with small plates without peripodia; median columns composed of small plates. *Perm.*, Turkey.——Fig. 223, *2*. **P. anatoliensis*; *2a,b,* part of oral surface showing lantern, aboral surface, ×1.3 (Kier, n).

Perischocidaris Neumayr, 1881, p. 174 [**Archaeocidaris harteiana* Bailey, 1874, p. 42; OD, M] [=*Prosechinus* Pomel, 1883, p. 113 (obj.); *Homotoechus* Sollas, 1892, p. 152 (obj.)]. Ambulacrum with 6 columns (in only known species), median columns elevated; interambulacra wider than ambulacra, with 5 columns in each area; large, perforate, primary tubercles on some interambulacral plates; amount of imbrication not known. *L.Carb.*, Ire.——Fig. 223,*3*. **P. harteiana* (Bailey); aboral surface, ×0.7 (87).

Proterocidaris DE KONINCK, 1882, p. 514 [**P. giganteus*; OD, M] [=*Fournierechinus* JACKSON, 1929, p. 67 (type, *F. deneensis*); ?*Jacksonechinus* LAMBERT, 1936, p. 39 (type, *J. andrewi* LAMBERT, 1936, p. 39); *Eupholidocidaris* KIER, 1956, p. 15 (type, *E. brightoni*)]. Low, large ambulacra and interambulacra with more than 2 columns; adorally ambulacra much more developed; plates of equal size; small perforate primary tubercles on some interambulacral and ambulacral plates. *Miss.*-



Penn., N.Am.-Eu.-?N.Afr.(Egypt).——FIG. 224,*1*. **P. giganteus,* L.Carb., Belg.; *1a,b,* aboral and oral faces, ×0.25, ×0.29 (97).

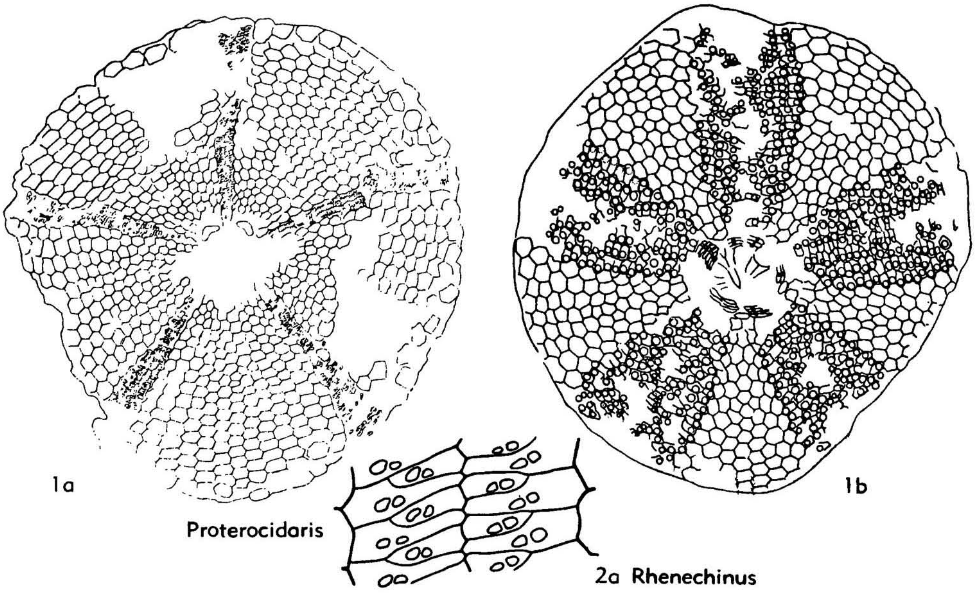
Rhenechinus DEHM, 1953 [**R. hopstatteri*; OD]. Ambulacrum with 4 columns, occluded plates alternating with primaries; interambulacrum with many regular columns. *Dev.,* Ger.——FIG. 224,*2*. **R. hopstatteri*; *2a,* part of amb, ×2.5; *2b,* part of oral surface, ×1 (42).

Family LEPIDESTHIDAE Jackson, 1896

[Lepidesthidae JACKSON, 1896, p. 206]

More than 2 columns in each ambulacrum, ambulacral plates not enlarged adorally. *Dev.-Perm.*

Lepidesthes MEEK & WORTHEN, 1868, p. 522 [**L. coreyi*; OD, M] [=*Hybochinus* WORTHEN & MILLER, 1883, p. 331 (type, *H. spectabilis*)]. Test



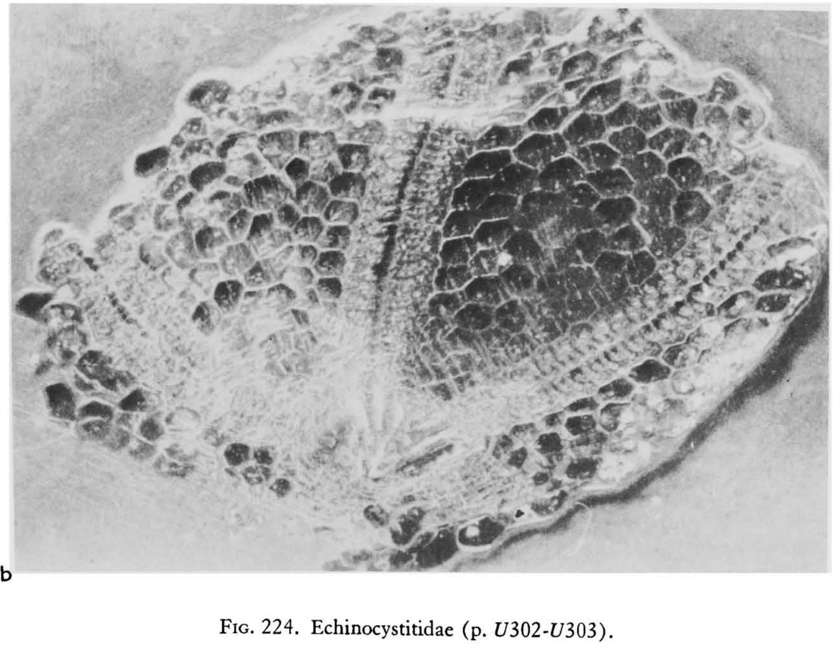
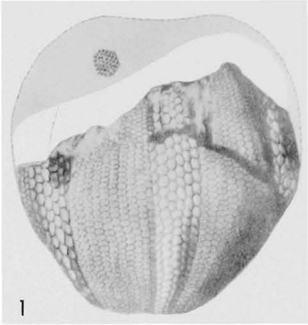
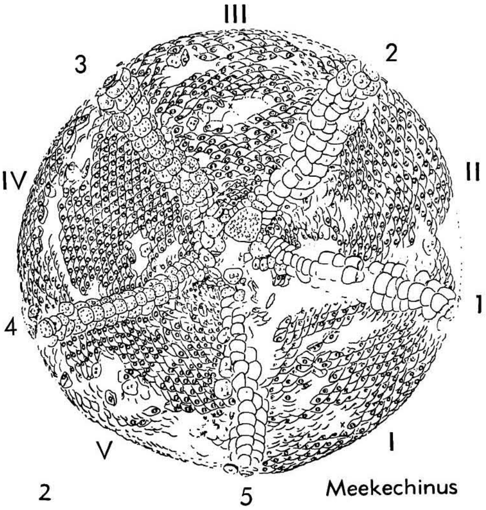


FIG. 224. Echinocystitidae (p. *U*302-*U*303).



Lepidesthes



Meekechinus

FIG. 225. Lepidesthidae (p. U303-U304).

high, plates strongly imbricate, ambulacra with many columns; interambulacra with few; ambulacra wider at mid-zone than interambulacra; no primary tubercles. *Dev.-Penn.*, Eu.-USSR-N. Am.-N.Afr.——FIG. 225,*1*. **L. coreyi,* Miss., USA (Ind.); lat. view, interamb. column central, ×0.8 (87).

Meekechinus JACKSON, 1912, p. 442 [**M. elegans*; OD]. Plates strongly imbricate; ambulacra with many columns; interambulacra with few; ambulacra much wider at mid-zone; small perforate primary tubercle on ambulacral and interambulacral plates; teeth serrated. *Perm.*, USA(Kans.).——FIG. 225,*2*. **M. elegans*; aboral view, ×1.5 (87).

Family LEPIDOCENTRIDAE Lovén, 1874

[Lepidocentridae LOVÉN, 1874, p. 39]

Only 2 columns of plates in each ambulacrum. *Ord.-Miss.*

Lepidocentrus MÜLLER, 1857, p. 258 [**L. eifelianus*; OD, M]. Pore pairs uniserial, all in contact with interambulacrum, adoral plates similar to adapical; interambulacrum wide, with many regular columns; small perforate primary tubercles on most of interambulacral plates. *Dev.-Miss.*, Eu.-N.Am.——FIG. 226,*3*. *L. mülleri* SCHULTZE, Dev., Ger.; lat. view, part of test showing amb and 2 interambs, ×1 (87).

Albertechinus STEARN, 1956, p. 741 [**A. montanus*; OD]. Ambulacra narrow, plates low, pore pairs uniserial, radial vessel almost isolated from interior by internal processes; interambulacra with many irregularly arranged plates; large primary tubercle on some interambulacral plates. *Dev.*, Can.——FIG. 226,*4*. **A. montanus*; part of crushed surface showing narrow amb and adjoining interambs, ×1 (156).

Aulechinus BATHER & SPENCER, 1934, p. 558 [**A. grayae*; OD]. Plates of test strongly imbricate, ambulacrum with deep median groove, radial vessel internally enclosed; ambulacral plates overlapping perradially, not fused; podial pores large, single or incompletely divided, notched; interambulacrum with numerous irregularly arranged plates; no primary tubercles. *Ord.*, Eng.——FIG. 226,*2*. **A. grayae*; lat. view, summit above (*M*, madreporite), ×2 (130).

Deneechinus JACKSON, 1929, p. 22 [**D. tenuisponus*; OD]. Test large, low; interambulacrum with many columns; each plate with several small perforate primary tubercles. *L.Carb.*, Belg.

Ectinechinus MACBRIDE & SPENCER, 1938, p. 95 [**E. lamonti*; OD]. Test elongated, plates strongly imbricate; ambulacrum with no median groove, radial vessel internally enclosed; podial pores double or incompletely divided; ambulacral plates overlapping perradially, not fused; interambulacrum with numerous irregularly arranged plates; no primary tubercles. *Ord.*, Eng.——FIG. 226,*1*. **E. lamonti*; lat. view, summit above, ×2 (130).

Eothuria MACBRIDE & SPENCER, 1938, p. 95 [**E. beggi*; OD]. Elongate test; plates strongly imbricated, ambulacrum curved, perradial groove slight or absent, radial vessel not internally enclosed, ambulacral plates overlapping perradially, not fused, each pore with many openings; interambulacrum with numerous more or less irregularly arranged plates; no primary tubercles; jaws reduced or absent. *Ord.*, Scot.(Girvan).——FIG. 226,*5*. **E. beggi*; *5a,* oblique lat. view showing apical disc; *5b,* similar view showing peristome, ×2 (130).

[MACBRIDE & SPENCER considered *Eothuria* to be a holothurian and not an echinoid. However, it has so many characters similar to *Aulechinus* and *Ectinechinus*, such as similar ambulacral and interambulacral plate arrangement with the same imbrication, and presence of a single genital plate, that it is here considered classifiable as an echinoid. It differs only from other echinoids in having many pores in each ambulacral plate, in having no oculars, and in having valvelike plates at the mouth in place of 5 teeth. It appears to be an offshoot from the *Aulechinus* and *Ectinechinus* line.]

Hyattechinus JACKSON, 1912, p. 291 [**H. beecheri*; OD]. Test low; ambulacra adorally wide, with

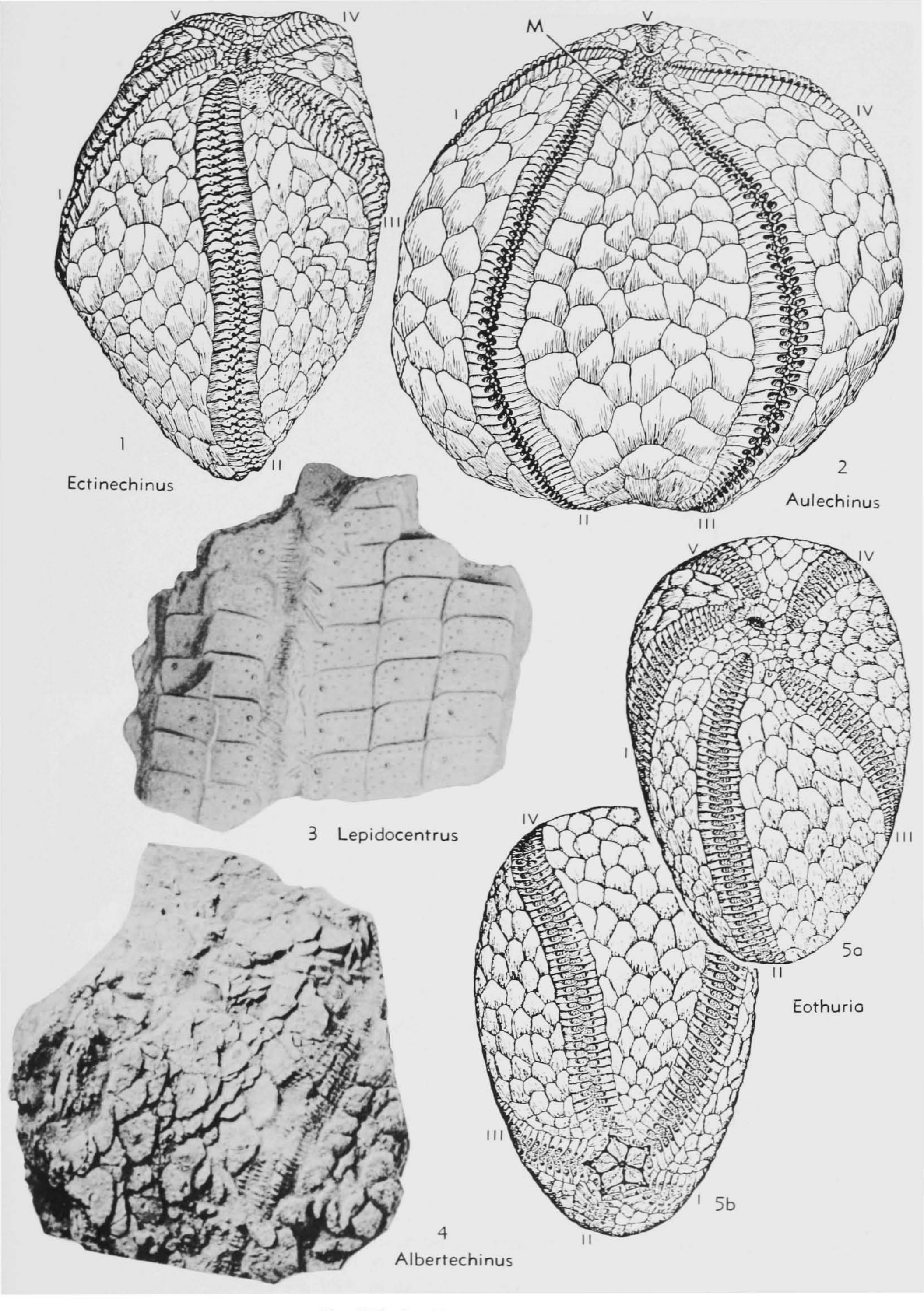


FIG. 226. Lepidocentridae (p. *U*304).

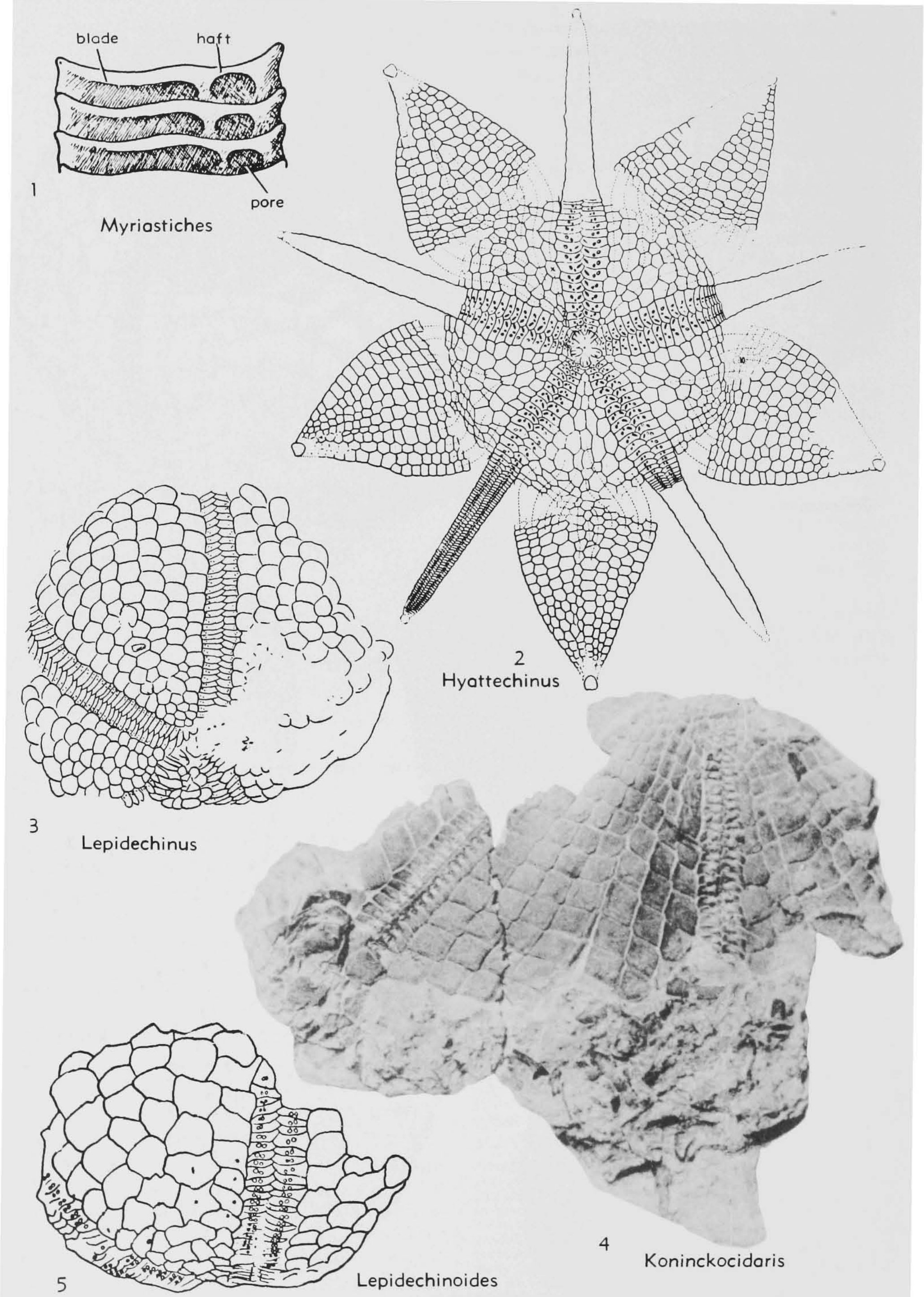
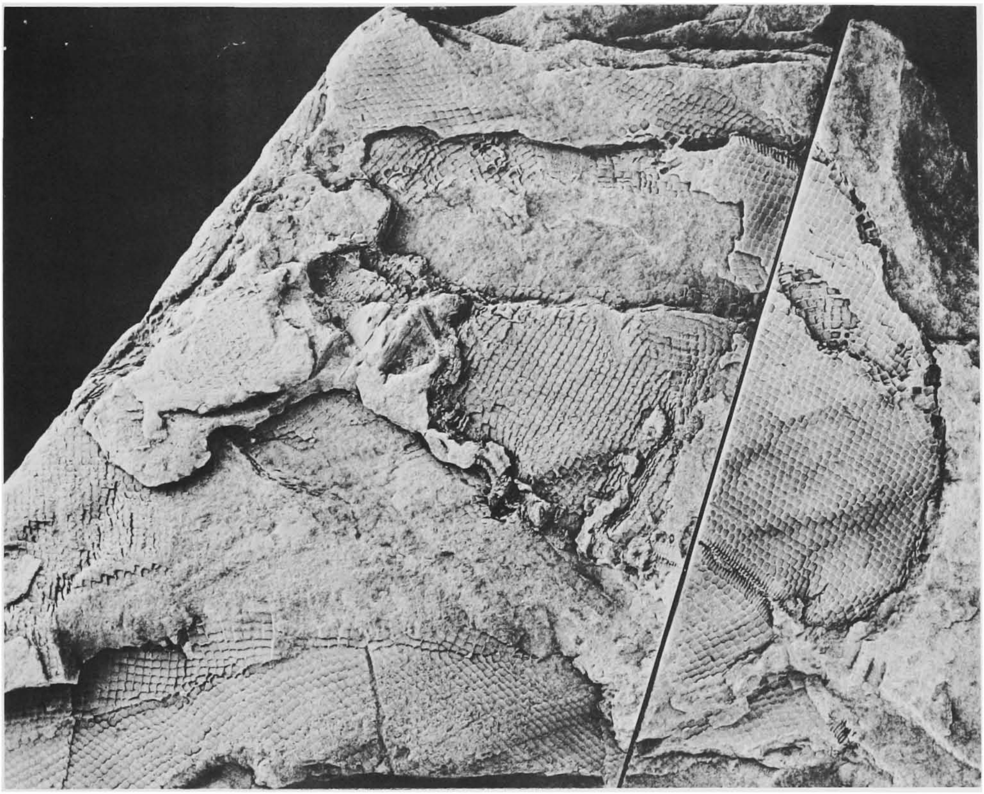


FIG. 227. Lepidocentridae (p. *U*304, *U*307).



1 Myriastiches

FIG. 228. Lepidocentridae (p. U307).

large peripodia, adapically narrow without peripodia; internal spinose processes on adoral ambulacral plates; interambulacrum with many columns, small perforate tubercles on some interambulacral plates. *L.Carb.(Miss.),* Eu.-N.Am.——FIG. 227,*2*. **H. beecheri*, USA(Pa.); plate diagram extending from centrally placed peristome, ×5.5 (87).

Koninckocidaris DOLLO & BUISSERET, 1888, p. 959 [**K. cotteaui*; SD, M]. Ambulacrum with high plates, pore pairs uniserial, internal ridge along perradial suture; interambulacrum with many regular columns; no primary tubercles. *Sil., ?L. Carb.,* N.Am.-?Eu.——FIG. 227,*4*. *K. silurica* JACKSON, Sil., USA(N.Y.); aboral part of test showing broad interambs and narrow ambs, ×1 (87).

Lepidechinoides OLSSON, 1912, p. 442 [**L. ithacensis*; SD, M]. Adoral plates similar to adapical; internally ambulacral plates opposite horizontal ambulacral sutures expanded laterally, fan-shaped; internal spinose processes on adoral portion of ambulacrum; interambulacrum with many columns; no primary tubercles. *Dev.,* N.Am.——FIG. 227,*5*. **L. ithacensis,* USA(N.Y.); adoral part of test showing wide interambs and narrow ambs, ×2 (25).

Lepidechinus HALL, 1861, p. 18 [**L. imbricatus*; OD, M] [=*Rhoechinus* KEEPING, 1876, p. 37 (type, *R. irregularis*)]. Adoral ambulacral plates similar to adapical; interambulacrum wide with many columns; only secondary tubercles. *Miss.,* N.Am.-Eu.——FIG. 227,*3*. **L. imbricatus,* Miss., USA(Iowa); adoral part of test, oblique view, ×1.9 (87).

Myriastiches SOLLAS, 1899, p. 700 [**M. gigas*; OD]. Pore pairs uniserial, near perradial suture, through plates; ambulacral, interambulacral plates small; interambulacrum with many small plates in regular columns (more than 32 in type-species); small spines, no tubercles. *Sil.,* Eng.——FIG. 227,*1*; 228, *1*. * *M. gigas*; 227,*1*, part of amb, ×18 (130); 228,*1*, part of oral surface, ×0.65 (Kier, n).

Palaeodiscus SALTER, 1857, p. 332 [**P. ferox*; OD, M]. Test very flexible; ambulacrum with external median groove, internal processes present but not covering radial canal, pore pairs uniserial, piercing ambulacral plates; interambulacrum with many regular columns; no primary tubercles. *Sil.,*

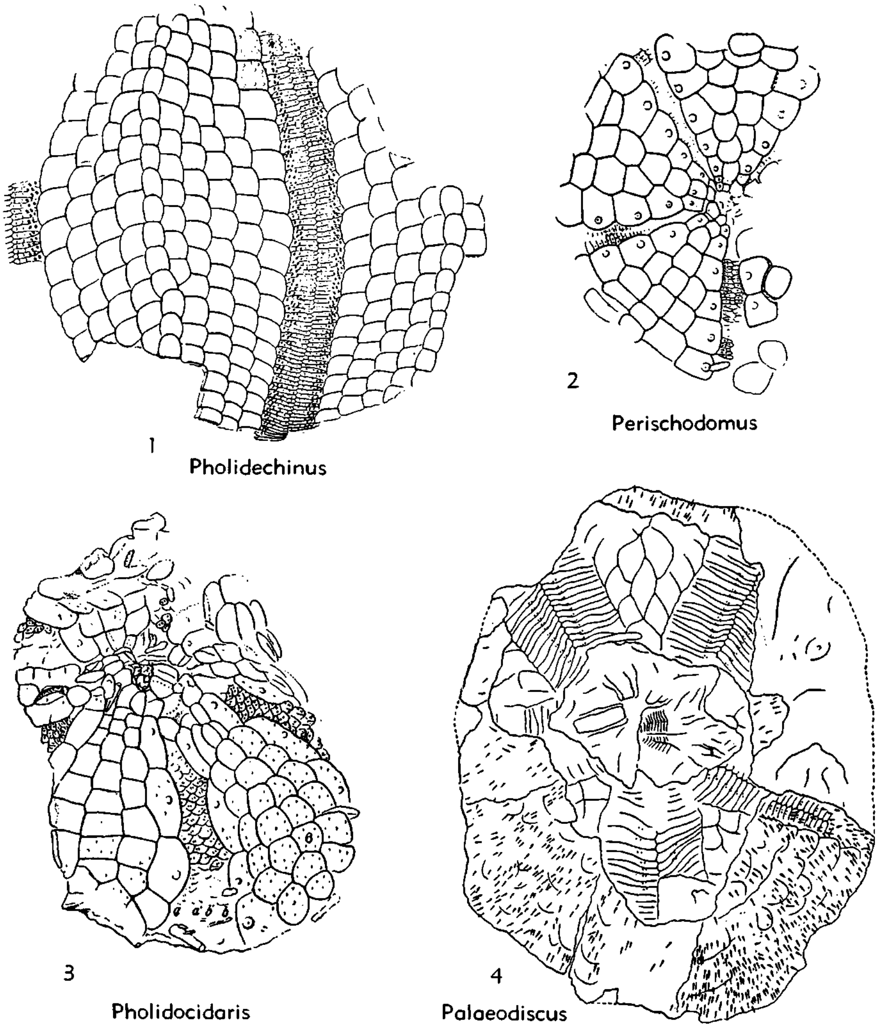


Fig. 229. Lepidocentridae (p. *U*307-*U*309).

Eng.——Fig. 229,*4*. **P. ferox;* peristomial region, ×2 (83).

Perischodomus M'Coy, 1849, p. 253 [**P. biserialis*; OD, M] [=*Tretechinus* Tornquist, 1897, p. 784 (type, *Perischodomus illinoisensis* Worthen & Miller, 1883, p. 333)]. Pore pairs biserial at ambitus, where some of ambulacral plates not in contact with interambulacra; adoral plates larger than adapical; interambulacrum wide with many columns; primary perforate tubercle on some interambulacral plates. *L.Carb.(Miss.),* Eu.-N.Am. ——Fig. 229,*2*. **P. biserialis,* Ire.; aboral surface, ×0.95 (87).

Pholidechinus Jackson, 1912, p. 299 [**P. brauni*; OD]. Adoral ambulacral plates similar in size to adapical, low; pore pairs uniserial to slightly biserial; interambulacrum with many regular columns; no primary tubercles. *Miss.,* USA(Ind.). ——Fig. 229,*1*. **P. brauni*; lat. view showing wide interambs and narrow ambs, ×1.05 (87).

Pholidocidaris Meek & Worthen, 1869, p. 78 (*nom. conserv.* ICZN, 1955) [**Lepidocentrus irregularis* Meek & Worthen, 1869, p. 78] [=*Protoechinus* Austin, 1860, p. 446 (type, *P. anceps*); *?Protocidaris* Whidborne, 1898, p. 202 (type, *Eocidaris? acuaria* Whidborne, 1896, p. 376)]. Ambulacra adorally much more developed; adapically adambulacral plates much larger than other interambulacral plates; adorally all interambulacral plates of same size; large perforate primary tubercle on adapical adambulacral and all adoral interambulacral plates; secondary tubercle on other plates. *?Dev., L.Carb.(Miss.),* Eu.-N.Am.——Fig. 229,*3*. **P. irregularis* (Meek

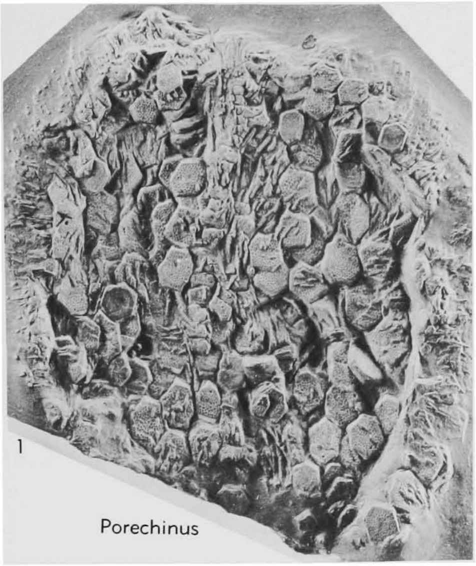


FIG. 230. Lepidocentridae (p. *U*309).

& Worthen), Miss., USA(Ind.); oblique view of apical region, ×0.9 (87).

Porechinus Dehm, 1961, p. 4 [**P. porosus*; OD]. Pore pairs uniserial, oblique, situated near middle of plate; inner pore of pair on edge of plate, not closed; interambulacrum with many columns; no primary tubercles. *Dev.*, Ger.——Fig. 230,*1*. **P. porosus*, interamb near summit, ambs at left and right, ×1 (Kier, n).

FAMILY UNCERTAIN

Devonocidaris Thomas, 1920, p. 212 [**D. jacksoni* Thomas, 1924, p. 500; SM Thomas, 1924]. Plates thin; perforate primary tubercle on interambulacral and larger ambulacral plates; teeth with median furrow on outer side. *Dev.*, Eu.-N.Am.

Tornquistellus Berg, 1899, p. 77 [**Leptechinus gracilis* Tornquist, 1897, p. 785] [=*Leptechinus* Tornquist, 1897, p. 785 (obj.) (*non Leptechinus* Gauthier, 1869)]. Known only from isolated interambulacral plates, thin, flat, wider than high, secondary tubercles. *Dev.*, Ger.

Order PALAECHINOIDA Haeckel, 1866

Plates not strongly imbricate, ambulacral plates bevel over interambulacra; interambulacrum of one or more than 2 columns; no perignathic girdle. *Sil.-Perm.*

Family PALAECHINIDAE M'Coy, 1849

[Palaechinidae M'Coy, 1849, p. 253] [=Palaeechinidae Jackson, 1912, p. 302]

Enlarged adradial ambulacral plates; interambulacrum with more than 2 columns; imperforate tubercles. *Miss.*

Palaechinus M'Coy, 1844, p. 172 [**P. ellipticus*; SD Lambert & Thiéry, 1910, p. 119] [=*Palechinus* Scouler in Griffith, 1840 (*nom. nud.*); *Palechtinus* Fischer de Waldheim, 1848, p. 247 (*nom. null.*); *Palaeechinus* Lovén, 1874, p. 40 (*nom. van.*)]. Ambulacrum with 2 columns of plates, pore pairs uniserial to slightly biserial. *L.Carb.(Miss.)*, Eu.-N.Am.——Fig. 231,*1*. *P. canadensis* Kier, Miss., Can.; *1a*, lat. view showing interamb, ×1; *1b*, apical region, ×1; *1c*, apical disc, ×5; *1d*, amb, ×4 (92).

Lovenechinus Jackson, 1912, p. 324 [*nom. conserv.* ICZN, 1955] [**Oligoporus missouriensis* Jackson, 1896, p. 184; OD] [=*Eriechinus* Pomel, 1883, p. 114 (type, *Palaechinus sphaericus* M'Coy, 1844, p. 172); *Typhlechinus* Neumayr, 1889, p. 363 (type, *Palaechinus sphaericus* M'Coy, 1844, p. 172)]. Ambulacrum with 4 columns of plates, consisting of 2 columns of narrow demiplates, 2 columns of wider occluded plates; pore pairs biserial. *L. Carb. (Miss.)*, Eu.-N. Am.-China.——Fig. 232,*1*. **L. missouriensis* (Jackson), USA (Mo.); *1a*, aboral view of int. mold, ×0.5; *1b*, amb and interamb plates, ×1.3 (87).

Maccoya Pomel, 1869, p. 46 [**Palaechinus gigas* M'Coy, 1844; OD]. Ambulacrum with 2 columns of plates, all in contact at median suture, at adradial suture every other plate nearly excluded from contact with interambulacra; pore pairs biserial. *L.Carb.(Miss.)*, Eu.-N.Am.——Fig. 231, *2*. *M. sphaerica* (M'Coy), Ire.; *2a*, oblique aboral view of test, ×1.2; *2b*, amb and interamb plates, ×2.6 (87).

Melonechinus Meek & Worthen, 1861, p. 396 [**Melonites multipora* Owen & Norwood, 1846, p. 225; OD] [=*Melonites* Norwood & Owen, 1846, p. 225 (*non* Lamarck, 1822, p. 615); *Melechinus* Quenstedt, 1875, p. 381 (obj.); *?Donbassechinus* Faas, 1941, p. 73 (type, *D. kumpani*)]. Ambulacrum with more than 4 columns of plates, consisting of 2 columns of narrow demiplates, 2 columns of wider occluded plates, and in addition one or more irregular columns of isolated plates between demi- and occluded plates; pore pairs multiserial. *L.Carb.(Miss.)*, Eu.-N.Am.-USSR-China.——Fig. 231,*3*; 232,*2*. **M. multiporus* (Owen & Norwood), USA(Mo.); 231,*3*, amb with bordering rows of interamb plates, ×2.3; 232,*2*, aboral view of test, ×1 (87).

Oligoporus Meek & Worthen, 1862, p. 472 [**Melonites danae* Meek & Worthen, 1861, p. 397; OD, M] [=*Melonopsis* Meek & Worthen, 1866, p. 249 (obj.)]. Ambulacrum with 4 columns of plates, consisting of 2 columns of wider occluded plates, and in addition scattered isolated plates in middle line of each half area; pore pairs multiserial. *Miss.*, N.Am.——Fig. 233,*1*. **O. danae* (Meek & Worthen), USA(Iowa); amb with bordering interamb plates at right, ×2.4 (87).

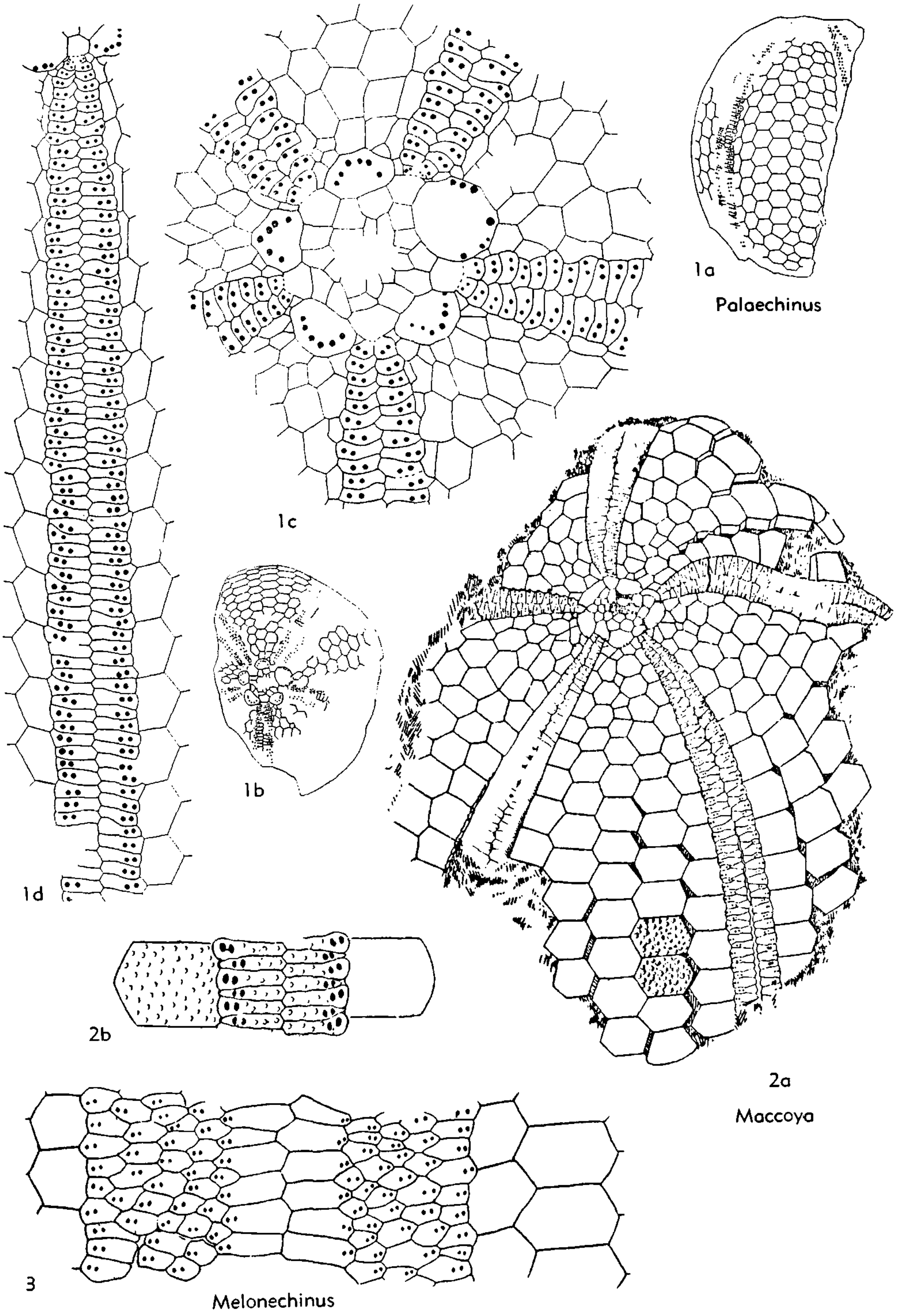


FIG. 231. Palaechinidae (p. U309).

