PART U
ECHINODERMATA 3
ASTEROZOA — ECHINOZOA

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VOLUME 1

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[Volume 1, p. i-xxx, 1-366a; Volume 2, p. 367-695]

INTRODUCTION

By Raymond C. Moore

The publication of *Treatise* Echinodermata 3 in advance of two other volumes allotted to this phylum, respectively numbered 1 and 2, seems anomalous, especially when it is learned that a discussion broadly dealing with characteristics and relationships of echinoderms as a whole has been assigned place at the beginning of Echinodermata 1. Such a chapter is logical as introduction to all others concerned with individual groups however these may be defined and arranged. Accordingly, a comprehensive section entitled "General Features of Echinodermata" has been prepared by Georges Ubaghs, of the Université de Liège. Completed in 1961, it has subsequently been revised twice, mostly in minor ways but with some important additions and subtractions. In my opinion the contribution by UBAGHS is one of outstanding value, one which will be studied with profit by neozoologists as well as paleontologists when it becomes available. Unhappy delay in its appearance is due to the tardy pace in completing fossil groups—all Paleozoic echinoderms—which belong in the same volume.

A disadvantage of the *Treatise* project is the "packaged" nature of volumes planned to contain designated taxonomic assemblages. So long as required parts of a package are unavailable, others remain in files with cumulative needs for revision. The fact that authors are not compensated financially calls for other incentives in order to finish tasks that have been accepted and a burden is placed on the editor (also unpaid) to plead for accomplishment of assignments. Thus, some *Treatise* units move at snail's pace. On the other hand, an advantage of arrangements is the possibility of sending to the press any volume as soon as it is ready. This explains the appearance of Echinodermata 3 in advance of Echinodermata 1 and 2.

At the time many years ago (1948) when the echinoderms were divided into three groups for purposes of the *Treatise,* the view was accepted that the phylum was divisible into two subphyla based essentially on mode of life—forms prevailingly sessile on one hand and others prevailingly free-moving on the other. These have been named Pelmatozoa and Eleutherozoa, respectively. Pelmatozoans were planned for treatment in Echinodermata 1 and 2, Eleutherozoa in Echinodermata 3. Eleutherozoans were interpreted to include starfishes, ophiuroids, echinoids, and holothuroids, with ophiocistioids as an afterthought.

The assignment to prepare descriptions and plan illustrations of fossil asteroids and ophiuroids was accepted in 1950 by W. K. SPENCER, who had published extensive studies of them in monographs of the Palaeontographical Society. By 1951 he had brought together rough notes, including directions for securing desired figures, mostly new drawings to be made under my direction. The notes were organized by me into typescript suitable for use in the *Treatise* and with minor changes this was approved in conferences at Dr. SPENCER's residence at Beaulieu-sur-Mer in southern France. This was in 1951 and 1952. At this time C. W. WRIGHT, of London, was invited to contribute information and some written discussions of post-Paleozoic asterozoans and later SPENCER and WRIGHT worked together to reshape classification that would coordinate previously divergent arrangements of suprageneric taxa based on the separate worlds of fossil and extant forms. In this important effort they were successful, as recounted briefly in introductory paragraphs of the contribution by SPENCER and WRIGHT on asterozoans in this volume. Not until ten years later, however, was a final version made ready, with numerous changes and additions for which WRIGHT is to be credited and thanked.

Initially, a considerable part of the *Treatise* presentation of Echinoidea was planned to be secured from H. L. HAWKINS, of the University of Reading, in part with the collaboration of R. V. MELVILLE, of the Geological Survey of Great Britain, one of his former students. MELVILLE in 1951 produced an excellent account of the general morphology of echinoids, with notes for preparation of figures, but HAWKINS found it infeasible to contribute. Then J. WYATT DURHAM, of the University of California (Berkeley) was invited to help and he accepted willingly. In 1954-55 he was awarded a Guggenheim Fellowship for echinoid studies in Europe and used this opportunity as a primary means of advancing the *Treatise* project in the realm of echinoids. One result of this study was the development of a revised classification of Echinoidea, published by DURHAM and MELVILLE in a *Journal of Paleontology* paper (1957) and proposed as the framework for taxonomic arrangement in the *Treatise.*

In 1960 I asked Durham to assume leadership in organizing the various needed chapters on these echinoderms, some of general scope and others for coverage of major systematic groups. With help from him various assignments were made, with result that the team of workers was enlarged to include P. M. KIER, H. B. FELL, D. L. PAWSON, C. D. WAGNER, and A. G.

FISCHER. Subsequent chapters in this volume by these paleontologists and by DURHAM and MELVILLE speak for themselves, but very much unseen and unrecorded effort is represented by correspondence on many problems and by editorial coordination of typescript and illustrations. An example of behind-the-scenes labor is preparation of an exhaustive list of all nominal genera of echinoids, fossil and Recent, with authorships, dates, and literature references—work done by DURHAM and WAGNER. Obviously, such a list is indispensable for achievement in reasonable degree of the *Treatise* aims of comprehensiveness and authoritativeness.

In connection with KIER's chapters on noncidaroid Paleozoic echinoids and cassiduloids in this volume, it is appropriate to mention two grants from the National Science Foundation to him for museum and field studies in Europe and work pursued in Washington, because, as recorded by him (KIER, 1962, p. 2), the underlying purpose of his researches was to provide a firm foundation for his *Treatise* chapters. Also, acknowledgment to the National Science Foundation for help to other *Treatise* contributors, in part through funds allotted under my direction, should be made. In aggregate the aid has been considerable and thus extremely important.

Judgment that the division of Echinodermata into subphyla named Pelmatozoa and Eleutherozoa, long accepted in textbooks and various monographic works, is untenable has become firm in the minds of at least several *Treatise* contributors who are specialists in the study of various echinoderm groups. This conclusion is not new, but to date it has received little attention and is not yet generally accepted. In the *Treatise* four subphyla are recognized—Homalozoa, Crinozoa, Asterozoa, and Echinozoa. The last two of those named are assigned to the present volume. The asterozoans contain a single class, Stelleroidea, composed of three subclasses, Somasteroidea, Asteroidea, Ophiuroidea; the subphylum is well delimited. The echinozoans are less easily discriminated, though the classes Echinoidea and Holothuroidea unquestionably belong here. The content of Echinozoa is discussed in a chapter by FELL and MOORE on "General Features and Relationships" of the subphylum and the inclusion of chapters devoted to Helicoplacoidea (by DURHAM and K. E. CASTER), Edrioasteroidea (by GERHARD REGNÉLL), Ophiocistioidea (by UBAGHS), and Cyclocystoidea (by R. V. KESLING) indicates classification of these groups in Echinozoa.

The homologies of morphological features observed in the subphyla, classes, and subclasses of echinoderms are very interesting from the standpoints of efforts to adopt uniform orientation, and reasonable correspondence in designation of parts, and especially of inquiries as to "natural" classification, evolution, and phylogeny of all groups. Difficulties and uncertainties are many. Even so, a chapter on the "Homology of Echinozoan Rays" is given by MOORE and FELL.

Description of the morphological features of holothurian sclerites and typescript and illustrations for systematic treatment of dissociated fossil holothurian sclerites were completed by DON L. FRIZZELL and HARRIET EXLINE (Mrs. FRIZZELL) as long ago as 1955. This material lodged ?patiently and ?peacefully in the editor's files for nine years, until it was returned at request of the authors for updating. Little change was needed, but at last this contribution was sent to the press. Meanwhile, D. L. PAWSON, a specialist on holothurians, who is an associate and former student of H. B. FELL at Victoria University of Wellington, New Zealand, had joined the staff of the Smithsonian Institution in Washington, D. C. He has assisted the FRIZZELLS and has been assisted by them on some points and has contributed a chapter of his own on "Phylogeny and Evolution of Holothuroids."

On behalf of the Geological Society of America, of the four paleontological societies that sponsor the *Treatise*, and of paleontologists and zoologists everywhere who will benefit from reference to Echinodermata 3, I express thanks and warm appreciation to the authors of the volume. Not least in deserving praise are Mrs. LAVON MCCORMICK and ROGER B. WILLIAMS, of my staff, for their prolonged, painstaking, able work on typescript, illustrations, and proofs, as well as work in libraries. Also, C. K. HYDER, editor of the University of Kansas Press, has continuously furnished very valuable aid.

ASTEROZOANS

By W. K. Spencer† and C. W. Wright
[†deceased; London]

CONTENTS

INTRODUCTION

In 1950 the late W. K. Spencer accepted responsibility for the section of the *Treatise* on Asterozoa. He invited me to prepare a contribution on the Mesozoic and Cenozoic members of the subclass Asteroidea. By 1953 he and I had, with great help from the Editor, R. C. Moore, virtually completed final typescript and illustrations on the basis of the then accepted classification, under which, in particular, Paleozoic Asteroidea were grouped in one ordinal arrangement and post-Paleozoic Asteroidea in a different and unrelated one.

In that year we both concluded that we should fail in our responsibility to the *Treatise* if we could not relate and integrate these two classifications. Much discussion and thought was devoted to this end. Shortly before Dr. Spencer's death in 1954 we had reached firm conclusions on the outline of a single classification and on the place therein of nearly all families of Asteroidea. Unfortunately the reorganization of the existing typescript could not be completed before Dr. Spencer died, although he left copious notes with both the Editor and myself. I have consequently undertaken reorganization of the whole text.

While this revision was proceeding Dr. H. Barraclough Fell told me of his exciting discovery that *Platasterias* is a living somasteroid and of some of the phylogenetic conclusions that flowed from his study of this genus. His subsequent work on the phylogeny of the sea stars, based on a thorough re-examination of many living forms of Asteroidea and Ophiuroidea, has led to a new appraisal, fully in accord with the paleontological evidence, of the fundamentals of the classification and evolution of Asterozoa. I have endeavored to take this into account so far as possible throughout the text.

In the original draft Dr. Spencer was responsible for most of the introductory matter and for the systematic description of the Paleozoic Asteroidea and all Ophiuroidea. Since his death I have rewritten most of the general matter and revised all the systematic part in the light of later information. Moreover, all extant genera of Asterozoa are now listed. Consequently the whole text is attributed to us jointly.

A number of new names of higher categories are introduced in the text. The need for this arises largely from the fundamental reclassification referred to above.

I must express my deep gratitude to the Editor, as I am sure Dr. Spencer would have wished to do, for his important contribution to our work in the repeated organization of our material, to Dr. H. B. Fell for timely information and much help, to Dr. Hans Hess, of Basel, for advance information about his work on fossil Ophiuroidea and to Miss Ailsa Clark, of the British Museum (Natural History), for ready assistance over Recent Asterozoa.

GENERAL CHARACTERS

DIAGNOSTIC FEATURES

The asterozoans are echinoderms distinguished by radial extensions from a central disc or body; the extensions are supported by calcified axes which are developed as sheaths around radial water vessels. Generally, these extensions have a distinct individuality and are called **arms**

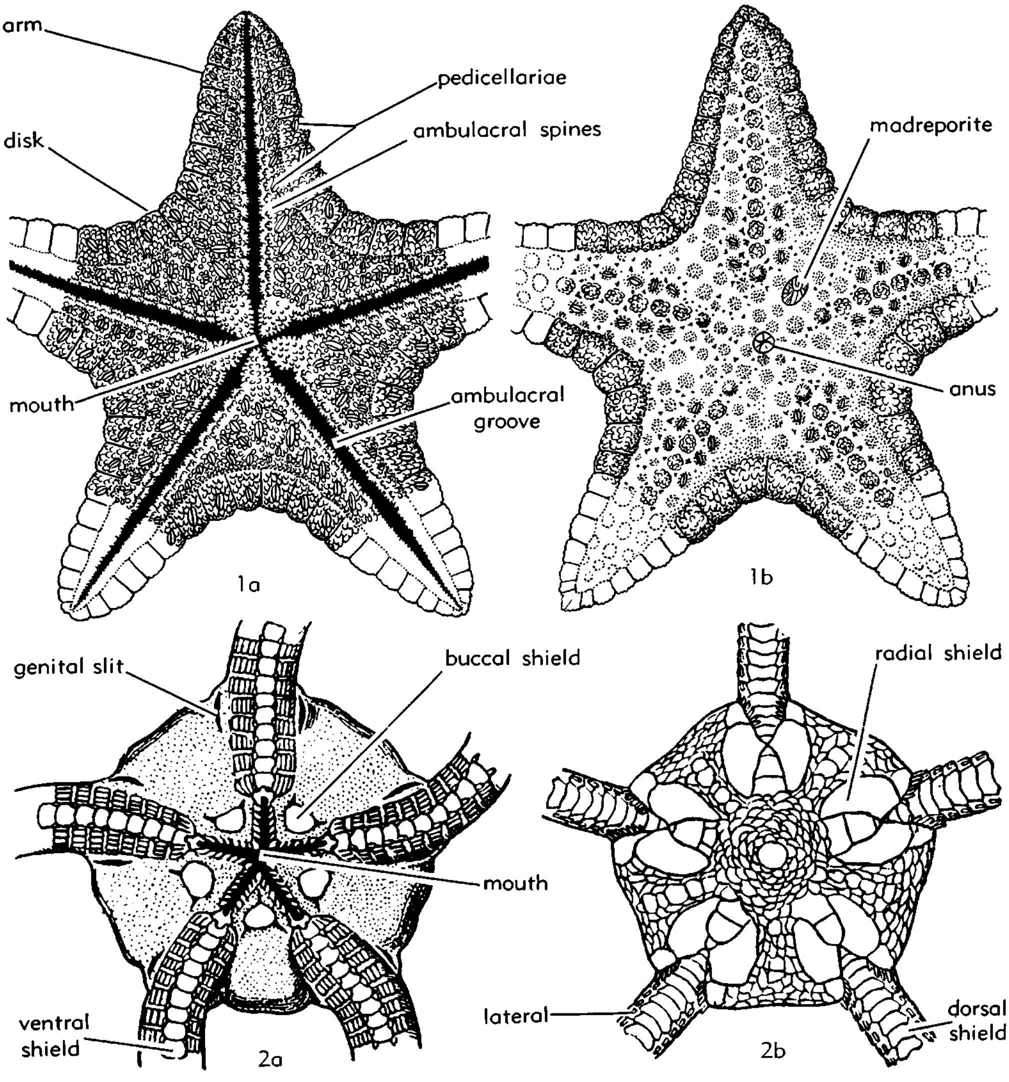

FIG. 1. Recent asterozoans, illustrating characteristic distinctions in form of asteroids and ophiuroids.

1. Starfish, *Anthenea flavescens,* common in shallow waters of the southwestern Pacific, showing features of its nearly flat underside (*1a,* oral surface) and more convex upper side (*1b,* aboral surface), ×1. The central disc is relatively large and the arms short. Narrow ambulacral grooves bordered by blunt spines radiate from the mouth. Pedicellariae and tubercles occur on both oral and aboral surfaces; they are arranged in rows of clusters on the upper surface (130).

2. Brittle-star, *Ophiura,* showing central disc and proximal (inner) parts of slender arms (*2a,* oral surface of one species; *2b,* aboral surface of another species), approx. ×2. Relatively large buccal shields are located interradially on the oral surface and pairs of large radial shields on the aboral surface; otherwise the disc is mainly covered by scalelike plates and granular ossicles. The arms bear rows of ventral (oral side), dorsal (aboral side), and lateral arm plates (137).

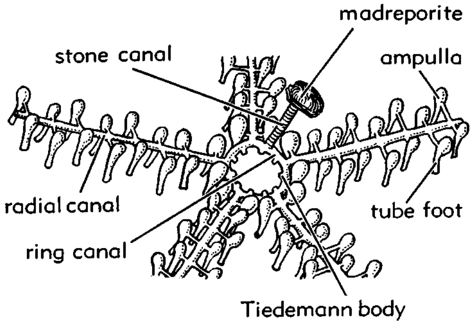

FIG. 2. Diagram of parts of starfish water-vessel system (104).

(Fig. 1). The mouth faces downward toward the sea floor and this side of the animal is called **oral.** Extending radially from the mouth along the oral surface to the extremities of the arms are rows of **tube feet,** which are mobile projections of the water-vessel system walled with soft tissue (Fig. 2). The surface opposite that bearing the mouth and tube feet is called **aboral.** In most asteroids it is characterized by the presence of a porous plate **(madreporite)** which acts as inlet to the water-vessel system; in most ophiuroids this plate is on the oral surface. Asterozoans are free-moving animals in the adult stage. Full-grown individuals range from a few millimeters to more than 50 cm. in diameter, measured from tip to tip of the outstretched arms.

Like other echinoderms, the asterozoans are exclusively marine. Living kinds in the main belong to two groups: asteroids, or starfishes, characterized in most taxa by lack of sharp separation of disc from arms; and ophiuroids, or brittle stars, distinguished by strong differentiation of the slender arms and rounded central disc. A group of correlative rank with primitive skeletal structures, the somasteroids, is represented by a few Paleozoic genera and a single extant species.

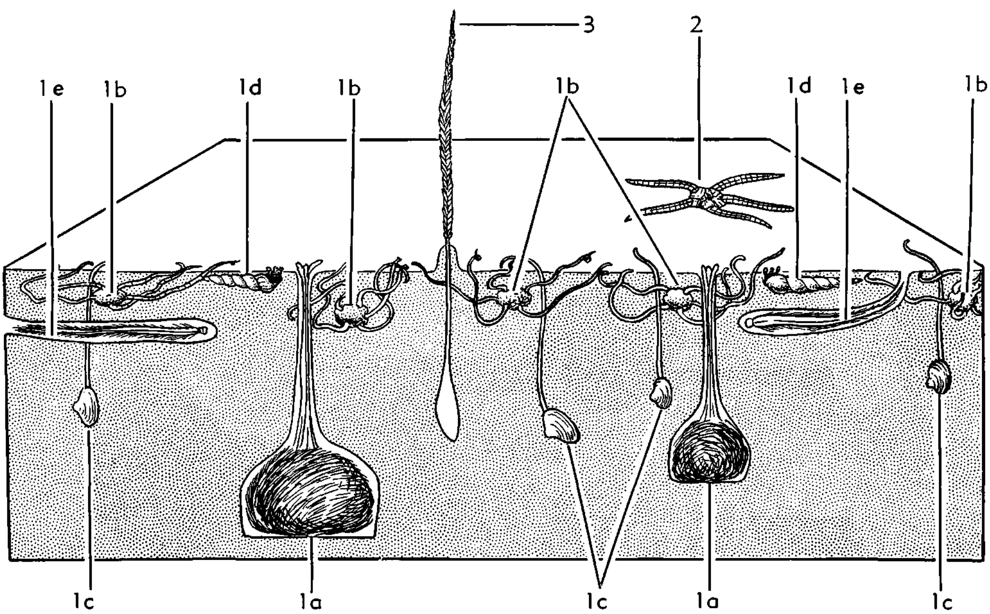

FIG. 3. Cross section of modern *Echinocardium-Turritella* community found in shallow seas, showing component groups of animals (101).

1. Animals living below surface of the sea floor, some in well-defined burrows; *1a,* sea urchin, *Echinocardium cordatum; 1b,* ophiuroid, *Amphiura filiformis; 1c,* pelecypod, *Abra nitida; 1d,* gastropod, *Turritella terebra; 1e,* worm.

2. Animals living on surface of sea floor; ophiuroid, *Ophiura texturata.*

3. Animals feeding in clear water above sea floor; anthozoan, *Virgularia mirabilis,* a suspension-feeder.

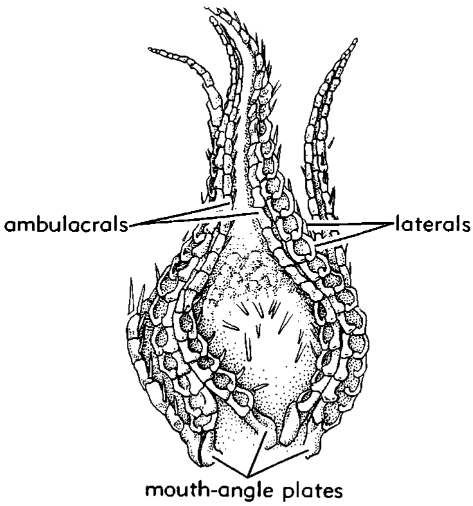

Fig. 4. Small Middle Ordovician ophiuroid (*Taeniaster spinosus*), Trenton, Ohio, with arms upraised, indicating withdrawal of animal into its burrow before death, ×5 (133).

MODE OF OCCURRENCE AS FOSSILS

The skeletal elements of Asterozoa consist of discrete ossicles which readily separate from each other after death, and accordingly the greater part of our knowledge of fossil forms is derived from specimens preserved under exceptional conditions that prevented the dissociation of interrelated hard parts. In the Paleozoic such specimens have been found particularly in lower Arenigian rocks of southern France, upper Arenigian of Czechoslovakia, Upper Ordovician deposits of Girvan, in Scotland, and in the Early Devonian Bundenbach Slates of Western Germany. These beds comprise sediments of ancient sea floors on and in which vigorous animal communities lived, with starfishes an important element. A corresponding community of the present day is illustrated in Figure 3. Such communities are divisible into three components: animals living under the surface of the sea floor, animals living on the surface, and animals feeding in clear water above the sea floor (2).

Preservation of intact skeletal parts requires rapid burial after death. It is evident that animals living below the sea floor are best suited for preservation, for the surrounding mud prevents scattering of discrete hard parts and tends both to seal the remains and to retard somewhat the decay of soft parts; some fossil asterozoans show that fine mud had time to infiltrate internal vessels, so that the original shape and course of these soft parts can be traced in the form of casts. The surrounding matrix also retained the animal in postures comparable to those assumed in life, as is well shown by some fossil ophiuroids (Fig. 4).

Specimens consisting of external molds, formed by solution of the calcite skeleton, are very useful for study by means of rubber casts which reveal the finest detail of surface characters and by gentle bending may show important features of ossicle junctions. Fossils preserved as calcite or pyrites may be less valuable because recrystallization tends to obliterate surface and structural characters.

In the Mesozoic, an excellent source of material, especially of Asteroidea, is the chalk of the Upper Cretaceous. Whole specimens occur, but are rare, while isolated ossicles or groups of ossicles, representing dissociated remains of single individuals, are abundant. The soft chalk in which they are embedded readily weathers away or can be cleaned, exposing the ossicles in perfect condition for examination. Many studies and reconstructions have been made from such ossicles (55, 74, 89). Since the chalk was laid down as a continuous deposit during a very long time, it is possible to follow in great detail the stages of evolution of several asteroid lineages.

Many other occurrences are known in Paleozoic and later rocks, in addition to those already mentioned. Occasionally, "starfish beds" containing abundant individuals of one or more species are observed, but, generally speaking, Asterozoa are rare fossils and well-preserved specimens are exceptional. In many marine formations no individuals have yet been discovered. Inevitably, therefore, the detailed history of the subphylum is rather poorly known and a good deal of speculation is necessary to make a connected story.

MORPHOLOGY AND FUNCTION

SKELETAL STRUCTURES

MAIN ELEMENTS

The skeletal structures in Asterozoa develop in the outer layers of the body and thus outline its shape. Component elements, or **ossicles,** may be classified in three groups: **axial elements,** comprising ossicles formed in the sheath of water vessels; **adaxial elements,** consisting of ossicles which adjoin and are in series with the axial skeleton; and **extraxial elements,** comprising all other ossicles. The distinction between these groups is well shown in the early starfish *Villebrunaster,* in which the whole oral surface is occupied by strongly contrasted ossicles of the axial and adaxial skeletons (Fig. 5). The components so closely follow in similar series that they may be said to be arranged in metameres.

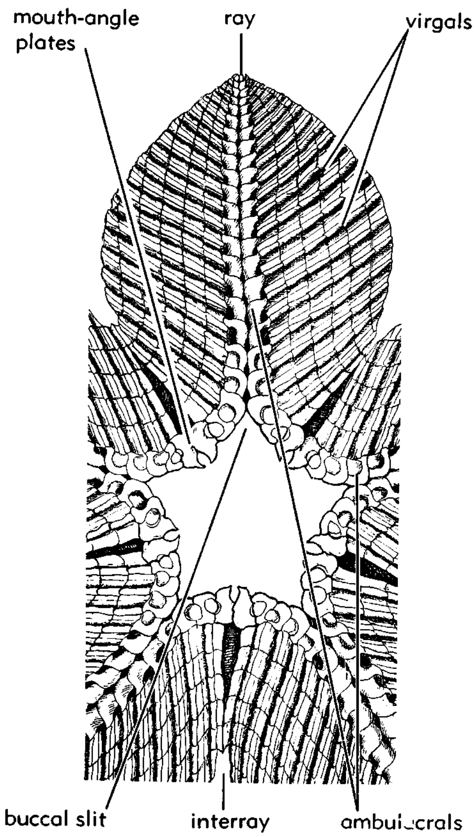

FIG. 5. Metameric segmentation of the skeleton of a primitive starfish, as shown by the oral surface of *Villebrunaster thorali* (reconstr.), ×5. The relatively large ossicles of the central disc and median part of the arms belong to the axial skeleton; others shown are adaxial elements. The double row of axial ossicles along each arm are ambulacrals, with basins for tube feet along their outer edges. Near the central opening the ambulacrals diverge to form V's of the mouth frame. In series with the ambulacrals are rod-shaped adaxial ossicles (virgals). Mouth-angle plates are located interradially, projecting into the central opening (131).

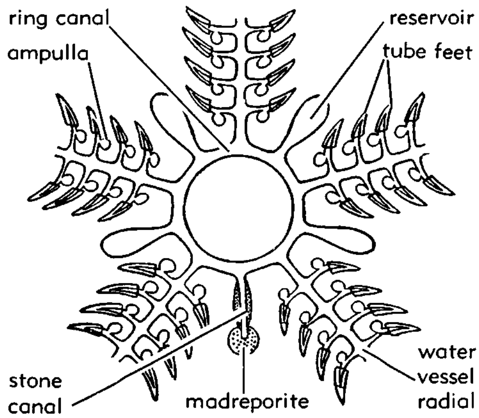

FIG. 6. Arrangement of water vessels in an extant asteroid (122).

The extraxial skeleton in *Villebrunaster* comprises triradiate ossicles making a wide-meshed network on the aboral surface, and not in series with the axial skeleton (see Fig. 20,*1*). A special extraxial plate is the madreporite which forms a sievelike opening from the outside into the water circulatory system. If present, it is located interradially; primitively, it was lateral in position but is on the aboral surface in most asteroids and on the oral surface in most ophiuroids and some early asteroids. The tube from the madreporite to the main water vessels is commonly calcified and is termed the **stone canal.**

AXIAL STRUCTURES

Arrangement. The pattern of axial skeletal elements exactly follows that of the main water vessels, one of which runs along the mid-line of each arm; a canal which encircles the mouth communicates between

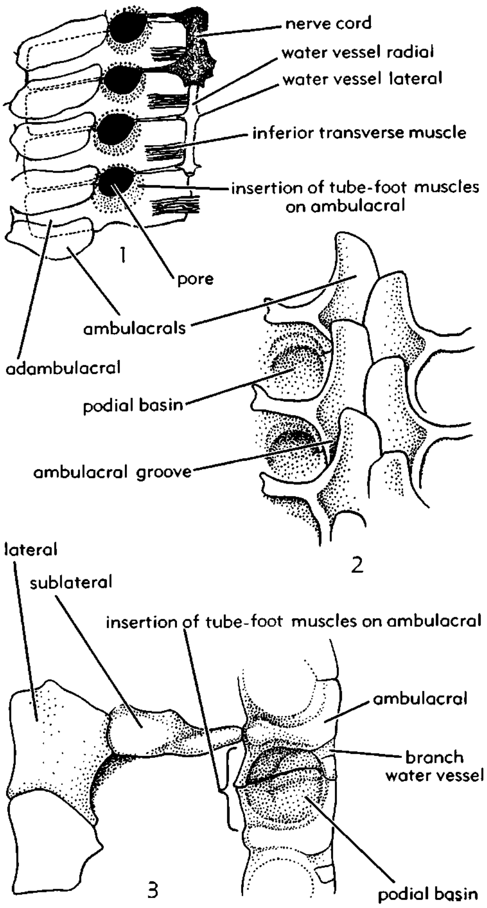

Fig. 7. Relationship between axial skeletal elements and seating of tube feet.——*1.* Structures visible along part of one side of ambulacrum of an extant starfish *(Astropecten irregularis)* with tube feet and spines attached to adambulacral and ambulacral ossicles removed and with parts of radial nerve cord and water vessel also cut away to show underlying structures (132).——*2.* Axial ossicles of primitive starfish (*Archegonaster*, U. Arenig.), showing structures corresponding with those in *1* (133).——*3.* Axial and adaxial ossicles of one side of arm of an early ophiuroid (*Eophiura*, U.Arenig.), showing basins for tube feet (133).

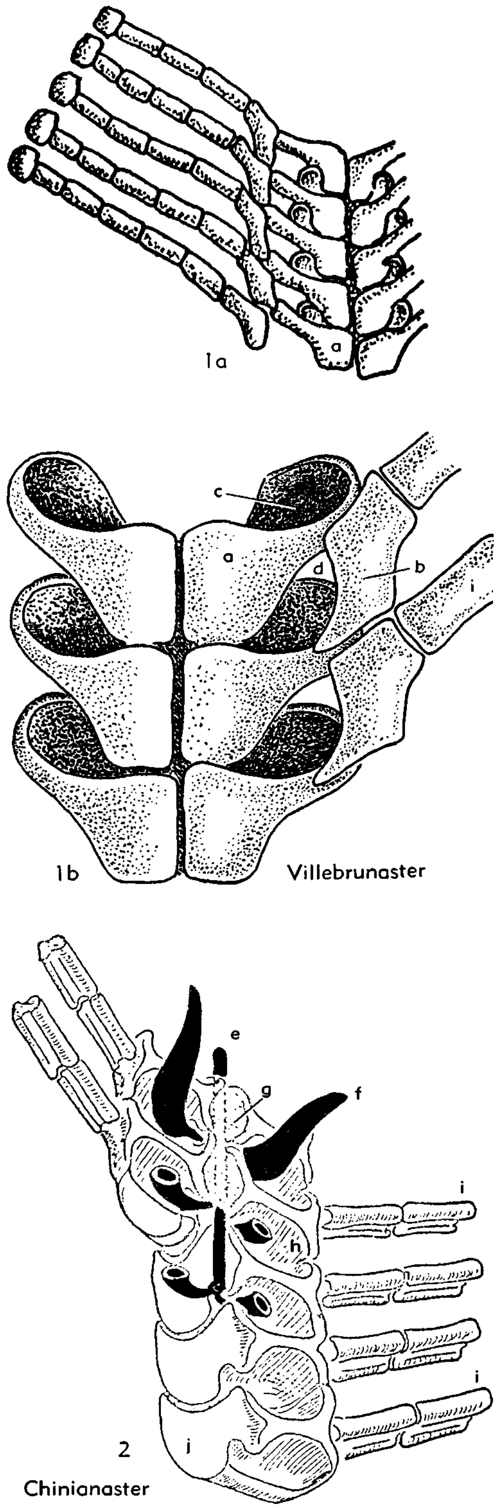

Fig. 8. Axial structures and tube feet of primitive somasteroids (108).——*1. Villebrunaster thorali* Spencer, L.Ord., Fr.; *1a,* arm skeleton near tip, ×6; *1b,* interpretation of mid-arm structure, ×10.——*2. Chinianaster levyi* Thoral, L.Ord., Fr. [Explanation: *a,* capitulum of ambulacral; *b,* adambulacral virgal; *c,* shelf of cupule (basin for tube foot); *d,* passage from cupule to arm interior; *e,* radial water vessel; *f,* tube foot; *g,* adductor muscle; *h,* cupule; *i,* virgal; *j,* ambulacral.]

the radial vessels of the arms and also connects with the stone canal (Fig. 6). The axial skeleton thus comprises the ossicles located along the water vessels of the arm and also the elements that form the **mouth frame.**

The axial skeleton is divided into segments, each of which corresponds with a branch water vessel approximately at right angles to the main canal. The branches are almost uniformly spaced. Each branch vessel emerges in a basin or depression readily recognizable in the skeleton. A tube foot is situated in each basin. Each of the ossicles that carry the basins is called an **ambulacral** (abbrev., *Amb,* pl. *Ambb*), the whole series along each arm forming an **ambulacrum.**

Relation of tube feet to their seatings. Fossil asterozoans commonly show in great detail the nature of the basins for the tube feet. The course of the water vessels and associated soft tissues can be determined by comparison with living starfishes (Fig. 7). The general relationship between water vessels and the axial skeleton has changed little since the time of the earliest known asterozoans. In all these primitive forms, whether somasteroids, asteroids, or ophiuroids, the seating of each tube foot was shared unequally between two ambulacrals, the larger part of the basin being located on the distal ossicles of the pair (Fig. 7,*2,3*). In Recent asteroids the basin is very shallow but still situated mostly on the distal ossicle (Fig. 7,*1,* shaded area, round pores).

The passage from the branch water vessel to the tube foot is distinguishable in many fossils as a break in the wall of the basin, just behind its transverse wall and situated on the proximal ambulacral, precisely as in extant asteroids. The derivation of this passage from a gap between adjacent ambulacrals can be seen from the situation in primitive somasteroids (Fig. 8).

Relation of structure to activities of tube feet. Minute details of the structure of the basins, as indicated by comparison with extant asteroids (71), are correlated with various activities of the tube feet. The chief of these are defined as protrusion and pointing. Protrusion is vigorous and extensive in extant forms. It is made possible by division of the tube foot into an internal sac, the **ampulla,** and an outward-directed closed tube, the **podium.** The tube foot is protruded by squeezing water from the ampulla into the podium and retracted by the reverse process (Fig. 9,*1a,b*).

It used to be thought that no Paleozoic asterozoans possessed passages between adjacent ambulacrals of the sort that imply the division of the tube foot into two parts, such as characterize extant asteroids (Fig. 10,*1*). It was necessary to suppose that if ampullae existed in Paleozoic forms they were situated outside the body cavity. Jaekel (38) suggested that the deeply hollowed basins in many Paleozoic asterozoans held external ampullae (Fig. 10,*2*) and that this provided a mechanism for protrusion

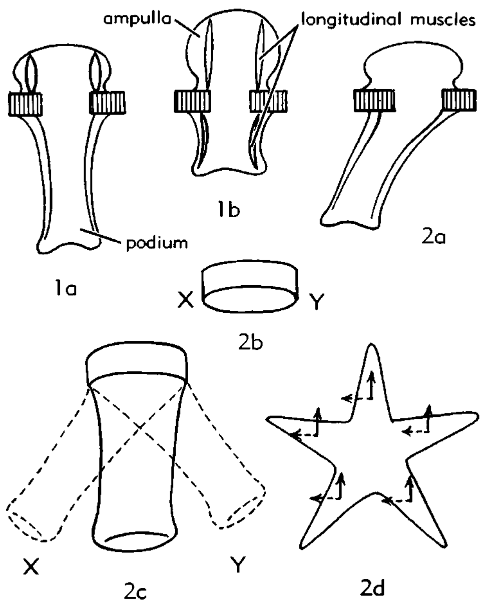

Fig. 9. Movements of tube feet (132).——*1.* Protrusion and contraction; *1a,* contraction of longitudinal muscle fibers in walls of the ampulla, reducing its volume so as to expel water into the podium and thus cause it to protrude; *1b,* contraction of longitudinal muscles of podium, expelling water into the ampulla and thus causing retraction of the tube foot.——*2.* Directional pointing; *2a,* deflection of podium accomplished by contraction of muscles on one side and simultaneous relaxation of those on the other; *2b,* muscle ring at base of podium in oblique view, contraction of fibers at X being accompanied by relaxation of those at Y and similarly for any other opposite parts of the ring; *2c,* diagram showing tube foot expanded in three directions; *2d,* changes in direction of locomotion of a starfish accompanied by corresponding changes in direction of pointing of podia, as indicated by the two sets of arrows.

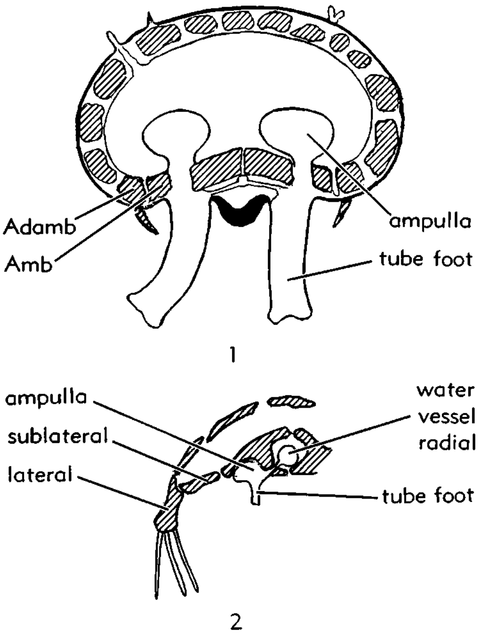

FIG. 10. Position of ampullae in relation to the body cavity of asterozoans.——*1.* Internal ampullae shown in cross section of arm of an extant asteroid (132).——*2.* External ampulla of an early ophiuroid *(Eophiura)* shown in cross section of arm, ampulla lodged in hollow of the ambulacral basin (114).

and retraction of the tube feet comparable with that of extant forms. In fact, most somasteroids and probably all Paleozoic asteroids had internal ampullae; the external ampullae are confined to Chinianasteridae (Fig. 8,*1b*) among somasteroids and to ophiuroids.

Directional protrusion or pointing of the tube feet is characteristic of living asterozoans. For example, in crawling, the podia are pushed outward in the direction of movement and in burrowing a sideways scooping action may be seen. SMITH (71) has shown that pointing of the podia is achieved by reciprocal contraction and relaxation of fibers on opposite sides of a ring of muscles between the wall of the upper part of the podium and the adjoining ambulacral (Fig. 9,*2a-d*). Thus, the angle of protrusion and the direction of pointing can be modified. Ancient asterozoans were probably able to point their tube feet like extant ones, for a well-defined narrow groove can be seen just inside the ambulacral basin in various early fossil asteroids and ophiuroids. This groove is plausibly interpreted as the line of insertion of the ring of muscle that controlled pointing.

Lever action of ambulacral ossicles. Asteroids are characterized by an arrangement of muscles attached to ambulacrals

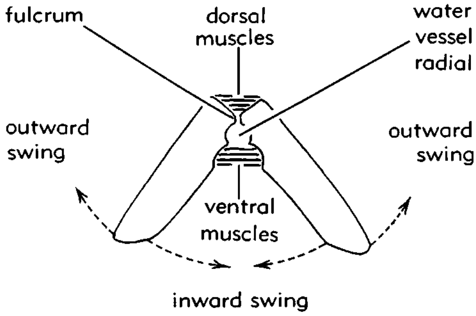

FIG. 11. Lever action of ambulacral ossicles (134).

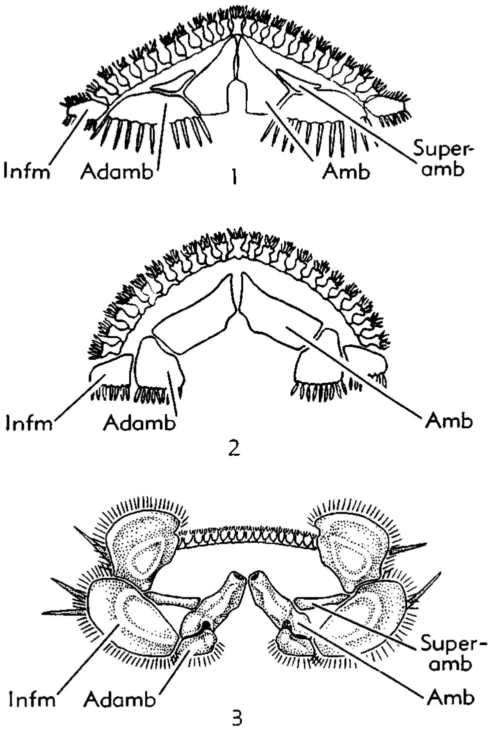

FIG. 12. Cross section of asteroid arms showing evolution of the ambulacral groove (133).——*1. Platanaster* (Ord.), with ambulacrals and adambulacrals at the same level.——*2. Schuchertia* (Ord.-Sil.), with ambulacrals arched above adambulacrals and rising well into the arm cavity.——*3. Astropecten* (Rec.), with steeply arched ambulacrals underlain by adambulacrals.

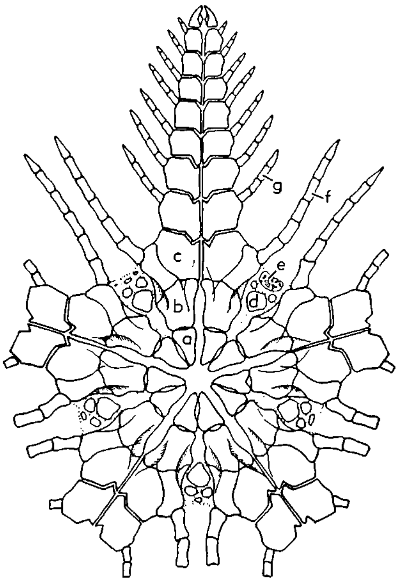

FIG. 13. *Chinianaster levyi* THORAL, L.Ord., Fr.; oral side of juvenile specimen, ×6.3 (108). [Explanation: *a-c*, 1st, 2nd, 3rd ambulacrals, *b* and *c* united syzygially; *d*, tegminal; *e*, inferred madreporite; *f*, oral pinnule; *g*, 4th metapinnule.]

that by a lever action allows opening or closing of the ambulacral groove. A pair of levers is formed by opposed bar-shaped ambulacrals arranged in an inverted V along the ambulacral groove on the oral surface of the arm; the fulcrum is near the tip of the V (Fig. 11). Excavations above and below the fulcrum provide for the insertion of dorsal and ventral muscles. Contraction of the dorsal muscles produces an outward swing of the lower ends of the bars, thus widening the ambulacral groove and assisting the protrusion of the tube feet. When the ventral muscles contract, the bars swing inward, narrowing the groove and sheltering the retracted tube feet.

The mouth-angle plates of primitive ophiuroids have a similar lever action, which was doubtless useful in digging burrows.

Ambulacral groove. The ambulacral groove with its arch formed by the ambulacrals is characteristic of asteroids. In this subclass the ambulacrals are invariably opposite one another, never alternating, as in somasteroids and early ophiuroids. In the earliest asteroid stage, exemplified by *Platanaster* (Fig. 12,*1*), the underside of the arm is flat and in substance of the ambulacrals interrupted by a shallow groove that carried the radial water vessel and radial nerve. A later stage, exemplified by *Schuchertia* (Fig. 12,*2*), shows a broad trough formed by transversely elongated ambulacrals, making an almost level roof of the groove which is bounded on either side by a wall of adambulacrals as innermost part of the adaxial skeleton. Subsequent deepening of the groove is accompanied by inward bending of these walls to make a nearly enclosed tube (Fig. 12,*3*).

Mouth frame. The mouth frame consists of the proximal ends of the rows of axial ossicles, more or less modified into an independent structure. There has been much argument about the origins and homologies of parts of the mouth frame, but a trustworthy conclusion appears to have been reached as a result of the latest studies by FELL (13) on primitive somasteroids. The following account is based on this work and therefore differs from standard descriptions.

Juvenile *Chinianaster* (Fig. 13) and *Villebrunaster* show that the proximal member of each ambulacral series is an acutely

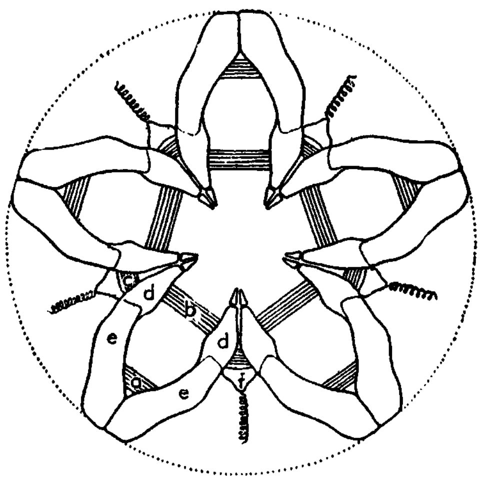

FIG. 14. Diagram of mouth frame of asteroid showing system of muscles that allows mouth-angle plates to be moved in and out (133). [Explanation: *a*, radial muscles between 1st ambulacrals; *b*, *c*, radial and interradial muscles attached to apophyses of mouth-angle plates; *d*, mouth-angle plate; *e*, 1st ambulacral; *f*, odontophore.]

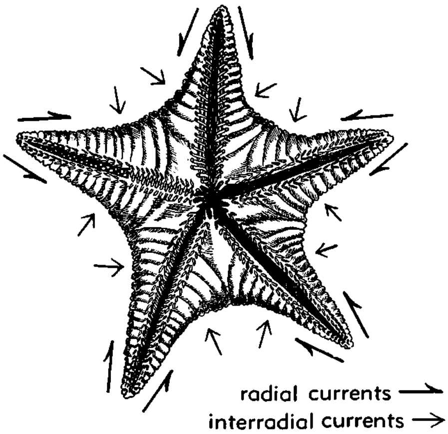

FIG. 15. Oral surface of recent asteroid *Porania,* showing large interradii and ciliate grooves; arrows indicate direction of flow of water currents (111).

triangular ossicle bordering the **buccal slit** and touching the adjacent ossicle of the neighboring axial series. These triangular ossicles are termed **mouth-angle plates.** The next two ambulacrals are united by syzygy into a massive ossicle which carries a complete cupule for a tube foot, as well as half cupules at either end. The differentiation of these elements of the mouth frame seems to be less distinct in adult *Chinianaster* and *Villebrunaster.* In the Recent *Platasterias,* the mouth-angle plates of each axial series have moved apart and superficially appear to be enlarged adambulacrals; the mouth frame thus appears to consist of powerful interradial "jaws" (pairs of mouth-angle plates of adjoining axial series) projecting between ends of the ambulacra. This is the typical appearance of the mouth frame of most Asteroidea, known as the **adambulacral type;** the mouth-angle plates have the appearance of specialized adambulacrals, whereas the apparent first ambulacrals are, in origin, fused second and third ambulacrals (Fig. 13).

A second type of mouth frame, termed **ambulacral type,** confined to the asteroid order Forcipulatida, is known. In this the mouth-angle plates are insignificant and most of the frame consists of the proximal ambulacrals, either straight or projecting into the mouth (see Fig. 63).

In some early Asteroidea with adambulacral mouth frames, an additional plate, the **torus,** is mounted on each pair of mouth-angle plates, projecting inward to the center of the mouth. Normally it carries several long spines. In *Cnemidactis,* for example, the five tori completely close the aperture. Forms without tori may have large spines that serve the same function.

In many forms the mouth frame was clearly more or less flexible, so that the mouth-angle plates could be moved in and out. The muscular system which allows this to be done (Fig. 14) involves an additional ossicle in each interradius, the **odontophore,** prominent in many early groups. Presumably this ossicle originally was an inframarginal which in the course of phylogeny became occluded from the margin and adapted as part of the "jaw" system. An analogous T-shaped plate is seen in somasteroids and some asteroids, but this may have a different origin.

The earliest Ophiuroidea (Stenurida) have deep radial V's, forming buccal slits, as in Somasteroidea, and somewhat similar mouth-angle plates. The "jaws" resemble those of Asteroidea of adambulacral type, but always have a torus.

ADAXIAL STRUCTURES

The adaxial skeleton of the somasteroid Chinianasteridae provides broad interradial tracts of grooves between parallel rows of narrow plates termed **virgals.** The rows are termed **metapinnules** and the whole structure is referred to as **metapinnular.** This arrangement of grooves persists in the extant somasteroid Platasteriidae but tends to be reduced and finally lost in the Paleozoic somasteroids. The sides of the grooves

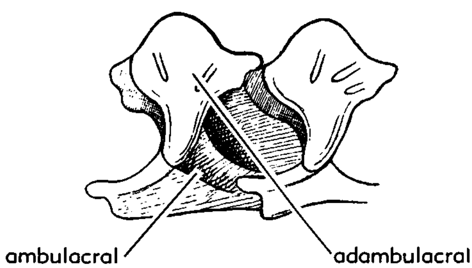

FIG. 16. Adaxial ossicles, termed adambulacrals, standing as wall at side of ambulacral groove; cross section of arm of *Archegonaster* (U.Arenig.), a somasteroid. Shelter for tube feet is provided by hollows between overhanging adambulacrals (133).

were ciliated, and thus water currents were produced from the periphery to the center of the arm. Many fossil and extant asteroids have analogous, if not homologous, systems for the production of such water currents. In principle, the currents serve two purposes—they bring small food particles to the ambulacral channel and thence to the mouth, and they also bring respiratory water to the tube feet and associated nerves, without which the tube feet become flaccid and do not function (70). The pattern of the oral surface and the arrangement of ciliary currents in the living asteroid *Porania* is much like that in *Chinianaster* (Fig. 15).

In later somasteroids and all asteroids some specialization of the primitive adaxial skeleton is observed. The row of ossicles next to the ambulacrals becomes continuous in a radial direction and the ossicles thicken to form a wall overhanging the ambulacral groove (Fig. 16); these ossicles are termed **adambulacrals.** They increase the depth of the ambulacral groove and shelter the podia when retracted; they are commonly armed with prominent spines.

The outermost row of virgals may similarly become continuous and form a row of **inferomarginals** (*Infm,* pl. *Infmm*). The intermediate rows may form a mosaic of ossicles, which in the most primitive asteroids (Platyasterida) retains the transverse series; but in most asteroids this pattern has been replaced by one composed of longitudinal (i.e., radial) gradients. The virgals of the row next to the adambulacrals, however, have become occluded in *Platasterias,* the living somasteroid, and rest across the internal surfaces of ambulacrals and adambulacrals; they are known as **superambulacral** ossicles. These persist in Platyasterida and Paxillosida but have disappeared in all but a very few other asteroids.

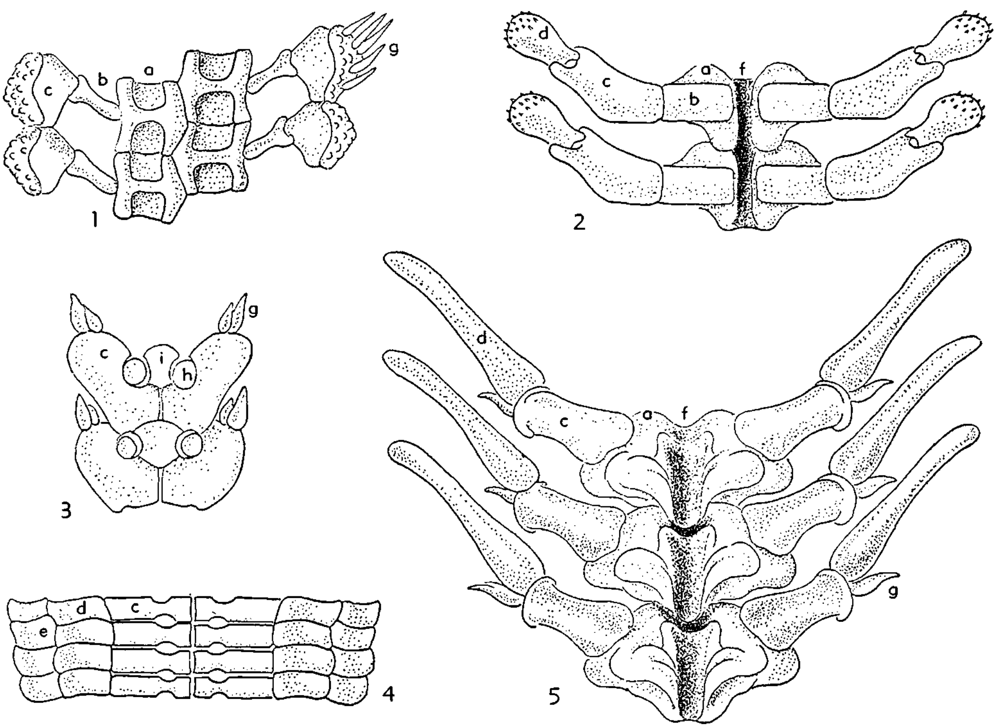

Fig. 17. Pinnate structure in Ophiuroidea (Fell).

1. Eophiura bohemica, ×2.3 (133).
2. Trichaster palmiferus, ×4 (108).
3. Ophiuraster symmetricus, ×13.5 (108).
4. Astrophyton sp., arm base, ×2 (119).
5. Asteronyx loveni, adoral view of arm skeleton dissection, ×6.7 (108).

[Explanations: *a.* ambulacral; *b,* virgal (sublateral); *c,* virgal (lateral); *d,* 3rd virgal; *e,* 4th virgal; *f,* hyponeural groove; *g,* lateral (secondary) spine; *h,* tentacle scale; *i,* ventral arm plate.]

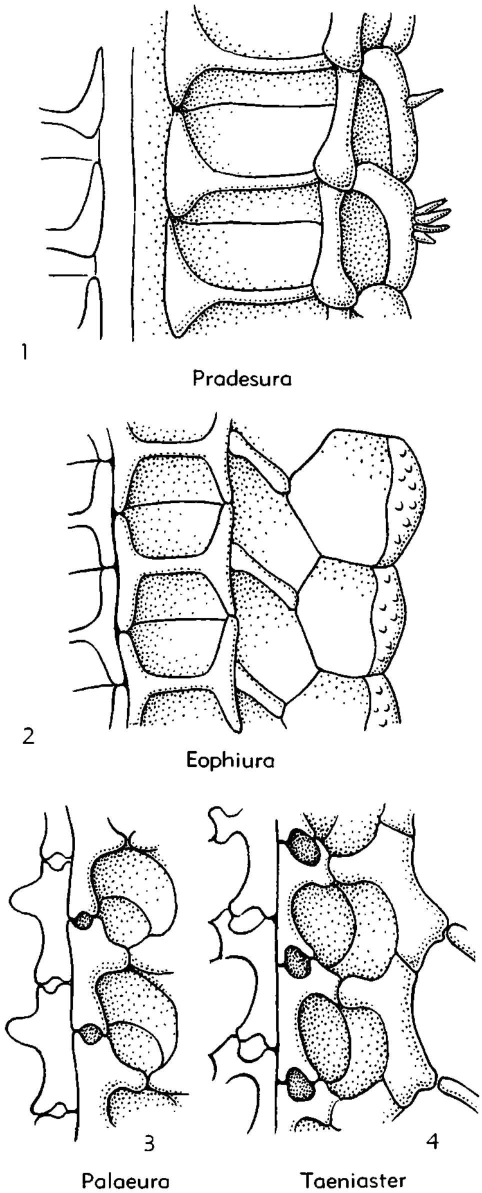

FIG. 18. Evolution of ambulacrals into vertebrae in arms of Ophiuroidea (133).——*1. Pradesura* (L. Arenig.), oldest known ophiuroid, has the basins for tube feet shared subequally by two ambulacrals with L-shaped ridges between, and an open ambulacral groove.——*2. Eophiura* (U.Arenig) has more equally shared basins, T-shaped ridges between, and closed ambulacral groove.——*3. Palaeura* (U. Arenig.) has the basins mostly on a single ambulacral, intervening ridges boot-shaped, and groove closed.——*4. Taeniaster,* much like *Palaeura,* has deeply excavated ridges for attachment of strong ventral muscles, and basins confined to single ambulacral.

OPHIUROID ARM (AXIAL AND ADAXIAL)

The most primitive ophiuroids show close resemblance to the contemporary somasteroids and, in particular, have a pinnate arm structure that is clearly derived from an ancestral metapinnular type. FELL has shown that several extant ophiuroids also preserve a distinctly pinnate arm structure, and he has demonstrated the homologies with the somasteroid arm (Fig. 17) (13). Even in a typical modern ophiuroid, the homology of lateral shield with a virgal can be made out (Fig. 17,5).

The critical development in the ophiuroid arm comprises fusion of the opposite ambulacrals to form single pieces that occupy most of the interior of the arm; these pieces, called **vertebrae,** articulated by a ball-and-socket joint. Associated with this step is transformation of the two inner rows of adaxial ossicles (homologues of first and second virgals) into side plates hinged to

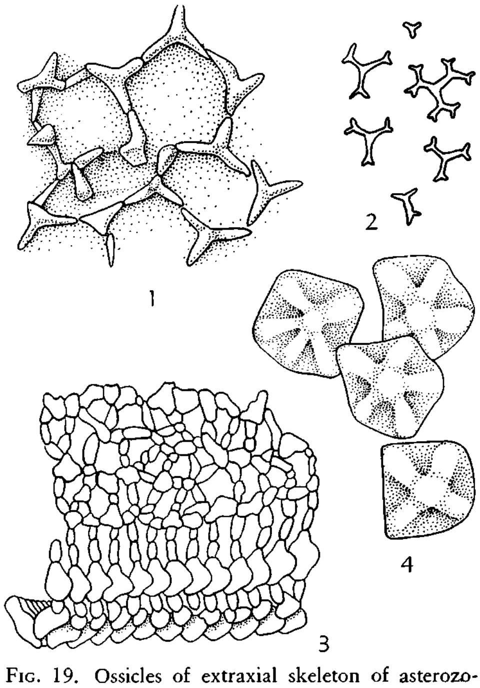

FIG. 19. Ossicles of extraxial skeleton of asterozoans.——*1.* Triradiate ossicles of aboral skeleton of an early somasteroid, *Chinianaster* (Arenig.) (133). ——*2.* The developing network for comparison with an echinoid plate, which at this stage consists of discrete radiate ossicles (112).——*3.* Network of ossicles on sides and aboral surface of an extant starfish, *Asterias rubens* (139).——*4.* Ossicles from aboral surface of an early ophiuroid, *Encrinaster,* showing stellate ridges (133).

the vertebrae to act as cover plates; the side plates are known as **sublaterals** (*SubL,* pl. *SubLL*) and **laterals** (*L,* pl. *LL*). The stages of alteration of ambulacrals into vertebrae are shown within the order Stenurida (Fig. 18). (One suborder, Proturina, shows no sign of the change. For convenience the arm segments of all Stenurida are referred to as ambulacrals.)

The vertebral type of axial skeleton permits increased mobility, for with it the arm can twist and turn. Each arm segment becomes an independent unit, since seating of the tube foot is no longer shared by two ossicles. Ability to twist is provided by muscle bands which border the ball-and-socket joints.

EXTRAXIAL STRUCTURES

The extraxial skeleton comprises ossicles not associated with the tube feet, mainly ossicles of the aboral surface. In their simplest form these are spicules with three narrow rays diverging from a small center, together forming a wide-meshed net (Fig. 19). The holes of the network provide for respiratory exchange between the body fluids and the surrounding water. Many asteroids have a network similar to that of *Chinianaster* (Fig. 19,*1*) but more substantially built, in which the nodal points of the ossicles commonly carry a small knob surmounted by a spine or group of spinelets **(paxilla)**. The knobs may be arranged in diagonal rows marking the course of channels on the aboral surface, along which water currents are driven by cilia; these currents flow over holes in the network, which generally are occupied by external gills (**papulae**) (Fig. 20), consisting of projecting folds of the body wall.

This general type of respiratory arrangement characterizes the Paxillosida, Spinulosida, and Forcipulatida of all periods. In the Valvatida, however, from Paleozoic Hudsonasteridae to living Goniasteridae, the aboral surface tends to be more or less completely covered by large solid ossicles. The papulae emerge as a rule from specific papular pores between them and these may be grouped into special papular areas. There may also be other arrangements to compensate for the reduction of the respiratory area. In Hudsonasteridae a loosely built group

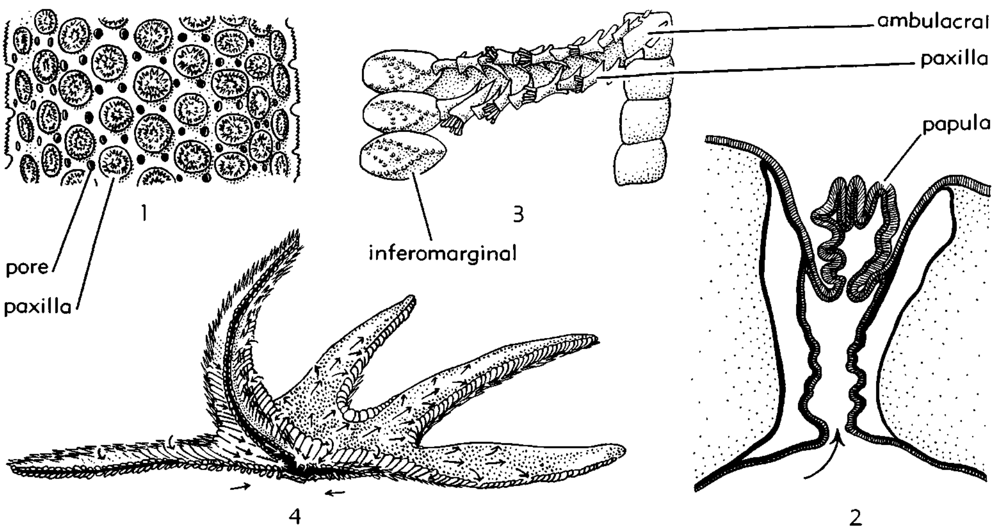

FIG. 20. Extraxial skeletal elements of the aboral surface of asteroids in relation to respiratory currents.

1. Diagonal channels on aboral surface of the extant *Chaetaster,* showing paxillae along borders of the channels and pores for papulae along the floors (118).

2. Cross section through a papula which has been withdrawn (118).

3. Diagonal channels on surface of the early Paleozoic *Platanaster* with the bordering paxillae fallen on their sides (133).

4. Diagram showing the way in which water collected on the aboral surface of a recent *Astropecten* is carried to the oral surface by intermarginal channels (111).

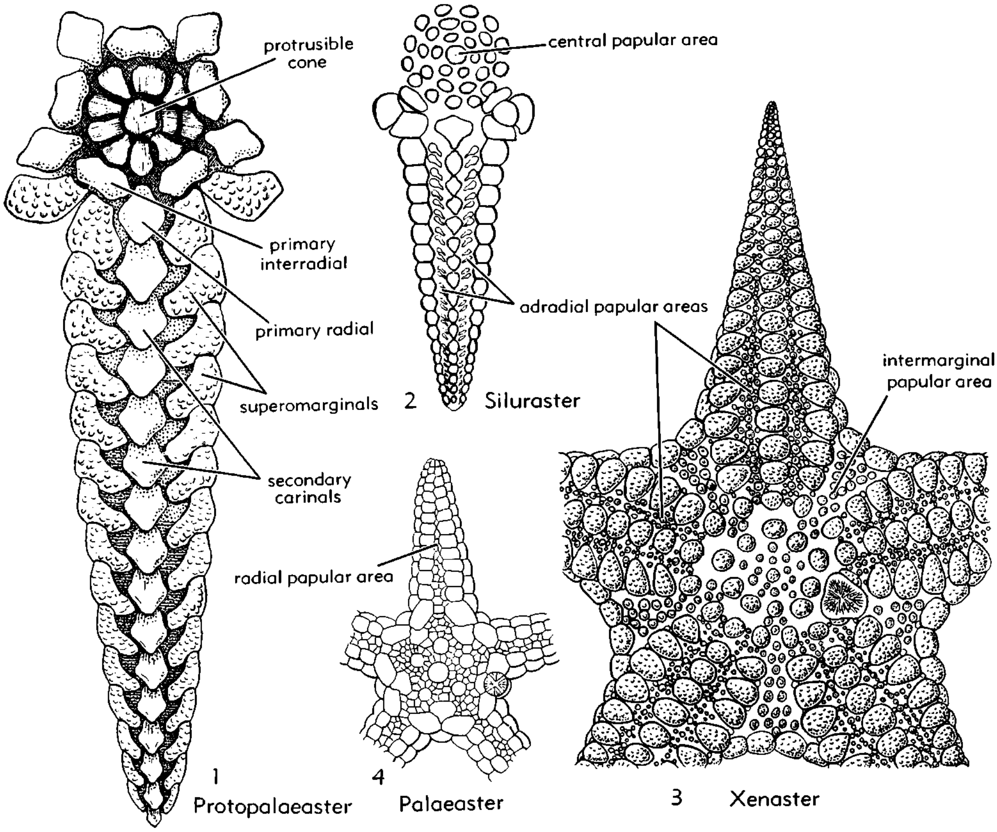

FIG. 21. Respiratory structures on aboral surface of early Valvatida (129).

1. *Protopalaeaster* (Hudsonasteridae), showing protrusible cone in center of disc, hinged to superomarginals through primary interradials (109).
2. *Siluraster* (Hudsonasteridae), showing central and adradial papular areas (133).
3. *Xenaster* (Xenasteridae) showing the addition of intermarginal papular areas (128).
4. *Palaeaster* (Palaeasteridae), showing radial papular areas consisting of numerous small ossicles (129).

of large ossicles in the center of the disc forms a **protrusible cone,** apparently for respiratory purposes; its ossicles are hinged to the superomarginals through the primary interradials (Fig. 21,*1*).

In *Siluraster* an adradial papular area occurs between carinals and superomarginals (Fig. 21,*2*). *Xenaster* has interradial intermarginal areas additionally (Fig. 21,*3*). Some *Mesopalaeaster* have an intermarginal area and in *Devonaster* they are of considerable extent; the abundant growth material of all ages found at Saugerties (57) shows that in ontogeny the young have an aboral surface like that of Hudsonasteridae and that older individuals develop successively adradial and intermarginal papular areas. In *Palaeaster* (Fig. 21,*4*) and *Neopalaeaster*, however, the whole of the middle of the upper surface of the arms becomes a respiratory area, being filled with small irregular ossicles. Generally, the appearance of additional respiratory areas seems to be correlated with a phylogenetic increase in size.

The extraxial skeleton of ophiuroids generally consists of overlapping scales which may show traces of their origin as components of a spicular web; scales on the aboral surface of *Encrinaster* (Ord.-Dev.) show the spicular rays surviving as stellate ridges with a shallow infilling between (Fig. 19,*4*). In many modern ophiuroids extraxial scales occupy considerable areas of the oral

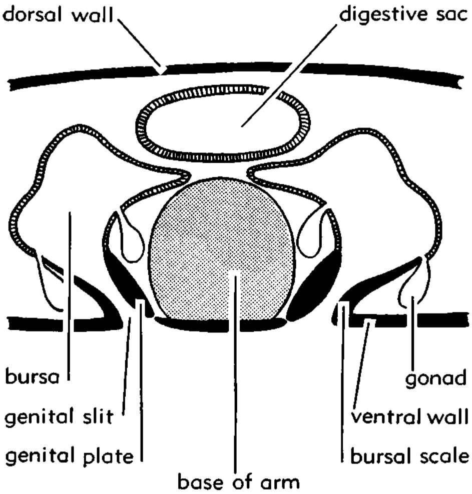

FIG. 22. Cross section of an ophiuroid disc showing gills and associated structures (115).

surface; this is mainly the consequence of extensions of the aboral skeleton downward to form pockets or pouches (**bursae**) for the internal gills. These constitute one of the main differences between ophiuroids and asteroids and presumably arose to meet the requirements of life in burrows. Damage to the delicate membrane of the respiratory surface is avoided by sinking it within the body wall (Fig. 22). Narrow slits allow the entry of water which is circulated within the cavity by ciliary action. The space for these internal gills is provided by secondary enlargement of the disc during ontogeny and by downgrowth of the aboral surface referred to above; during this process the madreporite migrates from a near-marginal aboral position to one very near the mouth. Since these characters are seen in the oldest known ophiuroid, *Pradesura,* they must be very stable features (Fig. 23,*3*).

Whereas early ophiuroids are characterized by a uniform covering of small scales, over a presumably flexible disc, a majority of later ophiuroids have a relatively stout and rigid covering (Fig. 24).

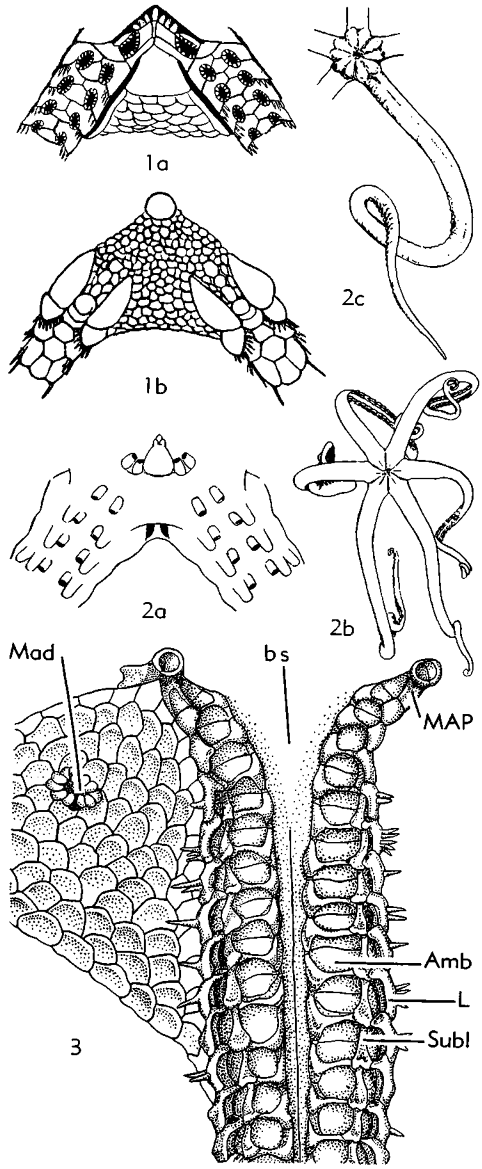

FIG. 23. Respiratory structures in ophiuroids.——*1.* Part of oral surface of the disc of *Ophiura* (Rec.); *1a,* arms covered ventrally by side shields (arm plates) and hexagonal small ventral shields, with pores for emergence of tube feet (or tentacles) surrounded by circlets of tentacle scales; gill slits along each side of arms with long genital bars at their outer edges; *1b,* radial shields on either side of base of arm, in aboral view (141).——*2. Asteroschema glutinosum* (Rec.); *2a,* part of disc and arms showing small openings of gill slits (shaded dark) in interrays; *2b,* entire animal, ×0.5; *2c,* disc and arm in aboral view, showing pairs of large radial shields, ×0.7 (120).——*3.* Oral surface of disc of *Pradesura,* oldest known ophiuroid, showing downgrowth of aboral surface of disc and accompanying movement of madreporite from lateral position, associated with internal position of gills, ×7 (133). [Explanation: *Amb,* ambulacrum; *bs,* buccal slit; *L,* lateral; *Mad,* madreporite; *MAP,* mouth-angle plate; *Subl,* sublateral.]

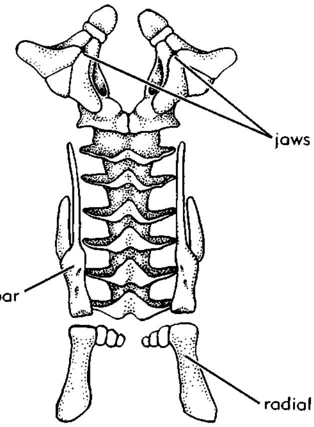

FIG. 24. Part of disc and arm base of *Ophiomyxa anisacantha* (Rec.); aboral view with radial shields (appearing as large marginal scales) upturned, showing simple articulation of the shields and genital bars and primitive jaws with feeble interradial musculature (120).

Scales persist but tend to become fused into larger ossicles. These normally include **radial shields** on the aboral surface of the disc and **genital bars** adjoining gill openings on the oral side. Each radial shield articulates with a genital bar, the shields being raised and lowered by muscles in aid of respiration; the shields are directly above the gill pouches, and by pressing against their flexible walls provide for the emptying and refilling of the pouches with water. Both paleontological and embryological evidence indicates that the radial shields are derived from fusion of scales at the edge of the disc. The marginal frame of enlarged scales in some Ordovician ophiuroids (e.g., *Euzonosoma*) was probably associated with pulse movement of the disc to circulate water in the burrow. Genital bars first appear in the Devonian.

In some early forms (e.g., *Stenaster* and *Stuertzaster*) and in Euryalina, the oral interrays of the disc are much reduced and the shape of the body and even some of the internal organs may resemble those of asteroids (14). In these forms the madreporite tends to retain its primitive lateral position and the gill pouches are concentrated about the center of the disc.

The density of calcification of the aboral skeleton varies considerably. In early members of the asteroid orders Paxillosida and Spinulosida the calcification of the central area of the disc is so weak that the mouth frame in the fossils is exposed in aboral view. Similar views of the mouth frame are commonly seen in early ophiuroids. Various extant asteroids and ophiuroids have the aboral surface covered by skin without any distinct ossicles in or below it.

Madreporite. As already mentioned, the madreporite was originally lateral but it migrated to the aboral or oral surface in various lineages. In early Spinulosida and Paxillosida, the madreporite, when recognizable, is a medium-sized rigid ossicle closely associated with a primary interradial but overlying neighboring ossicles (Fig. 25). In early Valvatida and Forcipulatida, however, it is a large thin, apparently flexible, plate situated in most genera on the oral edge of the side. This peculiar type of madreporite may have been concerned with both the water circulation and the hemal circulation. In modern Asteroidea

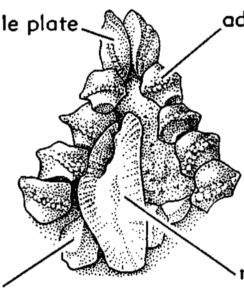

FIG. 25. Part of interradial aboral surface of *Palasterina primeva* (Sil.) showing flat madreporite overlying other ossicles (133).

[*Explanation of Figure 26*]

1. Comatulid crinoid, *Promachocrinus kerguelenensis,* pentacrinoid stage, ×12; *1a,b,* lateral and dorsal views.

2. Ophiuroid, *Ophiopyrgus wyvillethomsoni,* ×10; *2a,b,* lateral and aboral views.

3. Comatulid crinoid, *Eumorphometra aurora,* late pentacrinoid stage, ×12; *3a,b,* lateral and dorsal views.

4. Ophiuroid, *Ophiomastus stellamaris,* aboral view, ×30.

5. Ophiuroid, *Ophiomyxa* sp., aboral view of juvenile, ×15.

6. Asteroid, *Asterina* sp., ×15; *6a,b,* aboral views of larval stages.

7. Comatulid crinoid in early pentacrinoid stage, dorsal view showing circlet of infrabasals.

8. Ophiuroid, *Ophiosteira echinulata,* immature stage with basals still conspicuous, ×6.

[Explanation: *b*, basal; *c*, centrodorsal; *i*, infrabasal; *r*, radial; *t*, terminal.]

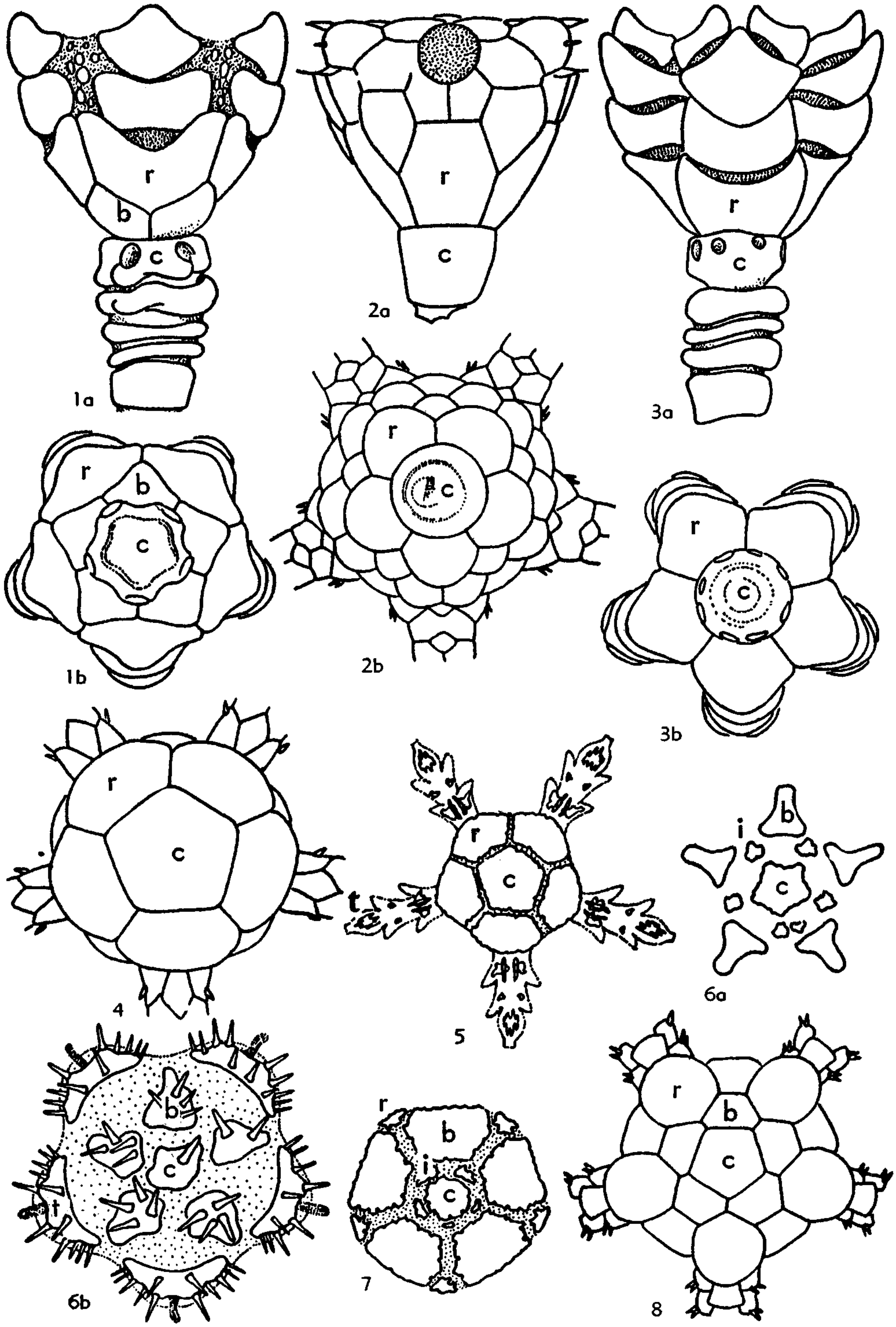

FIG. 26. Calyces of astroradiate echinoderms (108).
[*Explanation on facing page*]

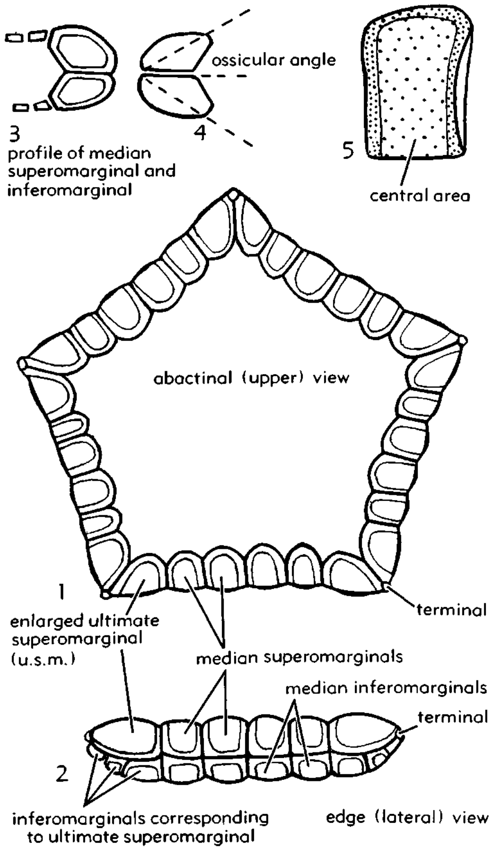

FIG. 27. Morphology of marginals in *Metopaster* (134).

it is almost solely concerned with the former function but in ontogeny a stage with both functions is seen; the very young asteroid has a heart, the **dorsal sac,** which lies near the opening of the water canal. In later life the activity of this heart is much diminished and it becomes embedded in the substance of the madreporite. The heart is very like that of *Balanoglossus.* The large flexible madreporite referred to above could well have capped a pulsating vesicle which retained its activity well into adult life. The primary interradial in juvenile asteroids forms such a cap, and this presumably accounts for the association of madreporite and a primary interradial in certain early forms.

Primary circlets. In early growth stages of both Asteroidea and Ophiuroidea the first-formed plates of the aboral skeleton are a few relatively large ossicles arranged in a pattern reminiscent of the structure of the calyx of Crinoidea. A centrale is surrounded by a circlet of five interradial plates and one of five radial plates. The homologies of these **primary circlets,** which in many groups persist in one form or another into the adult (Fig. 21), has been much discussed. It is clear that radial series **(carinals)** in adult asteroids are not homologous with the radials of crinoids or ophiuroids, but the basic calycinal system seems to be common to all three groups (Fig. 26) (13).

Marginals. At the edge of the body of many asteroids is a frame of enlarged ossicles called **marginals** (*M,* pl., *MM*). There may be only a single row or a lower row, homologous with the single row, and an upper one; the ossicles of the lower row are called **inferomarginals** (*InfM,* pl., *InfMM*) and of the upper **superomarginals** (*SupM,* pl., *SupMM*). The marginals may be rounded and sloping or square, forming a vertical wall at the edge of the body. Generally the marginals form a continuous frame, but in some early forms the arms are not fused together at their bases, so that the marginal frame is broken. In many Paxillosida, a central ridge occurs on each marginal, so that channels are developed over the edge of the frame, connecting with ciliated channels on the oral surface; in Cribellina similar grooves between marginals are occupied by papillated skin folds called **cribriform organs.** In some Goniasteridae (Valvatida) several distal marginals may be united in single enlarged ossicles, called **ultimate superomarginals** or **inferomarginals** (Fig. 27).

Superomarginals are normally placed directly over corresponding inferomarginals, but distally the correspondence may be less exact; in a few forms (e.g., *Trichasteropsis,* Paxillosida), the number of marginals differs markedly between upper and lower series. There is normally an equal number of marginals on either side of an interradial mid-line, but in a few families an odd **interradial** or **axillary marginal** is seen in either or both series.

In Notomyota the distal marginals are imbricate, thus allowing considerable flexure of the arms, by which means it is presumed that the animal swims.

Phylogenetically inferomarginals are derived from virgals and they are therefore part of the adaxial skeleton, whereas superomarginals are differentiated members of the extraxial skeleton of the aboral surface.

Terminals. Many and probably all asteroids have a single **terminal ossicle** at the tip of the arms, which in living and presumably fossil forms covers the base of an unpaired ocular tentacle. In some cases the terminals are large and have a characteristic shape.

Spines. Apart from protuberances that are one with the ossicles, most asterozoans bear spines. These originate, like ossicles of the oral and aboral skeleton, from radiate spicules, but they are formed at a higher level in the body wall than the ossicles. Paleontological evidence suggests that the spines are later-evolved skeletal elements that are secondarily attached to the older primary skeleton. A form of attachment common to all asterozoans is the ball-and-socket joint, very similar to that of echinoids (Fig. 28).

An important function of asterozoan spines is to clean the surface, especially in areas concerned with respiration. This is done by cilia on the spines that produce water currents from the base to tip of the spines, debris being thus lifted from the animal's surface. It is thus not surprising that spines and respiratory channels are commonly associated, particularly in asterozoans that have spines on paxillar shafts.

Various modifications of spines characterize different groups in Asteroidea and are of great classificatory importance. Paxillosida, many Valvatida, and some other groups carry, on the aboral surface or the margins, small ossicles with a ridged or pillar-like protuberance crowned by a tuft of spinelets or granules which are linked by muscles; these ossicles with their spines are known as **paxillae.** The tuft of spines can be opened or closed; when open, the network of paxillar spines provides effective protection for the papulae. In Pterasteridae (Spinulosida) the spines support a continuous supradorsal membrane, within which young are brooded.

Many Asteroidea carry **pedicellariae,** minute stalked, sessile, or sunken pincers. The stalked pedicellariae are formed of

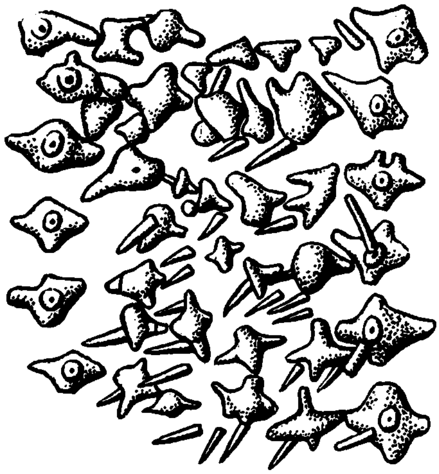

FIG. 28. Spines of *Promopalaeaster bellulus* showing perforated ball-and-socket attachment, like that of echinoids (129).

straight (forceps-like) or crossed (scissor-like) members embedded in tissue and attached to ossicles or spines; they occur in Forcipulatida (Fig. 29). Sessile pedicellariae consist of two or more opposed movable spines. Particularly in Valvatida, groups of such spines may be fused to form bivalved pedicellariae. Bivalved and other types occur in depressions in the aboral and marginal ossicles of Valvatida; such alveolate or foraminate pedicellariae are the only types commonly found in fossils.

SOFT PARTS

Following is a brief account of the soft parts of asterozoans other than those already dealt with in discussion of skeletal structures.

The **mouth** of asterozoans is in the center of the lower, oral, surface and opens into a sac-shaped stomach, which may be divided by a constriction. Paired extensions of the stomach reach into the arms in Asteroidea, where they form a liver. Most Asteroidea have an anus on the aboral surface, either in the center or close to it in an interradius, but some lack it, as do all Ophiuroidea.

In asteroids a **ring nerve** around the mouth gives rise to radial nerve cords that run along each ambulacral groove. The radial nerve is continuous with a general plexus of nerve fibers just under the epi-

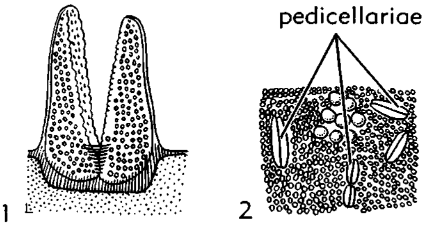

Fig. 29. Pedicellariae of Recent asteroids; *1*, forceps-like (forcipulate) pedicellaria of *Oreaster*, enlarged; *2*, bivalved (valvate) pedicellariae of *Culcita*, ×1 (118).

dermis of the whole body wall, including the podia; the plexus is thickened to form a marginal nerve cord along each side of the arms. In ophiuroids the nervous system is basically similar, but in forms with vertebrae the radial nerve has a ganglionic swelling in each vertebra; it gives off a branch into each podium and separate branches to the body wall and spines.

The asterozoan epidermis is liberally supplied with sensory cells, which are highly sensitive to touch or chemical stimuli. The ophiuroids have no special sense organs, but asteroids have a light-sensitive organ, generally pigmented, at the base of the terminal tentacle of each arm.

Asterozoa have a rather simple ring-and-radial hemal system.

ORIENTATION

Traces of bilateral symmetry are singularly few in Asterozoa. Several families of asteroids and all ophiuroids lack an anus; in most asteroids it is central or nearly so. There is no preferred direction of movement. Formally, orientation could be based on the position of the madreporite, save in the species or genera of asteroids with more than one, for example, *Acanthaster*, which has many. However, it is impossible to be certain that the position of the madreporite is homologous with that in other echinoderms. In any case, orientation in Asterozoa is of no practical and little theoretical importance.

FEEDING

Primitive somasteroids have a system of grooves on the oral side between the metapinnules, which are covered by small spines or plates and lead to the radial groove. These grooves clearly conduct water from the upper, aboral surface, primarily for feeding. Detrital particles falling on or near the sea star are thus swept by ciliary action, probably entangled in threads of mucus, to the mouth by way of the gaps between the aboral paxillae, along the interpinnular food grooves to the radial food groove and then to the mouth (Fig. 30). The living somasteroid *Platasterias* retains this method of suspension feeding and, in addition, captures relatively large food with its tube feet and passes it along the radial grooves to the mouth. The petaloid shape of the arms of somasteroids is probably associated with this system of food capture (11).

Similar methods of ciliary suspension-feeding persist in some living asteroids (e.g., *Porania*, Fig. 15). The frequent multi-armed forms among Paleozoic asteroids may also have been suspension-feeders, since the arms could constitute an effective net to catch drifting particles of food.

A development of this ciliary feeding is seen in mud-eating asteroids; *Ctenodiscus* (Goniopectinidae) plows through the upper layer of mud of the sea floor, entangling material in threads of mucus, which are then swept by ciliary action along channels on the oral surface to the radial groove and then to the mouth.

Typically, however, asteroids eat large food. Two main methods are observed in living forms. In the first, prey is passed to the mouth by the tube feet or the sea star positions itself with the mouth directly over the prey and the lips of the stomach

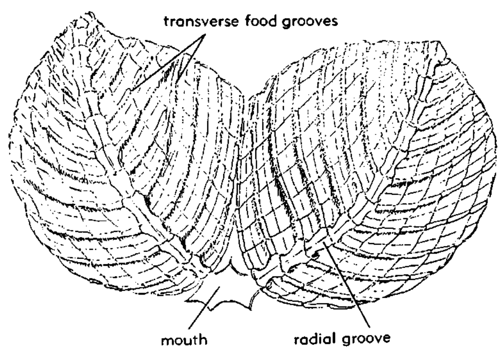

Fig. 30. Side view of *Villebrunaster thorali* (L.Ord., Fr.) with body flexed, showing transverse food grooves leading to radial groove and thence to mouth (133).

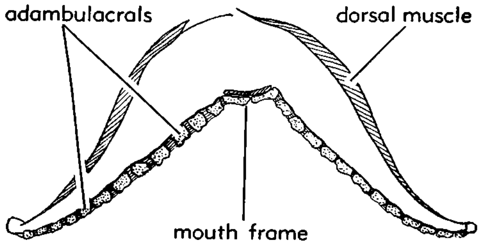

FIG. 31. Diagrammatic cross section of asteroid in position of feeding on large food, illustrating forces and resistances involved. The body is in the form of a dome supported by ends of the arms which give a firm grip on the sea floor. Resistance to collapse of the dome is provided by strong muscles which run from tips of the arms to the center of the dome, where they are firmly attached to each other, and by the chains of adambulacrals joined to each other by muscles, which run from a strong mouth frame below the center of the dome to tips of the arms (133).

are then everted through the mouth and draw the prey into the stomach. Living *Astropecten* has been observed to fill itself so full of small mollusks by this method that the upper surface is distended (42). This type of food capture is as old as the Ordovician, for specimens of *Girvanaster* have been found (U.Ord., W.Scot.) similarly dilated with small gastropods. Many modern asteroids eat other asteroids, ophiuroids, and echinoids. The predator digests the soft parts and ejects the hard remains. Fossil "pellets" consisting of such remains have been found in Upper Cretaceous chalks of western Europe; these are probably attributable to carnivorous asteroids. One specimen included identifiable remains of nine species of asteroids, two ophiuroids, and one echinoid (89).

The second method is that employed by *Asterias* and other members of its family. The sea star straddles a pelecypod and pulls open the upper valve with its tube feet; the lips of the stomach are then everted and inserted between the valves of the prey; the soft parts are then digested outside the mouth of the sea star, and the product is sucked in. This form of external digestion is applied to a variety of other prey, such as brachiopods, sickly fish, or coral polyps. An example of this system of feeding is supplied by a find of more than 400 *Devonaster* individuals associated with a bed of pelecypods (M.Dev., N.Am.).

How the strains involved in opening such large food are met is explained by Figure 31. The body, raised into a dome, is supported on the tips of the arms and prevented from collapse partly by long and strong dorsal muscles and partly by the chains of adambulacrals united by short muscles. The firm mouth frame supports the center of the dome. A specimen of

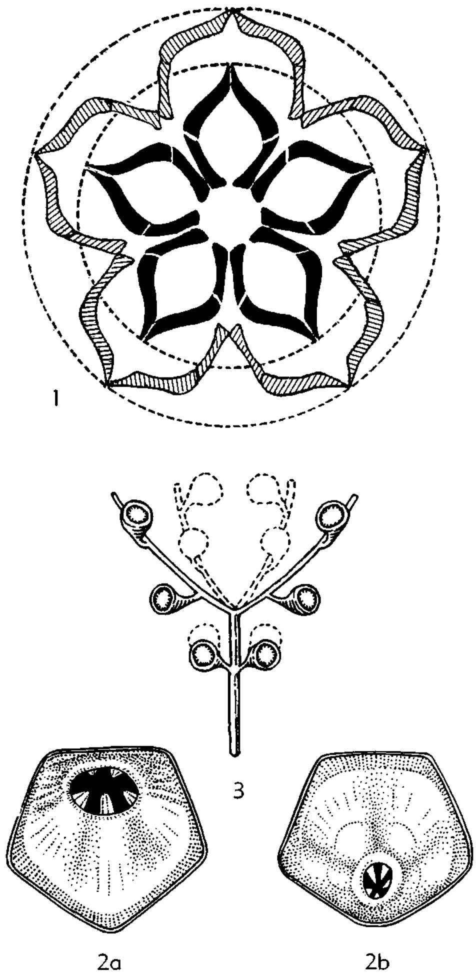

FIG. 32. Movements of echinoderm mouth parts useful for digging.——*1.* Ophiuroid mouth-frame movements associated with digging action of mouth-angle plates (133).——*2.* Movements of an echinoid's teeth showing position protruded *(2a)* and partly retracted *(2b)* (111).——*3.* Movements of second pair of buccal tentacles of an ophiuroid during digging action of mouth-angle plates; the tentacles are placed favorably for lateral scooping of loosened sediment and in some forms they are enlarged considerably (133).

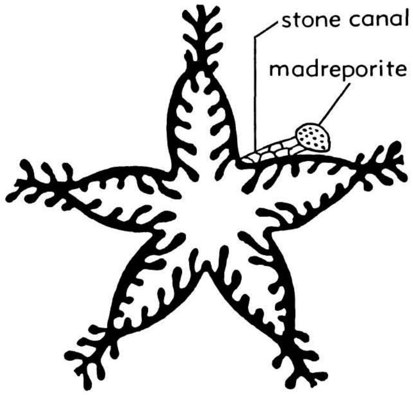

FIG. 33. Arrangement of buccal tentacles in *Eophiura;* these consist of tube feet disposed along edges of the buccal slits (133).

Ordovician *Salteraster* has been found in approximately this position.

Divergence of the first ophiuroids from the common stock of somasteroids may be associated with their living in burrows in the sea floor. The earliest ophiuroids (Arenig.) are found in nodules which show molds of some of the interior soft parts, indicating that the animals may have been buried in sediment at the time of death; moreover, central parts of the animal are preserved while distal parts of the arms are missing. The Recent *Amphiura* lives in a burrow with tips of the arms above or very near the sea bottom (Fig. 3). Where

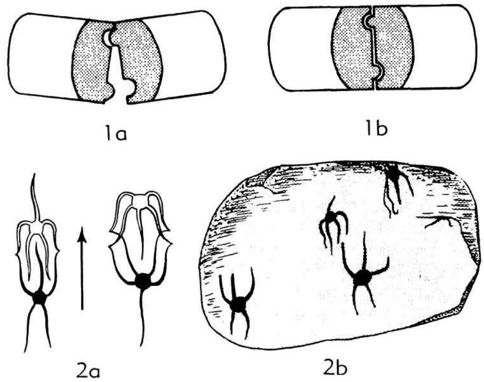

FIG. 35. Arm structure and movement in active bottom-dwelling ophiuroids (135).——*1.* Intervertebral joints of zygophiuroid vertebrae showing *(1a,b)* dorsal ball-and-socket and ventral peg-and-socket elements, latter maintaining linkage of vertebrae when the arm is used to push against the sea floor.——*2.* Position of arms in crawling; *2a, Ophiura* (Rec.) in first position (black) and at end of arm stroke (outline), showing inactive arm in front or rear (arrow shows direction of movement); *2b, Ophiaulax* (Dev.) in similar positions.

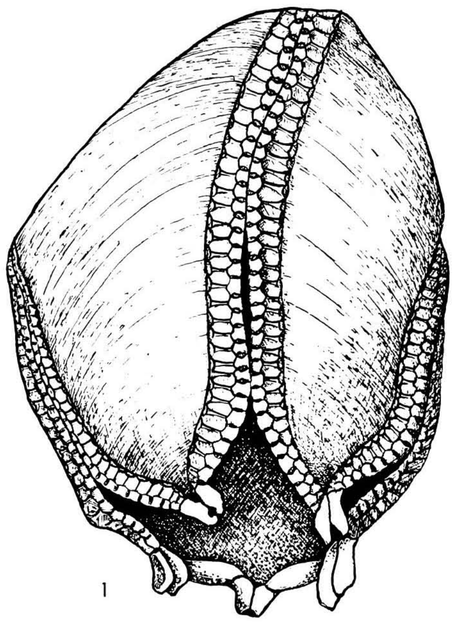

FIG. 34. *Cheiropteraster* (L.Dev.), showing downward projection of small mouth-angle plates for anchorage and diverging proximal ambulacrals next to the deep buccal slits, ×0.6 (133).

FIG. 36. *Onychaster flexilis* MEEK & WORTHEN (L. Carb.), intertwined in the arms of the crinoid *Barycrinus hoveyi* (103).

arm tips of early ophiuroids are preserved, they are generally pressed closely to the aboral surface of the disc, as if the arms had been withdrawn into the burrow before death (Fig. 4). As in living *Astropecten* (70), the tube feet may have been used as scoops in excavating, but the sediment was perhaps loosened by thrusts of the mouth-angle plates (Fig. 32,*1*) operating as do echinoids' teeth (Fig. 32,*2*); withdrawal of the cone of mouth-angle plates would swing the buccal tentacles into place to scoop away the loosened sediment (Fig. 32,*3*). While digging, the arms are bent upward and the disc is elongated to accommodate the animal to its narrow burrow.

Once in its burrow an ophiuroid can use only the tube feet of the tips of the arms for the capture of food; this is then passed along the series of tube feet protected by the lateral and sublateral plates and by rows of spines, until it reaches the mouth which is well provided with **buccal tentacles** (Fig. 33). The tunnel thus formed also serves for the passage of respiratory water. Arenigian ophiuroids (e.g., *Eophiura, Palaeura*) have been found in this position of feeding.

Other early ophiuroids, such as *Stenaster* (M.Ord.-U.Ord), had large soft slightly calcified discs providing a large food-collecting surface on the aboral side, which was connected by channels with the rows of tube feet on the oral surface. Presumably, they were sessile bottom-dwellers, living either as suspension-feeders or gathering organic detritus with their buccal tentacles, or both. *Cheiropteraster* (L.Dev., W.Ger.) had a large swollen disc anchored to the bottom by the mouth-angle plates (Fig. 34). The widely open buccal slits were bordered by buccal tentacles (only tube feet present in the genus) in a position to grasp food from debris floating near the bottom.

By Devonian time two groups had developed, with feeding habits associated with considerable structural modifications of the arms that allowed for active movement on the sea floor in one group and for a commensal life attached to crinoids and other hosts in the second. In the first of these (Ophiurida), the zygophiuroid joint is developed with a peg and a socket on the lower half of the vertebra, which allow the arm to swing downward rapidly (Fig. 35, *1*); the vertebral segments interlock during the swinging movement of the arm tip so as to push the animal along the sea floor. The arms are held in a characteristic posture during this process, two pairs of arms being used for propulsion and the fifth being inactive (Fig. 35,*2*). An abrupt change of direction is accomplished by using the inactive unpaired arm and the adjacent one of a pair, leaving the other arm of the pair to become inactive. *Ophiura*

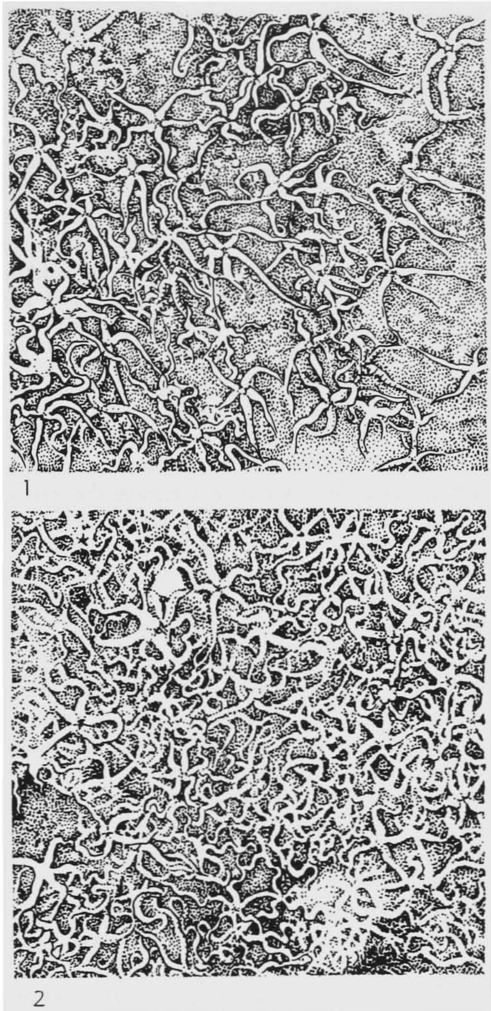

FIG. 37. Dense populations of ophiuroids in shallow water near Plymouth, England.——*1. Ophiothrix fragilis* in an area of 0.25 sq.m. at depth of 55 m.; about 100 individuals to 1 sq.m.——*2. O. fragilis* in an area of 0.25 sq.m. at depth of 48 m.; about 340 individuals to 1 sq.m. (from submarine photographs by H. G. Vevers, 1952).

can attain a speed of about 6 feet a minute, many times faster than an asteroid of comparable size using only its tube feet. Specimens of *Ophiaulax* (Dev.) have been found fossil in this "hunting" position (Fig. 35,*2b*). The system of vertebrae also allows the tips of the arms to coil around large prey and bring it to the mouth, like an elephant's trunk; in these forms the mouth-angle plates, used in earlier forms for digging burrows, now become jaws for crushing and tearing prey. Another important modification is the development of the laterals, which wrap around and are fixed to the vertebral axis. The laterals carry spines which may aid the grip of the arm on the bottom during movement; normally they do not entirely encase the arms, the gaps being filled by small dorsal and ventral plates.

The second of the two new groups in the Devonian (Phrynophiurida) had arms that could climb up and grip onto hosts such as crinoids by means of the vertical rolling of the arms and small hooked spines (Fig. 36). This group consists of suspension-feeders, collecting organic particles by their own ciliary action, aided by that of their hosts. Some extant members of the order, the "basket stars" (Gorgonocephalidae), have complex branched arms forming a tangle; they do not need the support of stalked animals but can support their food-gathering apparatus above the sea floor themselves.

Many living members of the order Ophiurida also retain the habit of suspension-feeding. Submarine photographs (Fig. 37) have shown very high densities of *Ophiothrix* in layers one above the other, apparently forming nets to capture food brought by tidal streams.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO ASTEROZOANS

The complex structures of asterozoans have given rise to many special terms. Variation in nomenclature and usage by specialists has greatly increased the number likely to be met in the literature. In the *Treatise* the number of such terms is kept to a minimum and in the following glossary many terms are mentioned merely as synonyms. Classification of terms is indicated typographically, boldface for most commonly used terms and italics for terms not recommended.

Many authors treat the names of particular ossicles ending in "al" as Latin nouns with a plural ending in "-ia" (e.g., ambulacral, pl. ambulacralia). In the *Treatise* such terms are treated as English words and the plurals formed by adding "-s" (e.g., ambulacrals).

abactinal. See aboral.

aboral. Applied to surface (or structures on it) opposite that bearing mouth and ambulacral grooves, or to direction away from mouth (*syn.*, abactinal, apical, dorsal).

accessory. Applied to ossicles of oral or aboral surface other than ossicles of primary circlet, carinals, ambulacrals, marginals, or terminal.

actinal. See oral.

actinostomial ring. See mouth frame.

adambulacral. Ossicle of series on oral surface of ray, next to ambulacrals (abbrev., *Adamb.*, pl., *Adambb*); derived from first virgal of primitive somasteroids.

adaxial. Applied to ossicles actually or in origin in transverse series wtih axial ossicles (i.e., with ambulacrals).

adoral. Directed toward mouth.

adradial. Ossicle of series on aboral surface of ray, between carinals and marginals (*syn.*, accessory radial, dorsolateral); also, directed toward axis of ray.

ambital. Pertaining to edge of body in plan view.

ambulacral. Ossicle of axial skeleton, one of double series of opposite or alternate ossicles formed along radial water vessel that constitutes axis of ray or arm (abbrev., *Amb*, pl., *Ambb*); also, pertaining to series of ambulacral ossicles.

ambulacral groove. Axial depression along oral surface of ray that is roofed by series of ambulacral ossicles.

ambulacral channel. Median channel between ambulacrals that houses radial water vessel and accompanying soft tissues.

ampulla (pl., **ampullae**). Dorsal saclike part of tube foot, either seated externally in cupule or internally and connecting with podium through podial pore; ampullae may be single or double.

anus. Vent of digestive tract, present only in some asteroids in which it is an inconspicuous pore near middle of aboral surface of disc.

apical. See aboral.

arc. Curved part of margin of asteroids in which arms are more or less distinct from disc in plan view; generally as interbrachial arc.

arm. Radial extension of body surrounding axis consisting of ambulacra; arms may be distinct from disc or not.

axial. Pertaining to axis formed by ambulacrals in sheath of radial water vessel in ray.

axil. Angle formed by junction of rays or arms in asteroids that have straight-sided arms and no interbrachial arcs.

axillary. In axil; generally applied to single large ossicle in axils of certain asteroids.

bivium. Part of asterozoan containing madreporite and ray on each side of it.

body wall. Integument, with any included calcareous skeleton, that encloses disc and arms.

brachial. See carinal.

buccal shield. Large, more or less triangular ossicle in interradial position adjoining mouth in ophiuroids (*syn.,* buccal plate).

buccal slit. Extension of mouth along axis of ray, bordered by single row of ambulacrals on each side (*syn.,* oral slit).

buccal tentacle. Tube foot on border of buccal slit.

bursa (pl., **bursae**). Internal gill pouch in ophiuroids, entered by gill slit.

caecal pore. See papular pore.

carinal. Ossicle of series along mid-line of aboral surface of ray, in line with primary radial if present (*syn.,* brachial, median dorsal, radial).

central plate. See centrale.

centrale. Prominent plate at center of aboral surface of disc in many asterozoans, center of primary circlet (*syn.,* central plate, centrodorsal).

centrodorsal. See centrale.

covering plate. Sometimes applied to laterals in certain primitive ophiuroids in which they can swing over ambulacral groove or to adambulacrals in certain asteroids.

cryptozonate. Referring to asteroids in which marginals are not conspicuously larger than other ossicles.

cupule. Cup-shaped depression on oral surface of ambulacrals in which tube foot is seated.

dental papilla. Scalelike ossicle projecting from jaw in ophiuroids.

disc. Central part of body, more or less distinctly separable from arms.

disc ambital. See intermarginal.

distal. Situated relatively farther away from mouth or center of disc; opposite of proximal.

dorsal. Same as aboral.

dorsal shield. Ossicles of series along mid-line of aboral surface of arm in ophiuroids (*syn.,* dorsal arm plate).

dorsolateral. See adradial.

fasciole. A specialized, heavily ciliated tract; applied to the intermarginal channel in some asteroids.

flooring plate. See ambulacral.

genital bar. Elongate ossicle along oral edge of gill slit at base of arm in ophiuroids.

genital papilla. Minute scalelike process adjoining gill slit.

genital slit. See gill slit.

gill slit. Fissure in disc of ophiuroids along side of base of arm, leading into bursa.

granules. Minute, more or less spherical skeletal elements situated on surface of ossicles, generally in pits or distributed in covering skin.

groove spine. Short blunt spines, generally recumbent, in clusters or rows bordering ambulacral grooves in many asteroids.

inferomarginal. Ossicle of a series along the oral edge of arms or disc or both (abbrev., *InfM,* pl., *InfMM*); in origin part of the adaxial skeleton, i.e., a virgal.

interactinal. See oral intermediate.

interbrachial. Between arms; applied to margin or surface of disc or to internal structures.

intermarginal. Small ossicle between rows of inferomarginals and superomarginals in some asteroids; also as epithet, applied to surface of one marginal adjoining next marginal.

intermediate. Apart from its common usage, applied specifically to ossicles of oral surface between adambulacrals and inferomarginals (*see* oral intermediate).

interradial. Indicating position midway between axis of adjacent rays or area between such rays.

interray. Area between a pair of adjacent rays.

jaw. Compound ossicle projecting into the mouth cavity in ophiuroids.

lateral. Ossicle of a series along the side of the arm in ophiuroids (abbrev., *L,* pl., *LL*) (*syn.,* side shield); in origin a virgal.

madreporite. Spongy or sievelike ossicle that serves as inlet to the water vascular system (abbrev., *Mad*); it is located interradially, lateral in some primitive asterozoans, but on the aboral surface in most asteroids and a few ophiuroids and on the oral surface in other ophiuroids.

marginal. Ossicle of a series along the ambitus (abbrev., *M,* pl., *MM*); either of inferomarginal or superomarginal series.

median dorsal. See carinal.

metapinnule. Structure running transversely outward from ambulacral and composed of series of more or less cylindrical ossicles called virgals; metapinnules constitute adaxial skeleton in most somasteroids and persist more or less modified in many asteroids and ophiuroids.

mouth. Entrance to digestive tract, invariably located in center of oral, or under, side of animal.

mouth-angle plate. More or less prominent ossicle projecting into mouth from proximal end of interray, forming pair with adjacent mouth-angle plate (abbrev., *MAP,* pl., *MAPP*); in origin part of series of ambulacrals.

mouth frame. Angulated girdle of ossicles surrounding mouth (*syn.,* actinostomial ring).

mouth shield. See buccal shield.

odontophore. Single axillary on distal edge of pair of mouth-angle plates in asteroids.

oral. Applied to surface of animal that contains mouth and in asterozoans is directed downward (*syn.,* actinal).

oral intermediate. Applied to ossicles of oral surface between adambulacrals and inferomarginals in asteroids, constituting part of adaxial skeleton (*syn.*, interactinal, ventrolateral).

oral papilla. Minute scalelike projection near mouth in ophiuroids.

oral slit. See buccal slit.

ossicle. Any individual calcified element of skeleton, but normally used for larger of such elements.

papilla (pl., **papillae**). Scalelike minute ossicle in ophiuroids.

papula (pl., **papulae**). Short protuberance of integument between ossicles of aboral or oral surface of asteroids that functions as external gill.

papular pore. Gap between ossicles for protrusion of papula (*syn.*, caecal, respiratory pore).

paxilla (pl., **paxillae**). Ossicle of extraxial skeleton with shaft surmounted by tuft of spinelets.

paxillose. With paxillae.

pedicellaria (pl., **pedicellariae**). Minute forceps- or pincer-like or valvate calcareous appendage borne on or in skin, ossicles, or spines of asteroids.

phanerozonate. With marginals conspicuously larger than other ossicles.

plate. See ossicle.

podial opening, podial pore. Passage between ambulacrals for emergence of tube foot.

podium (pl., **podia**). Cylindrical outer part of tube foot.

primary circlet. Ring of prominent ossicles on aboral surface, typically consisting of five radials and five interradials surrounding centrale.

proximal. Nearer mouth or center of disc; opposite of distal.

pustule. Minute boss on ossicle with central depression in which spine articulates.

radial. Prominent ossicle on aboral surface of asteroids, in line with mid-line of arm, forming part of primary circlet; commonly used in older literature for any ossicle in series with primary radial (*see* carinal); also applied to organs (e.g., canal, nerve) extending along arms.

radial shield. Relatively large ossicle comprising one of pair adjacent to base of arm on aboral surface of disc in many ophiuroids.

ray. Segment of body that includes one ambulacral axis.

respiratory pore. See papular pore.

ring canal. Part of water vascular system that forms canal around mouth, from which radial canals radiate.

side shield. *See* lateral.

spicule. Very minute irregular, cylindrical, or radiate skeletal element.

spine. Sharp or blunt, short or long skeletal element, attached to ossicle by muscle.

spine pit. Coarse or fine depression in ossicle in which spine or granule articulates.

stone canal. Calcified tube leading from madreporite to ring canal.

streptospondyline. Type of articulation between vertebrae in some ophiuroids, in which there is simple ball-and-socket joint.

sublateral. Small ossicle between ambulacral and lateral on side of arm of some primitive ophiuroids, homologous with adambulacral of asteroids (abbrev., *SubL*, pl., *SubLL*).

superambulacral. Internal ossicle lying across the inner junction of ambulacral and adambulacral in some asteroids; originating from occluded virgal.

superomarginal. Ossicle of series along edge of disc or arms or both, above series of inferomarginals (abbrev., *SupM*, pl., *SupMM*); modified ossicle of extraxial skeleton in origin.

supramarginal. See superomarginal.

tentacle. May be used for tube feet in general or specialized one.

tentacle pore. Same as podial pore, but more commonly used than that term in describing ophiuroids.

terminal. Single ossicle at tip of arm, appearing very early in ontogeny; in asteroids it protects ocular tentacle (*syn.*, ocular plate).

tooth papilla. *See* dental papilla.

torus (pl., **tori**). Flat ossicle, commonly carrying spines, projecting into mouth from mouth-angle plate in some asteroids and from jaws of all ophiuroids.

trivium. Part of body containing three rays, excluding bivium.

tube foot. Extensible water-filled organ consisting of cylindrical podium and sac-shaped ampulla, connected with radial water canal; tube feet form two or four rows along ambulacral axis.

ventral. See oral.

ventral shield. Ossicle of secondary origin on oral side of arm in ophiuroids.

ventrolateral. See oral intermediate.

vertebra (pl., **vertebrae**). Fused pair of opposite ambulacrals, articulating with neighboring vertebrae by ball-and-socket joints.

virgal. More or less rod-shaped ossicle of metapinnule.

water-vascular system. Assemblage of water-filled canals comprising stone canal, ring canal, radial canals, and tube feet.

zygophiuroid. Type of articulation of vertebrae in some ophiuroids in which are several peg-and-socket joints that limit movement in horizontal plane between vertebrae (*syn.*, zygospondyline).

zygospondyline. See zygophiuroid.

REPRODUCTION AND ONTOGENY

Little is yet known of reproduction and ontogeny of somasteroids, but FELL has published a remarkable figure of a juvenile stage of the most primitive genus, *Chinianaster,* which shows many features resembling those of comatulid crinoids (Fig. 13).

Most Asteroidea are bisexual, but hermaphroditic individuals occur and some species are always hermaphrodites. Genital organs *(gonads)* vary in number and position from a pair in each interradius to large numbers arranged in two rows along each arm. In bisexual forms these gonads normally discharge ova in very large numbers or sperm into the water where fertilization occurs. Some asteroids, however, brood their young and these generally have rather few eggs; the method of fertilization is unknown. Certain cold-water species hatch the eggs under their arched body; some Astropectinidae brood young among the paxillae of the aboral surface; some Brisingidae brood them in cages of long spines between the bases of the arms; a few species even brood young in their stomachs. In Pterasteridae, a **supradorsal membrane** supported on tops of the paxillae forms the roof of a brood chamber.

Normally the embryo, when it escapes from the egg, develops a ciliated band and projections known as **larval arms**; this distinguishes the **bipinnaria stage.** Later, three short arms appear with a sucker between them **(brachiolaria stage).** The embryo attaches itself to some object by the sucker and metamorphoses into a minute star at one end, which then breaks free from or absorbs the remainder. The bipinnaria or the brachiolaria stages may be omitted in certain genera.