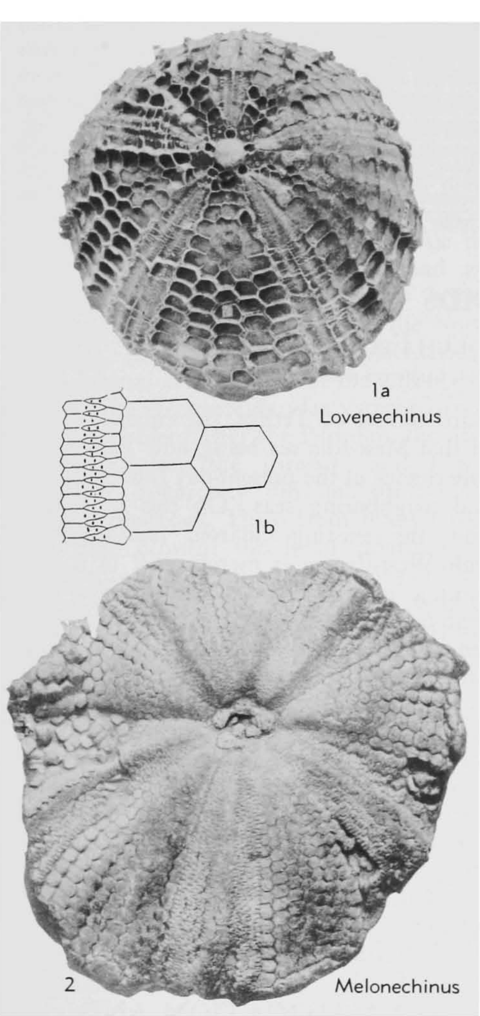


FIG. 232. Palaechinidae (p. *U*309).

Family CRAVENECHINIDAE Hawkins, 1946

[Cravenechinidae HAWKINS, 1946, p. 195]

Interambulacrum with one or 4 columns; adradial ambulacral plates enlarged; small perforate or imperforate primary tubercles on ambulacral and interambulacral plates. *Sil.-Perm.*

Cravenechinus HAWKINS, 1946, p. 195 [**C. uniserialis*; OD]. Ambulacrum with 8 series of pore pairs; perforate primary tubercles. *L.Carb.*, Eng.——FIG. 234,*4*. **C. uniserialis*; part of amb column, ×2 (82).

Gotlandechinus REGNÉLL, 1956, p. 158 [**G. balticus*; OD]. Ambulacrum with 4 columns of plates,

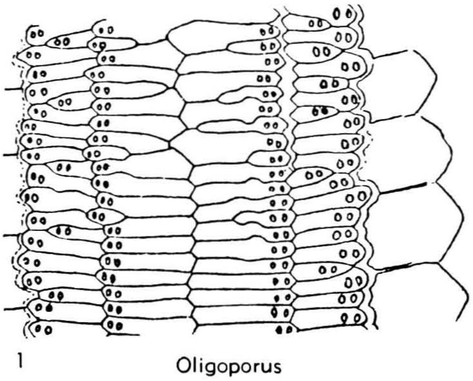


FIG. 233. Palaechinidae (p. *U*309).

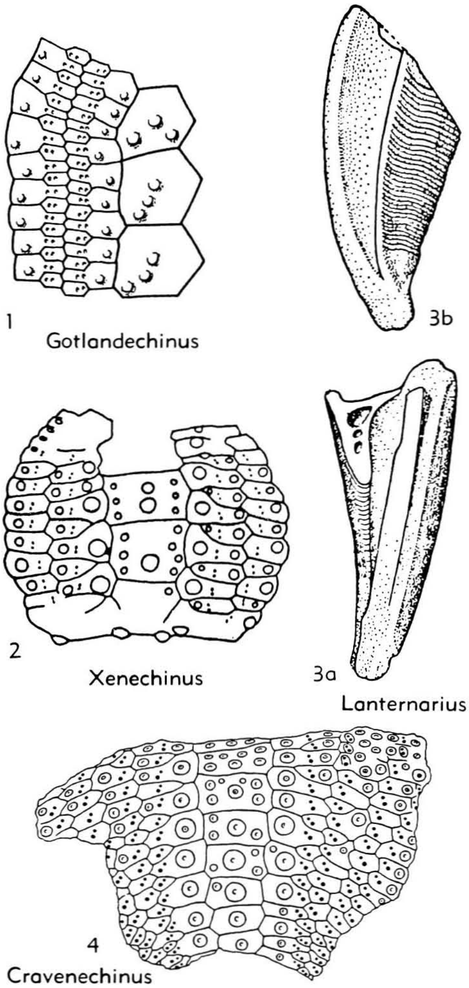


FIG. 234. Cravenechinidae *(1-2,4)*; Order and Family Uncertain *(3)* (p. *U*311-*U*312, *U*329).

pore pairs uniserial; 4 columns in each interambulacrum. *Sil.*, Sweden.——FIG. 234,*1*. **G. balticus*, Gotl.; amb column with interamb plates at right, ×2.5 (148).

Xenechinus KIER, 1958, p. 889 [**X. parvus*; OD]. Ambulacrum with 4 series of pore pairs; covered passageway on interior for radial vessel; imperforate primary tubercles. *Perm.*, USA(Tex.).——FIG. 234,*2*. **X. parvus*; interamb bordered by amb columns, ×8 (95).

FAMILY UNCERTAIN

Wrighthia *(sic)* POMEL, 1869, p. 46 [**Palechinus phillipsiae* FORBES, 1848; OD, M] [=*Wrightella* POMEL, 1883, p. 115 (obj.)]. Known only from one poorly described specimen showing portion of ambulacrum and interambulacrum. *?Sil.*, Eng.

Xysteria POMEL, 1883, p. 114 [**Palaechinus konigii* M'COY, 1844; OD, M]. Known only from few isolated interambulacral plates covered with secondary tubercles. *L.Carb.*, Ire.

CIDAROIDS

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INTRODUCTION

The cidaroids are the only surviving echinoids with authenticated Paleozoic representatives, and they are believed to be ancestral to all other surviving echinoids. They are here regarded as an order of the subclass Perischoechinoidea, the three extinct Paleozoic orders of which have already been treated in this volume. Cidaroids are of exceptional interest as archaic living echinoids with generalized morphological features.

To judge by their fossil abundance, cidaroids reached a peak of development in Mesozoic seas, and thereafter declined in Europe, the Mediterranean, and North America, playing only a minor role in the faunas of those regions after the Eocene. However, the group still flourishes in the Indo-West-Pacific, and another quite distinctive assemblage is conspicuous in the seas of Antarctica, where it apparently evolved in prolonged isolation.

Specimens of Indo-Pacific cidaroids were brought to Europe by travelers in the 17th and 18th centuries. These echinoids, by their exquisite symmetry and evident similarity to fossils, evoked the admiration of amateur naturalists, such as Queen LOUISA ULRIKA, of Sweden, whose cabinets were afterwards to be studied by LINNÉ and others.

The widespread extinction of northern cidaroid faunas, coupled with their survival in the Indo-West-Pacific regions, has long presented something of a mystery. However, it may well have been that the impoverishment of the Tertiary cidaroid fauna of Europe was the result of the southeastward retreat of Tethys, the cidaroid fauna of that Mesozoic sea being now part of the inheritance of the present-day Indian Ocean, and neighboring seas. On this interpretation, the existing cidaroid fauna of the Indo-West-Pacific is merely part of a continuing succession of Tethyan stocks and Tethys itself is simply a former northwestern extension of the Indian Ocean. The existing North Atlantic cidaroid fauna seems to be a late derivative of a small tropical Caribbean nucleus of genera derived from the Indo-Pacific. Whether or not the supposed recency of the Atlantic Ocean can be justified, such supposition offers a more reasonable interpretation of the changes in cidaroid faunas of North Atlantic regions than the earlier hypothesis of northern extinctions with simultaneous (and inexplicable) Indo-Pacific survivals.

CLASSIFICATION AND EVOLUTIONARY TRENDS

The oldest undoubted cidaroids are the Early Carboniferous Archaeocidaridae. These forms have a pluriserial structure of the interambulacra, a feature seen also in other Perischoechinoidea which were their precursors, and this structure doubtless was inherited from them. From these early cidaroids probably arose the family Miocidaridae, of which the oldest undoubted members are of Permian age (though a Carboniferous miocidarid seems to be represented by the incompletely known *"Miocidaris" cannoni* of North America). The Miocidaridae resemble the Archaeocidaridae in having a semiflexible test, in which the interambulacral plates overlap upon the ambulacra, but differ from them (and by the same token resemble modern cidaroids) in having biserial interambulacra. By late Triassic times the first representatives of the modern Cidaridae had appeared; these had a rigid test, but retained the simple uniserial arrangement of the ambulacral pores seen in the Miocidaridae and the perforate tubercles of the latter. By the Jurassic the other two families of cidaroids had appeared, the Psychocidaridae, with imperforate tubercles (still surviving in the North Pacific), and the extinct Diplocidaridae, with biserial arrangement of the ambulacral pores. The Archaeocidaridae vanished from the fossil record after the Permian, the Miocidaridae after the Jurassic, and Diplocidaridae apparently did not survive the Early Cretaceous. Thus, from mid-Cretaceous time onward the fossil cidaroids are represented only by families which still flourish today. Most cidaroids are now restricted to the tropics, especially of the Indo-West-Pacific region.

ECOLOGY

The structure of Paleozoic and early Mesozoic cidaroids parallels that of living forms sufficiently to imply that their ecology would not have differed materially from that of extant representatives of the order. The living forms are inactive echinoids, moving only slowly, mainly by using the large spines as levers or stilts. Shallow-water cidaroids hide during daylight hours in crevices or under stones. Large muscles occur at the base of the spines in one Antarctic genus *(Homalocidaris),* and it has been supposed that this implies a more active mode of progression (136a); recently, however, living specimens freshly dredged from the floor of the Ross Sea show that the animal, at least when lying on the ship's deck, scarcely moved the spines at all, and it is accordingly doubtful whether any cidaroid can move rapidly.

Cidaroids live at almost all depths, at least down to 4,000 m. Most species prefer hard bottom, such as reefs, and it is probable that short-spined forms, even in deeper offshore waters, contrive to make use of shell beds as temporary hard bottom. Forms with long slender spines seem to tolerate soft mud, and deep-sea cidaroids develop such spines. The shallow-water reef-dwelling genera do not conceal themselves by holding other objects over the test with the tube feet, as do other regular echinoids; this is because the tube feet of the aboral side have only vestigial or modified suctorial discs, serving as respiratory organs.

Cidaroids feed upon available bottom animals, including mollusks, tubicolous annelids, polyzoans, foraminifers, and sponges. Their teeth are strong enough to crush the hard parts of such organisms.

Development may be direct, the young stages being carried on the aboral side (e.g., *Austrocidaris,* see Fig. 241,*3*), or on the oral side (e.g., *Eurocidaris, Goniocidaris*); or indirect development, involving a pluteus larva, may occur, as described in the chapter on "Ontogeny" (*Treatise* Part S).

Various commensals, especially sponges, polyzoans, and cirripeds, may occur on the primary spines. Foraminifers and annelids occur among the secondary spines, and a holothuroid *(Taeniogyrus cidaris)* coils itself around the primary spines of *Stylocidaris.* Parasitic gastropods, and other parasites, occur either externally or as endoparasites. Remains of such organisms may be found with fossil cidaroids, or the evidence of their work may be apparent as borings in fossil cidaroid skeletal parts.

Certain genera of extant cidaroids (e.g., *Eucidaris, Phyllacanthus*) exhibit marked preference for seas in which the surface temperature does not go beyond definite limits throughout the year; among genera named their distribution at present falls within the winter isotherms for approximately 15° C. On the basis of such distribution patterns, estimates of Tertiary sea temperatures have been made, yielding results not inconsistent with other data (56).

MORPHOLOGY OF HARD PARTS

Cidaroids, in common with other echinoids, have a complex skeleton, the individual parts of which may exhibit specific or higher taxonomic characters, or both. In *Goniocidaris,* for example, there are at least 3,000 separate skeletal elements of some 60 different shapes and sizes, some with elab-

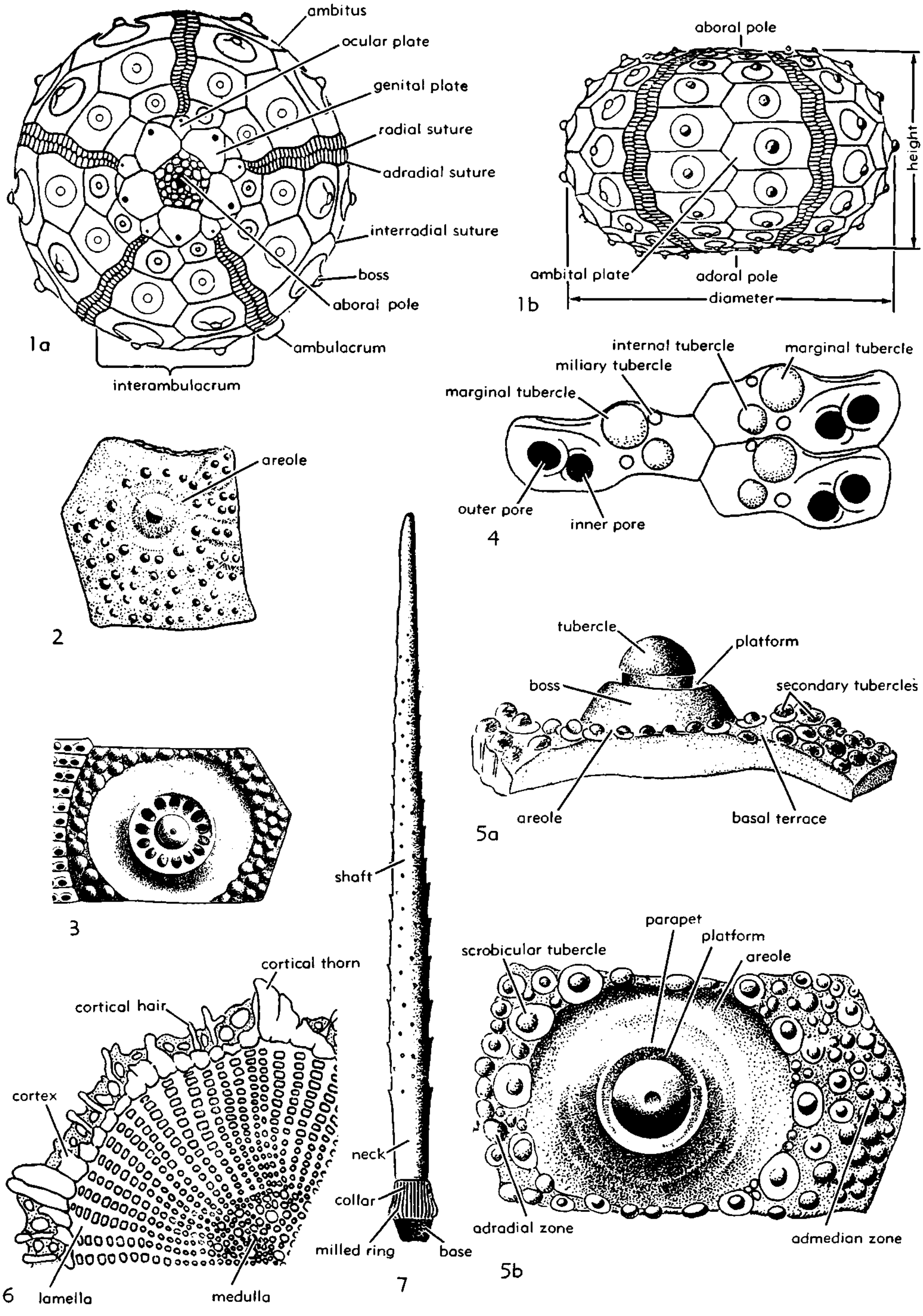

Fig. 235. Morphological features of cidaroid echinoids (Fell, n).——*1a,b.* Aboral and lateral views of test.——*2,3.* Interambulacral plates.——*4.* Part of ambulacrum.——*5a,b.* Side and external views of interambulacral plate.——*6.* Part of cross section of spine, enl.——*7.* Side view of spine.

orate microscopic detail. Of these, only 600, at most, would normally be of any paleontological significance—that is, several associated plates or rarely a single plate or spine sufficient to yield a generic or specific determination. In general, recognition is difficult from isolated skeletal pieces. Again, some forms cannot be placed in correct systematic position on the basis of the skeleton alone, even when complete, because pedicellariae are required to yield a final determination; fortunately, not many cidaroid genera are so difficult to identify, though it is probable that many fossil genera would be subdivided if adequate information on the nature of their pedicellariae or larvae was available. Although pedicellariae are occasionally found on fossils, as a rule, the only parts of the cidaroid skeleton of value in paleontology are whole or partial tests, ambulacral and interambulacral plates, and primary spines. These structures are briefly explained in the following paragraphs, illustrated by Figure 235.

The **test** (Fig. 235,*1a,b*) is the outer (though mesodermal) shell formed by vertical columns of plates. All Cenozoic genera have 20 columns of plates, but a larger number occur in some Paleozoic cidaroids (e.g., Archaeocidaridae, see Fig. 237), and in the Cretaceous genus *Tetracidaris* (see 254,*3*), such genera being termed **pluriserial.** A pluriserial condition occurs temporarily in the young stage of some living cidaroids, and fossils suggest that the pluriserial pattern is the original one for the order. The upper surface of the test is termed **aboral,** or adapical, and the lower surface **oral.** The major circumference of the test, always horizontal, is termed the **ambitus,** and the adjacent skeletal plates are called **ambital plates.** Thus the whole test may be thought of as a globe, in which the plates are arranged in vertical meridians, the ambitus forming the equator. Of the vertical series of plates, five double (or multiple) columns carry pores for tube feet, and are termed **ambulacra,** or in abbreviated form **ambs.** Five intervening double (or multiple) columns of plates, carrying large tubercles, are termed the **interambulacra,** or in short **interambs.**

The ambulacra (Fig. 235,*4*) are divisible into an outer **poriferous area,** and an inner, broader **interporiferous area.** The poriferous area is marked on each component amb plate by the presence of two similar pores, termed a **pore pair.** These correspond to the points of ingress and egress of ambulacral fluid circulating in the tube foot of the living animal; thus each pore pair corresponds to one tube foot. It is of systematic importance whether the pore pair is horizontally or obliquely placed, and whether the two pores are each provided with a distinct wall (**nonconjugate pores**), or united by a common depressed groove (**conjugate pores**). Nonconjugate pores are illustrated in Figure 235,*4*, conjugate pores are shown in Figure 247, *1e.* The interporiferous area carries various rounded **tubercles,** of which usually one on each plate is distinguished as a larger **marginal tubercle,** adjoining the pore pair. The vertical series of such marginal tubercles is termed the **marginal series;** it may be straight, or sinuous, as also the vertical series of pore pairs. The other tubercles are termed the inner tubercles. All tubercles, in life, carry small spines, distinguished as **ambulacral spines.** Very small **miliary tubercles** may also occur for the attachment of **pedicellariae,** which are small grasping or toilet organs of complex structure, but their paleontological significance is slight. A third pore may occur near the pore pair; this is for the emergence of the nerve supplying the tube foot and is termed the **neuropore.** A neuropore, if enlarged, may form a significant systematic character in some Antarctic genera, but it is not at present known in fossils.

Each interambulacral plate bears a single large prominence, the **boss** (Fig. 235,*2,3,5*). Surmounting the boss is a **platform** on which is placed a central rounded **tubercle** (or **mamelon**). The tubercle articulates with a hemispherical cup on the base of a large spine, called the **primary spine** (Fig. 235,*7*). In most cidaroids a central **perforation** on the tubercle provides in life for a strand of connective ligament which runs to a corresponding perforation in the cup of the spine. In the Psychocidaridae no perforation is seen on the tubercles (at least of the adoral hemisphere), such tubercles being termed **imperforate** (e.g., *Tylocidaris,* see Fig. 252,*3*). The platform is commonly surrounded by a low **parapet,** and its surface may be **crenulate** (e.g., *Histocidaris,* Fig. 235,*4*) or **noncrenulate** (e.g., *Goniocidaris,* Fig. 235,*5*). The boss is surrounded by a broad, saucer-shaped shallow depression, the **areole,** which is devoid of sculpture. The outer margin of the areole, usually somewhat more deeply depressed, is termed the **scrobicule.** It serves as the region for the origin of muscles which move the spine. Surrounding the scrobicule and situated at a higher level than the rest of the plate is a more or less continuous ring of smaller tubercles, the **scrobicular tubercles.** Each of these usually has a miniature areole, and in life it carries a small spine, the **scrobicular spine.** The rest of the plate is usually covered by many small tubercles termed **secondary tubercles** and **miliary tubercles.** In some genera the scrobicular ring of tubercles is incomplete above and below, so that the areoles of adjacent plates are **confluent** (e.g., *Rhabdocidaris,* see Fig. 245,*2*), whereas in other genera (e.g., *Stereocidaris,* see Fig. 242,*3*), the areoles are widely separated. Characters such as these aid identification of isolated plates of fossils. The genus *Dicyclocidaris* is peculiar in having an inner ring of tubercles within the areole (see Fig. 239,*2b*) and *Porocidaris* has radially placed slots in the same position (see Fig. 244,*2f*); these seem to be specialized features of the muscle-attachment surface.

Plates are separated by **sutures,** rigid in post-Triassic genera, but imbricated and evidently movable in earlier cidaroids, where the test must have been more or less flexible. The latter feature accounts for the dislocation of plates in *Archaeocidaris* (see Fig. 237,*3a*), for example, and to lesser extent in *Dicyclocidaris* (see Fig. 239,*2c*). Imbricating test plates occur in other perischoechinoid orders of the Paleozoic and are also seen in the extant orders Diadematoida and Echinothurioida, where the condition may well be an inheritance from Paleozoic ancestors, as inferred in the case of the Cidaroida.

The **spines,** or radioles, comprise the large **primary spines** carried by the **primary tubercles,** and smaller **secondary spines** carried on **secondary** (and **scrobicular**) **tubercles.** Usually only the former are of paleontological significance. The base of a primary spine articulates with the tubercle of its plate by means of the cup-shaped depression in its lower surface, termed the **acetabulum.** Spines carried on crenulate tubercles are correspondingly crenulate around the margin of the acetabulum (e.g., *Histocidaris,* see Fig. 240,*1f*). Above the base is a more or less conspicuous **milled ring** and **collar,** both of which are striated, to serve as attachments for muscles arising from the areole (Fig. 235,*7*). In some another distinct region occurs just beyond the collar, termed the **neck.** In all, the greater part of the spine is distinguished as the **shaft;** this may be cylindrical, flattened, fluted, smooth, or thorny; it usually tapers but it may expand into a blade, or into a hollow trumpet-like structure, or the whole organ may be modified into a cup or umbrella. These variations are often of value in narrowing the field of possible affinity of fossil fragments, as can be observed by studying the illustrations here given in the systematic section. The microscopic structure of spines is complex, and usually preserved in fossils, even when secondarily impregnated by mineral calcite. It is studied by transverse sections. At the center is the **medulla** (Fig. 235,*6*). Radiating from it are many fine vertical **lamellae** or septa, united to each other by intervening **trabeculae.** The whole structure forms a 3-dimensional mesh, the **stereom,** through which the living tissue (**stroma**) ramifies. Nearly always an outer, denser, zone is observed, the **cortex,** also of calcite, on which **flutings** or **cortical hairs** (of calcite) or other structures may develop; this is nonliving in the adult, and consequently epizoic animals can adhere to the spines of cidaroids. The microscopic detail of the transverse section often aids in identification of spines.

The usual zoological keys to the identification of cidaroids are difficult to apply to fossils, for the pedicellariae and other finer details are almost always lost. If, however, attention is paid to the sum total of available characters exhibited by spines, and amb and interamb plates, as given in the diagnoses which follow, many fossils can be classified in taxa which are unlikely to differ substantially from those used for living forms.

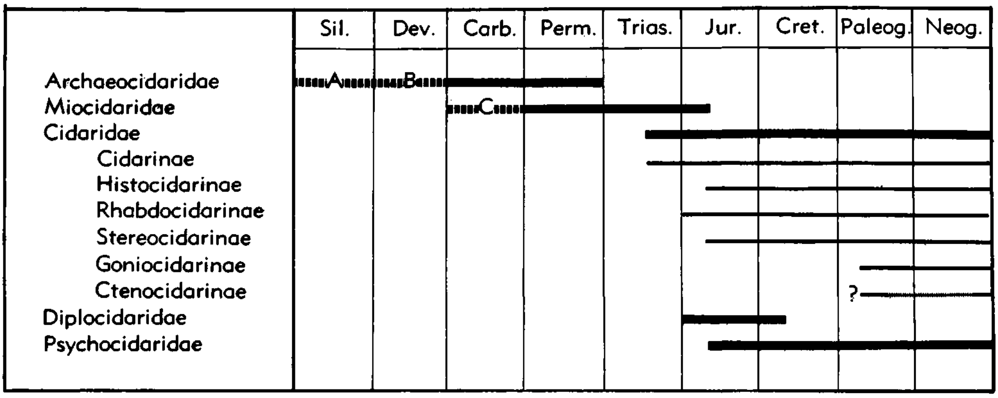

FIG. 236. Stratigraphic distribution of cidaroid family and subfamily assemblages. [*A* represents *Silurocidaris* only, archaeocidarid affinity uncertain; *B* represents *Nortonechinus* and *Xenocidaris*, archaeocidarid affinity uncertain; *C* represents *"Miocidaris" cannoni* JACKSON, miocidarid affinity very probable but genus uncertain.] (Fell, n.)

STRATIGRAPHICAL DISTRIBUTION

The known stratigraphical range of the families and subfamilies of Cidaroida is shown in Figure 236. Owing to the present inability to classify fossil genera on the basis of pedicellariae, the fossil genera are doubtless more inclusive than Recent ones, and would be more subdivided if their pedicellariae were available. It has therefore seemed undesirable to indicate the number of genera known for each family and subfamily by variation in the thickness of lines showing their time range, for such treatment of the data would probably be misleading. Accordingly, Figure 236 shows no more than the recorded time ranges.

Order CIDAROIDA Claus, 1880

[*nom. correct.* MORTENSEN, 1935 (*pro* Cidaroidea MORTENSEN, 1928)] [=Cidaridae CLAUS, 1880]

Test subspherical, radially symmetrical, rigid or with imbricating plates; base resorbed during growth. Ambs of 2 columns; each plate with a single pore pair, not uniting in compound plates, though grouped in diads or triads in some. Interambs conspicuously wider than ambs, of 2 or more columns; each interamb plate with one enlarged primary tubercle, carrying an enlarged corticate (rarely decorticate) primary spine; areole conspicuous, usually defined by scrobicular ring of secondary tubercles. Lantern present; teeth not keeled. Peristome covered (in life) by imbricating plates; no gills or gill slits. Apical system enclosing periproct. No spheridia. Pedicellariae of 2 types; globiferous, with a median venom cell; and tridentate (usually lacking). *U.Sil.-Rec.*

Family ARCHAEOCIDARIDAE M'Coy, 1844

Test flexible; interamb plates pluriserial (in 4 or more columns), imbricating over amb plates at adradial sutures; primary tubercles perforate, noncrenulate; amb pores uniserial. *U.Dev.-Perm.*

Archaeocidaris M'COY, 1844, p. 173 [**Cidaris urii* FLEMING, 1828; OD, M] [*nom. conserv.* ICZN, Op. 370, 1955] [=*Echinocrinus* L. AGASSIZ, 1841 (obj.) (suppressed ICZN Op. 370, 1955); *Palaeocidaris* DESOR, 1846 (type, *Cidarites nerei* MÜNSTER, 18??); *Eocidaris* DESOR, 1856 (type, *Cidaris laevispina* SANDBERGER, 18??); *Cidarotropus* POMEL, 1883 (type, *Archaeocidaris wortheni* HALL, 18??; *Permocidaris* LAMBERT, 1899 (type, *Cidaris forbesiana* DE KONINCK, 18??)]. Test subspherical, probably depressed adorally and adapically. Amb plates tending to form triads, with irregular enlargement of each successive third plate. Interamb plates in 4 columns (at least ambitally), interradial series imbricating more or less upon adradial and adradial more or less upon amb series. Primary spines smooth, striate, or spinulose, or with lateral expansions, but without terminal clavate or discoid shaft; cortex reduced (or ?absent), medulla (in some or all) hollow. *L. Carb.*, Eu., N.Am.; *Perm.*, N.India.——FIG. 237,*1*. *A. immanis* KIER, Penn., Okla.; *1a*, test, lat., ×0.7; *1b*, amb, ×2.1 (largest known cidaroid).

——Fig. 237,*2*. *A. blairi* (Miller), Miss., USA (Mo.); oral view, lantern, ×1.4.——Fig. 237,*3*. *A. aliquantula* Kier, Miss., USA(Iowa); *3a,b,* interamb plates, spines, ×2.9 (96).——Fig. 237,*4*. *A. rossica* (von Buch), Carb., USSR; *4a,b,* test aboral, oral, ×1.4 (87).

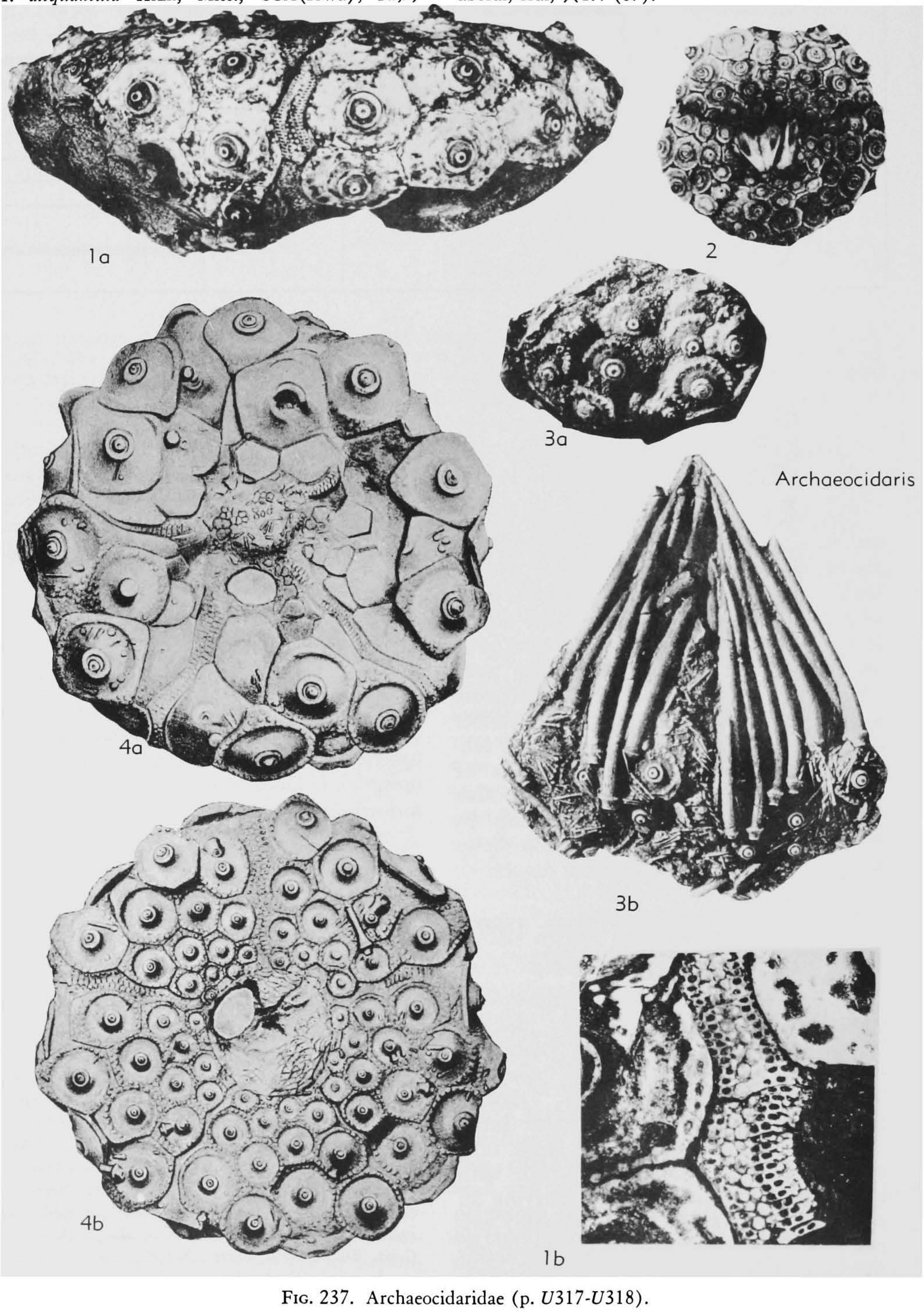

Fig. 237. Archaeocidaridae (p. *U*317-*U*318).

Lepidocidaris MEEK & WORTHEN, 1873, p. 478 [**L. squamosa*; OD, M]. Like *Archaeocidaris,* but amb triads more conspicuous and more regular, and interamb plates in 6 to 8 columns, with scrobicular ring surrounded by raised tumid area. *Miss.,* N. Am.——FIG. 238,5. **L. squamosa,* USA(Ill.); *5a,b,* parts of test, ×2.8, ×0.7 (87).

Nortonechinus THOMAS, 1920, p. 481 [**N. welleri*;

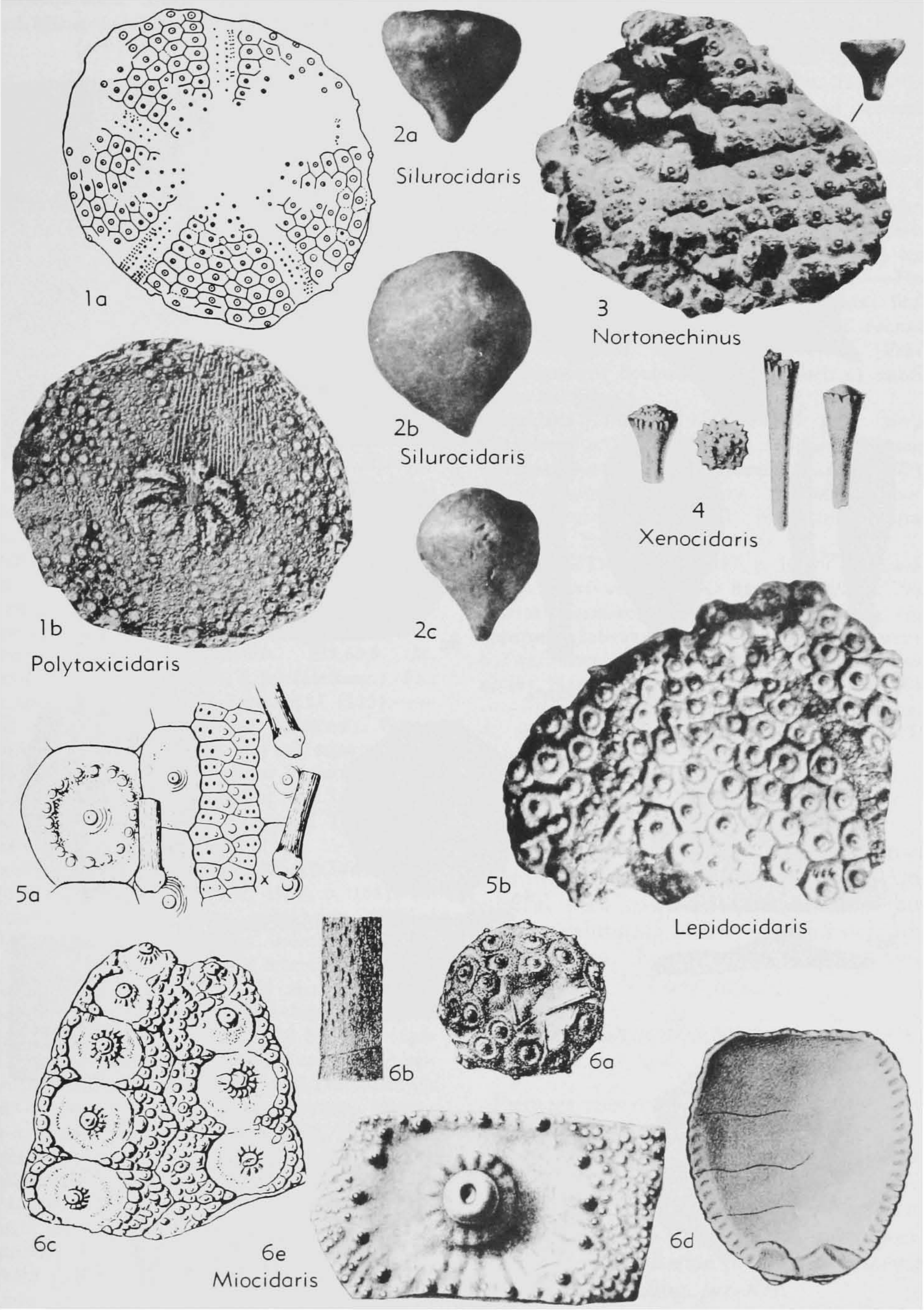

FIG. 238. Archaeocidaridae *(1-5)*; Miocidaridae *(6)* (p. *U*319-*U*321).

OD]. Primary spines short, shaft expanded into terminal disc; interambs as in *Lepidocidaris*; ambs unknown. *U.Dev.*, N.Am.(Iowa).——FIG. 238,*3*. **N. welleri*; interamb plates, ×2 (162).

Polytaxicidaris KIER, 1958, p. 10 [**P. dyeri*; OD]. Like *Lepidocidaris* but amb primary tubercles mostly perforate, no triads; and scrobicular ring marginal, with no surrounding tumid area. *Miss.*, N.Am.(Ind.).——FIG. 238,*1*. **P. dyeri*; *1a,b*, holotype, oral, ×1.4 (96).

?**Silurocidaris** REGNÉLL, 1956, p. 165 [**S. clavata*; OD]. Primary spines clavate, shaft spheroidal; test unknown. *U.Sil.*, Sweden.——FIG. 238,*2*. **S. clavata*; *2a-c*, spine shafts, ×2.8 (94a).

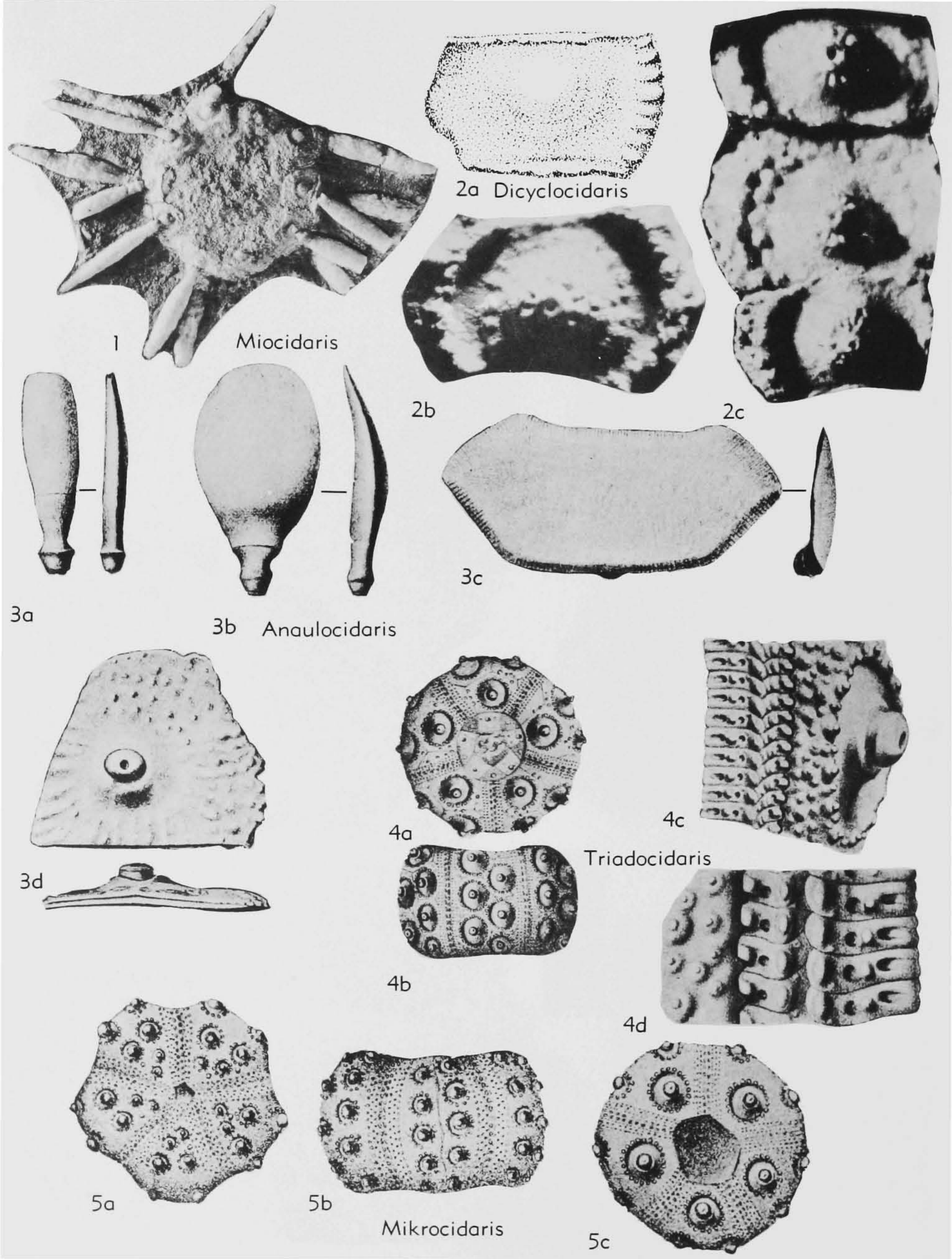

FIG. 239. Miocidaridae (p. *U321*).

?**Xenocidaris** Schultze, 1866, p. 126 [*_X. clavigera_; OD, M]. Primary spines as in _Nortonechinus,_ but more slender and with terminal spinulose ring. Test unknown. _M.Dev.,_ Eu.(Ger.); _U.Dev.,_ N.Am. (Iowa).——Fig. 238,_4_. *_X. clavigera,_ M.Dev., Ger.; spines, ×1.4 (136a).

Family MIOCIDARIDAE Durham & Melville, 1957

[_nom. nov. pro_ Streptocidaridae Lambert, 1900=Streptocidarinae Mortensen, 1928 (_nom. correct.,_ not based upon any generic name)]

Test partly flexible, interamb plates in 2 columns, plates imbricating adorally and adradially, beveled over adjoining amb plates. Primary tubercles perforate. Amb plates uniserial, with nonconjugate pores, not forming diads or triads. _L.Carb.-L.Jur._

Miocidaris Döderlein, 1887, p. 40 [*_M. cassiani_ Bather, 1909 (_non. subst. pro Cidaris klipsteini_ Desor); SD Bather, 1909, p. 84] [=_Eotiaris_ Lambert, 1900]. Test small to medium-sized. Areoles well developed, more or less confluent. Primary tubercles perforate, crenulate, bearing cylindrical spines with granular ornament on shaft. Ambs narrow, plates probably supported in membrane, overlapped by denticulate, beveled adradial margin of interamb plates. Tridentate pedicellariae present, with globular head and elongate jaws (known in _M. lorioli_ only). _?L.Carb.,_ N.Am.; _Perm.-L.Jur.,_ Eu.-Asia.——Fig. 238,_6a,b_. _M. lorioli_ Lambert & Thiéry, L.Jur.(Hettang.), Fr.; _6a,_ test, aboral, ×0.7; _6b,_ spine, ×11 (115).——Fig. 238,_6c,d_. _M. keyserlingi_ (Geinitz), Perm., Hung.; _6c,d,_ interamb ext. and int. aspects, ×4.2 (10).——Fig. 238,_6e_. _M. planus_ Bather, U.Trias. (Carn.), Hung.; interamb plate, ×3.5 (10).——Fig. 239,_1_. _M. pakistanensis_ Linck, L.Trias., Pak.; test with spines, aboral, ×0.7 (118).

Anaulocidaris Zittel, 1879, p. 486 [*_Cidaris buchi_ Münster, 1843; SD Bather, 1909, p. 168]. Interambulacral plates thin, imbricating adradial edge not denticulate, areoles indistinct, without scrobicular tubercles. Primary tubercles noncrenulate, without parapet or basal terrace. Primary spines strongly depressed, shield-shaped, imbricating so that upper edges are covered by lower edges of spines immediately adapical, completely obscuring aboral hemisphere of test. _U.Trias.(Carn.),_ Eu.——Fig. 239,_3_. _A. testudo_ Bather, Hung.; _3a-c,_ spines in ext. and lat. aspects, ×2.3; _3d,_ interamb plate, ext. and lat. aspects, ×3.3 (11).

?**Aplocidaris** Lambert & Thiéry, 1909, p. 31 [*_Cidaris helenae_ de Regny, 1903; OD]. Test very small, interamb plates with noncrenulate primary tubercle, and single ring of scrobicular tubercles, areole ill-defined; no other secondary tubercles. Ambs very narrow, without tubercles, sutures oblique. Primary spines compressed, with denticulate margins. [Possibly juvenile stage of some miocidarid. Family assignment doubtful owing to lack of imbricating test plates.] _U.Trias.(Nor.),_ Eu.

Dicyclocidaris Fell, 1950, p. 83 [*_D. denticulata_; OD]. Like _Miocidaris,_ but with 2 rings of scrobicular tubercles on ambital plates, inner ring developed on floor of areole; spines cylindrical, thorny. _U.Trias.(Carn.),_ N.Z.——Fig. 239,_2_. *_D. denticulata_; _2a-c,_ int. and ext. aspects of interamb plates, ×5.3 (54).

?**Mikrocidaris** Döderlein, 1887, p. 39 [*_Cidaris pentagona_ Münster, 1843; SD Lambert & Thiéry, 1909, p. 140] [=_Microcidaris_ Lambert & Thiéry, 1909, p. 140 (_nom. van._)]. As _Triadocidaris,_ but test very small (3-5 mm.), and test plates not beveled. _U.Trias.(Carn.),_ Eu.——Fig. 239,_5a,b_. *_M. pentagona_ (Münster), Aus.; _5a,b,_ test, aboral, lat., ×5.4.——Fig. 239,_5c_. _M. venusta_ (Münster), Aus.; test, aboral, ×7 (116). [Family assignment doubtful owing to lack of imbricating test plates.]

Pachycidaris Thiéry, 1928, p. 179 [*_P. thieryi_ Collignon & Lambert, 1928 (=_Cidaris spinosa_ Cotteau, _partim, non C. spinosa_ Agassiz); OD]. Primary spines very thorny. Ambulacral marginal tubercles developed irregularly. _U.Jur. (Oxford.),_ Eu.

Triadocidaris Döderlein, 1887, p. 39 [*_Cidaris subsimilis_ Münster, 1843; SD Bather, 1909, p. 79]. Test as _Miocidaris,_ but tubercles noncrenulate, and uppermost interamb plate hypertrophied in some. _U.Trias.(Carn.),_ Eu.——Fig. 239,_4a,b_. *_T. subsimilis,_ Hung.; _4a,b,_ test aboral, lat., ×0.7 (116).——Fig. 239,_4c,d_. _T. persimilis_ Bather, Hung.; _4c,_ amb, interamb, ×6.5; _4d,_ amb plates, ×13 (11).

Family CIDARIDAE Gray, 1825

Test rigid. Interambulacral plates in 2 columns. Primary tubercles perforate. Ambulacral pore pairs uniserial aborally, but in some exhibiting pluriserial tendencies on adoral region, though never forming compound plates. _U.Trias.-Rec._

Subfamily HISTOCIDARINAE Mortensen, 1928

[_nom. transl._ Fell, herein (_ex_ Histocidarina Mortensen, 1928)]

Primary tubercles strongly crenulate. Primary spines cylindrical, not clavate; either smooth or thorny. Secondary spines elongate, erect, more or less flattened, but not squamiform. Pores nonconjugate, conspicuous wall separating inner from outer pore. Tridentate pedicellariae present, globiferous pedicellariae wanting. _Jur.-Rec._

Histocidaris Mortensen, 1903, p. 22 [*_Porocidaris elegans_ A. Agassiz, 1879; OD]. Test usually well arched, flattened at apex and peristome. Interambulacral plates broader than high, their areoles large, more or less confluent below ambitus. Apical plates partly naked, especially genital plates; genital pore usually entirely enclosed by genital plate. Primary spines cylindrical throughout most or all of their length, tip tapering or widening in some; collar short (not more than *ca.* 3 mm.), not swollen midway. *Oligo.*, N.Z.; *Mio.*, N.Afr.; *Rec.*, IndoPac.-Carib.——FIG. 240,*1*. *H. mackayi* FELL, M.Oligo., N.Z.; *1a*, test (holotype) aboral, ×1.35; *1b*, test (paratype), lat., ×1.35; *1c*, in-

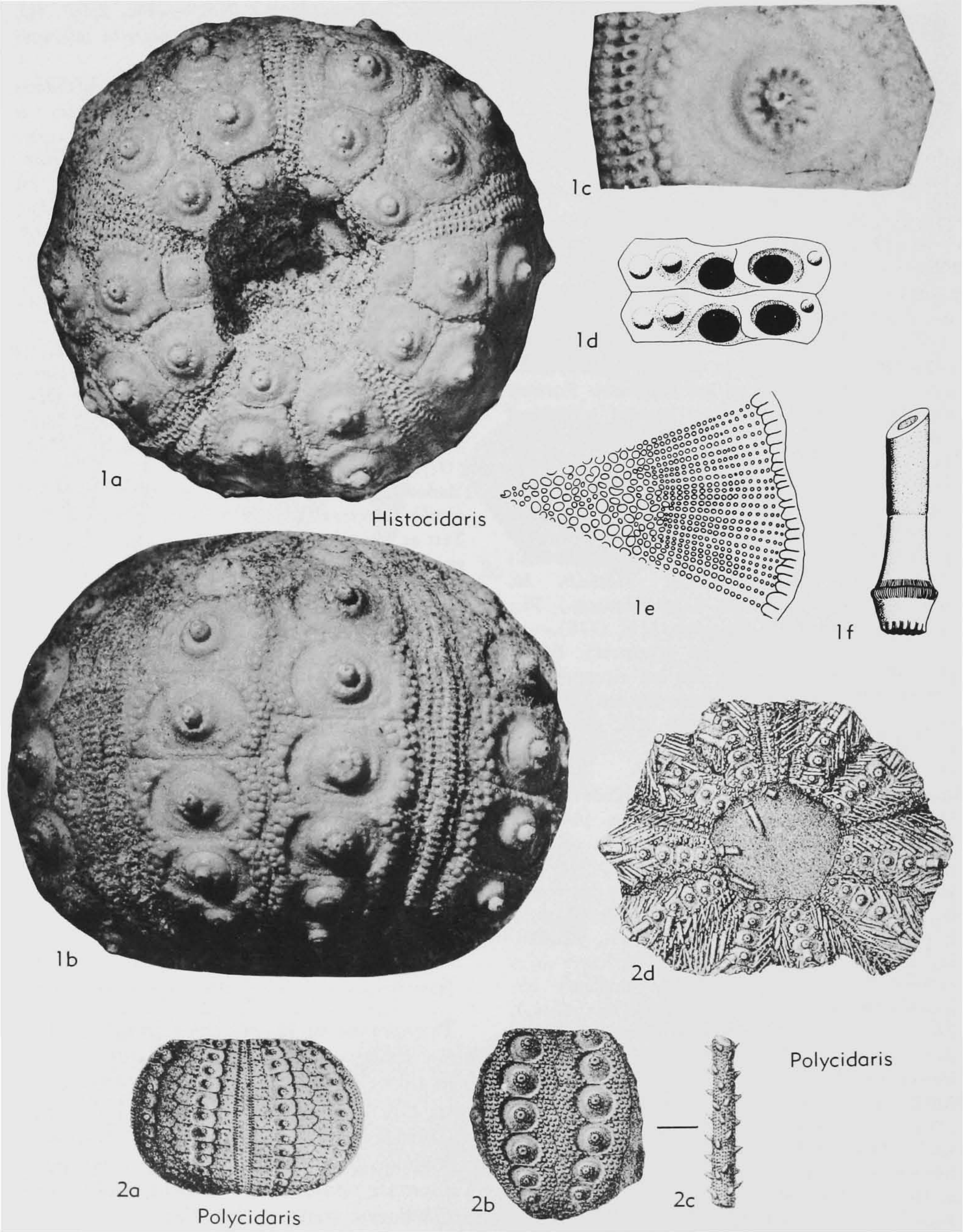

FIG. 240. Cidaridae (Histocidarinae) (p. *U322-U323*).

teramb plate with attached amb plates, ×3.3; *1d*, amb plate, ×13.5; *1e*, transv. sec. of spine, ×27; *1f*, base of spine, ×2.7 (56).

Polycidaris Quenstedt, 1858, p. 644 [**Cidarites multiceps* Quenstedt, 1858] [*non Polycidaris* Bettoni, 1900 (=*Loriolella* Fucini, 1904)]. Interambulacral plates relatively numerous (up to 15), and broader than high; areoles all confluent, scrobicular rings reduced to undulating line of tuberculation on either side of areole series. Ambulacra straight. Primary spines probably slender, thorny. *Jur.(Bajoc.-Oxford.)*, Eu.——Fig. 240, *2a*. **P. multiceps* (Quenstedt), Oxford., Ger.; lat., ×0.8 (145).——Fig. 240,*2b,c*. *P. legayi* Sauvage, Portland., Fr.; *2b*, interamb, ×0.8; *2c*, spine, ×2.7 (27c).——Fig. 240,*2d*. *P. spinulosa* Roemer, Bajoc., Fr.; peristome and adoral part of test, with adhering spines, ×1.35 (27c).

Poriocidaris Mortensen, 1909, p. 53 [**Porocidaris purpurata* Wyville Thomson, 1874; OD] [=*Porocidaris* A. Agassiz, 1872 (*non* Desor, 1855)]. Like *Histocidaris* but primary spines tapering and with long collar (10-20 mm.), especially apical spines, where collar may occupy 0.3 length of whole spine. Tridentate pedicellariae with only 2 valves. *Rec.*, Atl.-?Ind.O.

Procidaris Pomel, 1883, p. 109 [**Cidaris edwardsi* Wright, 1855; SD Mortensen, 1928]. Like *Polycidaris* but marginal ambulacral tubercles perforate. Primary spines slender, cylindrical, smooth. *L.Jur.-M.Jur.*, Eu.——Fig. 241,*1,2*. **P. edwardsi*, L.Jur.(Charmouth.), Eng.; *1*, test, lat., ×1; *2*, test plates, ambs at right, interamb at left, ×2.7 (172).

Subfamily CTENOCIDARINAE Mortensen, 1928

[*nom. transl.* Fell, herein (*ex* Ctenocidarina Mortensen, 1928)]

Primary tubercles noncrenulate on oral hemisphere, subcrenulate or noncrenulate on aboral hemisphere. No horizontal sutural grooves. Ambulacral pore pairs placed obliquely on plate; 2 pores confluent or separated by very narrow wall, thickness of which does not exceed 0.5 of pore diameter. No tridentate pedicellariae. Large and small globiferous pedicellariae present. *?Eoc.*, Patagonia; *Rec.*, Antarctic-N.Z.-S.Pac.

Ctenocidaris Mortensen, 1910, p. 3 [**C. speciosa*; OD]. Test low. Interambulacra with or without ill-defined, naked, slightly sunken median area; areoles rather deep, proximal 4 or 5 usually confluent; all primary tubercles noncrenulate; scrobicular tubercles not conspicuously differentiated from other secondaries. Ambulacral pores commonly confluent, neuropore inconspicuous. Apical system and peristome approximately half of horizontal diameter; ocular pore usually surrounded by circular wall; female genital pore not entirely enclosed by genital plate. Primary spines cylindrical, with numerous thorns irregularly scattered on shaft or (less commonly) arranged in longitudinal rows; oral primaries coarsely serrate or spatulate, not spearhead-shaped. Secondary spines clavate. Globiferous pedicellariae without end tooth. *Rec.*, Antarctic.

Aporocidaris Agassiz & Clark, 1907, p. 36 [**Porocidaris milleri* A. Agassiz, 1898; OD]. Like *Ctenocidaris* but test high, arched or conical, very thin and fragile. Areoles shallow. Neuropore conspicuous. Median ambulacral area rather naked, slightly sunken, weak grooves in median area at terminations of horizontal ambulacral sutures. Primary spines long, slender, with sparse, irregular thorns; oral primaries spearhead-shaped, serrate, distally curved; secondary spines erect, cylindrical or weakly clavate. *Rec.*, Antarctic (littoral)-Pac. (abyssal).

Austrocidaris H. L. Clark, 1907, p. 212 [**Temnocidaris canaliculata* A. Agassiz, 1863; OD] [*non Temnocidaris* Cotteau, 1863]. Like *Ctenocidaris* but conspicuous, sunken, median furrow present in both interambulacra and ambulacra. Areoles well separated, deep; primary tubercles subcrenulate aborally, noncrenulate adorally. Pores not confluent. Primary spines with rather smooth, slender, cylindrical shaft; secondary spines flattened, somewhat adpressed. *?Eoc.*, Patagonia; *Rec.*, subantarctic.——Fig. 241,*3*. **A. canaliculata* (A. Agassiz), Rec., subantarctic; lat., with juveniles adhering to adapical region, ×1.35 (163).

Eurocidaris Mortensen, 1909, p. 30 [**Cidaris nutrix* Wyville Thomson, 1876; OD]. Like *Ctenocidaris* but having flattened scrobicular spines. *Rec.*, Antarctic.

Homalocidaris Mortensen, 1928, p. 67 [**Austrocidaris gigantea* H. L. Clark, 1925; OD]. Like *Ctenocidaris* but interambulacra without slightly sunken, naked median area; areoles large, deep, separated by narrow ridges. Ambulacral pores confluent. Primary spines cylindrical, shaft smooth, milled ring very conspicuous. *Rec.*, Antarctic.

Notocidaris Mortensen, 1909, p. 17 [**Goniocidaris mortenseni* Koehler, 1900; OD]. Like *Ctenocidaris*, but differing in primary spines, which are more or less compressed, with longitudinal rows of spinules on shaft or longitudinal ridges; oral primaries conspicuously spearhead-shaped. [*Ctenocidaris* has, *Notocidaris* lacks, a coat of calcareous hairs on the shaft, a difference unlikely to have paleontological significance, however.] *?Plio.*, N.Z.; *Rec.*, Antarctic.

Ogmocidaris Mortensen, 1921, p. 151 [**O. benhami*; OD]. Like *Austrocidaris* but small globiferous pedicellariae with end tooth and developing in adult stage small adapical umbrella-shaped spines, other spines elongate, cylindrical, and slender. [The occurrence (here first recorded) of umbrella-shaped adapical spines in this genus, and the character of the small globiferous pedicellariae, suggest that it is transitional to the Goniocidarinae, to which subfamily the genus might with equal right be referred.] *Rec.*, N.Z.——FIG. 242,*1*. **O. benhami*; *1a*, interamb plate with ambs at left, ×6.7; *1b*, amb plates, ×13.5 (56).

Rhynchocidaris MORTENSEN, 1909, p. 5 [**R. triplopora;* OD]. Like *Ctenocidaris* but with neuropore

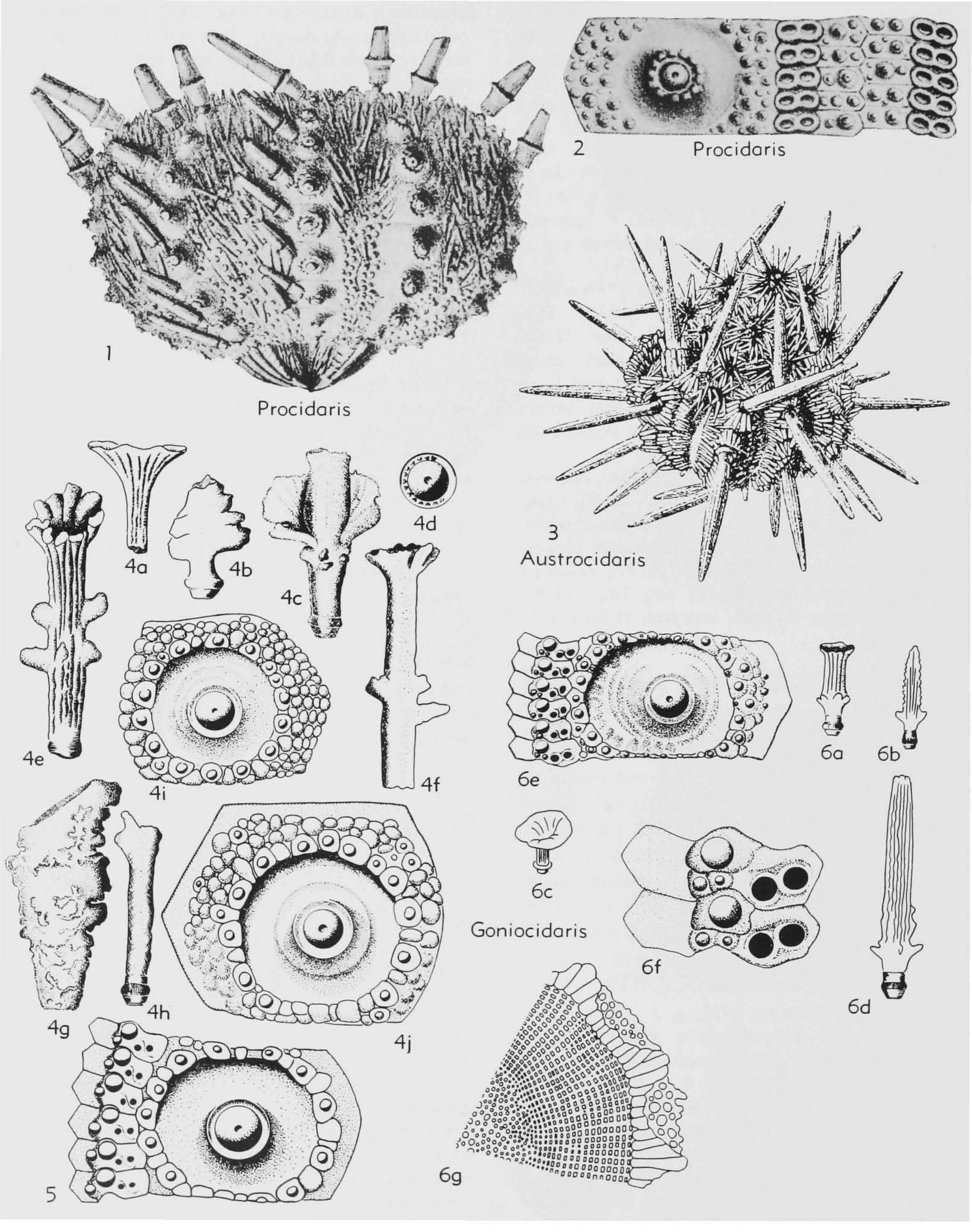

FIG. 241. Cidaridae (Histocidarinae) *(1,2)*, (Ctenocidarinae) *(3)*, (Goniocidarinae) *(4-6)* (p. *U323*, *U325*).

so strongly developed that ambulacral plates (on adoral side at least) appear to carry pore-triplets in place of pore pairs. *Rec.,* Antarctic.

Subfamily GONIOCIDARINAE Mortensen, 1928

[*nom. transl.* FELL, herein (*ex* Goniocidarina MORTENSEN, 1928)]

Test usually flattened above and below. Grooves or pits, or both, on horizontal sutures of interambulacra and ambulacra, commonly confluent with median vertical grooves. Primary tubercles adorally noncrenulate, aborally noncrenulate or weakly subcrenulate. Pores nonconjugate, close together. Tridentate pedicellariae unknown. Globiferous pedicellariae present, small forms with end tooth, large forms without it. *Eoc.-Rec.*

Goniocidaris DESOR in AGASSIZ & DESOR, 1846, p. 337 [**Cidarites tubaria* LAMARCK, 1816; SD MORTENSEN, 1928, p. 150] [=*Stephanocidaris* A. AGASSIZ, 1863 (*non* AGASSIZ, 1872); *Adelcidaris* COTTON & GODFREY, 1942 (*nom. van.*)]. Median parts of horizontal sutures sunken or naked, forming conspicuous grooves in interambulacra and ambulacra; grooves commonly confluent with vertical furrow or median suture. Pores horizontal or, less commonly, oblique. Adapical primary spines with terminal disc or cup (developed only at maturity). *Eoc.,* Australia; *Rec.,* Indo-W.Pac.

G. (Goniocidaris) DESOR, 1846; *emend.* MORTENSEN, 1928 [**Cidarites tubaria* LAMARCK, 1816; SD MORTENSEN, 1928, p. 150]. Primary spines without basal disc, having instead basal spurs; shaft with coarse ridges or thorns. *Eoc.,* S.Australia; *Oligo.,* N.Z.; *Mio.,* India-Australia; *Plio.,* Iran-Australia; *Rec.,* Indo-W.Pac., incl. SE.Afr.——FIG. 241,*4*. *G. hebe* FELL, U.Oligo., N.Z.; *4a-h,* spines, ×1.35; *4i,j,* interamb plates, ×4.——FIG. 241,*5*. *G. pusilla* FELL, L.Mio., N.Z.; amb plates (left) and interamb, ×10.——FIG. 241,*6*. *G. umbraculum* HUTTON, Rec., N.Z.; *6a-d,* spines, ×2; *6e,* amb plates (left) and interamb, ×4; *6f,* amb plate, ×13.5; *6g,* transv. sec. of spine, ×27 (56).

G. (Aspidocidaris) MORTENSEN, 1928, p. 67 [**Goniocidaris alba*; OD]. Basal disc, and usually also very large terminal disc, present on primary spines; secondary spines short, flattened, with transversely straight-cut termination. *Rec.,* Japan-Indon.-Australia-N.Z.——FIG. 242,*2*. *A. parasol* FELL, Rec., N.Z.; test with spines (holotype), ×1.35 (Fell, n).

G. (Cyrtocidaris) MORTENSEN, 1927, p. 264 [**Goniocidaris tenuispina*; OD]. Basal disc, and usually also large terminal disc with indented edge, present on primary spines; shaft long, slender, thorny, secondary spines long, slender, pointed. *Rec.,* Philip.

G. (Discocidaris) DÖDERLEIN, 1885, p. 80 [**D. mikado*; OD]. Discs repeated serially at intervals along proximal part of shaft of ambital primary spines. *Rec.,* Japan-Indon.

G. (Petalocidaris) MORTENSEN, 1903, p. 18 [**Goniocidaris florigera* A. AGASSIZ, 1879; OD]. Primary spines with basal disc, shaft coarsely thorny; secondary spines flattened, thorny at base. *Rec.,* Japan-Indon.

Psilocidaris MORTENSEN, 1927, p. 282 [**P. echinulata*; OD]. Like *Schizocidaris* but primary spines long (3 to 5 times test horizontal diameter) and slender and lacking calcareous investment of shaft. Apical system conspicuously larger than peristome. *Rec.,* Indon. (abyssal).

Rhopalocidaris MORTENSEN, 1927, p. 272 [**Cidaris hirsutispinus* DE MEIJERE, 1904; OD]. Like *Psilocidaris* but secondary spines clavate, and apical system not conspicuously larger than peristome. Small abyssal forms less than 20 mm. diameter. *Rec.,* Japan-Indon.

Schizocidaris MORTENSEN, 1903, p. 25 [**S. assimilis*; OD]. Neither basal nor apical discs, shaft covered by smooth, glabrous calcareous investment which is supported between thorns by erect, columnar, calcareous cortical hairs. Secondary spines smooth, flattened, not clavate. *Rec.,* Indon.

Subfamily STEREOCIDARINAE Lambert, 1900

[*nom. transl.* FELL, herein (*ex* Stereocidaridae LAMBERT, 1900)]

Test robust, usually well arched. Interambulacra with more or less distinct horizontal sutural grooves on aboral side, upper areoles and tubercles commonly more or less rudimentary; interambulacral plates tending to be higher than broad on aboral side so that areoles there tend to be widely separated. Pores nonconjugate. Upper primary spines more or less reduced; secondary spines flattened, more or less adpressed. Globiferous pedicellariae usually without end tooth. *U.Jur.-Rec.*

Stereocidaris POMEL, 1883, p. 110 [**Cidaris cretosa* MANTELL, 1835; SD LAMBERT & THIÉRY, 1909 (Feb., p. 31; *non* Mar., 1909, where *C. merceyi* was designated, p. 152)] [=*Typocidaris* POMEL, 1883 (type, *Cidaris malum* A. GRAS); *Phalacrocidaris* LAMBERT, 1902 (type, *Dorocidaris japonica* DÖDERLEIN, 1885); *Anomocidaris* AGASSIZ & CLARK, 1907 (type, *Cidaris tenuispinus* YOSHIWARA, 1898)]. Test robust. Interambulacral plates high, especially aboral ones; rarely more than 7 plates in column, upper 1 to 3 having areole, tubercle, and spine more or less rudimentary; areoles deep, well separated, even on adoral side; intervening tumid surfaces densely covered by secondary and miliary tubercles. Primary tubercles noncrenulate or aborally subcrenulate. Ambulacra usually sinuate; pores nonconjugate. Primary spines with neck approximately twice length of collar, shaft commonly flaring toward tip; scrobicular spines flattened, adpressed around areole; other secondary spines squamiform or spiniform, densely packed. Tridentate pedicellariae present or absent; large globiferous pedicellariae without end-tooth, small globiferous pedicellariae with or without them. *Cret.*, Eu.-N.Am.; *Eoc.*, Eu.-Australia; *Oligo.*, N.Z.; *Mio.*, Australia-?Indon.; *Plio.*, Australia-N.Z.; *Rec.*, Indo-W.Pac. incl. SE. Afr., but not yet known from Australasia, where it may be expected). [Note on synonymy: *Typocidaris* POMEL, 1883, p. 111 (type, *Cidaris malum* A. GRASSÉ) is

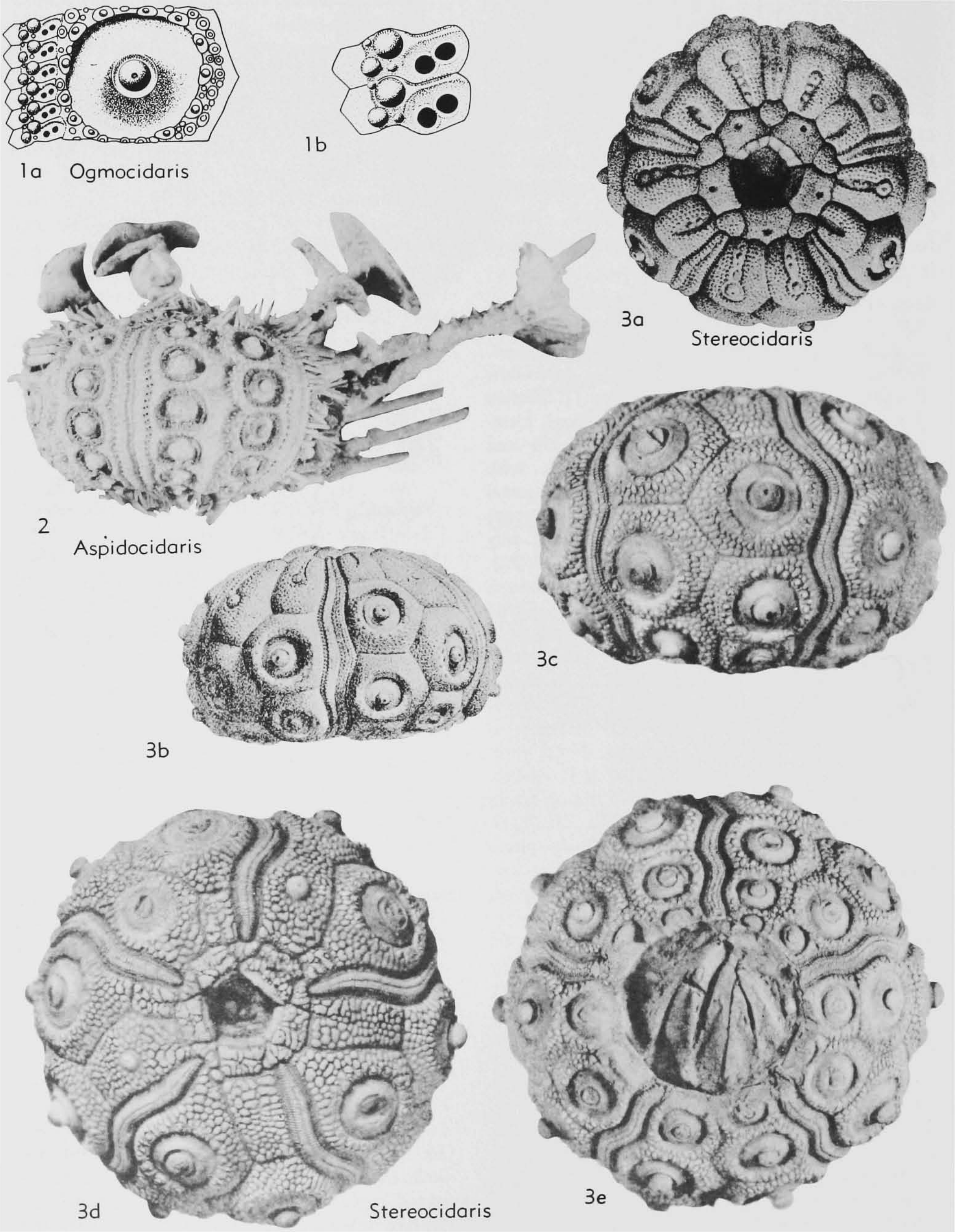

FIG. 242. Cidaridae (Ctenocidarinae) *(1)*, (Goniocidarinae) *(2)*, (Stereocidarinae) *(3)* (p. *U323-U327*).