The skeleton begins to form as rods or spicules that expand to form flat plates with holes, typically 11 at first on the aboral surface (five terminals, five interradials, and one centrale). Later ossicles form between these original ones and push out the terminals so that they remain at the tips of the arms. In Goniasteridae the marginals are formed immediately proximal to the terminals. A series of very young Upper Cretaceous *Metopaster* is known from Denmark and England (55).

Many starfishes reproduce by fission and regeneration of the missing parts. *Linckia* (Ophidiasteridae) normally casts off single arms, which then regenerate the whole of the rest of the body.

Ophiuroidea are typically bisexual but some species are hermaphrodites. A few bisexual species have minute males permanently attached to the much larger females. Stenurida and Oegophiurida have gonads arranged serially inside the arms. More advanced forms have few to many gonads attached to the inner wall of the bursae; when ripe, they discharge into the bursae and thence through the bursal slits into the water. Some species brood their young in the bursae or the ovaries.

In forms in which the eggs are discharged into the sea, the embryo escapes from the egg in the **blastula stage,** much earlier than in Asteroidea. The free larva gradually develops into a **pluteus** similar to that of echinoids, with arms supported by skeletal rods. The hard and soft parts of the final stage gradually develop within the pluteus, the larval arms are absorbed, and the larva falls finally to the sea floor.

Reproduction by fission also occurs in some ophiuroids.

PHYLOGENY AND EVOLUTION

Recent work has demonstrated that the major subdivisions of sea stars appeared very early in geological history and that most of the higher taxa were extraordinarily long-lived (Fig. 38). Somasteroids and platyasterid asteroids persist to the present day, while the earliest known asteroids and ophiuroids are almost contemporary with the earliest somasteroids. One cannot therefore rule out the possibility that Stelleroidea had a long history in the Cambrian. If, however, as seems to be true, somasteroids are derived directly from crinoids, which are not yet known before the Ordovician, it is natural to assume that somasteroids originated no earlier than the Late Cambrian and that divergence from them of asteroids and ophiuroids was relatively rapid.

Only in the case of Platyasterida can we trace the course of this divergence in any detail. *Platanaster* differs little from some somasteroids, and even in its asteroid ambulacral furrow it is not really far from the condition seen in the living somasteroid *Platasterias.* Thereafter, Platyasterida are known only from the Devonian *Palasteriscus,* which seems to be merely a decalcifying offshoot of *Platanaster,* and by the Recent family Luidiidae. *Luidia* has diverged more fundamentally, by the development of strap-shaped arms and by telescoping and reduction of the metapinnules to form a pavement of squarish plates on the oral surface of the arms.

Paxillosida, Valvatida, and Forcipulatida are all present by the end of the Ordovician and at their first appearance they are very distinct from one another and from Somasteroidea. We do not yet know enough even to speculate usefully on the steps by which they diverged from Somasteroidea or its derivative, Platyasterida. There are undoubtedly whole groups of Late Cambrian and Early Ordovician sea stars of which so far we know nothing. However, the presence of superambulacral ossicles in many Paxillosida suggests their derivation from *Luidia*-like Platyasterida, a supposition supported by the regular occurrence in both groups of intermarginal fascioles. So far as morphology is concerned, it is conceivable that the other two suborders were derived from the same source, but there is nothing in geological occurrence to support this.

The Spinulosida include some Recent forms that retain suggestive somasteroid features, such as traces of metapinnular structure and interradial slots, and the suborder presumably, therefore, was derived from primitive Platyasterida or directly from the Somasteroidea.

The earliest known asteroid is, in fact, a member of the Paxillosida (Hemizonina) —namely, the Lower Ordovician *Petraster.* The Petrasteridae persisted into the Silurian, occurring in Europe, North America, and Australia. From Early Silurian to Triassic there is a widespread group, Palasterinidae, whose latest member, the Triassic *Trichasteropsis,* may by paedomorphy have given rise to the important stock of the Diplozonina, which first appeared in the Early Jurassic; the morphological gap, however, is considerable. Although the numerous Jurassic members can be distinguished generically from Recent forms, they all seem to belong to the Recent family Astropectinidae, which is abundant and widespread at the present day.

In living faunas two distinct groups generally are associated taxonomically with the Astropectinidae. They are here separated, following FISHER (17), as the suborders Cribellina and Notomyotina. The Cribellina show a number of apparently primitive characters, which in the Porcellanasteridae are combined with a highly specialized appearance. All members of the suborder are characterized by cribriform organs, a type of specialized fasciole, between some or all of the marginals. *Ctenodiscus* (Goniopectinidae) has channels between all marginals, with simple cribriform organs that consist of webbed spinelets, and the channels continue across the oral surface to the ambulacra. *Ctenodiscus* also has superambulacrals and true paxillae. These features suggest derivation from early Astropectinidae by development of the marginal fascioles in the direction of cribriform organs. Indeed, *Craspidaster* (Astropectinidae) differs from other members of its family in having the marginal channels covered by webbed spinelets; it thus neatly represents a transitional type between the Astropectinidae and Goniopectinidae. The Porcellanasteridae would then be derived from Ctenodiscinae by further specialization and localization of the cribriform organs, accompanying a change of ecology that allowed the general disappearance of spinulation of the body surface. If the Cribellina were thus derived from Diplozonia, one must assume that they reverted secondarily to having single ampullae. The only alternative possibility, an unlikely one, would be that they originated independently from early Somasteroidea and never passed through a stage with double ampullae. However, until early fossil representatives are found, one cannot speculate further about the suborder's history.

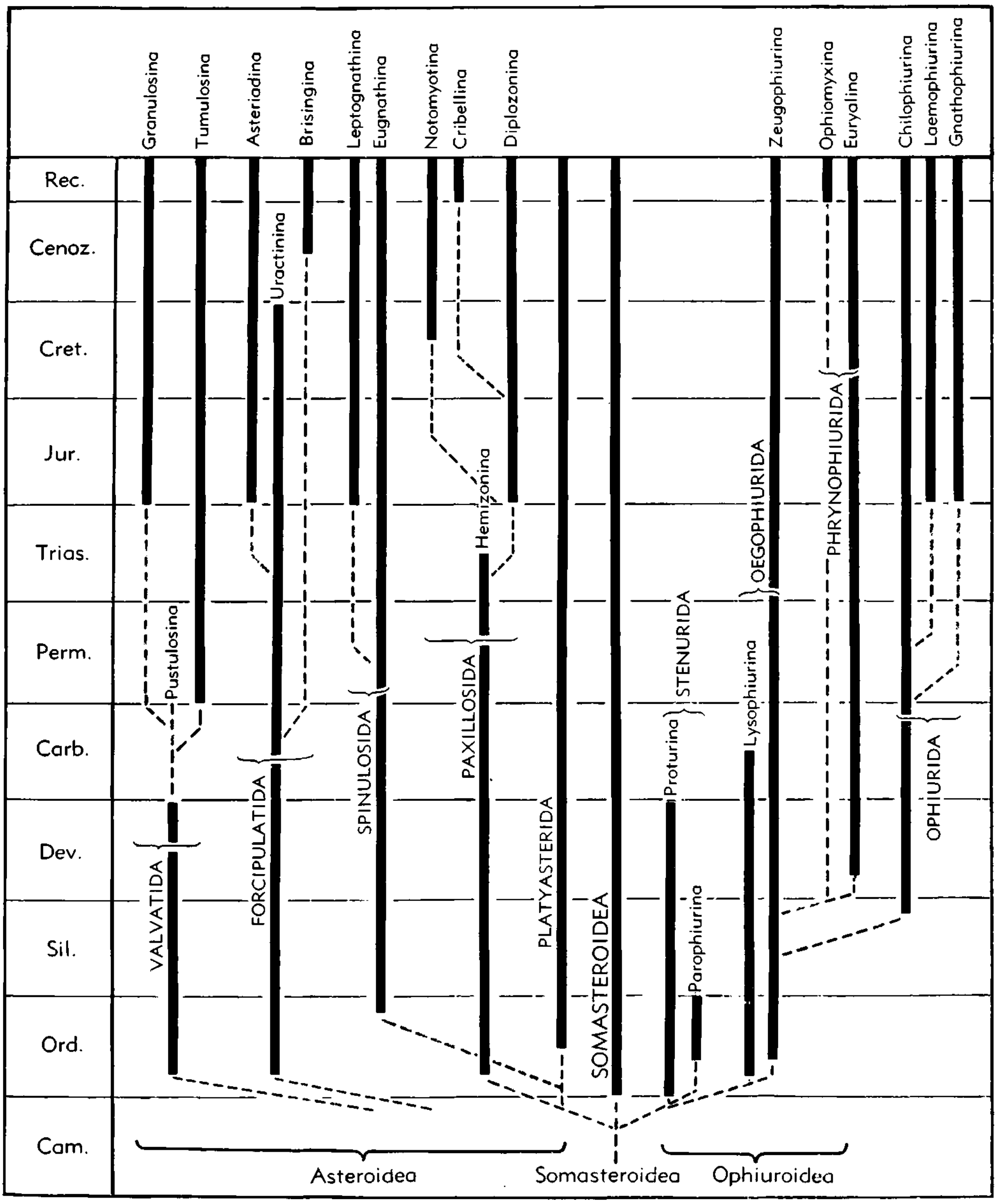

FIG. 38. Phylogeny of Asterozoa (134).

Notomyotina are characterized chiefly by longitudinal muscles in the arms; these with associated imbricate marginals are presumably an adaptation for swimming. The only known fossils consist of dissociated ossicles from the Cretaceous. They show close resemblance to certain living species. Thus, no useful discussion of phylogeny is possible, but it is likely that the suborder had a long history.

Species assigned to the order Valvatida provide a large proportion of known fossil Asteroidea, but, even so, our knowledge of the succession of species and genera is very limited. The first Valvatida (Palaeasteraceae) generally are small, having short wedge-shaped arms with inferomarginal frame extending to the arm tips; the aboral surface is composed of rather few large ossicles and is thus markedly paedomorphic. Such forms characterize the Middle and Upper Ordovician. Later forms tend to be larger and to lose the paedomorphic character of the aboral surface by introduction of accessory ossicles between the initial large ones; in addition, the bases of adjoining arms fuse and the large interbrachial axillary ossicles are occluded from the margin.

Promopalaeasteraceae have the inferomarginal frame limited and not extending to the arm tips; the arm becomes rounded in section, with the ambulacral segments compressed and the proximal ambulacrals in four rows, as in Forcipulatida. Presumably, this superfamily represents a continuation of the trends seen already in Palaeasteraceae. The Monasteridae, however, found only in the Permocarboniferous of Australia, have diverged in a different direction; here the adambulacrals are exceptionally wide and occupy most of the oral surface of the arms.

The Mesozoic Stauranderasteridae closely resemble *Monaster,* except that they have adambulacrals of more normal width. It would seem that the Stauranderasteridae are less aberrant descendants of the same group from which *Monaster* had diverged.

Early in the Jurassic the family Sphaerasteridae appeared, including forms with a closely fitting armature of ossicles and with no produced arms. The Jurassic *Sphaeraster* was hemispherical but an almost spherical genus survives to the present day. This group is probably derived from early Stauranderasteridae.

The Goniasteridae include many Mesozoic and Recent genera, whose general similarity is marked. They presumably originated in Palaeasteraceae, but there is a large gap in the late Paleozoic. The abundant Cretaceous forms allow recognition of some phyletic series which include links with a few Recent genera, but the detailed phylogeny of most of the family remains unknown. It was among Upper Cretaceous Goniasteridae that parallel evolution in several species series led to an orthogenetic interpretation. Many features that supported this interpretation are now known to be consequences of allometric growth, and there is no reason to postulate any process other than normal selection operating on a number of separate stocks in various niches in one broad environment.

The Oreasteridae are characterized by a high swollen disc, some with large tubercles or stout spines. They may have a superficial resemblance to certain Stauranderasteridae, but their young stages are flat and have inferomarginals and superomarginals like those of Goniasteriadae. They are thus probably derived from that family, but their coarsely reticulate aboral skeleton has diverged considerably from the tessellate one of the Goniasteridae.

The Ophidiasteridae are common in Recent seas but are known as fossils only from the Upper Cretaceous and Cenozoic. With their long cylindrical arms, they much resemble some Paleozoic forms, such as *Promopalaeaster,* but it is impossible to say if there is any direct connection.

The Spinulosida include a wide range of living forms that mostly have not evolved pedicellariae but tend to have groups of unmodified spinelets on their surface. This is a primitive feature, and the order seems to include a variety of stocks that separated at different times from the Platyasterida or even perhaps Somasteroidea. The Recent Tremasterinae retain metapinnular structure, and the Lower Jurassic Tropidasteridae show considerable resemblance to Palasteriscidae (Platyasterida).

Most of the known fossil Spinulosida belong to a suborder characterized by large spade-shaped mouth-angle plates, which persists from Ordovician to the present day. It includes several multiarmed genera, Recent and fossil, and already by the Silurian it had produced forms with reduced skeleton that apparently lived anchored by the jaws as suspension-feeders. The other suborder, characterized by small mouth-angle plates, includes some Recent forms of very primitive type but is virtually unrepresented by fossils.

The source of the Forcipulatida, all members of which have an "ambulacral" mouth frame, is unknown. They appeared early in the Ordovician. The Paleozoic suborder Uractinina mostly have very small discs and long narrow arms. They seem to be closely related to each other and to form in general a single evolving series. The only exception is the family Compsasteridae, which has spindle-shaped arms and somewhat resembles the Asteriidae (Asteriadina). However, there is no evidence among Compsasteridae of the pedicellariae which characterize the later suborder. The Compsasteridae and Asteriidae overlap in the Early Jurassic, and it may therefore be reasonable to derive the latter from the former. One stock of Uractinina, the Arthrasteridae, persisted until late in the Late Cretaceous.

The Brisingina, virtually unknown as fossils, comprise most peculiar forms. With their long narrow arms, small disc, and high axillary ossicle, they certainly resemble the Uractinina, and it is likely that they originated before the end of the Paleozoic.

The earliest order of Ophiuroidea, the Stenurida, includes forms that show a distinct metapinnular structure reminiscent of the Somasteroidea, but even the Pradesuridae (Early Ordovician) are quite distinct from Somasteroidea in their typically ophiuroid disc, covered with scales, and long slender arms. The order also includes forms that are losing the metapinnular aspect of the arms and tending toward typical ophiuroids in their arms structure.

The development of vertebral type of axial structure is carried further in Oegophiurida as early as the Ordovician and this order has recently been shown to persist to the present day (12). A single known Recent species retains a number of primitive "nonophiuroid" features.

Various specialized offshoots in both these early orders occur, particularly forms with globose or bag-shaped discs that seem to have been sessile suspension-feeders.

The remaining ophiuroids fall into two orders, Phrynophiurida and Ophiurida, with fully developed vertebrae of various types. Both these orders first appeared at the beginning of the Devonian and have persisted in large variety to the present day. They were derived presumably from different stocks within the Oegophiurida, but the detailed course of their evolution is not yet known. The Euryalina (Phrynophiurida) developed a type of vertebra that allowed vertical coiling of the arms and thus the ability to cling to other sessile organisms, particularly crinoids; this attribute is first seen in the Carboniferous. Ophiurida, on the other hand, became adapted for free movement on the sea floor, though many forms are actually sessile suspension-feeders. Although considerable evolutionary radiation of a minor sort has occurred in both groups, the earliest forms are much like modern ones, and there have been no changes of fundamental importance. Moreover, the fossil record is poor compared with the abundant and varied Recent fauna, most members of which probably have a long history.

CLASSIFICATION

Linné in 1758 grouped all sea stars known to him in a single genus, *Asterias,* which was divided into three sections, of which the second, Stellatae, was equivalent to Asteroidea as now known, and the third, Radiatae, to Ophiuroidea plus Comatulae. The Stellatae corresponded to Linck's (1733) Stellae fissae and the Radiatae to his Stellae integrae. Lamarck (1801) recognized a "family" called les Stellérides, coordinate with his les Échinides; he established *Ophiura*, leaving asteroids and euryalids in *Asterias. Euryale* was set up by Oken in 1815. Lamarck in 1816 within an order termed radiaires échinodermes distinguished a section (les Stellérides) that included comatules, euryales, ophiures, and asteries. He thus finally separated Asteroidea and Ophiuroidea. By 1835 Agassiz had proposed Stellérides as an order of echinoderms, including in it the two families Asteriadae and Ophiuridae. Two years later Burmeister named the combined group Asteroidea, of which Hypostoma Gray, 1840 (as a class), is a synonym. Forbes (1840), first in post-Linnean times, named Ophiuroidea at the suprafamilial level.

Zittel (1879), largely following Bronn (1860), divided a class Asteroidea into two orders, Ophiuridae, with suborders Euryaleae and Ophiureae, and Stelleridae, with suborders Encrinasteriae and "Asteriae verae" (91). The Encrinasteriae included a group of fossil forms, mainly Devonian, with marginals and stout petaloid arms. Schöndorf (62) divided this group into two parts, one including forms with opposite ambulacrals, which he referred to Asteroidea, and the other with alternate ambulacrals, which he thought could not be referred either to Asteroidea or Ophiuroidea and therefore assigned to a new subclass, Auluroidea. Subsequently Spencer (1930) showed that these forms had good ophiuroid characters and so he abandoned Schöndorf's subclass. Zittel's "Asteriae verae" were long known as Euasteriae (Bronn's term) or Euasteroidea, in contrast with Encrinasteriae.

Ludwig demonstrated that the Asteroidea and Ophiuroidea were built on a common plan, and he found in the ontogeny of Ophiuroidea what he regarded as an asteroid stage (42).

Gregory (1899) established a class Stelleroidea with subclasses Asteroidea and Ophiuroidea: he recalled (25, p. 238) that these taxa are usually ranked as distinct classes but stated correctly that "no definite line of separation can be drawn between them" and that they are "constructed upon the same fundamental plan," "contain the same variations from the typical arrangement," and have "not a single constant difference between them." This is the view adopted in the *Treatise* and generally accepted by palaeontologists. Some neontologists, however, have argued for a wider separation of Asteroidea and Ophiuroidea, primarily on embryological grounds. The facts of palaeontology and also the occurrence among living forms of certain Ophiuroidea with asteroid characters outweigh the embryological evidence. That ophiuroid larvae at certain stages differ from asteroid larvae and resemble those of echinoids is presumably due to separate evolution of the pelagic larvae of Ophiuroidea (on which the pressures of selection operate just as much as on the adults) and convergence with echinoid larvae. Some biochemical evidence suggests closer affinity between ophiuroids and echinoids than between ophiuroids and asteroids (36, p. 700); but even if this is found to be valid in wider investigation it still would not outweigh the morphological and paleontological evidence.

Finally, Spencer (77) based a third subclass, Somasteroidea, on certain Lower Ordovician sea stars and demonstrated that they were ancestral both to Asteroidea and to Ophiuroidea. Fell subsequently recognized a living species of somasteroid (11) and put the relationship of the three subclasses on a firm basis (13).

Subdivision of Asteroidea above family level began in 1875, when Perrier established two unnamed sections, one with stalked and straight or crossed pedicellariae and quadriserial tube feet (family Asteriidae), the other with sessile pincer-shaped or valvate pedicellariae and biserial tube feet (six other families).

Viguier (1878) had two subclasses of a class Asteroidea based on nature of the mouth ring (86). The first, "Asteries ambulacraires," was characterized by predominance of the proximal functional ambulacral plates in the mouth ring and feebleness of the mouth-angle plates, by stalked, straight, or crossed pedicellariae, and by quadriserial tube feet (families Asteriidae, Heliasteridae, Brisingidae), the second by the predominance of adambulacral plates, to which the mouth-angle plates are assimilated, in the mouth ring, by sessile pincer-shaped or valvate pedicellariae and by biserial tube feet (seven families).

Perrier in 1884 regarded the pedicellariae, although on fallacious grounds, as more important than other characters for classification and amplified his previous scheme (53). He divided the Asteroidea into four orders according to characters of the pedicellariae as follows: Forcipulatae (families Brisingidae, Pedicellasteridae, Asteriidae, Heliasteridae), Spinulosae (Echinasteridae, Pterasteridae, Asterinidae), Valvatae (Linckiidae, Goniasteridae, Asteropsidae), and Paxillosae (Archasteridae, Astropectinidae).

Sladen (1889) rejected Perrier's classification and established only two orders: Phanerozonia characterized by conspicuous marginals, and Cryptozonia, with marginals reduced or absent in the adult. Since some Cryptozonia have a phanerozonate stage in ontogeny, he regarded Phanerozonia as the more primitive order (67). A number of families cannot be definitely assigned to the Phanerozonia or Cryptozonia and in practice Sladen's classification has been combined in various ways with PERRIER's. FISHER, for example, maintained the Phanerozonia to include PERRIER's Paxillosae and Valvatae and ranked it with Spinulosae and Forcipulatae (17).

The classification adopted for Asteroidea in the *Treatise* is essentially a combination of that of PERRIER and VIGUIER, modified in the light of paleontological evidence and the work of FELL. The four Recent orders of PERRIER are seen on a variety of evidence, including characters of the mouth ring and mouth-angle plates, to have their roots in Paleozoic families. The Luidiidae, however, are Recent survivors of the Paleozoic order Platyasterida, which represent the simplest modification of Somasteroidea to asteroid status. The Asteroidea are thus divided into five orders, Platyasterida, Paxillosida, Valvatida, Spinulosida, and Forcipulatida.

Above family level, the Ophiuroidea were split by most 19th-century authors into two divisions, ophiurids and euryalids, variously graded. BELL (1892), however, was struck by the importance of the system of articulation of the vertebrae. Accordingly, he divided the Ophiuroidea into three groups, Streptophiurae, with simple ball-and-socket articulation; Cladophiurae, with hour-glass-shaped articulatory surfaces; and Zygophiurae, in which free lateral movement of the arms was limited by processes and pits at sides of the vertebrae (1). GREGORY (1897) added Lysophiurae for Paleozoic form, with a double series of alternating ambulacrals instead of vertebrae (24).

JAEKEL, in 1923, erected a class "Brachioidea," divided into two subclasses, Parophiura, for certain early Paleozoic forms, and Ophiura (38). However, MATSUMOTO (1915) proposed an entirely new classification based on internal skeletal structures (45). Within the class Ophiuroidea he established two subclasses, Oegophiuroidea, for a group of Paleozoic forms, and Myophiuroidea, for the remainder. The latter subclass contained four orders, Phrynophiurida, Laemophiurida, Gnathophiurida, and Chilophiurida.

SPENCER (1951) recognized the subclass Ophiuroidea containing an order, Stenurida, with two suborders, co-ordinate with an order Ophiurida for the rest; within the Ophiurida he included as suborders MATSUMOTO's Oegophiuroidea and Myophiuroidea (77).

FELL (1962) has shown that MATSUMOTO's Oegophiuroidea and Phrynophiuroidea should stand as orders co-ordinate with the Stenurida, while MATSUMOTO's other orders could, if accepted, best be regarded as suborders of the Ophiurida (of which MATSUMOTO's Myophiuroidea is really a synonym, 12). This is the classification adopted in the *Treatise*. However, MURAKAMI has recently (1963) published a classification of extant ophiuroids derived from that of MATSUMOTO but based primarily on details of the jaw structure (52). He has distinguished the following orders and suborders: Phrynophiurida, Laemophiurida, Gnathophiurida, and Chilophiurida, with three suborders set up by himself in 1947, Trematophiurina, Holophiurina, and Agmatophiurina. Whether this rearrangement will find general acceptance remains to be seen.

OUTLINE OF CLASSIFICATION

The figures in parentheses indicate numbers of included genera. Where there is no oblique stroke, the figure represents fossil genera, some of which may have Recent species. Where there is an oblique stroke, the figure before it represents genera known as fossils (possibly including Recent species), while the figure after the oblique stroke represents Recent genera with no known fossil species. Figures after a colon (:) indicate numbers of subgenera exclusive of nominotypical subgenera.

Asterozoa *(subphylum)* (182/556:14). *L.Ord.-Rec.*
- Stelleroidea *(class)* (182/556:14). *L.Ord.-Rec.*
  - Somasteroidea *(subclass)* (7/1). *L.Ord.-Rec.*
    - Goniactinida *(order)* (7/1). *L.Ord.-Rec.*
      - Chinianasteridae (1). *L.Ord.*
      - Villebrunasteridae (2). *L.Ord.*
      - Platasteriidae (/1). *Rec.*
      - Archegonasteridae (1). *L.Ord.*
      - Archophiactinidae (3). *U.Ord.-U.Dev.*
  - Asteroidea *(subclass)* (111/288:12). *L.Ord.-Rec.*
    - Platyasterida *(order)* (3). *M.Ord-Rec.*
      - Palasteriscidae (2). *M.Ord.-L.Dev.*
      - Luidiidae (1). *Mio.-Rec.*
    - Paxillosida *(order)* (13/41:2). *L.Ord.-Rec.*
      - Hemizonina *(suborder)* (6). *L.Ord.-Trias.*
        - Petrasteridae (1). *L.Ord.-Sil.*
        - Lepidasteridae (2). *M.Sil.-U.Dev.*
        - Palasterinidae (3). *Sil.-Trias.*

Diplozonina *(suborder)* (7/20:2). *L.Jur.-Rec.*
Astropectinidae (7/20:2). *L.Jur.-Rec.*
Astropectininae (7/19:2). *L.Jur.-Rec.*
Craspidasterinae (/1). *Rec.*
Cribellina *(suborder)* (/13). *Rec.*
Goniopectinidae (/4). *Rec.*
Goniopectininae (/2). *Rec.*
Ctenodiscinae (/2). *Rec.*
Porcellanasteridae (/9). *Rec.*
Notomyotina *(suborder)* (1/8). *L.Cret.-Rec.*
Benthopectinidae (1/8). *L.Cret.-Rec.*
Valvatida *(order)* (69/93:2). *L.Ord.-Rec.*
Pustulosina *(suborder)* (27). *L.Ord.-L.Carb.*
Palaeasteraceae *(superfamily)* (22). *L.Ord.-L. Carb., ?Permocarb.*
Palaeasteridae (2). *M.Sil., ?Permocarb.*
Hudsonasteridae (6). *L.Ord.-U.Sil.*
Hudsonasterinae (4). *L.Ord.-U.Ord.*
Coccasterinae (1). *M.Sil.-U.Sil.*
Silurasterinae (1). *M.Ord.*
Neopalaesteridae (1). *L.Carb.*
Mesopalaesteridae (6). *U.Ord.-U.Dev.*
Mesopalaeasterinae (3). *U.Ord.-U.Dev.*
Lepidactininae (2). *M.Sil.-L.Dev.*
Clarkeasterinae (1). *U.Dev.*
Xenasteridae (5). *L.Dev.*
Family Uncertain (2).
Promopalaeasteraceae *(superfamily)* (5). *M. Ord.-Sil.*
Promopalaeasteridae (3). *M.Ord.-Sil.*
Eoactinidae (2). *Sil.*
Tumulosina *(suborder)* (6/1). *Permocarb.-Rec.*
Monasteridae (1). *Permocarb.*
Stauranderasteridae (3). *M.Jur.-U.Cret.*
Sphaerasteridae (2/1). *M.Jur.-Rec.*
Granulosina *(suborder)* (36/92:2). *L.Jur.-Rec.*
Odontasteridae (1/5). *M.Jur.-Rec.*
Chaetasteridae (/1). *Rec.*
Archasteridae (1). *?Mio., Rec.*
Goniasteridae (30/44:2). *L.Jur.-Rec.*
Goniasterinae (5/11:1). *U.Cret.-Rec.*
Chitonasterinae (/1). *Rec.*
Athenoidinae (/5). *Rec.*
Hippasteriinae (1/2:1). *U.Cret.-Rec.*
Nectriinae (/2). *Rec.*
Pseudarchasterinae (2/2). *U.Jur.-Rec.*
Pycinasterinae (2). *L.Jur.-Mio.*
Subfamily Uncertain (20/22).
Oreasteridae (/20). *Rec.*
Ophidiasteridae (4/19). *U.Cret.-Rec.*
Radiasteridae (/2). *Rec.*
Spinulosida *(order)* (15/72:2). *M.Ord.-Rec.*
Eugnathina *(suborder)* (13/23:2). *M.Ord.-Rec.*
Taeniactinidae (4). *U.Ord.-L.Carb.*
Lepyriactinidae (1). *L.Sil.*
Schuchertiidae (1). *M.Ord.-Sil.*
Helianthasteridae (3). *Dev.*
Solasteridae (2/7). *L.Jur.-Rec.*
Tropidasteridae (1). *L.Jur.*
Korethrasteridae (/4). *Rec.*
Pythonasteridae (/3). *Rec.*
Pythonasterinae (/1). *Rec.*
Myxasterinae (/2). *Rec.*
Pterasteridae (/9:2). *Rec.*
Leptognathina *(suborder)* (2/49). *L.Jur.-Rec.*
Asterinidae (/17). *M.Jur.-Rec.*
Asterininae (/12). *Rec.*
Anseropodinae (/3). *Rec.*
Tremasterinae (/2). *M.Jur., Rec.*
Ganeriidae (/8). *Rec.*
Poraniidae (/13). *Rec.*
Echinasteridae (1/1). *?U.Cret., Rec.*
Valvasteridae (1/1). *L.Jur.-Rec.*
Acanthasteridae (/1). *Rec.*
Mithrodiidae (/1). *Rec.*
Metrodiridae (/1). *Rec.*
Forcipulatida *(order)* (11/82:6). *L.Ord.-Rec.*
Uractinina *(suborder)* (10). *L.Ord.-U.Cret.*
Cnemidactinidae (1). *Ord.*
Urasterellidae (5). *L.Ord.-Permocarb.*
Calliasterellidae (3). *L.Carb.-U.Cret.*
Protarthrasterinae (1). *L.Carb.*
Calliasterellinae (1). *U.Carb.*
Arthrasterinae (1). *U.Cret.*
Compsasteridae (1). *L.Dev.-L.Jur.*
Asteriadina *(suborder)* (1/65:6). *L.Jur.-Rec.*
Heliasteridae (/1). *Rec.*
Zoroasteridae (/7). *Rec.*
Asteriidae (1/57:6). *?L.Jur., M.Jur.-Rec.*
Asteriinae (1/45:6). *?L.Jur., M.Jur.-Rec.*
Pedicellasterinae (/5). *Rec.*
Labidiasterinae (/4). *Rec.*
Pycnopodiinae (/2). *Rec.*
Neomorphasterinae (/1). *Rec.*
Brisingina *(suborder)* (/17). *L.Oligo.-Rec.*
Brisingidae (/17). *L.Oligo.-Rec.*
Ophiuroidea *(subclass)* (63/266:2). *L.Ord.-Rec.*
Stenurida *(order)* (10). *L.Ord.-U.Dev.*
Proturina *(suborder)* (6). *L.Ord.-U.Dev.*
Pradesuridae (2). *L.Ord.-L.Dev.*
Phragmactinidae (1). *U.Ord.*
Rhopalocomidae (2). *U.Sil.-U.Dev.*
Bdellacomidae (1). *U.Sil.-L.Dev.*
Parophiurina *(suborder)* (4). *L.Ord.-L.Dev.*
Eophiuridae (1). *L.Ord.*
Palaeuridae (2). *L.Ord.-L.Dev.*
Stenasteridae (1). *M.Ord.-U.Ord.*
Oegophiurida *(order)* (21/1). *L.Ord.-Rec.*
Lysophiurina *(suborder)* (15). *M.Ord.-L.Carb.*
Encrinasteridae (7). *U.Ord.-L.Carb.*
Protasteridae (8). *M.Ord.-L.Carb.*
Zeugophiurina *(suborder)* (6/1). *L.Ord.-Rec.*
Lapworthuridae (3). *L.Ord.-L.Dev.*
Furcasteridae (2). *U.Ord.-L.Carb.*
Klasmuridae (1). *U.Dev.*
Ophiocanopidae (1). *Rec.*
Phrynophiurida *(order)* (4/69). *L.Dev.-Rec.*
Ophiomyxina *(suborder)* (/23). *Rec.*
Ophiomyxidae (/23). *Rec.*
Ophiomyxinae (/16). *Rec.*
Ophiobyrsinae (/7). *Rec.*
Euryalina *(suborder)* (4/46). *L.Dev.-Rec.*
Eospondylidae (2). *L.Dev.*
Onychasteridae (1). *Miss.*
Asteronychidae (1/1). *?U.Cret., Rec.*
Asteroschematidae (/6). *Rec.*
Gorgonocephalidae (/33). *Oligo.-Rec.*
Euryalidae (/6). *Rec.*
Ophiurida *(order)* (26/194:2). *Sil.-Rec.*
Chilophiurina *(suborder)* (18/90:2). *Sil.-Rec.*
Ophiurinidae (5). *Sil.-L.Carb.*
Ophiuridae (10/48). *L.Carb.-Rec.*
Aganasterinae (1). *L.Carb.*
Ophiurinae (7/30). *L.Carb.-Rec.*
Ophiolepidinae (2/18). *?Perm., Rec.*

SYSTEMATIC DESCRIPTIONS

Subphylum ASTEROZOA Zittel, 1895

Echinoderms characterized by generally depressed star-shaped body, composed of central disc with mouth on underside and symmetrical radiating arms; axial skeleton along arms protects radial water vessels and nerves; tube feet normally confined to lower side of body. *L.Ord.-Rec.*

In addition to genera known as fossils, Recent genera are listed with author, date, type-species, and synonymy, but generally diagnoses of genera not yet found fossil are omitted, despite the probability that most Recent asterozoan genera are of considerable geological age. Many fossil asterozoans have been referred to extant genera. Not all of these attributions are justified and some have been omitted here.

Class STELLEROIDEA Lamarck, 1816

[*nom. transl. et correct.* Gregory, 1900 (*pro* les Stellérides Lamarck, 1816)]

Characters of subphylum. *L.Ord.-Rec.*

Subclass SOMASTEROIDEA Spencer, 1951

Asterozoans with oral surface bearing shallow radial channels formed by recumbent ambulacrals, which in at least some forms can be raised to form temporary ambulacral furrows; tube feet seated in broad basins, which may or may not communicate with body cavity; radial water vessel enclosed to varying extent between ambulacrals. Axial skeleton consisting of ambulacrals in double series, generally in opposite pairs but apparently alternating in some forms, each ambulacral typically giving rise to transverse series of ossicles (**metapinnules**), consisting of more or less rod-like elements (**virgals**), which may be undifferentiated (Chinianasteridae) or differentiated into adambulacral, intermediate, and marginal ossicles; between metapinnules are food-groove channels on oral surface covered with small plates or protected by spines; jaws composed of proximal pairs of ambulacrals and their reduced metapinnules; aboral surface typically bearing paxillae with tetraradiate bases (11, 13, 77). *L.Ord.(Tremadoc.)-Rec.*

Order GONIACTINIDA Spencer, 1951

Characters of subclass. *L.Ord.-Rec.*

Family CHINIANASTERIDAE Spencer, 1951

Ambulacral skeleton of stout barrel-shaped ossicles, not forming any groove; tube feet exclusively external, set in cupules, pointed and covered with minute plates (as in Ophiocistioidea). Arms petaloid, formed from simple metapinnules which end in free marginal radiole; undifferentiated virgals flanged, carrying row of small plates on either side which cover channels. Mouth-angle plates subtriangular, elongate. Buccal slits extending into arm bases. Aboral surface with widely spaced paxillae. *L.Ord.(Tremadoc.)-L.Ord.(Arenig.).*

Chinianaster Thoral, 1935 [**C. levyi*; OD]. Characters of family. *L.Ord.*, S.Fr.——Fig. 39,*4*. **C. levyi*; oral surface (reconstr.), ×3.5 (133). (See also Fig. 8,*2*; 13.)

Family VILLEBRUNASTERIDAE Fell, 1963

Tube feet not plated, with internal ampulla; cupules communicating with internal cavity between wings on ambulacrals; water tube enclosed by capitula of ambulacrals; virgals differentiated into adambulacral, oral intermediate, and marginal elements; metapinnules of distal part of arms ending

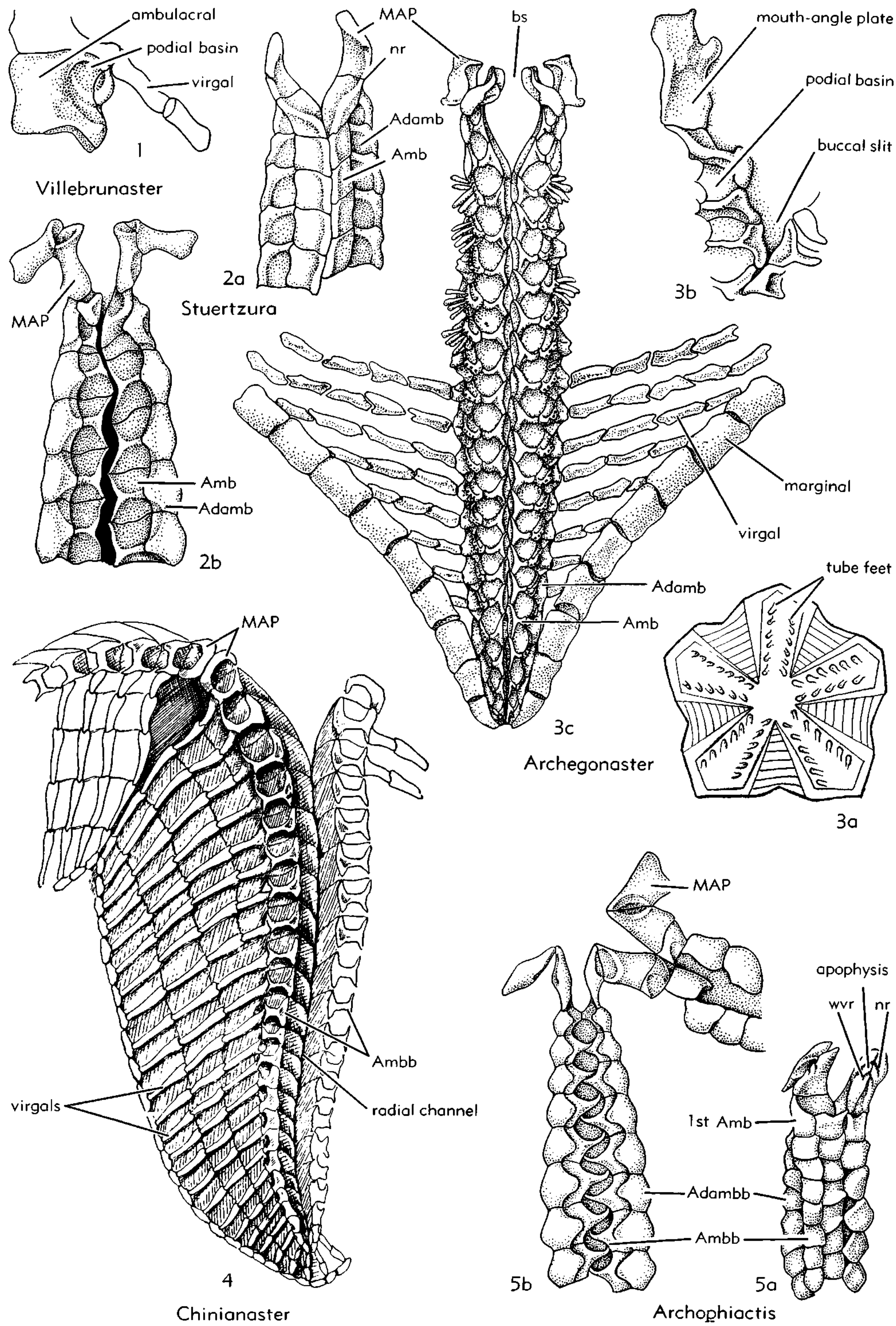

FIG. 39. Chiniasteridae *(4);* Villebrunasteridae *(1);* Archegonasteridae *(3),* Archophiactinidae *(2,5).* [Explanation: *Adamb,* adambulacrum; *Amb(b),* ambulacrum; *bs,* buccal slit; *MAP,* mouth-angle plate; *nr,* nerve-ring groove, *wvr,* water-vascular-ring groove.] (p. *U*39, *U*41-*U*42).

in distinct marginals without terminal radioles. Intermediate virgals forming walls of food grooves, apparently without cover plates. *L.Ord.*

Villebrunaster Spencer, 1951 [**V. thorali*; OD]. Arms petaloid. Metapinnules of slender virgals, undifferentiated except for marginals on distal part of arms and adambulacrals; ambulacrals changing in shape along arms. *L.Ord.*, S.Fr.——Fig. 39,*1*. **V. thorali*; ambulacrals showing podial basin and virgals, enl. (133). (See also Fig. 8.)

Ampullaster Fell [**A. ubaghsi*; OD]. Body more or less pentagonal, with rhombic arms separated by deep, narrow interradial clefts. Proximal metapinnules of slender virgals except for adambulacrals; distal ones of few strong virgals of which outermost are marginals. *L.Ord.*, S.Fr.——Fig. 40,*1*. **A. ubaghsi*; oral view, ×5 (108).

Family PLATASTERIIDAE Caso, 1945

Arms petaloid, separated by deep interradial fissures. Metapinnules consisting of virgals differentiated into adambulacral, occluded superambulacral, marginal, and terminal elements; adambulacrals and marginals forming walls of interpinnular grooves, covered by erectile series of small plates on either side; ambulacrals with adambulacrals erectable to form temporary ambulacral furrow of asteroid type. *Rec.*

Platasterias Gray, 1871 [**P. latiradiata*; OD]. Characters of family. *Rec.*, Nicaragua.

Family ARCHEGONASTERIDAE Spencer, 1951

More or less pentagonal in outline with no interradial clefts; continuous series of marginals running along edge of body and adambulacrals along shallow radial grooves but metapinnules otherwise reduced to few rows of virgals near distal ambulacrals. Capitula of ambulacrals imbricating. *L.Ord. (U.Arenig.).*

A few specimens are preserved as horizontally flattened pentagons but most are elongated vertically, with distal ambulacrals flexed over the aboral surface so that upward stretched tube feet could grasp food (Fig. 39,*3a*). The mouth frame, as in primitive ophiuroids, has deep clefts at summit of mouth-angle plates, which indicate position of muscles for digging; the first pair of buccal tube feet projected directly into the mouth. The reduction of ossicles denotes transition to the Archophiactinidae.

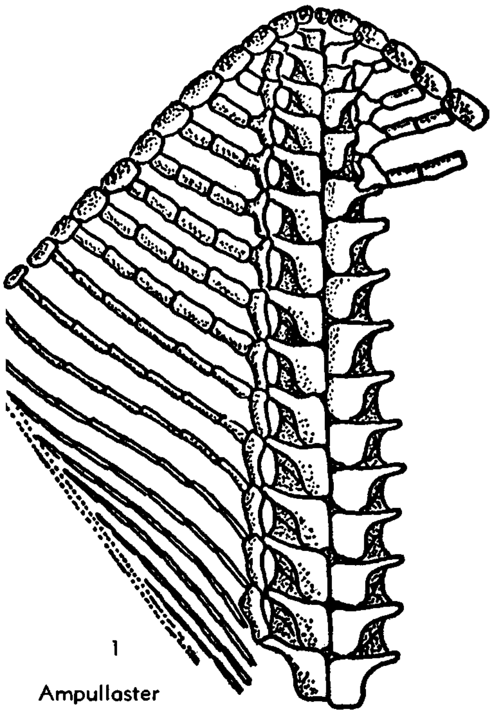

Fig. 40. Villebrunasteridae (p. *U*41).

Ball-and-socket joints between axial ossicles allowed flexing when the animal assumed a feeding posture.

Archegonaster Jaekel, 1923 [**A. pentagonus* Spencer, 1951; SM]. *L.Ord.(U.Arenig.)*, Czech. ——Fig. 39,*3*. **A. pentagonus*; *3a*, diagram of arms flexed over aboral surface in feeding posture; *3b*, part of mouth frame from inner side, ×3; *3c*, part of oral surface reconstructed, ×3 (133).

Family ARCHOPHIACTINIDAE Spencer, 1927

Adaxial skeleton reduced to adambulacrals only. No buccal slits. *U.Ord.-U.Dev.*

The aboral surface was probably much swollen and nearly devoid of skeleton. The family was probably sessile.

Archophiactis Spencer, 1925 [**A. grayae*; OD]. Adambulacrals broad; aboral surface of ambulacrals rounded; mouth-angle plates elongate, stout. *U.Ord.*, Scot.——Fig. 39,*5*. **A. grayae 5a,b*, aboral and oral surfaces of proximal part of arm and part of mouth frame, ×5 (133).

Stuertzura Gregory, 1897 [**Protaster brisingoides* Gergory, 1889; OD] [=*Stürtzura* Gregory, 1897]. Adambulacrals narrow; aboral surface of ambulacrals ridged; mouth-angle plates long, narrow. *Sil.*, Australia.——FIG. 39,*2*. **S. brisingoides* (GREGORY); *2a,b*, aboral and oral surfaces of proximal part of arm and part of mouth frame, ×5 (133).

Lepidasterina RUEDEMANN, 1916 [**L. gracilis*; OD]. Multiarmed, with ossicles of radial groove as in *Stuertzura. U.Dev.*, USA(N.Y.).

Subclass ASTEROIDEA de Blainville, 1830

[*nom. transl.* GREGORY, 1900, p. 239 (*ex* order Asteroidea BURMEISTER, 1837, p. 467, *nom. correct. pro* order Asteridea DE BLAINVILLE, 1830, p. 216] [=order Astroides DE BLAINVILLE, 1822; order Asteriodea FLEMING, 1822, order Cirrhigrada FORBES, 1841; class Asterioidea BRONN, 1860, p. 240] [Diagnosis prepared by W. K. SPENCER & C. W. WRIGHT. Research on authorship and synonymy of subclass by H. B. FELL & J. WYATT DURHAM]

Asterozoans having relatively broad arms with considerable hollow space within ossicular frame; arms normally not separated from central disc; oral side bearing open ambulacral grooves which carry rows of tube feet, proximal tube feet in some early stocks forming buccal tentacles. Respiration through skin of aboral surface, which is commonly folded into external gills (papulae). Spines or granules generally well distributed over surface both of skin and of bare ossicles. Later genera commonly carrying pedicellariae. *L.Ord.-Rec.*

Order PLATYASTERIDA Spencer, 1951

Arms 5 to many; ossicles in transverse gradients emerging from axial ossicles; ambulacrals erect and ambulacra furrowed; single row of marginals, when present, channeled so that marginal grooves link with vestigial food grooves on oral surface, which persist as respiratory fascioles (13). *M.Ord.-Rec.*

Family PALASTERISCIDAE Gregory, 1900

[=Palaechinasteridae STÜRTZ, 1890 (invalid because not founded on generic name); Platanasteridae SPENCER, 1919]

Arms 5, adambulacrals very broad, with flat spines on long transverse ridge; ambulacral grooves very shallow, aboral surface swollen, with many parallel rows of paxillae; axillary broad, breastplate-shaped. *M. Ord.-L.Dev.*

Platanaster SPENCER, 1919 [**P. ordovicus*; OD]. Single row of marginals present. *M.Ord.*, Eng. (Shrops.).——FIG. 41,*1*; 42,*1*. **P. ordovicus*; 41,*1a*, oral side of arm, ×2; 41,*1b*, part of same, ×6; 42,*1*, aboral surface, ×1 (133). (See also Fig. 12,*1*.)

Palasteriscus STÜRTZ, 1886 [**P. devonicus*; OD]. Like *Platanaster* but lacking marginals. *L.Dev.*, Ger.——FIG. 41,*2*; 42,*2*. **P. devonicus*; 41,*2*, apical view of ambulacrals showing pegs, ×5; 42,*2*, aboral surface, ×0.5 (133).

Family LUIDIIDAE Verrill, 1899

Arms 5 to many, normally strap-shaped, adambulacrals, oral intermediate ossicles, and inferomarginals in regular transverse series as in *Platanaster*, recalling metapinnules; superambulacrals present. Aboral surface covered with paxillae not in wholly regular rows. *Mio.-Rec.*

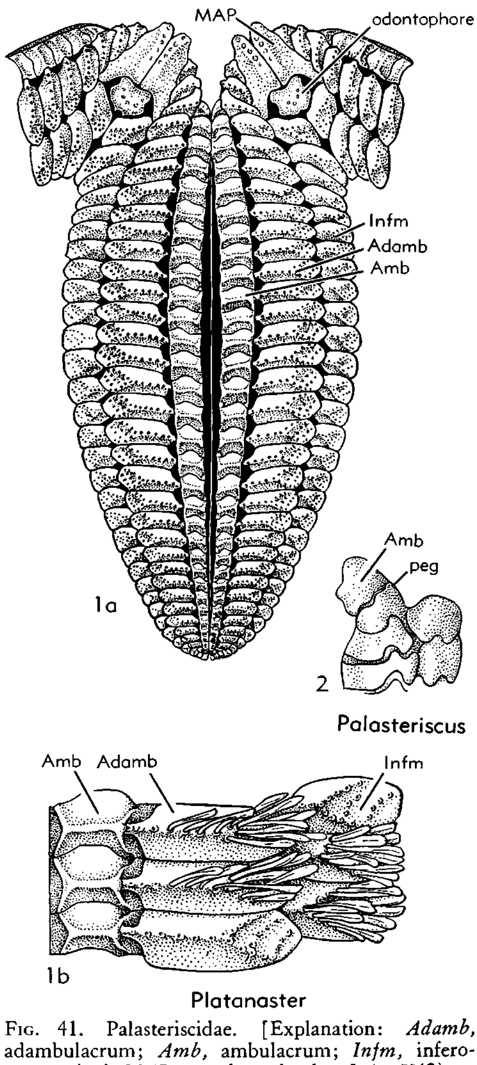

FIG. 41. Palasteriscidae. [Explanation: *Adamb*, adambulacrum; *Amb*, ambulacrum; *Infm*, inferomarginal; *MAP*, mouth-angle plate.] (p. *U*42).

Luidia Forbes, 1839 [**L. fragillissima* (=**Asterias ciliaris* Philippi, 1837); OD ICZN Opin. 129] [=*Hemicnemis* Müller & Troschel, 1840; *Petalaster* Gray, 1840; *Luydia* Düben & Koren, 1847; *Astrella* Perrier, 1882; *Integraster, Quinaster, Penangaster, Denudaster, Senegaster, Alternaster, Armaster, Maculaster* Döderlein, 1920]. Except for *Hemicnemis, Luydia,* and *Armaster,* synonyms may all be justifiable names for subgenera. *Mio.,* Hung.; *Rec.*——Fig. 42,*3*. *L. hungarica* Rakusj; oral surface of arm showing transverse gradients of ambulacrals, adambulacrals, oral intermediate ossicles, and inferomarginals, ×5 (124).

Order PAXILLOSIDA Perrier, 1884

[*no. correct.* Spencer & Wright, herein (*pro* Paxillosa)]

Mouth frame adambulacral, mouth-angle plates prominent, in many forms with keel and median furrow, marginal frame (when present) separated from mouth frame by interradial area with small ossicles. No transverse gradients. Interradial arc even, without axillary. Ambulacral areas never compressed. Tube feet in 2 rows. *L.Ord.-Rec.*

Many of this order have marginals channeled to form more or less specialized intermarginal fascioles, normally connecting with furrows on the oral side, presumably to conduct respiratory water from aboral to oral surface.

Suborder HEMIZONINA Spencer, 1951

[*nom. transl. et correct.* Spencer & Wright, herein (*pro* Hemizonida)] [=Gnathasterina Spencer, 1951]

No superomarginals or only on arms. Aboral surface generally with well-developed stellate ossicles. *L.Ord.-Trias.*

Family PETRASTERIDAE Spencer, 1951

[=Uranasteridae Spencer, 1916]

Arms 5; inferomarginals well developed; axillary area on oral surface with small ossicles or granules. *L.Ord.-Sil.*

Petraster Billings, 1858 [**Palasterina rigidus* Billings, 1857; OD] [=*Uranaster* Gregory, 1899]. Characters of family. *L.Ord.-Sil.,* Wales-Eire-Czech.-Australia.——Fig. 43,*4*. *P. kinahani* (Baily), L.Ord., Wales; *4a,* part of aboral surface of arm, ×4; *4b,* oral surface of arm and mouth region, ×2; *4c,* part of aboral surface, including aboral view of inferomarginals, adambulacrals, and mouth-angle plates, ×4 (133).

Family LEPIDASTERIDAE Gregory, 1899

Arms many, inferomarginals well devel-

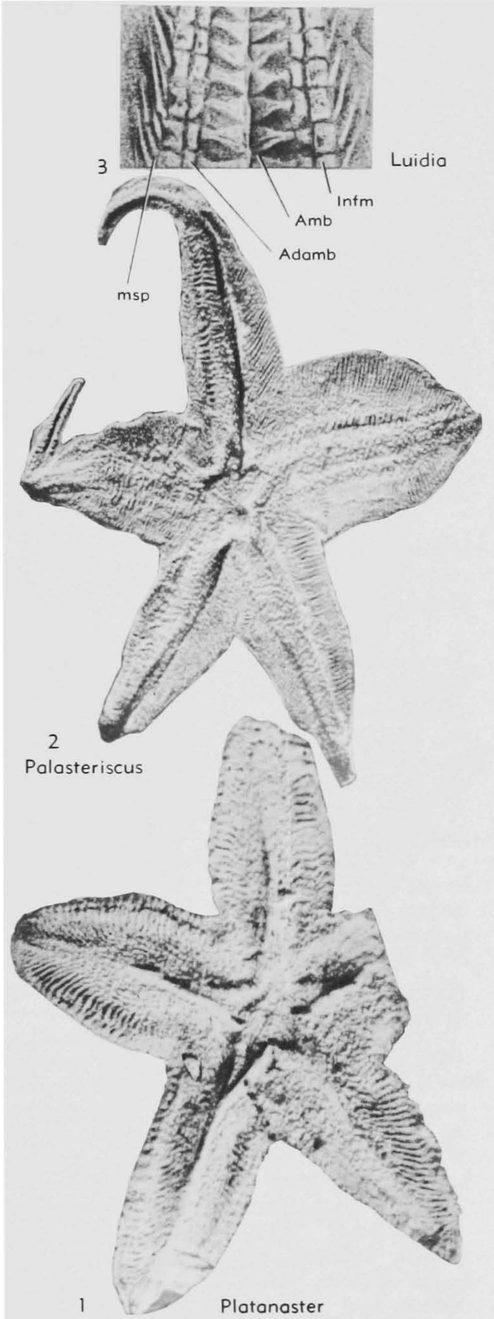

Fig. 42. Palasteriscidae *(1,2)*; Luidiidae *(3)*. [Explanation: *Adamb,* adambulacrum; *Amb,* ambulacrum; *Infm,* inferomarginal; *MAP,* mouth-angle plate; *msp,* marginal spine.] (p. *U*42-*U*43).

oped; oral interradial areas with large or small ossicles. *M.Sil.-U.Dev.*

Lepidaster Forbes, 1850 [**L. grayi*; OD]. Interradial areas with small ossicles. *M.Sil.*, Eng.——Fig. 43,6. **L. grayi*; part of oral surface, ×2 (133).

Devonistella Spencer, 1927 [**Helianthaster filiciformis* Woodward, 1874; OD]. Interradial areas

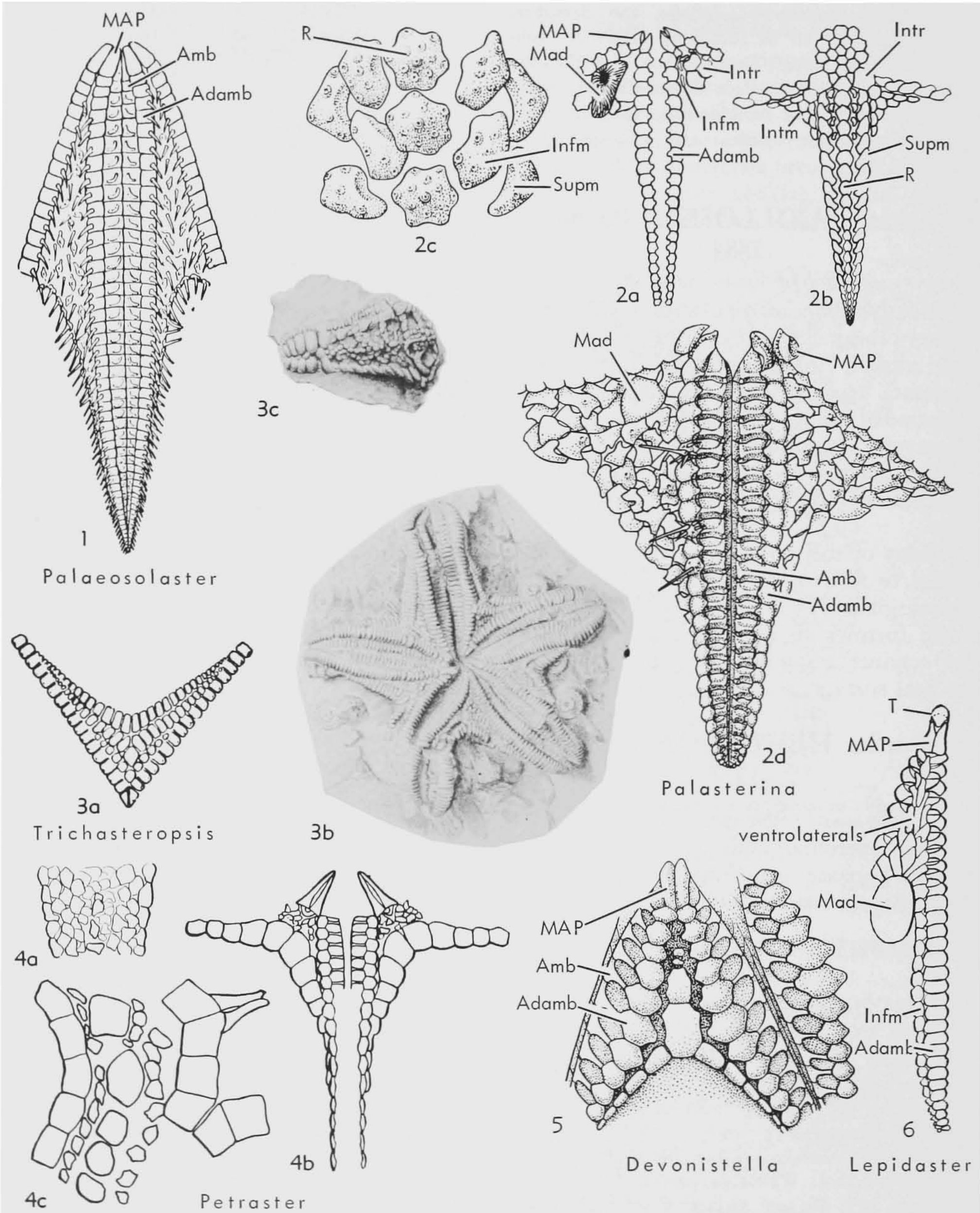

Fig. 43. Petrasteridae *(4)*; Lepidasteridae *(5,6)*; Palasterinidae *(1-3)*. [Explanation: *Adamb*, adambulacral; *Amb*, ambulacral; *Infm*, inferomarginal; *Intm*, intermarginal; *Intr*, interradial; *Mad*, madreporite, *MAP*, mouth-angle plate; *R*, radial; *Supm*, superomarginal; *T*, torus.] (p. *U*43-*U*45).

with few large ossicles. *U.Dev.*, Eng.——FIG. 43, *5.* **D. filiciformis* (WOODWARD); part of oral surface, ×3 (133).