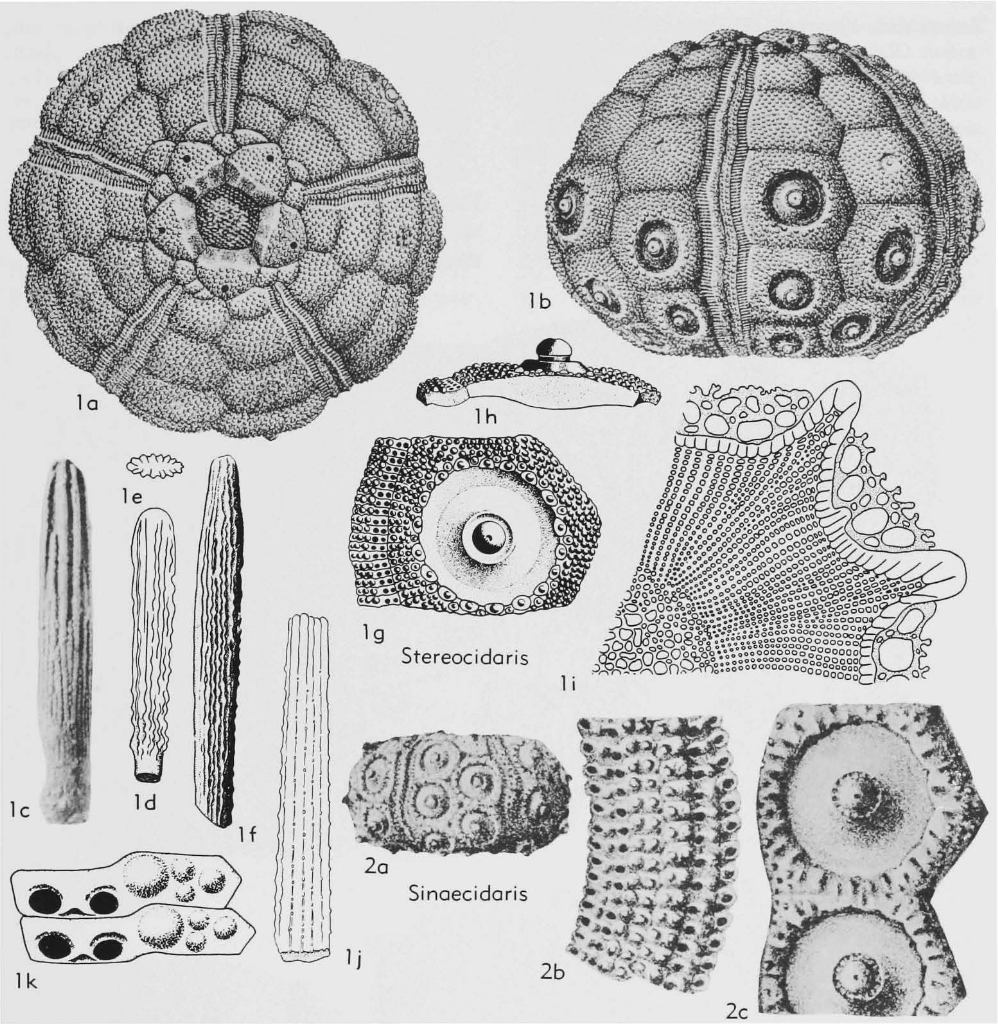

FIG. 243. Cidaridae (Stereocidarinae) (p. *U325-U327*).

founded on forms with grooved sutures and fully developed upper areoles; *Phalacrocidaris* LAMBERT, 1902 (type, *Dorocidaris japonica* DÖDERLEIN) for forms having atrophied upper areoles but no sutural grooves as in *S. merceyi* (COTTEAU). *Anomocidaris* AGASSIZ & CLARK, 1907, is a junior objective synonym of *Phalacrocidaris*. The characters supposed to distinguish *Typocidaris* and *Phalacrocidaris*, however, intergrade, and these genera must be united with *Stereocidaris*.]——FIG. 242,*3a,b*. *S. sceptifera* (MANTELL), U.Cret., Eng.; *3a,b*, test, aboral, lat., ×0.7 (173).——FIG. 242,*3c-e*; 243,*1c*. *S. hudspethensis* COOKE, M.Cret., N.Am.(Tex.); 242,*3c-e*, test, lat., aboral, oral, ×0.7 (23); 243,*1c*, spine, ×1.35 (23).——FIG. 243,*1a,b*. *S. merceyi* (COTTEAU), M.Cret., Fr.; aboral, lat., ×1 (27a).——FIG. 243,*1d-i*. *S. hutchinsoni* FELL, L.Pleist., N.Z.; *1d-f*, spines, ×1.35; *1g,h*, interamb and amb plates, ×2; *1i*, transv. sec. of spine, ×27 (56).——FIG. 243,*1j,k*. *S. striata* (HUTTON), L.Oligo., N.Z.; *1j*, spine, ×2.7; *1k*, amb plates, ×13.5 (56).

Compsocidaris IKEDA, 1939, p. 160 [**C. pyrsacantha*; OD]. Like *Stereocidaris* but test with only sparsely scattered secondary tubercles instead of dense tuberculation. Primary spines cylindrical, ridged, not thorny. *Rec.*, Bonin Is.

Sinaecidaris FOURTAU, 1921, p. 9 [**S. gauthieri*; OD]. Like *Stereocidaris* but primary tubercles distinctly crenulate throughout interambulacra. *Cret.*, Egypt.——FIG. 243,*2*. **S. gauthieri*; *2a*, test lat., ×1; *2b*, amb plates, ×6.7; *2c*, interamb plates, ×2.7 (65).

Temnocidaris Cotteau, 1863, p. 355 [**T. magnifica*; OD] [*non Temnocidaris* A. Agassiz, 1863 (=*Austrocidaris* H. L. Clark, 1907)]. Numerous conspicuous grooves and porelike impressions scattered over all coronal plates (probably accommodating globiferous pedicellariae); horizontal sutural grooves, and vertical zigzag groove on interambulacral mid-line. Primary tubercles noncrenulate; pores subconjugate; primary spines cylindrical, slender, finely thorny. *U.Cret.*, Eu.——Fig. 244,*1*. **T. magnifica*, Fr.; *1a*, test (holotype), lat., ×0.85; *1b*, amb plates, ×3.5; *1c*, amb plates, ×8.5; *1d,e*, interamb plates, ×0.85, ×3.5 (27).

Subfamily RHABDOCIDARINAE Lambert, 1900

[*emend.* Fell, herein]

Test robust, without sutural grooves. Pores conjugate or subconjugate. Primary spines large, robust. *L.Jur.-Rec.*

Rhabdocidaris Desor, 1855, p. 39 [**Cidaris orbigny-*

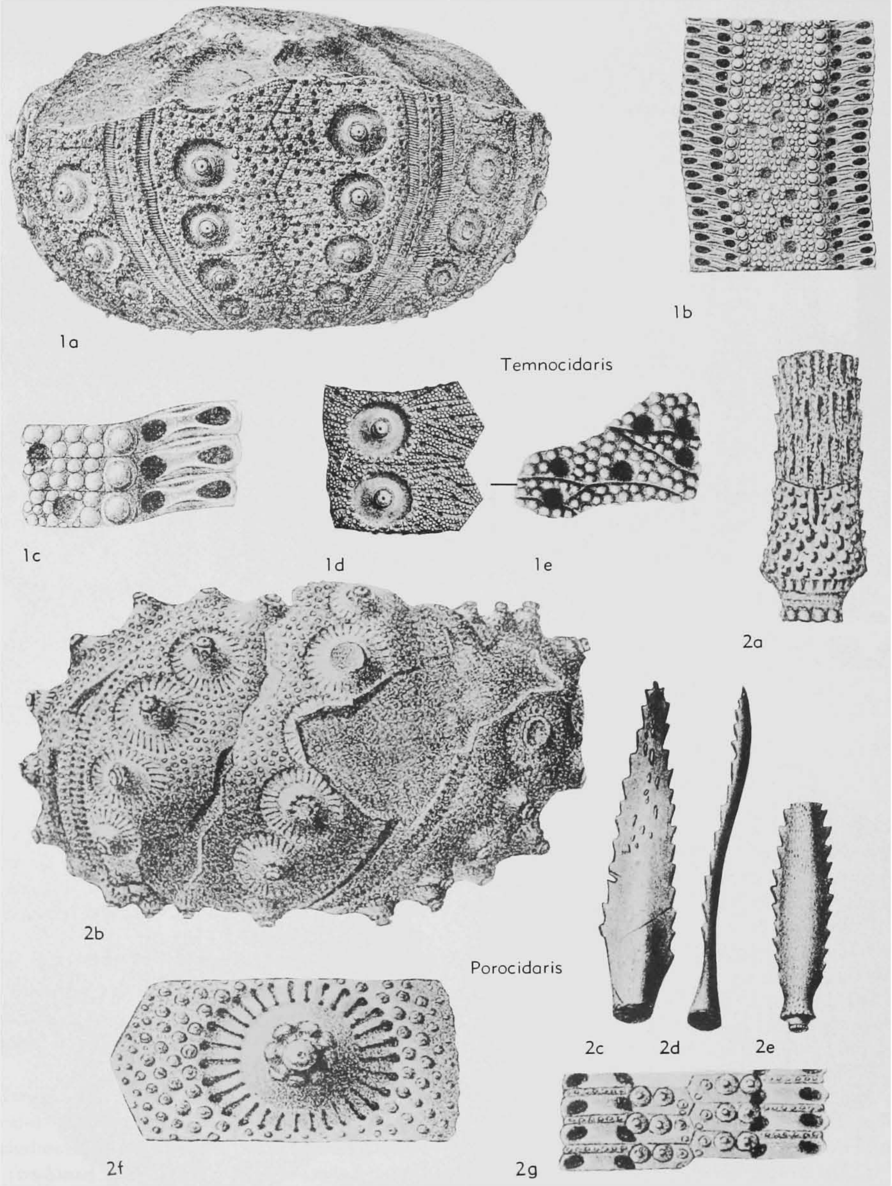

Fig. 244. Cidaridae (Stereocidarinae) *(1)*, (Rhabdocidarinae) *(2)* (p. *U*328, *U*330).

ana L. Agassiz; SD Lambert & Thiéry, 1910, p. 136]. Test spherical, slightly flattened at apex and peristome, usually large (diam. ± 100 mm.). Areoles circular, shallow, not confluent; primary tubercles strongly crenulate. Ambulacra sinuate, pores conjugate. Primary spines long, typically depressed and expanded to form broad, obcordate or fan-shaped plates, shaft bearing longitudinal, radiating series of thorns. *L.Jur.-Eoc.,* Eu.——Fig. 245,*1*. **R. orbignyana* (Agassiz), Jur., Fr.; *1a,* test, lat., ×0.75; *1b,c,* spines, ×0.75.——Fig. 245,*2*. *R. rhodani* Cotteau, Jur., Fr.; interamb plates, ×0.9.——Fig. 245,*3*. *R. copeoides* Desor, Jur., Fr.; *3a,b,* spines, ×0.75 (27d).

Actinocidaris Mortensen, 1928, p. 73 [**Phyllacanthus thomasi* A. Agassiz & H. L. Clark, 1907; OD]. Like *Prionocidaris* but primary spines thick, cylindrical or fusiform, finely tuberculated, surface of shaft covered by coarse reticulate layer formed by thick, anastomosing cortical, calcareous hairs. Pores subconjugate. *Rec.,* Hawaii.

Chondrocidaris A. Agassiz, 1863, p. 18 [**C. gigantea*; OD]. Test low, height half of diameter, flattened above, sides arched. Areoles shallow, not

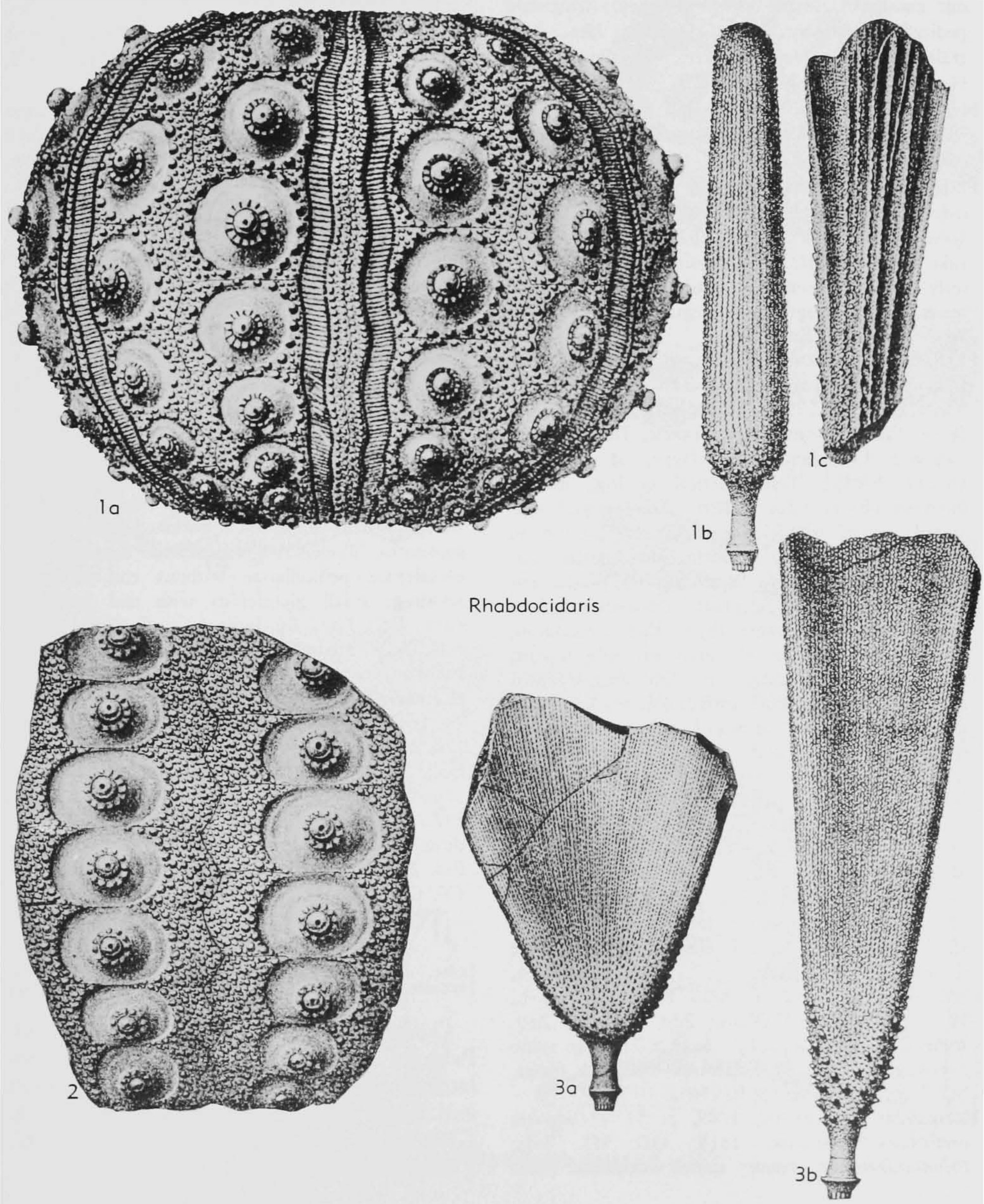

Fig. 245. Cidaridae (Rhabdocidarinae) (p. *U*329).

confluent, primary tubercles noncrenulate. Ambulacra straight or sinuate, pores conjugate. Madreporite not conspicuously enlarged. Whole surface of corona, save for areoles and poriferous area, densely coated in uniform, small, hyaline, more or less spinuliform tubercles; areoles carry small, conical, adpressed secondary spines, attached to sides (not tops) of tubercles. Primary spines thick, commonly with dense hair at base of shaft, with coarse thorns which tend to unite into longitudinal lamellae, latter spreading fanlike at tips; cortex thin. Large globiferous pedicellariae without end-tooth, small ones with them; tridentate pedicellariae present. *Oligo.*, Australia; *Mio.*, Australia-Fiji-Indon.-Madag.; *Rec.*, IndoPac. (incl. Hawaii but not New Zealand).

Megacidaris Thiéry, 1928, p. 180 [**Cidarites horrida* Merian, 1880; OD]. Sutures oblique. Pores conjugate. *M.Jur.(Bajoc.)*, Eu.

Parhabdocidaris Thiéry, 1928, p. 181 [**Rhabdocidaris varusensis* Cotteau, 1880; OD] [=*Parrhabdocidaris* Mortensen, 1928 *(nom. van.)*]. Like *Rhabdocidaris* but ambulacral plates irregularly arranged, some as diads, some in simple series, with corresponding irregularity of marginal tubercles. *U.Jur.*, Eu.

Phyllacanthus Brandt, 1835, p. 67 [**Cidarites (Phyllacanthus) dubia*; OD, M] [*nom. conserv.* ICZN, Op. 208, 1954] [=*Leiocidaris* Desor, 1855 (type, *Cidaris imperialis* Lamarck, 1816); *Aulacocidaris* Lambert, 1903 (type, *A. lamberti* (Savin, 1903)]. Test spherical or low, usually flattened above, sides arched. Areoles well separated, central part elevated, carrying prominent, noncrenulate primary tubercle. Madreporite conspicuously larger than other genital plates, encroaching on small periproct. Scrobicular tubercles conspicuously larger than other secondaries, usually with distinct elevation on side toward areole. Pores conjugate, but with wall elevated aborally. Primary spines cylindrical, thick, robust, with fine granules arranged in regular longitudinal series on shaft; cortex thick; primary radial lamellae (as seen in transverse section) arising in fanlike clusters from projecting portions of medulla. Secondary spines broad, flat, squamiform, closely adpressed. Globiferous pedicellariae without end-tooth. *Oligo.*, Australia-N.Z.; *Mio.*, Australia-N.Z.-Fiji Is.-India; *Plio.*, Australia; *Rec.*, Australia (5 of 6 species), IndoPac.——Fig. 246, *1*. *P. wellmanae* Fell, U.Mio., N.Z.; *1a,b*, part of test, lat., and aboral, ×1.3; *1c*, amb plates, ×13.——Fig. 246,*2*. *P. titan* Fell, U.Oligo.-L. Mio., N.Z. (*2a,b*, U.Oligo.; *2c-f*, L.Mio.); *2a-f*, spines (*2a*, ×4; *2b*, ×1.3; *2c-f*, ×0.7); *2g*, spine transv. sec., ×26; *2h,i*, amb and interamb plates, ×1.7; *2j*, amb plates, ×10 (56).

Plococidaris Mortensen, 1909, p. 51 [**Cidarites verticillata* Lamarck, 1816; OD, M]. Like *Prionocidaris* but primary spines verticillate. Pores subconjugate. *Mio.*, India-Madag.; *Rec.*, IndoPac. (but not N.Z.).

Porocidaris Desor, 1855, p. 46 [**Cidarites schmidelii* Münster, 1843; SD Lambert & Thiéry, 1910, p. 108]. Like *Rhabdocidaris* but ambulacra straight. Areoles circular and shallow (as in *Rhabdocidaris*) but confluent, each with circle of radiating, porelike or slitlike marginal depressions. Primary spines partly known only, orals flattened, coarsely serrate, collar more or less tuberculate. *Eoc.*, Eu.-N.Afr.——Fig. 244,*2*. **P. schmidelii* (Münster), Egypt; *2a*, base of spine, ×2.8 (27e); *2b*, test, lat., ×1.1; *2c-e*, spines, ×1.1 (44); *2f*, interamb plate, ×2.1; *2g*, amb plates, ×8.5 (121). [=*Procidaris* Pávay, 1875, p. 230 *(nom. van.)*.]

Prionocidaris A. Agassiz, 1863, p. 18 [**Cidarites pistillaris* Lamarck, 1816; OD] [=*Stephanocidaris* A. Agassiz, 1872 (*non* 1863); *Schleinitzia* Studer, 1880 (type, *S. crenularis*); *?Pleurocidaris* Pomel, 1883 (type not designated, genus of doubtful validity)]. Test arched or low, more or less flattened at apex, thin and somewhat fragile. Primary tubercles noncrenulate adorally, weakly subcrenulate or noncrenulate aborally; areoles shallow, well separated save for lowermost 2 or 3, which may be confluent. Pores distinctly conjugate or subconjugate. Primary spines usually long, tapering, with coarse thorns in longitudinal series; less commonly cylindrical, smooth or widened distally, or with thorns arranged in whorls; cortex thin; oral primaries with relatively long collar, tipped by rudimentary shaft. Secondary spines not adpressed, larger ones flattened, smaller ones spiniform. Tridentate pedicellariae slender; large globiferous pedicellariae without end tooth, or wanting; small globiferous with end tooth. *U.Cret.*, Eu.; *Eoc.*, Eu.-India-Australia-N.Z.; *Oligo.*, N.Z.; *Mio.*, Medit.(Sardinia-Malta)-Australia; *Rec.*, IndoPac. (but not N.Z.).——Fig. 247,*1a-d*. *P. marshalli* Fell, M.Eoc., N.Z.; *1a-c*, spines, ×1.5; *1d*, part of transv. sec. of spine, ×30 (56).——Fig. 247,*1e-g*. *P. canaliculata* (Duncan & Sladen), Eoc., N.India; *1e*, amb plates, ×3.75; *1f*, test lat., ×0.75; *1g*, interamb plates, ×1.5 (47).——Fig. 247,*1h*. *P. sismondai* (K. Mayer), Mio., Eu. (Sardinia); test lat., with spines, ×0.7 (107).——Fig. 247,*1i*. *P. mitchelli* (Emmons), M.Eoc., USA (N. Car.); test, oral, ×0.75 (22).

Subfamily CIDARINAE Gray, 1825

[*nom. transl.* Fell, herein (*ex* Cidaridae Gray, 1825)] [=Cidarina Mortensen, 1928, *plus* Stylocidarina Mortensen, 1928 *(partim)*]

Corona without sutural pits or grooves. Primary tubercles crenulate or noncrenulate; but if crenulate, primary spines short and thick. Pores horizontal, nonconjugate. Globiferous and tridentate pedicellariae. *U.Trias.(Rhaet.)-Rec.*

Cidaris LESKE, 1778, p. 74 [**Echinus cidaris* LINNÉ, 1758, approx. limited in 1761] [=*Cidarites* AUCTT. (*non* LAMARCK, 1816) (=*Phyllacanthus* BRANDT, 1835); *Orthocidaris* A. AGASSIZ, 1863 (type, *Cidaris papillata* LESKE, 1878); *Dorocidaris* A. AGASSIZ, 1869 (type, *Cidaris papillata* LESKE, 1878); *Papula* BAYLE, 1878]. Areoles generally deep, well separated; primary tubercles noncrenulate adorally, aborally noncrenulate or (exceptionally) subcrenulate. Primary spines with more or less distinct longitudinal regular rows of spinules, sometimes forming ridges. Oral primaries flattened, smooth, slightly serrate. Large and small globiferous pedicellariae with end tooth; tridentate pedicellariae present. *Rec.,* Atl.-Medit.-Ind.O.——FIG. 247,*2*. **C. cidaris* (LINNÉ); test, lat., ×0.75 (136a).

[It is unfortunate that the primary type of the order and family, *Cidaris cidaris* (LINNÉ), should belong to a small group of Atlantic forms characterized by the presence of end teeth on large and small globiferous pedicellariae,

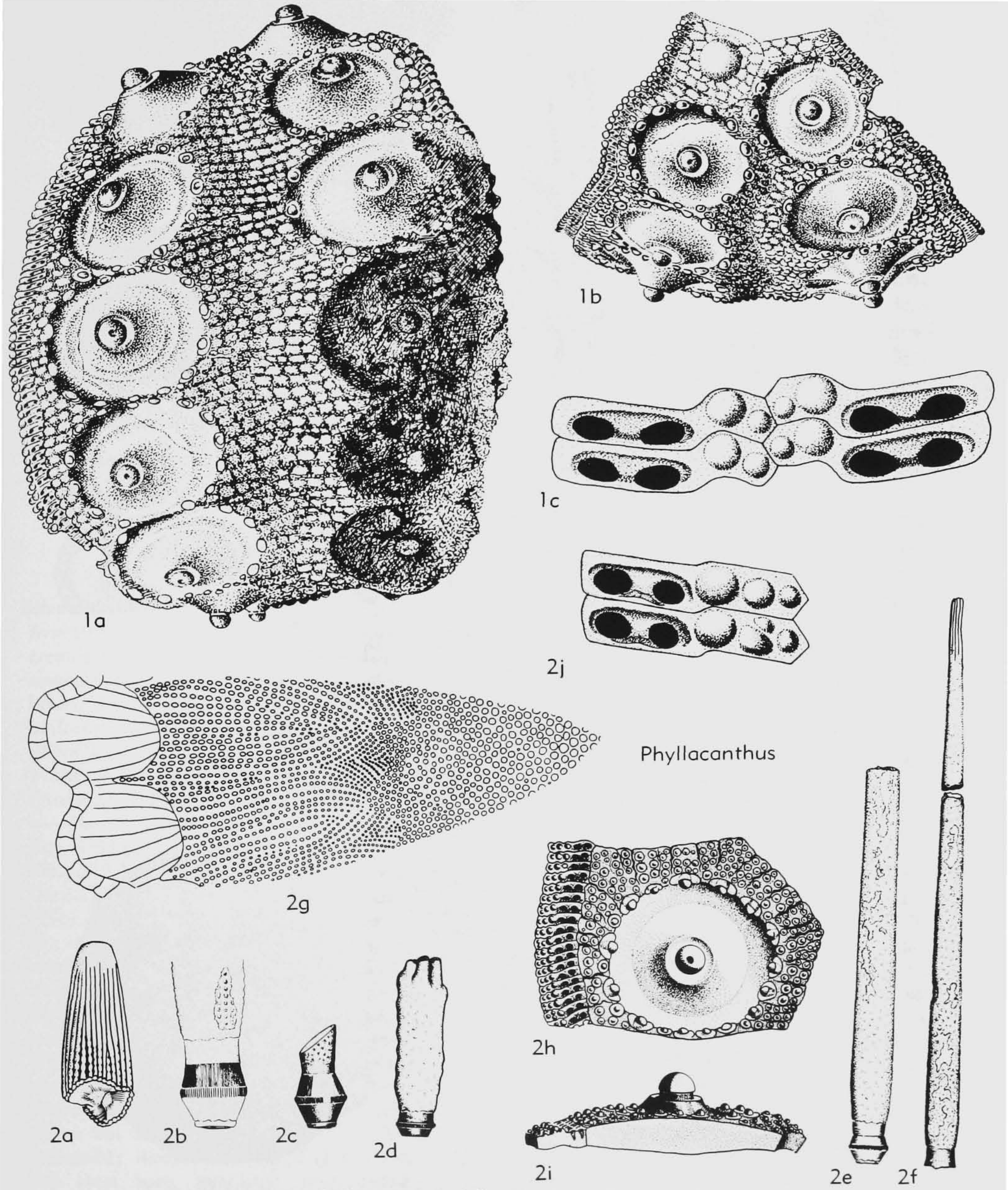

FIG. 246. Cidaridae (Rhabdocidarinae) (p. U330).

features of very slight paleontological significance; in fact, no valid fossil species has yet been described for the genus *Cidaris*. On the other hand, since it is the primary type-genus, it has long been the practice to assign to it all fossil species whose precise generic position has not been established. In this sense the name is without taxonomic validity, and should therefore be distinguished in some way—such as *"Cidaris,"* or *"Cidaris"* s.l. (=*Cidarites* auctt., *non Cidaris* LESKE).] [=*Cidarites* LAMARCK, 1816, p. 52 (=jr. hom., ICZN Art. 20, 56b)—MOORE.]

Alpicidaris LAMBERT, 1910, p. 4 [**A. cureti*; OD]. Ambulacral plates tending to form diads or triads, especially adorally, where one marginal tubercle occurs on every 2nd or 3rd plate. Primary tubercles noncrenulate; areoles transversely oval, not well separated, more or less confluent below ambitus. Spines unknown. *L.Cret.(Hauteriv.)*, Eu.——FIG. 248,*1*. **A. cureti*, Fr.; *1a*, test, lat., ×1.1; *1b*, amb plates, ×2.2 (115).

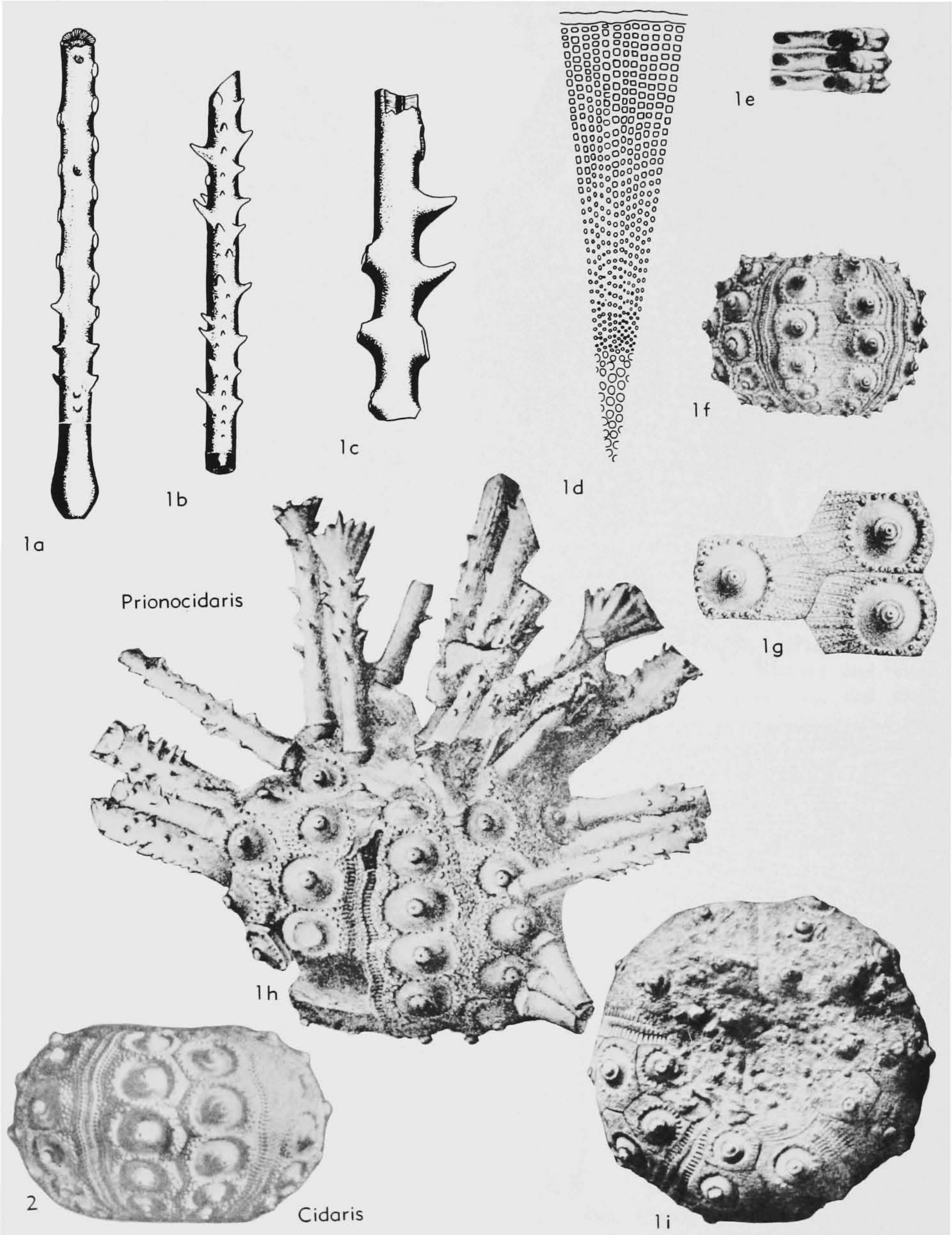

FIG. 247. Cidaridae (Rhabdocidarinae) *(1)*, (Cidarinae) *(2)* (p. *U*330-*U*331).

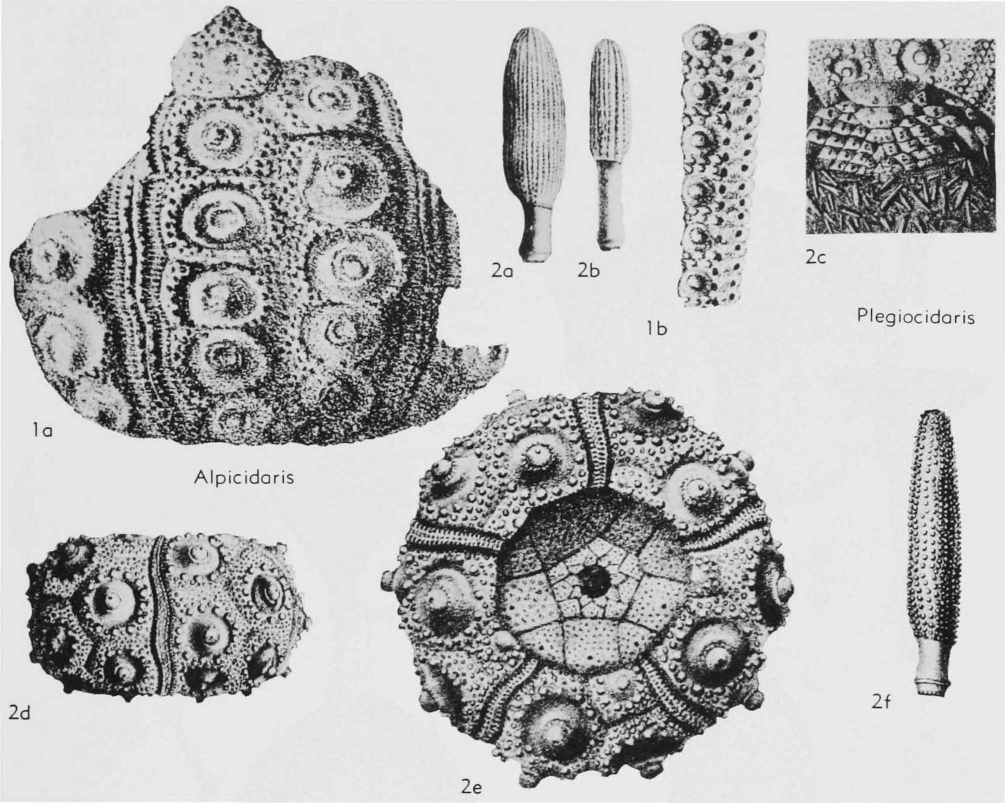

FIG. 248. Cidaridae (Cidarinae) (p. *U332*, *U337*).

Balanocidaris LAMBERT, 1910, p. 4 [**Cidaris glandifera* MÜNSTER, 1843; OD]. Primary tubercles noncrenulate. Primary spines glandiform. Ambulacra sinuous, pore-zone narrow, interporiferous area broad, densely tuberculate, tubercles arranged in uniform longitudinal and horizontal rows. *U.Trias. (Carn.)*, Eu.; *Jur.*, Eu.-?Calif.; *U.Cret.*, Eu.-?Calif. ——FIG. 249,*2a,b*. *?B. pleracantha* (AGASSIZ), U.Cret., Fr.; *2a,b*, spines, ×0.9 (44).——FIG. 249,*2c,d*. *?B. californica* (CLARK), M. Jur., USA(Calif.); *2c,d*, spines, ×1.8 (22).——FIG. 249,*2e,f*. **B. glandifera* (MÜNSTER), Jur., Ger.; *2e*, spine, ×0.9 (44); *2f*, amb plates, ×1.8 (27c).——FIG. 249,*2g*. *B. roysii* (DESOR), Jur., Fr.; spine, ×1.8 (27c).

Calocidaris H. L. CLARK, 1907, p. 211 [**Dorocidaris micans* MORTENSEN, 1903; OD]. Like *Cidaris* but shaft of primary spines smooth, glabrous; all primary tubercles noncrenulate. *Rec.*, W.Indies.

Centrocidaris A. AGASSIZ, 1904, p. 32 [**Goniocidaris doederleini* A. AGASSIZ, 1898; OD]. Like *Stylocidaris* but ambulacra broad (*ca.* half as wide as interamb); median ambulacral and interambulacral areas bare, somewhat depressed, but not forming well-defined grooves; primary spines with smooth, glabrous surface; large globiferous pedicellariae with or without end tooth. *Rec.*, W.C.Am. (Cocos I.-Galapagos Is.).

Cyathocidaris LAMBERT, 1910, p. 12 [**Cidaris cyathifera* AGASSIZ; OD]. Corona high, subspherical. Interambulacral plates high, primary tubercles noncrenulate. Ambulacra sinuous, simple throughout. Primary spines of aboral side cup-shaped or trumpet-shaped, some with central prominence. *U.Cret.*, Eu.-Antarctic; *Eoc.*, *?Mio.*, Eu.——FIG. 249,*1a-c*. **C. cyathifera* (AGASSIZ), U.Cret. (Senon.), N.Fr.; *1a-c*, spines, ×0.9 (27a).——FIG. 249,*1d*. *C. erebus* LAMBERT, U.Cret., Antarctic, spine, ×0.9 (108).——FIG. 249,*1e*. *C. crateriformis* (GÜMBEL), Eoc., Fr.; spine, ×0.9 (27e).——FIG. 249,*1f-h*. *C. nordenskioldi* LAMBERT, Cret., Antarctic; *1f-h*, spines, ×0.9 (108).

Eucidaris POMEL, 1883, p. 109 [**Cidarites metularia* LAMARCK, 1816; SD CLARK & BATHER, 1909, p. 88] [=*Cidaris* A. AGASSIZ, 1872 (*non* LESKE, 1778); *Gymnocidaris* A. AGASSIZ, 1863 (type, *Cidarites metularia* LAMARCK, 1816) (*non* L. AGASSIZ, 1838)]. Like *Stylocidaris* but madreporite slightly larger than other genital plates; primary spines typically cylindrical, truncate, otherwise fusiform or clavate; shaft abruptly trun-

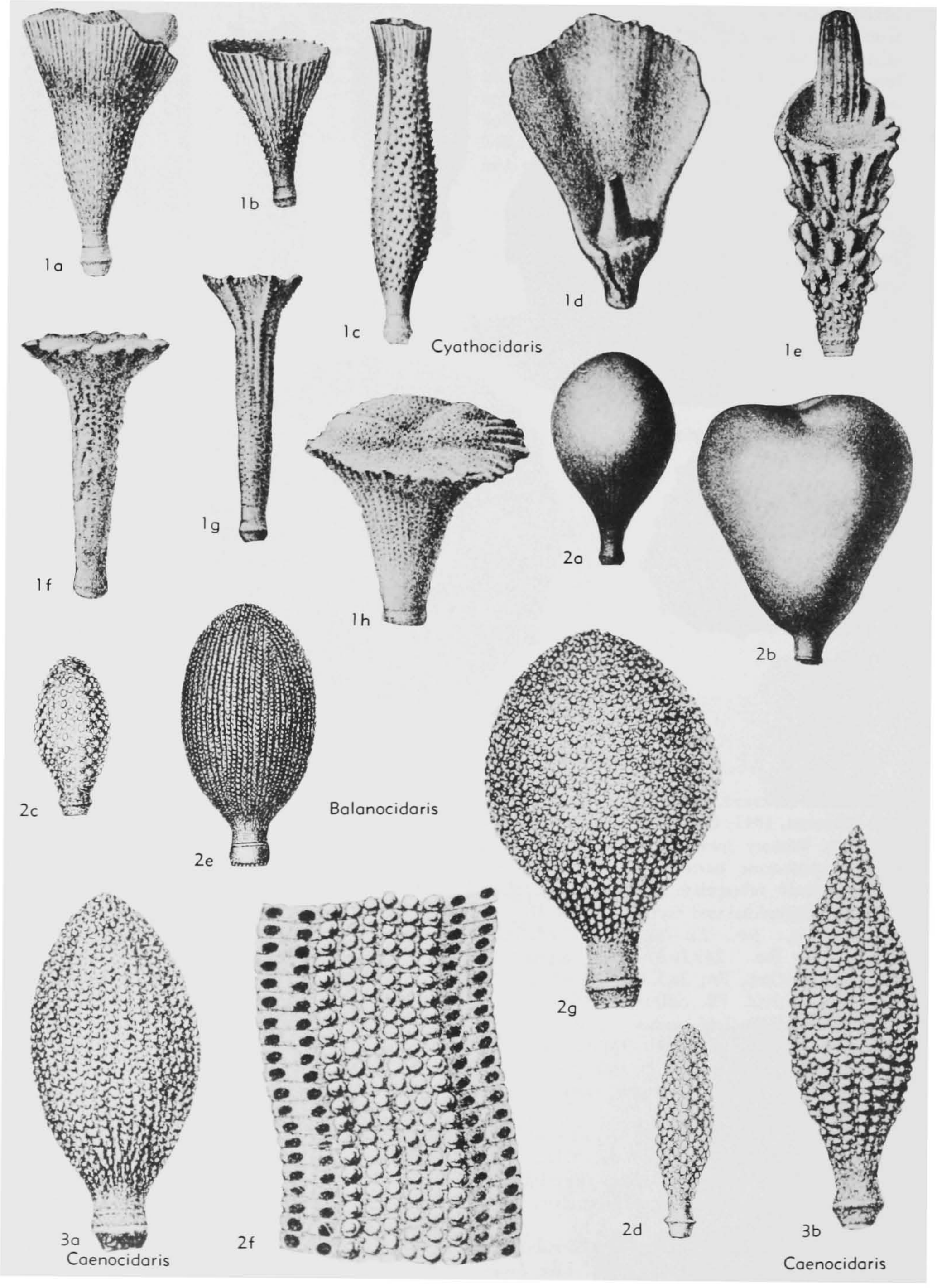

Fig. 249. Cidaridae (Cidarinae) *(1,2)*; Psychocidaridae *(3)* (p. *U*333, *U*339).

cate, terminating in crown with central prominence, and with low, rounded warts disposed in regular, longitudinal series; secondary spines adpressed; tridentate pedicellariae of 2 types, valves either straight or curved. *U.Eoc.,* N.Z.; *Oligo.,* N.Z.; *Mio.,* Fiji-?Australia-Calif.-W.Indies; *Plio.,* Calif.; *Rec.,* trop. and subtrop.——FIG. 250,*1a-f*. *E. strobilata* FELL, U.Eoc.-L.Oligo., N.Z. (*1-3,* U. Eoc.; *4-6,* L.Oligo.); *1a-f,* spines, ×2.8.——FIG. 250,*1g,h*. *E. coralloides* FELL, L.Oligo., N.Z.; *1g,h,* spine, lat. and top, ×2.1 (56).

Hesperocidaris MORTENSEN, 1928, p. 73 [**Dorocidaris panamensis* A. AGASSIZ, 1898; OD]. Like *Stylocidaris* but primary spines cylindrical, not tapering, some conspicuously expanded at tip, with low granules arranged in longitudinal series. *?Eoc.,* Calif.; *Rec.,* Calif.-W.Panama-Ecuador.

Kionocidaris MORTENSEN, 1932, p. 165 [**K. striata*; OD]. Like *Stylocidaris* but primary spines columnar, slightly tapering, with about 25 shallow flutes on shaft, low elevations between flutes and regular longitudinal series of pores in surface of distal region. *Rec.,* Natal.

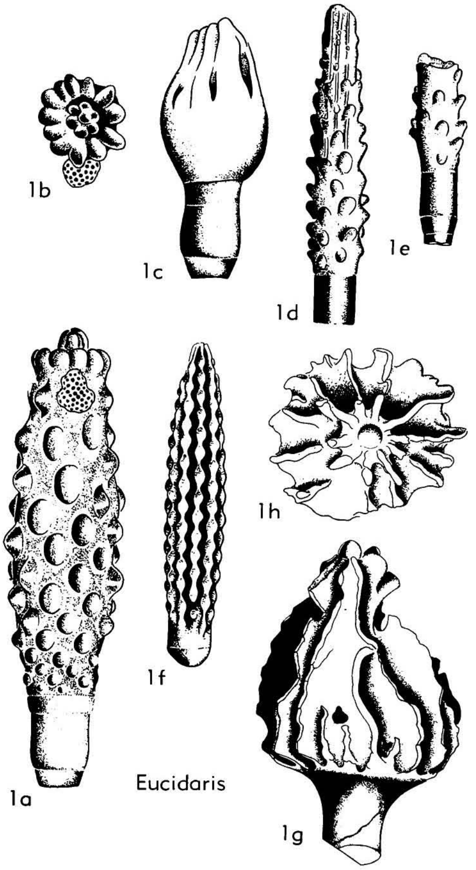

FIG. 250. Cidaridae (Cidarinae) (p. *U*333, *U*335).

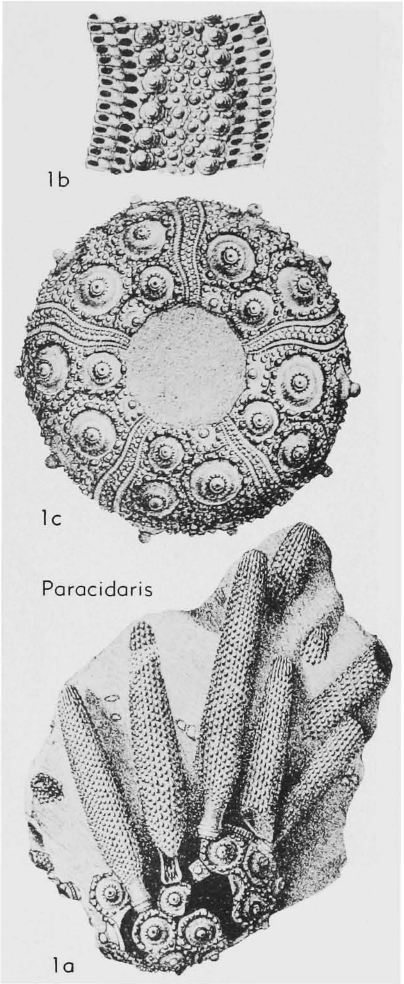

FIG. 251. Cidaridae (Cidarinae) (p. *U*335, *U*337).

Lissocidaris MORTENSEN, 1939, p. 11 [**L. fusca*; OD]. Like *Calocidaris,* but cortex layer of spines covered by thick anastomosing layer of hairs which coalesce to produce smooth, glabrous investment about shaft. *Rec.,* Ind.O. (Maldive Is.).

Paracidaris POMEL, 1883, p. 109 [**Cidarites florigemma* PHILLIPS, 1829; SD LAMBERT & THIÉRY, 1910, p. 135]. Ambulacral plates simple but tending to form diads, especially adorally, where one marginal tubercle occurs on only every alternate plate. Primary tubercles crenulate; areoles rounded, well separated; scrobicular tubercles larger than other secondaries; primary spines thick, clavate or fusiform, collar short, shaft with coarse, uniform spinules in regular longitudinal series. *U. Trias.(Rhaet.)-U.Jur.(Portland.),* Eu.——FIG. 251, *1*. **P. florigemma,* U.Jur.(Oxford.), Fr.; *1a,* test

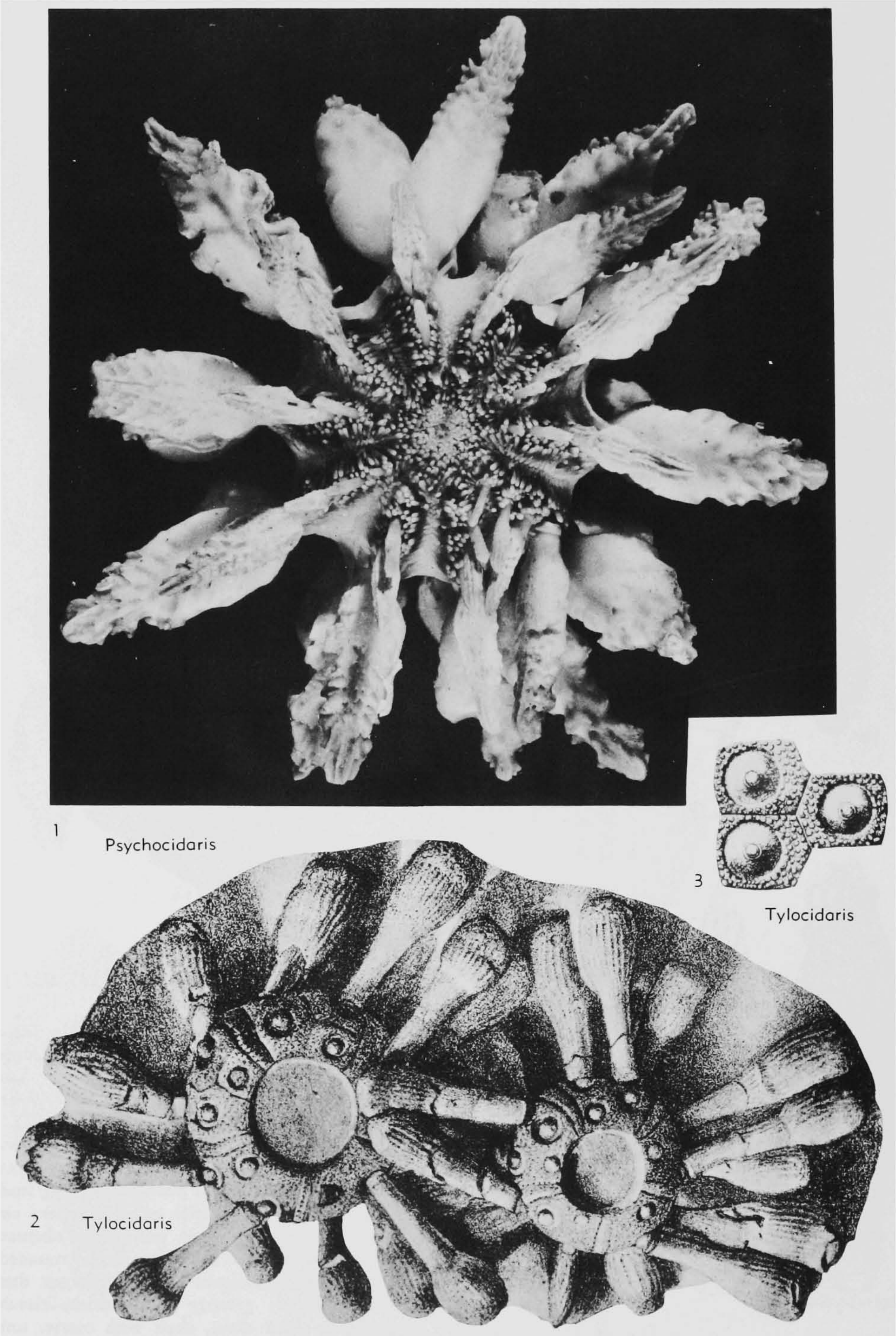

FIG. 252. Psychocidaridae (p. *U*338-*U*339).

with spines, ×0.7; *1b,* amb plates, ×3.5; *1c,* test, aboral, ×1.4 (27c).

Plegiocidaris Pomel, 1883, p. 109 [**Echinus coronatus* von Schlotheim, 1820; SD Lambert & Thiéry, 1910, p. 135]. Like *Paracidaris* but ambulacra simple throughout corona, becoming pluriserial only on peristome. Primary radioles with long cylindrical collar, and cylindrical shaft as long as collar or 2 or 3 times longer, diameter of shaft twice that of collar; transition from collar to shaft oblique, with abrupt change in diameter of spine. *U.Trias.(Nor.)-U.Jur.,* Eu.——Fig. 248, *2a-e.* **P. coronata* (von Schlotheim), U.Jur. (Oxford.), Ger.; *2a,b,* spines, ×1; *2c,* peristome, ×2.25; *2d,e,* test, lat., aboral, ×1, ×1.3 (145). ——Fig. 248,*2f. P. cervicalis* Agassiz, U.Jur.(Oxford.), Fr.; spine, ×0.75 (44).

Stylocidaris Mortensen, 1909, p. 52 [**Cidaris*

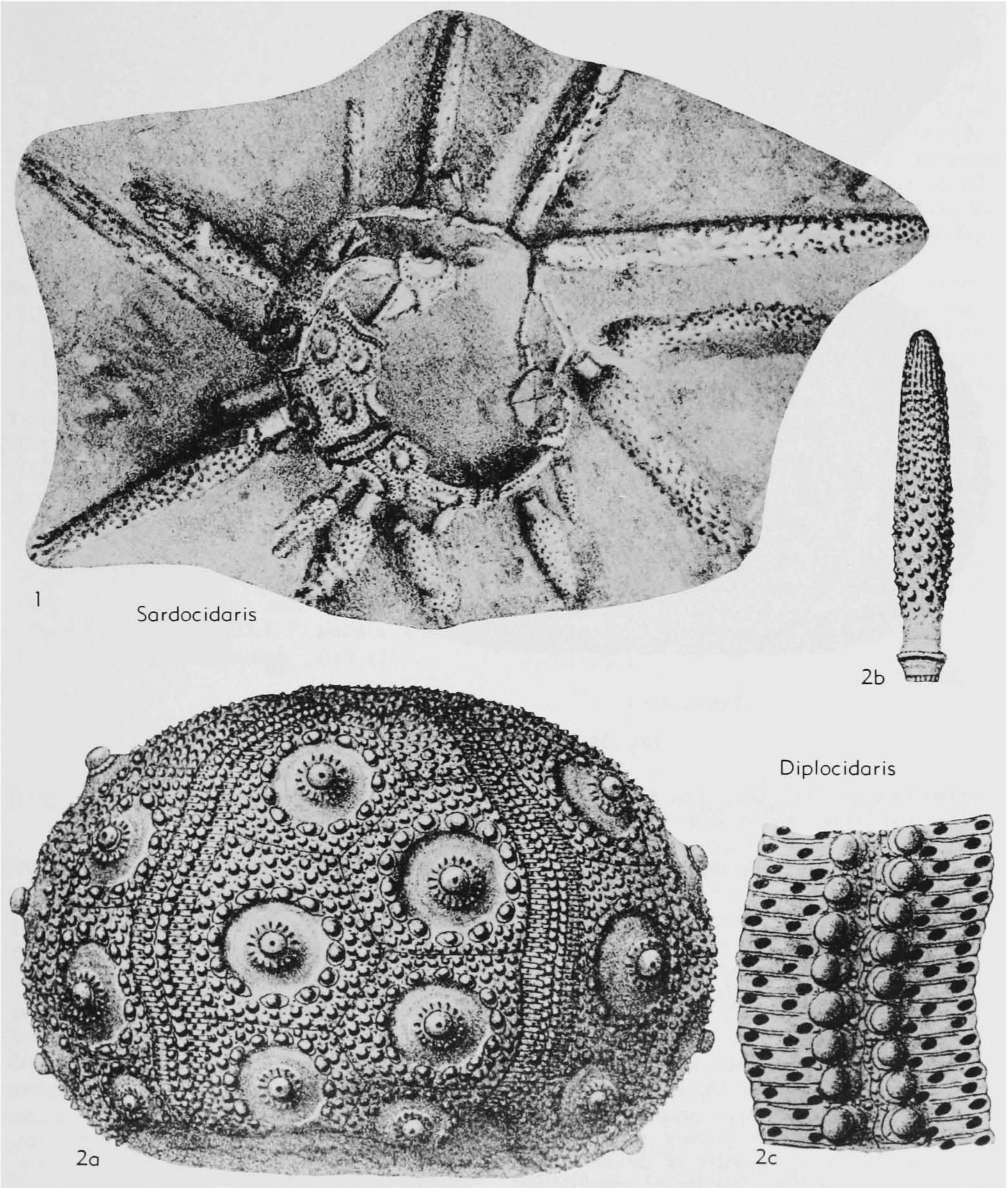

Fig. 253. Psychocidaridae *(1)*; Diplocidaridae *(2)* (p. *U*339).

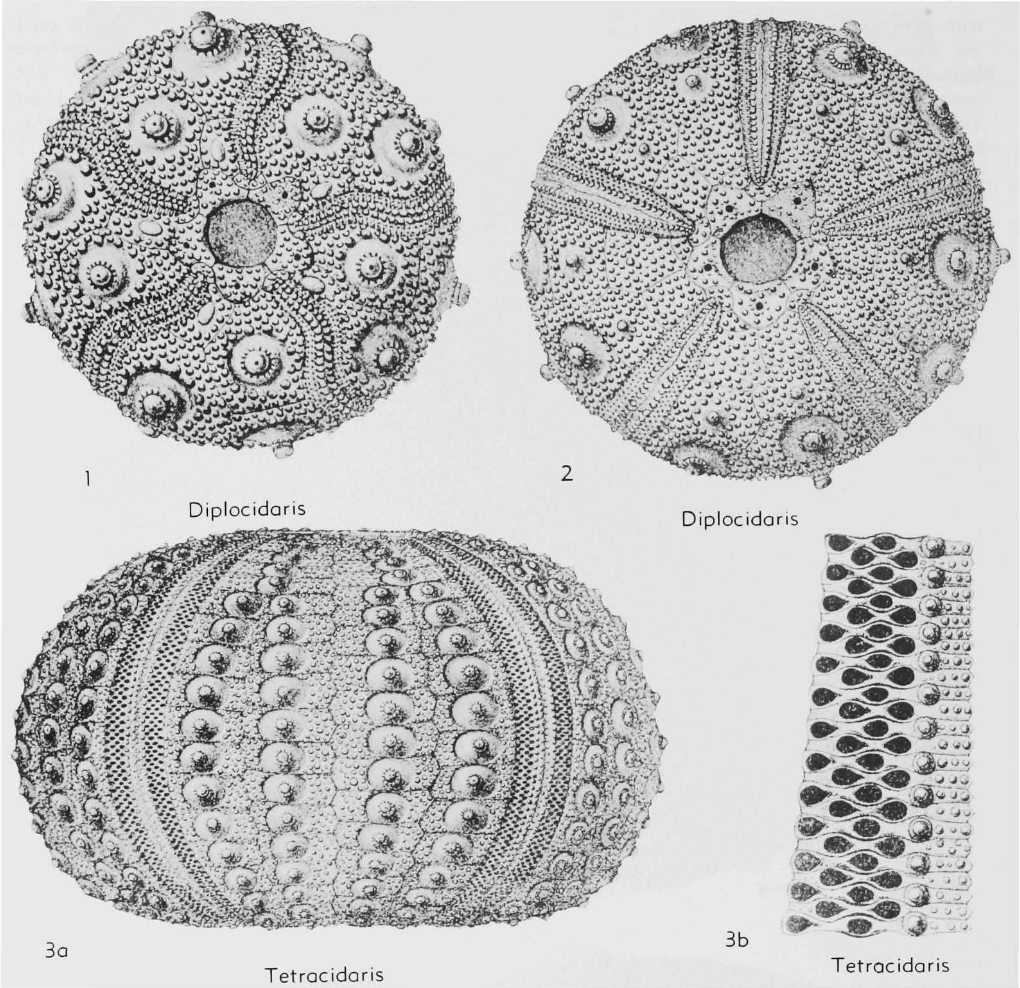

FIG. 254. Diplocidaridae (p. *U*339).

affinis PHILIPPI, 1845; OD]. Test usually flattened above and below. Areoles deep or shallow, well separated, only proximal 2-3 confluent; primary tubercles noncrenulate adorally, some weakly subcrenulate aborally, especially in young stages, otherwise noncrenulate aborally. Primary spines usually tapering to point; secondary spines more or less flattened, not adpressed. Tridentate pedicellariae slender; large globiferous without small end-tooth, globiferous with them. *Mio.*, Medit.; *Rec.*, trop. and subtrop. seas.

Tretocidaris MORTENSEN, 1903, p. 28 [**Dorocidaris bartletti* A. AGASSIZ, 1880; OD]. Like *Cidaris* but areoles very shallow, well separated; primary tubercles all noncrenulate. Primary spines cylindrical, coarsely thorny, spinules in distinct longitudinal ridges, end in some forms conspicuously widened; shorter spines commonly more or less cup-shaped. *Rec.*, trop. Atl.

Family PSYCHOCIDARIDAE Ikeda, 1936

Primary tubercles imperforate. Pores nonconjugate, commonly separated by prominent wall. No peristomial interradial plates; peristomial ambulacral plates in double series. *U.Jur.-Rec.*

Psychocidaris IKEDA, 1935, p. 386 [**P. ohshimai*; OD]. Test low, of moderate size, flattened above and below, plates robust with rigid sutures. Apical system nearly half of horizontal diameter. Madreporite scarcely larger than other genital plates. Areoles large, sunken; primary tubercles large, hyaline, noncrenulate; few upper ones (immature) weakly perforate. Upper primary spines glandiform, ambital primaries longer, somewhat flattened, oral primaries cylindrical; all primaries, save orals, with coarse irregular thorns; cortex bulky, spongy, containing cavities (dry spines having density of *ca.* 0.6). Large globiferous pedicellariae without poison chamber. *Rec.*, Bonin Is. (180 m.).——FIG. 252,*1*. **P. ohshimai*; oral view of test with spines, ×0.9 (Fell, n).

Anisocidaris THIÉRY, 1928, p. 181 [**Cidaris bajocensis* COTTEAU, 1880; OD]. Like *Caenocidaris*, but pore zones widened, pores nonconjugate. *M. Jur.(Bajoc.)*, Eu.

Caenocidaris THIÉRY, 1928, p. 180 [**Cidaris cucumifera* AGASSIZ, 18??; OD]. Like *Merocidaris* but adoral ambulacral plates biserial. *M.Jur.(Bajoc.)*, Eu.——FIG. 249,*3*. **C. cucumifera* (AGASSIZ), Fr.; *3a,b*, spines, ×1.8 (27c).

Merocidaris THIÉRY, 1928, p. 180 [**Cidaris honorinae* COTTEAU, 1880; OD]. Adoral primary tubercles imperforate, noncrenulate; aboral primary tubercles perforate, crenulate. *Jur.(Bajoc.-Kimmeridg.)*, Eu.

Sardocidaris LAMBERT, 1907, p. 22 [**S. piae*; OD]. Like *Psychocidaris* but primary spines long, cylindrical, tapering, not glandiform. *M.Cret.*, N. Afr.; *Mio.*, Eu.——FIG. 253,*1*. **S. piae*, L.Mio., Eu.(Sardinia); test with spines, ×1 (107).

Tylocidaris POMEL, 1838, p. 109 [**Cidaris clavigera* KÖNIG, 1820; SD LAMBERT & THIÉRY, 1910, p. 156]. Like *Psychocidaris* but primary spines with fine spinules, not coarse thorns, on glandiform and other spines, spinules scattered irregularly or in regular longitudinal series. *U.Cret.*, Eu.(Eng.-Fr.-Denm.); *L.Eoc.*, N.Am.——FIG. 252,*2*. **T. clavigera* (KÖNIG), Eng.; tests with spines, oral, ×0.9 (173).——FIG. 252,*3*. *T. walcotti* (CLARK), L.Eoc., USA(N.J.); interamb, ×0.9 (22).

Family DIPLOCIDARIDAE Gregory, 1900

Plates of ambulacra arranged in diads throughout, marginal tubercles developed on alternate plates only, pore zone biserial. Primary tubercles perforate. *Jur.-Cret.*

Diplocidaris DESOR, 1855, p. 44 [**Cidaris gigantea* AGASSIZ, 18??; SD LAMBERT & THIÉRY, 1910, p. 138] [=*Alternocidaris* QUENSTEDT, 1873 (obj.)]. Interambulacral plates in 2 columns throughout; primary tubercles crenulate. Pores conjugate or subconjugate, uppermost more or less rudimentary. Primary spines cylindrical, short, granulated. *L.Jur.-L.Cret.*, Eu.——FIG. 253,*2*. **D. gigantea*, U.Jur. (Kimmeridg.), Fr.; *2a,b*, test lat., spine, ×1; *2c*, amb plates, ×4.——FIG. 254,*1*. *D. miranda* (AGASSIZ), U.Jur.(Kimmeridg.), Fr.; test, aboral, ×0.8.——FIG. 254,*2*. *D. etalloni* DE LORIOL, U. Jur.(Raurac.), Fr.; test, aboral, ×0.7 (27c). [=?*Diplotiaris* QUENSTEDT, 1872, p. 36.]

Tetracidaris COTTEAU, 1872, p. 445 [**T. reynesi*; OD]. Interambulacral plates in 4 columns at ambitus, in 2 columns adapically and adorally. Pores distant but nonconjugate. Primary tubercles crenulate. Primary spines cylindrical, slender. *L.Cret. (Neocom.)*, Eu.——FIG. 254,*3*. **T. reynesi*, Fr.; *3a*, test, lat., ×0.8; *3b*, amb plates, ×4 (28).

Order and Family UNCERTAIN

Lanternarius REGNÉLL, 1956, p. 171 [**L. latens*; OD]. Known only from lantern; pyramids large, adperradial walls adapically with internal excavation; epiphyses narrow, but uniting over moderately deep foramen magnum. *Sil.*, Sweden (Gotl.).——FIG. 234,*3*. **L. latens*; *3a,b*, parts of lantern, ×3 (148).

EUECHINOIDS

By H. BARRACLOUGH FELL (with sections by R. V. MELVILLE and by H. B. FELL and D. L. PAWSON)

[Victoria University of Wellington, New Zealand; transferred to Harvard University]

Subclass EUECHINOIDEA Bronn, 1860

[Diagnosis and discussion by H. B. FELL]

Test composed of 5 bicolumnar ambs and 5 alternating bicolumnar interambs. Plates imbricating, or joined by flexible integument, or (more usually) united by rigid sutures. Anus and surrounding periproct either placed within apical system (endocyclic condition) or secondarily translocated to interamb 5, which is termed posterior interamb (exocyclic condition). Lantern present or absent, or present only in juvenile stage. Gills and gill slits present or absent. Spheridia present. Pedicellariae present, including ophicephalous types. *?Carb., U. Trias.-Rec.*

The included groups are here classified as 18 orders which, following proposals of DURHAM & MELVILLE (52), may be arranged in four superorders, namely Diadematacea, Echinacea, Gnathostomata, and Atelostomata. The evolutionary trends exhibited are so diverse as to require separate treatment under the subsidiary taxa. In general, however, the first two superorders are characterized by remaining predominantly radially symmetrical subspherical forms, similar to the Cidaroida, but differing conspicuously in exhibiting a persistent trend toward compounding of the ambulacral plates, especially in groups of three.

The Diadematacea achieve this compounding by a different method from that observed in the Echinacea; the details are given under the superorders. In addition, many of the Echinacea achieve a greater complexity of jaw structure than is found in the Diadematacea.

The other two superorders, Gnathostomata and Atelostomata, retain simple amb plates, without compounding of the elements, but differ in structure of the dental apparatus, which tends to disappear in the postembryonic stages of development, and in the degree to which a secondary bilateral symmetry comes to be superimposed upon the earlier radial symmetry. All members of the Gnathostomata and Atelostomata are exocyclic, that is, the anus and periproct have entered the posterior interamb. One group of Diadematacea, however, the Pygasteroida, also shows an early exocyclic condition, and the structure of the jaws and other features suggest that the Pygasteroida do not share a common derivation with that of the other exocyclic groups.

This implies that the older classification, in which all exocyclic echinoids were grouped in one taxon, the Irregularia, is unlikely to reflect natural relationships, and accordingly should be discarded (52). In practice, however, the older term Irregularia does virtually correspond to the two taxa Gnathostomata and Atelostomata, here recognized, differing only by including the Pygasteroida, a very small group. Similarly, the older taxon Regularia (including all endocyclic forms, i.e., forms in which the anus remained within the apical system) corresponds to the groups Perischoechinoidea, Diadematacea, and Echinacea, excluding only the Pygasteroida.

Although the classification here employed seems superficially to differ widely from that in general use hitherto, including that used in MORTENSEN's monograph (136), the differences are more apparent than real, for, as DURHAM & MELVILLE (65) have stressed, MORTENSEN himself demonstrated that the probable affinities of the various taxa are those implicit in the arrangement here presented.

DIADEMATACEA

By H. BARRACLOUGH FELL

INTRODUCTION

The Diadematacea comprise an assemblage of Euechinoidea all characterized by retaining a lantern of the same type as found in the Cidaroida (aulodont dentition). Most members of the group also have well-developed gills and gill slits, and the tubercles are always perforate. The amb plates in primitive, older genera retain the simple structure seen in cidaroids, but in most Diadematacea they tend to become compounded; in the latter case, the compounding follows the so-called diadematoid or arbacioid patterns, as defined below.

The assemblage is here regarded as comprising four orders, grouped to form a taxon of higher status to which DURHAM & MELVILLE (65) assigned the rank of superorder. The origins of the Diadematacea are not entirely clear, but recent opinion derives all from a cidaroid ancestry (65). This topic is referred to below (p. *U*344), where a polyphyletic derivation is considered as possible, though improbable. The earliest Diadematacea, so far known, are of Late Triassic age, though it is possible that some fragmentary Lower Carboniferous fossils may be referable to the group. The three surviving orders are mainly deep-water forms of cosmopolitan distribution, though one family, the Diadematidae, comprises littoral and sublittoral representatives found in tropical and subtropical waters, especially of the Indo-Pacific. One order (Pygasteroida) is extinct. The extant members are all more or less venomous, the spines either carrying terminal venom glands or producing a toxic secretion over the shaft itself, which is sharp and fragile and capable of penetrating the skin of predators.

MORPHOLOGY

The test and other skeletal features have fundamentally the structure seen in Cidaroida; hence the only aspects requiring particular mention are those which differ from that order.

GENERAL NATURE OF TEST

The body shape is subspherical, ranging from high subconical forms among the Pedinoida (e.g., *Leiopedina,* see Fig. 267,*3*) to depressed hemispherical or rotular forms, as in the other orders. In the Pygasteroida (see Fig. 270, 271) the anus and periproct lie partly or entirely in one interamb, giving an axis of bilateral symmetry, but despite this, the overall radial symmetry remains conspicuous, and the body does not lose its hemispherical or rotular form, though it may be truncated posteriorly in *Pygaster* (see Fig. 271).

The size of the body ranges from small forms of *ca.* 10 mm. horizontal diameter, to large ones up to *ca.* 150 mm. diameter (e.g., *Micropyga, Asthenosoma*).

As in some of the Paleozoic orders, a persistent tendency to develop imbricating plates is seen, imparting more or less flexibility to the test. This is especially marked in the order Echinothurioida and in some families of Diadematoida, especially the Diadematidae and Micropygidae. In the orders Pedinoida and Pygasteroida such flexibility is lacking.

APICAL SYSTEM

The apical system shows very great variation, and is evidently indicative of some major trends of evolution within the Diadematacea. A completely monocyclic apex characterizes two families of Diadematoida, namely the Aspidodiadematidae and Micropygidae. In these forms the ocular and genital plates are all broadly in contact with the centrally placed periproct; an example is *Tiaridia,* an early aspidodiadematid (see Fig. 261).

In the family Diadematidae the apex is typically monocyclic also, but in the type-genus *Diadema* the anterior oculars (especially oculars II and III) tend to become exsert, probably indicating an incipient rearward movement of the periproct. The same tendency, more strongly expressed, is seen in the order Pygasteroida, where all the anterior oculars (II, III, and IV) become exsert, the posterior oculars I and V are not only in direct contact with the periproct, but are actually thrust aside by it as it moves into the posterior interamb (interamb 5) (see Fig. 271).

An intermediate condition is seen in the Lissodiadematidae, among the diadematoid families, where the posterior oculars I and V become insert, oculars II, III, and IV being exsert; or only ocular II may be exsert. All examples cited so far may be regarded as forming a sequence indicative of a persistent tendency for the periproct and anus to move backward along the axis amb III-interamb 5. There remain two orders where no such trend is conspicuous. One of these is the Echinothurioida, where the apical system is initially dicyclic, but with increasing age all oculars become insert, thus transforming the apex to a monocyclic type. A further development occurs in some echinothurioid genera, by which the oculars and genitals become separated, by resorption of their adjacent borders, or insertion of other tissue between them.

Present opinion derives the Echinothurioida from Cidaroida (52). Since the development of Cidaroida shows that the dicyclic apex is secondary to the monocyclic pattern, it appears unlikely that the initial dicyclic condition of Echinothurioida could be primitive. In such case, the adult monocyclic apex in Echinothurioida must be a tertiary condition, produced by resorption of the adapical margins of the genital plates, the periproct apparently remaining central. An alternative hypothesis, however, derives the Echinothurioida, not from Cidaroida, but from some other Paleozoic order—for example, the lepidocentrid Echinocystitoida (as postulated by MORTENSEN, 136b); so far as can be gathered from the fragmentary remains of Paleozoic echinocystitoids, the oculars seem to have been broadly insert (136b), though exceptionally they were exsert, as in *Lepidechinus* (87). The latter case, then, might imply that the exsert oculars of young Echinothurioida could be primitive. On the whole, however, the balance of evidence from other characters is not in favor of MORTENSEN's hypothesis, and hence it seems more likely that the dicyclic juvenile apex of Echinothurioida is a secondary condition, perhaps derived from a cidaroid ancestry.

Similar considerations apply to the remaining diadematacean order, the Pedinoida; here the apex is typically dicyclic throughout life, all oculars being broadly exsert (see Fig. 263,*1c*). It is possible that in some pedinoid genera (e.g., *Echinopedina*) the posterior oculars became insert, but the evidence at present is insufficient. Such insertion of the posterior oculars would not be surprising, however, for other evidence suggests that the Pygasteroida arose from a pedinoid ancestry, which would imply a backward movement of the anus and periproct in some pedinoids, with consequent insertion of oculars I and V.

PERISTOME

The peristome, like the apical system, shows wide variation in structure, and here again we may detect major evolutionary trends. In all Diadematacea there is evidence of the development of gills, but in some of the Echinothurioida the gills are secondarily lost during growth, and in no member of that order are the gills strongly developed. Thus, the peristome in Echinothurioida never shows very conspicuous gill slits, and in adults of some genera there may be no evident gill slits at all. Clearly such cases are secondary and not comparable with the condition in Cidaroida, where the absence of gill slits is due to the complete lack of gills from that order.

In other orders of Diadematacea gill slits are generally conspicuous, though exceptionally they may be inconspicuous or lacking, as in the pygasteroid *Pileus* (see Fig. 270,*3a*). The major divergence in peristome structure concerns the plating, however, and relationship of the ambs. In the Echinothurioida, as also in Cidaroida, but no other group, the ambs and interambs extend across the peristome, the peristomial amb plates carrying pore pairs, arranged like spokes in continuation of the ambs on the test itself (see Fig. 256,*2a*).

In all other Diadematacea the peristome lacks such plates, and instead has five pairs of oral plates. Such oral plates occur in the juvenile stages of Echinothurioida (136b, 52), and hence it may be inferred that the multiplated peristome of adult Echinothurioida is a secondary condition, and does not indicate a direct derivation of that order from the Paleozoic Echinocystitoida, where multiplated peristome structure also occurs (52).

AMBULACRA

The ambulacra exhibit a persistent tendency toward compounding of the plates by fusion. The compounding follows a pattern, termed diadematoid, in which successive groups of three plates unite to form one plate, the middle element being always larger than the other two elements. In simplest cases the individual amb plates remain distinguishable, each carrying a single pore pair, though a large primary tubercle usually develops only on every third plate; an example is *Plesiodiadema* (see Fig. 261,*1b*). Each of the plates carrying an enlarged tubercle is called a primary amb plate, and its unmodified adjacent neighbors are termed secondary plates.

A group of three, that is, a primary together with the adjacent secondaries on either side of it, is termed a triad. Occasionally, two instead of three plates are associated, and such pairs are termed diads. A more advanced example of compounding is seen in *Astropyga* (see Fig. 259,*5*), where the two secondaries have fused to the intervening primary, and the compound plate consequently carries three successive pore pairs arranged in a short arc. Such plates are termed trigeminate. Numerous other examples are given in illustrations accompanying this chapter, and in all cases the primary is the middle element.

Sometimes the compounding may proceed further, leading to polyporous amb plates. The exact manner in which this occurs varies. An example of a compound polyporous plate derived from the fusion of three trigeminate plates is seen in *Pelanechinus* (see Fig. 256,*2b*). This also illustrates a further process, by which some of the secondary plates become restricted to the outer part of the compound plate; that is, they fail to make contact with the radial mid-line and suture. Such secondaries are termed demiplates. Demiplates are also seen in trigeminate plates (e.g., *Phormosoma,* Fig. 257,*2*), where a large primary is flanked by a demiplate on either side. This latter pattern is sometimes termed arbacioid (for it also occurs in the order Arbacioida), but it is obviously only a variety of diadematoid pattern.

Complex patterns derived from diadematoid or arbacioid compounding are illustrated in the Echinothurioida (see Fig. 257), where the demiplates may be excluded from both the adradial and perradial margins of the amb, and may be very reduced in size. Such occluded demiplates may give a multicolumnar or pluriserial aspect to the amb in which they occur, but study of the patterns seen in the Echinothurioida makes it clear that the resemblance to pluriserial Paleozoic genera is superficial, and that the fundamental pattern is diadematoid. Hence the view advanced by MORTENSEN (136b), which related the Echinothurioida to the pluriserial perischoechinoids of the Paleozoic, does not bear close examination, and has been rejected by DURHAM & MELVILLE (52). There remain, however, more puzzling Echinothurioida (e.g., *Sperosoma*; see Fig. 257,*7*) in which the complexity of amb structure invites closer comparison with that of Paleozoic Echinocystitoida than with other Echinothurioida, and perhaps the notion of affinity between the Echinothurioida and the pluriserial Paleozoic echinoids cannot altogether be ruled out.