Family PALASTERINIDAE Gregory, 1899

[=Palaesterinidae STÜRTZ, 1890 (not founded on included genus); Lindstroemasterininae GREGORY, 1899; Palaeosolasteridae SCHUCHERT, 1914; Protactininae SPENCER, 1926; Palaeosolasteridae LEHMANN, 1957]

Arms 5 to many; interradial arcs without differentiated marginals. *Sil.-Trias.*

Palasterina M'COY, 1851 [**Uraster primaevus* FORBES, 1848; OD] [=*Palaeasterina* ETHERIDGE, 1881; *Lindstroemaster* GREGORY, 1899; *Hisingeraster, Pseudopalasterina* STÜRTZ, 1900; *?Protactis* SPENCER, 1927; *?Archasterina* LEHMANN, 1957]. Arms 5, more or less cylindrical, bounded distally by adambulacrals; interradial areas aborally with few to many well-calcified ossicles. Odontophore weak to strong. Aboral surface of arms with rather large hexagonal marginals and carinals, in some forms with small intermediate ossicles. Larger ossicles may be pustulose and bear various spines. *L. Sil.-L. Dev.*, Ger.-Eng.-Sweden.——FIG. 43,*2.* **Palasterina primaeva* (FORBES), U.Sil., Eng.; *2a,b,* oral and aboral surfaces of arm and part of disc, ×3; *2c,* ossicles of aboral surface, ×15 (133).——FIG. 43,*2d. P. antiqua* (HISINGER), U.Sil., Eng.; oral surface, ×5 (133).

Palaeosolaster STÜRTZ, 1899 [**P. gregoryi*; OD] [=*Echinasterias, Echinostella* STÜRTZ, 1899; *Echinodiscus* STÜRTZ, 1899 (*non* WORTHEN & MILLER, 1883); *Echinodiscaster* DELAGE & HÉROUARD, 1904; *Echinodiscites* SCHUCHERT, 1914]. Arms many. Oral and aboral intermediate ossicles subequal, each carrying single spine. *L.Dev.*, Ger. ——FIG. 43,*1.* **P. gregoryi*; part of oral surface, ×0.5 (133).

Trichasteropsis ECK, 1879 [*pro Trichaster* QUENSTEDT, 1875 (*non* AGASSIZ, 1836)] [**Asterias cilicia* QUENSTEDT, 1852 (=**Asterias weissmanni* MÜNSTER, 1843); OD]. Superomarginals much longer than inferomarginals, row of minute intermarginals present proximally. Ossicles in axillary areas in regular rows. *Trias.*, Ger.——FIG. 43, *3.* **T. weissmanni* (MÜNSTER); *3a,* part of oral surface, diagrammatic; *3b,c,* oral surface and aboral view of arm, ×1 (128).

Suborder DIPLOZONINA Spencer & Wright, new suborder

Regular double rows of marginals; aboral skeleton typically of true paxillae but early forms may have granular tessellate plates; superambulacral plates present. Tube feet pointed, without sucking discs; ampullae double. *L.Jur.-Rec.*

Family ASTROPECTINIDAE Gray, 1840

[incl. Plutonasteridae SLADEN, 1889; Priamasterinae KOEHLER, 1912 (*nom. transl. et correct.* FISHER, 1917 (*ex* Priamastérïdées KOEHLER, 1912)]

Disc generally rather small; arms long and pointed, normally straight-sided, rarely petaloid; contact facets between marginals smaller in most genera than sides of these plates, leaving ridges on them and narrow channels between adjacent marginals for marginal fascioles; aboral surface covered with tessellate ossicles in some Mesozoic genera but otherwise with true paxillae; oral interradial areas with flat ossicles extending greater or less distance into arms; superambulacral ossicles present. Tube feet pointed, without sucking discs; ampullae double (26). *L.Jur.-Rec.*

Subfamily ASTROPECTININAE Gray, 1840

[*nom. transl.* SLADEN, 1899 (*ex* Astropectinidae GRAY, 1840)]

Marginal fascioles not webbed. *L.Jur.-Rec.*

Genera known as fossils are described first in alphabetical order, after the type-genus; those known only as extant genera are then listed in alphabetical order.

Astropecten GRAY, 1840 [**Asterias aranciaca* LINNÉ, 1758; SD FISHER, 1908] [=*Stellaria* NARDO, 1834 (*non* SCHMIDT in MÖLLER, 1832); *Astropectinides* VERRILL, 1914]. Intermarginal facet small, not angular; inferomarginals with irregularly distributed horseshoe-shaped tubercles, which bear long spines of varying size. Typical paxillae. *U. Mio.(Torton.)-Rec.*——FIG. 12,*3. A.* sp., Rec.; cross section of arm, enl. (133).

Advenaster HESS, 1955 [**A. inermis*; OD]. Lateral facets of marginals large so that intermarginal fasciole is very small; outer face only of marginals and all other ossicles except ambulacrals with pustules bearing fine spines. *L.Jur.(Bajoc.)*, Switz. ——FIG. 44,*1.* **A. inermis*; oral surface (reconstr.), ×1 (113).

Cuneaster HESS, 1955 [**C. hauteriviensis*; OD]. Intermarginal facets small, more or less quadrangular; ridge on marginals high and narrow so that intermarginal channel is wide. *L.Cret. (Hauteriv.)-L.Eoc.(Ypres.)*, Eu.——FIG. 44,*2.* **C. hauteriviensis*, L.Hauteriv., Switz.; side views of superomarginal and inferomarginal, ×4 (113).

Lambertella MERCIER, 1935 [**L. Valettei*; OD]. Ridge on marginals projecting laterally in club-shaped prominence with narrow neck, few or no spines or granules. [Known only from isolated marginals.] *M.Jur.(Bathon.), ?U.Cret.(Turon.)*, Fr.-?Eng.——FIG. 44,*5.* **L. valettei*, Bathon., Fr.; *5a,b,* aboral and profile views of ?superomarginal, ×3 (121).

Lophidiaster SPENCER, 1913 [**L. ornatus*; OD]. Intermarginal facet small, rounded; inferomarginals with rugosities but no horseshoe-shaped tubercles; typical paxillae. *L.Cret.(L.Alb.)-L.Mio.(Burdigal.),* Eu.-Can.

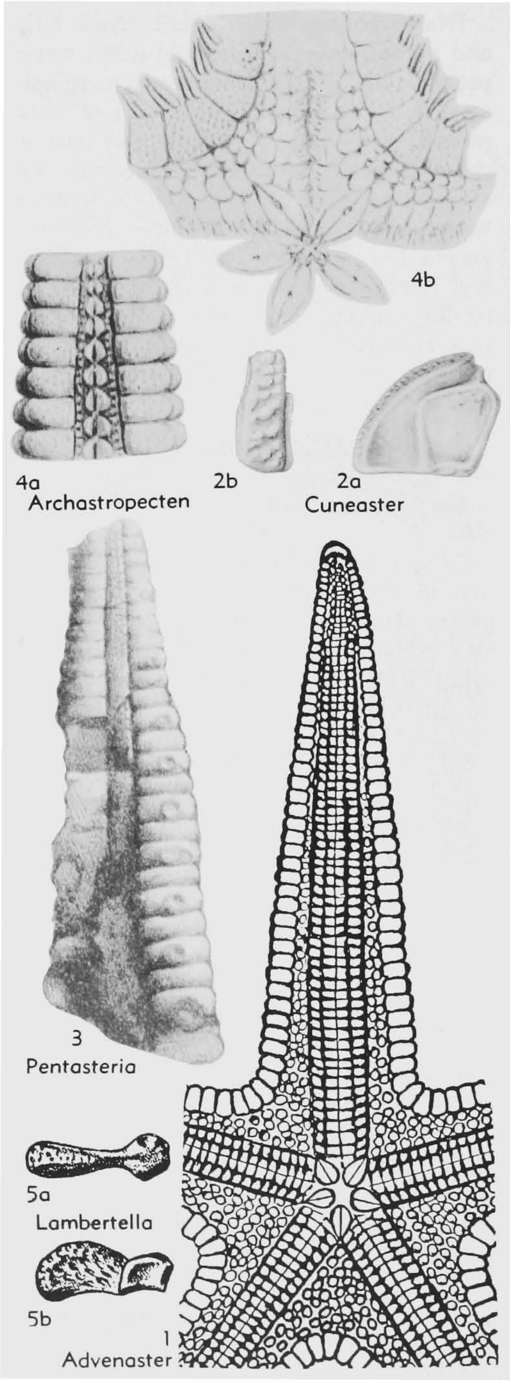

FIG. 44. Astropectinidae (Astropectininae) (p. U45-U46).

Pentasteria VALETTE, 1929 [*non* DE BLAINVILLE, 1834, in syn. in D'ORBIGNY, 1852 (*ex Pentasterias* AGASSIZ, 1842, *nom. correct. pro Pentastéries* DE BLAINVILLE, 1830)] [**P. boisteli*; OD] [=*Crenaster* D'ORBIGNY, 1850; *?Triboletia* DE LORIOL, 1908; ICZN pend.]. Lateral facets of marginals large; inferomarginals with rugosities and irregular row of large horseshoe-shaped tubercles; superomarginals with fine spine pits and (in some forms) large socket for stout spine; aboral surface covered by tessellated plates with pits; no paxillae. *L.Jur.-L.Eoc.,* Eu.

P. (Pentasteria). Some though not all superomarginals with short stout spine in large socket. *M.Jur.(Oxford.)-L.Cret.(Valangin.),* Eu.——FIG. 44,*3*. *P. (P.) rectus* M'COY, Oxford., Eng.; aboral view of part of arm showing large sockets for spines on superomarginals, ×1 (139).

P. (Archastropecten) HESS, 1955 [**Astropecten huxleyi* T. WRIGHT, 1862; OD]. No stout spines on superomarginals. *L.Jur.(?Pliensbach., Aalen.)-L.Eoc.(Ypres.).*——FIG. 44,*4*. *P. (A.) cotteswoldiae* (BUCKMAN), Bathon., Eng. (Oxfords.); *4a,* part of aboral, surface of arm showing superomarginals without large sockets, ×2; *4b,* oral surface of part of disc and arm, ×3 (139).

Plesiastropecten PEYER, 1944 [**P. hallovensis*; OD]. Only specimen too badly preserved for characters to be ascertained; marginals with long spines; aboral paxillae having stellate bases with 4 or 6 points. *L.Jur.(Hettang.),* Switz.

Astromesites FISHER, 1913 [**A. compactus*; OD]. *Rec.*

Bathybiaster DANIELSSON & KOREN, 1883 [**Astropecten pallidus* DANIELSSON & KOREN, 1877 (=**Archaster vexillifer* WYVILLE-THOMSON, 1873); OD] [=*Phoxaster* SLADEN, 1885 (*nom. nud.*); *Phoxaster* SLADEN, 1889; *?Ilyaster* DANIELSSON & KOREN, 1883]. *Rec.*

Blakiaster PERRIER, 1881 [**B. conicus*; OD] [=*?Bunodaster* VERRILL, 1909]. *Rec.*

Ctenophoraster FISHER, 1906 [**C. hawaiiensis*; OD]. *Rec.*

Ctenopleura FISHER, 1913 [**C. astropectinides*; OD]. *Rec.*

Dipsacaster ALCOCK, 1893 [**D. sladeni*; OD]. *Rec.*

Dytaster SLADEN, 1889 [**D. nobilis*; SD FISHER, 1919] [=*Crenaster* PERRIER, 1885 (*non* D'ORBIGNY, 1850); *Dytaster* SLADEN, 1885 (*nom. nud.*)]. *Rec.*

Koremaster FISHER, 1913 [**Dytaster (Koremaster) evaulus*; OD]. *Rec.*

Leptychaster SMITH, 1876 [**L. kerguelenensis*; OD] [=*Leptoptychaster* SMITH, 1879; *Priamaster* KOEHLER, 1912]. *Rec.*

L. (Leptychaster). *Rec.*

L. (Parastropecten) LUDWIG, 1905 [**Parastropecten inermis*; OD] [=*Glyphaster* VERRILL, 1909]. *Rec.*

L. (Trophodiscus) FISHER [**Trophodiscus almus*; OD]. *Rec.*

Lonchotaster SLADEN, 1889 [**L. tartareus*; SD FISHER, 1919] [=*Lonchotaster* SLADEN, 1885 *(nom. nud.)*]. *Rec.*

Macroptychaster H.E.S. CLARK, 1962 [**Leptoptychaster accrescens* KOEHLER, 1920; OD]. *Rec.*

Mimastrella FISHER, 1916 [**Mimaster cognatus* SLADEN, 1889; OD]. *Rec.*

Patagiaster FISHER, 1906 [**P. nuttingi*; OD]. *Rec.*

Persephonaster WOOD-MASON & ALCOCK, 1891 [**P. croceus*; OD] [=*Psilasteropsis* FISHER, 1906]. *Rec.*

Plutonaster SLADEN, 1885 [**Archaster bifrons* WYVILLE-THOMSON, 1873; OD]. *Rec.*

Psilaster SLADEN, 1885 [**Astropecten andromeda* MÜLLER & TROSCHEL, 1842; OD] [=*Ripaster* KOEHLER, 1906; *Phidiaster* KOEHLER, 1909]. *Rec.*

Tethyaster SLADEN, 1889 [**Asterias subinermis* PHILIPPI, 1837; SD A. M. CLARK & A. H. CLARK, 1954] [=*Moiraster* SLADEN, 1889; *Sideriaster* VERRILL, 1899; *Anthosticte* FISHER, 1911]. *Rec.*

Thrissacanthias FISHER, 1916 [**Persephonaster penicillatus* FISHER, 1904; OD]. *Rec.*

Tritonaster FISHER, 1906 [**T. craspedotus*; OD]. *Rec.*

Subfamily CRASPIDASTERINAE Fisher, 1916

Marginal and oral fascioles webbed. *Rec.*

Craspidaster SLADEN, 1889 [**Archaster hesperus* MÜLLER & TROSCHEL, 1840; OD] [?=*Nauricia* GRAY, 1840 *(nom. dub.)*]. *Rec.*

Suborder CRIBELLINA Fisher, 1911

Arms five, short or long, disc large; marginals normally thin and lamelliform, high, naked or covered with membrane, smooth or with few large spines; cribriform organs between all or some marginals. No intestine or anus in most forms; tube feet pointed, without sucking disc; ampullae single. *Rec.*

Family GONIOPECTINIDAE Verrill, 1889

Abactinal surface paxillose; cribriform organs between all marginals; oral surface with transverse rows of ossicles separated by channels covered by webbed spinelets, continuous from cribriform organs to ambulacrals; superambulacral ossicles present. *Rec.*

Subfamily CTENODISCINAE Sladen, 1889

Marginals moderately solid; cribriform organs consisting solely of webbed spinelets. No intestine. *Rec.*

Ctenodiscus MÜLLER & TROSCHEL, 1842 [**Asterias polaris* SABINE, 1821 (=**A. crispata* RETZIUS, 1805); OD] [=*Anodiscus* PERRIER, 1869]. *Rec.*

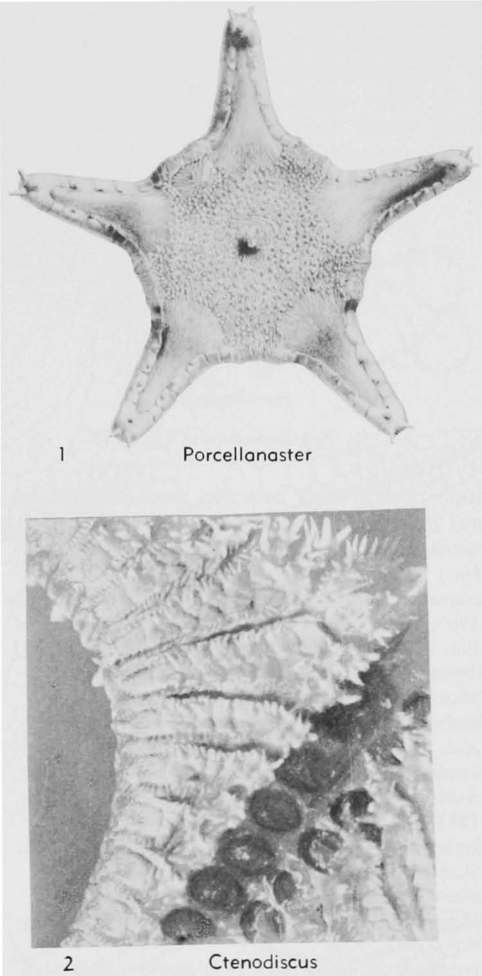

FIG. 45. Goniopectinidae (Ctenodiscinae) *(2)*; Porcellanasteridae *(1)* (p. *U*47-*U*48).

——FIG. 45,*2*. **C. crispatus* (RETZIUS); part of aboral surface, enl. (110).

Pectinidiscus LUDWIG, 1900 [**P. annae*; OD]. *Rec.*

Subfamily GONIOPECTININAE Verrill, 1889

Cribriform organs composed of discrete spinelets covered by single-webbed series. Well-developed intestine and intestinal caecum. *Rec.*

Goniopecten PERRIER, 1881 [**G. demonstrans;* OD]. *Rec.*

Prionaster VERRILL, 1889 [**P. elegans*; OD]. *Rec.*

Family PORCELLANASTERIDAE Sladen, 1883

Marginals very thin; cribriform organs highly developed but (with single excep-

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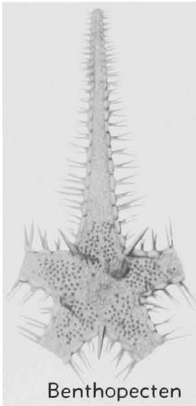


FIG. 46. Benthopectinidae (p. U48).

tion) present only between some marginals; oral interradial areas without channels. *Rec.*

Porcellanaster WYVILLE-THOMSON, 1877 [**P. ceruleus*; OD] [=*Caulaster* PERRIER, 1882; *Albatrossaster* LUDWIG, 1907 (*pro Albatrossia* LUDWIG, 1905, *non* JORDAN & EVERMANN, 1898)]. *Rec.*——FIG. 45,*1*. **P. ceruleus*; aboral surface, ×2 (130).

Abyssaster MADSEN, 1961 [**Hyphalaster tara* WOOD-MASON & ALCOCK, 1891; OD]. *Rec.*

Benthogenia FISHER, 1911 [**B. cribellosa*; OD]. *Rec.*

Eremicaster FISHER, 1905 [**Porcellanaster tenebrarius* FISHER, 1905 (=**P. gracilis* SLADEN, 1883); OD]. *Rec.*

Hyphalaster SLADEN, 1883 [**Hyphalaster inermis* SLADEN, 1883; SD MADSEN, 1961]. *Rec.*

Lysaster BELL, 1909 [**L. lorioli*; OD]. *Rec.*

Sidonaster KOEHLER, 1909 [**S. vaneyi*; SD MADSEN, 1961]. *Rec.*

Styracaster SLADEN, 1883 [**S. horridus*; SD MADSEN, 1961] [=*Machairaster* PERRIER, 1884 (*nom. nud.*); *Chunaster* LUDWIG, 1907]. *Rec.*

Thoracaster SLADEN, 1883 [**T. cylindratus*; OD]. *Rec.*

Suborder NOTOMYOTINA Ludwig, 1910

[=Myonota VERRILL, 1914]

Arms flexible, with pair of dorsal muscle bands, perhaps allowing swimming; marginals alternate, imbricating with long spines; no superambulacral plates. Pedicellariae pectinate; tube feet with sucking discs, ampullae double. *L.Cret.-Rec.*

Family BENTHOPECTINIDAE Verrill, 1894

[*nom. transl.* VERRILL, 1899 (*ex* Benthopectininae VERRILL, 1894)] [=Pararchasterinae SLADEN, 1889]; Pontasterinae VERRILL, 1894; Cheirasteridae LUDWIG, 1910]

Disc small, arms long and slender; odd interradial marginal in each series present in some genera. *L.Cret.-Rec.*

Benthopecten VERRILL, 1884 [**B. spinosus*; OD] [=*Pararchaster* SLADEN, 1885]. Odd interradial superomarginal more prominent than others; superomarginals bearing 1 primary spine and inferomarginals 1 or 2. [An undescribed species probably belonging to this genus occurs in Albian rocks of England.] *?L.Cret.(U.Alb.)*, Eng., *Rec.*——FIG. 46,*1*. *B. armatus* (SLADEN), Rec.; aboral view, ×1 (130).

Acontiaster DÖDERLEIN, 1921 [**A. bandanus*; OD]. *Rec.*

Cheiraster STUDER, 1883 [**C. gazellae*; OD]. *Rec.*

Gaussaster LUDWIG, 1910 [**G. vanhoffeni*; OD]. *Rec.*

Luidiaster STUDER, 1883 [**L. hirsutus*; OD] [=*Acantharchaster* VERRILL, 1894; *Marcellaster* KOEHLER, 1907; *Marcelaster* KOEHLER, 1908]. *Rec.*

Myonotus FISHER, 1911 [**Acantharchaster intermedius* FISHER, 1900; OD]. *Rec.*

Nearchaster FISHER, 1911 [**Acantharchaster aciculosus* FISHER, 1910; OD]. *Rec.*

Pectinaster PERRIER, 1885 [**P. filholi*; OD]. *Rec.*

Pontaster SLADEN, 1885 [**Astropecten tenuispinus* DÜBEN & KOREN, 1846; OD]. *Rec.*

Order VALVATIDA Perrier, 1884

[*nom. correct.* SPENCER & WRIGHT, herein (*pro* "Valvata" PERRIER, 1884)]

Mouth frame of adambulacral type; mouth-angle plates relatively inconspicuous and normally only distinguishable from succeeding adambulacrals by their subtrigonal outline; infero- and superomarginals, if present, normally equal in number and without intermarginal channels; adambulacrals without transverse ridge. Ambulacrals normally in 2, rarely in 4 rows. Pedicellariae, when present, generally valvate and with bases sunk into substance of ossicles. *L.Ord.-Rec.*

Suborder PUSTULOSINA Spencer, 1951

[*nom. transl. et correct.* SPENCER & WRIGHT, herein (*ex* Pustulosa SPENCER, 1951)]

Marginals with many small undifferentiated spines elevated on small tubercles (pustules); superomarginals generally within frame of inferomarginals and loosely connected. Pedicellariae unknown. *L.Ord.-L.Carb.*

Superfamily PALAEASTERACEAE S. A. Miller, 1889

[*nom. transl.* SPENCER & WRIGHT, herein (*ex* Palaeasteridae S. A. MILLER, 1889)]

Ambulacral furrow generally closed by

short quadrangular adambulacrals. Inferomarginal frame reaches to ends of the arms. *L.Ord.-L.Carb., ?Permocarb.*

Family PALAEASTERIDAE S. A. Miller, 1889

Single axillary in each arc dividing row of inferomarginals that borders arms, which are thus not fully fused at base; superomarginals lying within inferomarginals; no carinals present but irregular small plates occurring along mid-line of arms; aboral surface of disc with distinct primary circlets, ossicles of which are separated by many

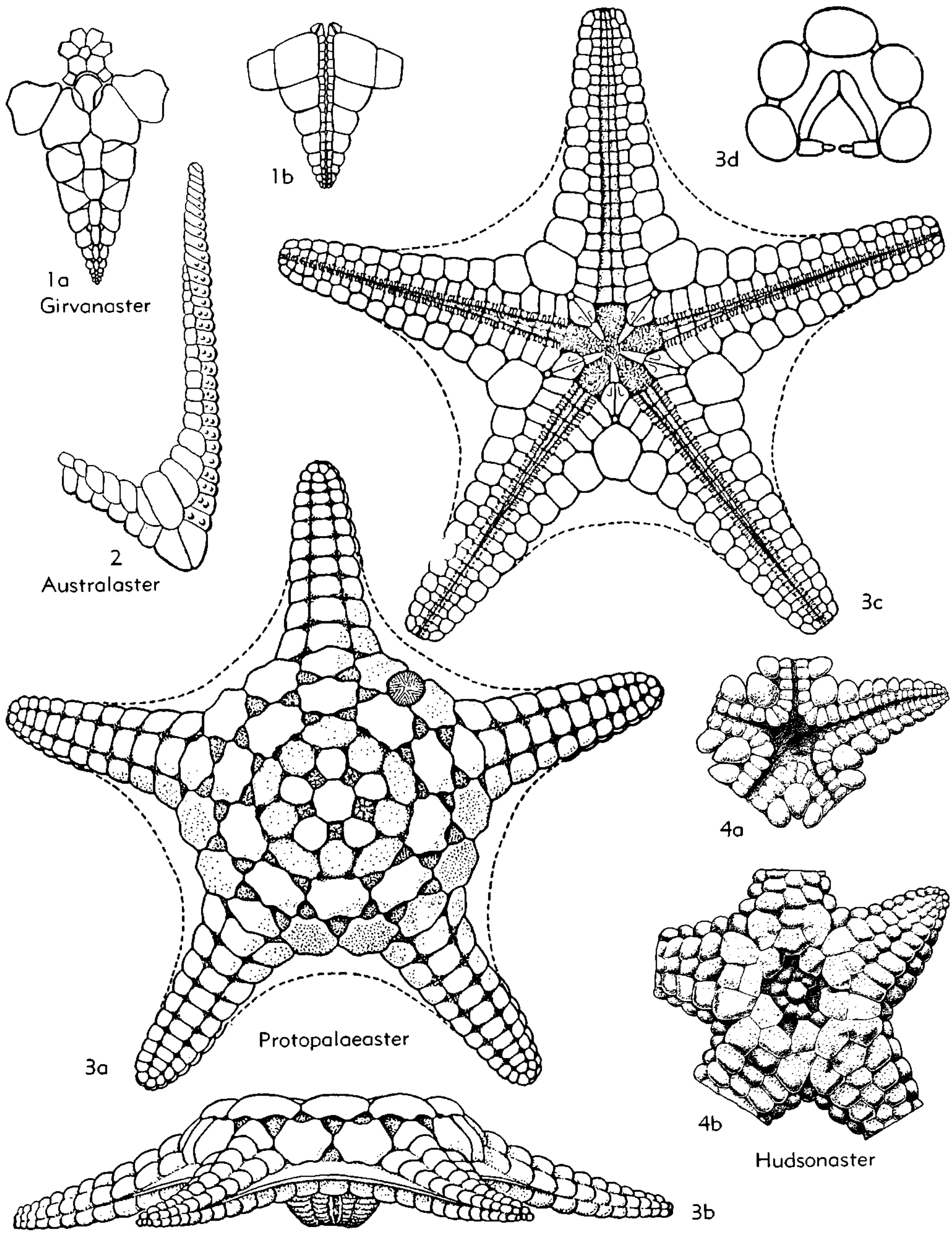


FIG. 47. Palaeasteridae *(2)*; Hudsonasteridae (Hudsonasterinae) *(1,3-4)* (p. *U*50).

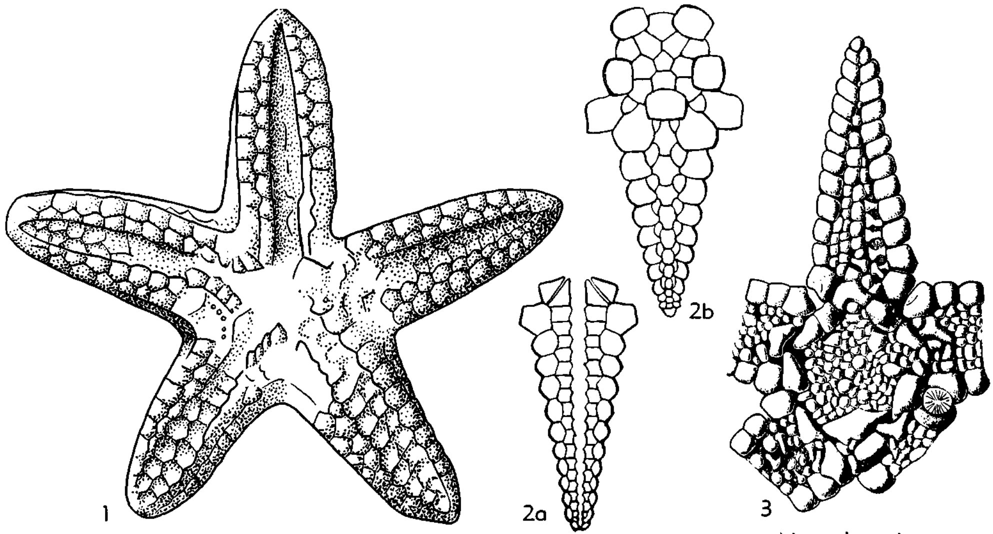


FIG. 48. Hudsonasteridae (Hudsonasterinae) *(1)*, (Coccasterinae) *(2)*, Neopaleasteridae *(3)* (p. *U*51).

small plates, probably forming rigid structure. *M.Sil., ?Permocarb.*

Palaeaster HALL, 1852 [**P. niagarensis*; OD]. Characters of family. *M.Sil.,* N.Am.——FIG. 21,*4*. **P. niagarensis,* USA(N.Y.); aboral side, ×2 (129).

?Australaster SCHUCHERT, 1914 [**Palaeaster (Monaster) giganteus* ETHERIDGE, 1892; OD] [=*Monaster* GREGORY, 1899 *(non* ETHERIDGE, 1892; ICZN pend.)]. Large, with slender arms; adambulacrals increasing in width and inferomarginals decreasing distally; aboral surface unknown. *Permocarb.,* New S. Wales.——FIG. 47,*2*. **A. giganteus* (ETHERIDGE); oral view, ×1 (129).

Family HUDSONASTERIDAE Schuchert, 1914

[=Protopalaeasteridae RASMUSSEN, 1962]

Single axillary with free distal edge dividing strong frame of inferomarginals bordering arms which generally are unfused but tend to join at base in some genera; superomarginals within frame of inferomarginals; aboral surface of arms generally consisting of superomarginals and row of carinals only, but with additional rows of ossicles in Silurasterinae; aboral surface of disc with centrale and primary circlets which may form protrusible cap, presumably for respiratory purposes; ambulacrals rarely exposed; in some genera apparently blocky, without large basins for tube feet, in others with strong T-shaped ridges and basins between; ampullar pores present in some genera but minute and may occur generally despite emphasis in descriptions on their absence. *L.Ord.-U.Sil.*

The strongly calycinal aboral skeleton of hudsonasterids is probably due to paedomorphic evolution from the young of an ancestral form and is not in itself necessarily a primitive feature.

Subfamily HUDSONASTERINAE Schuchert, 1914

Aboral arm skeleton composed of superomarginals and carinals only; protrusible cap present on central disc. *L.Ord.-U.Ord.*

Hudsonaster STÜRTZ, 1900 [**Palasterina rugosa* BILLINGS, 1857; OD]. Arms subtriangular, with broad base, clearly not fused. *U.Ord.,* N.Am.——FIG. 47,*4*. *H. incomptus* (MEEK), U.Ord.(Richmond.); Ohio; *4a,b,* oral and aboral sides, ×2 (129).

Girvanaster SPENCER, 1916 [**G. sculptus*; OD]. Axillaries very large; proximal superomarginals large; protrusible cap narrow. *U.Ord.,* Scot.——FIG. 47,*1*. **G. sculptus*; *1a,b,* oral and aboral sides, ×6 (133).

Protopalaeaster HUDSON, 1912 [**P. narrawayi*; OD] [=*Belaster* SPENCER, 1916; *Ordoviciaster* FEDOTOV, 1936]. Proximal superomarginals not conspicuously large; arms tending to fuse; ambulacrals apparently without T-shaped ridge. *L.Ord.-U.Ord.,* N.Am.-Eng.-Turkestan.——FIG. 47,*3*. **P. narrawayi,* L.Ord., USA(Minn.); *3a-c,* aboral, lat. view, oral view, ×2; *3d,* cross section of arm, ×4 (40). (See also Fig. 21,*1*.)

?**Macroporaster** RAYMOND, 1921 [**Asterias matutinus* HALL, 1847; OD]. Similar to *Hudsonaster* but ambulacrals with T-shaped ridges forming wide basins for tube feet. *M.Ord.,* N.Am.——FIG. 48,*1*. **M. matutinus* (HALL); oral surface, ×1.5 (126).

Subfamily COCCASTERINAE Spencer & Wright, new subfam.

Like Hudsonasterinae but no protrusible cap on disc. *M.Sil.-U.Sil.*

Coccaster SPENCER, 1916 [**C. bulbiferus*; OD]. Primary radials much swollen. *M.Sil.-U.Sil.,* Eng. ——FIG. 48,*2*. **C. bulbiferus*, Herefords.; *2a,b,* aboral and oral sides, ×5 (133).

Subfamily SILURASTERINAE Spencer & Wright, new subfam.

Aboral arm skeleton with rows of small intermediate ossicles between carinals and superomarginals. *M.Ord.*

Siluraster JAEKEL, 1903 [**S. perfectus*; OD] [=*Caractacaster* SPENCER, 1916]. Characters of subfamily. *M.Ord.,* W.Eng.-Czech.——FIG. 21,*2*. *S. caractaci* (SPENCER), Eng.(Heref.); aboral side, ×3 (133).

Family NEOPALAEASTERIDAE Schuchert, 1915

Very like Palaeasteridae except that superomarginals overlie inferomarginals, but it is not certain whether axillary has free edge or is enclosed by inferomarginals. [A doubtful family. Lower Silurian species from Sweden ascribed to *Neopalaeaster* probably belongs to Palaeasteridae.] *L.Carb.*

Neopalaeaster SCHUCHERT, 1915 [**Palaeaster crawfordsvillensis* S. A. MILLER, 1880; OD]. Characters of family. *Miss.,* N.Am.——FIG. 48,*3*. **N. crawfordsvillensis* (MILLER), Miss., USA(Ind.); aboral side, ×2 (129).

Family MESOPALAEASTERIDAE Schuchert, 1914

[*nom. transl.* SPENCER & WRIGHT, herein (*ex* Mesopalaeasterinae SCHUCHERT, 1915)]

Axillaries enclosed by first pair of inferomarginals and arms fused at base; aboral skeleton with rows of small intermediate ossicles separating carinals from superomarginals. *U.Ord.-U.Dev.*

Large numbers of *Devonaster* found at Saugerties, N.Y. (RUEDEMANN, 1915) show various stages of development. The earliest has stellate aboral ossicles, as in *Petraster*. In the next, the aboral surface passes through a *Hudsonaster* stage. Finally, the large ossicles become separated by lightly calcified areas, which allowed the extrusion of papulae.

Subfamily MESOPALAEASTERINAE Schuchert, 1915

With papular areas on aboral surface at base of arms on either side of primary radial. *U.Ord.-U.Dev.*

Mesopalaeaster SCHUCHERT, 1914 [**Palaeaster shafferi* HALL, 1868; OD] [=?*Argaster* HALL, 1868].Disc compact, small; arms narrow, straight-sided. [FOERSTE (1919) distinguished *Hemipalaeaster* as a subgenus (type, *H. schucherti*, OD), since its row of carinals is not continuous but interrupted proximally. This seems to be of only specific importance.] *U.Ord.,* N.Am.-Scot.——FIG. 49,*2a*. *M. primus* SPENCER, U.Ord., Scot.; part of oral surface, ×6 (133).——FIG. 49,*2b,c*. **M. shafferi* (HALL), U.Ord., USA(Ohio); *2b,* oral side of young individual, ×5; *2c,* aboral side of adult, ×2 (133).

Arisaigaster SPENCER, 1953 [**Palaeaster parviusculus* BILLINGS, 1860; OD]. Disc large; arms short and broad. *U.Ord.-U.Sil.,* E.Can.-Scot.-Eng.——FIG. 49,*3a*. *A. leintwardinensis* SPENCER, U.Sil., Eng.; aboral side, ×9 (133).——FIG. 49,*3b*. **A. parviusculus* (BILLINGS), L.Sil., N.Scotia; oral side, ×4 (129).

Devonaster SCHUCHERT, 1914 [**Palaeaster eucharis* HALL, 1868; OD]. Disc large, arms broad and slightly petaloid; aboral surface of disc covered with small irregular plates which also extend between carinals and superomarginals which are well within frame of inferomarginals. *M.Dev.-U.Dev.,* N.Am.——FIG. 49,*4*. **D. eucharis* (HALL), M.Dev., USA(N.Y.); *4a,b,* aboral and oral sides, ×1 (129).

Subfamily LEPIDACTININAE Spencer, 1918

[*nom. transl.* SPENCER & WRIGHT, herein (*ex* Lepidactinidae SPENCER, 1918)]

Differs from Mesopalaeasterinae in having no papular areas at base of arms. *M.Sil-L.Dev.*

Lepidactis SPENCER, 1918 [**L. wenlocki*; OD]. Inferomarginals not extending to end of arms. *M. Sil.,* Eng.——FIG. 49,*1*. **L. wenlocki*; *1a,b,* oral and aboral sides of arm, ×2 (133).

Spaniaster SCHÖNDORF, 1907 [*pro Coelaster* SANDBERGER, 1855 (*non* AGASSIZ, 1835)] [**Coelaster latiscutatus* SANDBERGER, 1855; OD] [=?*Miomaster* SCHÖNDORF, 1909]. Inferomarginals extending to end of arms. *L.Dev.,* W.Eu.

Subfamily CLARKEASTERINAE Spencer & Wright, new subfamily

Like Mesopalaeasterinae but with double row of narrow carinals; primary radials swollen as in *Coccaster*. *U.Dev.*

Clarkeaster RUEDEMANN, 1916 [**Palaeaster clarki* CLARKE & SWARTZ, 1913; OD]. Characters of subfamily. *U.Dev.*, E.N.Am.——FIG. 49,*5*. **C. clarki* (CLARKE & SWARTZ); aboral side, ×2 (127).

Family XENASTERIDAE Gregory, 1899

[=Palaeogoniasteridae STÜRTZ, 1890 (invalid because not founded on generic name); Palaeostellidae LEHMANN, 1957]

Like Mesopalaeasteridae but with more than single ossicle in each axillary area; arms wedge-shaped, flattened orally and with narrow ambulacrals. *L.Dev.*

Xenaster SIMONOVITSCH, 1871 [**X. margaritatus*; OD] [=?*Archaeasterias* MÜLLER, 1855; *Archasterias* SIMONOWITSCH, 1871]. Two pairs of inferomarginals incorporated within marginal frame; superomarginals subordinate to inferomarginals; few intermediate ossicles on oral side. *L.Dev.*, Ger.——FIG. 21,*3*. **X. margaritatus*; part of aboral surface showing intermarginals between rows of superomarginals and small arc of inferomarginals; also lightly calcified space between carinals and superomarginals, ×1.5 (128).

Agalmaster SCHÖNDORF, 1909 [**A. miellensis*; SD SCHUCHERT, 1914]. Two pairs of inferomarginals

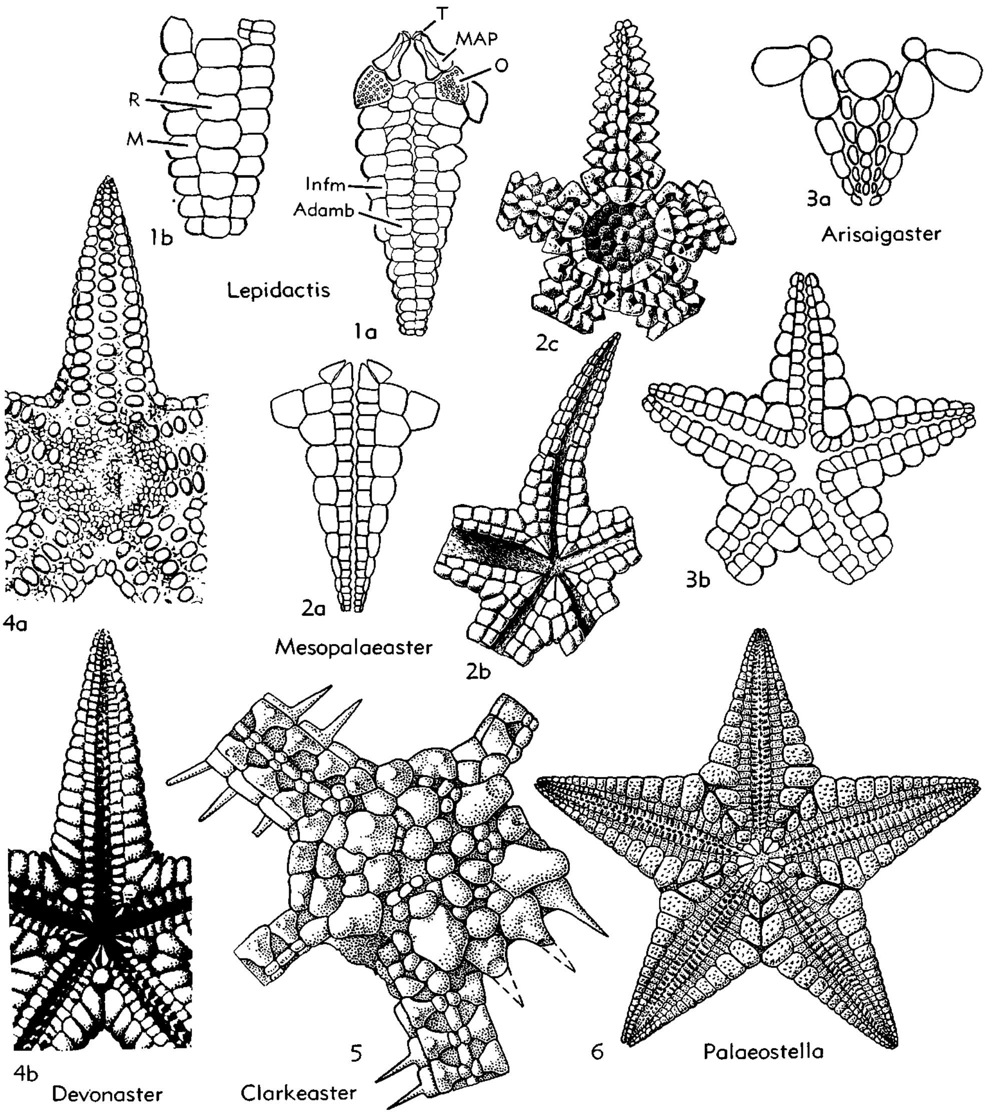


FIG. 49. Mesopalaeasteridae (Mesopalaeasterinae) *(2-4)*, (Lepidactininae) *(1)*, (Clarkeasterinae) *(5)*; Xenasteridae *(6)*. [Explanation: *Adamb*, adambulacral; *Infm*, inferomarginal; *M*, marginal; *MAP*, mouth-angle plate; *O*, odontophore; *R*, radial *T*, torus.] (p. *U*51-*U*53).

inside marginal frame; superomarginals prominent; oral intermediate plates numerous. *L.Dev.*, Ger.

Palaeostella Stürtz, 1890 [**P. solida*; OD] [=*Palaenectria* Stürtz, 1893; *Eifelaster* Schöndorf, 1909]. Like *Agalmaster* but with no oral intermediate plates. *L.Dev.*, Ger.——Fig. 49,6. *P. follmanni* (Schöndorf); oral side, ×1.5 (128). (128).

Rhenaster Schöndorf, 1909 [**R. schwerdi*; OD]. No interray accessory plates on oral or aboral side. *L.Dev.*, Ger.

Trimeraster Schöndorf, 1909 [**T. parvulus*; OD]. Only single pair of inferomarginals inside marginal frame. *L.Dev.*, Ger.

Family and Subfamily UNCERTAIN

Eostella Lehmann, 1957 [**E. hunsrueckiana*; OD]. Marginals apparently T-shaped. [The single known specimen is too badly preserved for its characters and affinities to be made out.] *L.Dev.*, Ger.

Hunsrueckaster Lehmann, 1957 [**H. peregrinus*; OD]. [The single known specimen is too badly preserved for its characters and affinities to be made out.] *L.Dev.*, Ger.

Superfamily PROMOPALAEASTERACEAE Schuchert, 1914

[*nom. transl.* Spencer & Wright, herein (*ex* Promopalaeasteridae Schuchert, 1914)]

Marginal frame not reaching end of arms; adambulacrals broad; ambulacrals exposed and proximally may form 4 rows; arms well produced. *M.Ord.-Sil.*

Family PROMOPALAEASTERIDAE Schuchert, 1914

[=Anorthasterinae Schuchert, 1915]

Arms fused at base and generally more or less cylindrical; ambulacrals compressed and proximally in 4 rows; adambulacrals broad. *M.Ord.-Sil.*

Promopalaeaster Schuchert, 1914 [**Palaeaster granulosus* Meek, 1872 (*non* Hall, 1868) (=**Palaeaster speciosus* Meek, 1872); OD]. Characters of family. *M.Ord.-Sil.*, N.Am.-Scot.-Australia.——Fig. 50,*2a,b*. *P. magnificus* (Miller), U.Ord.(Richmond.), USA(Ohio); *2a*, aboral side of distal part of arm, ×3; *2b*, oral side of interradial area, ×3 (129).——Fig. 50,*2c,d*. *P. elizae* Spencer, U.Ord., Scot.; *2c*, oral view of ambulacrals and adambulacrals; *2d*, part of oral side showing inferomarginals enclosing 2 axillary ossicles between interradial arc and mouth frame, ×6 (133).

Anorthaster Schuchert, 1914 [**Palaeaster miamiensis* S. A. Miller, 1880]. Original diagnosis

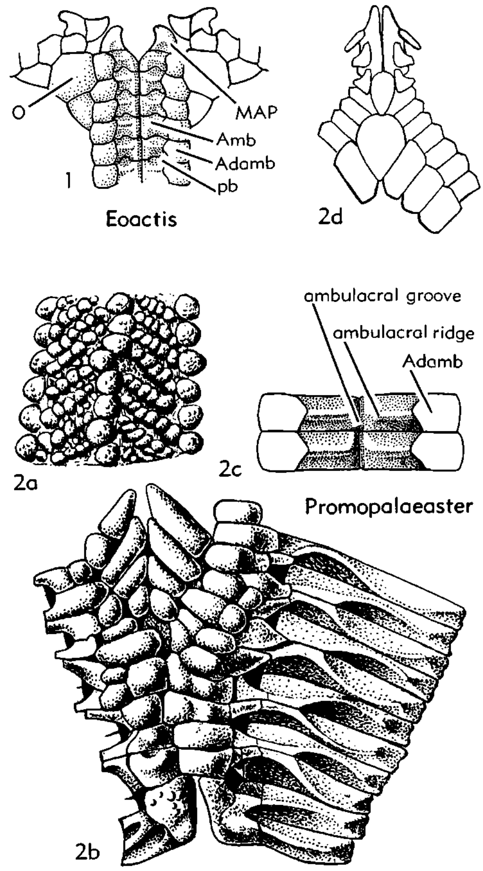


Fig. 50. Promopaleasteridae *(2)*; Eoactinidae *(1)*. [Explanation: *Adamb*, adambulacral; *Amb*, ambulacral; *MAP*, mouth-angle plate; *O*, odontophore; *pb*, podial basin.] (p. *U*53).

states "aberrant Promopalaeasteridae with the axillary and interbrachial areas composed entirely of adambulacral pieces" but may be founded on a pathological or damaged individual. *U.Ord.*, USA(Ohio).

?**Kyraster** Lehmann, 1957 [**K. inermis*; OD]. Single known specimen badly preserved, may belong in this family. *L.Dev.*, Ger.

Family EOACTINIDAE Spencer, 1919

Marginal frame confined to few ossicles in arm axils. *Sil.*

Eoactis Spencer, 1914 [**E. simplex*; OD]. Axillary large, hexagonal. *L.Sil.*, Eng.-N.Am.——Fig. 50,*1*. **E. simplex*, part of oral surface near mouth, ×8 (133).

Yarravaster Spencer, 1950 [**Caractacaster yarraensis* Withers & Keeble, 1934; OD]. Axillary rounded, swollen. *Sil.*, Australia.

Suborder TUMULOSINA Spencer & Wright, new suborder

This suborder is erected for a presumed phyletic assembly of peculiar forms characterized by a high swollen disc covered with rather large ossicles notched in one way or another to allow for extrusion of papulae. The Monasteridae in many ways resemble early Palaeasteraceae, from which presumably they were derived. The Stauranderasteridae, though lacking the characteristic wide adambulacrals of Monasteridae, closely resemble the family in other important characters. The Sphaerasteridae probably were derived from Early Jurassic Stauranderasteridae and tended to a closely plated spherical form. *Permocarb.-Rec.*

Family MONASTERIDAE Schuchert, 1915

Disc large, tumid; arms club-shaped, with steep lateral borders formed by inferomarginals, which are visible in aboral aspect and

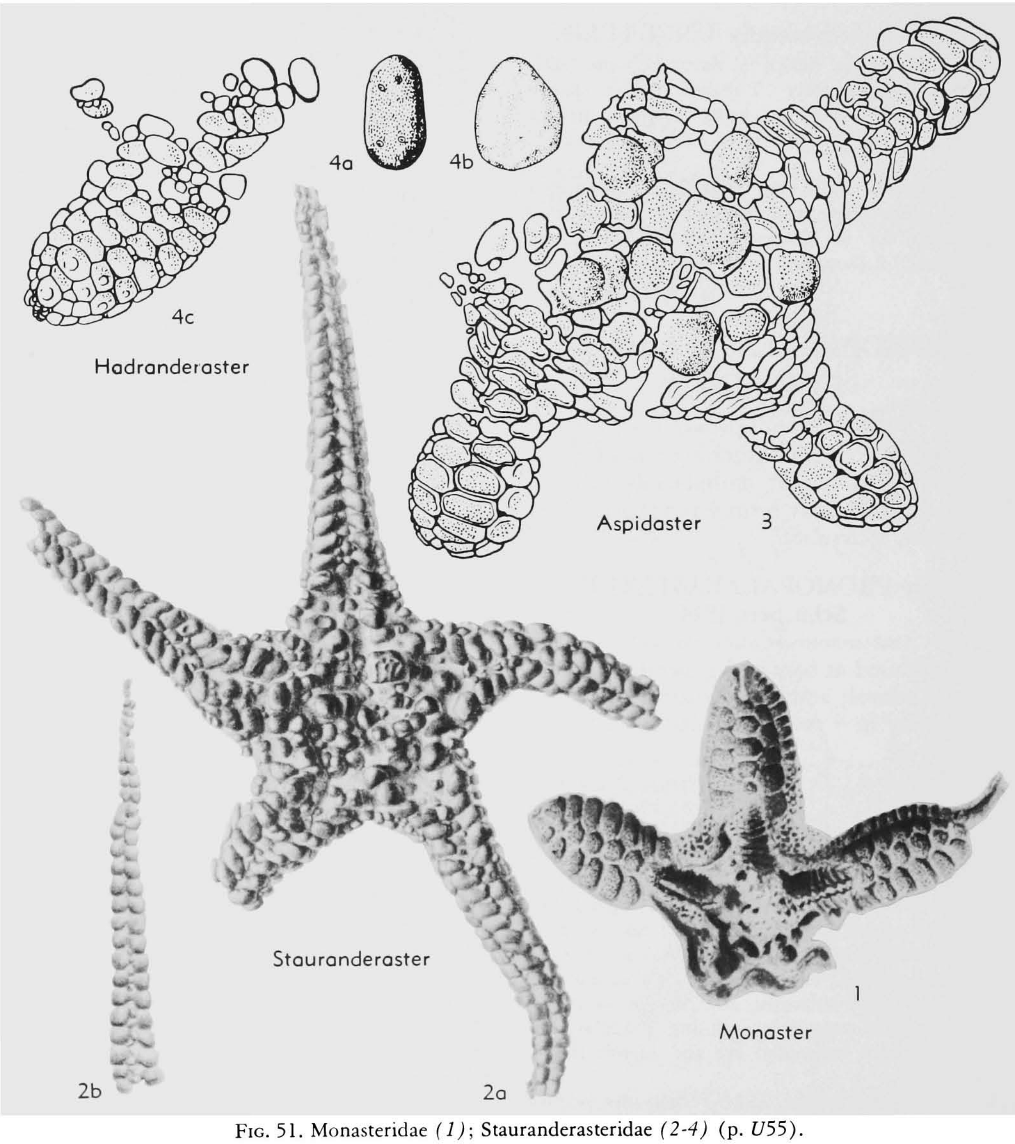


FIG. 51. Monasteridae *(1)*; Stauranderasteridae *(2-4)* (p. *U55*).

are twice as numerous as superomarginals, a series of which adjoins row of swollen carinals; adambulacrals exceptionally wide, occupying most of oral surface of arms; disc with centrale and primary interradials larger than remaining ossicles, most of which are spindle-shaped. *Permocarb.*

Monaster ETHERIDGE, 1892 [**Palaeaster clarkei* DE KONINCK, 1877; SD SCHUCHERT, 1914; ICZN pend.] [=*Etheridgaster* GREGORY, 1899]. Characters of family. *Permo-Carb.,* Australia(New S. Wales).——FIG. 51,*1*. **M. clarkei* (DE KONINCK); aboral surface, ×1 (107).

Family STAURANDERASTERIDAE Spencer, 1913

Some forms closely resembling Monasteridae except that adambulacrals are square and inferomarginals are no more numerous than superomarginals; other forms with long narrow arms and intermarginals may occur; aboral skeleton of disc consisting of massive spindle- or breastplate-shaped ossicles notched at corners to allow protrusion of papulae and including prominent centrale and primary interradials. *M.Jur.-U.Cret.*

Stauranderaster SPENCER, 1907 [**Oreaster boysii* FORBES, 1848; OD]. Arms long, narrow, and straight-sided; carinals weak or absent. *U.Jur. (Kimmeridg.)-U. Cret.(Maastricht.),* Eu. - N. Am. (Tex.).——FIG. 51,*2*. *S. coronatus* (FORBES), U. Cret.(Cenoman.), Eng.; *2a,* aboral surface; *2b,* lat. view of arm showing intermarginals, ×0.75 (131).

Aspidaster DE LORIOL, 1884 [**A. delgadoi*; OD]. Disc high and swollen; arms club-shaped with large carinals; marginals and ossicles of disc generally with smooth rabbet edge. *M.Jur. (Bathon.)-U.Cret.(Dan.),* Eu.——FIG. 51,*3*. *A. bulbiferus* (FORBES), U.Cret.(Santon.), Eng., aboral side, ×1 (131).

Hadranderaster SPENCER, 1907 [**Pentaceros abbreviatus* SPENCER, 1905 (=**Oreaster simplex* GEINITZ, 1871); OD] [=*?Stauraster* VALETTE, 1928]. Marginals hexagonal or rounded, extremely thick, lacking smooth rabbet edge. *?L.Jur.(Charmouth.), M. Jur.(Bathon.) - U. Cret.(Campan.),* W. Eu.——FIG. 51,*4*. **H. simplex* (GEINITZ), U.Cret.(Santon.), Eng.; *4a,b,* lat. and profile views of marginal, ×2 (133); *4c,* aboral side of arm, ×1 (131).

Family SPHAERASTERIDAE Schöndorf, 1906

Body high, domed, and slightly pentagonal to globular, without produced arms, covered with close-fitting plates (3, 58). *M.Jur.-Rec.*

Sphaeraster QUENSTEDT, 1875 [*pro Sphaerites* QUENSTEDT, 1852 (*non* DUFTSCHMID, 1805)] [**Sphaerites punctatus* QUENSTEDT, 1852; SD A. M. CLARK, 1962]. Domed, with flat or slightly concave base, square inferomarginals and high, short, wide superomarginals forming ambital margin, broken only by ends of ambulacra; aboral surface covered by large thin hexagonal plates with pores for papulae along their sutures; oral interradial areas with close-fitting small plates. *U.Jur.(Oxford.),* Ger.——FIG. 52,*2*. **S. punctatus* (QUENSTEDT); *2a,b,* upper and lower views of fragment, ×1 (123).

Podosphaeraster A. M. CLARK, 1962 [**P. polyplax*; OD]. Spherical, with no ambital margin or distinct marginals, ambulacra reaching equator; more abactinal plates than in *Sphaeraster,* covered with thin skin containing granules. *Rec.*——FIG. 52,*3*. **P. polyplax*; dorsolateral view, ×2.5 (102).

Valettaster LAMBERT, 1914 [*pro Tholaster* SPENCER, 1913 (*non* SEUNES, 1896)] [**Oreaster ocellatus* FORBES; SD RASMUSSEN, 1950; ICZN Opin. 331] [=*?Asteriaceros* VALETTE, 1934]. Apparently like *Sphaeraster* in shape but aboral ossicles thick, irregular, generally low cones. *M.Jur.(Bathon.)-U.Cret.(Maastricht.),* Eu.——FIG. 52,*1*. **V. ocellatus* (FORBES), U.Cret.(Santon.), Eng.; *1a,* oral side, ×1; *1b,* ossicle, ×2 (131).