INTERAMBULACRA

The interambs present relatively little complexity, the main features which vary being the number of primary tubercles developed on each plate, and the number of vertical series in which the tubercles are arranged. It may be presumed that the more primitive forms would inherit a single primary tubercle on each interamb plate, as seen in cidaroids, and that the development of enlarged secondary tubercles (or additional primaries, since the two categories are not separable) is a secondary feature.

As in the Cidaroida, the primary tubercles can be either crenulate or noncrenulate. In all Diadematacea the tubercles are perforate.

The primary spines of Diadematacea are nearly always hollow, owing to the incomplete development of the medulla; this feature recalls the Archaeocidaridae. A notable exception is the order Pedinoida, where the spines are solid (at least in those cases where spines are known). The family Aspidodiadematidae is unique in having septate medullary structure; hence the central lumen of spines is divided by transverse sheets of stereom into a series of loculi. In some Echinothurioida the medulla may be almost entirely filled in, producing a secondarily solid spine; an example is *Araeosoma thetidis* (see Fig. 256,*1*). The external form of the primary spines may be significant in classification. Among Echinothurioida, for example, the subfamily Echinothuriinae is characterized by primary spines on the oral surface with terminal hooves (see Fig. 256,*1c,e*). Many of the diadematoid genera carry primary and secondary spines which have spinous processes arranged in spirals.

SPHERIDIA AND PEDICELLARIAE

Minute organs of balance termed spheridia, and pedicellariae of various types, occur on the amb plates in Diadematacea. In general their paleontological significance is slight, and they are seldom found on fossils, though the pits in which spheridia lie are sometimes observable; for example, in *Plesiodiadema* (see Fig. 261,*1b*) a spheridian pit occurs on the lower edge of the lowest plate of each triad, and similar pits are seen in the corresponding position in *Aspidodiadema* (see Fig. 261,*2*).

LANTERN

In the lantern, the structure is essentially as in Cidaroida, the teeth carrying no keel, and the foramen magnum being open above; this condition is described as aulodont. The perignathic girdle is also developed, the auricles comparable with those of cidaroids, though secondarily reduced in the post-Mesozoic Echinothurioida. This latter feature points to a cidaroid ancestry rather than to derivation from Echinocystitoida (where auricles are unknown).

CLASSIFICATION AND EVOLUTIONARY TRENDS

In the light of the foregoing review, the main groups of Diadematacea may be distinguished as follows: One stock, the order Echinothurioida, retains a peristome of cidaroid type, on which uncompounded poriferous amb plates form radial series (separated by interradial series), the test amb plates being variously compounded on a diadematoid plan, the test flexible, the spines hollow, and tubercles noncrenulate. The group has apparently given rise to no derivatives.

Another ordinal assemblage, the Diadematoida, shares diadematoid amb-compounding tendencies and hollow spines, but differs in having five pairs of oral plates on the peristome. Two families of Diadematoida have noncrenulate tubercles and a more or less flexible test; these are the Lissodiadematidae and Micropygidae, both deep-water groups. Two other families, Diadematidae and Aspidodiadematidae, have crenulate tubercles, and a more or less imbricate test (flexible only in the Diadematidae); they are distinguished mainly by their spines which are septate in the Aspidodiadematidae, nonseptate in the Diadematidae.

A third ordinal stock, the Pedinoida, differs from the preceding groups in having solid spines and a rigid test; the tubercles are noncrenulate. The diadematoid structure of the ambs, and the supraordinal characters point to a common origin with the other orders.

The remaining order, Pygasteroida, comprises a small group of genera with an exocyclic periproct, resembling the Pedinoida in other features (the nature of the dentition being uncertain, however); these are inferred to have arisen from some pedinoid ancestry (52). Both the Pedinoida and Pygasteroida are uniform assemblages, each comprising a single family. With exception of the Echinothurioida, the structure of the apex in Diadematacea points to an incipient anteroposterior axis along which bilateral symmetry becomes increasingly evident in the later families, Lissodiadematidae, Diadematidae, and in the Pygasteroida.

From the morphological features reviewed above it appears that origins of the Diadematacea probably lie among some Paleozoic cidaroid stock, and that the assemblage is more uniform than MORTENSEN (136b) believed. DURHAM & MELVILLE (52) drew attention to the fact that the oldest known echinothurioid (*Pelanechinus*) more closely resembled the Pedinoida than do extant Echinothurioida, and the amb structure of *Pelanechinus* is clearly diadematoid (see Fig. 256,*2*). It is therefore reasonable to infer a common ancestry for the orders Diadematoida, Pedinoida, and Echinothurioida. The order Pygasteroida appears to be a derivative of the Pedinoida.

ECOLOGY

Except for the Diadematidae, and the genus *Asthenosoma* among the Echinothurioida, the Diadematacea are predominantly deep-water forms. This fact, combined with the more or less imbricate and consequently fragile test structure, makes them rather rare as fossils. Most extant forms appear to be scavengers rather than predators, and the deep-water genera feed largely on detrital material, including leaves and wood of terrestrial plants, swept out to sea by rivers, subsequently sinking to the bottom. The Diadematidae are essentially littoral and sublittoral forms in tropical and subtropical seas, some genera (e.g., *Diadema, Echinothrix*) inhabiting coral reefs. These have very long, brittle, hollow spines able to puncture the skin of predators and when broken off, producing dangerous wounds on account of toxins in their substance. Various fishes and crustaceans shelter between the longer spines, secure from attack by larger animals. Parasites include gastropods and a crab (*Eumedon*) which enters and inhabits the rectum of *Echinothrix*. The reef-dwelling Diadematidae feed on tubicolous and encrusting organisms attached to the coral or substrate. Some Diadematidae have light-sensitive areas on the skin of the aboral and oral surfaces of the test, sometimes conspicuous on account of

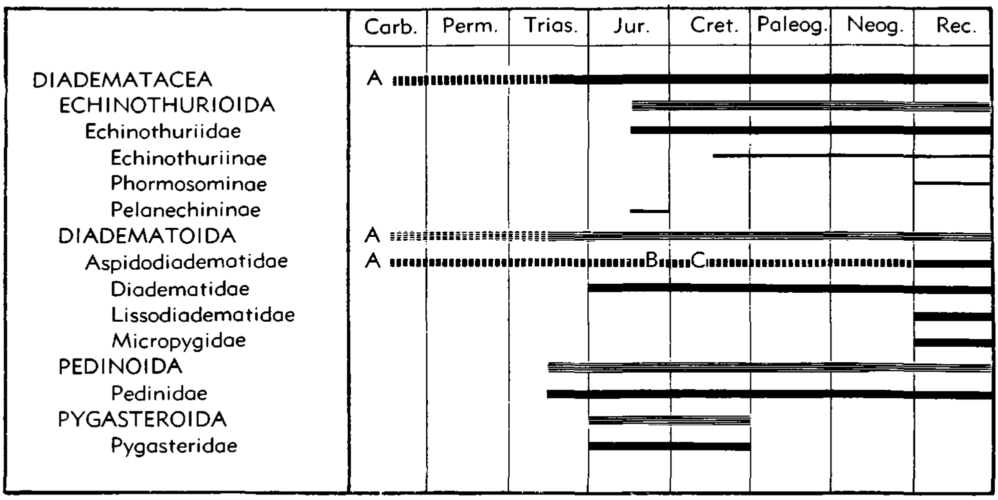

FIG. 255. Stratigraphic distribution of Diadematacea. [*A*, genus indet.; *B*, *Eosalenia* only; *C*, *Tiaridia* only; aspidodiadematid affinity of *A* possible, of *B* and *C* probable.]

the blue pigment which they contain. They are recorded as capable of detecting the shadows of approaching objects, toward which the defensive spines can be directed. The dermis which invests the whole test and spines is usually a blackish or dark purplish color.

The Echinothurioida are also venomous, but for a different reason, namely the development of poison glands on the spines, especially secondary spines. These may terminate in an acuminate tip, which is invested by venom glands (see Fig. 257,*6*). The most dangerous species are those of the shallow-water genus *Asthenosoma,* which is often entangled in fishermen's nets in the tropical and subtropical Indo-Pacific; cases of fatal injury to man are recorded from Japan (GISLÉN, 1933). *Asthenosoma,* unlike the deep-water genera of Echinothurioida, feeds on organic detritus available in littoral situations, and MORTENSEN (136b) observed intertidal specimens in Indonesia feeding selectively upon feces derived from village sewage.

Little is known of the ecology of Pedinoida. The extant species are exclusively archibenthal, and it is inferred that the fossils probably frequented similar environments on the continental slope, down to 2,000 m. The living forms apparently feed on bottom detritus and organisms such as foraminifers. The fossil genus *Pedina* was occasionally gregarious (e.g., *P. sublaevis*); species of the surviving genus *Caenopedina* appear to be rare and solitary.

Of the Pygasteroida nothing is known as to their ecology, but from the general similarity of the test structure to that of the surviving nucleolitid *Apatopygus,* it may be inferred that they probably rested upon soft bottom (shell grit or sand), and fed upon detritus.

STRATIGRAPHICAL DISTRIBUTION

The recorded time ranges of the families and subfamilies are indicated in Figure 255. Owing to the fragility of the test, it is impracticable to represent the peaking of genera by variation in thickness of the lines, for sampling on the basis of fossils is by no means comparable with that on the basis of extant forms, and such comparison would give misleading emphasis to Recent genera.

Superorder DIADEMATACEA Duncan, 1889

[=Aulodonta *sensu* MORTENSEN, 1940, *plus* Echinothuriidae THOMSON, 1872, *plus* Pygasteridae DUNCAN, 1900]

Test rigid or flexible, plates united by sutures or by membranous interstices, or imbricating beveled margins; without conspicuous bilateral symmetry. Primary tubercles perforate. Periproct endocyclic or exocyclic. Perignathic girdle complete in adult. Lantern well developed at all stages, aulodont. Gills and gill slits normally present in adult (exceptionally lacking, as secondary feature). Amb plates simple or (more usually) compounded in diadematoid or arbacioid groups, or in more complex arrangements derived from diadematoid pattern. *?L.Carb., U.Trias.-Rec.*

Order ECHINOTHURIOIDA Claus, 1880

Test low hemispherical to rotular, flexible, with imbricating plates or interstitial membranous junctions. Ambs and interambs extending in bicolumnar series across peristome. Peristomial amb plates simple, amb plates of test compounded in diadematoid (or derived) patterns, in some simulating pluriserial columns. Periproct endocyclic. Apical system dicyclic in young stages, becoming monocyclic in adult; five genital pores. Tubercles noncrenulate. Spines striate, usually hollow, exceptionally with secondary medullary infilling. Gills and gill slits inconspicuous, or lost in adult. Spheridia present aborally and adorally, located in pits beside pore pairs. Pedicellariae present, including tridentate, tridactylous,, triphyllous, and ophicephalous types. *U.Jur.-Rec.*

Family ECHINOTHURIIDAE Thomson, 1872

Characters of order. *U.Jur.(Oxford.)-Rec.*

Subfamily ECHINOTHURIINAE Thomson, 1872

[=Asthenosominae MORTENSEN, 1934]

Ambs trigeminate. Adoral primary spines with terminal hoof. Teeth with rounded tip. *U.Cret.(Senon.)-Rec.*

Echinothuria WOODWARD, 1863, p. 327 [**E. floris*; OD]. Test large (to 100 mm. diameter). Ambs and interambs of equal width, almost devoid of tubercles. Amb plates comprising enlarged primaries, with alternating demiplates located in pairs about midway across horizontal suture; primaries with or without primary tubercle, and few scattered secondary tubercles. No membranous interstices between succeeding test plates. Apical system, oral surface and spines unknown. *U.Cret. (Senon.),* Eng.——FIG. 256,*3*. **E. floris*; *3a,* test aboral, ×1; *3b,* amb aboral, ×4 (173).

Araeosoma MORTENSEN, 1903, p. 53 [**Calveria fenestratum* THOMSON, 1872, p. 494; OD]. Test large, depressed. Conspicuous membranous interstices between plates, especially of aboral surface. Primary amb plates entire, much larger than demiplates. Pores on oral surface arranged in three series on either side of the interporiferous area. *?U.Cret.(Senon.),* Eu.(Denm.-Fr.); *Plio.,* N.Z.; *Rec.,* IndoPac.-Atl., shelf-archibenthal. —— FIG. 256,*1a,b*. *A.* sp. aff. *A. thetidis* (H. L. CLARK), Plio., N.Z.; *1a,* transv. sec. of spine, ×85; *1b,* fragments of associated adapical test plates, ×7 (here first recorded).——FIG. 256,*1c*. *A. violaceum* MORTENSEN, Rec., Atl.; adoral spine shaft and hoof, ×8.5 (136b).——FIG. 256,*1d*. *A.? bruennichi* RAVN, U.Cret., Denm.; hoof, ×8.5 (147).——FIG. 256,*1e*, *A.? mortenseni* RAVN, U. Cret., Denm.; adoral spine shaft and hoof, ×8.5 (147).——FIG. 257,*6*. *A. thetidis* (H. L. CLARK), Rec., N.Atl. (360 m.); secondary spine with venom sac, ×29 (136b).

Asthenosoma GRUBE, 1868, p. 42 [**A. varium*; OD] [=*Cyanosoma* SARASIN, 1886 (type, *C. urens,* =*A. varium*)]. Like *Araeosoma* but pores arranged in 3 dense series on both adoral and aboral surfaces of test, and more slender and elongate hoof on adoral spines. Aboral spines completely invested by dermis, secondary spines with venom glands strongly developed, capable of inflicting lethal stings. *U.Cret.,* Eu.; *Rec.,* IndoPac., littoral and sublittoral.——FIG. 257,*8a,b*. **A. varium,* Ind.O.; *8a,b,* amb (aboral), juv. and adult, ×2.8 (136b).——FIG. 257,*8c*. *A. striatissimum* RAVN, *U.Cret.,* Denm., hoof, ×8.5 (147).

Calveriosoma MORTENSEN, 1934, p. 163 [**Calveria hystrix* THOMSON, 1872; OD] [=*Calveria* THOMSON, 1872 (preocc.)]. Like *Araeosoma* but membranous interstices between test plates conspicuous only on oral side. *Rec.,* N.Atl.-N.Pac. (160-1,800 m.).——FIG. 257,*4*. **C. hystrix* (THOMSON), N.Atl.; amb plates, ×4.3 (136b).

Hapalosoma MORTENSEN, 1903, p. 64 [**Asthenosoma pellucidum* A. AGASSIZ, 1879; OD]. Like *Araeosoma* but lacking primary tubercles from admedian regions of amb and interamb plates. *Rec.,* Indon.-Japan (shelf-archibenthal). —— FIG. 257,*3*. **H. pellucidum* (AGASSIZ), Indon.(Kei Is.); amb, adapical, ×5.7 (3).

Hygrosoma MORTENSEN, 1903, p. 59 [**Phormosoma petersii* A. AGASSIZ, 1880; OD]. Pores on oral surface arranged in single series placed near abradial margin of amb. Aboral demiplates small, wholly enclosed within primary plates, which alone reach abradial margin of amb. *Rec.,* IndoPac.-Atl. (200-3,000 m.).

Sperosoma KOEHLER, 1897, p. 304 [**Sperosoma grimaldii*; OD]. Test large. Primary amb plates divided into 2 parts by longitudinal (adradial) fissure, adradial portion carrying pore pair, adradial nonporiferous area. *Rec.,* IndoPac.-Atl. (300-2,300 m.).——FIG. 257,*7*. **S. grimaldii,* E.Atl.; amb adoral, ×4.3 (136b).

Tromikosoma MORTENSEN, 1903, p. 62 [**T. koeh-*

leri; OD] [=*Echinosoma* Pomel, 1883, p. 108 (*non* Audinet-Serville, 1839; *nec* Semper, 1868; *nec* Wollaston, 1854)]. Pores on oral surface arranged in single series placed near adradial margin of amb. Demiplates on aboral surface forming transverse pairs, outer member reaching ab-

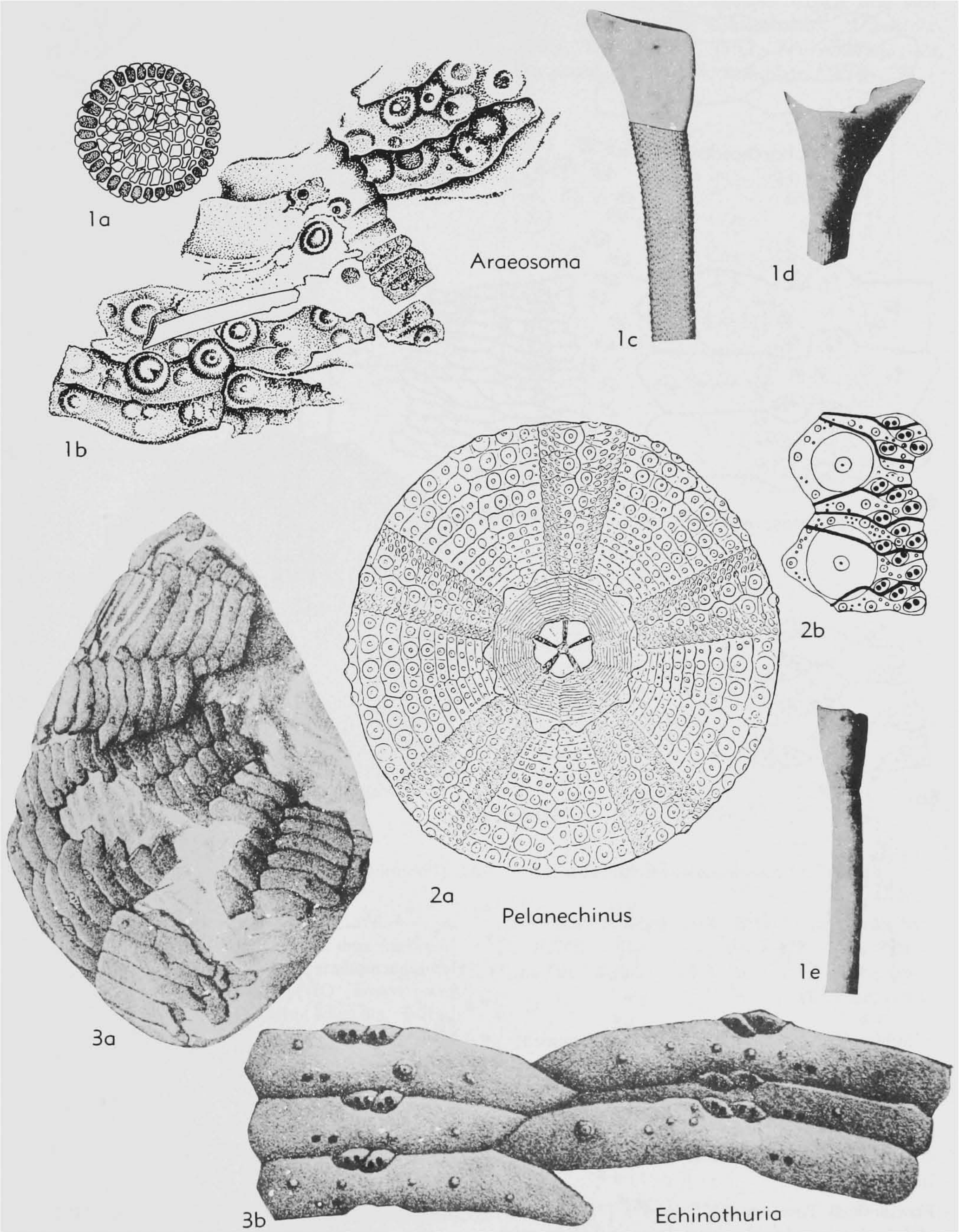

Fig. 256. Echinothuriidae (Echinothuriinae) *(1,3)*, (Pelanechininae) *(2)* (p. *U*346, *U*349-*U*350).

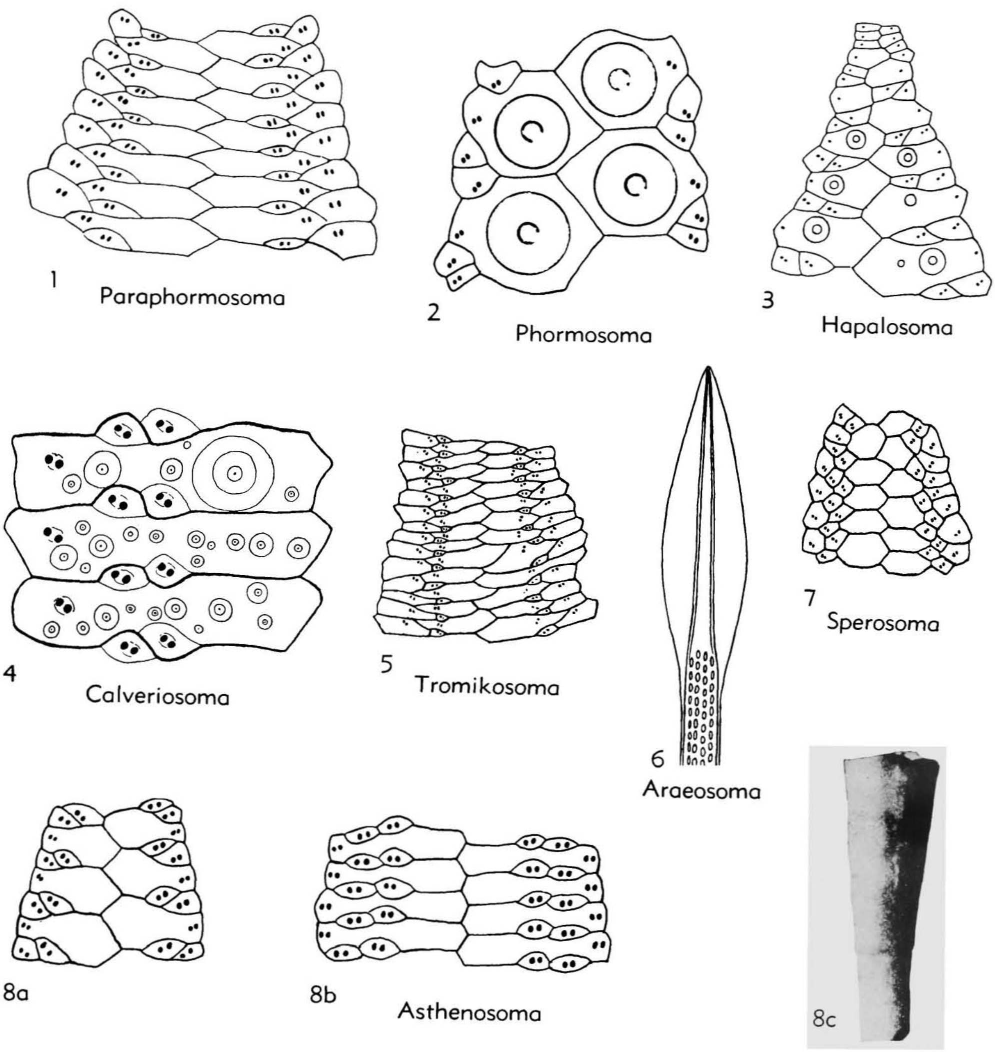

FIG. 257. Echinothuriidae (Echinothuriinae) *(3-8)*, (Phormosomatinae) *(1-2)* (p. *U*346-*U*348).

radial margin of amb. *Rec.*, IndoPac.-Atl. (deep water only, 850-3,500 m.).——FIG. 257,*5*. *T. panamense* A. AGASSIZ, E.Pac. (2,400-3,300 m.); amb, ×2.9 (3).

Subfamily PHORMOSOMATINAE Mortensen, 1934

[*nom. correct.* FELL, herein (*pro* Phormosominae MORTENSEN, 1934, p. 162)]

Ambs polyporous, plates triple-comclavate, without terminal hoof. Teeth acuminate. *Rec.*

Phormosoma THOMSON, 1872, p. 493 [**P. placenta*; OD]. Areoles of oral surface large and deep, with raised margin, giving honeycomb appearance to lower side of test. *Rec.*, IndoPac.-Atl. (shelf-abyssal).——FIG. 257,*2*. **P. bursarium* A. AGASSIZ, IndoPac.; amb adoral, ×2.9 (136).

Hemiphormosoma MORTENSEN, 1934, p. 162 [**H. paucispinum*; OD]. Distal (ambital) plates alone having enlarged areoles. Primary tubercles not forming regular series. *Rec.*, Indon. (4,000 m.).

Paraphormosoma MORTENSEN, 1934, p. 162 [**Phormosoma alternans* DE MEIJERE, 1902; OD]. Areoles not enlarged. Primary tubercles arranged in regular series from aboral to oral surface. *Rec.*, Indon. (archibenth.).——FIG. 257,*1*. **P. alternans*; amb, ×3.6 (136b).

Subfamily PELANECHININAE Groom, 1887

[*nom. transl.* GREGORY, 1900 (*ex* Pelanechinidae GROOM, 1887)]

Ambs polyporous, plates triple-compounded from successive diadematoid triads. *U.Jur.*, Eu.

Pelanechinus Keeping, 1878, p. 924 [**Hemipedina corallina* Wright, 1856; OD, M]. Test to 100 mm. diameter. Amb plates bearing one enlarged primary tubercle, its areole formed (more or less) by 3 primary amb elements, with which are associated 6 other demiplates; pores of each compound amb plate arranged in 3 arcs of 3. Up to 4 primary tubercles on ambital interamb plates. Conspicuous gill clefts. Plates of peristome in regular series, ambs here with pores in double series. Pedicellariae tridentate (coarse and slender), possibly also ophicephalous. *U.Jur.(Oxford.)*, Eng.——Fig. 256,2. **P. corallinus*; *2a*, test adoral, ×0.57; *2b*, amb plates, ×2.9 (77).

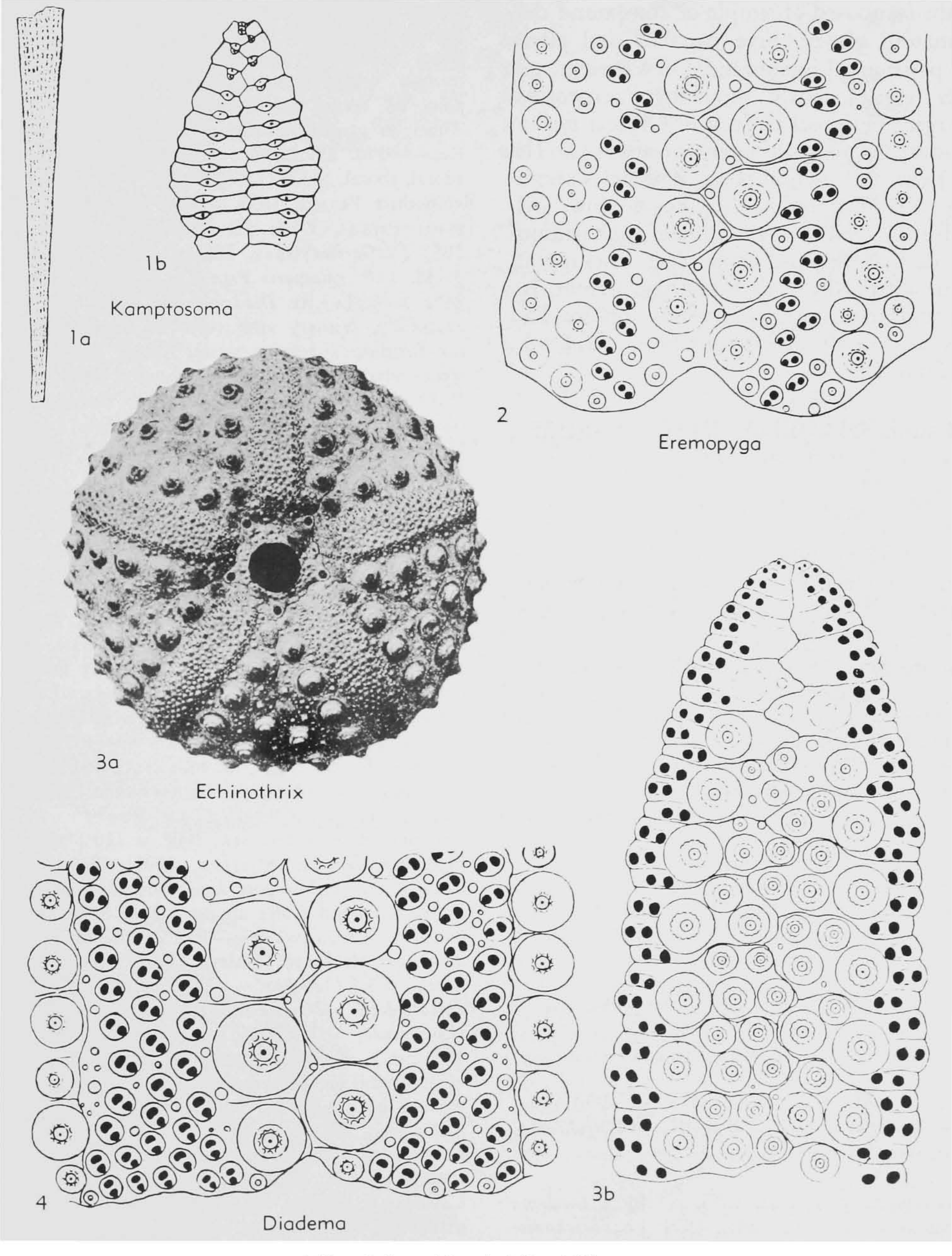

Fig. 258. Diadematidae (*U*350-*U*352).

Order DIADEMATOIDA Duncan, 1889

[=Diademaria Haeckel, 1896; Diademida Delage & Hérouard, 1903; Centrechinoida Jackson, 1912)]

Test subspherical, depressed hemispherical or pentagonal; rigid or flexible, plates usually imbricated internally. Ambs and interambs not extending across peristome, ambs composed of simple or compound diadematoid plates. Five pairs of oral plates on peristomial membrane. Gills present, gill slits conspicuously notching peristomial margin. Periproct endocyclic. Apical system monocyclic, or with anterior oculars (II, III, IV) exsert; 5 genital pores. Tubercles crenulate or noncrenulate. Spines hollow, cylindrical, typically verticillate. Spheridium on each compound amb plate (lacking in some adapically). Pedicellariae present, including tridentate, triphyllous, ophicephalous, and rarely globiferous types. *?L.Carb., U.Trias.-Rec.*

Family DIADEMATIDAE Gray, 1855

[*nom. correct.* Zittel, 1879, *pro* Diademadae Gray, 1855] [=Centrechinidae Jackson, 1912]

Test of moderate to large size, usually somewhat flattened, commonly rather flexible. Primary tubercles crenulate. Primary and secondary spines usually hollow and verticillate, not divided internally by transverse septa. *L.Jur.-Rec.*

Diadema Gray, 1825, p. 246 [*_Echinometra setosa_ Leske, 1778; ICZN Op. 206, 1954] [=_Centrechinus_ Jackson, 1912 (obj.)]. Test large (to 110 m.), subhemispherical, depressed, not flexible. Primary amb tubercles conspicuous in 2 regular series. Ambulacral spines not conspicuously unlike others; primary spines of oral surface not clavate, not expanded distally, or invested by dermis. No globiferous pedicellariae; no spines on buccal plates. Oculars I, IV, and V insert. *?U.Cret.*, Eu., *Rec.*, IndoPac.-Atl. ——Fig. 258,*4*. *_D. setosum_ (Leske), IndoW.Pac., littoral; amb adoral, ×6.2 (136c).——Fig. 259,*4*. *D.? ebroicense* Caffin, U.Cret.(Cenon.), Fr.; *4a,b,* spines, ×2.2 (17).

Astropyga Gray, 1825, p. 426 [*_Cidaris radiata_ Leske, 1778; OD]. Like *Eremopyga,* but porezones more or less widened adorally, aboral surface of test not conspicuously naked. Spines with central lumen filled by loose mesh of stereom. *Rec.*, IndoPac.-Carib.——Fig. 259,*5*. *A. pulvinata* (Lamarck), Gulf Panama; amb aboral, ×5 (136c).

Centrostephanus Peters, 1855, p. 109 [*_Diadema longispina_ Philippi, 1845; OD] [=_Thrichodiadema_ A. Agassiz, 1863 (type, *T. rodgersii*, p. 354); *Echinodiadema* Verrill, 1867 (*non* Cotteau, 1869) (type, *E. coronata*, p. 580)]. Like *Diadema* but retaining embryonic adoral amb plate in adult unresorbed, with pore pair intact; globiferous pedicellariae occur, and spines on buccal plates. *?Mio., Plio.*, S.Eu., *Rec.*, IndoPac.-Atl. ——Fig. 259,*2*. *C. rubricingulus* H. L. Clark, Carib.; amb adoral, ×10 (136c).

Chaetodiadema Mortensen, 1903, p. 1 [*_C. granulatum_; OD]. Test rounded, depressed; somewhat flexible. Amb plates imbricated adorally, interamb plates imbricated aborally (observable only internally, where directions appear reversed). Pore pairs on adoral side arranged in single series. Tubercles greatly reduced adorally. *Rec.*, IndoW.Pac.——Fig. 259,*1*. *_C. granulatum_; _1a,b,_ amb, adoral, aboral, ×3.6 (136c).

Echinothrix Peters, 1853, p. 484 [*_Echinus calamaris_ Pallas, 1774; SD Mortensen, 1940, p. 283] [=_Garelia_ Gray, 1855 (type, *G. aequalis*, p. 38, =_E. calamaris_ Pallas); *Savignya* Desor, 1855 (obj.)]. Like *Diadema,* but ambs widened adapically, primary amb tubercles inconspicuous, not forming 2 regular series. Aboral ambulacral spines small, setiform, barbed distally. *Rec.*, Indo-W.Pac.——Fig. 258,*3*. *E. diadema* Linné; *3a,* test (holotype in collection of Queen Louisa Ulrika), aboral, ×0.75 (129); *3b,* amb, aboral, ×5.5 (136c).

Eodiadema Duncan, 1889, p. 339 [*_E. granulatum_ Wilson, 1889, pl. 10, fig. 5; OD]. Test small to medium. Ambs composed of simple plates, pores arranged in single straight series, except near peristome where they are arranged in triads and form incipient compound trigeminate plates of diademoid type. Amb primary tubercles perforate, one to each plate, except adorally, where only middle plate of each triad carries tubercle. Oculars I and V insert. Spines long and slender, verticillate (not known in type-species). *L.Jur.*, Eu.——Fig. 260,*1*. *_E. granulatum,_ Eng.; _1a,_ test, lat., ×0.75; *1b,* amb and interamb, ×6; *1c,* peristome, ×2.25; *1d,* apical system, ×3 (170).

Eremopyga Agassiz & Clark, 1908, p. 110 [*_Astropyga denudata_ de Meijere, 1902; OD]. Like *Chaetodiadema,* but pore zones adorally arranged in triads, aboral plates almost naked. Spines hollow. *Rec.*, China-Indon.——Fig. 258,*2*. *_E. denudata_ (de Meijere), Malaya (70-275 m.); amb adoral, ×5.6 (136c).

Goniodiadema Mortensen, 1939, p. 549 [*_G. mauritiense_; OD]. Test large (horiz. diam. to 110 mm.), depressed though not flattened, somewhat flexible; ambitus pentagonal, rounded angles formed by interambs. Pore zones uniserial adorally. *Rec.*, Maurit.(archibenthal).

Kamptosoma Mortensen, 1903, p. 60 [*_Phormosoma asterias_ A. Agassiz, 1881; OD] [=_Cuenotia_ Lambert & Thiéry, 1914 (obj.)]. Amb plates of diademoid triads only at extreme adapical region, elsewhere forming diads, with alternate plates occluded as small demiplates. Ambital primary spines flattened and expanded distally, others cylindrical, hollow, more or less thorny. [The affinities of this genus are obscure, and hitherto it has been classified as an aberrant echinothurioid; the crenulate tubercles suggest, however, that it is a

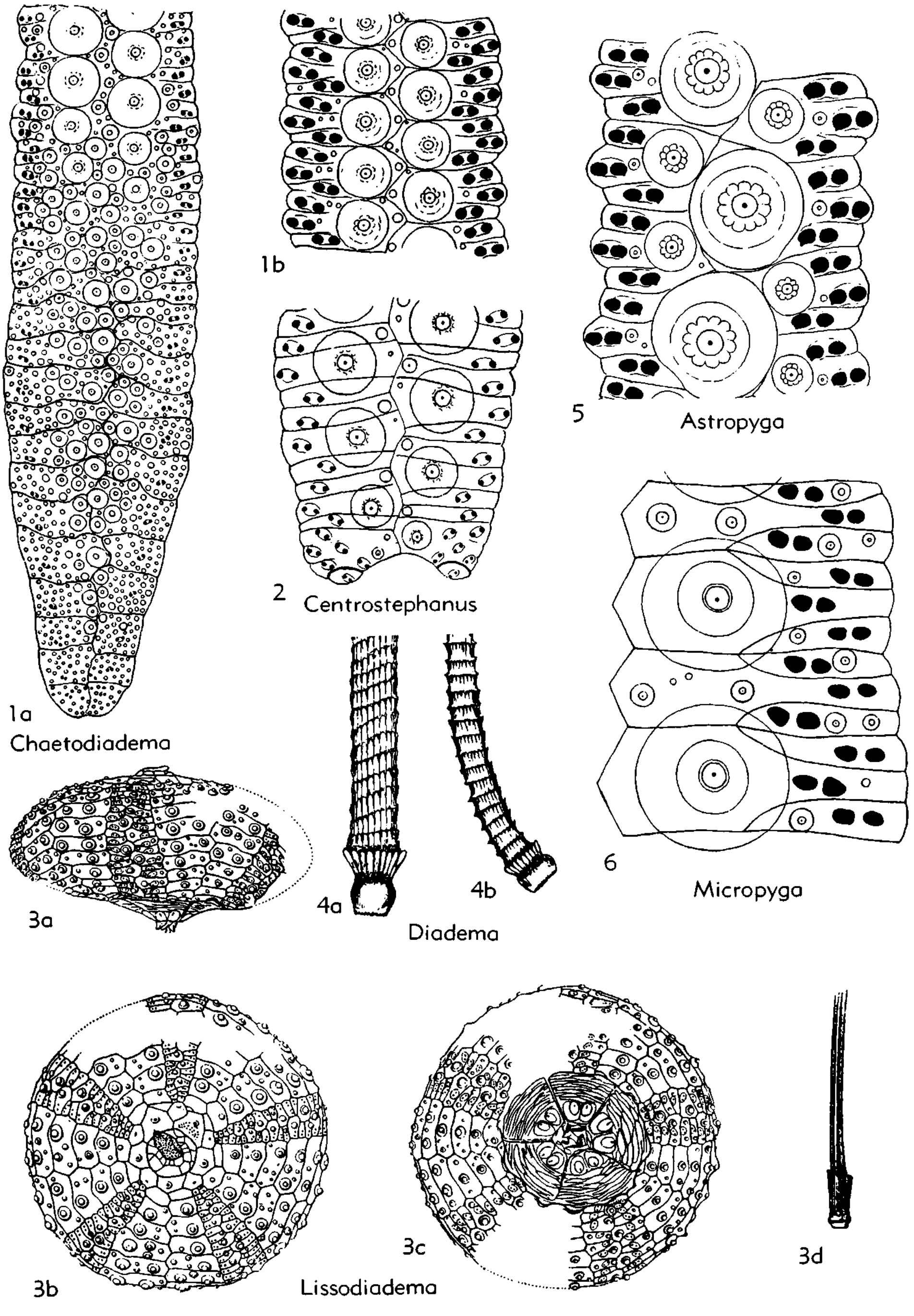

FIG. 259. Diadematidae *(1-2,4-5)*; Lissodiadematidae *(3)*; Micropygidae *(6)* (p. *U*350, *U*352).

diadematid adapted for abyssal life.] *Rec.,* C.Pac.-SE.Pac.(abyssal, 4,000-5,000 m.).——Fig. 258,*1.* **K. asterias* (A. Agassiz), SE.Pac.; *1a,* ambital radiole, ×19; *1b,* amb adapical region with ambital and part of subambital region, ×1.5 (3).