Suborder GRANULOSINA Perrier, 1894

[*nom. transl. et correct.* SPENCER & WRIGHT, herein (*ex* Granulosa PERRIER, 1894)]

Marginals conspicuous, invariably fewer than adambulacrals, in two series, opposite; aboral ossicles arranged in calycinal system in young, which generally cannot be distinguished in adults, ossicles generally covered with spines or granules in shallow sockets. Pedicellariae, if present, generally valvate and sunk in ossicles. *L.Jur.-Rec.*

Family ODONTASTERIDAE Verrill, 1889

[=Gnathasterinae PERRIER, 1894]

Pentagonal or broadly stellate, with odd interradial marginal in each series, more paxillose than most Goniasteridae; mouth-angle plates triangular, generally bearing recurved spines with glassy tips. *M.Jur.-Rec.*

Odontaster VERRILL, 1880 [**O. hispidus*; OD] [=*Gnathaster* SLADEN, 1889; *Gnathodon* VERRILL, 1899; *Peridontaster* KOEHLER, 1920; *Epidontaster* KOEHLER, 1921; *Gymnognathaster* DÖDERLEIN, 1928]. One spine common to each pair of mouth-angle plates. [A Jurassic species doubtfully belongs here.] *?M.Jur.(Bajoc.* or *Bathon.),* N.Z.; *Rec.*

Acodontaster VERRILL, 1899 [**Gnathaster elongatus*

SLADEN, 1889; OD] [=*Heuresaster* BELL, 1908; *Pseudodontaster* KOEHLER, 1912; *Tridontaster* KOEHLER, 1920; *Metadontaster* KOEHLER, 1921]. *Rec.*

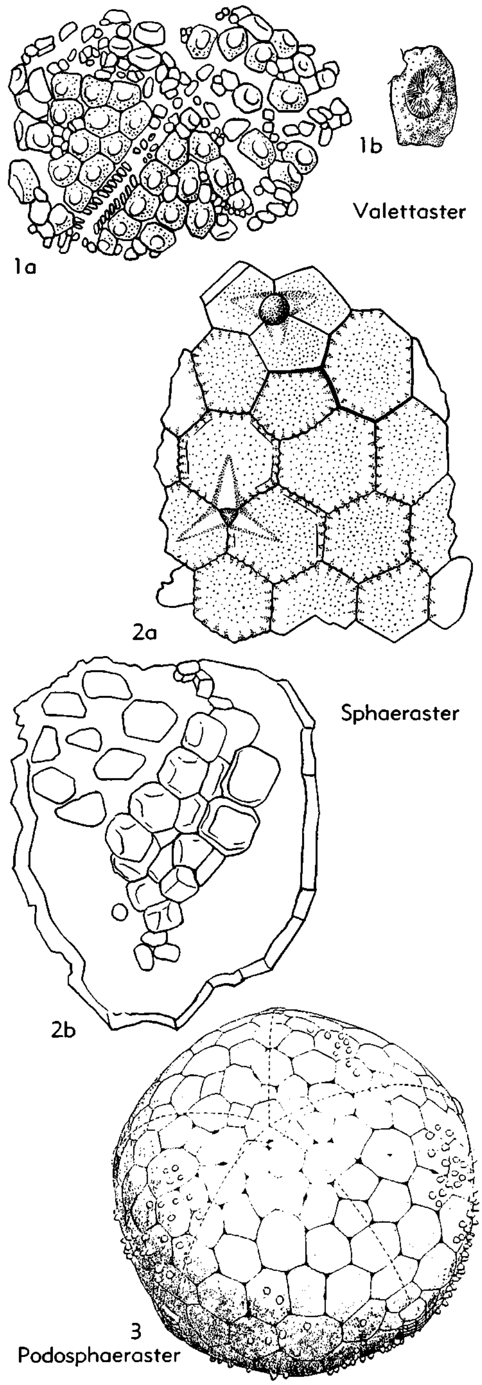


FIG. 52. Sphaerasteridae (p. U55).

Asterodon PERRIER, 1891 [**Goniodiscus singularis* MÜLLER & TROSCHEL, 1842; SD FELL, 1953] [=*Diplodontias* FISHER, 1908 (*pro Goniodon* PERRIER, 1894, *non* HERRICK, 1888)]. *Rec.*

Eurygonias FARQUAR, 1913 [**E. hylacanthus*; OD]. *Rec.*

Hoplaster PERRIER, 1882 [**H. spinosus*; OD]. *Rec.*

Family CHAETASTERIDAE Sladen, 1889

[*nom. transl.* LUDWIG, 1897 (*ex* Chaetasterinae SLADEN, 1889)]

Marginals small, with odd interradial marginal in each series; spinelets of paxillae slender and glassy; superambulacral plates present; calcareous interbrachial septa. Ampullae single. *Rec.*

The position of this family is altogether doubtful.

Chaetaster MÜLLER & TROSCHEL, 1840 [**Asterias subulata* LAMARCK, 1816 (=**Asterias longipes* RETZIUS, 1805); OD]. *Rec.*

Family ARCHASTERIDAE Viguier, 1878

Superficially like Astropectinidae but tube feet with sucking discs; aboral ossicles tabulate and paxilliform, with internal imbricating ridges, arranged in oblique transverse rows on either side of conspicuous radial series. *?Mio.,Rec.*

Archaster MÜLLER & TROSCHEL, 1840 [**A. typicus*; OD]. Characters of family. Interradial arcs pointed. *?Mio.*, S.Afr., *Rec.*

Family GONIASTERIDAE Forbes, 1841

Pentagonal to narrowly stellate forms generally with large disc; marginals prominent, opposite, normally with no odd interradial marginal; plates on both oral and aboral surfaces in close contact; aboral plates flat, tabulate or paxilliform, with or without spines or granules but in several genera they may be tumid. Pedicellariae most commonly alveolate or valvate. *L.Jur.-Rec.*

Many Mesozoic genera belong here, but their phylogeny and therefore detailed taxonomy are determined only for a few groups. Few Cenozoic forms are known and it is therefore difficult to link the Mesozoic with abundant Recent genera. Hence, organization into subfamilies can only be provisional; certain groups of genera are distinct but there remain a large number of genera that must still be assigned to Goniasteridae, *incertae sedis,* but which probably ought to be grouped into several subfamilies.

Subfamily GONIASTERINAE Forbes, 1841

Shape varying from pentagonal to rather long-armed but all genera agree in having rather few and large marginals, normally with slightly sunken edge ("rabbet edge" of SPENCER) and raised smooth or distantly granulate central area; aboral plates may be flat and smooth, granulate or papillate, or may be raised into round tubercles. There is a strong tendency to specialization of distal superomarginals which may represent up to 7 marginals fused into an enlarged ultimate superomarginal. The subfamily comprises a series of genera radiating or secondarily derived from the Cretaceous and Cenozoic *Metopaster*. *U.Cret.-Rec.*

Goniaster AGASSIZ, 1835 [**Asterias tesselatus* LAMARCK, 1816; OD] [=*Phaneraster* PERRIER, 1894]. Prominent rounded or bluntly pointed tubercles on aboral plates, particularly on primary circlet and carinals; enlarged ultimate superomarginals. *Rec.*

Ceramaster VERRILL, 1899 [**Asterias granularis* RETZIUS, 1783; OD] [=?*Petalastrum* DE GREGORIO, 1895; *Philonaster* KOEHLER, 1909]. Like *Metopaster* in shape and marginal ornament but with no enlarged ultimate superomarginals and many more marginals (up to 18 in half arc) and with tabulate (not flat) aboral ossicles; arms not upturned strongly as in *Recurvaster*. *?U. Cret.(Maastricht.)*, Eu., *Rec.*——FIG. 53,*1*. *C.? dividuus* (RASMUSSEN), Maastricht., Denm.; *1a,b*, side and aboral views, ×1 (125).

Metopaster SLADEN, 1893 [**Goniaster (Goniodiscus) parkinsoni* FORBES, 1848; SD RASMUSSEN, 1950 (ICZN Opin. 331)] [=*Mitraster* SLADEN, 1893; *Ravniaster* BRÜNNICH-NIELSEN, 1943; ?*Dictydaster* MERCIER, 1935]. Pentagonal, with sharp-pointed arms; rarely with arms slightly produced; marginals very large and few (2 to 5 superomarginals in half arc); enlarged ultimate superomarginals corresponding to 2 to 7 inferomarginals; central area of marginals with fine pits for granules or smooth, surrounded by distinct narrow area with several rows of setae. *U. Cret.(Cenoman.)-Mio.*, Eu.-N.Am.-N.Z. —— FIG. 53,*3*. **M. parkinsoni* (FORBES), Santon., Eng.; *3a,b*, aboral and lat. views, ×1 (131); *3c*, profile of superomarginals and inferomarginals, ×2 (133). (See also Fig. 27.)

Recurvaster BRÜNNICH-NIELSEN, 1943 [**R. stevensensis* (=**Metopaster tumidus radiatus* SPENCER, 1913); OD]. Differs from *Metopaster* in having no enlarged ultimate superomarginals, more marginals, and arms produced and upturned, making distal marginals skew. *U.Cret.(Campan.)-Eoc.*, NW.Eu.——FIG. 53,*2*. **R. radiatus* (SPENCER), Campan., Denm.; *2a,b*, aboral and lat. views of arm, ×1; *2c*, profile of superomarginal and inferomarginal, ×1 (125).

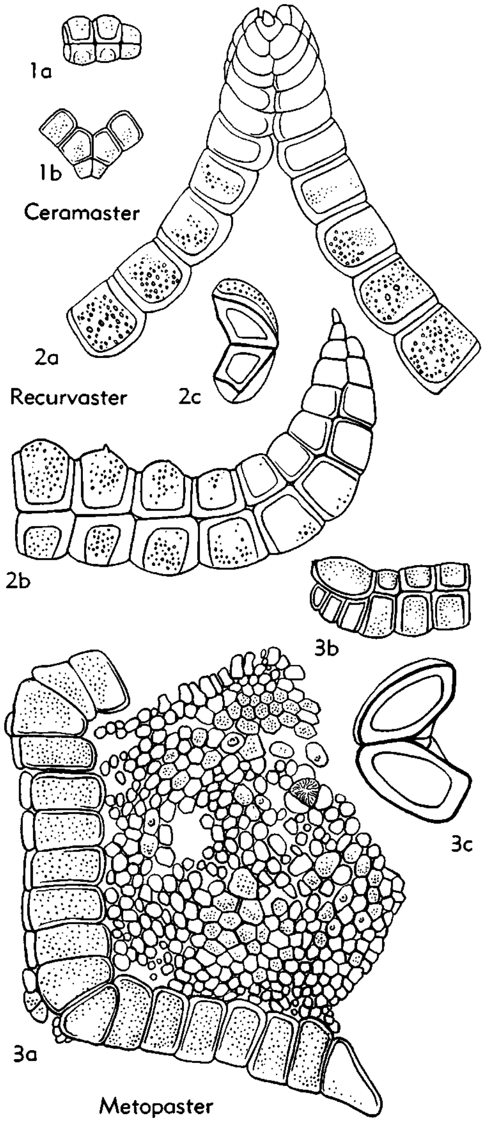


FIG. 53. Goniasteridae (Goniasterinae) (p. *U57*).

Spenceria FOURTEAU, 1914 [**Metopaster teilhardi* DE LORIOL, 1908; OD]. Ultimate inferomarginals seemingly enlarged like superomarginals. [Probably a young *Metopaster*.] *U.Cret.(Santon.)*, Eng.

Sphaeriodiscus FISHER, 1910 [**Stephanaster bourgueti* PERRIER, 1894]. Only differs from *Metopaster* in that last few superomarginals are not united in single ossicle, penultimate superomarginals normally larger than median ones. *U.Cret. (Campan.)*, Eng., *Rec.*

Cladaster VERRILL, 1899 [**C. rudis*; OD]. *Rec.*

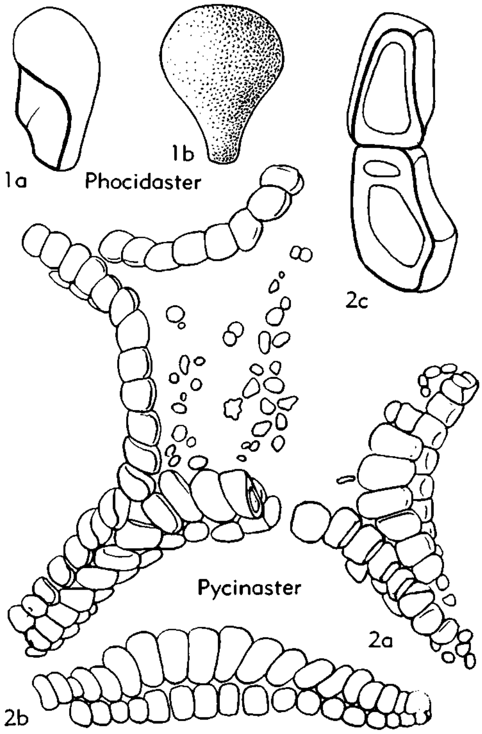


FIG. 54. Goniasteridae (Pycinasterinae) (p. U59).

Iconaster SLADEN, 1889 [**Astrogonium longimanum* MÖBIUS, 1859; OD]. *Rec.*

I. (Iconaster). *Rec.*

I. (Glyphodiscus) FISHER, 1917 [**Iconaster periectus* FISHER, 1913; OD]. *Rec.*

Pentagonaster GRAY, 1840 [**P. pulchellus*; OD] [=*Astrogonium* MÜLLER & TROSCHEL, 1842; *Stephanaster* AYRES, 1851]. Pentagonal or with moderately long arms, which have broad rounded ends; marginals with smooth central area; distalmost or one proximal to it in upper and lower series may be enlarged; inferomarginals corresponding with superomarginals except at extreme tip of arm. [There is very little difference between *Pentagonaster, Tosia,* and *Metopaster.*] *Rec.*

Pergamaster KOEHLER, 1920 [**P. tessellatus* (=?*Pentagonaster incertus* BELL, 1908)]. *Rec.*

Plinthaster VERRILL, 1899 [**Pentagonaster perrieri* SLADEN, 1889; OD] [=*Pyrenaster* VERRILL, 1889]. *Rec.*

Pontioceramus FISHER, 1911 [**P. grandis*; OD]. *Rec.*

Tesselaster H. L. CLARK, 1941 [**T. notabilis*; OD]. *Rec.*

Toraster A. M. CLARK, 1952 [**Astrogonium tuberculatum* GRAY, 1847]. *Rec.*

Tosia GRAY, 1840 [**T. australis*; OD]. *Rec.*

Tosiaster VERRILL, 1914 [**Tosia arcticus* VERRILL, 1909; OD]. *Rec.*

Subfamily CHITONASTERINAE Fisher, 1911

Disc small, arms moderately long, straight-sided, covered by membrane; aboral ossicles each with stout spine, like those present in vertical series on marginals; 3 similar spines on each adambulacral. *Rec.*

Chitonaster SLADEN, 1889 [**C. cataphractus*; OD] [=*Chitonaster* SLADEN, 1885 *(nom. nud.)*]. *Rec.*

Subfamily ANTHENOIDINAE Fisher, 1919

[=Leptogonasterinae PERRIER, 18--]

Body enclosed by thin membrane, generally covering or covered by granules; plates of aboral surface tending to be stellate; secondary aboral plates generally present. *Rec.*

Anthenoides PERRIER, 1881 [**A. peircei*; OD] [=*Leptogonaster* SLADEN, 1889; *Antheniaster* VERRILL, 1899]. *Rec.*

Atelorias FISHER, 1911 [**A. anacanthus*; OD]. *Rec.*

Ogmaster VON MARTENS, 1865 [**Goniodiscus capella* MÜLLER & TROSCHEL, 1842; OD] [=*Dorigona* GRAY, 1866]. *Rec.*

Siraster H. L. CLARK, 1915 [**S. tuberculatus*; OD]. *Rec.*

Stellaster GRAY, 1840 [**S. childreni* (=**Asterias equestris* RETZIUS, 1805)]. *Rec.*

Subfamily HIPPASTERIINAE Verrill, 1899

Aboral surface covered by well-spaced larger ossicles packed with intercalated smaller ones, in internal view forming coarse network; marginals with conical tubercles or stout spines. *U.Cret.-Rec.*

Hippasteria GRAY, 1840 [**H. europaea* (=**Asterias phrygiana* PARELIUS, 1768); OD (other included species is synonym)]. Disc large, arms short; marginals bare except for few large tubercle-like spines and granules around edge; larger aboral ossicles tumid and smooth except for marginal granules. *U.Cret.*, N.Z., *Rec.*

H. (Hippasteria) [=*Euhippasteria* DONS, 1938]. *U.Cret.*, N.Z., *Rec.*

H. (Nehippasteria) DONS, 1938 [**H. (N.) insignis*; OD]. *Rec.*

Cryptopeltaster FISHER, 1904 [**C. lepidonotus*; OD]. *Rec.*

Evoplosoma FISHER, 1906 [**E. forcipifera*; OD]. *Rec.*

Subfamily NECTRIINAE Perrier, 1894

Superambulacral plates present; with intermarginal as well as aboral papulae. *Rec.*

Nectria GRAY, 1840 [**Asterias ocellifera* LAMARCK, 1816; OD]. *Rec.*

Nectriaster H. L. CLARK, 1946 [**Mediaster monacanthus* H. L. CLARK, 1916; OD]. *Rec.*

Subfamily PSEUDARCHASTERINAE Sladen, 1889

Abactinal plates paxilliform or tabulate; superambulacra present, at least in rudimentary form. Pedicellariae, if present, spiniform, fasciolar, or incipiently bivalved. *U.Jur.-Rec.*

Pseudarchaster SLADEN, 1889 [**P. discus*; SD FISHER, 1911] [=*Pseudarchaster* SLADEN, 1885 *(nom. nud.)*]. Aboral plates paxilliform, in radial rows of which several extend along arm; marginals thick, with fasciolated grooves between; oral intermediate plates in transverse and longitudinal series; mouth-angle plates large and prominent. *U.Eoc.-L.Mio.*, N.Z., *Rec.*

Aphroditaster SLADEN, 1889 [**A. gracilis*; OD] [=*Aphroditaster* SLADEN, 1885 *(nom. nud.)*]. Doubtfully distinct from *Pseudarchaster. Rec.*

Paragonaster SLADEN, 1889 [**P. ctenipes*; SD FISHER, 1919]. Single series of flat granulose plates extending along aboral surface of arm between superomarginals. *U.Jur.-Mio.*, N.Z., *Rec.*

Perissogonaster FISHER, 1913 [**P. insignis*; OD]. Only differs from *Paragonaster* in having odd interradial marginal in each series. *Rec.*

Subfamily PYCINASTERINAE Spencer & Wright, n. subfamily

Very robust forms with rather small disc and long arms; superomarginals high, swollen, with rounded profile, and with large hollows for intermarginal muscles; spines almost absent; marginals and aboral ossicles may have feeble rugosities. Alveolar pedicellariae. *L.Jur.-Mio.*

This group seems to have no close relationship with any other Mesozoic Goniasteridae.

Pycinaster SPENCER, 1907 [*pro Pycnaster* SLADEN, 1891 (*non* POMEL, 1883)] [**Goniaster (Goniodiscus) angustatus* FORBES, 1848; OD]. Characters of subfamily. *L.Jur.-Mio.*, W.Eu.——FIG. 54,*2*. **P. angustatus* (FORBES), U.Cret.(Santon.), Eng. (Kent); *2a,b,* aboral and lat. views, ×1; 2c, profile of superomarginal and inferomarginal, ×2 (131).

?**Phocidaster** SPENCER, 1913 [**P. grandis*; OD]. Known only from large interradial superomarginals, which are high, short, club-shaped, with swollen aboral end; surface consisting of fine shallow spine pits separated by rugosities. *Cret. (U.Alb.-Cenoman.),* Eng.——FIG. 54,*1*. **P grandis,* U.Alb., Devon; *1a,b,* profile and lat. views of superomarginal, ×2 (139).

Subfamily UNCERTAIN

Without thorough revision of the family the remaining fossil and Recent members cannot be satisfactorily placed in subfamilies. Some of the following genera might perhaps be placed in Goniasterinae, but most of them should obviously be assigned to one of several unnamed subfamilies. The subfamilial name Mediasterinae VERRILL, 1914, is available for one group. In the following account genera known as fossils are listed first in alphabetical order, then those known only as living forms.

Calliaster GRAY, 1840 [**C. childreni*; OD]. Arms rather long; marginals large, with large bosses that carry short stout spines; radial lines of stout spines on aboral surface and still larger spines on ossicles of primary circlet. *U.Eoc.-U.Oligo.*, N.Z., *Rec.*

Calliderma GRAY, 1847 [**C. emma*; OD] [=*Tomidaster* SLADEN, 1891]. Disc large, with short arms passing evenly into wide interradial arcs; marginals short, wide, relatively larger than in *Comptonia* and wider than in *Tylasteria,* with fine hexagonal spine pits and, irregularly, large shallow depressions; tessellate close-fitting oral and aboral plates. Valvate pedicellariae may be abundant. *U.Cret.(Cenoman.)-Oligo.*, Eu., *Rec.* ——FIG. 55,*6*. *C. smithiae* (FORBES); *6a,b,* oral and aboral sides, ×1 (Cenoman., Eng., Sussex) (131); *6c,* profile of superomarginal and inferomarginal, ×2 (Turon., Eng., Devon) (133).

Cenomanaster WRIGHT, 1951 [*pro Jacobella* MERCIER, 1935 (*non* JEANNET, 1908)] [**Jacobella cenomanensis* MERCIER, 1935; OD]. Disc rather large; arms narrow at base, long, straight-sided, tapering very gradually, with superomarginals not in contact; marginals short, wide, with granules; single large tubercle on aboral side of superomarginals; aboral ossicles granulose, irregularly rounded; some with conical tubercle. *U.Cret. (Cenoman.),* Fr.——FIG. 56,*4*. **C. cenomanensis* (MERCIER), Sarthe; aboral side, ×1 (121).

Chomataster SPENCER, 1913 [**C. acules*; OD] [=?*Huraeaster* VALETTE, 1915]. Long slender arms sharply demarcated from disc; interradial margins generally straight, with wedge-shaped superomarginal at junction with arm; marginals tall, those of arm and interray differing in profile, generally with fine close spine pits. *U.Cret. (Santon.-Maastricht.),* NW.Eu.——FIG. 55,*3*. *C.* sp., Campan., Eng.(Norfolk); aboral side, ×1 (139).

Comptonia GRAY, 1840 [**C. elegans*; OD]. Arms long, slender, distinct from slightly curved or straight interradial arcs; marginals square and rather small on arms, short and wide in interrays, with fine, close spine pits. Large valvate pedicellariae common. *L.Cret.(Apt.-U.Alb.), ?U.Cret. (Santon.),* Eng.-?Egypt-?Can.——FIG. 55,*5*. *C. comptoni* (FORBES), U.Alb., Eng.; *5a,b,* aboral and lat. views, ×1 (131).

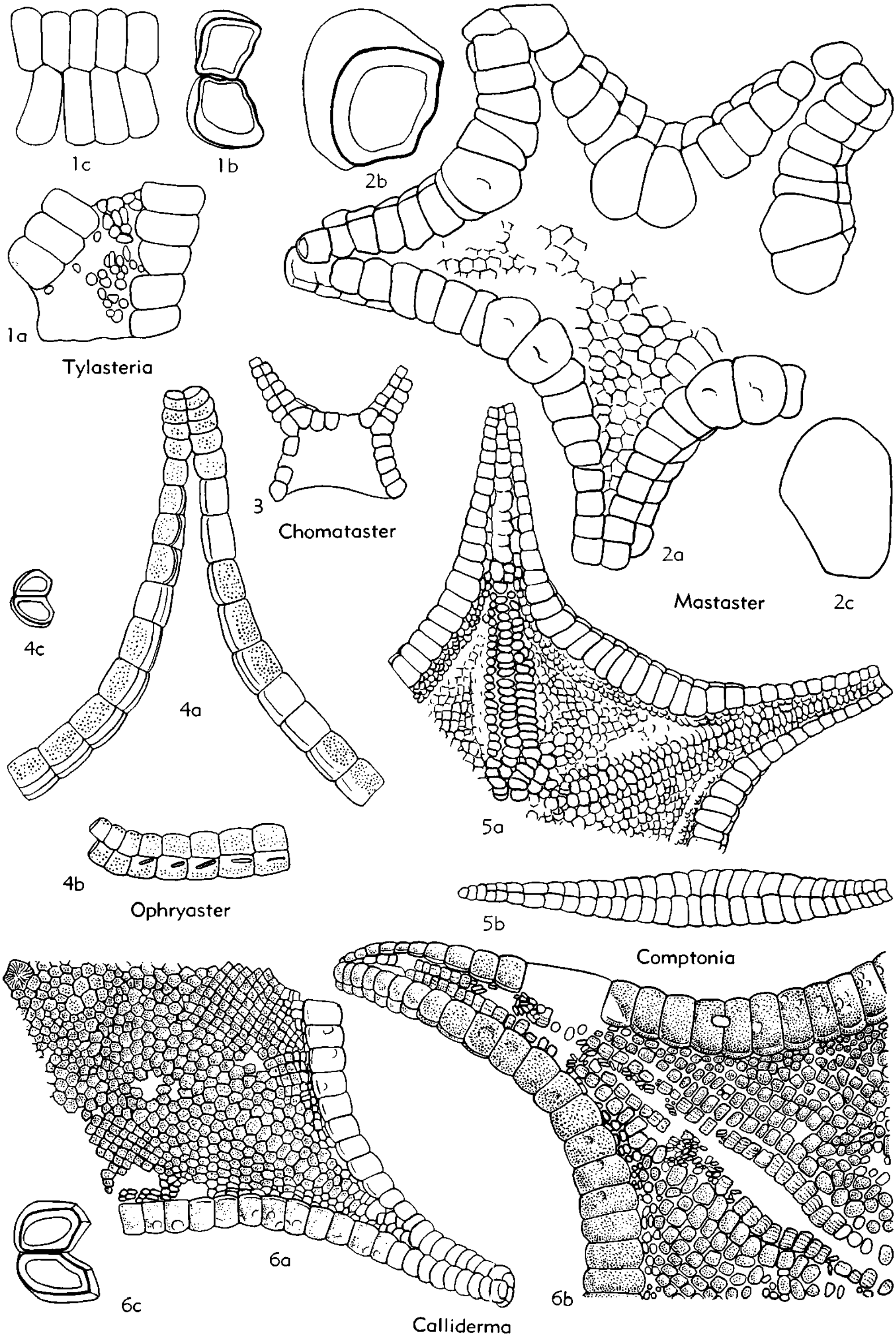


FIG. 55. Goniasteridae (subfamily uncertain) (p. U59, U62-U63).

Cottreauaster Wright, 1951 [*pro Spenceraster* Cottreau, 1929 (*non* Lambert, 1913)] [**Spencer-aster lamarei* Cottreau, 1929; OD]. Disc small, arms long, narrow, straight-sided, flexible; marginals small, tumid with fine granules; superomarginals with tubercles or spines, aboral plates irregular. *M.Jur.(Bathon.)*, Fr.——Fig. 56,*3*. **C. lamarei* (Cottreau), Orne; aboral side, ×2 (105).

Crateraster Spencer, 1913 [**Asterias quinqueloba* Goldfuss, 1822; OD, ICZN Opin. 331] [=*Austinaster* Adkins, 1928]. Pentagonal to stellate, with arms slightly produced; marginals large, rather few (4 to 7 in half arc), more or less op-

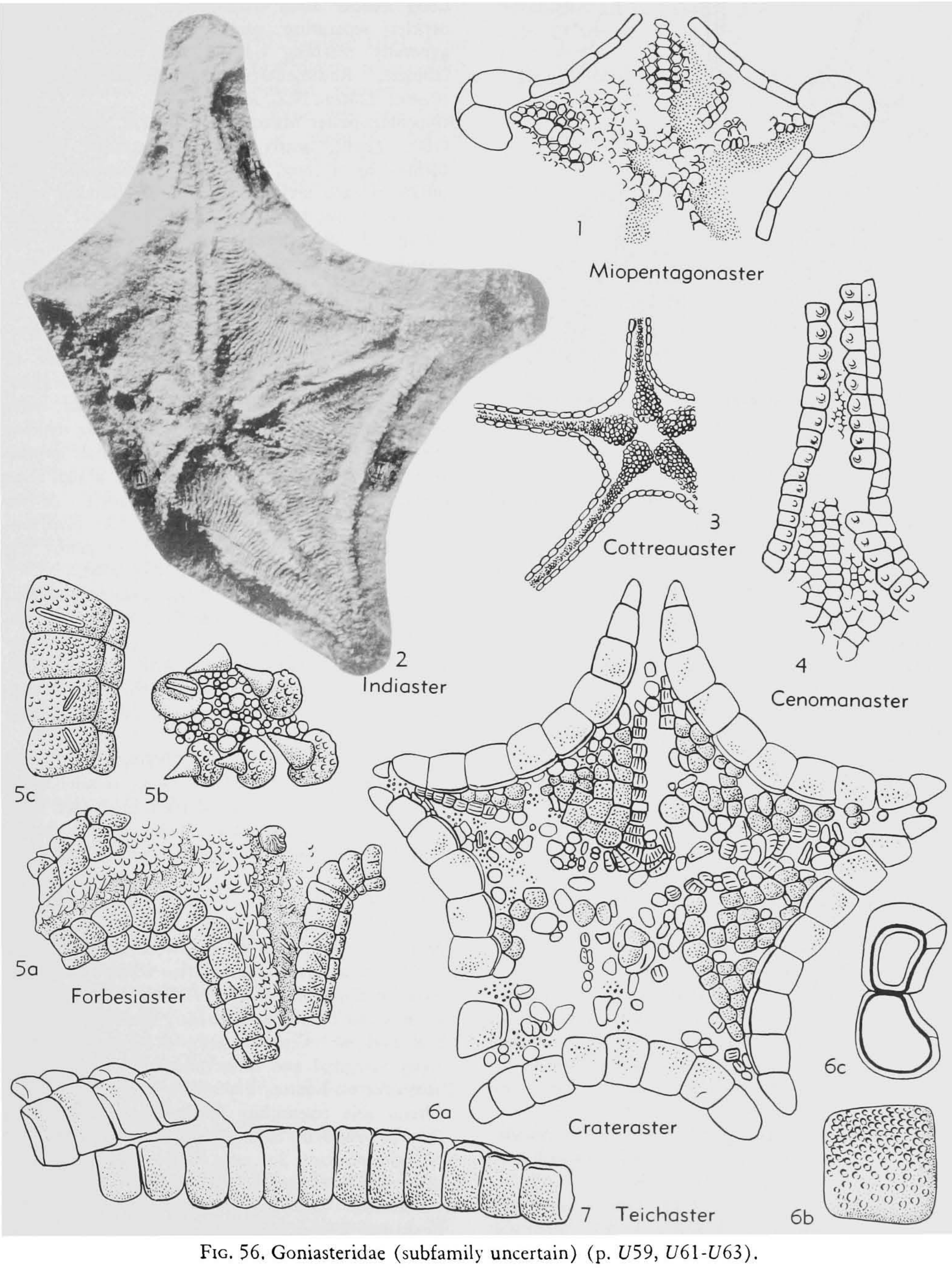


Fig. 56. Goniasteridae (subfamily uncertain) (p. *U*59, *U*61-*U*63).

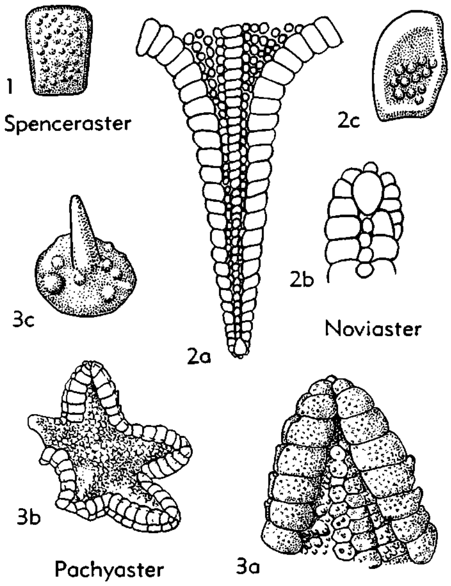


FIG. 57. Goniasteridae (subfamily uncertain) (p. U62-U63).

posite, last few superomarginals in contact on mid-line of arm; marginals with distinct lateral and oral or aboral faces, lateral faces at least with shallow crater-like pits; profile of marginals like that of some Jur. *Tylasteria;* oral and aboral ossicles large, tessellate. *Cret.(U.Alb.-Campan.),* Eu.-N.Am.——FIG. 56,*6*. **C. quinqueloba* (GOLDFUSS), Santon., Eng.(Kent); *6a,* oral side, ×1 (131); *6b,* lat. face of marginal, ×2 (131); *6c,* profile of superomarginal and inferomarginal, ×2 (133).

Forbesiaster DE LORIOL, 1909 [**F. wrighti*; OD]. Arms wide at base, rounded at tip; no distinct interradial arc; marginals twice as wide as long, with widely spaced pits for granules and short spines around edges; aboral ossicles irregular, rounded or tumid, largest with granules and round conical spines. Large bivalved pedicellariae on most superomarginals. *U.Cret.(Santon.),* Egypt. ——FIG. 56,*5*. **F. wrighti*; *5a,* aboral side, ×1; *5b,* part of aboral surface, ×4; *5c,* superomarginals, ×2 (117).

Indiaster RAO, 1957 [**I. krishna*; OD]. Small, very short marginals; interradial areas on oral surface with rows of rod-shaped ossicles that simulate metapinnules. *M.Jur.(U.Bathon.),* India(Cutch). ——FIG. 56,2. **I. krishma*; oral surface, ×6 (Rao).

Leptogonium POMEL, 1887 [**L. mauritanicum*; OD]. Figure only; not recognizable beyond family. *Plio.(Sahelian),* N.Afr.(Alg.).

Mastaster MERCIER, 1935 [**M. villersensis*; OD]. Like *Tylasteria* but with fewer, bulkier marginals and 2 very large highly swollen superomarginals in center of each interray. *U.Cret.(Cenoman.-Turon.),* Eng.-Fr.——FIG. 55,*2*. **M. villersensis*; *2a,* aboral side, ×1 (Cenoman., Fr.); *2b,c,* profile and lat. views of interradial superomarginal, ×2 (Cenoman., Eng.) (139).

Mediaster STIMPSON, 1857 [**M. aequalis*; OD] [=*Isaster* VERRILL, 1894 (*non* DESOR, 1858)]. Long slender arms with several series of aboral ossicles separating superomarginals, one series generally reaching tip of arm; aboral ossicles tabulate. Rudimentary superambulacral ossicles present. *L.Mio.,* N.Z., *Rec.*

Miopentagonaster MERCIER, 1935 [**M. calloviensis*; OD]. Small, nearly straight interradial margin formed by 4 long, narrow, low granulose marginals in each series; distally much smaller marginal is followed by large terminal; aboral ossicles hexagonal, granulose, with marked spaces for papulae; carinals slightly raised and larger than other ossicles. *U.Jur.(Callov.),* Fr.——FIG. 56,*1*. **M. calloviensis,* Calvados, aboral side, ×2 (121).

Noviaster VALETTE, 1929 [**N. lissajousi*; OD]. Arms long, straight-sided, moderately wide at base, tips blunt; interradial arcs rounded; superomarginals regular, distinctly skew, tumid, with large tubercles on faces between adjoining ossicles, surface with fine hexagonal pits; carinals prominent, 3 rows, reduced to 1 distally, along arms ending in large tumid oval ossicle. *M.Jur.(Bathon.),* Eng.-Fr.——FIG. 57,*2*. **N. lissajousi,* Fr.; *2a,* aboral side, ×1; *2b,* tip of arm, ×4; *2c,* profile of superomarginal, ×4 (136).

Nymphaster SLADEN, 1889 [**Nymphaster protentus* SLADEN, 1889 (=**Pentagonaster arenatus* PERRIER, 1881 (obj.); SD FISHER, 1917] [=*Nymphaster* SLADEN, 1885 *(nom. nud.)*]. Arms long, slender, sharply distinct from disc; superomarginals in contact for whole length of arms; aboral plates tessellate. *L.Mio.,* N.Z.-Cuba, *Rec.*

Ophryaster SPENCER, 1913 [**Nymphaster oligoplax* SLADEN, 1891; OD]. Long slender arms passing into evenly rounded interradial arcs, marginals large, long, narrow, blocky, slightly tumid, with close or distant hexagonal or circular spine pits, which are generally absent from edge of superomarginals next to aboral ossicles; superomarginals in contact along distal part only of arms; no space for papulae between aboral ossicles. Long low bivalved pedicellariae common. *U.Cret.(Turon.-Campan.)-Mio.,* NW.Eu.——FIG. 55,*4*. *O. magnus* SPENCER, Campan., Denm.; *4a,b,* aboral and lat. views of arm, ×1; *4c,* profile of superomarginal and inferomarginal, ×1 (125).

Pachyaster DE LORIOL, 1909 [**P. aegyptiacus*; OD]. Aboral side resembling *Forbesiaster,* of which it may be synonym, based on juvenile.——FIG. 57,*3*. **P. aegyptiacus*; *3a,* arm, ×3; *3b,* aboral side, ×1; *3c,* aboral ossicle, ×20 (117).

Spenceraster LAMBERT, 1913 [*pro Trachyaster* SPENCER, 1913 (*non* POMEL, 1883)] [**Nymphaster rugosus* SPENCER, 1907; SD SPENCER &

WRIGHT, herein]. Small, with short narrow arms and rounded interradial arcs; superomarginals in contact along mid-line of arms; marginals few, low, nearly as long as wide, with evenly curved profile, surface covered with rugosities but generally with narrow smooth band around edge. *Cret.(U.Alb.-Cenoman.),* Eng.——FIG. 57,*1*. **S. rugosus* (SPENCER), aboral side of superomarginal, ×4 (133).

Teichaster SPENCER, 1913 [**T. favosus*; OD]. Arms more produced than in *Crateraster,* from which it is derived; body high but flat; marginals with high vertical lateral face; spine pits large, shallow, close, hexagonal or circular. *U.Cret.(Campan.)-Mio.,* Eu.——FIG. 56,*7*. **T. favosus,* U.Cret.(Maastricht.), Eng.(Norfolk); lat. view of fragment, ×1 (139).

Tylasteria VALETTE, 1930 [*pro Tylaster* SPENCER, 1913 (*non* DANIELSSON & KOREN, 1881)] [**Asterias jurensis* GOLDFUSS, 1822; OD]. Robust, with large disc and tapering arms, moderately broad at base; interradial arc well rounded; marginals wider than long, slightly tumid, profile evenly curved or square or undercut, densely covered by generally hexagonal spine pits; aboral plates large, flat, with hexagonal pits. *M.Jur.(Bajoc.)-L.Cret.(Alb.),* Eu.——FIG. 55,*1*. **T. jurensis* (GOLDFUSS), U.Jur.(Oxford.), Ger.; *1a,c,* oral and lat. views; *1b,* profile of superomarginal and inferomarginal (123).

Amphiaster VERRILL, 1868 [**A. insignis*; OD]. *Rec.*

Astroceramus FISHER, 1906 [**A. callimorphus*; OD]. *Rec.*

Astrothauma FISHER, 1913 [**A. euphylacteum*; OD]. *Rec.*

Circeaster KOEHLER, 1909 [**Circeaster marcelli* KOEHLER, 1909; SD SPENCER & WRIGHT, herein].

Eugoniaster VERRILL, 1899 [**Pentagonaster investigatoris* ALCOCK, 1893; OD]. *Rec.*

Gigantaster DÖDERLEIN, 1924 [**G. weberi*; OD]. *Rec.*

Gilbertaster FISHER, 1906 (**G. anacanthus*; OD]. *Rec.*

Johannaster KOEHLER, 1909 [**J. superbus*; OD]. *Rec.*

Lithosoma FISHER, 1911 [**L. actinometra*; OD]. *Rec.*

Litonotaster VERRILL, 1889 [**Pentagonaster intermedius* PERRIER, 1884; OD]. *Rec.*

Lydiaster KOEHLER, 1909 [**L. johannae*; OD]. *Rec.*

Mahabissaster MACAN, 1938 [**M. zengi*; OD]. *Rec.*

Mariaster A. H. CLARK, 1916 [**Johannaster giganteus* GOTO, 1914; OD]. *Rec.*

Milteliphaster ALCOCK, 1893 [**M. woodmasoni*; OD]. *Rec.*

Notioceramus FISHER, 1940 [**N. anomalus*; OD]. *Rec.*

Peltaster VERRILL, 1899 [**P. hebes* =(**Goniaster nidarosiensis* STORM, 1881); OD]. *Rec.*

Progoniaster DÖDERLEIN, 1924 [**P. atavus*; OD]. *Rec.*

Pseudogoniodiscaster LIVINGSTONE, 1930 [**P. wardi*; OD]. *Rec.*

Rosaster PERRIER, 1894 [**Pentagonaster alexandri* PERRIER, 1881; OD] [=*Nereidaster* VERRILL, 1899]. *Rec.*

Sibogaster DÖDERLEIN, 1924 [**S. digitatus*; OD]. *Rec.*

Styphlaster H. L. CLARK, 1938 [**S. notabilis*; OD]. *Rec.*

Family OREASTERIDAE Fisher, 1911

[=Pentacerotidae GRAY, 1841; Antheneinae FISHER, 1911]

Disc large, generally high and swollen, even cushion-like in adult, with robust arms or none; younger stages generally resembling Goniasteridae; body normally covered with thick granulose membrane; marginals large; intermarginals may be present; abactinal skeleton reticulate, composed of stellate plates, in many forms bearing stout spines. Papulae numerous, in special areas; calcareous interbrachial septa. *Rec.*

Oreaster MÜLLER & TROSCHEL, 1842 [**Asterias reticulatus* LINNÉ, 1758; OD] [=*Pentaceros* (SCHULZE, 1760 (*non. binom.*)) GRAY, 1840 (*non* CUVIER & VALENCIENNES, 1829)]. *Rec.*

Anthaster DÖDERLEIN, 1915 [**Oreaster valvulatus* MÜLLER & TROSCHEL, 1843; OD]. *Rec.*

Anthenea GRAY [**A. chinensis* (=**Asterias pentagonula* LAMARCK, 1816); OD] [=*Hosia* GRAY, 1840; *Hosea* GRAY, 1866]. *Rec.*——FIG. 1,*1*. *A. flavescens* (GRAY), Rec.; *1a,b,* oral and aboral surfaces, ×1 (130).

Asterodiscus GRAY, 1847 [**A. elegans*; OD]. *Rec.*

Bothriaster DÖDERLEIN, 1916 [**B. primigenius*; OD]. *Rec.*

Choriaster LÜTKEN, 1869 [**C. granulatus*; OD]. *Rec.*

Culcita AGASSIZ, 1836 [**Asterias discoidea* LAMARCK, 1816 (=**Asterias schmideliana* RETZIUS, 1805); OD] [=*Randasia* GRAY, 1840; *Goniodiscus* MÜLLER & TROSCHEL, 1842; *Goniodiscoides* FISHER, 1906]. *Rec.*

Goniodiscaster H. L. CLARK, 1909 [**Asterias pleyadella* LAMARCK, 1816; OD]. *Rec.*

Gymnanthenea H. L. CLARK, 1938 [**Anthenea globigera* DÖDERLEIN, 1916; OD]. *Rec.*

Halityle FISHER, 1913 [**H. regularis*; OD] [=*Culcitaster* H. L. CLARK, 1915]. *Rec.*

Monachaster DÖDERLEIN, 1916 [**Goniodiscus sanderi* MEISSNER, 1892; OD]. *Rec.*

Nidorellia GRAY, 1840 [**Pentaceros (Nidorellia) armatus*; OD]. *Rec.*

Paulia GRAY, 1840 [**P. horrida*; OD] [=*Pauliella* LUDWIG, 1905]. *Rec.*

Pentaceraster DÖDERLEIN, 1916 [**Asterias mammillatus* AUDOUIN, 1827; OD]. *Rec.*

Pentaster DÖDERLEIN, 1935 [*pro Pentaceropsis* SLADEN, 1889 (*non* STEINDACHNER & DÖDERLEIN,

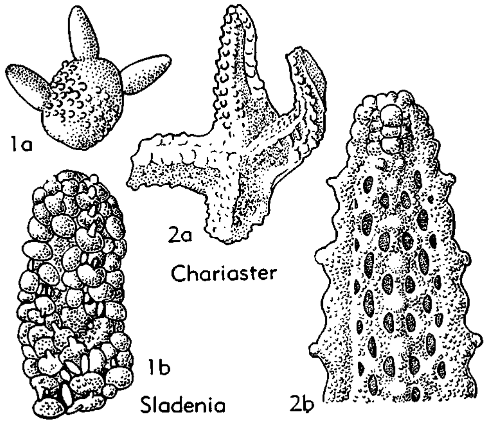


FIG. 58. Ophidiasteridae (p. *U64*).

1884)] [**Asterias obtusata* BORY DE SAINT VINCENT, 1827; OD]. *Rec.*

Poraster DÖDERLEIN, 1916 [**Oreaster productus* BELL, 1884 (=**Oreaster superbus* MOÖBIUS, 1859); OD]. *Rec.*

Protoreaster DÖDERLEIN, 1916 [**Asterias nodosa* LINNÉ, 1758; OD]. *Rec.*

Pseudanthenea DÖDERLEIN, 1916 [**Anthenea grayi* PERRIER, 1876; OD]. *Rec.*

Pseudoreaster VERRILL, 1899 [**Asterias obtusangulus* LAMARCK, 1816; OD]. *Rec.*

Stellasteropsis DOLLFUS, 1936 [**S. fouadi*; OD]. *Rec.*

Family OPHIDIASTERIDAE Verrill, 1867

[=Linckiidae PERRIER, 1875]

Disc small, arms long and slender, generally more or less cylindrical; body normally covered by granulose membrane; marginals small; aboral skeleton tessellate; small superambulacral plates generally present. Pedicellariae foraminate or excavate, or lacking. *U.Cret.-Rec.*

Ophidiaster AGASSIZ, 1835 [**Asterias ophidianus* LAMARCK, 1816; OD] [=?*Tamaria* GRAY, 1840; *Chione* GISTL, 1847]. *Rec.*

Austrofromia H. L. CLARK, 1921 [**Fromia polypora* H. L. CLARK, 1916; OD]. *Rec.*

Bunaster DÖDERLEIN, 1896 [**B. ritteri*; OD]. *Rec.*

Certonardoa H. L. CLARK, 1921 [**Scytaster semiregularis* MÜLLER & TROSCHEL, 1842; OD]. Like *Nardoa*, but oral surface of arms flat, not convex, and cross section of arms triangular at base; aboral ossicles in regular radial series on proximal part of arms. Papulae in groups, as in *Nardoa*, but none on oral surface. *Mio.*, Formosa, *Rec.*

Chariaster DE LORIOL, 1909 [**C. elegans*; OD]. Marginals in 2 prominent rows, with large mammillate tubercles generally on alternate ossicles; aboral surface flat but with median row of tubercles on distal part of arm formed by swollen intersections of long ossicles; adambulacrals with 2 rows of spines. *U.Cret.(Santon.)*, Egypt.——FIG. 58,*2*. **C. elegans*; *2a*, aboral side, ×1; *2b*, tip of arm, ×4 (117).

Cistina GRAY, 1840 [**C. columbiae*; OD]. *Rec.*

Copidaster A. H. CLARK, 1948 [**C. lymani*; OD]. *Rec.*

Dactylosaster GRAY, 1840 [**Asterias cylindrica* LAMARCK, 1816; SD H. L. CLARK, 1921]. *Rec.*

Dissogenes FISHER, 1913 [**D. styracia*; OD]. *Rec.*

Ferdina GRAY, 1840 [**F. flavescens* GRAY, 1840; SD FISHER, 1919]. *Rec.*

Fromia GRAY, 1840 [**Asterias milleporella* LAMARCK, 1816; OD]. *Rec.*

Gomophia GRAY, 1840 [**G. egyptiaca*; OD]. *Rec.*

Hacelia GRAY, 1840 [**Ophidiaster (Hacelia) attenuatus*; OD]. *Rec.*

Leiaster PETERS, 1852 [**L. coriaceus*; SD FISHER, 1919] [=*Lepidaster* VERRILL, 1871 (*non* FORBES, 1850)]. *Rec.*

Linckia NARDO, 1834 [**L. typus* (=**Asterias laevigatus* LINNÉ, 1758); OD] [=*Cribella* AGASSIZ, 1835 (*non* FORBES, 1841); *Acalia* GRAY, 1840; *Catantes*, *Undina* GISTL, 1847]. Arms cylindrical; aboral ossicles not in regular longitudinal series; adambulacrals with 2 or 3 rows of granules. No pedicellariae. *U.Cret.*, Eng., *Rec.*

Nardoa GRAY, 1840 [**Asterias variolata* RETZIUS, 1805; SD H. L. CLARK, 1921] [=*Melia* GISTL, 1847]. *Rec.*

Narcissia GRAY, 1840 [**N. teneriffae* (=**Asterias canariensis* D'ORBIGNY, 1839); OD]. *Rec.*

Neoferdina LIVINGSTONE, 1931 [**Ferdina cumingi* GRAY, 1840; OD]. *Rec.*

Pharia GRAY, 1840 [**Ophidiaster (Pharia) pyramidatus*; OD]. *Rec.*

Phataria GRAY, 1840 [**Linckia (Phataria) unifascialis*; OD]. *Rec.*

Plenardoa H. L. CLARK, 1921 [**Linckia semiseriata* MARTENS, 1865; OD]. *Rec.*

Pseudophidiaster H. L. CLARK, 1916 [**P. rhysus*; OD] [=*Pseudolinckia* H. L. CLARK, 1916, *lapsus*]. *Rec.*

Sladenia DE LORIOL, 1909 [**Nardoa? fourteaui* DE LORIOL, 1904; OD]. Arms broadly flattened, rounded at tip; marginals rather large, mostly bearing short, stout spines; aboral ossicles oval, tumid, spinose; adambulacrals with ?2 rows of spines. *U.Cret.(Santon.)*, Egypt.——FIG. 58,*1*. **S. fourteaui* (DE LORIOL); *1a*, aboral ossicle, enl.; *1b*, aboral side of arm, ×1 (Loriol).

Family RADIASTERIDAE Fisher, 1916

[=Mimasterinae SLADEN, 1889]

Marginals small and subpaxilliform; membranous interbrachial septa and superambulacral plates present; aboral plates consisting of penicillate paxillae; oral intermediate plates imbricated in transverse series. *Rec.*

Radiaster PERRIER, 1881 [**R. elegans*] [=*Mimaster* SLADEN, 1882]. *Rec.*

Gephyriaster FISHER, 1910 [**Mimaster swifti* FISHER, 1905]. *Rec.*

Order SPINULOSIDA Perrier, 1884

[*nom. correct.* SPENCER & WRIGHT, herein (*pro* Spinulosa PERRIER, 1884)] [=Velata PERRIER, 1894]

Mouth frame adambulacral; mouth-angle plates prominent, not keeled; marginal frame only rarely present except in juveniles; mouth-angle plates placed on prominent axillary if marginals are present. Pedicellariae, if present, generally consisting of grouped spines. Aboral skeleton reticulate, imbricate or absent, in many forms consisting of regular rows of paxillae, but in early family Taeniactinidae consisting of 3 rows of rather large plates in each radius. *M.Ord.-Rec.*

Since so few fossil forms are yet known, classification of this order must be provisional.

Suborder EUGNATHINA Spencer & Wright, new suborder

Mouth-angle plates large, spade- or plowshare-shaped, with conspicuous marginal and suboral spines; ambulacral furrows wide; adambulacral spines pectinate. *M. Ord.-Rec.*

Family TAENIACTINIDAE Spencer, 1927

[=Calyptactininae SPENCER, 1930]

Aboral surface of arms with 3 rows of prominent ossicles in each radius. *U.Ord.-Miss.*

Taeniactis SPENCER, 1927 [**T. wenlocki*; OD]. Oral interrays with few scattered ossicles; aboral skeleton confined to disc and bases of arms. *L.Sil.*, Scot.——FIG. 59,*3*. **T. wenlocki*; *3a*, individual with arms flexed upward, ×3; *3b,c*, oral and aboral surfaces, ×7.5 (133).

Baliactis SPENCER, 1922 [**B. ordovicus*; OD] [=*Leioactis, ?Palaeactis* LEHMANN, 1957]. Oral interrays bearing large broad axillary. *U.Ord.-Dev.*, Eng.-Ger.——FIG. 59,*2a,b*. *B. devonicus* SPENCER, L.Dev., Ger.; oral side of proximal part of arm, ×1 (133).

Calyptactis SPENCER, 1930 [**C. spinosus*; OD]. Aboral skeleton of closely fitting ossicles; arms apparently normally enrolled in life. *L.Carb. (Miss.)*, Eng.-N.Am.——FIG. 59,*4*. *C. demissus* (MILLER), Miss., USA; aboral side of enrolled specimen, ×1 (133).

Lepidasterella SCHUCHERT, 1914 [**L. babcocki* (=**Helianthaster gyalum* CLARKE, 1908); OD]. Arms 24 or more, with 3 rows of carinal and superomarginal ossicles on aboral surface. *U.Dev.*, N.Am.——FIG. 59,*5*. **L. gyalum* (CLARKE), USA (N.Y.); aboral side, ×1 (129).

Family LEPYRIACTINIDAE Spencer & Wright, new family

Aboral skeleton reduced, none preserved in fossils; adambulacrals very narrow, mouth-angle plates much elongated. *L.Sil.*

Lepyriactis SPENCER, 1927 [**L. nudus*; OD]. Arms 5. *L.Sil.*, Scot.——FIG. 59,*6*. **L. nudus; 6a,b*, oral and aboral views of proximal part of arm, ×3; *6c*, aboral view of 2 neighboring mouth-angle plates showing grooves for water vascular ring and neural ring, ×3 (133).

Family SCHUCHERTIIDAE Schuchert, 1915

Aboral skeleton not differentiated and all ossicles alike; inferomarginals present, with large axillaries abutting mouth-angle plates. *M.Ord.-Sil.*

Schuchertia GREGORY, 1899 [**Palasterina stellata* BILLINGS, 1858] [=*Trentonaster* STÜRTZ, 1900]. Characters of family. *M.Ord.-Sil.*, N.Am.-Scot.-Australia.——FIG. 59,*1*. *S. wenlocki* SPENCER, Sil., Scot.; oral view of arm, ×3 (133).

Family HELIANTHASTERIDAE Gregory, 1899

[*nom. transl.* SPENCER & WRIGHT, herein (ex Helianthasterinae GREGORY, 1899)] [=Palaechinasteridae STÜRTZ, 1890 (invalid because not based on included genus)]

Adambulacrals narrow, with single large spine or several at outer edge; aboral surface reticulate or granular. *Dev.*

Helianthaster ROEMER, 1863 [**H. rhenanus*; OD]. Arms 14 to 16, rather rigid; disc moderately large; aboral surface granular. *L.Dev.*, Ger.——FIG. 59,*7*. **H. rhenanus*; oral surface of arm, ×1 (133).

Echinasterella STÜRTZ, 1890 [**E. sladeni*; OD]. Arms 5, rather long and slender; adambulacrals with single spine; aboral surface reticulate, with small spines. *L.Dev.-U.Dev.*, Ger.——FIG. 60,*2*. **E. sladeni*, L.Dev.; X-ray view, ×0.5 (116).

Hystrigaster LEHMANN, 1957 [**H. horridus*; OD]. Arms 5, rather short, broad at base; long spines on aboral surface and in 2's or 3's on outer edge of adambulacrals. *L.Dev.*, Ger.——FIG. 60,*1*. **H. horridus*; X-ray view, ×0.5 (116).

Family SOLASTERIDAE Perrier, 1884

Disc rather large, arms long, 5 to many; aboral skeleton normally open and irregularly reticulate, rarely with large imbricating paxillate plates; oral intermediate plates present; single or double row of marginal paxillae. *L.Jur.-Rec.*

Solaster Forbes, 1839 [**Asterias endeca* Linné,

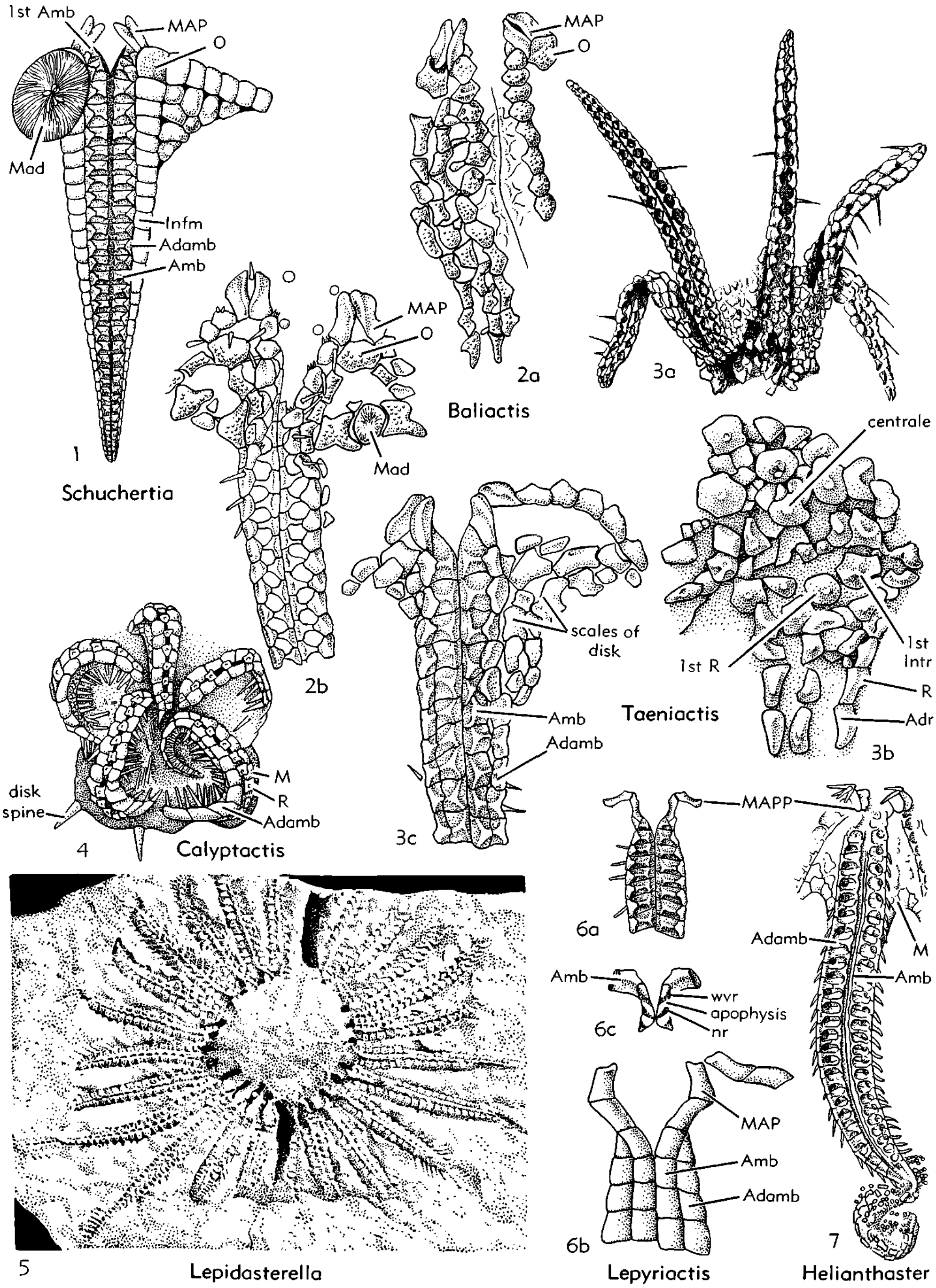


Fig. 59. Taeniactinidae *(2-5)*; Lepyriactinidae *(6)*; Schuchertiidae *(1)*; Helianthasteridae *(7)*. [Explanation: *Adamb*, adambulacral; *Adr*, adradial; *Amb*, ambulacral; *Infm*, inferomarginal; *Intr*, interradial; *M*, marginal; *Mad*, madreporite; *MAP*, mouth-angle plate; *nr*, nerve-ring groove; *O*, odontophore; *R*, radial; *wvr*, water-vessel-ring groove.] (p. *U65*).

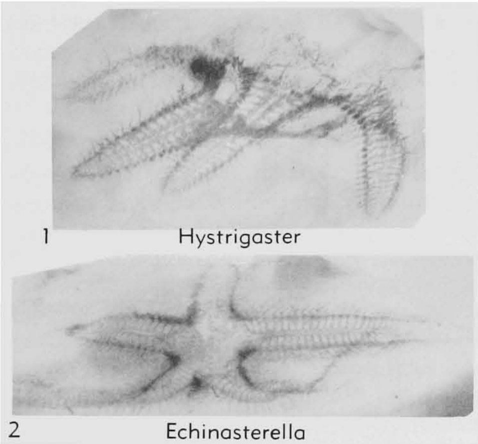


FIG. 60. Helianthasteridae (p. *U65*).

1771; OD] [=*Endeca, Polyaster* GRAY, 1840]. Arms 7 to 17 in Recent species; series of large marginal paxillae, with or without second smaller series. [Jurassic specimens rare, one with abnormally small disc and 33 arms.] *L.Jur.(Pliensbach.)-M.Jur.(Bathon.),* Eu.; *Rec.,* cosmop.——FIG. 61,2. *S.? moretonis* FORBES, Bathon., Eng.(Glos.); part of oral surface, ×1 (139).

Crossaster MÜLLER & TROSCHEL, 1840 [**Asterias papposus* LINNÉ, 1767; OD]. *Rec.*

Cuenotaster THIÉRY, 1920 [*pro Leucaster* KOEHLER, 1912 (*non* GAUTHIER, 1877)] [**Leucaster involutus* KOEHLER, 1912; OD]. *Rec.*

Heterozonias FISHER, 1910 [**Crossaster alternatus* FISHER, 1906; OD]. *Rec.*

Laetmaster FISHER, 1908 [*pro Ctenaster* PERRIER, 1881 (*non* AGASSIZ, 1836)] [**Ctenaster spectabilis* PERRIER, 1881; OD]. *Rec.*

Lophaster VERRILL, 1878 [**Solaster furcifer* DÜBEN & KOREN, 1884; OD] [=*Sarkaster* LUDWIG, 1905]. Arms 5; marginal paxillae in 2 well-developed rows. *Plio.,* Eng.; *Rec.*

Paralophaster FISHER, 1940 [**Solaster godefroyi* KOEHLER, 1912; OD] [=*Myoraster* FISHER, 1940]. *Rec.*

Rhipidaster SLADEN, 1889 [**R. vannipes*; OD]. *Rec.*

Xenorias FISHER, 1913 [**Rhipidaster (Xenorias) polyctemis*; OD]. *Rec.*

Family TROPIDASTERIDAE Wright, 1880

Arms 5 to many; adambulacrals broad,

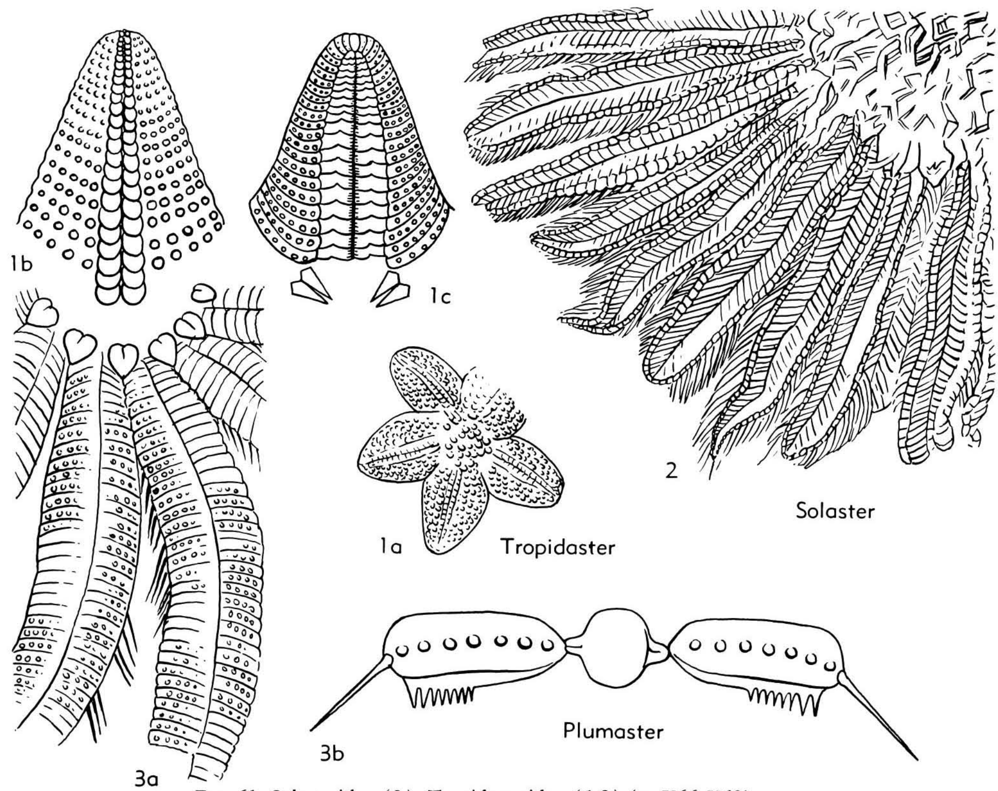


FIG. 61. Solasteridae *(2)*; Tropidasteridae *(1,3)* (p. *U66-U68*).

with transverse ridge carrying single row of spines; aboral surface with rows of spines. *L.Jur.*

Tropidaster FORBES, 1850 [**T. pectinatus*; OD]. Small, with 5 bluntly petaloid arms; ambulacral grooves wide, bordered by wide adambulacrals bent in middle and bearing 5 small spines which project into ambulacral furrow; continuous with adambulacrals are short wide inferomarginals with raised ridge and 8 or more long spines covering intermarginal grooves; mouth-angle plates prominent, plowshare-shaped; aboral surface with radial double row of overlapping rounded plates, otherwise covered with transverse rows of blunt conical spines. *L.Jur.(Pliensbach.),* Eng.——FIG. 61,*1*. **T. pectinatus,* Eng.(Glos.); *1a,* aboral side, ×1; *1b,c,* diagrammatic aboral and oral views, ×2 (139).

?**Plumaster** WRIGHT, 1861 [**P. ophiuroides*; OD]. Arms many, narrow at base, widest at mid-length; adambulacrals short, wide, with row of 8 long slender spines and row of small spines on distal margins; mouth-angle plates prominent. *L.Jur. (Pliensbach.),* Eng.——FIG. 61,*3*. **P. ophiuroides,* Eng.(Yorks.); *3a,* oral side, ×1; *3b,* adambulacrals, enl. (139).

Family KORETHRASTERIDAE Danielsson & Koren, 1884

Superficially like Solasteridae but without oral intermediate plates and with spines of adambulacrals and inferomarginals forming single series; aboral skeleton formed of rounded plates or wide mesh of isolated tufts of spinelets; marginals not paxilliform. *Rec.*

Korethraster THOMSON, 1873 [**K. hispidus*; OD]. *Rec.*

Anareaster FELL & H. E. S. CLARK, 1959 [**A. ganymede*; OD]. *Rec.*

Peribolaster SLADEN, 1889 [**P. folliculatus*; OD] [=*Peribolaster* SLADEN, 1885 (*nom. nud.*)]. *Rec.*

Remaster PERRIER, 1894 [**Korethraster (R.) palmatus*; OD]. *Rec.*

Family PYTHONASTERIDAE Sladen, 1889

[*nom. transl.* PERRIER, 1894 (*ex* Pythonasterinae SLADEN, 1889)]

Arms 5 to 10, long, cylindrical; aboral surface with bundles of long spinelets in webbed or ensacculated groups; mouth-angle plates and adambulacrals with combs of webbed spinelets. *Rec.*

Subfamily PYTHONASTERINAE Sladen, 1889

Pythonaster SLADEN, 1889 [**P. murrayi*; OD] [=*Pythonaster* SLADEN, 1885 (*nom. nud.*)]. *Rec.*

Subfamily MYXASTERINAE Perrier, 1894

Myxaster PERRIER, 1885 [**M. sol*; OD]. *Rec.*

Asthenactis FISHER, 1906 [**A. papyraceus*; OD]. *Rec.*

Family PTERASTERIDAE Perrier, 1875

Cross-shaped or lobed aboral plates bearing groups of spinelets which support membrane, distinct from aboral surface, forming cavity for young which escape by central valved aperture, termed osculum; lateral spines on adambulacrals either supporting oral web or merging in oral surface; no oral intermediate plates; mouth-angle plates broad and plowshare-shaped; internal septa membranous. *Rec.*

Pteraster MÜLLER & TROSCHEL, 1842 [**Asterias militaris* O. F. MÜLLER, 1776; OD]. *Rec.*

P. (Pteraster) [=*Pterasterides* VERRILL, 1909; ?*Lophopteraster* VERRILL, 1895]. *Rec.*

P. (Retaster) PERRIER, 1878 [**Pteraster capensis* GRAY, 1847; SD FISHER, 1911] [=*Hexaster* PERRIER, 1891; *Temnaster* VERRILL, 1894]. *Rec.*

P. (Apterodon) FISHER, 1940 [**Pteraster stellifer* SLADEN, 1882; OD]. *Rec.*

Benthaster SLADEN, 1882 [**Benthaster wyvillethomsoni* SLADEN, 1882; SD SPENCER & WRIGHT, herein]. *Rec.*

Calyptraster SLADEN, 1882 [**C. coa*; OD]. *Rec.*

Cryptaster PERRIER, 1885 [**C. personatus*; OD]. *Rec.*

Diplopteraster VERRILL, 1880 [**Pteraster multipes* SARS, 1877; OD]. *Rec.*

Euretaster FISHER, 1940 [**Retaster insignis* SLADEN, 1882; OD]. *Rec.*

Hymenaster THOMSON, 1873 [**H. pellucidus*; OD]. *Rec.*

Hymenasterides FISHER, 1911 [**H. zenognathus*; OD]. *Rec.*

Marsipaster SLADEN, 1882 [**M. spinosissimus* SLADEN, 1882; SD SPENCER & WRIGHT, herein]. *Rec.*

Suborder LEPTOGNATHINA Spencer & Wright, new suborder

Mouth-angle plates small, triangular; ambulacral furrows narrow. *L.Jur.-Rec.*

This suborder includes a variety of isolated families, of which some are clearly very primitive, but their geological record is poor.

Family ASTERINIDAE Gray, 1840

Minute marginals normally present; aboral skeleton composed of imbricated plates bearing grouped or single spinelets or granules; oral intermediate plates in regular transverse series, in some species consisting of virgals; interradial slits or dorsal depressions present in Tremasterinae. *M. Jur.-Rec.*

Known genera of this family are Recent except for a yet undescribed Middle Jurassic form from Switzerland.

Subfamily ASTERININAE Gray, 1840

Papulae widely distributed. Aboral ossicles thick. *Rec.*

Asterina NARDO, 1834 [**Asterias minuta* (=**Asterias gibbosa* PENNANT, 1777); OD] [=*Ctenaster* AGASSIZ, 1835; *Asteriscus* MÜLLER & TROSCHEL, 1840; *Asterinides* VERRILL, 1914]. *Rec.*

Allopatiria VERRILL, 1913 [**Patiria ocellifera* GRAY, 1840; OD]. *Rec.*

Asterinopsis VERRILL, 1914 [**Asterias penicillaris* LAMARCK, 1816; OD]. *Rec.*

Desmopatiria VERRILL, 1914 [**D. flexilis*; OD]. *Rec.*

Disasterina PERRIER, 1875 [**D. abnormalis*; OD] [=*Habroporina* H. L. CLARK, 1921]. *Rec.*

Manasterina H. L. CLARK, 1938 [**M. longispina*; OD]. *Rec.*

Nepanthia GRAY, 1840 [**Nepanthia maculata* GRAY, 1840; SD VERRILL, 1914] [=*Parasterina* FISHER, 1908]. *Rec.*

Paranepanthia FISHER, 1917 [**Nepanthia platydisca* FISHER, 1913; OD]. *Rec.*

Patiria GRAY, 1840 [**P. coccinea* GRAY, 1840 (=**Asterias miniata* BRANDT, 1835); OD] [=*Callopatiria, Enoplopatiria* VERRILL, 1914]. *Rec.*

Patiriella VERRILL, 1914 [**Asterina (Asteriscus) regularis* VERRILL, 1867; OD]. *Rec.*

Pseudonepanthia A. H. CLARK, 1916 [**P. gotoi*; OD]. *Rec.*

Tegulaster LIVINGSTONE, 1933 [**T. emburyi*; OD]. *Rec.*

?Socomia GRAY, 1840 *(nom. dub.)*. *Rec.*

Subfamily ANSEROPODINAE Fisher, 1903

[=Palmipedinae SLADEN, 1889]

Papulae in narrow radial band. Ossicles of papular area stellate. Other aboral ossicles thin, scalelike, with a downward projection that meets an upward process from an oral ossicle, forming or supporting pillar for disc. *Rec.*

Anseropoda NARDO, 1834 [**Asterias membranacea* RETZIUS, 1805; (=**Asterias placenta* PENNANT, 1777); OD] [=*Palmipes* AGASSIZ, 1835; *Carna* GISTL, 1848]. *Rec.*

Kampylaster KOEHLER, 1920 [**K. incurvatus*; OD]. *Rec.*

Mirastrella FISHER, 1940 [**M. biradialis; OD*]. *Rec.*

Subfamily TREMASTERINAE Fisher, 1903

[*ex* SLADEN, 1889, provisional]

Papulae in radial areas, wider than in Anseropodinae. With interradial slits or aboral depressions. *M.Jur., Rec.*

Tremaster VERRILL, 1879 [**T. mirabilis*; OD]. *Rec.*

Stegnaster SLADEN, 1889 [**Pteraster inflatus* HUTTON, 1872; OD]. *Rec.*

Genus undescribed assigned to this subfamily. *M. Jur.(Bajoc.),* Switz.

Family GANERIIDAE Sladen, 1889

[incl. Cryasteridae KOEHLER, 1906 (as Cryasteridés, *nom. correct.* FISHER, 1911)]

Large marginals normally present but may be small and confined to interrays; aboral skeleton imbricate, reticulate, or reduced to minute plates in skin. *Rec.*

Ganeria GRAY, 1847 [**G. falklandica*; OD]. *Rec.*

Aleutiaster A. H. CLARK, 1939 [**A. schafferi*; OD]. *Rec.*

Cycethra BELL, 1881 [**C. simplex* (=**Goniodiscus verrucosus* PHILIPPI, 1857); OD] [=*Lebrunaster* PERRIER, 1891]. *Rec.*

Leilaster A. H. CLARK, 1938 [**Korethraster radians* PERRIER, 1881; OD]. *Rec.*

Magdalenaster KOEHLER, 1907 [**M. arcticus*; OD]. *Rec.*

Perknaster SLADEN, 1889 [**P. fuscus* SLADEN, 1889; SD FISHER, 1940] [=*Cribraster* PERRIER, 1888; *Cryaster* KOEHLER, 1906; *Cribellopsis* KOEHLER, 1917]. *Rec.*

Scotiaster KOEHLER, 1908 [**S. inornatus*; OD]. *Rec.*

Tarachaster FISHER, 1913 [**T. tenuis*; OD]. *Rec.*

Family PORANIIDAE Perrier, 1894

[=Gymnasteriidae SLADEN, 1889; Asteropidae FISHER, 1908]

Marginals varying from prominent, more or less overlapping, smooth, or with few spines, to absent; aboral skeleton loosely tessellate or reticulate, covered by skin which is smooth, granulose, or spinulose; extreme forms may have no solid skeleton except some axial elements. *Rec.*

Porania GRAY, 1840 [**Asterias gibbosus* LEACH, 1817 (=**Asterias pulvillus* O. F. MÜLLER, 1788); OD] [=*Glabraster* A. H. CLARK, 1916].*Rec.*——FIG. 15,*1*. *P.* sp., Rec.; oral surface (111).

Asteropsis MÜLLER & TROSCHEL, 1840 [*pro Asterope* MÜLLER & TROSCHEL, 1840 (*non* HÜBNER, 1819)] [**Asterias carinifera* LAMARCK, 1816; OD] [=*Gymnasteria* GRAY, 1840, December (*non* PHILIPPI, 1840, June)]. *Rec.*

Chondraster VERRILL, 1895 [**Porania grandis* VERRILL, 1878; OD]. *Rec.*

Dermasterias PERRIER, 1875 [**D. inermis* (=**Asteropsis imbricata* GRUBE, 1857); OD]. *Rec.*

Marginaster PERRIER, 1881 [**M. pectinatus* PERRIER, 1881; SD SLADEN, 1889] [=*Cheilaster* BELL, 1892]. *Rec.*

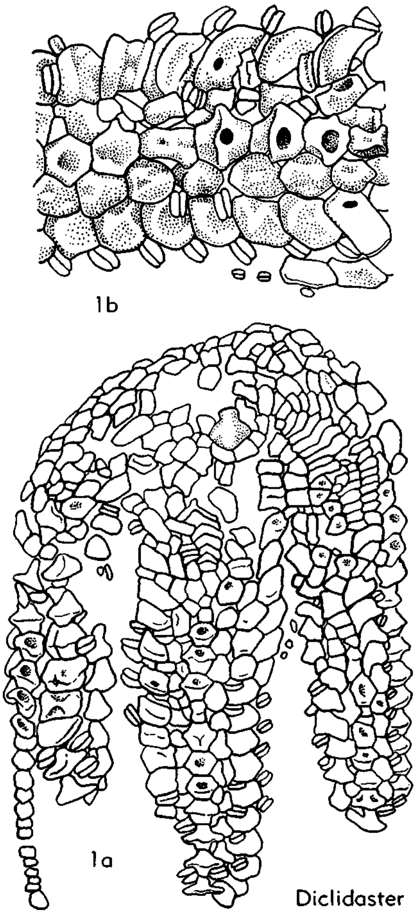


FIG. 62. Valvasteridae (p. U70).

Petricia GRAY, 1847 [**P. punctata* (=**Asterias vernicina* LAMARCK, 1816); OD]. *Rec.*

Poraniella VERRILL, 1914 [**P. regularis*; OD]. *Rec.*

Poraniomorpha DANIELSSON & KOREN, 1881 [**P. rosea*; OD] [=*Rhegaster* SLADEN, 1883; *Lasiaster* SLADEN, 1889; *Culcitopsis* VERRILL, 1914]. *Rec.*

Poranisca VERRILL, 1914 [**P. lepida*; OD]. *Rec.*

Pseudoporania DONS, 1936 [**P. stormi*; OD]. *Rec.*

Sphaeriaster DONS, 1939 [*pro Sphaeraster* DONS, 1938 (*non* QUENSTEDT, 1875)] [**Sphaeraster berthae* DONS, 1938; OD]. *Rec.*

Spoladaster FISHER, 1940 [**Cryaster brachyactis* H. L. CLARK, 1923; OD]. *Rec.*

Tylaster DANIELSSON & KOREN, 1881 [**T. willei*; OD]. *Rec.*

Family ECHINASTERIDAE Verrill, 1867

[*non* Echinasterina GRAY, 1840, based on *Echinaster* GRAY, 1840 (*non* MÜLLER & TROSCHEL, 1840)]

Disc small, arms long and slender; aboral ossicles reticulate, with spines single or in small groups. Pedicellariae lacking; ampullae single. *?U.Cret., Rec.*

Echinaster MÜLLER & TROSCHEL, 1840 [**Asterias seposita* LAMARCK, 1816 (*non* RETZIUS, 1783) (=**Asterias sagena* RETZIUS, 1805); SD FISHER, 1913] [*non Echinaster* GRAY, 1840 (see *Acanthaster*)] [=*Othilia, Rhopia* GRAY, 1840; *Henricides* VERRILL, 1914]. *Rec.*

Cribraster PERRIER, 1891 [**C. sladeni*; OD]. *Rec.*

Dictyaster WOOD-MASON & ALCOCK, 1891 [**D. xenophilus*; OD]. *Rec.*

Henricia GRAY, 1840 [**H. oculata* (=**Asterias sanguinolenta* O. F. MÜLLER, 1776); OD] [=*Cribella* FORBES, 1841 (*non* AGASSIZ, 1835); *Cribrella* LÜTKEN, 1857 (*non* AGASSIZ, 1835); *Magdalenaster* KOEHLER, 1907; *Cyllaster* A. H. CLARK, 1916; *Spinohenricia* HEDING, 1936]. Marginals more or less distinguishable; aboral surface with many spinelets in groups or on ridges; single doubtful specimen found fossil (7). *?U.Cret.* (Calif.), *Rec.*

Plectaster SLADEN, 1889 [**Echinaster decanus* MÜLLER & TROSCHEL, 1843; OD]. *Rec.*

Poraniopsis PERRIER, 1891 [**P. echinaster*; OD (other included species is synonym)] [=*Poraniopsis* PERRIER, 1888 (*nom. nud.*); *Lahillea* DE LORIOL, 1904; *Alexandraster* LUDWIG, 1905; *Ortmannia* DE LORIOL, 1906]. *Rec.*

Rhopiella FISHER, 1940 [**R. koehleri*; OD]. *Rec.*

Thyraster IVES, 1890 [**Echinaster serpentarius* MÜLLER & TROSCHEL, 1842; OD]. *Rec.*

Family VALVASTERIDAE Viguier, 1878

[*nom. correct.* FISHER, 1911 (*pro Valvasteridés* VIGUIER, 1878)] [=Valvasterinae KOEHLER, 1910]

Marginals conspicuous; aboral ossicles regularly arranged, with small triangular papular areas between, with isolated spinelets. Pedicellariae large, low, bivalved on superomarginals and small, 2-jawed on aboral surface; ampullae double. *L.Jur.-Rec.*

Valvaster PERRIER, 1876 [**Asterias striata* LAMARCK, 1816; OD]. *Rec.*

Diclidaster DE LORIOL, 1897 [**D. gevreyi*; OD]. Short wide imbricating plates at base of arms; some aboral ossicles bearing perforations (?for stalked pedicellariae). *L.Jur.(Hettang.)*, Fr.——FIG. 62,*1*. **D. gevreyi*, Ardêche; *1a*, oblique aboral view, arms turned down, ×2; *1b*, part of arm, ×4 (117).

Family ACANTHASTERIDAE Sladen, 1889

Many arms; madreporites numerous. Upright, 2-jawed pedicellariae; well-developed interbrachial septa; ampullae double. *Rec.*

Acanthaster GERVAIS, 1841 [*pro Echinaster* GRAY, 1840 (*non* MÜLLER & TROSCHEL, 1840)] [**A.*

echinus (=**Asterias planci* LINNÉ, 1758); OD]. *Rec.*

Family MITHRODIIDAE Viguier, 1879

[*nom. transl.* PERRIER, 1894 (*ex* Mithrodiinae VIGUIER, 1879)]

Whole surface, including spines, overlaid with rough granules, tubercles or spinelets; no interbrachial septa; ampullae double. *Rec.*

Mithrodia GRAY, 1840 [**M. spinulosa* (=**Asterias clavigera* LAMARCK, 1816); OD] [=*Heresaster* MICHELIN, 1844]. *Rec.*

Family METRODIRIDAE Sladen, 1889

[*nom. transl.* FISHER, 1917 (*ex* Metrodirinae SLADEN, 1889)]

Abactinal surface and marginals covered with skin, bearing isolated skin-covered spines. *Rec.*

Metrodira GRAY, 1840 [**M. subulata*; OD] [=*Scaphaster* DE LORIOL, 1899]. *Rec.*

Order FORCIPULATIDA Perrier, 1884

[*nom. correct.* SPENCER & WRIGHT, herein (*pro* Forcipulatae PERRIER, 1884)]

Mouth of ambulacral type; madreporite always on aboral surface. Pedicellariae, when present, always straight or crossed. *L.Ord.-Rec.*

Suborder URACTININA Spencer & Wright, new suborder

[=Urasterina SPENCER, 1951 (name misleading because *Uraster* is synonym of *Asterias* of suborder Asteriadina)]

Arms typically narrow and well produced with parallel sides; aboral ossicles with numerous paxillae set on shafts in diagonal rows; in Arthrasterinae aboral ossicles are reduced to 5 rows and paxillar shafts broadened to form ridges; ambulacrals, except in some late Devonian and Carboniferous forms, not compressed; adambulacrals typically with median ridge carrying row of stout spines; single primary interradial present in earlier genera; odontophore high and wedge-shaped. Pedicellariae unknown. [For comparison of mouth frame with that of Asteriadina see Fig. 63, 64. Most Uractinina are Paleozoic but Compsasteridae linger into L. Jur. and a genus of Calliasteridae is rather common in U.Cret.] *L.Ord.-U.Cret.*

Family CNEMIDACTINIDAE Spencer, 1918

Arms steep-sided, with upper row of close ossicles (?inferomarginals) knit with row of adambulacrals which have flat oral surface; aboral surface with rows of small paxillae; oral side with wide mouth and several divergent ambulacrals arranged as if bordering buccal slits, aborally fused into closed girdle. Most apertures closed orally by 5 flaps, in same position as tori in ophiuroids but in horizontal plane. [The only described genus is M.Ord.-U.Ord. but undescribed material is known from L.Ord. of Czech.] *Ord.*

Cnemidactis SPENCER, 1918 [**Urasterella girvanensis* SCHUCHERT, 1914; OD]. Characters of family. *M.Ord.-U.Ord.*, Can.-Scot.——FIG. 63,*4*; 64,*1*. **C. girvanensis* (SCHUCHERT), U.Ord., Scot.; 63,*4*, part of mouth frame; 64,*1*, cross section of arm, oral surface of interray, ×5 (133).

Family URASTERELLIDAE Schuchert, 1914

[=Roemerasterinae GREGORY, 1900]

Arms rounded in section; adambulacra disc-shaped, with transverse ridge carrying stout spines, aboral ossicles paxilliform, subequal, in diagonal series, each corresponding with segment of ambulacral skeleton; ambulacrals not compressed. *L.Ord.-Permocarb.*

Urasterella M'COY, 1851 [**Uraster ruthveni* FORBES, 1858; OD] [=*Roemeraster, Palasteracanthion, Protasteracanthion* STÜRTZ, 1886]. Aboral side of arms flat, many paxillae with unequal-sized bases. *M. Ord. - Permocarb.*, Can.-Scot.-Ger.-USSR. ——FIG. 64,*6a,b*. **U. ruthveni* (FORBES), U.Sil., Eng.; *6a*, oral side of arm, ×2; *6b*, aboral side, ×5 (133).——FIG. 64,*6c,d*. *U. thraivensis* SPENCER, U.Ord., Scot.; *6c*, oral side, ×2; *6d*, aboral side, ×3 (133).——FIG. 64,*6e*. *U. verruculosa* LEHMANN, L.Dev., Ger.; aboral side, ×1 (116). (See Fig. 63,2.)

Bohemaster JAEKEL, 1923 [**B. primula*; OD]. Unrecognizable member of family. *L.Ord.*, Czech.

Phillipsaster SPENCER, 1950 [**Palaeaster coronella* SALTER, 1857; OD]. Like *Salteraster* but with only slightly swollen arms. *Sil.*, Eng.-E.Can.-Australia. ——FIG. 64,*3*. **P. coronella* (SALTER), L.Sil., Eng., part of aboral surface, ×5 (133).

Salteraster STÜRTZ, 1893 [**Palaeaster asperrima* SALTER, 1857; OD]. Arms strongly swollen, with single row of carinals separated from marginals by many paxillae. *M.Ord.-Sil.*, N.Am.-Eng.-Australia.——FIG. 64,*4a,b*. **S. asperrimus* (SALTER), U.Ord., Eng.(Heref.); *4a*, cross section of arm, ×5; *4b*, oral side of arm, ×2 (133).——FIG. 64,*4c*. *S. grandis* (MEEK), U.Ord.(Richmond.), USA(Ohio); specimen with arms folded together, ×1 (129).

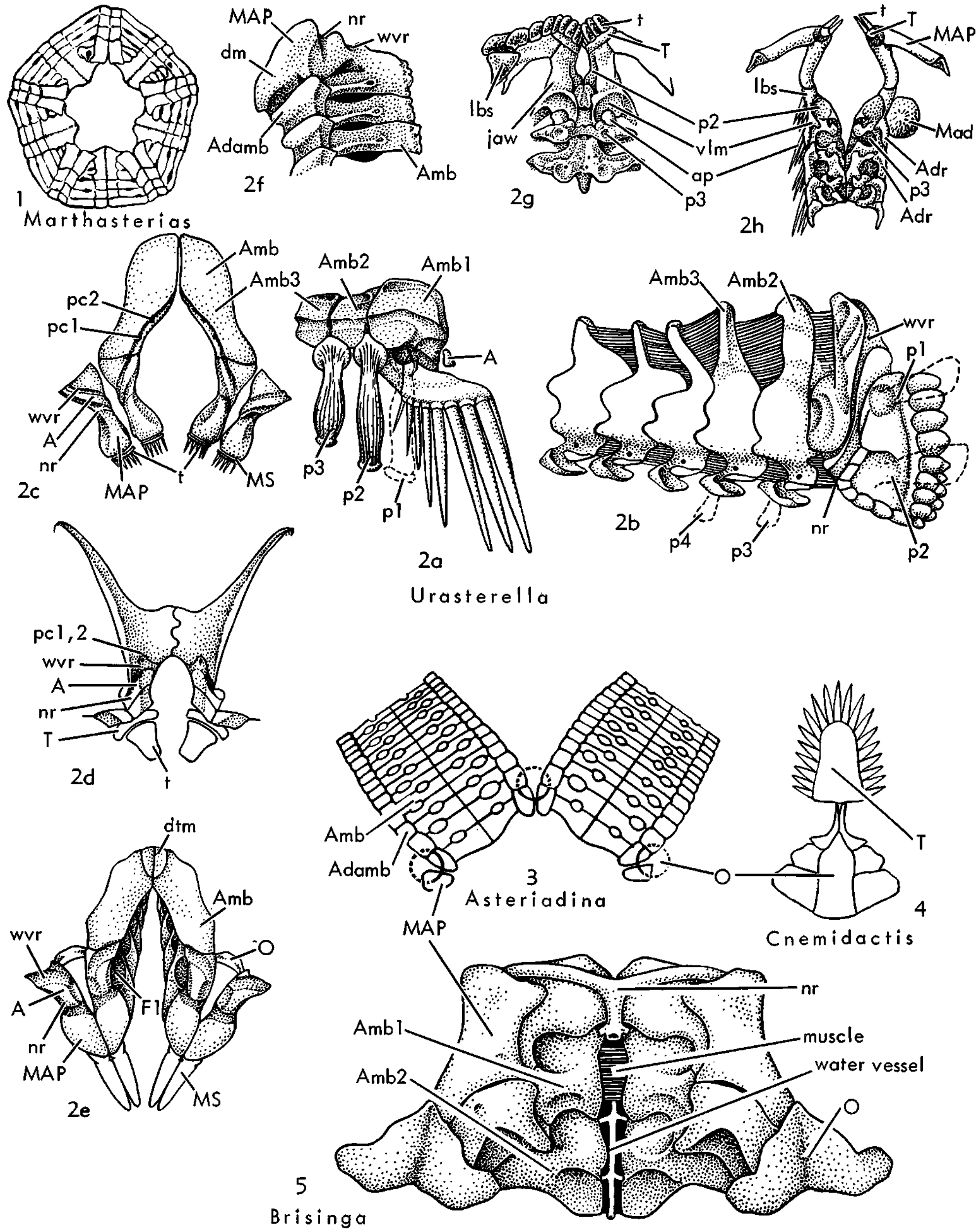


FIG. 63. Mouth frames of ambulacral type.——*1.* Aboral aspect of frame of *Marthasterias glacialis*, Rec. (86).——*2a-h.* Frame of *Urasterella* in oral aspect (133).——*3.* Diagram of ambulacral type of mouth frame as in Asteriadina, oral aspect (Spencer, n).——*4.* Part of frame of *Cnemidactis*, Ord., showing flap-like torus (29).——*5.* Part of frame of *Brisinga*, Rec., oral aspect (133). [Explanation: *A,* apophysis; *Adamb,* adambulacral; *Adr,* adradial; *Amb,* ambulacral; *ap,* articular peg (lateral hinge); *dm,* dental muscle attachment; *dtm,* dorsal transverse muscle attachment; *lbs,* lateral buccal shield; *Mad,* madreporite; *MAP,* mouth-angle plate; *MS,* mouth spine; *nr,* nerve-ring groove; *O,* odontophore; *p,* podial (tube foot) basin; *pc,* podial canal (to tube foot); *T,* torus; *t,* tooth (teeth); *vlm,* ventral longitudinal muscle attachment; *wvr,* water-vessel-ring groove.] (p. U71, U76-U77).

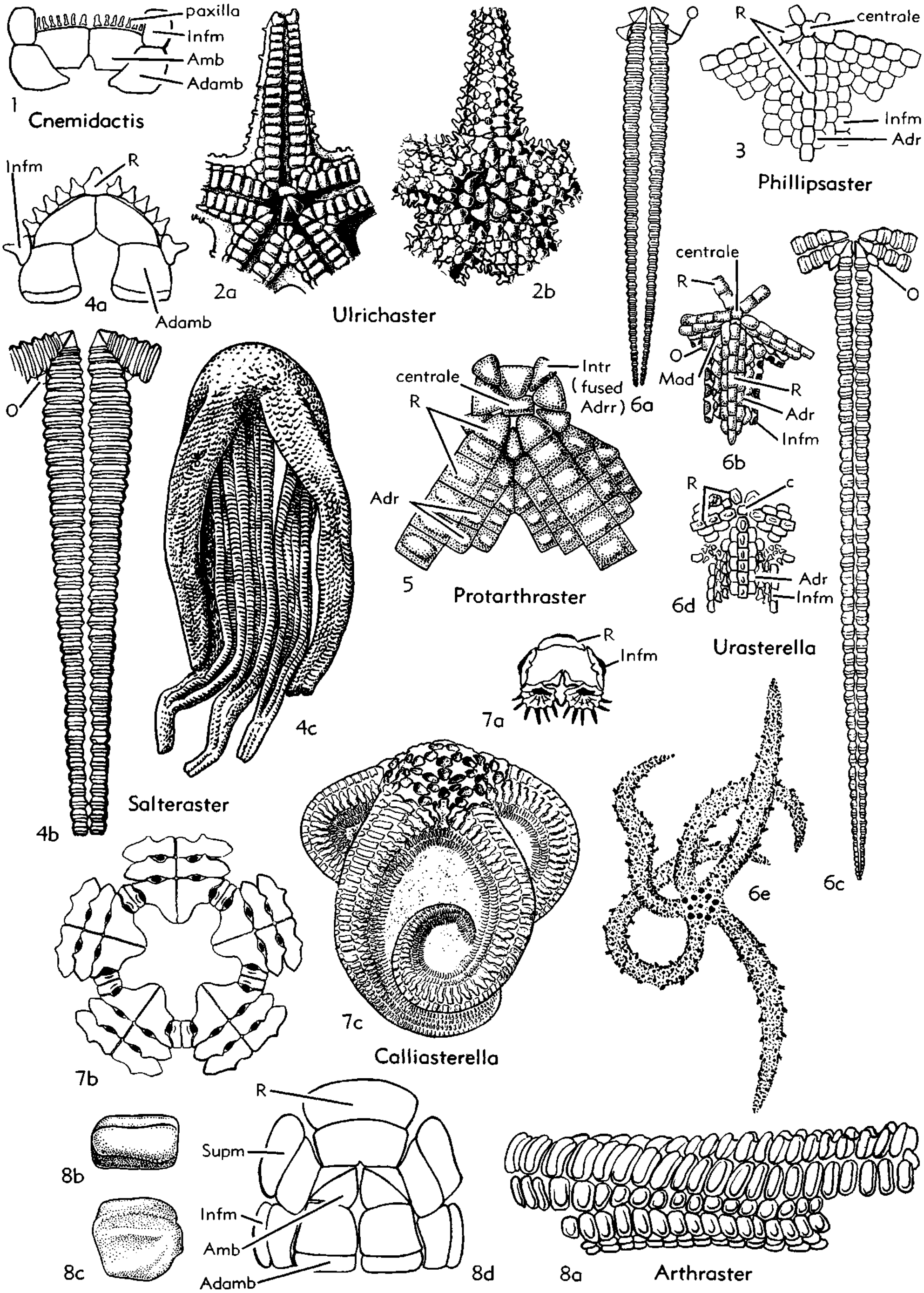


FIG. 64. Cnemidactinidae *(1)*; Urasterellidae *(2-4,6)*; Calliasterellidae (Protarthrasterinae) *(5)*, (Calliasterellinae) *(7)*, Arthrasterinae *(8)*. [Explanation: *Adamb*, adambulacral; *Adr*, adradial; *Amb*, ambulacral; *Infm*, inferomarginal; *Intr*, interradial; *Mad*, madreporite; *O*, odontophore; *R*, radial; *Supm*, superomarginal.] *(U71, U74)*.

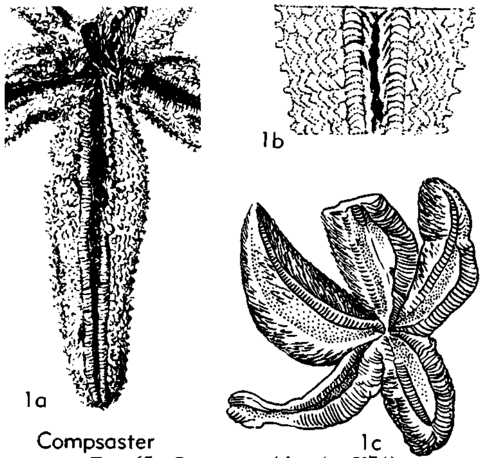


FIG. 65. Compsasteridae (p. U74).

Ulrichaster SPENCER, 1950 [**Urasterella ulrichi* SCHUCHERT, 1915]. Median oral surface of arms with 2 rows of ossicles, highly swollen in adults. *M. Ord.-L. Sil.,* N. Am.-Scot.——FIG. 64,*2*. **U. ulrichi* (SCHUCHERT), M.Ord.(Blackriv.), USA (Minn.); *2a,* oral side, ×3; *2b,* aboral side, ×2 (129).

Family CALLIASTERELLIDAE Schöndorf, 1910

[=Arthrasteridae SPENCER, 1918]

Disc small; arms long and straight-sided; oral face of adambulacrals with prominent transverse ridge; aboral ossicles of arms transversely elongate and bearing median ridge; with 5 primary radials. *L.Carb.-U. Cret.*

Subfamily PROTARTHRASTERINAE Spencer, 1918

Aboral ossicles in several rows, those along mid-line of arms with transverse ridge, others with paxillae. *L.Carb.*

Protarthraster SPENCER, 1918 [**Palaeaster longimanus* WHIDBORNE, 1896; OD]. Arms well rounded in section, inferomarginals on oral surface. *L.Carb.,* Eng.——FIG. 64,*5*. **P. longimanus* (WHIDBORNE); aboral surface, ×5 (133).

Subfamily CALLIASTERELLINAE Schöndorf, 1910

Aboral ossicles of arm reduced to 3 rows, no superomarginals present. *U. Carb.*

Calliasterella SCHUCHERT, 1914 [*pro Calliaster* TRAUTSCHOLD, 1879 (*non* GRAY, 1840)] [**Calliaster mirus* TRAUTSCHOLD, 1879; OD]. Arms enrolled toward oral side, as in *Calyptactis. U.Carb.,* Eu.(USSR).——FIG. 64,*7*. **C. mira* (TRAUTSCHOLD); *7a,* section of arm, ×1; *7b,* ossicles of mouth region from oral side, ×2; *7c,* reconstruction, ×0.5 (128).

Subfamily ARTHRASTERINAE Spencer, 1918

Aboral ossicles of arm in 5 rows of inferomarginals, superomarginals, and carinals. *U.Cret.*

Arthraster FORBES, 1848 [**A. dixoni*; OD]. Arms semicircular in section; arm ossicles more or less equal, short and wide, with tumid surface rising to smooth or rugose or pitted rounded transverse ridge. *U.Cret.(Turon.-Maastricht.),* Eng.-Fr.——FIG. 64,*8*. **A. dixoni,* Turon., Eng.; *8a,* side of arm, ×1; *8b,c,* top and side of marginal, ×2; *8d,* cross section of arm, ×2 (133).

Family COMPSASTERIDAE Schuchert, 1914

Arms swollen and fusiform; ambulacrals and adambulacrals numerous, compressed; ambulacrals transversely elongate, almost linear; aboral surface bearing many paxillae, with tall shafts. *L.Dev.-L.Jur.*

Compsaster WORTHEN & MILLER, 1883 [**C. formosus*; OD] [=*Jaekelaster* STÜRTZ, 1900; *Schlueteraster* LEHMANN, 1957]. Characters of family. *L. Dev.-L. Jur. (Bathon.),* Eng.-Ger.-N. Am.——FIG. 65,*1a,b*. **C. formosus,* U.Miss.(Chester.), USA (Ill.); *1a,* oral side, ×1; *1b,* part of same, ×2 (129).——FIG. 65,*1c*. *C. spiniger* (WRIGHT), Bathon., Eng.; *1c,* oral side, ×2 (139).

Suborder ASTERIADINA Fisher, 1928

Many ossicles of aboral surface modified to form crossed pedicellariae, basal plate representing spine, pincers on its summit comprising modified spinelets. *L.Jur.-Rec.*

Family HELIASTERIDAE Viguier, 1878

Disc large, with many (up to 50) short arms, divided internally from disc by wall. *Rec.*

Heliaster GRAY, 1840 [**Asterias helianthus* LAMARCK, 1816; SD H. L. CLARK, 1909]. *Rec.*

Family ZOROASTERIDAE Sladen, 1889

Disc small, arms normally long, subcylindrical, with ossicles in close radial series. Pelicellariae straight only. *Rec.*

Zoroaster WYVILLE THOMSON, 1873 [**Z. fulgens*; OD]. *Rec.*

Bythiolophus FISHER, 1916 [**B. acanthinus*; OD]. *Rec.*

Cnemidaster SLADEN, 1889 [**C. wyvillei*; OD]. *Rec.*

Mammaster PERRIER, 1894 [**Zoroaster sigsbeei* PERRIER, 1881; OD]. *Rec.*
Myxoderma FISHER, 1905 [**Zoroaster (Myxoderma) sacculatus*; OD]. *Rec.*
Pholidaster SLADEN, 1889 [**P. squamatus*; SD FISHER, 1919]. *Rec.*
Prognaster PERRIER, 1891 [**P. grimaldii*; OD]. *Rec.*

Family ASTERIIDAE Gray, 1840

Arms 5 to many; body swollen; ambulacrals and adambulacrals numerous, compressed; adambulacrals transversely elongate, ambulacrals narrow. Tube feet normally in 4 rows; pedicellariae straight and crossed. Aboral skeleton generally reticulate. Division into subfamilies is difficult. Neomorphasterinae and Pedicellasterinae are distinct groups, but Labidiasterinae and Pycnopodiinae perhaps less so. Attempts to divide the remainder have not been wholly successful, and therefore here they are all left in Asteriinae. *?L.Jur., M.Jur.-Rec.*

Subfamily ASTERIINAE Gray, 1840

[=Stichasteridae PERRIER, 1885;. Coscinasteriinae, Notasteriinae FISHER, 1923]

Characters most closely similar to those of *Asterias*. [Includes a wide range of genera which lack features of other subfamilies.] *?L.Jur., M.Jur.-Rec.*

Asterias LINNÉ, 1758 [**A. rubens*; SD NORMAN, 1865] [=*Stellonia* NARDO, 1834; *Uraster* AGASSIZ, 1835; *Asteracanthion* MÜLLER & TROSCHEL, 1840; *Allasterias* VERRILL, 1909; *Parasterias* VERRILL, 1914]. Disc fairly large, arms 5 or 6, rather broad and short; aboral skeleton open network with spines in nearly regular series along midline and margin of arms but elsewhere spaced irregularly. [Fossils can only be provisionally placed in the restricted genus.] *?L.Jur.(Pliensbach.), M.Jur.(Oxford.), Rec.*, cosmop.——FIG. 66,*1*. *A.? gaveyi* (FORBES), L.Jur., Pliensbach., Eng. (Glos.); *1a*, oral side of arm, ×1; *1b*, ambulacrals and adambulacrals, ×3 (139).
Adelasterias KOEHLER, 1914 [**Diplasterias papillosa* KOEHLER, 1906; OD]. *Rec.*
Allostichaster VERRILL, 1914 [**Asteracanthion polyplax* MÜLLER & TROSCHEL, 1844; OD]. *Rec.*
Anasterias PERRIER, 1875 [**A. minuta*; OD] [=*Asteroderma* PERRIER, 1888; *Parastichaster* KOEHLER, 1920; *Eremasterias* FISHER, 1930]. *Rec.*
A. (Anasterias). *Rec.*
A. (Sporasterias) PERRIER, 1894 [**Asterias rugispina* STIMPSON, 1860; (=**Asteracanthion antarcticum* LÜTKEN, 1856); OD]. *Rec.*
A. (Kalyptasterias) KOEHLER, 1923 [**K. conferta*; OD]. *Rec.*
Aphanasterias FISHER, 1923 [**A. pycnopodia*; OD]. *Rec.*

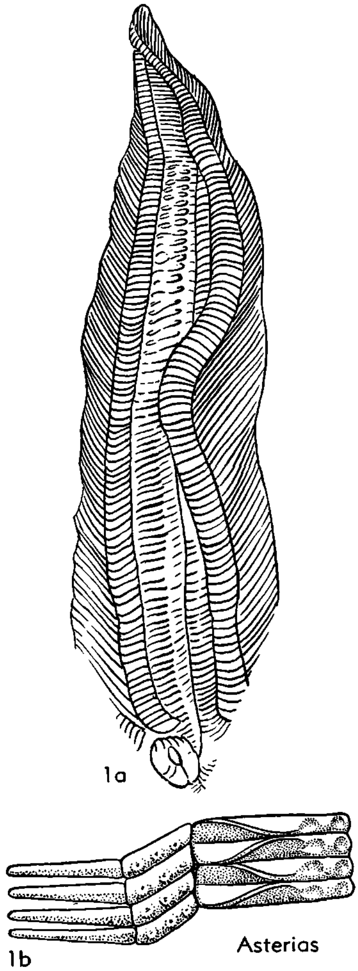


FIG. 66. Asteriidae (Asteriinae) (p. *U*75).

Aphelasterias FISHER, 1923 [**Asterias japonica* BELL, 1881; OD]. *Rec.*
Astrometis FISHER, 1923 [**Asterias sertulifera* XANTUS, 1860; OD]. *Rec.*
Astrostole FISHER, 1923 [**Margaraster? scaber* HUTTON, 1872; OD]. *Rec.*
Australiaster FISHER, 1923 [**Coscinasterias dubia* H. L. CLARK, 1909; OD]. *Rec.*
Caimanaster A. M. CLARK, 1962 [**C. acutus*; OD]. *Rec.*
Carlasterias DA COSTA, 1952 [**Mortensenia lusitanica* DA COSTA, 1941; OD] [=*Mortensenia* DA COSTA, 1941 (*non* DÖDERLEIN, 1905)]. *Rec.*
Calvasterias PERRIER, 1875 [**C. asterinoides*; OD] [=*Stichorella* KOEHLER, 1920]. *Rec.*
Coscinasterias VERRILL, 1867 [**C. muricata*; OD]. *Rec.*
C. (Coscinasterias). *Rec.*
C. (Stolasterias) SLADEN, 1889 [**Asterias tenui-*

spina LAMARCK, 1816; SD FISHER, 1923] [=*Lytaster, Polyasterias* PERRIER, 1894]. *Rec.*

Cosmasterias SLADEN, 1889 [**Asteracanthion sulcifer* PERRIER, 1869 (=**Asteracanthion luridum* PHILIPPI, 1858; SD FISHER, 1930)] [=*Comasterias* PERRIER, 1891; *Quadraster* PERRIER, 1896]. *Rec.*

Cryptasterias VERRILL, 1914 [**Diplasterias turqueti* KOEHLER, 1906; OD]. *Rec.*

Displasterias PERRIER, 1888 [**Asterias brandti* BELL, 1881; ICZN pend.] [=*Podasterias* PERRIER, 1894; *Koehleraster* FISHER, 1922; *Bathyasterias* FISHER, 1930]. *Rec.*

Distolasterias PERRIER, 1896 [**Asterias (Stolasterias) stichantha* SLADEN, 1889; OD]. *Rec.*

Evasterias VERRILL, 1914 [**Asterias troscheli* STIMPSON, 1862; OD]. *Rec.*

Gastraster PERRIER, 1894 [**Pedicellaster margaritaceus* PERRIER, 1882; OD]. *Rec.*

Granaster PERRIER, 1894 [**Stichaster nutrix* STUDER, 1885; OD] [=*Hemiasterias* VERRILL, 1914]. *Rec.*

Icasterias FISHER, 1923 [**Asterias panopla* STUXBERG, 1878; OD]. *Rec.*

Kenrickaster A. M. CLARK, 1962 [**K. pedicellaris*; OD]. *Rec.*

Leptasterias VERRILL, 1866 [**Asteracanthion muelleri* SARS, 1844; OD] [=*Ctenasterias* VERRILL, 1914]. *Rec.*

L. (Leptasterias). *Rec.*

L. (Endogenasterias) DJAKONOV, 1938 [**Asteracanthion groenlandicum* STEENSTRUP, 1857; OD]. *Rec.*

L. (Eoleptasterias) DJAKONOV, 1938 [**Asteracanthion ochetense* BRANDT, 1835; OD]. *Rec.*

L. (Hexasterias) FISHER, 1930 [**Asteracanthion polaris* MÜLLER & TROSCHEL, 1842; OD]. *Rec.*

L. (Nesasterias) FISHER, 1930 [*L. (N.) stolacantha*; OD]. *Rec.*

Lethasterias FISHER, 1923 [**Asterias nanimensis* VERRILL, 1914; OD]. *Rec.*

Lysasterias FISHER, 1908 [**Anasterias perrieri* STUDER, 1885; OD] [=*Anasterias* LUDWIG, 1903 (*non* PERRIER, 1885); *Paedasterias* VERRILL, 1914]. *Rec.*

Marthasterias JULLIEN, 1878 [**M. foliacea* (=**Asterias glacialis* LINNÉ, 1758); OD]. *Rec.*

Meyenaster VERRILL, 1913 [**Asterias gelatinosus* MEYEN, 1834; OD]. *Rec.*

Neosmilaster FISHER, 1930 [**Asterias georgianus* STUDER, 1885; OD]. *Rec.*

Notasterias KOEHLER, 1911 [**N. armata*; OD] [=*Autasterias* KOEHLER, 1911]. *Rec.*

Orthasterias VERRILL, 1914 [**O. columbiana* (=**Asterias koehleri* DE LORIOL, 1897); OD]. *Rec.*

Perissasterias H. L. CLARK, 1923 [**P. polyacantha* H. L. CLARK, 1923; SD FISHER, 1926]. *Rec.*

Pisaster MÜLLER & TROSCHEL, 1840 [**Asteracanthion margaritifer* (=**Asterias ochraceus* BRANDT, 1835); OD] [=*Calliasterias* FEWKES, 1889]. *Rec.*

Psalidaster FISHER, 1940 [**P. mordax*; OD]. *Rec.*

Pseudechinaster H. E. S. CLARK, 1962 [**P. rubens*; OD]. *Rec.*

Saliasterias KOEHLER, 1920 [**S. bracheata*; OD]. *Rec.*

Sclerasterias PERRIER, 1891 [**S. guernei*; OD] [=*Eustolasterias* FISHER, 1923]. *Rec.*

Smilasterias SLADEN, 1889 [**Asterias (S.) scalprifera* SLADEN, 1889; SD FISHER, 1930] [=*Nanaster* PERRIER, 1894]. *Rec.*

Stenasterias VERRILL, 1914 [**Asterias (Leptasterias) macropora* VERRILL, 1909; OD]. *Rec.*

Stephanasterias VERRILL, 1871 [**Asteracanthion albulus* STIMPSON, 1853]. *Rec.*

Stichaster MÜLLER & TROSCHEL, 1840 [**S. striatus* (=**Asterias aurantiaca* MEYEN, 1834 (not invalidated by *A. aranciaca* LINNÉ, 1758); OD] [=*Tonia* GRAY, 1840; *Coelasterias* VERRILL, 1867 (*nom. nud.*); *Coelasterias* VERRILL, 1871]. *Rec.*

Stichastrella VERRILL, 1914 [**Asterias rosea* O. F. MÜLLER, 1776; OD]. *Rec.*

Stylasterias VERRILL, 1914 [**Asterias forreri* DE LORIOL, 1887; OD]. *Rec.*

Tarsastrocles FISHER, 1923 [**Hydrasterias verrilli* FISHER, 1903; OD]. *Rec.*

Triplasterias ENGELS & SCHROEVERS, 1961 [**T. mercatoris*; OD]. *Rec.*

Uniophora GRAY, 1840 [**U. globifera* (=**Asterias granifera* LAMARCK, 1816); OD]. *Rec.*

Urasterias VERRILL, 1909 [**Asteracanthion linckii* MÜLLER & TROSCHEL, 1842; OD]. *Rec.*

Subfamily PEDICELLASTERINAE Fisher, 1918

Alone in family with first proximal adambulacrals wholly or partly separated interradially. Tube feet may be biserial throughout. *Rec.*

Pedicellaster SARS, 1861 [**P. typicus*; OD]. *Rec.*

Ampheraster FISHER, 1923 [**Sporasterias marianus* LUDWIG, 1905; OD]. *Rec.*

Anteliaster FISHER, 1923 [**A. coscinactis*; OD]. *Rec.*

Hydrasterias SLADEN, 1889 [**Asterias (H.) ophidion*; OD]. *Rec.*

Peranaster FISHER, 1923 [**Pedicellaster chirophorus* FISHER, 1917; OD]. *Rec.*

Tarsaster SLADEN, 1889 [**T. stoichoides*; OD]. *Rec.*

Subfamily LABIDIASTERINAE Verrill, 1914

Arms many, long and slender. One spine on each inferomarginal, wreathed with crossed pedicellariae. No oral intermediate plates. Aboral skeleton very open or obsolescent. *Rec.*

Labidiaster LÜTKEN, 1871 [**L. radiosus*; OD] [=?*Gymnobrisinga* STUDER, 1884; *Labidiastrella* VERRILL, 1914]. *Rec.*

Coronaster PERRIER, 1885 [**C. parfaiti*; OD] [=*Heterasterias* VERRILL, 1914]. *Rec.*

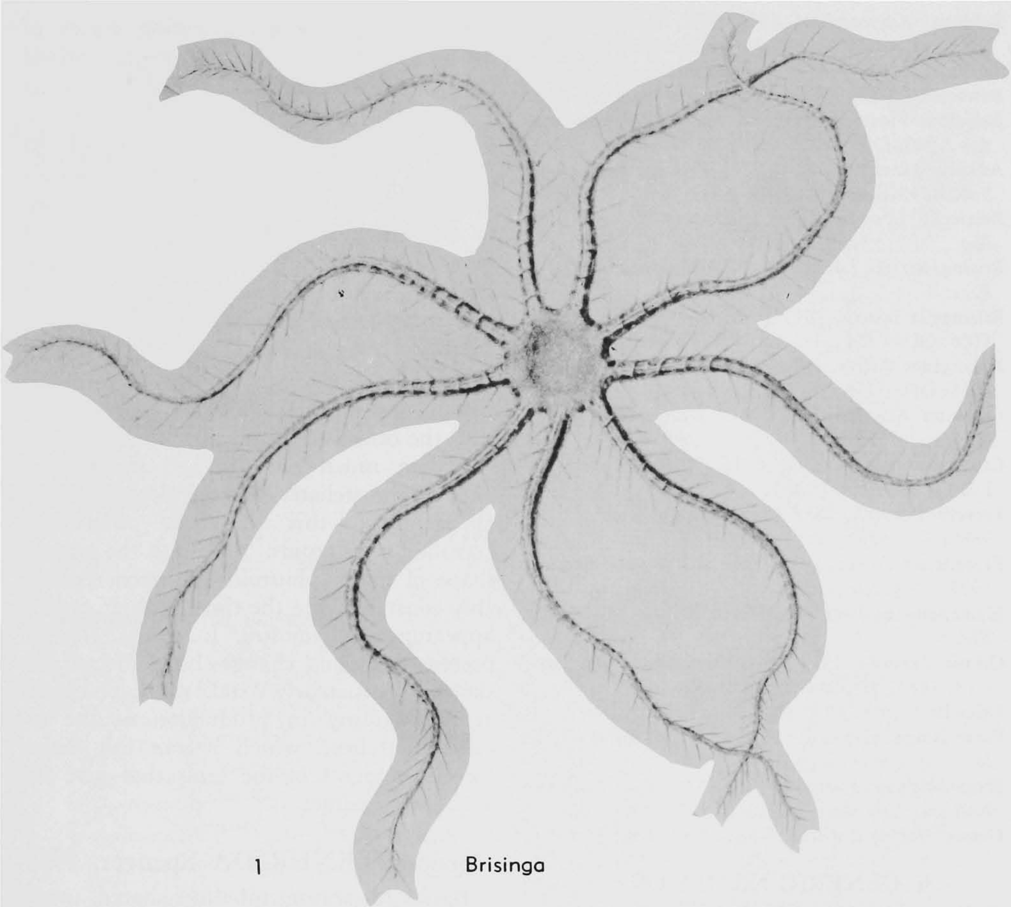


FIG. 67. Brisingidae (p. U77).