Kierechinus Philip, 1963, p. 1104 [**Pedinopsis melo* Kier, 1957, p. 845; OD]. Like *Pedinothuria,* but with about 12 primary tubercles on each interamb plate. Radioles imperfectly verticillate. *L.Eoc.,* Somalia (Auradu), N.Afr.

Palaeodiadema Pomel, 1887, p. 318 [**Pseudodiadema fragile* Wiltshire; OD] [=*Helikodiadema* Gregory, 1896 (obj.) *(nom. van.)*]. Test fragile, of moderate size, low, flattened above, slightly rounded below, plates apparently somewhat imbricated. Amb plates simple aborally, trigeminate adorally, where pores are arranged in arcs of 3. Primary tubercles of ambs and interambs in distinct longitudinal series, secondary tubercles of interambs few, and not distinctly arranged in series; plates otherwise rather naked. Apical system large, probably monocyclic. Peristome large, gill slits indistinct. Radioles slender, verticillate. *Cret.(Cenoman.-Senon.),* Eu.-N.Afr.——Fig. 260, *3.* **P. fragile* (Wiltshire), Senon., Eng.; *3a,* amb adoral, ×7.5 (74); *3b,* spine, ×4.5 (173); *3c,d,* test, aboral, oral, ×1.9 (173).

Pedinothuria Gregory, 1897, p. 119 [**P. cidaroides*; OD]. Test small (*ca.* 12 mm. horizontal diameter), depressed, flattened above and below. Amb pores uniserial aborally, becoming biserial at ambitus, and assuming trigeminate arcs of 3 adorally; occluded demiplate in each triad below ambitus. Primary tubercles small on ambs, occurring on alternate, or every 3rd plate. Primary tubercles large on interambs, areole occupying most of plate. Few secondary tubercles. Apical system large. Peristome smaller than apical system, with very deep gill slits. Spines unknown. *M.Jur.(Bathon., ?U.Jur.(Sequan.),* Eu.(Ger.-Fr.).——Fig. 260,*2.* **P. cidaroides,* Ger.; *2a,b,* test (holotype), lat., oral, ×3.4; *2c-e,* amb plates, aboral, ambital, adoral, all ×19 (74).

Family LISSODIADEMATIDAE Fell, n. fam.

Primary tubercles noncrenulate. Primary spines hollow, not verticillate. Outer tube feet not specialized. *Rec.*

Lissodiadema Mortensen, 1903, p. 393 [**L. lorioli*; OD] [=*Leptodiadema* Agassiz & Clark, 1907 (type, *L. purpureum*]. Test small (25 mm. diam.), flattened above and below, delicate, somewhat flexible by imbrication of alternate interamb plates across interradius. Amb plates trigeminate, pores forming straight series. Spines smooth, slightly curved basally. *Rec.,* Indon.-Hawaii (littoral).——Fig. 259,*3.* *L. purpureum* (Agassiz & Clark), Hawaii; *3a-c,* test, lat., aboral, oral, ×4.3; *3d,* spine, ×4.3 (4).

Family MICROPYGIDAE Mortensen, 1904

Primary tubercles noncrenulate. Primary spines hollow, not verticillate. Pore pairs forming double series; outer series of tube feet converted into umbrella-shaped structures containing anchor-shaped spicules. Amb plate trigeminate, but arcs of pore pairs of successive compound plates reversed, so that successive primaries have pores displaced alternately inward or outward. *Rec.*

Micropyga A. Agassiz, 1879, p. 274 [**M. tuberculata*; OD] [=*Rotapedina* Lambert & Thiéry, 1914 (obj.) *(nom. van.)*]. Test large (up to 140 mm. diam.), low hemispherical, flattened adorally, flexible. Primary tubercles in conspicuous longitudinal series. Gill clefts deep. Spines of moderate length, thorny. *Rec.,* IndoW.Pac.——Fig. 259,*6.* **M. tuberculata,* Indon., amb, ×5.8 (136c).

Family ASPIDODIADEMATIDAE Duncan, 1889

[=Aspidodiademinae Delage & Hérouard, 1903; Aspidodiademina Mortensen, 1939]

Test of small to moderate size (20 to 40 mm. diam.), fragile, ovoid or spherical, interamb plates slightly imbricating adorally, as seen from within. Apical system monocyclic. Primary tubercles crenulate. Primary spines hollow, central lumen transversely divided by delicate fenestrated plates which are connected by vertical calcareous strands, verticillate, ambital spines elongated and curved so that apex is directed downward. Apical system monocyclic. *?U.Jur., Rec.*

Aspidodiadema A. Agassiz, 1878, p. 188 [**A. tonsum*; OD]. Amb plates compounded in normal diadematoid triads, of which primary median components are much larger than upper and lower elements, and median primary tubercles resemble primary interamb tubercles in size and form; secondary components of triads without primary tubercles. *Rec.,* IndoPac.-Carib.(archibenthal).——Fig. 261,*2.* **A. tonsum,* Indon.; amb at ambitus, ×6.5 (136c).

Eosalenia Lambert, 1905, p. 311 [**E. miranda*; OD]. Test as *Aspidodiadema,* but adapical amb plates arranged in diads, with primary tubercle on every second plate (as in Saleniidae). Apical system large, but not otherwise known. Spines unknown. *U.Jur.(Bathon.),* Fr.——Fig. 261,*4.* **E. miranda; 4a-c,* test, lat., oral, aboral, ×1.1; *4d,* amb, ×5.7; *4e,* interamb plates, ×4.3 (115).

Plesiodiadema Pomel, 1883, p. 106 [**Aspidodiadema microtuberculatum* A. Agassiz, 1879; OD] [=*Dermatodiadema* A. Agassiz, 1898 *(nom.*

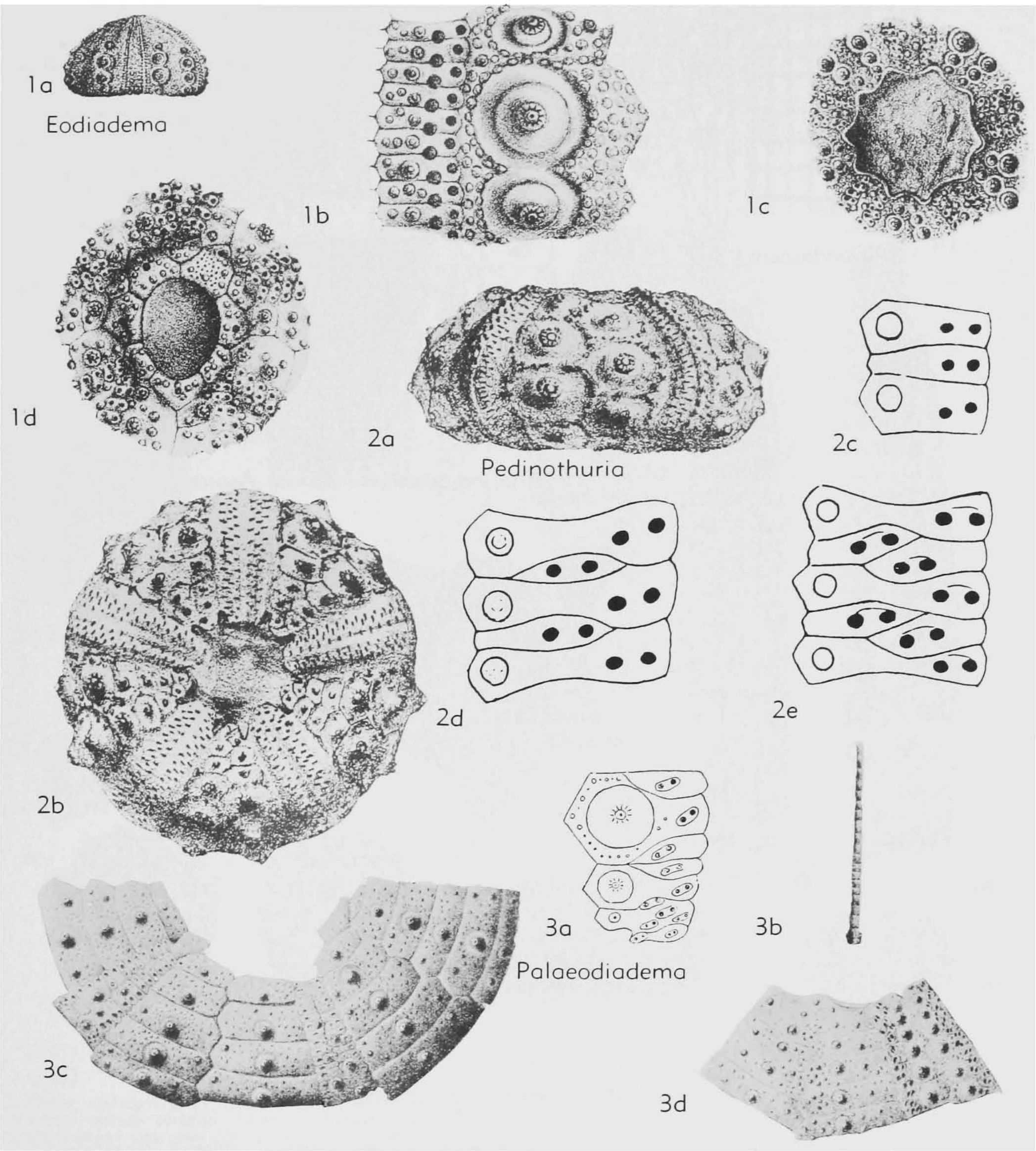

Fig. 260. Diadematidae (p. *U*350, *U*352).

van.)] [*non Plesiodiadema* Duncan, 1885, p. 433 (=*Polydiadema* Lambert, 1888)]. Like *Aspidodiadema,* but amb plates all (or nearly all) simple, arranged in triads, primary tubercle of each median plate not enlarged, other 2 plates of triad without primary tubercle. *Rec.,* IndoPac.-Atl. (archibenthal-abyssal, 300-3,900 m.).——Fig. 261, *1a. P. indicum* (Döderlein), Indon., 300-520 m.; long. sec. of primary spine, ×36 (136c).——Fig. 261,*1b. P. antillarum* (A. Agassiz), trop. Atl., 750-3,000 m., adoral amb, ×13 (136c).

Tiaridia Pomel, 1883, p. 97 [**Hemicidaris batnensis* Cotteau; OD, M]. Test like *Aspidodiadema,* but adapical amb plates like *Plesiodiadema* (with primary tubercle on every third plate). Apical system as *Aspidodiadema,* but genitals extending outward into interambs. *U.Cret.(Cenoman.),* N. Afr.(Alg.).——Fig. 261,*3.* **T. batnensis* (Cot-

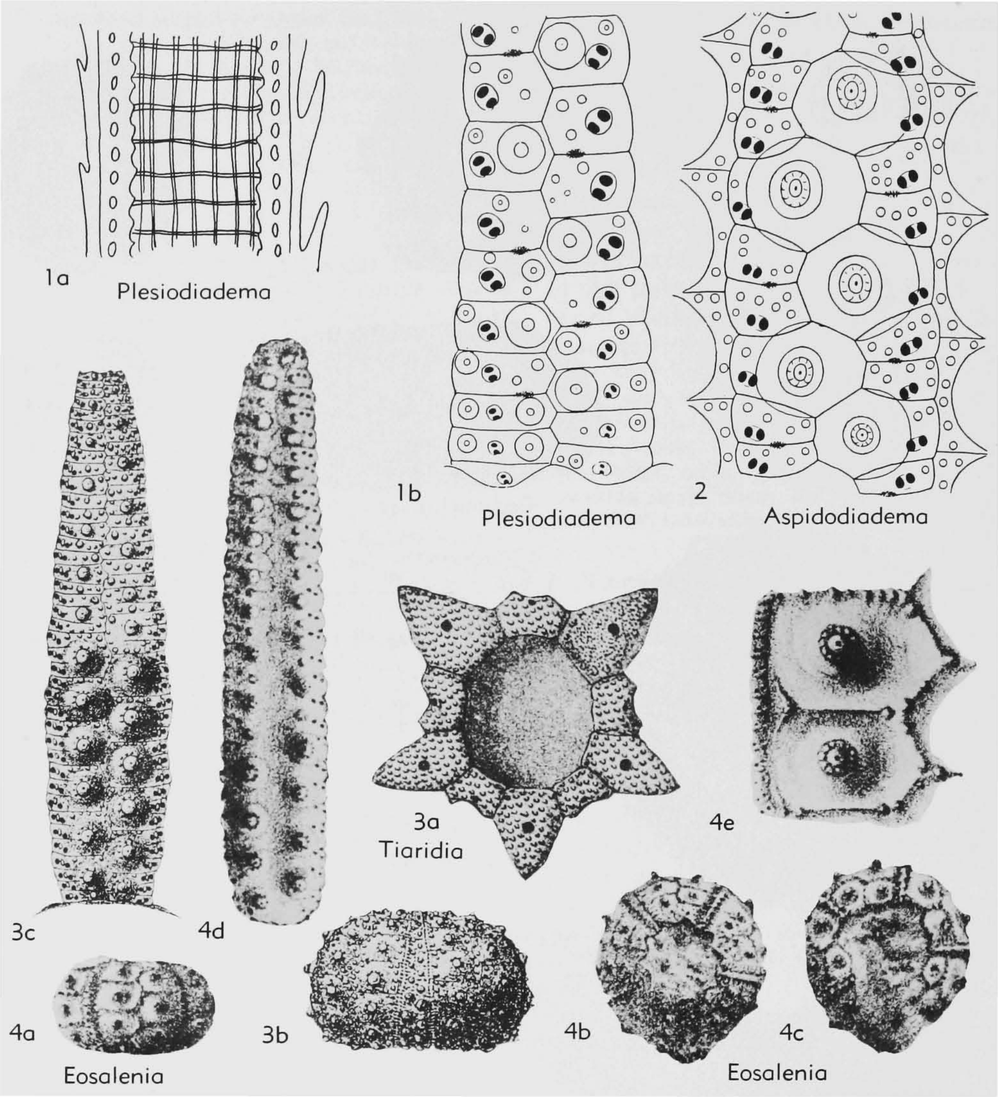

FIG. 261. Aspidodiadematidae (p. *U*352-*U*354).

TEAU); *3a*, apical system, ×4.3 (136c); *3b*, test, lat., ×1.1; *3c*, amb, ×5 (31).

Family UNCERTAIN

The following genera cannot at present be assigned to families, but are probably diadematoids.

Ancylocidaris MILLER, 1929, p. 334 [**A. spenceri*; OD]. Test low, small (9 mm. horiz. diam.). Amb plates simple, with oblique pore pair close to abradial edge. Interamb plates chevron-shaped, angle directed adorally. Other features unknown. *Jur.*, N.Am.

Endeodiadema DE LORIOL, 1890, p. 90 [**E. lepidum*; OD]. Like *Eodiadema* but amb plates all simple (not forming triads adorally) and pore pairs set obliquely. *M.Jur.(Callov.)*, Eu.(Port.).——FIG. 262,*5*. **E. lepidum*; *5a,b*, interamb, amb, ×7.8 (124).

Engelia TORNQUIST, 1908, p. 408 [**Cidaris laqueata* QUENSTEDT, 1875; OD]. Amb plates with pore zone situated some distance from abradial margin, which carries marginal series of small tubercles. *L.Jur.*, Eu.(Ger.).——FIG. 262,*3*. **E. laqueata* (QUENSTEDT); *3a*, amb (*fide* TORNQUIST), ×2.3 (164); *3b*, amb (*fide* QUENSTEDT), ×3.9

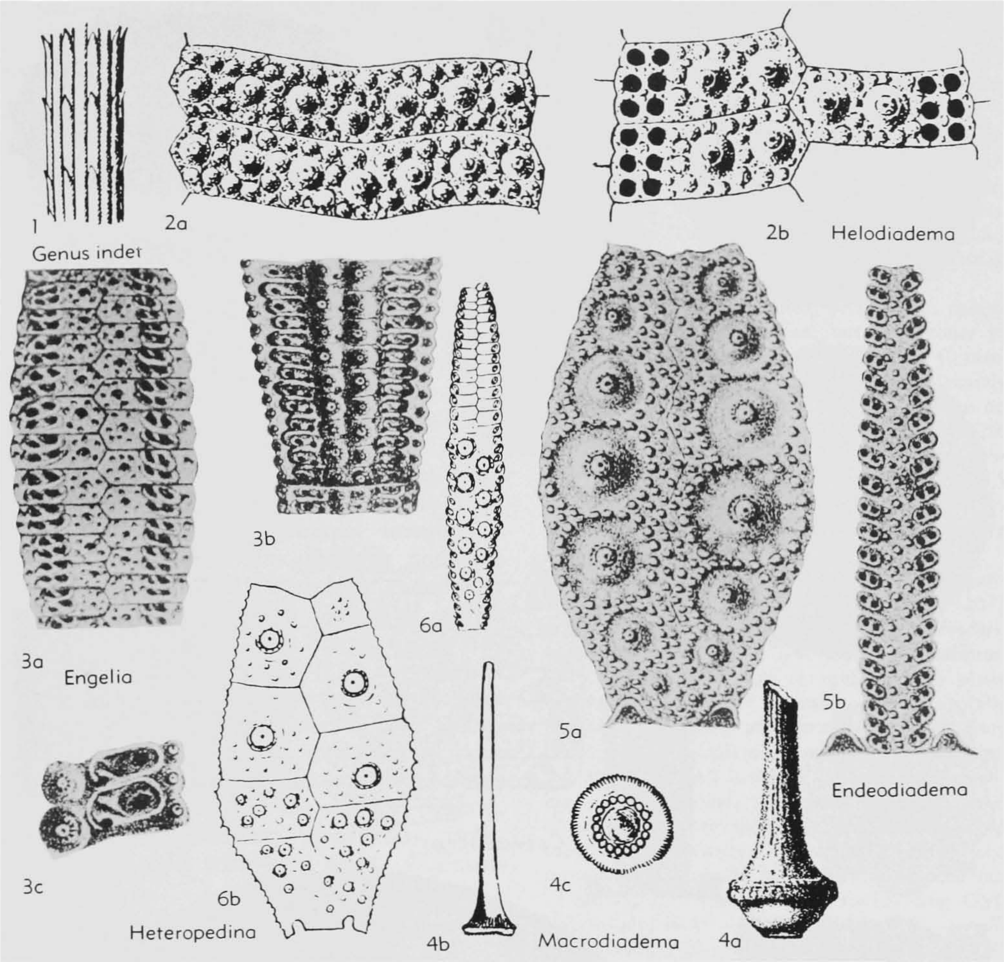

FIG. 262. Family Uncertain (p. *U*354-*U*357).

(145); *3c,* amb plate (*fide* QUENSTEDT), ×6.2 (145).

[Other characters given by QUENSTEDT (145) for the type-species include perforate, crenulate primary tubercles on every second amb plate (as in Fig. 262,*3b*), but TORNQUIST (164) illustrated the tubercles as imperforate noncrenulate (as in Fig. 263,*3a*), and a detail published by QUENSTEDT (145) shows large primary crenulate perforate tubercles to every amb plate. These contradictions prohibit exact classification of *Engelia.* MORTENSEN (136c) suggested that QUENSTEDT'S original material contained parts of three genera, and he nominated the illustration here shown in Fig. 262,*3a,* as the type of *Engelia,* leaving unsettled whether or not it is identical with all, or only part, or no part, of QUENSTEDT'S original material.]

Helodiadema MORTENSEN, 1939, p. 550 [**Cottaldia rotula* W. B. CLARK; OD]. Test small, globular. Ambs trigeminate, tubercles perforate, crenulate, 2 or 3 in horizontal row in each compound plate. Interambs with up to 11 tubercles on each plate, in horizontal series, secondaries not distinguishable from primary tubercles, all crenulate, perforate. Plates otherwise covered by granulation. Apical system dicyclic. Peristome large, gill slits small. Radioles unknown. *L.Cret.,* N.Am.——FIG. 262,*2.* **H. rotula* (CLARK), Washita, USA(Tex.); *2a,b,* interamb, amb, ×14 (22).

Heteropedina MICHALET, 1895, p. 71 [**H. moteti*; OD]. Test small (20 mm.). Adoral amb plates trigeminate, carrying well-developed crenulate perforate tubercle; adapical amb plates simple primaries, without primary tubercles, and almost devoid of secondary tubercles. Pore zones almost straight. Adoral interamb plates with irregularly arranged small primary tubercles, perforate and finely crenulate, similar to amb primary tubercles; aboral interamb plates each with one large tubercle which is perforate (possibly crenulate nature doubtful); uppermost plate of each interamb without tubercle. Apical system and peristome large.

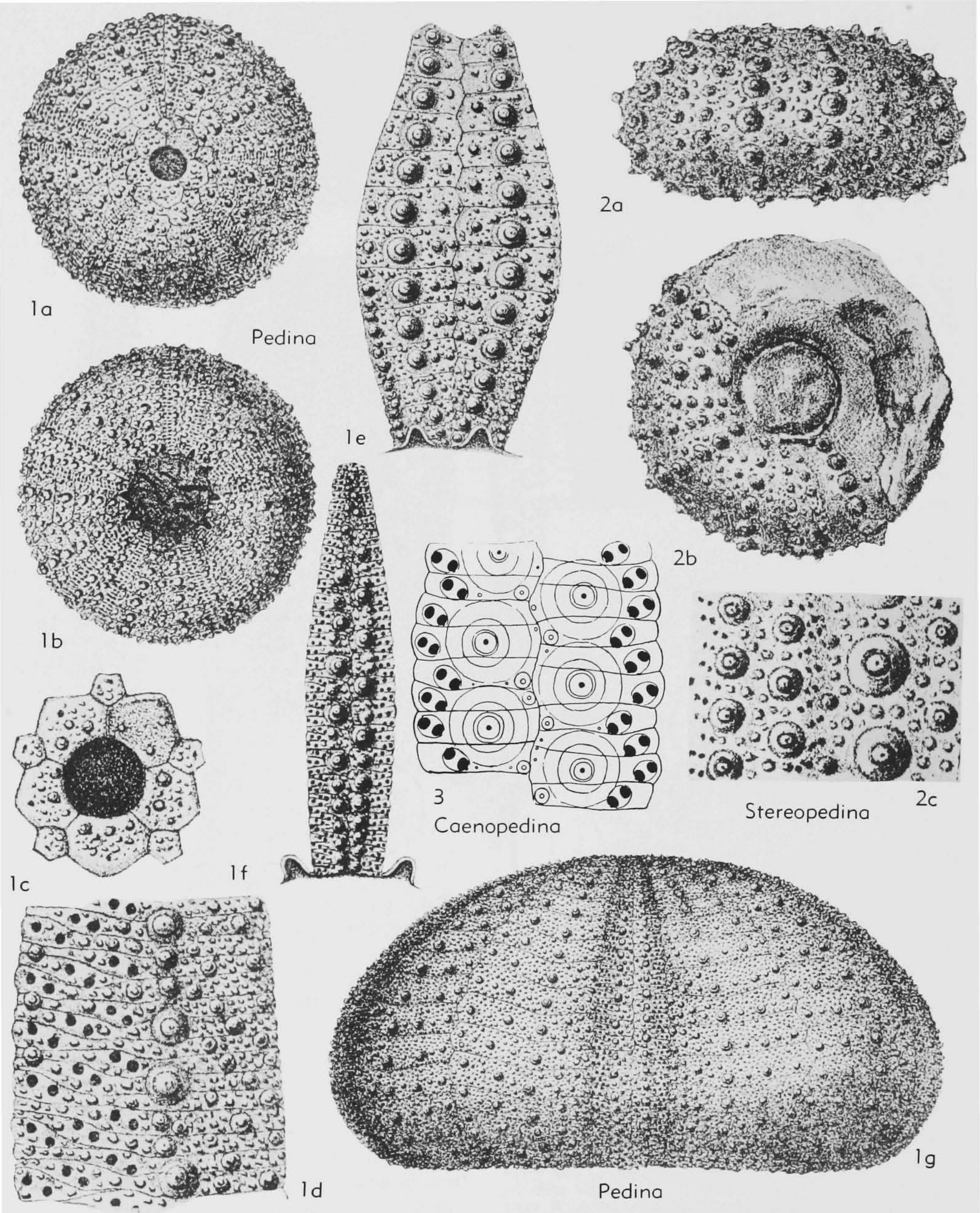

FIG. 263. Pedinidae (p. *U*357).

Spines unknown. *U.Jur.(Bathon.)*, Fr.——FIG. 262,6. **H. moteti*; *6a,b,* amb, interamb, ×3.1 (136c).

Macrodiadema LAMBERT, 1897, p. 6 [**M. ciplyensis*; OD]. Primary radiole with slender, finely striated shaft, and broad, short basal region, margin of acetabulum crenulate. Test and other structures unknown. *U.Cret.*, Fr.——FIG. 262,*4a.* **M. ciplyensis*; spine, lat., ×1.8 (103).——FIG. 262, *4b,c. M. buccinifera* (CAFFIN); *4b,* spine, lat., ×1.8; *4c,* base from below, ×3.5 (17).

Genus indet., ?fam. Aspidodiadematidae. *L.Carb.,* Ger.——Fig. 262,*1*. Spine, ×5.5 (152). [Suggests an aspidodiadematid, but internal structure of spines unknown. No diadematoid is with certainty known from the Paleozoic. Mortensen (136c), however, is inclined to see in this fossil some possible archaic diadematoid, rather than the perischoechinoid *Pholidocidaris*, to which Schmidt (152) has attributed it.]

Order PEDINOIDA Mortensen, 1939

[*nom. transl.* Fell, herein (*ex* suborder Pedinina Mortensen, 1939, p. 547)]

Test subspherical, high subconical to depressed hemispherical or rotular; rigid though fragile, plates not imbricating. Ambs and interambs not extending across peristome. Ambs composed of simple or compounded diadematoid plates. Five pairs of oral plates on peristomial membrane. Gills present; gill slits shallow, notching peristomial margin. Periproct endocyclic. Apical system dicyclic; 5 genital pores. Tubercles noncrenulate. Spines finely striate, more or less thorny (but not verticillate); primaries solid, secondaries hollow. Spheridia unknown in fossils (but placed near tube foot of adoral secondary element of amb plates in living genus *Caenopedina*, where they continue to the adapical region). Pedicellariae including globiferous, ophicephalous, and tridentate types. *U.Trias.-Rec.*

Family PEDINIDAE Pomel, 1883

[*nom. transl.* Gregory, 1900 (*ex* Pedininae, *nom. correct.* Duncan, 1889, *pro les* Pediniens Pomel, 1883)] [=Propedinidae Lambert, 1937 (*nom. van.*, based on jr. obj. syn. of *Pedina*)]

Characters of order. *U.Trias.(Rhaet.)-Rec.*

Pedina L. Agassiz, 1838, p. 4 [**P. sublaevis*; SD Savin, 1905] [=*Megapedina* Lambert & Thiéry, 1910 (type, *Pedina charmassei* Cotteau, 1885); *Propedina* Lambert & Thiéry, 1925 (obj.) *(nom. van.)*; *Hectopedina* Thiéry, 1928; *Atlasaster* Lambert, 1931]. Test medium-sized to large (100 mm. horiz. diam.), more or less depressed, rather fragile. Pore pairs arranged in arcs of 3, adoral pair outermost. Primary ambulacral tubercles occurring on both oral and aboral hemispheres. Scattered secondary tubercles. *Jur.(Pliensbach.-Oxford.)*, Eu., Madag.; *Mio.*, S.Am.

P. (Pedina). Single series of primary tubercles in each column, but primary ambulacral tubercles lacking from some compound plates and interambulacral ones not contiguous throughout. *Jur. (Pliensbach.-Oxford.)*, Eu.-Madag.——Fig. 263,*1a-f*. **P. (P.) sublaevis*, Callov., Fr.; *1a,b*, test aboral, adoral, ×1.2; *1c*, apical system, ×2.7; *1d*, amb detail, ×6; *1e,f*, interamb, amb, ×2 (27c).——Fig. 263,*1g*. *P. (P.) gigas* A. Agassiz, Bathon., Fr.; test, lat., ×0.85 (27c).

P. (Stereopedina) de Loriol, 1902, p. 11 [**Stereopedina ameghinoi*; OD, M]. Like *P. (Pedina)*, but primary ambulacral tubercles forming regular vertical series, present on all amb plates. *Mio.*, S.Am.(Patagonia).——Fig. 263,*2*. **P. (S.) ameghinoi* (de Loriol); *2a,b*, test, lat., aboral, ×1.7; *2c*, detail of test, ×3.5 (125).

Caenopedina A. Agassiz, 1869, p. 256 [**C. cubensis*; OD]. Like *Hemipedina*, but pore zones in arcs of 3 throughout. Test not exceeding 40 mm. horiz. diam. Generally brightly colored, mainly deep-sea forms, usually with bands of pigment on finely thorny spines. *Rec.*, IndoPac.-Carib. (20-2,000 m.).——Fig. 263,*3*. *C. diomedeae* Mortensen, Gulf of Panama (840 m.); amb, ×5.5 (136c). [=*Coenopedina* Pomel, 1883, p. 99 *(nom. null.)*; *Coenodiadema* Bather, 1900, p. 86 *(nom. null.)*.]

Diademopsis Desor, 1855, p. 79 [**Echinus serialis* L. Agassiz, 1840; SD Bather, 1909, p. 109] [=*Hecistocyphus* Pomel, 1883 (type, *Diademopsis bonissenti* Cotteau)]. Test small to medium-sized, low hemispherical or rotular. Amb plates compound trigeminate adorally, simple aborally but every 3rd plate with primary tubercle. Pore zones straight, except near peristome, where forming arcs of 3. All ambulacral components reaching radial mid-line. Interamb plates low and broad, with more than one series of enlarged tubercles, secondaries resembling primary and forming series parallel to primary series. *U.Trias. (Rhaet.)-U.Jur.(Kimmeridg.)*, Eu.(Fr.-Eng.-Ger.-Switz.-Italy)-N.Afr.——Fig. 264,*2*. **D. serialis* (L. Agassiz); *2a-c*, test lat., oral, aboral, ×0.85 (44); *2d*, interamb, ×2.1 (27c).——Fig. 265,*2a,b*. *D. michelini* (Cotteau), L.Jur.(Hettang.), Switz.; *2a,b*, interamb, amb, ×1.8 (27c).——Fig. 265,*2c*. *D. micropora* (L. Agassiz), Rhaet., Fr.; interamb, ×1.8 (27c).——Fig. 265,*2d*. *D. heeri* Merian, Rhaet., Fr.; test with spines, ×0.9 (44).

Echinopedina Cotteau, 1866, p. 117 [**Echinus gacheti* Desmoulins; OD] [=*Hebertia* Lambert, 1910, p. 2 (obj.); (*non Hebertia* Michelin, 1859, =*Echinopsis* L. Agassiz, 1840)]. Test subspherical, of moderate size (to 40 mm. diam.). Pore zones arranged in arcs of 3, of which adapical pair is very slightly nearer adradial margin than others (hence obscurely inverse), but not forming 3 vertical series. Only single vertical series of primary tubercles in amb sand interambs. *Eoc.*, Eu., N.Afr.-Carib.——Fig. 267,*1*. **E. gacheti* (Desmoulins), Fr.; test, lat., ×1.2 (31).

Hemipedina Wright, 1855, p. 2 [**Pedina etheridgei* Wright, 1854; SD Lambert, 1900, p. 6] [=*Leiodiadema* Quenstedt, 1873 (obj.); *Miopedina* Pomel, 1883 (type, *Hemipedina tubercu-*

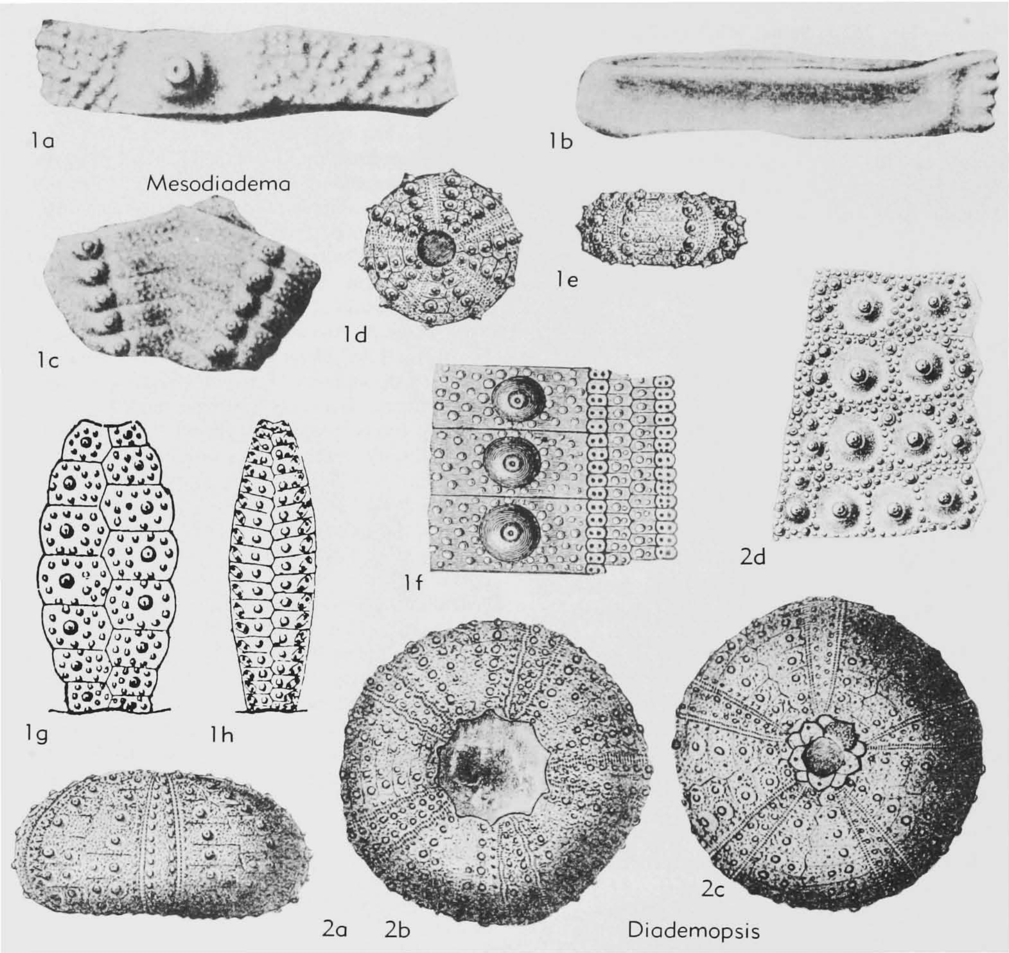

FIG. 264. Pedinidae (p. U357-U359).

losa Wright, 1860; *Archaeodiadema* Gregory, 1896 (type, *A. thompsoni*)]. Like *Diademopsis,* but interamb plates high and narrow, with only single series of primary tubercles, single large primary tubercle and areole of each interamb plate lying near its center. *L.Jur.(Pliensbach.)-U.Cret. (Cenoman.),* Eu. (Eng.-Fr.-Ger.-Switz.)-?Iran.——Fig. 266,*2a-d.* **H. etheridgei,* J.Jur.(Toarc.), Eng.; *2a,* apical system (holotype), ×7.5 (136c); *2b-d,* test, lat., aboral, oral, ×4.2 (172).——Fig. 266,*2e*; 267,*5. H. tuberculosa* Wright, Oxford., Eng.; 266,*2e,* test aboral, with spines, ×1.25 (172); 267,*5a,b,* amb, interamb, ×4 (27c). [=*Psilosalenia* Quenstedt, 1873, p. 256.]

Leiopedina Cotteau, 1866, p. 114 [**Codechinus tallevignesi* Cotteau, 1856; OD, M] [=*Chrysomelon* Laube, 1868, p. 13 (obj.)]. Test large (to 60 mm. diam.), as high as broad, or higher, subglobular to subconical. Pore zones broad, pore pairs in oblique arcs of 3, in inverse sequence (adapical pore outermost), forming 3 well-defined vertical series. Outermost pore pairs not differing from others. *Eoc.(Lutet.),* Eu.(Fr.-Ger.).——Fig. 267,*3.* **L. tallevignesi* (Cotteau), Fr.; *3a,* amb (adoral), ×2 (27e); *3b,* amb plates, ×3.3 (136c); *3e,* test, lat., ×0.9 (31).

Loriolipedina Lambert, 1910, p. 133 [**L. alpina*; OD]. Like *Leiopedina,* but outermost pore pairs of each series elongate. *Eoc.,* Eu.——Fig. 267,*6.* **L. alpina,* Switz.; *6a,* amb and interamb plate, ×2; *6b,* test, lat., ×0.7 (120).