Plazaster FISHER, 1941 [**Labidiaster borealis* UCHIDA, 1938; OD]. *Rec.*

Rathbunaster FISHER, 1906 [**R. californicus*; OD]. *Rec.*

Subfamily PYCNOPODIINAE Stimpson, 1862
[*nom. transl.* VERRILL, 1914 (*ex* Pycnopodiidae STIMPSON, 1862)]

Inferomarginals with two spines, heavily wreathed with pedicellariae. No oral intermediate plates. Aboral skeleton obsolescent. *Rec.*

Pycnopodia STIMPSON, 1862 [**Asterias helianthoides* BRANDT, 1835; OD]. *Rec.*

Lysastrosoma FISHER, 1922 [**L. anthosticta*; OD]. *Rec.*

Subfamily NEOMORPHASTERINAE Fisher, 1923

Primary aboral plates conspicuously enlarged. Aboral skeleton of closely imbricated, sparsely granulated ossicles in regular radial series. *Rec.*

Neomorphaster SLADEN, 1889 [*pro Glyptaster* SLADEN, 1885 (*non* HALL, 1852)] [**N. eustichus* (=**Stichaster talismani* PERRIER, 1891); OD] [=*Calycaster* PERRIER, 1891]. *Rec.*

Suborder BRISINGINA Fisher, 1928
[=Euclasteroidea TORTONESE, 1958]

Arms many, sharply distinct and readily separated from very small disc; odontophore visible on edge of disc; ambulacrals and adambulacrals not compressed; pairs of ambulacrals articulated end to end; aboral skeleton weak. Crossed pedicellariae abundant; papulae in many species lacking. *L. Oligo.-Rec.*

Family BRISINGIDAE Sars, 1875

Characters of suborder. [A single fossil of unidentified genus is known from California.] *L.Oligo.-Rec.*

Brisinga ASBJORNSEN, 1856 [*B. *endecacnemos*; OD].*Rec.*——FIG. 67,*1*. *B. mediterranea* PERRIER; aboral surface, slightly enlarged (Perrier). *Rec.*
Astrocles FISHER, 1917 [**A. actinodetus*; OD]. *Rec.*
Astrolirus FISHER, 1917 [**Brisinga panamensis* LUDWIG, 1905; OD]. *Rec.*
Astrostephane FISHER, 1917 [**Brisinga moluccana* FISHER, 1916; OD]. *Rec.*
Belgicella LUDWIG, 1903 [**B. racowitzana*; OD]. *Rec.*
Brisingaster DE LORIOL, 1883 [**B. robillardi*; OD]. *Rec.*
Brisingella FISHER, 1917 [**Brisinga fragilis* FISHER, 1906; OD]. *Rec.*
Brisingenes FISHER, 1917 [**Brisinga mimica* FISHER, 1916; OD]. *Rec.*
Colpaster SLADEN, 1889 [**C. scutigerulus*; OD]. *Rec.*
Craterobrisinga FISCHER, 1916 [**Brisinga panopla* FISHER, 1906; OD]. *Rec.*
Freyella PERRIER, 1885 [**Freyella spinosa* PERRIER, 1885; SD FISHER, 1917]. *Rec.*
Freyellaster FISHER, 1918 [**Freyella fecunda* FISHER, 1905; OD]. *Rec.*
Hymenodiscus PERRIER, 1884 [**H. agassizi*; OD]. *Rec.*
Odinia PERRIER, 1885 [**Odinia semicoronata* PERRIER, 1885; SD FISHER, 1917]. *Rec.*
Odinella FISHER, 1940 [**O. nutrix*; OD]. *Rec.*
Parabrisinga HAYASHI, 1948 [**P. pellucida*; OD]. *Rec.*
Stegnobrisinga FISHER, 1916 [**Brisinga (Stegnobrisinga) placoderma* FISHER, 1916; OD]. *Rec.*
Genus? Brisingid species. *Oligo.*, USA(Calif.).

GENERIC NAMES OF INDETERMINATE OR UNRECOGNIZABLE STATUS APPLIED TO FOSSIL ASTEROIDEA

Coelaster AGASSIZ, 1836 [**C. couloni*; OD] Not figured. Unrecognizable. *L.Cret.(Neocom.)*, Switz.
Cribellites TATE, 1864 [**C. carbonarius*; OD]. No species figured. Possibly a urasterellid. *Carb.*, Eire.
Cupulaster FRITSCH, 1893 [**C. pauper*; OD] Unidentifiable juvenile. *U.Cret.(Turon.)*, Czech.
Palmasterias SAVI & MENEGHINI, 1851 [*non* BLAINVILLE in GERVAIS, 1842, unrecognized asteroid]. Stated by NEAVE to be a crinoid.
Rumanaster POPESCU-VOITESTI, 1911 [**R. uhligi*; OD]. Unidentifiable terminals and ?marginals of a phanerozonate form. *Eoc.*, Rumania.

Subclass OPHIUROIDEA Gray, 1840

[*nom. transl.* GREGORY, 1900, p. 259 (*ex* order Ophiuroidea D'ORBIGNY, 1852, p. 132, *nom. correct. pro* order Ophiurida GRAY, 1840, p. 132] [=order Ophiuridae ZITTEL, 1880, p. 439] [Diagnosis prepared by W. K. SPENCER & C. W. WRIGHT. Research on authorship and synonymy by H. B. FELL]

Asterozoa with disc in almost all forms sharply distinct from slender elongate arms; most primitive forms retaining traces of metapinnular structures in arms, derived from Somasteroidea, but in most of subclass bulk of arm cavity filled with complex ossicles of axial skeleton; ossicles of adaxial skeleton forming side plates, primitively movable but in advanced forms firmly fixed to axial ossicles. Respiration by means of gills which typically are placed in enlarged interrays. Spines inconspicuous or absent except on lateral edges of arms and jaws. *L.Ord.(Arenig.)-Rec.*

Some ophiuroid stocks contain forms in which the internal gills are concentrated near the center of the body, the interrays being then much reduced and the general body shape stellate. Some Paleozoic fossils apparently of this type have often been classified as asteroids. Although the general shape of most ophiuroids has been remarkably constant since the time of their earliest appearance (*Pradesura,* L.Arenig.) to the present, profound changes have affected the skeletal, particularly axial, structure of the arms, resulting in production of the so-called vertebrae, which permit the snake-like movements of the arms that give the subclass its name.

Order STENURIDA Spencer, 1951

Basins for seating tube feet shared, usually subequally, by 2 ambulacrals; arm joints and musculature allowing only simple movements; buccal slits present in many genera. *L.Ord.(L.Arenig.)-U.Dev.*

In one of the two suborders, Proturina, the ambulacrals remain in a primitive condition; in the other, Parophiurina, some stocks have ambulacrals that approach the condition of vertebrae.

Suborder PROTURINA Spencer & Wright, new suborder

Tube enclosing radial water vessel not strengthened along its adradial edges; ambulacral basins shallow. *L.Ord.(L.Arenig.)-U.Dev.*

The Pradesuridae are the oldest known Ophiuroidea. When first introduced they exhibited a typical ophiuroid disc and long slender arms; these were burrowing forms. They were then absent from known faunas

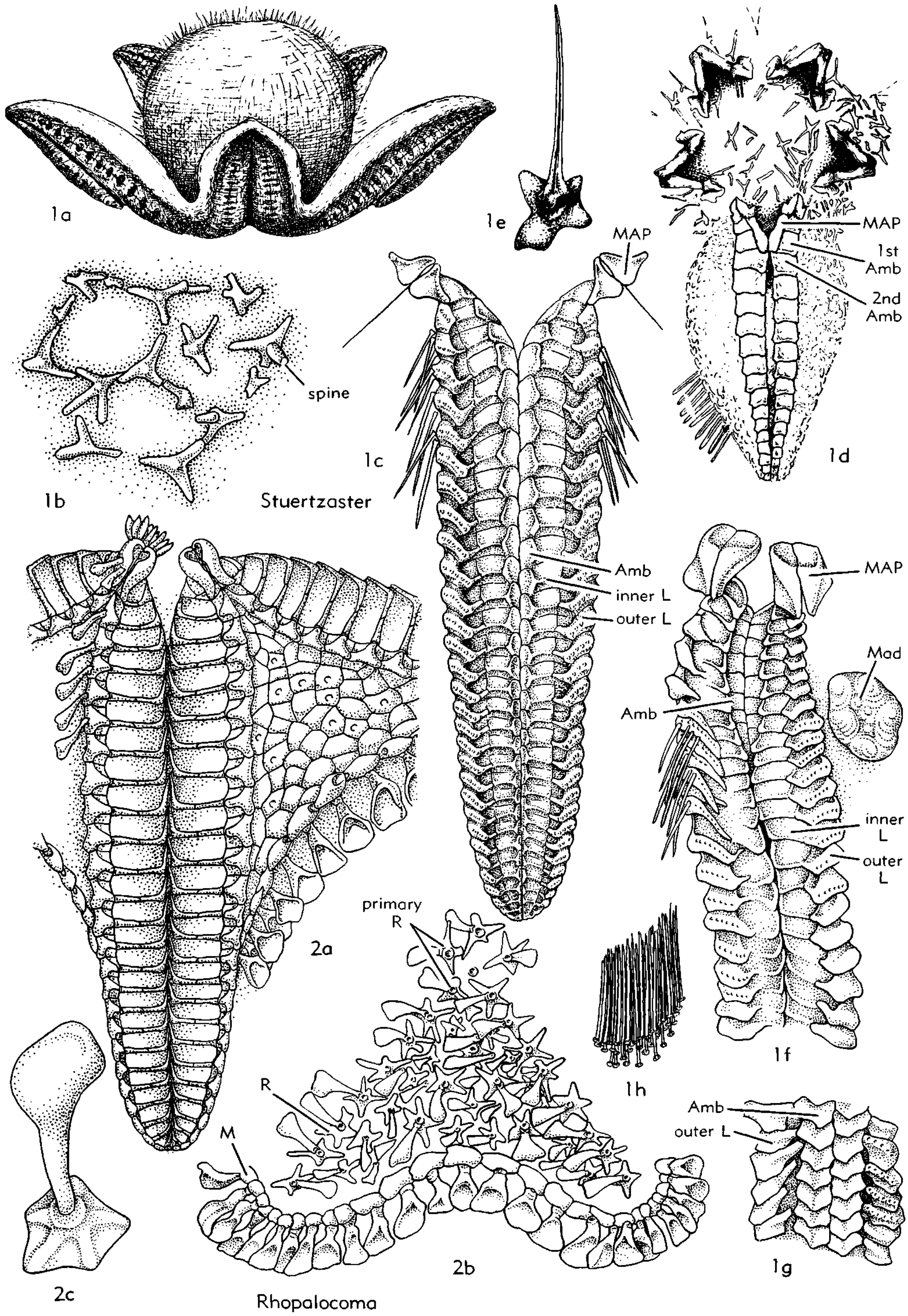


FIG. 68. Pradesuridae *(1);* Rhopalocomidae *(2).* [Explanation: *Amb,* ambulacral; *L,* lateral; *M,* marginal; *Mad,* madreporite; *MAP,* mouth-angle plate; *R,* radial.] (p. *U*80-*U*81).

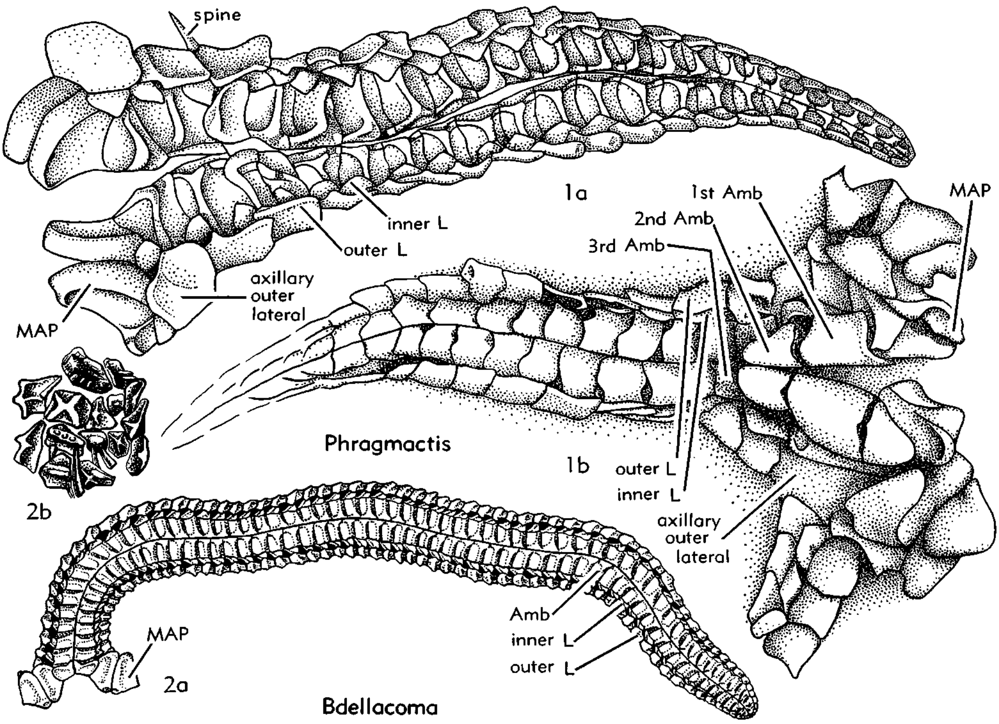


FIG. 69. Phragmactinidae *(1)*; Bdellacomidae *(2)*. [Explanation: *Amb*, ambulacral; *L*, lateral; *MAP*, mouth-angle plate.] (p. *U*81).

until the Late Silurian when they appeared in the lagoonal fauna at Leintwardine (Shropshire). Their general form was completely changed, for they exhibited high swollen aboral surface and short swollen arms. Evidently they had emerged to live on the sea floor. Several fossil specimens may be found crowded together on one slab, an indication of suspension feeding. The Rhopalocomidae, Phragmactinidae, and Bdellacomidae, whose ancestry is still unknown, are found in the same fauna as Pradesuridae, as well as later.

Family PRADESURIDAE Spencer, 1951

Laterals subventral, with only narrow swing. *L.Ord.-L.Dev.*

Earliest forms have a typical ophiuroid disc, undifferentiated proximal ambulacrals and laterals with narrow oral edges, whereas later ones have a swollen disc with reduced oral interrays, differentiated proximal ambulacrals and laterals with broad oral edges. All are assumed to have been sessile but not living in burrows.

Pradesura SPENCER, 1951 [**Palaeura jacobi* THORAL, 1935; OD]. Mouth-angle plates subtriangular; oral interrays large; aboral surface of disc covered with overlapping scales, each with central spine; madreporite small and thick with few grooves; proximal ambulacrals undifferentiated, buccal slits elongate; laterals with narrow oral edge. *L.Ord.(L.Arenig.)*, S.Fr.——FIG. 18,*1*, 23,*3*. **P. jacobi* (THORAL); 18,*1*, basins for tube feet; 23,*3*, oral surface of part of disc and arm, ×7 (133).

Stuertzaster ETHERIDGE, 1899 [*pro Palaeocoma* SALTER, 1857 (*non* D'ORBIGNY, 1850)] [**Palaeocoma marstoni* SALTER, 1857; SD SCHUCHERT, 1914] [=*Erinaceaster* LEHMANN, 1957]. Arms rather short, with rounded ends; aboral surface of disc highly swollen, with wide-meshed network of radiate spicules; oral interrays slight; mouth-angle plates subtriangular to elongate; proximal ambulacrals differentiated; laterals with broad oral edge. *U.Sil.-L.Dev.*, Eng.-Ger.——FIG. 68,*1a-d*. **S. marstoni* (SALTER), U.Sil., Eng. (Heref.); *1a*, profile, ×2; *1b*, part of aboral skeleton, ×8; *1c*, oral surface of arm; *1d*, ambulacrals and mouth frame in aboral view, ×3 (133).——FIG. 68,*1e*. *S. spinosissimus* (ROEMER), L.Dev., Ger.; ossicles of aboral surface, ×5 (133).——FIG. 68,*1f-h*. *S. colvini* (SALTER), U.Sil., Eng. (Heref.); *1f*, oral surface of arm, ×1; *1g*, aboral surface of part of arm, ×5; *1h*, aboral ossicles (133).

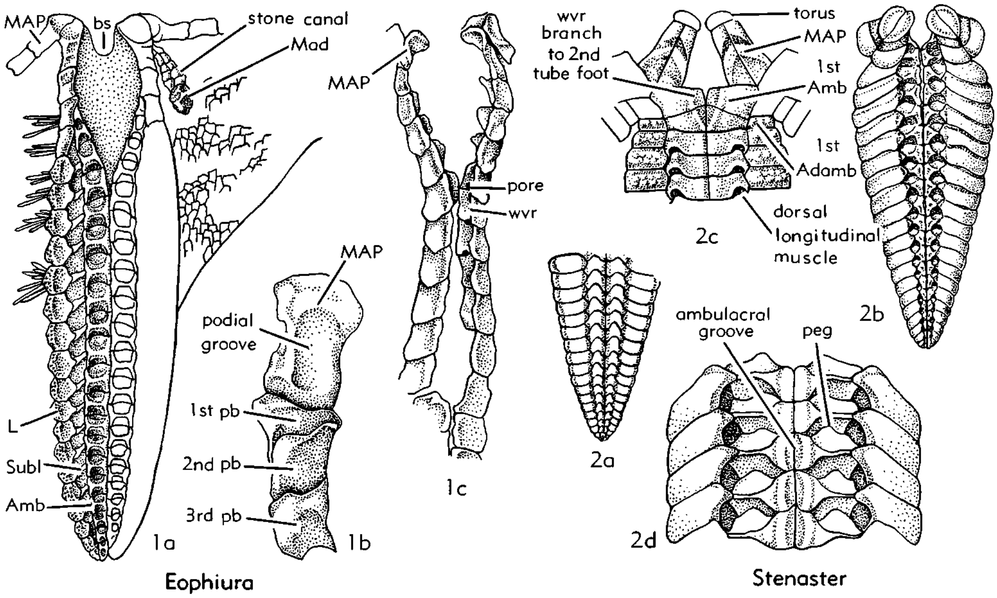


FIG. 70. Eophiuridae *(1)*, Stenasteridae *(2)*. [Explanation: *Adamb*, adambulacral; *Amb*, ambulacral; *bs*, buccal slit; *L*, lateral; *Mad*, madreporite; *MAP*, mouth-angle plate; *pb*, podial basin; *Subl*, sublateral: *wvr*, water-vessel-ring groove.] (p. *U*82).

Family PHRAGMACTINIDAE Spencer, 1951

[*nom. correct.* SPENCER & WRIGHT, herein (*ex* Phragmactidae SPENCER, 1951)]

Laterals embracing sides of arms; proximal buccal tentacles well developed; no aboral skeleton. *U.Ord.*

Phragmactis SPENCER, 1940 [**P. grayae*; OD]. Laterals with spines on low ridge; single interradial ossicles in position of buccal shields; mouth-angle plates short, deeply excavated for first buccal tentacles; proximal ambulacrals differentiated. *U. Ord.*, Scot.——FIG. 69,*1*. **P. grayae*, Girvan; *1a,b*, oral and aboral surfaces of arm, ×10 (133).

Family RHOPALOCOMIDAE Spencer & Wright, new family

Laterals subventral, with wide swing, bearing row of spines along their oral edge; ambulacral grooves wide; sublaterals well exposed. *U.Sil.-U.Dev.*

Rhopalocoma SALTER, 1857 [**Palaeocoma (R.) pyrotechnica*; OD]. Arms 5, short and blunt; disc with large oral interrays bordered by more or less cylindrical marginals, each bearing large club-shaped spine; proximal ambulacrals not differentiated; mouth-angle plates elongate; laterals articulating with sublaterals by ball-and-socket joints. *U.Sil.*, Eng.(Heref.).——FIG. 68,*2*. **R. pyrotechnica*; *2a*, oral surface of arm, ×6; *2b,c*, aboral ossicles, ×6, ×8 (133).

Ptilonaster HALL, 1868 [**P. princeps*; OD]. Arms 10; conical spine on each lateral; disc domed, with spicular skeleton; madreporite well developed near edge; mouth-angle plates elongate, wedge-shaped. *U.Dev.*, USA(N.Y.).

Family BDELLACOMIDAE Spencer & Wright, new family

Laterals embracing sides of very long narrow arms and bearing long spines; aboral skeleton composed of stout ossicles. *U.Sil.-L.Dev.*

Bdellacoma SALTER, 1857 [**Palaeocoma (B.) vermiformis*; OD]. Characters of family. *U.Sil.-L. Dev.*, Eng.-Ger.——FIG. 69,*2*. **B. vermiformis*, U.Sil., Eng.(Heref.); *2a*, oral surface of arm, ×4; *2b*, aboral ossicles, ×4 (133).

Suborder PAROPHIURINA Jaekel, 1923

[*nom. transl.* SPENCER & WRIGHT, herein (*ex* subclass Parophiura JAEKEL, 1923)]

Ambulacrals with strong median (adradial) ridges, completely enclosing radial channel; their distal ends not sufficiently elongated to form complete cups for seating tube feet. *L.Ord.-L.Dev.*

Members of this suborder have undifferentiated ambulacrals adjoining the buccal slits and thus all these plates resemble one

1 Medusaster

FIG. 71. Palaeuridae (p. U82).

another, as in *Pradesura* and early somasteroids. The canal leading to the madreporite is calcified, simulating the stone canal of asteroids; it is most readily seen in *Eophiura.*

Rather than coin a new subordinal name, it seems best to revive, redefine, and translate JAEKEL's name for a subclass that was erected primarily for *Eophiura* and *Palaeura.*

Family EOPHIURIDAE Schöndorf, 1910

[*non* Eophiuridae STÜRTZ, 1900 (*recte* Eophiuritidae) =Furcasteridae STÜRTZ, 1900]

Extremities of arms blunt; ambulaterals alternating; laterals and sublaterals in independent series. *L.Ord.*

Eophiura JAEKEL, 1903 [**E. bohemica* SCHUCHERT, 1914; SM]. Well-developed ball-and-socket joints between laterals and sublaterals, giving them wide swing; spines on laterals forming continuous border except at ends of arms where they are broadly scattered; buccal slits very deep, bordered by 5 or 6 ambulacrals; basins for tube feet deep, rounded. *L.Ord.(U.Arenig.),* Czech.——FIG. 70,*1*. **E. bohemica*; *1a,* part of oral surface, ×1; *1b,* angle of mouth frame from side, ×2.5; *1c,* mouth frame and ambulacrals from above, ×1 (133). (See Figs. 7,*3*; 10,*2*; 18,*2*.)

Family PALAEURIDAE Spencer, 1951

Like Eophiuridae but arm extremities tapering and no sublaterals visible; ambulacrals with incipient boot-shaped median ridge; disc rounded, with conspicuous interradial areas and well-defined scales. *L. Ord.-L.Dev.*

Palaeura JAEKEL, 1903 [**P. neglecta* SCHUCHERT, 1914; SM]. Arms 5. *L.Ord.(U.Arenig.),* Czech. ——FIG. 18,*3*. **P. neglecta* SCHUCHERT; ambulacrals (133).

Medusaster STÜRTZ, 1890 [**M. rhenanus*; OD]. Arms many. *L.Dev.,* Ger.——FIG. 71,*1*. **M. rhenanus*; aboral surface (116).

Family STENASTERIDAE Schuchert, 1914

Ambulacrals oposite, not alternating; laterals broad, each with several rows of pustules; disc with swollen aboral surface and reduced oral interrays. *M.Ord-U.Ord.*

Stenaster BILLINGS, 1858 [**S. salteri* (=**Uranaster obtusus* FORBES, 1848; SD SCHUCHERT, 1914] [=*Tetraster* NICHOLSON & ETHERIDGE, 1880]. *M.Ord.-U.Ord.,* Can.-Eu.-W.Asia.——FIG. 70,*2*. **S. obtusus* (FORBES), U.Ord., Scot.; *2a,b,* aboral and oral surface of arm, ×2.5; *2c,* mouth frame from aboral side, ×5; *2d,* aboral surface of arm, ×5 (133).

Order OEGOPHIURIDA Matsumoto, 1915

[*nom. transl. et correct.* FELL, 1962 (*ex* Oegophiuroidea MATSUMOTO, 1915)]

Hyponeural groove covered by soft skin, forming canal not closed over by ventral arm plates; disc covered by skin with or without granules or by imbricating scales; in Encrinasteridae scales at margin may fuse to form narrow frame of stout ossicles; madreporite lateral in early forms, though not so heavily calcified as in Stenurida, tending to move to oral side; no oral or radial shields, dorsal or ventral arm plates, genital plates or bursae; each ray with only 2 buccal tentacles; paired serial gonads extending along proximal part of arms. Gastric caeca entering arms (12). *L.Ord.-Rec.*

The laterals are fused with the sublaterals but junction of the components can be recognized in some cases (Fig. 73,*3*). The inner ends of the fused ossicles are articulated to the axial ossicles and can rotate to act as cover plates; as in Stenurida, they may be subventral in some families and wrapped round the side of the arms in others.

FELL's recognition of *Ophiocanops* as a living member of this largely Paleozoic order allows the soft-part characters to be diagnosed.

Large-scale models of vertebrae of fossil oegophiurids demonstrate their general resemblance to those of most modern ophiuroids (Fig. 72). An important functional difference lies in the very weak development of the ventral peg-and-socket joint; if any fossil oegophiurids had emerged from living

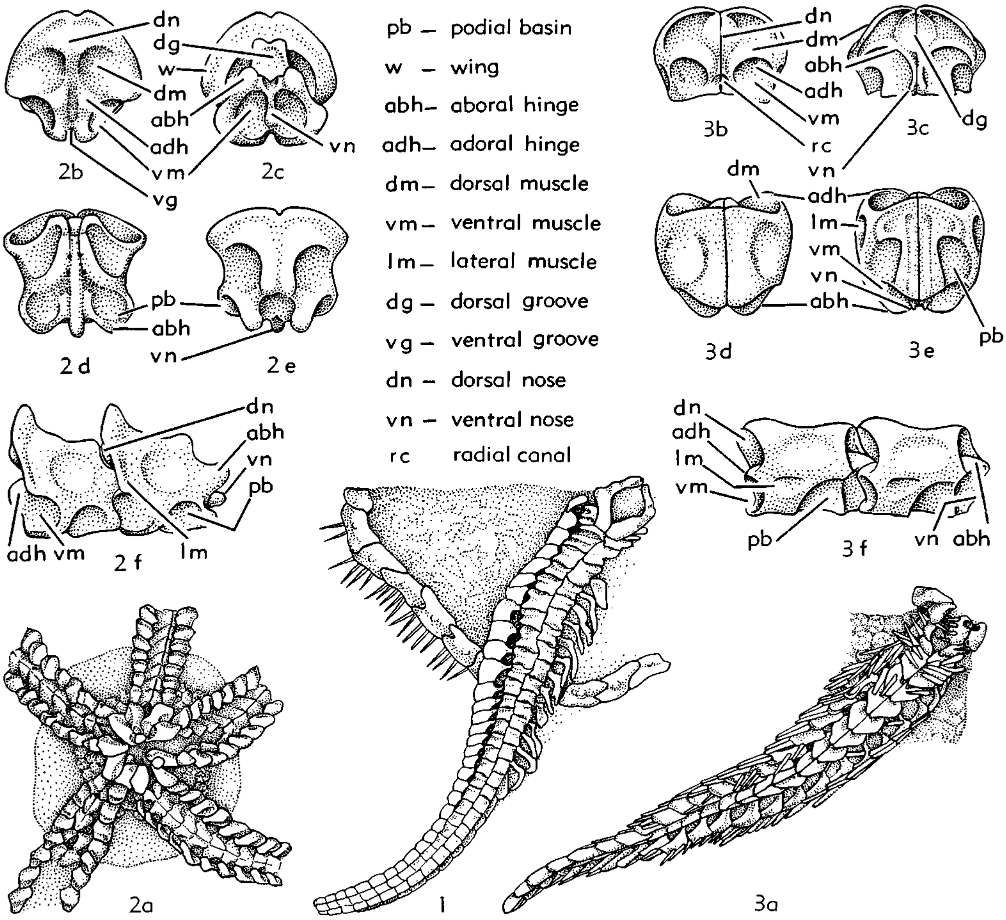


FIG. 72. Structural features of Oegophiurida (133).

1. Encrinaster grayae, U.Ord., Scot.; aboral surface showing marginal frame with slight spicular skeleton within frame, also showing ambulacrals with vertebrae and mouth frame from aboral side, ×2.

2. Vertebrae of *Hallaster* sp., Sil.. N.Am.; *2a,* disc and arm bases from oral side, ×2.5; *2b-f,* vertebra in adoral, aboral, apical, oral, and lateral views, enlarged.

3. *Ophiura* sp., Rec.; *3a,* oral surface of arm and part of disc, ×5; *3b-f,* vertebra in adoral, aboral, apical, oral, and lateral views, enlarged.

in burrows, they could not move speedily on the sea floor. The vertebrae have characteristic boot-shaped median ridges, under which lies the radial water vessel. As in Stenurida, the structure and muscles of the mouth frame allowed biting movements by the interradially placed mouth-angle plates, but the radial components, which remain passive in the bite, are different; in Stenurida, they comprise several ossicles in each ray but in Oegophiurida only a single pair. They move backwards in the initial stages of the bite, overriding the vertebrae (Fig. 73,*1,2*). The single row of long horizontal spines on the torus are quite unlike the vertically pointed teeth of typical Ophiurida.

Suborder LYSOPHIURINA Gregory, 1896

[*nom. correct.* SPENCER & WRIGHT, herein (*pro* Lysophiurae GREGORY, 1896)]

Halves of vertebrae alternating. *M.Ord.-L.Carb.*

Family ENCRINASTERIDAE Schuchert, 1914

[=Palaeobrisingidae STÜRTZ, 1890 (not founded on generic name) *(nom. nud.)*; Aspidosomatidae GREGORY, 1899 (*Aspidosoma* is junior homonym); Schoenasteridae SCHUCHERT, 1915; Euzonosomatidae SPENCER, 1930; Cheiropterasteridae SPENCER, 1930]

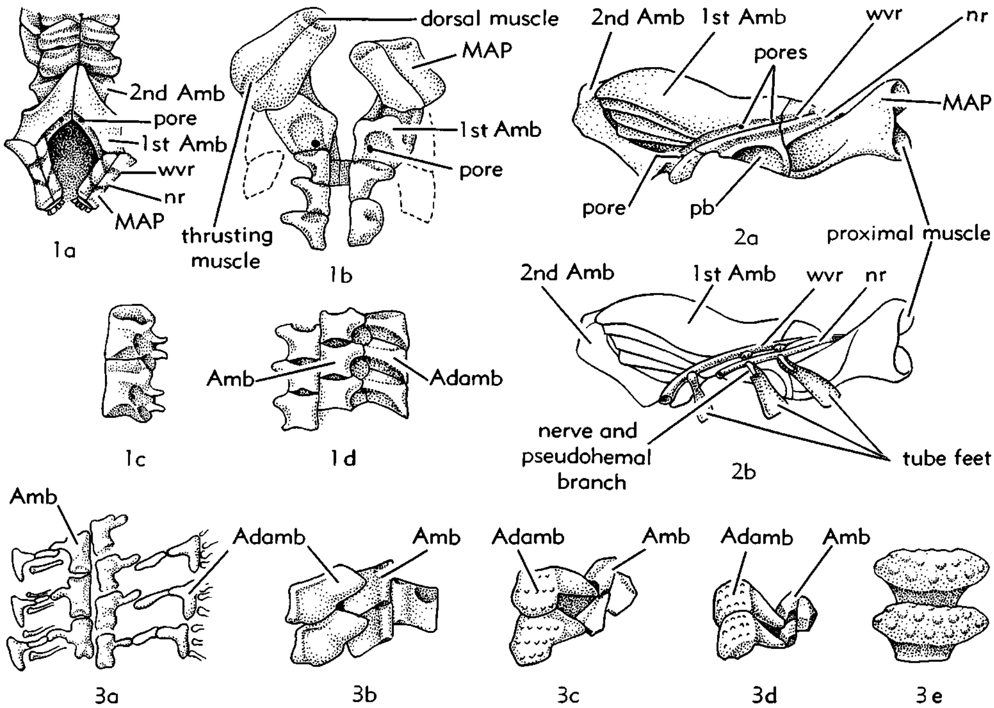


FIG. 73. Mouth frame, ambulacrals, and laterals of fossil Oegophiurida (133).

1. Encrinaster; 1a,b, E. grayae, U.Ord., Scot., apical and oral views of mouth frame showing low first pair of ambulacrals, reduced second ambulacrals, large cups for second buccal tentacles, and perforations in each cup for branch water vessel, ×10; *1c,* ambulacrals of *E. grayae* showing cups for tube feet and groove for outward swing of laterals, ×10; *1d, E. eifelensis,* L.Dev., Ger., showing laterals in outward position.

2. Lapworthura sp.; *2a,b,* inner views indicating large first two buccal tentacles and first ambulacral overriding next one, ×10.

3. Euzonosoma; 3a, laterals of *E. tischbeinianum* formed by fusion of two components, oral view, ×6; *3b-d,* laterals of *E. orbitoides,* apical and two oral views, ×10; *3e,* rows of pustules on laterals and grooves between adjacent ossicles of young *E. orbitoides,* ×20. [Explanation: *Adamb,* adambulacral; *Amb,* ambulacral; *MAP,* mouth-angle plate; *nr,* nerve-ring groove; *pb,* podial basin; *wvr,* water-vessel-ring groove.]

Laterals subventral, commonly with broad oral face, elongate transversely and with curved sutures, producing appearance of rope twists; oral interrays well developed; margin commonly bounded by frame of ossicles. *U.Ord.-L.Carb.*

Typical forms first discovered in the Lower Devonian of Germany were assigned to *Aspidosoma* or *Encrinaster* and thought to have affinities with Asteroidea. SCHÖNDORF (62) showed that they differed from modern Asteroidea and Ophiuroidea by having the radial water vessel enclosed as a canal within the ambulacrals but he gave too much importance to this feature in erecting a new suborder, Auluroidea; most early Ophiuroidea have such a feature and it persists in modern Euryalidae; the Encrinasteridae also have typical ophiuroid vertebrae.

Laterals of most genera of the Encrinasteridae have broad oral faces bearing rows of pustules, superficially resembling adambulacrals of Asteroidea (Fig. 73, *1c*). The stenurid *Stenaster* has laterals with similar oral face and with typical ophiuroid attachment to ambulacrals, so that they operate as cover plates with wide lateral swing.

A tendency for the disc to become swollen is carried to an extreme in *Cheiropteraster,* which also has tube feet confined to proximal parts of the arms and alongside deep buccal slits.

Encrinaster Haeckel, 1866 [**Aspidosoma arnoldi* Goldfuss, 1848; SD Schuchert, 1914] [=*Aspidosoma* Goldfuss, 1848 (*non* Fitzinger, 1845)]. Arms with many axial and adaxial elements; strong musculature between ambulacrals; marginal frame well marked. *U.Ord.-L.Carb.*, Eng.-Scot.-Ger.——Fig. 73,*1a-c*; 74,*3a-c*. *E. grayae* Spencer, U.Ord., Scot.(Girvan); 73,*1a-c*, mouth frame and ambulacrals, ×10; 74,*3a*, oral side of arm and part of disc, ×3.3; *3b*, part of oral surface of arm, ×10; *3c*, adambulacrals and ambulacrals in wide part of arm, ×10 (133).——Fig. 73,*1d*. *E. eifelensis* Schöndorf, L.Dev., Ger.; laterals (128).

Cheiropteraster Stürtz, 1890 [**C. giganteus*; OD].

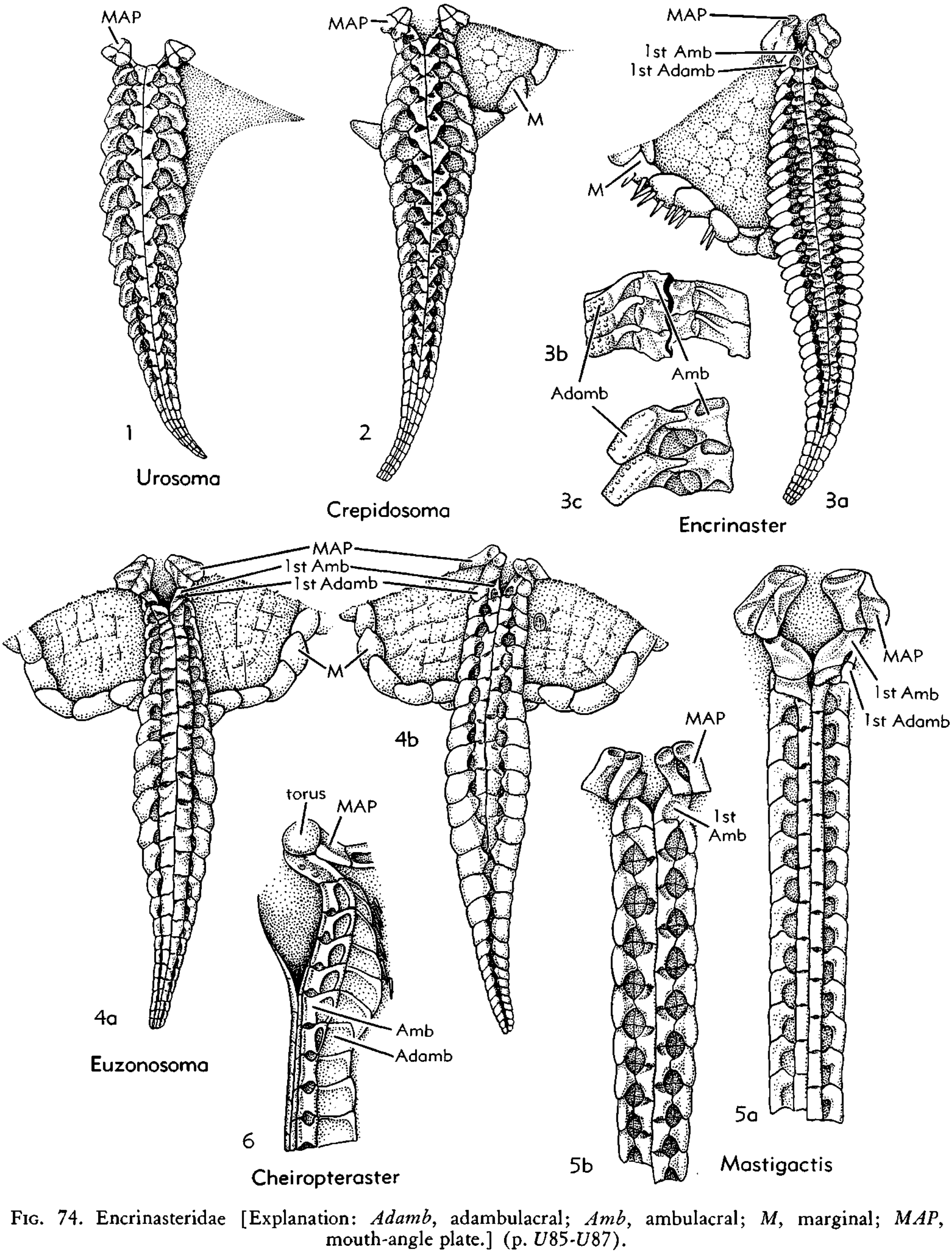


Fig. 74. Encrinasteridae [Explanation: *Adamb*, adambulacral; *Amb*, ambulacral; *M*, marginal; *MAP*, mouth-angle plate.] (p. *U*85-*U*87).

Vertebral boots elongate; lateral T-shaped, with prominent small spines at edge; proximal ambulacrals divergent, barely differentiated, disc highly swollen, covered by thick skin with granules but no visible scales; tube feet confined to bases of arms. *L.Dev.*, Ger.——FIG. 74,*6*. **C. giganteus*; area near mouth showing ambulacrals and laterals, ×1 (133). (See also Fig. 34.)

Crepidosoma SPENCER, 1930 [**C. wenlocki*; OD]. Like *Euzonosoma* but mouth frame weaker. *L.Sil., ?L.Dev.*, Scot.-Ger.——FIG. 74,*2*. **C. wenlocki*, L.Sil., Scot.; oral surface, ×7.5 (133).

Euzonosoma SPENCER, 1930 [**E. orbitoides*; OD]. [=*?Schoenaster* MEEK & WORTHEN, 1860 (virtually unrecognizable); *Jovaster* KEYES & BEANE, 1934; *Hymenosoma* LEHMANN, 1957]. Arms distinctly petaloid; laterals widest at middle of arm length; proximal ambulacrals well developed; fewer axial and adaxial elements in arms than in *Encrinaster*; mouth frame strong; marginal frame strong. *U. Ord.-U. Dev.*, Scot.-Ger.-USA (N.Y.-Ill.).——FIG. 73,*3*; 74,*4*. **E. orbitoides*, U.Ord., Scot.(Girvan); 73,*3*, laterals; 74,*4a,b*, aboral and oral surfaces of arm and part of disc, ×5 (133).

Loriolaster STÜRTZ, 1886 [**L. mirabilis*; OD]. Like *Cheiropteraster* but vertebral boots short; laterals deep, with short spines at edge; proximal ambulacrals in form of bow. *L.Dev.*, Ger.

Mastigactis SPENCER, 1930 [**Eugasterella aranea* RUEDEMANN, 1916; OD]. Arms long, narrow, straight-sided; vertebral boots elongate; mouth-

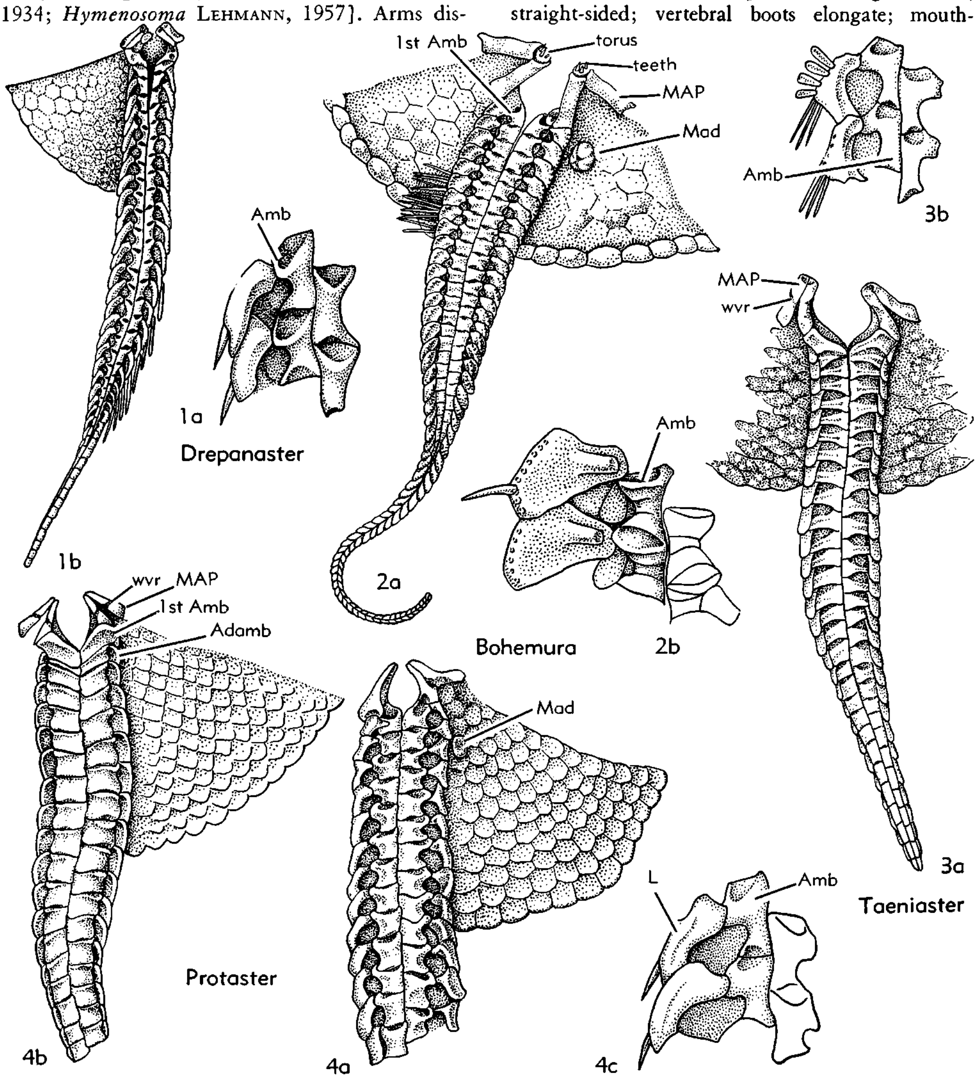


FIG. 75. Protasteridae. [Explanation: *Adamb*, adambulacral; *Amb*, ambulacral; *L*, lateral; *Mad*, madreporite; *MAP*, mouth-angle plate; *wvr*, water-vessel-ring groove.] (p. *U*87).

angle plates stout. *U.Ord.-U.Dev.*, Scot.-N.Am. ——FIG. 74,*5*. **M. aranea* (RUEDEMANN), U.Ord., Scot.(Girvan); *5a,b,* aboral and adoral surfaces of arm, ×4 (133).

Urosoma SPENCER, 1930 [**Uraster hirudo* FORBES, 1848; OD]. Like *Crepidosoma* but no marginal frame. *M.Ord.-U.Dev.*, Eu.-N.Am.——FIG. 74,*1*. **U. hirudo* (FORBES), U.Sil., Eng.; part of oral surface, ×7.5 (133).

Family PROTASTERIDAE S. A. Miller, 1889

[=Palaeophiuridae GREGORY, 1897; Taeniasteridae GREGORY, 1899; Palaeophyomyxidae STÜRTZ, 1900]

Laterals wrapped around sides of arms, forming side shields; edges of disc may be thickened but have no well-developed marginal frame; oral edges of ambulacrals narrow; laterals with vertical ridge bearing short or long spines; groove spines commonly present. *M.Ord.-L.Carb.*

Protaster FORBES, 1849 [**P. sedgwickii*; OD] [=*Eugaster* HALL, 1860; *Eugasterella* SCHUCHERT, 1914]. Depressions for attachment of dorsal arm muscles weak; laterals with articulating nose near oral edge. *M.Ord.-L.Carb.*, Eng.-USA(N.Y.).——FIG. 75,*4a,b*. **P. sedgwickii*, U.Sil., Eng.; *4a,b,* oral and aboral sides of arm and part of disc, ×0.6 (133).——FIG. 75,*4c*. *P. salteri* (FORBES), M.Ord., Wales; part of arm showing ambulacrals and laterals, ×20 (133).

Aulactis SPENCER, 1930 [**A. orthopaeda*; OD]. Vertebrae with wide shallow median groove on aboral side. *M.Ord.*, Wales.

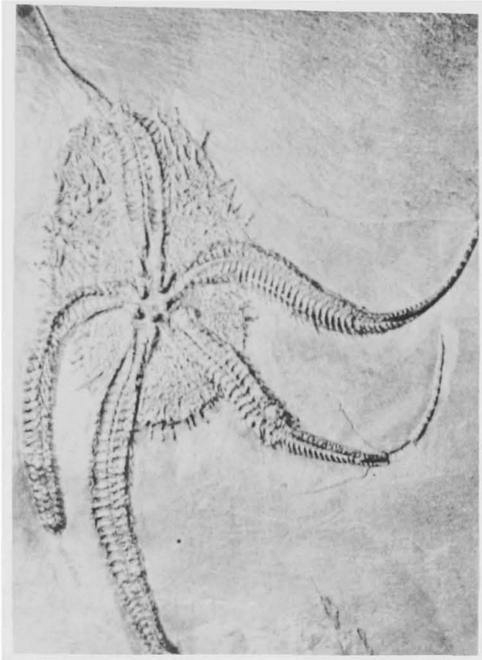
Bohemura JAEKEL, 1903 [**B. jahni*; OD]. Musculature like that of *Protaster* but articulating nose of laterals plain, distant from oral edge. *U.Ord.-L.Carb.*, Eu.-W.Asia.——FIG. 75,*2a*. **B. jahni*, U.Ord., Czech.; oral side of arm and part of disc, ×1 (133).——FIG. 75,*2b*. *B. groomi* SPENCER, U.Ord., Wales; part of arm showing ambulacrals and laterals, ×10 (133).

Drepanaster WHIDBORNE, 1898 [**Protaster scabrosus* WHIDBORNE, 1896; OD]. Arms very long and narrow; muscle depressions as in *Taeniaster*. *U.Ord.-L.Carb.*, N.Am.-Eng.-Scot.——FIG. 75,*1a*. **D. scabrosus*, L.Carb., Eng.(Devon.); part of arm showing ambulacrals and laterals, ×10 (133). ——FIG. 75,*1b*. *D. grayae* SPENCER, U.Ord., Scot.; oral side of arm and part of disc, ×2 (133).

?**Inyoaster** PHLEGER, 1936 [**I. bradleyi*; OD]. Unrecognizable. *Ord.*, Calif.

Mastigophiura LEHMANN, 1957 [**M. grandis*; OD]. Differs from *Taeniaster* only in having large spines on disc, perhaps only a specific difference. *L.Dev.*, Ger.——FIG. 76,*1*. **M. grandis*; oral side, ×0.5 (116).

Palaeophiura STÜRTZ, 1890 [**P. simplex*; OD]. Vertebral boots long, narrow; laterals with spine-like ridge projecting considerably outward. *L. Dev.*, Ger.



1 Mastigophiura

FIG. 76. Protasteridae (p. *U*87).

Taeniaster BILLINGS, 1858 [**Palaeocoma spinosa* BILLINGS, 1857; SD SCHUCHERT, 1914] [=*Alepidaster* MEEK, 1872; *Protasterina* ULRICH, 1878; *Bundenbachia* STÜRTZ, 1886; *Palaeophiomyxa* STÜRTZ, 1890]. Arms not conspicuously narrow; depressions for aboral muscles deep. *M.Ord.-L. Dev.*, N.Am.-Ger.——FIGS. 75,*3*. **T. spinosus* (BILLINGS), M.Ord.(Trenton.), Ont.; *3a,* aboral side and part of disc, ×2; *3b,* part of arm showing ambulacrals and laterals, ×20 (133). (See also Fig. 4, 18,*4*.)

Suborder ZEUGOPHIURINA Matsumoto, 1929

[*nom. transl. et correct.* FELL, 1963 (*ex* Zeugophiuroidea MATSUMOTO, 1929)]

Halves of vertebrae opposite, separate or fused. *L.Ord.-Rec.*

Members of this suborder in general structure closely resemble Protasteridae except in position of the vertebral halves. They are distinguished from early Ophiurida only by position of the laterals; in Zeugophiurina they are separated by a wide groove that exposes the oral surface of the vertebrae, except for a covering of soft skin,

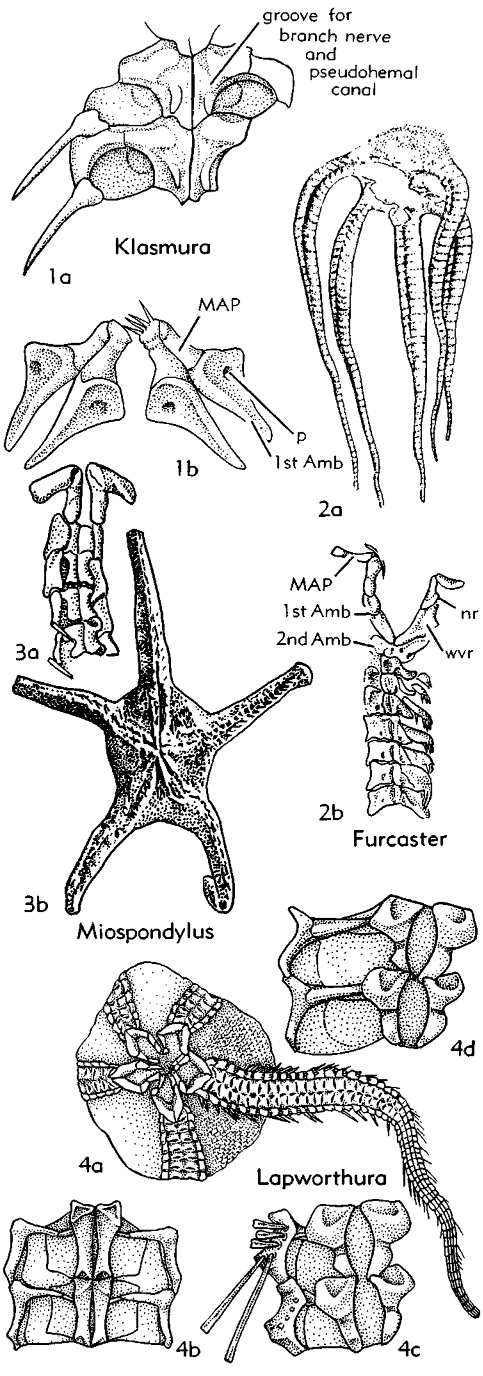


FIG. 77. Lapworthuridae *(3-4)*; Furcasteridae *(2)*; Klasmuridae *(1)*. [Explanation: *Amb*, ambulacral; *MAP*, mouth-angle plate; *nr*, nerve-ring groove; *p*, podial basin; *wvr*, water-vessel-ring groove.] (p. *U*88-*U*89).

whereas in Ophiurida the laterals meet and cover the oral surface of the vertebrae.

Specimens of the earliest genus, *Hallaster*, are found with arms upflexed, indicating a burrowing habit. Later genera (e.g., *Lapworthura, Klasmura*) were probably emergent. *Klasmura* seems to have lived commensally with crinoids.

Family LAPWORTHURIDAE Gregory, 1897

[=Hallasteridae SPENCER, 1925]

Disc large, arms robust, with short or long conical spines, generally set in row not parallel to arm axis. *L.Ord.-L.Dev.*

Lapworthura GREGORY, 1897 [**Protaster miltoni* SALTER, 1857; OD]. Arms low, broad; basins for tube feet large; laterals with elongate noses, vertical spines long, in rows at wide angle to arm axis. *U.Ord.-Sil.*, Eng.-Scot.-Australia.——FIG. 77, *4*. **L. miltoni* (SALTER), M.Sil., Eng.(Heref.), *4a*, aboral side of disc and arm, ×1.5; *4b-d*, arm showing ambulacrals and laterals, enl. (133).

Hallaster STÜRTZ, 1886 [**Protaster forbesi* HALL, 1861 (=**Palaeocoma cylindrica* BILLINGS, 1857); OD] [=*Taeniura* GREGORY, 1897 (*non* MÜLLER & HEULE, 1837); *Hypophiura* JAEKEL, 1903]. Vertical spines longer than arm segment; basins for tube feet narrow, boots with blunt toe; laterals with short noses. *L.Ord.-L.Dev.*, N.Am.-Scot.——FIG. 72,*2*. **H. cylindricus* (BILLINGS), M.Ord.(Trenton.), Ont.; *2a*, oral side of disc and arm bases; *2b-f*, vertebrae (133).

Miospondylus GREGORY, 1897 [**Ophiura rhenana* STÜRTZ, 1893; OD]. Arms moderately high; vertical spines mostly short and unequal, long spines lying across ambulacral groove. *L.Dev.*, Ger.——FIG. 77,*3*. **M. rhenanus* (STÜRTZ), Bundenbach; *3a*, side view of arm, ×3; *3b*, oral side, ×0.7 (133).