Mesodiadema Neumayr, 1889, p. 372 [**Hemipedina marconissae* Desor, 1858; OD]. Test small, depressed. Pore pairs in single straight series. Amb plates simple, uniform, not forming triads, each with single small primary tubercle. Interamb plates each with single small primary tubercle, placed near adradial edge, remainder of amb plate covered by granulation. Peristome small. Apical system and spines unknown. *?U.Trias.,* Hung.; *L.*

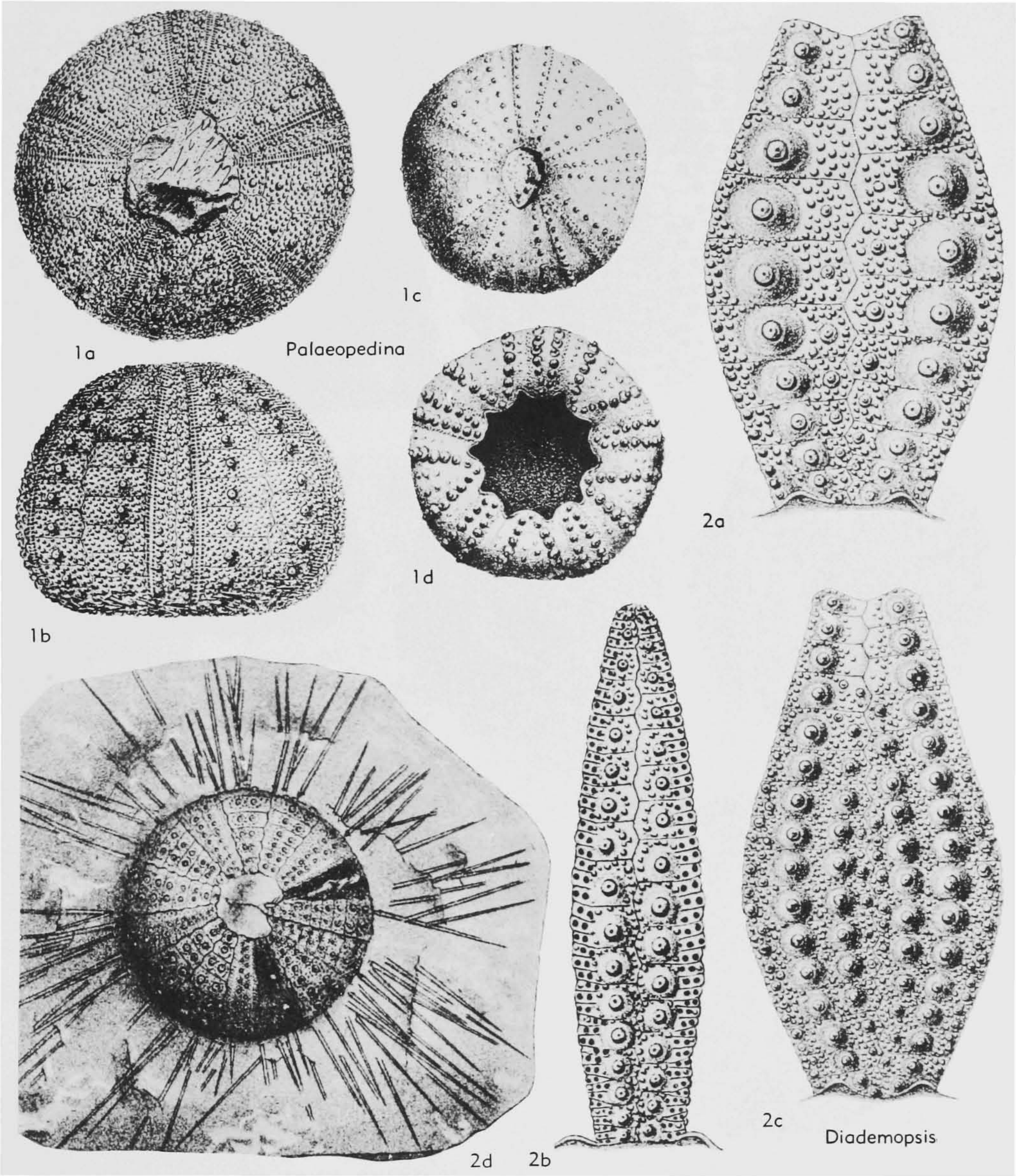

FIG. 265. Pedinidae (p. *U*357, *U*360).

Jur.(Toarc.), Fr.-N.Italy.——FIG. 264,*1a-c. M. latum* BATHER, ?U.Trias. (Carn.), Hung.; *1a,b,* interamb plates, ext., int., ×8.5; *1c,* interamb (adoral), ×3.5 (11).——FIG. 264,*1d-f.* **M. marconissae* (DESOR), L.Jur., N.Italy; *1d,e,* test, aboral, lat., ×1.4; *1f,* detail of amb and interamb, ×5.6 (139).——FIG. 264,*1g,h. M. angeliacense* VALETTE, L.Jur.(Charmouth.), Fr.; *1g,h,* interamb, amb (latter with oblique pores), ×? (165).

Micropedina COTTEAU, 1866, p. 822 [**Echinus olisiponensis* FORBES, 1850; OD]. Test small to medium-sized (25-40 mm.), subglobular to subconical. Pore pairs arranged in arcs of 3, of which adapical pair lies outermost (inverse). Numerous enlarged tubercles in both ambs and interambs, forming many series. Peristome small. Spines slender, longitudinally striate. *U.Cret.(Cenoman.-Senon.),* Eu.-N.Afr.-India.——FIG. 267,*2a-d. M. olisiponensis cotteaui* COQUAND, Cenoman., Fr.; *2a,* amb, aboral, ×?; *2b,c,* test, aboral, lat., ×1.2;

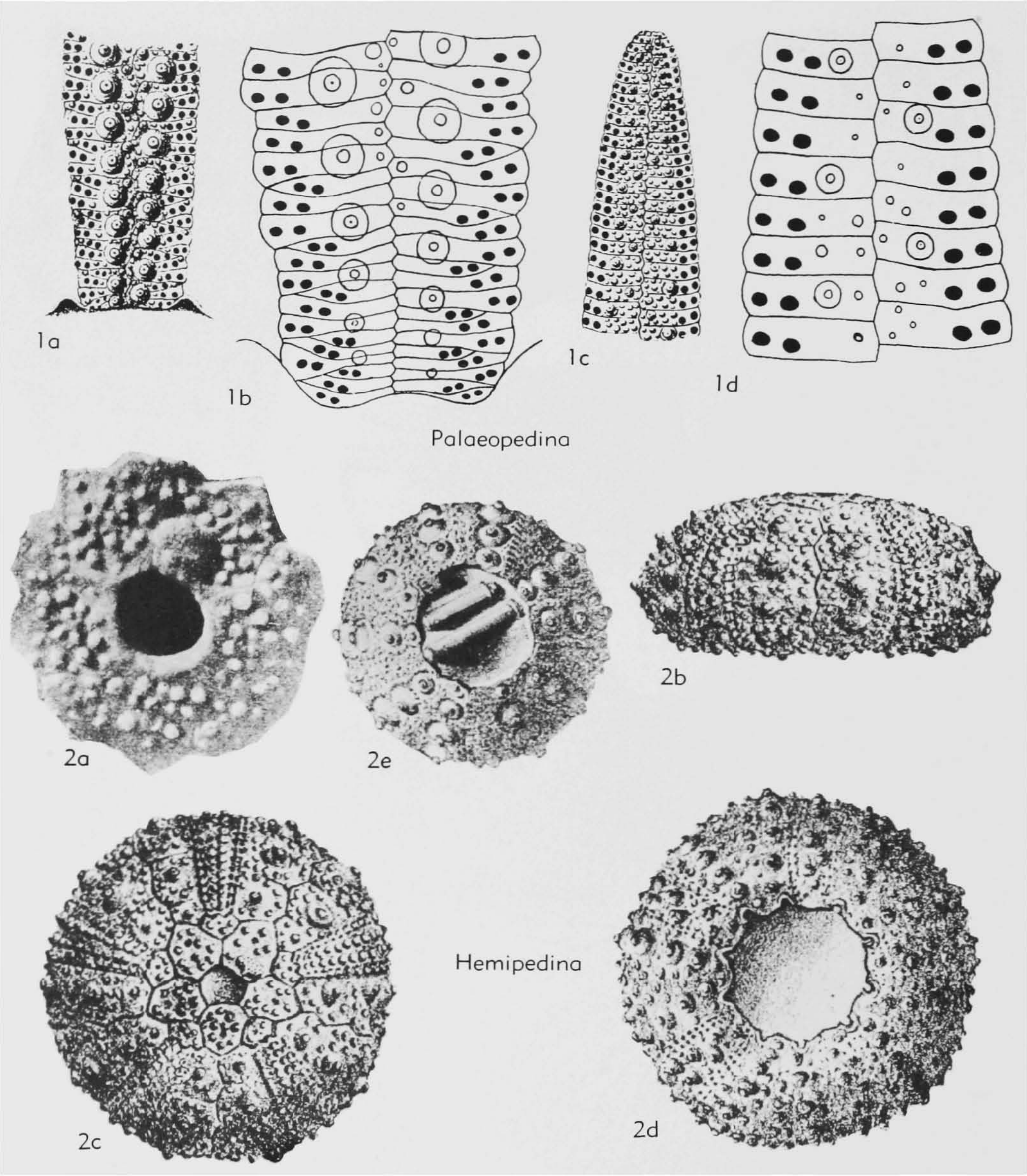

FIG. 266. Pedinidae (p. U357-U358, U360).

2d, apical system, ×5.5 (27a).——FIG. 267,*2e,f.* **M. olisiponensis* (FORBES), Cenoman., Port.; *2e,f,* amb, interamb, ×7 (157).

Palaeopedina LAMBERT, 1900, p. 22 [**Diadema globulus* L. AGASSIZ, 18??; OD]. Test small to medium-sized, subglobular or subhemispherical. Apical system elongate in anteroposterior axis, periproct displaced toward interamb 5; suranal plate may be present. Primary tubercles in single series, without conspicuous areoles, but secondary tuberculation present. [Young stages of *Plesiechinus* (Pygasteroida) resemble *Palaeopedina,* and erroneously have been referred to the genus (52).] *L.Jur.(Hettang.),* Eu.——FIG. 265,*1a,b,*; 266,*1.* **P. globulus* (AGASSIZ), S.Fr.; 265,*1a,b,* test, aboral, lat., ×0.9 (27c); 266, *1a,b,* amb adoral, ×2.1, ×5 (27c); 266,*1c,d,* amb aboral, ×2.1, ×5 (136c).——FIG. 265,*1c,d. P. bonei* (WRIGHT), Bajoc., Eng.; *1c,d,* test, aboral, oral, ×1.8 (172). [*P. bonei* is regarded by BATHER (1909) as probably a young *Pygaster*; the similarity suggests probable close relationship of pedinids and pygasterids.].

Phalacropedina LAMBERT, 1900, p. 30 [**Hemi-*

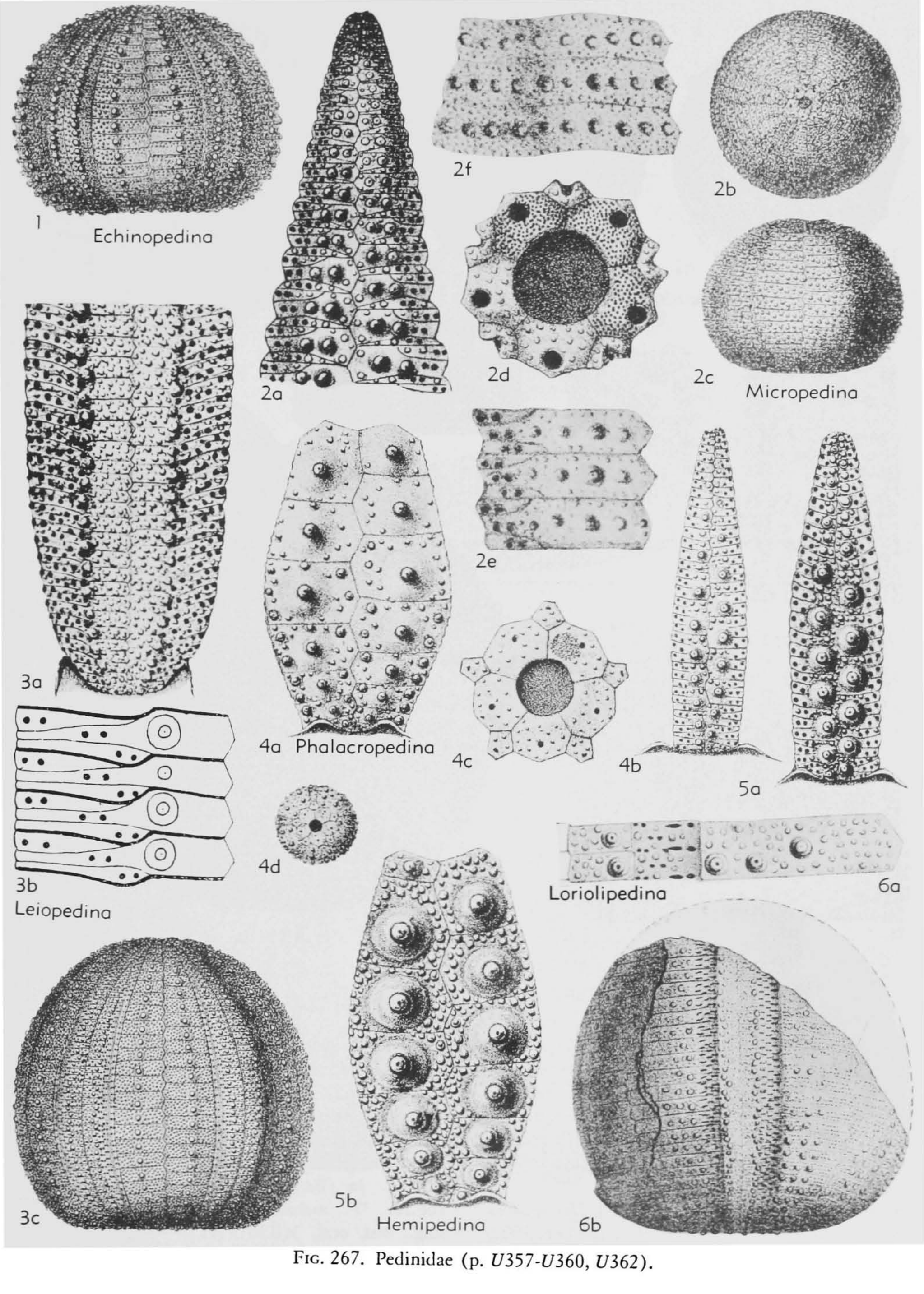

FIG. 267. Pedinidae (p. *U*357-*U*360, *U*362).

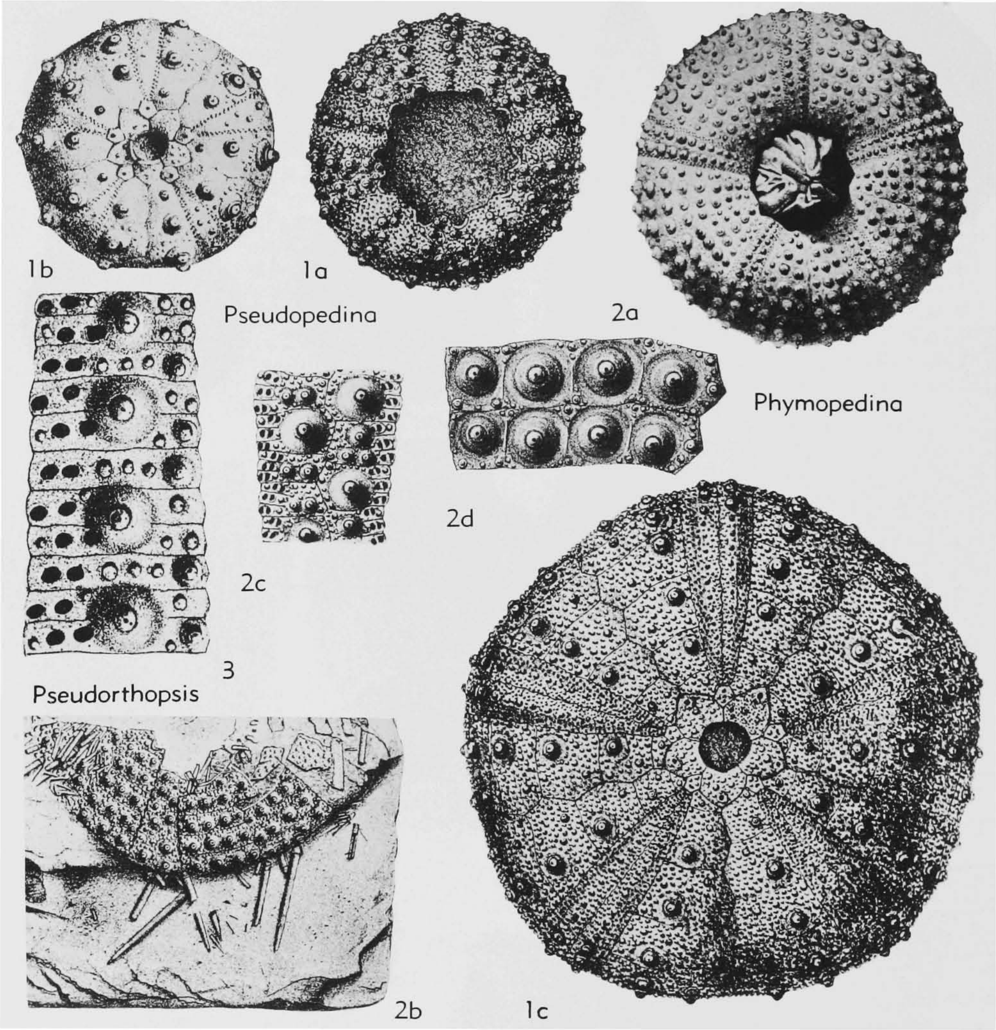

FIG. 268. Pedinidae (p. U362-U365).

pedina guerangeri COTTEAU, 1858; OD]. Like *Hemipedina,* but secondary tubercles very sparse, plates thus being almost naked, and primary areoles indistinct. *U.Jur.(Oxford.-Kimmeridg.),* Eu.——FIG. 267,*4*. **P. guerangeri* (COTTEAU), Oxford., Fr.; *4a-c,* interamb, amb, apical system, ×2.7; *4d,* test, aboral, ×0.9 (27c).

Phymopedina POMEL, 1883, p. 100 [**Hemipedina marchamensis* WRIGHT, 1855; SD LAMBERT, 1900, p. 28]. Test large (horiz. diam. *ca.* 70 mm.), hemispherical, depressed. Amb plates trigeminate, pores in indistinct arcs of 3, arcs more oblique adorally and crowded at peristome; adoral pore pair of each triad placed outermost. Primary amb tubercles as large as interamb primaries; amb primaries in single vertical series; either one enlarged primary on every compound plate or larger and smaller primary tubercles on alternate plates. Interamb primary and secondary tubercles similar, forming transverse series on each plate, and up to 4 vertical series on each column. Spines finely striated. *Jur.(Bathon.-Portland.),* W.Eu.——FIG. 268,*2a*. **P. marchamensis* (WRIGHT), Oxford, Eng.; test, oral, ×0.55 (172).——FIG. 268,*2b,c*. *P. legayi* (COTTEAU), Bathon., Fr.; *2b,* test, aboral, with spines, ×0.55; *2c,* amb detail, ×1.5 (27c). ——FIG. 268,*2d*. *P. bouchardi* (WRIGHT), Portland., Eng.; ambital interamb plates, ×1.5 (27c).

Pseudorthopsis SÁNCHEZ ROIG, 1949, p. 37 [**Echinopedina cubensis* COTTEAU, 1881, pl. 1; OD].

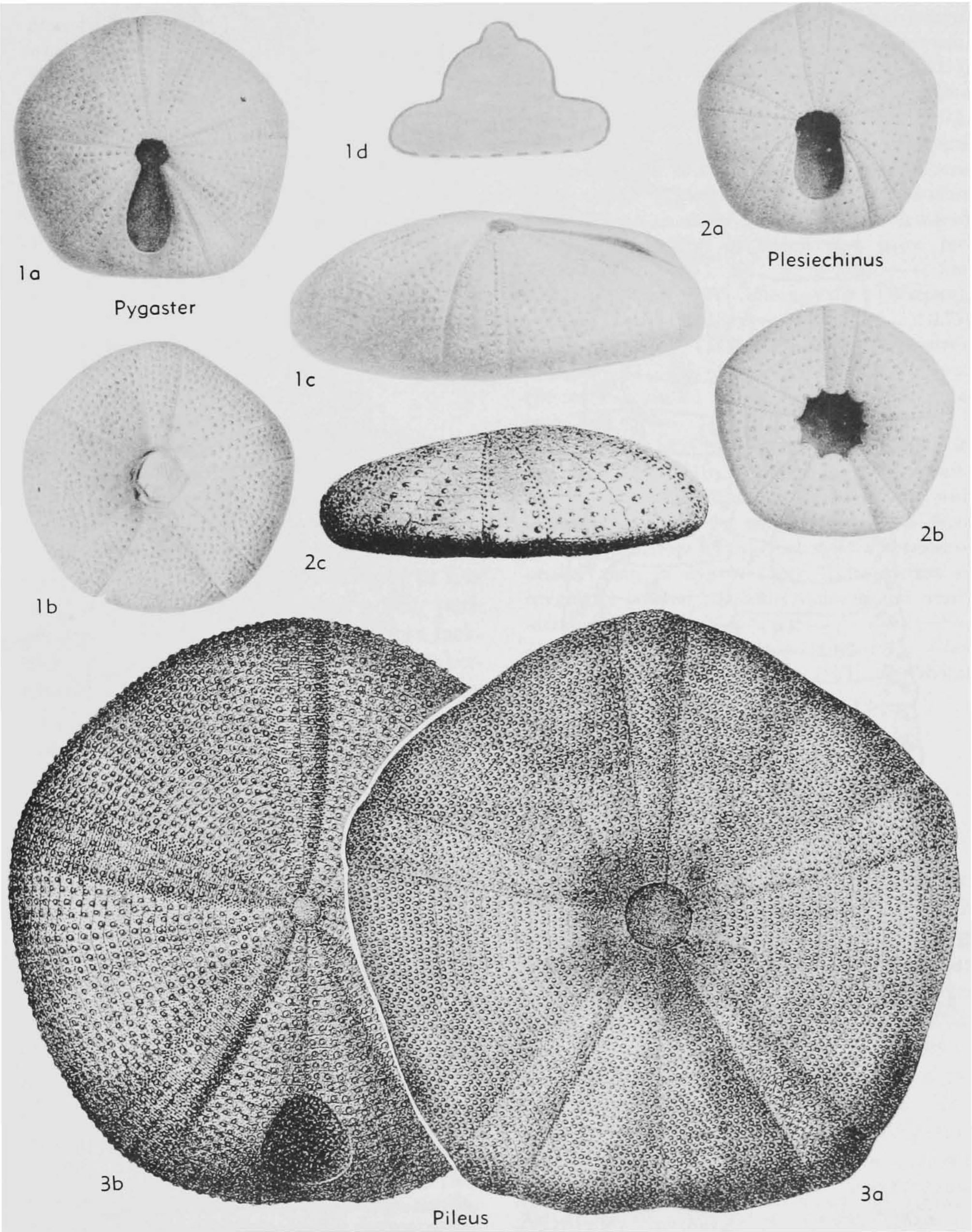

Fig. 269. Pygasteridae (p. *U*365).

Like *Echinopedina,* but pore pairs not inverse. *Eoc.,* Cuba.——Fig. 268,*3. *P. cubensis* (Cotteau); amb, ×4 (30).

Pseudopedina Cotteau, 1858, p. 9 [**Pedina bakeri* Wright, 1854; OD]. Like *Pedina,* but without aboral primary ambulacral tubercles. *M.Jur. (Bajoc.-Bathon.),* Eu.——Fig. 268,*1a,b. *P. bakeri* (Wright), Bajoc., Eng.; *1a,* test, oral, ×0.9

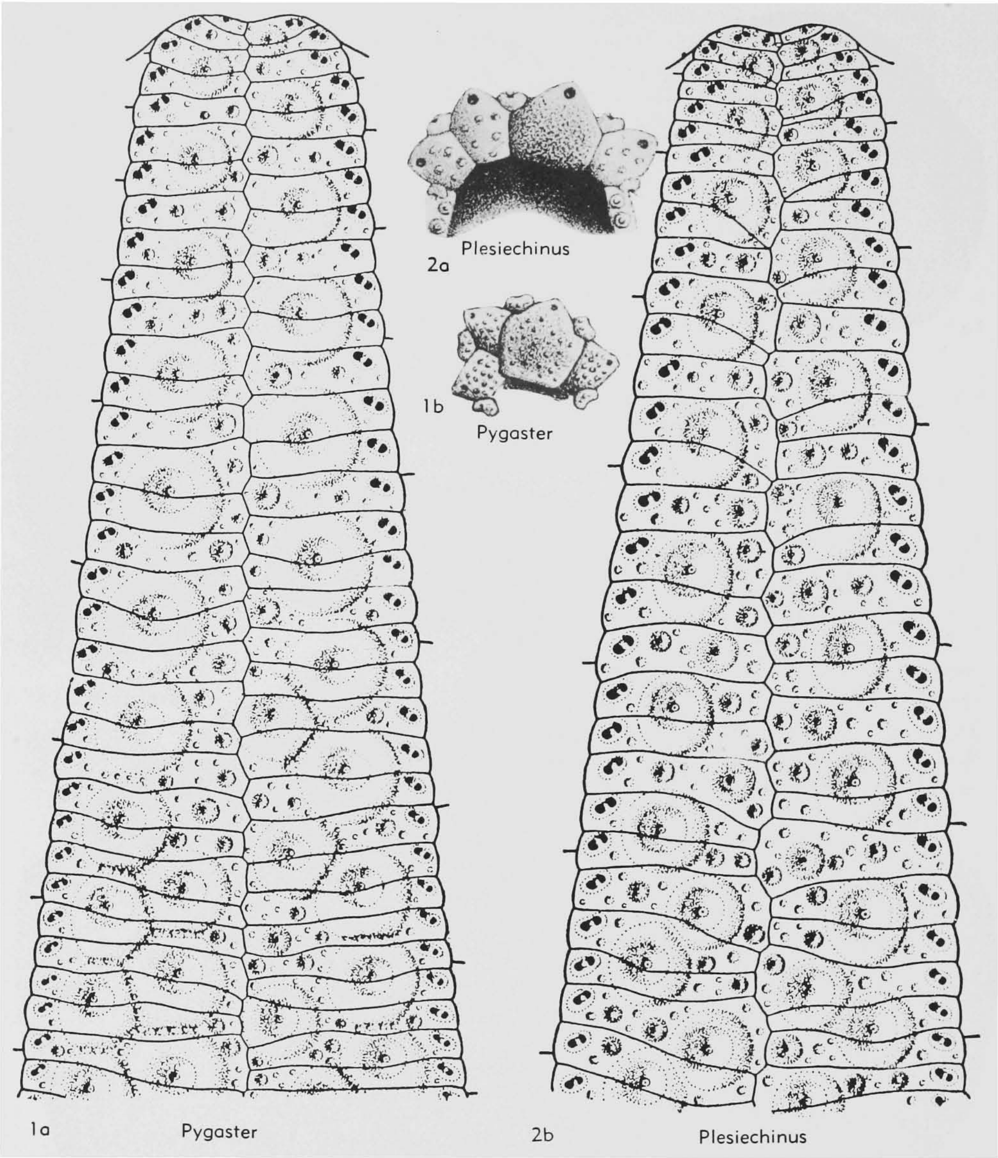

FIG. 270. Pygasteridae (p. *U*365).

(27a); *1b,* test, aboral, immature, ×1.8 (172). ——FIG. 268,*1c*. *P. divionensis* (MICHELIN), Bajoc., Fr.; test aboral, ×0.9 (27a).

Stenechinus ARNOLD & CLARK, 1927, p. 13 [**S. regularis*; OD]. Test subglobular, of moderate size. Pore zones in narrow, straight series, not widening at peristome. Amb plates trigeminate, median component bearing large primary tubercle close to pore pair, and adoral components on ambital amb plates excluded from radial mid-line (hence demiplates). Interamb plates each with large central primary tubercle, and scattered secondary tubercles. *?Eoc.,* Jamaica.

Family UNCERTAIN

The following genus is insufficiently known, but may provisionally be associated with the Pedinidae.

Leptocidaris QUENSTEDT, 1858, p. 644 [**L. triceps*;

OD]. Test small, depressed subspherical. Ambs trigeminate (?diadematoid), amb plates without primary tubercle except 3 ambital plates, each of which has single conspicuous tubercle. Interambs with single vertical series of primary tubercles on each column. Apical system, peristome and spines unknown. *U.Jur.(Oxford.),* Ger.

The following genera have earlier been associated with the Pedinidae, but are here excluded from the family as it now seems probable that the tubercles are crenulate.

Dumblea Cragin, 1893 [**D. symmetrica*; OD]. Here assigned to Pseudodiadematidae (see p. U386).

Farquharsonia Currie, 1927 [**F. somaliensis*; OD]. Here listed as *incertae sedis.*

Order PYGASTEROIDA
Durham & Melville, 1957

[=Pileatoida Lambert, 1900 *(partim)*] [Materials for this order prepared by R. V. Melville]

Medium-sized to large Diadematacea with rigid corona; apical system with four or five genital plates and four genital pores; periproct outside apical system; ambulacra lacking compound plates; interambulacral tubercles smooth, in regular vertical and horizontal series; radioles with solid axis; girdle composed of strong auricles suported by buttresses, apophyses rudimentary; teeth triangular in section, keeled and buttressed. *L.Jur.-U.Cret.*

Members of this order have been discussed by Hawkins (1911; 1918; 1920), while the reasons for establishing it as a separate order are given by Durham & Melville (1957) and Melville (1962).

Family PYGASTERIDAE Lambert, 1900

Characters of order. *L. Jur.-U.Cret.*

Pygaster J. L. R. Agassiz, 1836, p. 18 [**Clypeus semisulcatus* Phillips, 1829, SD Savin, 1905, p. 187] [=*Macropygus* Desor, 1857 (type, *Pygaster truncatus* Agassiz); ?*Echinoclypus* Pomel, 1869; *Megapygus* Hawkins, 1912 (type, *Pygaster umbrella*)]. Medium-sized, more or less depressed; apical system in contact with periproct, but genital 5 missing, and genital 3 with oculars II, III, and IV excluded; pore pairs uniserial throughout, or very weakly triserial adorally; elongated pits in transverse sutures of adoral interambulacral plates. *M. Jur. (Bajoc.)-U. Cret. (Cenoman.),* Eu.——Fig. 269,*1a-c*; 270,*1*. **P. semisulcatus* (Phillips), U. Oxford., Eng.; 269,*1a,b*, aboral, oral, ×0.7 (172); 269,*1c*, lat., ×1.1 (172); 270,*1a*, adoral portion of ambulacrum, enl. (81); 270,*1b*, apical system, ×2.5 (172).——Fig. 269,*1d*. *P. trigeri* Cotteau, Bathon., Fr.; cross section of tooth, ×45 (131).

Plesiechinus Pomel, 1883 [**Pygaster macrostoma* Wright, 1861; SD Hawkins, 1917, p. 167]. Differs from *Pygaster* in having plates of apical system arranged in arc around apical edge of periproct, with which all 4 genitals (but not oculars II, III, IV) are in contact; and in more pronounced triserial arrangement of adoral pore pairs. *Jur. (Pliensbach.-Bathon.),* Eu., W. N. Am. —— Fig. 269,*2*; 270,*2a*. **P. macrostoma* (Wright), Bathon., Eng.; 269,*2a,b*, aboral, oral, ×0.75; 269,*2c*, lat., ×1 (172); 270,*2a*, apical system, enlarged (172).——Fig. 270,*2b*. *P. ornatus* (Buckman), Bajoc., Eng.; adoral part of ambulacrum, enl. (81).

Pileus Desor, 1856 [**Pygaster pileus* J. L. R. Agassiz, 1847; OD]. Large, high-arched or subconical in profile; apical system compact, with imperforate genital 5; periproct separated from apical system, low on adapical surface; peristome smaller than in *Pygaster*; pore pairs biserial or irregularly triserial adapically, minute and nearly uniserial adorally. *U.Jur.(Oxford.),* Eu.——Fig. 269,*3*. **P. pileus* (Agassiz), Oxford., Fr. *(3a)*, Port. *(3b)*; *3a,* oral, ×0.7 (27b); *3b,* aboral, ×0.7 (124).

Order UNCERTAIN

Family HETEROCIDARIDAE
Mortensen, 1934

Ambs straight, comprising trigeminate (or ?polyporous) diadematoid plates. Interambs broad, each plate with 2 to 4 large primary tubercles arranged in horizontal row; tubercles also forming vertical series, with 6 to 8 such vertical series at ambitus. Adradial margin of interamb plates apparently imbricating upon amb plates. All primary tubercles perforate, crenulate. Peristome large, pentagonal, gill slits indistinct (or ?absent). Primary spines of cidaroid type, with granulated cortex. Lantern and apical system unknown. [The general aspect of the test recalls the Diadematoida, but the cidaroid character of the spines is opposed to such affinity, pointing rather to Hemicidaroida or even Cidaroida; no precise relationships can be suggested until the lantern structure is known.] *Jur.(Domer.-Oxford.).*

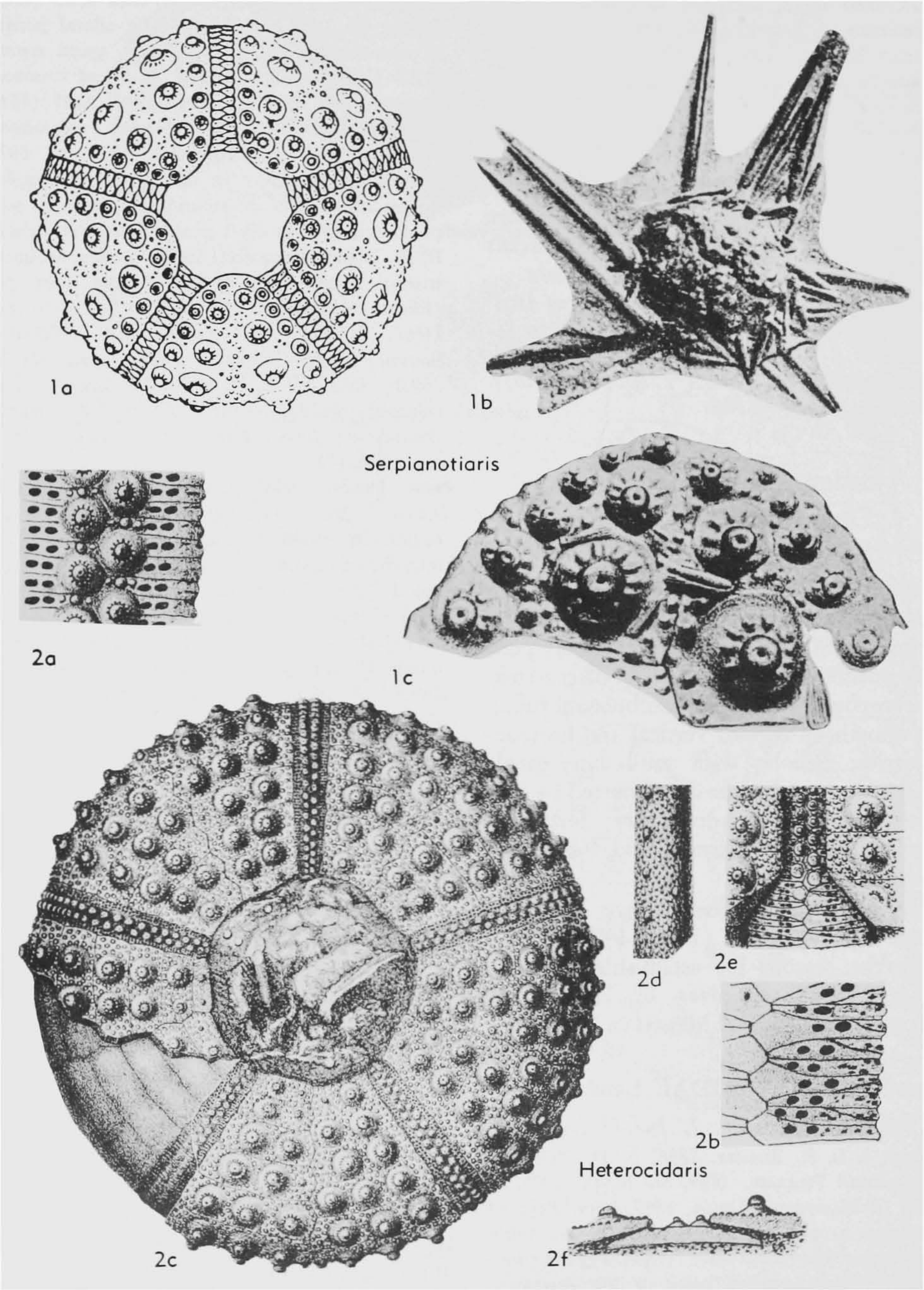

FIG. 271. Heterocidaridae *(2)*; Order and Family Uncertain *(1)* (p. *U366-U367*).

Heterocidaris COTTEAU, 1860, p. 17, 378 [**H. trigeri*; OD] [*non Heterocidaris* HALL, 1861 (=*Pholidocidaris* MEEK & WORTHEN)] [=*Heteroechinus* QUENSTEDT, 1874, p. 370]. Test low hemispherical, flattened below, large (more than 100 mm. diam.); other characters as for family. *Jur.(Domer.-Oxford.)*, Eu.-N.Am.——FIG. 271,*2*. **H. trigeri*, Bajoc., Fr.; *2a,b*, amb ext., int., ×4; *2c*, test aboral, ×0.6 (36); *2d*, spine fragment, ×2 (27c); *2e,f*, amb ext. (with supposedly im-