Family FURCASTERIDAE Stürtz, 1900

[=Eoluidiidae GREGORY, 1897; Eophiuridae (*recte* Eophiuritidae), Palaeospondylidae STÜRTZ, 1900]

Like Lapworthuridae but with subequal needle-shaped spines in rows close to sides of arms and parallel to arm axes. *U.Ord.-Miss.*

Furcaster STÜRTZ, 1886 [**F. palaeozoicus* (=**Protaster leptosoma* SLATER, 1857); OD] [=*Palastropecten, Eoluidia* STÜRTZ, 1886; *Squamaster* RINGUEBERG, 1886; *Eophiurites* STÜRTZ, 1900; *Palaespondylus, Palaeospondylus* STÜRTZ, 1900 (*non* TRAQUAIR, 1890); *Sympterura* BATHER, 1905; *Gregoriura* CHAPMAN, 1907; *Rhodostoma* SOLLAS & SOLLAS, 1912]. Interior of laterals with long vertical ridges normal to adoral edge; vertebrae with median hollow; mouth frame petaloid;

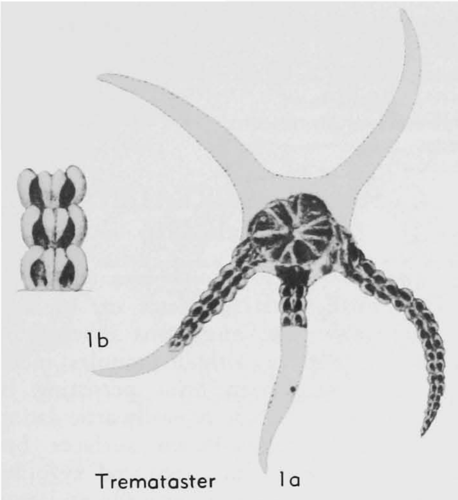


FIG. 78. Furcasteridae (p. *U89*).

fossils showing arms stiffly upright. *U.Ord.-Miss.*, Eu.-N.Am.-Australia.——FIG. 77,*2*. **F. leptosoma* (SALTER), L.Dev., Ger.; *2a*, specimen with raised arms, ×1; *2b*, part of aboral surface of arm, ×2.5 (133).

Tremataster WORTHEN & MILLER, 1883 [**T. difficilis*; OD]. Imperfectly known but apparently like *Furcaster* except that arms are flexuous. *Miss.*, USA(Ill.).——FIG. 78,*1*. **T. difficilis*; *1a*, oral surface; *1b*, part of arm, enl. (138).

Family KLASMURIDAE Spencer, 1925

Laterals with single long flat hollow spine; disc and arms covered by thick skin and long spines; mouth frame stout; madreporite ventral. *U.Dev.*

Klasmura RUEDEMANN, 1916 [**K. mirabilis*; OD]. Arms generally enrolled; specimens found in association with crinoids, with which they probably lived commensally. *U.Dev.*, USA(N.Y.).——FIG. 77,*1*. **K. mirabilis*; *1a*, part of oral surface, ×10; *1b*, oral side of mouth frame, ×10 (133).

Family OPHIOCANOPIDAE Mortensen, 1933

Laterals with rather few stout spines more or less parallel to arm axis, those on oral surface hooked and with course serrations, as in Euryalina; madreporite marginal; articulation of vertebrae tending to euryaline type (streptospondylous) (12). *Rec.*

Ophiocanops KOEHLER, 1922 [**O. fugiens*; OD]. *Rec.*

Order PHRYNOPHIURIDA Matsumoto, 1915

Disc and arms covered with skin; radial shields and genital plates articulating by simple facet or transverse ridge on each plate; peristomial plates large, entire or double or triple; oral frames entire, without well-developed lateral wings; dorsal arm plates absent or rudimentary; lateral arm plates ventral or subventral. *L.Dev.-Rec.*

Suborder OPHIOMYXINA Fell, 1962

Disc and arms covered by thick soft skin overlying plates and scales. *Rec.*

Family OPHIOMYXIDAE Ljungman, 1866

Characters of suborder. *Rec.*

Subfamily OPHIOMYXINAE Ljungman, 1866

[*nom. transl.* MATSUMOTO, 1915 (*ex* Ophiomyxidae LJUNGMAN, 1866)]

Oral shields small; adoral plates long and slender; vertebrae long and slender, articular peg well developed. *Rec.*

Ophiomyxa MÜLLER & TROSCHEL, 1840 [**Ophiura pentagona* LAMARCK, 1816; OD]. *Rec.*

Astrogeron VERRILL, 1899 [**Ophiogeron supinus* LYMAN, 1883; OD]. *Rec.*

Neoplax BELL, 1884 [**N. ophiodes*; OD]. *Rec.*

Ophiodera VERRILL, 1899 [**Ophiomyxa serpentaria* LYMAN, 1883; OD]. *Rec.*

Ophiogeron LYMAN, 1878 [**O. edentulus*; OD]. *Rec.*

Ophiohelus LYMAN, 1880 [**Ophiohelus umbella* LYMAN, 1880; SD H. L. CLARK, 1915]. *Rec.*

Ophiohyalus MATSUMOTO, 1915 [**O. gotoi*; OD]. *Rec.*

Ophiohymen H. L. CLARK, 1911 [**O. gymnodiscus*; OD]. *Rec.*

Ophioleptoplax H. L. CLARK, 1911 [**O. megapora*; OD]. *Rec.*

Ophiolycus MORTENSEN, 1933 [**O. inermis*; OD]. *Rec.*

Ophiomora KOEHLER, 1907 [**O. elegans*; OD]. *Rec.*

Ophiosciasma LYMAN, 1878 [**O. attenuatum*; OD]. *Rec.*

Ophioscolex MÜLLER & TROSCHEL, 1842 [**O. glacialis*; OD] [=*Ophiocynodus* H. L. CLARK, 1911]. *Rec.*

Ophiostiba MATSUMOTO, 1915 [**O. hidekii*; OD]. *Rec.*

Ophiostyracium H. L. CLARK, 1911 [**O. trachyacanthum*; OD]. *Rec.*

Ophiosyzygus H. L. CLARK, 1911 [**O. disacanthus*; OD]. *Rec.*

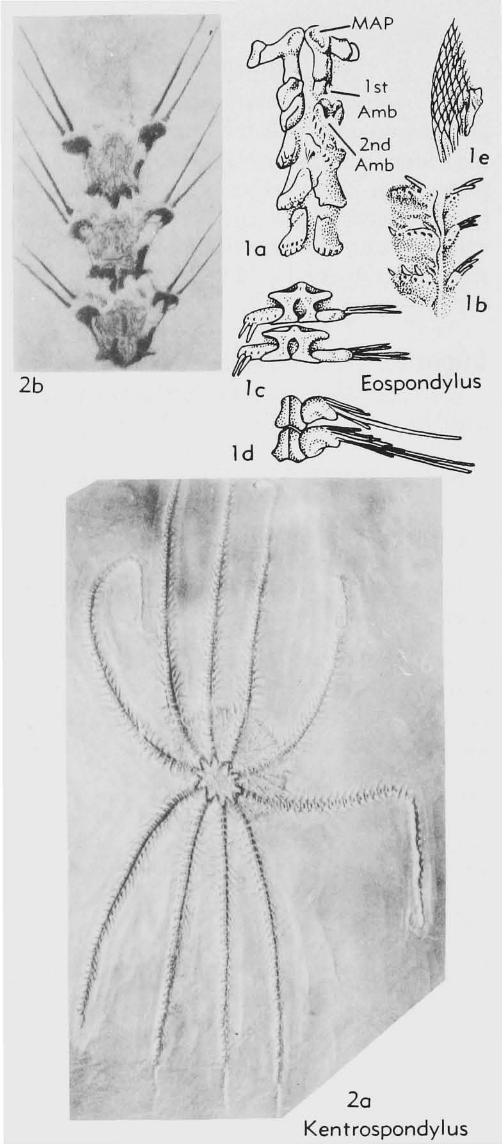


FIG. 79. Eospondylidae. [Explanation: *Amb*, ambulacral; *MAP*, mouth-angle plate.] (p. U90).

Subfamily OPHIOBYRSINAE Matsumoto, 1915

Oral shields and adoral plates fused together, massive; vertebrae short and thick, articular peg rudimentary or lacking. *Rec.*

Ophiobyrsa LYMAN, 1878 [**O. rudis*; OD]. *Rec.*

Astrogymnotes H. L. CLARK, 1914 [**A. catasticta*; OD] [=*Ophiovesta* KOEHLER, 1931]. *Rec.*

Ophiobrachion LYMAN, 1883 [**O. uncinatus*; OD]. *Rec.*

Ophiobyrsella VERRILL, 1899 [**Ophiobyrsa serpens* LYMAN, 1883; OD]. *Rec.*

Ophiophrixus H. L. CLARK, 1911 [**O. acanthinus*; OD]. *Rec.*

Ophioschiza H. L. CLARK, 1911 [**O. monacantha*; OD]. *Rec.*

Ophiosmilax MATSUMOTO, 1915 [**O. mirabilis*; OD]. *Rec.*

Suborder EURYALINA Lamarck, 1816

[*nom. correct.* FELL, 1962 (*pro* Euryalae MÜLLER & TROSCHEL, 1840, *nom. transl. ex* euryales LAMARCK, 1816)]

Disc small, with no plates or, in later forms, scales; disc and arms covered by thick skin, with or without granules; metapinnular structure in arms persisting in some genera; vertebrae typically articulating by broad hourglass-shaped surfaces but Onychasteridae retaining reduced zygophiuroid peg; arms coiling vertically and may branch. *L.Dev.-Rec.*

Family EOSPONDYLIDAE Spencer & Wright, new family

Arms 5 or 10; laterals well separated on aboral surface but closely approximated on oral surface of arms; laterals large and sickle-shaped. *L.Dev.*

Eospondylus GREGORY, 1897 [*pro Ophiurella* STÜRTZ, 1886 (*non* AGASSIZ, 1834] [**Ophiurella primigenia* STÜRTZ, 1886; OD]. Arms 5; vertical spines unequal, some very long; disc covered with smooth overlapping scales. *L.Dev.*, Ger.——FIG. 79,*1*. **E. primigenius* (STÜRTZ); *1a,b,* proximal part and side of arm; *1c,d,* oral and aboral surface of arm; *1e,* part of disc, ×5 (133).

Kentrospondylus LEHMANN, 1957 [**K. decadactylus*; OD]. Arms 10, very long and slender, round in section; vertical spines more or less equal, very long; disc with granules, some bearing long slender spines. *L.Dev.*, Ger.——FIG. 79,*2*. **K. decadactylus*; *2a,* aboral surface, ×0.5; *2b,* arm, enl. (116).

Family ONYCHASTERIDAE Miller, 1889

Arms 5, but may branch; laterals small. *L.Carb.*

This family closely resembles Recent Euryalina in the narrow high vertebrae with intervertebral articulation concentrated in the center of the ossicles, small laterals, small basins for the tube feet, and branching of the arms. The movement of the arms in *Onychaster*, however, was restricted by the small zygophiuroid peg (Fig. 80,2).

Onychaster MEEK & WORTHEN, 1868 [**O. flexilis*; OD]. Characters of family. *L.Carb.(Miss.)*, N. Am.-Eng.-Scot.——FIG. 80,*1*. *O. barrisi* (HALL),

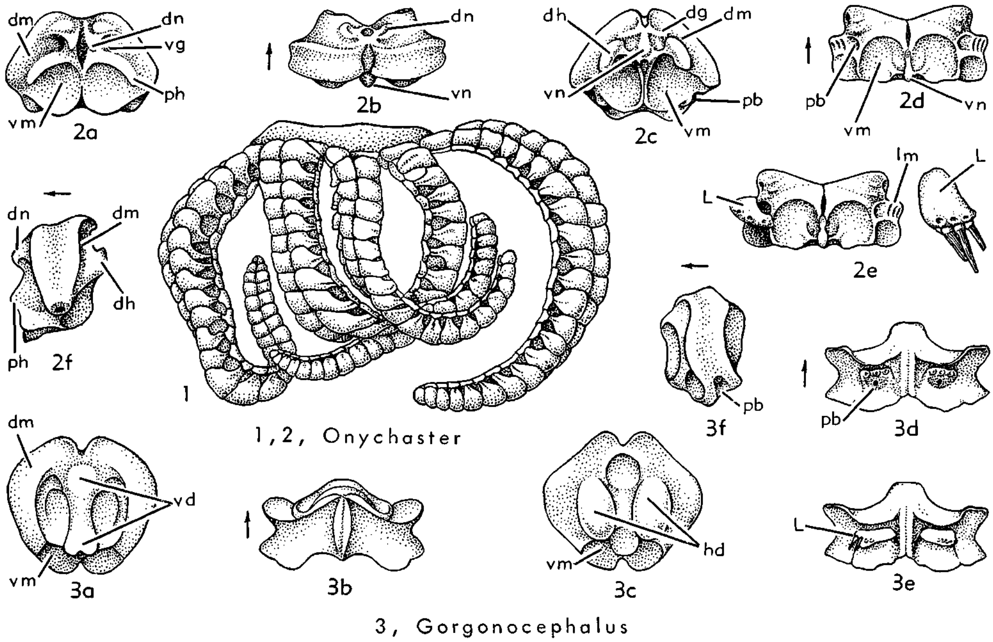


FIG. 80. Onychasteridae *(1-2)*; Gorgonocephalidae (3) (p. *U*90-*U*91).

Eng.(Devon.); side view, ×2 (133).——FIG. 80, *2,3.* **O. flexilis*, USA(Ind.); vertebrae *(2a-f)* compared with *Gorgonocephalus* (Rec.) *(3a-f)*, enlarged: *a*, proximal face; *b*, aboral side (arrow toward mouth); *c*, distal face; *d*, oral side, with laterals removed; *e*, oral side with laterals in position; *f*, lateral view (arrow toward mouth) (133).

Family ASTERONYCHIDAE Müller & Troschel, 1842

Arms not branched; distinct metapinnular structure; vertebrae with ventral furrow; distal arm joints not long and slender; distally lateral arms spines may be transformed into hooklets that do not have perforated lamina. Gonads restricted to disc. *?U.Cret., Rec.*

Asteronyx MÜLLER & TROSCHEL, 1842 [**A. loveni*; OD]. Disc and arms covered aborally by naked skin; more than 3 arm spines, outer ones modified as hooklets. [Isolated ossicles from Upper Cretaceous may belong here.] *?U.Cret.(Senon.)*, W.Eu., *Rec.*

Astrodia VERRILL, 1899 [**A. tenuispina*; OD]. *Rec.*

Family ASTEROSCHEMATIDAE Verrill, 1899

Similar to Asteronychidae but gonads extending at least midway along arms. *Rec.*

Asteroschema OERSTED & LÜTKEN, 1856 [**Asterias oligactes* PALLAS, 1788; OD] [=*Laspalia* LJUNGMAN, 1872 (*non* GRAY, 1840)]. *Rec.*

Astrobrachion DÖDERLEIN, 1927 [**Ophiocreas constrictus* FARQUAR, 1900; OD]. *Rec.*

Astrocharis KOEHLER, 1904 [**A. virgo*; OD]. *Rec.*

Astroscolex MORTENSEN, 1933 [**Ophiocreas adhaerens* STUDER, 1884; OD]. *Rec.*

Ophiocreas LYMAN, 1879 [**O. lumbricus*; OD]. *Rec.*

Ophiuropsis STUDER, 1884 [**O. lymani*; OD]. *Rec.*

Family GORGONOCEPHALIDAE Ljungman, 1867

[*incl.* Astrotominae MATSUMOTO, 1915]

Arms simple or branching; ventral furrow open; dorsal surface of arms bearing hooks without lamina of regularly arranged holes. [An undescribed genus occurs in the Oligocene of New Zealand (FELL, *in litt.*).] *Oligo.-Rec.*

Gorgonocephalus LEACH, 1815 [**Asterias caput-medusae* LINNÉ, 1758; SD H. L. CLARK, 1915]. *Rec.*——FIG. 80,*3*. *G.* sp.; *3a-f*, vertebrae (see under *Onychaster*, p. U90 for details).
Asteroporpa OERSTED & LÜTKEN, 1856 [**A. annulata* LÜTKEN, 1856; OD]. *Rec.*
Astracme DÖDERLEIN, 1927 [**Astrophyton mucronatum* LYMAN, 1869; OD]. *Rec.*
Astroboa DÖDERLEIN, 1911 [**Astrophyton clavatum* LYMAN, 1861; OD] [=*Astrorhaphis* DÖDERLEIN, 1911]. *Rec.*
Astrocaneum DÖDERLEIN, 1911 [**Astrophyton spinosum* LYMAN, 1875; OD] [=*Astrocynodus* A. H. CLARK, 1918]. *Rec.*
Astrochalcis KOEHLER, 1905 [**A. tuberculosus*; OD]. *Rec.*
Astrochele VERRILL, 1878 [**A. lymani*; OD]. *Rec.*
Astrochlamys KOEHLER, 1911 [**A. bruneus*; OD]. *Rec.*
Astrocladus VERRILL, 1899 [**Euryale verrucosum* LAMARCK, 1816 (=**Asterias euryale* RETZIUS, 1783); OD]. *Rec.*
Astroclon LYMAN, 1879 [**A. propugnatoris*; OD]. *Rec.*
Astrocnida LYMAN, 1872 [**Trichaster isidis* DUCHASSAING, 1850; OD]. *Rec.*
Astroconus DÖDERLEIN, 1911 [**Astrophyton australe* VERRILL, 1876; OD]. *Rec.*
Astrocrius DÖDERLEIN, 1927 [**Astrotoma sobrinus* MATSUMOTO, 1912; OD]. *Rec.*
Astrocyclus DÖDERLEIN, 1911 [**Astrophyton caecilia* LÜTKEN, 1856; OD]. *Rec.*
Astrodendrum DÖDERLEIN, 1911 [**Gorgonocephalus sagaminus* DÖDERLEIN, 1902; OD]. *Rec.*
Astrodictyum DÖDERLEIN, 1927 [**Astrophyton panamense* VERRILL, 1867; OD]. *Rec.*
Astroglymna DÖDERLEIN, 1927 [*pro Astrodactylus* DÖDERLEIN, 1911 (*non* HOGG, 1839)] [**Astrophyton sculptum* DÖDERLEIN, 1896; OD]. *Rec.*
Astrogomphus LYMAN, 1869 [**A. vallatus*; OD]. *Rec.*
Astrogordius DÖDERLEIN, 1911 [**Astrophyton cacaoticum* LYMAN, 1874; OD]. *Rec.*
Astrohamma DÖDERLEIN, 1930 [**Astrothamnus tuberculatus* KOEHLER, 1923; OD]. *Rec.*
Astrohelix DÖDERLEIN, 1930 [**Astrotoma bellator* KOEHLER, 1904; OD]. *Rec.*
Astrophyton FLEMING, 1828 [**Euryale muricatum* LAMARCK, 1816; SD H. L. CLARK, 1915]. *Rec.*
Astroplegma DÖDERLEIN, 1928 [**A. expansum*, OD]. *Rec.*
Astrospartus DÖDERLEIN, 1911 [**Euryale mediterraneus* RISSO, 1826; OD]. *Rec.*
Astrostephanus DÖDERLEIN, 1930 [**Astrotoma vecors* KOEHLER, 1904; OD]. *Rec.*
Astrothamnus MATSUMOTO, 1915 [**Astrotoma echinacea* MATSUMOTO, 1912; OD]. *Rec.*
Astrothorax DÖDERLEIN, 1911 [**A. misakiensis*; OD]. *Rec.*
Astrothrombus H. L. CLARK, 1909 [**A. rugosus*; OD]. *Rec.*
Astrotoma LYMAN, 1875 [**A. agassizii*; OD]. *Rec.*
Astrozona DÖDERLEIN, 1930 [**Astrogomphus munitus* KOEHLER, 1904; OD]. *Rec.*
Conocladus H. L. CLARK, 1909 [**C. oxyconus*; OD]. *Rec.*
Ophiocrene BELL, 1894 [**O. oenigma*; OD]. *Rec.*
Schizostella A. H. CLARK, 1952 [**S. bifurcata*; OD]. *Rec.*

Family EURYALIDAE Gray, 1840

[=Trichasteridae DÖDERLEIN, 1911]

Metapinnular structure may survive; *Trichaster*, for example, has metapinnules consisting of 3 virgals; ventral groove closed and radial canal and nerve enclosed within vertebrae; distal arm joints long and slender; no dorsal hooks on arms but distally lateral spines may be modified into hooklets, which have a perforated lamina. Gonads extending into arms. *Rec.*

Euryale? liasica QUENSTEDT, 1876, of which the figures suggest *Trichaster*, is reported by SEILACHER (1953) to consist of casts of resting places of normal ophiuroids, the traces of moving arm tips simulating branching arms.

Euryale OKEN, 1815 [**Euryale asperum* LAMARCK, 1816; SD H. L. CLARK, 1915]. *Rec.*
Asteromorpha LÜTKEN, 1869 [**A. steenstrupii* (=**Asteroschema rousseaui* MICHELIN, 1862); OD]. *Rec.*
Asterostegus MORTENSEN, 1933 [**A. tuberculatus*; OD]. *Rec.*
Astroceras LYMAN, 1879 [**A. pergamena*; OD]. *Rec.*
Sthenocephalus KOEHLER, 1898 [**S. indicus*; OD]. *Rec.*
Trichaster AGASSIZ, 1836 [**Euryale palmiferum* LAMARCK, 1816; OD]. *Rec.*

Order OPHIURIDA Müller & Troschel, 1840

[*nom. correct.* FELL, 1960 (*pro* Ophiureae MÜLLER & TROSCHEL, 1840)] [=Myophiuroidea MATSUMOTO, 1917]

Ambulacral grooves closed by growth of laterals on oral side toward mid-line of arms. Vertebrae subcylindrical, generally with zygophiuroid joints; vertebral halves opposite and united in pairs; dorsal and ventral shields (arm plates) present in all except most primitive forms. Radial shields, genital plates and buccal shields also generally present; no independent madreporite; stone canal opens on buccal shield. *Sil.-Rec.*

Earliest Ophiurida occur in Silurian rocks of the Argentine, followed by those of Devonian rocks in Belgium and western Germany. Minute details visible in Belgian specimens (35) show some features transitional between Oegophiurida and Ophiurida and others typically ophiurid. All stages in differentiation of aboral skeletal elements of disc into large units are found; the process begins at the margin and continues inward. *Ophiurina* (L.Dev.) has merely a thickened margin, whereas *Ophiaulax* (U. Dev.) and *Stephanoura* (U.Dev.) have a strong marginal frame not unlike that of *Euzonostoma*. Ossicles in the marginal frame of *Stephanoura* are incipient radial shields, for they articulate with a genital bar. In *Aganaster* (Miss.) the radial shields are fused in pairs and cover most of the disc except the center, which is occupied by a centrale and a primary circlet, as in some early Mesozoic ophiurids. *Stephanoura* also has small buccal shields.

Generic names were proposed for many of the early Mesozoic ophiurids by AGASSIZ (1835) and D'ORBIGNY (1850). They were founded on somewhat generalized characters. Later it was recognized that these groups had a distinctly modern aspect and T. WRIGHT and others placed them in Recent genera. With stricter standards of generic diagnosis, these identifications cannot all be maintained and in many cases essential diagnostic characters are not sufficiently exposed or preserved in the fossils. Attribution to Recent genera, or even families, is therefore often doubtful.

Suborder CHILOPHIURINA Matsumoto, 1915

[*nom. transl. et correct.* SPENCER & WRIGHT herein (*ex* Chilophiurida MATSUMOTO, 1915)]

Radial shield and genital plate articulate by 2 condyles and 1 pit on each plate. Genital plates and scales barlike. Peristomial plates large or small, normally double or triple. Oral frames with or without well-developed lateral wings. Oral papillae very well developed. *Sil.-Rec.*

The above is MATSUMOTO's diagnosis, applicable to the Recent forms. As here arranged, the suborder includes also the primitive transitional Paleozoic genera which lack fully developed radial shields.

Family OPHIURINIDAE Gregory, 1897

Disc tending to have marginals lengthened in some genera to form incipient short radial shields. Lateral shields wrapped well around arms but narrow dorsal and ventral shields may be present. Spines short, parallel or at slight angle to arm axis. *Sil.-Miss.*

Ophiurina STÜRTZ, 1890 [**O. lymani*; OD]. Disc with thickened margin but no plates visible; covered by granulose skin. No dorsal or ventral shields. Arm spines on low ridge. *L.Dev.*, Ger.——FIG. 81,*2*. **O. lymani*; *2a,b*, parts of aboral and oral surfaces, ×1 (133).

Argentinaster RUEDEMANN, 1916 [**A. bodenbenderi*; OD]. Marginal frame narrow. Lateral shields high, swollen. *Sil.*, Arg.

Ophiaulax UBAGHS, 1941 [**Protaster decheni* DEWALQUE, 1881; OD]. Like *Ophiurina* but disc bordered by well-developed marginals, dorsal shields present and arm spines on distinct ridge. *U.Dev.*, Belg.-Fr.——FIG. 81,*1*. **O. decheni* (DEWALQUE), Belg.; *1a,b*, oral and aboral surfaces, ×1 (135).

Silesiaster SCHWARZBACH & ZIMMERMANN, 1936 [**S. longivertebralis*; OD]. Only poor material known, but close to *Ophiurina*. *L.Carb.*, Ger.

Stephanoura UBAGHS, 1941 [**S. belgica*; OD]. Disc covered by slight skeleton, with incipient radial shields and interradial plates at margin; center with weak skeleton. Arms with ventral shields, arm spines on strong ridge, tentacle pores large. *U.Dev.*, Belg.——FIG. 81,*3*. **S. belgica*; *3a,b*, oral and aboral surfaces, ×1 (135).

Family OPHIURIDAE Lyman, 1865

Disc covered with thick scales or plates; primary circlet commonly prominent. No granulation. Radial shields normally stout. Genital papillae commonly present; oral papillae few; no dental papillae; an unpaired infradental papilla at apex of each jaw. Arms inserted laterally in and fused with disc. Arms short or moderately long, stout, widest at base, tapering rapidly. Arm plates all well developed. Arm spines short, flat on arm. *L.Carb.-Rec.*

Subfamily AGANASTERINAE Stürtz, 1900

[*nom. transl.* SPENCER & WRIGHT, herein (*ex* Aganasteridae STÜRTZ, 1900)]

Disc with large radial shields, united in pairs. *Miss.*

Aganaster MILLER & GURLEY, 1890 [**Protaster? gregarius* MEEK & WORTHEN, 1869; OD] [=*Ophiopege* BÖHM, 1893 (obj.)]. Characters of subfamily. *Miss.*, N.Am.-Scot.——FIG. 81,*4*. **A. gregarius* (MEEK & WORTHEN), L.Miss., USA (Ind.); *4a,b*, aboral surface; *4c*, oral surface of disc with exposed jaws; *4d*, side of arm; *4e*, oral surface of arm; *4f,g*, part of oral and aboral surfaces; all ×1 (133).

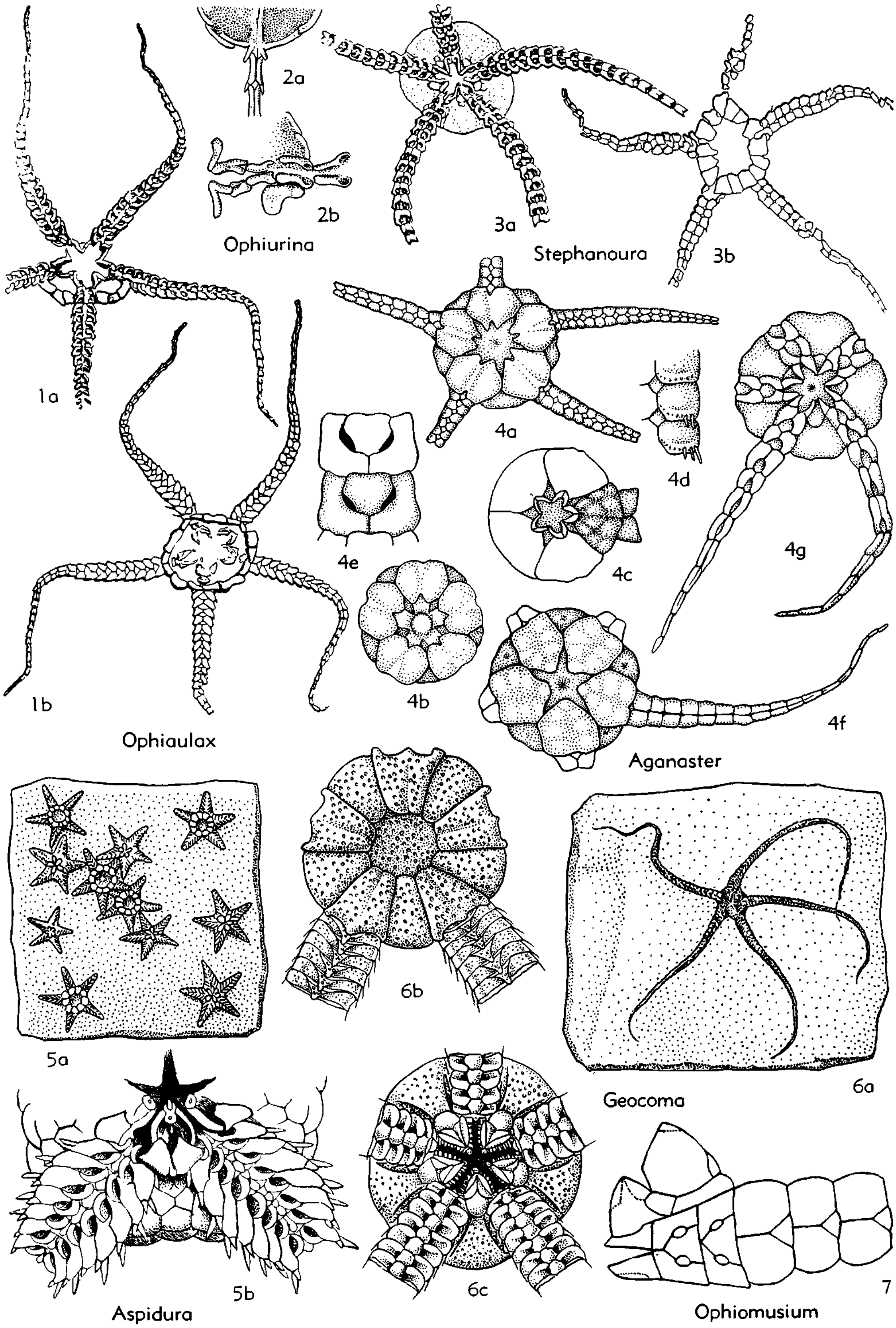


FIG. 81. Ophiurinidae *(1-3)*; Ophiuridae (Ophiurinae) *(5-6)*, (Aganasterinae) *(4)*, (Ophiolepidinae) *(7)* (p. *U*93, *U*95-*U*96).

Subfamily OPHIURINAE Lyman, 1865

[*nom. transl.* FELL, 1960 (*ex* Ophiuridae LYMAN, 1865)] [=Cholasteridae WORTHEN & MILLER, 1883; Ophiomastinae MATSUMOTO, 1915]

Second oral tentacle pore opening more or less entirely outside oral slit. *U.Miss.-Rec.*

MATSUMOTO divided Recent genera into two groups, the first with several proximal lateral shields extraordinarily wide and the disc merely with primaries and radial shields, the second without any wide lateral shields and with secondary scales on the disc.

Ophiura LAMARCK, 1801 [**Asterias ophiura* LINNÉ, 1758; OD] [=*Ophioglypha* LYMAN, 1860; *Ophioglyphina* LUDWIG, 1886; *Ophiozea* A. H. CLARK, 1920]. Disc covered with scales; primary plates inconspicuous. Edge of disc notched at base of arms, notch being filled with rudimentary dorsal arm plates. Ventral shields generally triangular, broader than long, not touching each other. Arm comb normally present but not continuous across arm base. Arm spines vestigial. [Many little-known Mesozoic forms have been referred to this genus.] *?Jur., U.Cret.-Rec.,* cosmop.——FIG. 1,2. *Ophiura* spp., Rec.; *2a,b,* oral and aboral surfaces, ×2 (137).

Amphiophiura MATSUMOTO, 1915 [**Ophioglypha bullata* WYVILLE-THOMSON, 1873; OD]. Arms gradually tapering with blunt end. Arm spines in single row, well spaced. Oral shield large. *Oligo.,* N.Am.; *U.Mio.,* Sakhalin; *Rec.*

Anophiura H. L. CLARK, 1939 [**A. simplex*; OD]. *Rec.*

Anthophiura H. L. CLARK, 1911 [**A. axiologa*; OD]. *Rec.*

Aplocoma D'ORBIGNY, 1852 [**Acroura agassizi* MÜNSTER, 1831; OD]. Arms moderately long. Dorsal and ventral shields small and well separated. [A doubtful genus.] *L.Jur.,* Eng.-Ger.——FIG. 82,*1a*. *A. leckenbyi* (FORBES), Pliensbach., Eng.; aboral side, ×1 (139).——FIG. 82,*1b,c*. *A. murravii* (FORBES), Pliensbach., Eng.; oral and aboral surfaces, ×1 (139).

Aspidophiura MATSUMOTO, 1915 [**A. watasei*; OD]. *Rec.*

Aspidura AGASSIZ, 1835 [**Ophiura loricata* GOLDFUSS, 1826; OD]. Arms short, very broad at base. Disc surface consisting solely of centrale, primary circlet and radial shields. *M.Trias.,* Bulg.-Ger.——FIG. 81,*5*. **A. loricata* (GOLDFUSS); *5a,* slab with specimens showing aboral surface, ×1; *5b,* oral side, ×10 (141).

Astrophiura SLADEN, 1879 [**A. permira*; OD]. *Rec.*

Cholaster WORTHEN & MILLER, 1883 [**C. peculiaris*; OD]. Disc apparently much as in *Aspidura* except that secondary scales occur. Arms abruptly truncated, ending in enlarged ossicles in only known specimen, but this may be pathological. *U.Miss.,* USA(Ill.).——FIG. 83,*1*. **C. peculiaris*; *1a,* aboral view, ×1; *1b,* part of arm, enl. (138).

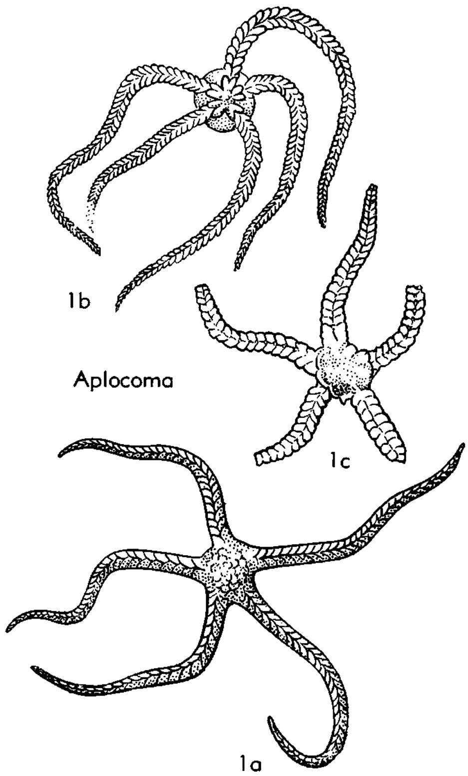


FIG. 82. Ophiuridae (Ophiurinae) (p. *U*95).

Dictenophiura H. L. CLARK, 1923 [**Ophiura carnea* LÜTKEN, 1858; OD]. *Rec.*

Euvondria FELL, 1961 [**E. floretta*; OD]. *Rec.*

Geocoma D'ORBIGNY, 1850 [**Ophiura carinata* MÜNSTER in GOLDFUSS, 1833; OD]. Radial shields large, reaching almost to center of disc. *L.Jur.,* ——FIG. 81,*6*. **G. carinata* (MÜNSTER); *6a,* aboral side, ×1; *6b,* aboral surface of disc, ×7; *6c,* oral surface of arm, ×7 (141).

Gymnophiura LÜTKEN & MORTENSEN, 1897 [**G. mollis*; OD]. *Rec.*

Haplophiura MATSUMOTO, 1915 [**Ophiozona gymnopora,* H. L. CLARK, 1909; OD]. *Rec.*

Homalophiura H. L. CLARK, 1915 [**Ophioglypha inornata* LYMAN, 1878; OD]. *Rec.*

Ophiochalcis KOEHLER, 1931 [**O. aspera*; OD]. *Rec.*

Ophiochorus H. L. CLARK, 1939 [**O. granulatus*; OD]. *Rec.*

Ophiochrysis KOEHLER, 1904 [**O. ornata*; OD]. *Rec.*

Ophiocrossota H. L. CLARK, 1928 [**Ophioglypha multispina* LJUNGMAN, 1867; OD]. *Rec.*

Ophiocten LÜTKEN, 1955 [**O. kroyeri* (=**Ophiura*

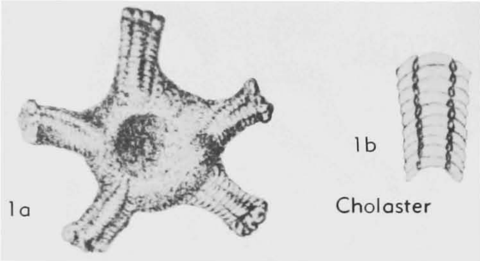


FIG. 83. Ophiuridae (Ophiurinae) (p. U95).

sericea FORBES, 1852); OD]. Primary plates more or less conspicuous. Disc not notched at arm base. Arm comb normally continuous across arm base. *Jur.,* Ger.-Eng.; *Mio.,* USSR; *Rec.*

Ophiogona STUDER, 1876 [**O. laevigata*; OD] [=*Ophiagona* LÜTKEN, 1877; *Ophiomaria* A. H. CLARK, 1916]. *Rec.*

Ophiomastus LYMAN, 1878 [**O. tegulitius*; OD]. *Rec.*

Ophiomisidium KOEHLER, 1914 [**O. speciosum*; OD]. *Rec.*

Ophionotus BELL, 1902 [**O. victoriae*; OD]. *Rec.*

Ophiophycis KOEHLER, 1901 [**O. mirabilis*; OD]. *Rec.*

Ophiopleura DANIELSSON & KOREN, 1877 [**O. borealis*; OD] [=*Luetkenia* DUNCAN, 1878 (*non* CLAUS, 1864)]. *Rec.*

Ophioplinthus LYMAN, 1878 [**Ophioplinthus medusa* LYMAN, 1878; SD H. L. CLARK, 1915]. *Rec.*

Ophiopyrgoides H. L. CLARK, 1939 [**Ophiopyrgus trispinosus* KOEHLER, 1904; OD]. *Rec.*

Ophiopyrgus LYMAN, 1878 [**O. wyvillethomsoni*; OD]. *Rec.*

Ophiosteira BELL, 1902 [**O. antarctica*; OD] [=*Ophiomages* KOEHLER, 1923]. *Rec.*

Ophiotjalfa MORTENSEN, 1915 [**O. vivipara*; OD]. *Rec.*

Ophiotypa KOEHLER, 1897 [**O. simplex*; OD]. *Rec.*

Ophiuraster H. L. CLARK, 1939 [**O. perissus*; OD]. *Rec.*

Ophiuroglypha HERTZ, 1926 [**Ophioglypha lymani* LJUNGMAN, 1870; OD]. *Rec.*

Ophiurolepis MATSUMOTO, 1915 [**Ophiolepis carinata* STUDER, 1876; OD]. *Rec.*

Stegophiura MATSUMOTO, 1915 [**Ophiura nodosa* LÜTKEN, 1855; OD]. *Rec.*

Theodoria FELL, 1961 [**Amphiophiura relegata* KOEHLER, 1922; OD]. *Rec.*

Subfamily OPHIOLEPIDINAE Ljungman, 1867

[*nom. transl.* MATSUMOTO, 1915 (*ex* Ophiolepididae LJUNGMAN, 1867)]

Second oral tentacle pores opening inside oral slits. *?Perm.,Rec.*

Ophiolepis MÜLLER & TROSCHEL, 1840 [**Ophiura annulosa* DE BLAINVILLE, 1834 (*non* LAMARCK, 1816); SD LYMAN, 1865 (=**Ophiolepis superba* H. L. CLARK, 1915)]. *?U.Trias.(Rhaet.),* Fr.; *Rec.*

Amphipholizona H. L. CLARK, 1915 [**A. delicata*; OD]. *Rec.*

Ophioceramis LYMAN, 1865 [**Ophiolepis januarii* LÜTKEN, 1856; OD]. *Rec.*

Ophioceres KOEHLER, 1922 [**O. incipiens*; OD]. *Rec.*

Ophiocrates KOEHLER, 1904 [**O. lenta*; OD]. *Rec.*

Ophiocypris KOEHLER, 1931 [**O. tuberculosus*; OD]. *Rec.*

Ophiolebella MORTENSEN, 1936 [**Ophiolebes biscutifer* E. A. SMITH, 1879; OD]. *Rec.*

Ophiolipus LYMAN, 1878 [**O. agassizii*; OD]. *Rec.*

Ophiomidas KOEHLER, 1904 [**O. alatus* KOEHLER, 1904; SD H. L. CLARK, 1915]. *Rec.*

Ophiomusium LYMAN, 1869 [**O. eburneum*; OD] [=*Ophiomusa* HERTZ, 1927; *?Ophiuraster* MILLER, 1958 (*non* H. L. CLARK, 1939)]. Disc and arm plates not obscured by skin, disc covered by regular porcelaneous plates and radial shields. Dorsal and ventral arm plates minute, not developed in distal part of arm where lateral arm plates meet on dorsal and ventral mid-lines. Tentacle pores 2 to 5. Continuous ridge of fused oral papillae round edge of jaw. *?Perm.-?Trias., L.Jur.-Rec.,* cosmop.——FIG. 81,7. *O. granulosum* (ROEMER), U.Cret.(Senon.), Eng.; oral surface of proximal part of arm, ×5 (125).

Ophiopenia H. L. CLARK, 1911 [**O. disacantha*; OD]. *Rec.*

Ophiophyllum LYMAN, 1878 [**O. petilum*; OD]. *Rec.*

Ophioplocus LYMAN, 1861 [**Ophiolepis imbricata* MÜLLER & TROSCHEL, 1842; OD]. *Rec.*

Ophiosphalma H. L. CLARK, 1941 [**Ophiomusium planum* LYMAN, 1878; OD]. *Rec.*

Ophioteichus H. L. CLARK, 1938 [**O. parvispinum*; OD]. *Rec.*

Ophiothyreus LJUNGMAN, 1871 [**O. goesi*; OD]. *Rec.*

Ophiotitanos SPENCER, 1907 [**O. tenuis*; OD]. Disc heavily granulate, except for feebly swollen radial shields. Dorsal arm plates distinctly swollen. Five short arm spines. Tentacle pores along whole length of arm. *U.Cret.,* Eng.——FIG. 84,*1*. **O. tenuis,* Cenoman., Eng.(Kent); aboral view, ×2 (113).

Ophiozona LYMAN, 1865 [**Ophiolepis impressa* LÜTKEN, 1859; SD H. L. CLARK, 1915]. *Rec.*

Ophiozonella MATSUMOTO, 1915 [**Ophiozona longispina* H. L. CLARK, 1908; OD]. *Rec.*

Ophiozonoida H. L. CLARK, 1915 [**O. picta*; OD] [=*Ophiotylos* MURAKAMI, 1943]. *Rec.*

Family OPHIOLEUCIDAE Matsumoto, 1915

Arms long and slender, commonly constricted at nodes, inserted ventrally below disc and not firmly fused with it. Arm spines few, small and adpressed. Disc with granules and spinules. Continuous series of oral papillae along free margin of jaws. *Rec.*

Ophioleuce KOEHLER, 1904 [**Ophioleuce seminudum* KOEHLER, 1904; SD H. L. CLARK, 1915]. *Rec.*

Amphitarsus H. L. CLARK, 1941 [**A. mirabilis*; OD]. *Rec.*

Ophiocirce KOEHLER, 1904 [**O. inutilis*; OD]. *Rec.*

Ophiernus LYMAN, 1878 [**O. vallincola*; OD]. *Rec.*

Ophiopallas KOEHLER, 1904 [**O. paradoxa*; OD]. *Rec.*

Ophioperla KOEHLER, 1912 [**O. ludwigi* (=**Ophiura koehleri* BELL, 1908); OD]. *Rec.*

Ophiopyren LYMAN, 1878 [**Ophipyren longispinus* LYMAN, 1878; SD H. L. CLARK, 1915]. *Rec.*

Ophiotrochus LYMAN, 1878 [**O. panniculus*; OD]. *Rec.*

Family OPHIOCOMIDAE Ljungman, 1867

[=Ophiospilinae MATSUMOTO, 1915]

Arms stout, widest at some distance from base. Arm spines long, at angle to arm. Oral frame with well-developed lateral wings. Teeth stout, quadrangular. Oral papillae border each jaw. Dental papillae in clump at apex of each jaw. *?U.Cret.,Rec.*

Ophiocoma AGASSIZ, 1836 [**Ophiura echinata* LAMARCK, 1816; SD H. L. CLARK, 1915]. Disc granulate. Arm spines solid. tentacle scales short, leaflike. *?U.Cret.(Cenoman.),* Eng.; *Rec.*

Ophiarthrum PETERS, 1851 [**O. elegans*; OD]. *Rec.*

Ophiocomella A. H. CLARK, 1939 [**O. caribbaea*; OD]. *Rec.*

Ophiocomina KOEHLER, 1920 [**Asterias nigra* ABILDGAARD, 1789; OD]. *Rec.*

Ophiomastix MÜLLER & TROSCHEL, 1842 [**Ophiura annulosa* LAMARCK, 1816; OD] [=*Acantharachna* E. A. SMITH, 1877]. *Rec.*

Ophiopsila FORBES, 1843 [**O. aranea*; OD] [=*Ophianoplus* M. SARS, 1857]. *Rec.*

Ophiopteris E. A. SMITH, 1877 [**O. antipodum*; OD]. *Rec.*

Family OPHIONEREIDIDAE Ljungman, 1867

[*nom. transl.* SPENCER & WRIGHT, herein (*ex* Ophionereidinae LJUNGMAN, 1867)] [=Ophiochitonidae MATSUMOTO, 1915]

Arms robust, not constricted at nodes, widest some distance from base. Keel on mid-line of ventral and commonly also on dorsal shields. Arms inserted ventrally below disc and not fused with it. Arm spines long, at angle to arm. Disc large and flat, with no granules or spines. *Rec.*

Ophionereis LÜTKEN, 1859 [**Ophiura reticulata* SAY, 1825; SD LYMAN, 1865]. *Rec.*

O. (Ophionereis). *Rec.*

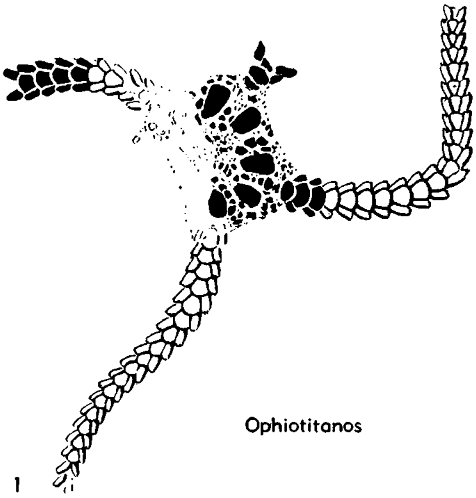


FIG. 84. Ophiuridae (Ophiolepidinae) (p. *U*96).

O. (Ophiotriton) DÖDERLEIN, 1896 [**O. semoni*; OD]. *Rec.*

O. (Ophiocrasis) H. L. CLARK, 1911 [**O. dictydisca*; OD]. *Rec.*

Ophiochiton LYMAN, 1878 [**O. fastigatus*; OD]. *Rec.*

Ophiodesmus ZIESENHENNE, 1940 [**O. amphilogus*; OD]. *Rec.*

Ophiodoris KOEHLER, 1904 [**Ophiodoris malignus* KOEHLER, 1904; SD H. L. CLARK, 1915]. *Rec.*

Ophioplax LYMAN, 1878 [**O. ljungmani*; OD]. *Rec.*

Family OPHIODERMATIDAE Ljungman, 1867

[=Ophiarachninae MATSUMOTO, 1915]

Arms inserted laterally and firmly fused with disc, moderately long, stout, widest at base. Granules cover disc scales of both surfaces and commonly jaws also. Unpaired infradental papillae at apex of each jaw. *L.Jur.-Rec.*

Ophioderma MÜLLER & TROSCHEL, 1840 [**Asterias longicauda* RETZIUS, 1805; SD H. L. CLARK, 1915]. *Rec.*

Bathypectinura H. L. CLARK, 1909 [**Pectinura lacertosa* LYMAN, 1883; OD]. *Rec.*

Cryptopelta H. L. CLARK, 1909 [**Ohiopeza aster* LYMAN, 1879; OD] [=*?Ophiodyscrita* H. L. CLARK, 1938]. *Rec.*

Diopederma H. L. CLARK, 1913 [**Ophiura daniana* VERRILL, 1867; OD]. *Rec.*

Distichophis ELY, 1942 [**D. clarki*; OD]. *Rec.*

Ophiarachna MÜLLER & TROSCHEL, 1842 [**Ophiura incrassata* LAMARCK, 1816; SD LÜTKEN, 1869]. *Rec.*

Ophiarachnella LJUNGMAN, 1872 [**Ophiarachna gorgonia* MÜLLER & TROSCHEL, 1842; SD H. L. CLARK, 1915]. *Rec.*

FIG. 85. Ophiodermatidae (p. U98).

Ophiochaeta LÜTKEN, 1869 [*O. hirsuta; OD]. Rec.

Ophiochasma GRUBE, 1868 [*O. adspersa (=*Ophiarachna stellata LJUNGMAN, 1867); OD] [=Ophiopinax BELL, 1884]. Rec.

Ophioclastus MURAKAMI, 1943 [*O. hataii; OD]. Rec.

Ophioconis LÜTKEN, 1869 [*Pectinura forbesi HELLER, 1862; OD]. Rec.

Ophiocormus H. L. CLARK, 1915 [*O. notabilis; OD] [=Ophiostegastus MURAKAMI, 1944]. Rec.

Ophiocryptus H. L. CLARK, 1915 [*O. maculosus; OD]. Rec.

Ophioncus IVES, 1889 [*O. granulosus; OD]. Rec.

Ophiopaepale LJUNGMAN, 1871 [*O. goesiana; OD]. Rec.

?**Ophiopetra** HESS, 1962 [*O. lithographica; OD]. Arm spines 3. Ventral shields pentagonal, dorsal shields triangular. [Perhaps belongs to Ophionereididae.] *U.Jur.(Kimmeridg.)*, Fr.——FIG. 85,*1*. *O. lithographica; aboral surface, ×10 (Hess).

Ophiopeza PETERS, 1851 [*O. fallax; OD] [=Ophiopsammus LÜTKEN, 1869] *?M.Jur.(Bathon.), Rec.*

Ophiopezella LJUNGMAN, 1871 [*Ophiarachna spinosa LJUNGMAN, 1867; SM LYMAN, 1882]. Rec.

Ophiurochaeta MATSUMOTO, 1915 [*Ophiochaeta mixta LYMAN, 1878; OD]. Rec.

Ophiuroconis MATSUMOTO, 1915 [*O. monolepis; OD]. Rec.

Ophiurodon MATSUMOTO, 1915 [*Ophioconis grandisquama KOEHLER, 1904; OD]. Rec.

Palaeocoma D'ORBIGNY, 1850 [*Ophiura milleri PHILLIPS, 1829; OD]. Arms cylindrical. Disc with or without granules. Radial shields large; other parts of disc lightly calcified. Dorsal shields broad, touching along most of length of arm. Ventral shields similar. Lateral shields high. Arm spines rudimentary. *L.Jur.*, Eu.——FIG. 86,*1*. *P. milleri (PHILLIPS); Pliensbach., Eng.(Yorks.); *1a*, part of aboral surface of arm, ×3; *1b*, aboral surface of disc, ×1 (139).——FIG. 86,*1c*. *P. escheri* (HEER), Hettang., Switz.; oral side (reconstr.), ×3.6 (113).

Pectinura FORBES, 1843 [*P. vestita; OD]. Rec.

Schizoderma NIELSEN, 1932 [*S. diplax; OD]. Rec.

Toporkovia DJAKONOV, 1954 [*T. fragilis; OD]. Rec.

Suborder LAEMOPHIURINA Matsumoto, 1915

[*nom. transl. et correct.* SPENCER & WRIGHT, herein (*ex* Laemophiurida MATSUMOTO, 1915)]

Radial shields and genital plates articulate by means of transverse ridge or simple facet on either plate. Peristomial plates large, normally entire. Oral frames entire, without well-developed lateral wings. Dorsal arm plates commonly very small; lateral arm plates well developed, generally meeting in pairs dorsally and ventrally. *L.Jur.-Rec.*

Family OPHIACANTHIDAE Perrier, 1891

[=Ophiomycetidae VERRILL, 1899]

Arms slender, commonly constricted at nodes. Dorsal and ventral arm plates very small. Arm spines long, numerous, at angle to arm, commonly glassy and serrate. Disc with granules and spinules. Distal vertebrae may be partly divided longitudinally by series of pores. *L.Jur.-Rec.*

Ophiacantha MÜLLER & TROSCHEL, 1842 [*O. spinulosa 1842 (=*Asterias bidentata RETZIUS, 1805); SD H. L. CLARK, 1915] [=Ophiectodia, Ophientodia, Ophiopristis, Ophioscalus, Ophiotreta VERRILL, 1899; Ophiodiplax KOEHLER, 1911]. Disc covered with thin skin bearing granules and stumpy spines. Arm spines hollow. *L.Jur.(Pliensbach.)*, Switz.; *Rec.*

Amphipsila VERRILL, 1899 [*A. maculata; OD]. Rec.

Glaciacantha FELL, 1961 [*G. jason; OD]. Rec.

Microphiura MORTENSEN, 1911 [*M. decipiens; OD]. Rec.

Ophiacanthella VERRILL, 1899 [*Ophiacantha troscheli LYMAN, 1878; OD]. Rec.

Ophialcaea VERRILL, 1899 [*Ophiacantha tuberculosa LYMAN, 1878; SD H. L. CLARK, 1915]. Rec.

Ophiambix LYMAN, 1880 [*O. aculeatus; OD]. Rec.

Ophientrema VERRILL, 1899 [*Ophiacantha scolopendrica LYMAN, 1883; OD]. Rec.

Ophioblenna LÜTKEN, 1859 [*O. antillensis; OD]. Rec.

Ophiocamax LYMAN, 1878 [*O. vitrea; OD]. Rec.

Ophiochondrella VERRILL, 1899 [*Ophiochondrus squamosus LYMAN, 1883; OD]. Rec.

Ophiocopa LYMAN, 1883 [*O. spatula; OD]. Rec.

Ophiocymbium LYMAN, 1880 [*O. cavernosum; OD]. Rec.

Ophiodaces KOEHLER, 1922 [*O. inanis; OD]. Rec.

Ophiodelos KOEHLER, 1931 [**O. insignis*; OD]. *Rec.*

Ophiodictys KOEHLER, 1922 [**O. uncinatus*; OD]. *Rec.*

Ophiogema KOEHLER, 1922 [**O. punctata*; OD]. *Rec.*

Ophioglyphoida CHAPMAN, 1934 [**Ophiacantha (Ophioglyphoida) fosteri*; OD]. Doubtful, as aboral surface unknown. *L.Cret.(Alb.),* Australia.

Ophiolebes LYMAN, 1878 [**Ophiolebes scorteus* LYMAN, 1878; SD H. L. CLARK, 1915]. *Rec.*

Ophiolimna VERRILL, 1899 [**Ophiacantha bairdi* LYMAN, 1883; OD]. *Rec.*

Ophiologimus H. L. CLARK, 1911 [**O. hexactis*; OD]. *Rec.*

Ophiomedea KOEHLER, 1906 [**O. duplicata*; OD]. *Rec.*

Ophiomelina KOEHLER, 1922 [**Ophiomitrella placida* KOEHLER, 1904; OD]. *Rec.*

Ophiomitra LYMAN, 1869 [**Ophiomitra valida* LYMAN, 1869; SD VERRILL, 1899]. *Rec.*

Ophiomitrella VERRILL, 1899 [**Ophiacantha laevipellis* LYMAN, 1883; OD]. *Rec.*

Ophiomyces LYMAN, 1869 [**Ophiomyces frutectosus* LYMAN, 1869; SD H. L. CLARK, 1915]. *Rec.*

Ophiomytis KOEHLER, 1904 [**O. weberi*; OD]. *Rec.*

Ophiophrura H. L. CLARK, 1911 [**O. liodisca*; OD]. *Rec.*

Ophiophthalmus MATSUMOTO, 1917 [**Ophiacantha cataleimmoida* H. L. CLARK, 1911; OD] [=*Ophiosemnotes* MATSUMOTO, 1917]. *Rec.*

Ophiopinna HESS, 1960 [**Geocoma elegans* HELLER, 1858; OD]. Disc covered with small thin scales. Base of arms with cuff of short wide plates. Teeth rather weak, skittle-shaped. Four square and 2 elongate mouth papillae. Proximal part of arm with about 10 arm spines, but on middle part dorsal arm plates are rudimentary or absent and some normal spines are transformed into tall feather-shaped spines, arranged in double dorsal row. Ventral arm plates keeled. Distal part of arm excessively long and thin. *?L.Jur.(Pliensbach.), M.Jur.(Callov.),* Fr.-Switz.——FIG. 88,*1*. **O. elegans* (HELLER), Callov., Fr. (Ardéche); *1a,b,* aboral and oral surfaces of disc, ×5; *1c,d,* aboral and lateral views of arm, ×5; *1e,* growth stages in natural position, ×2 (Hess).

Ophioplinthaca VERRILL, 1899 [**Ophiomitra dipsacos* LYMAN, 1878; OD]. *Rec.*

Ophioprium H. L. CLARK, 1915 [**Ophiacantha curvicornis* LYMAN, 1883; OD]. *Rec.*

Ophioripa KOEHLER, 1922 [**O. marginata*; OD]. *Rec.*

Ophiosparte KOEHLER, 1922 [**O. gigas*; OD]. *Rec.*

Ophiothamnus LYMAN, 1869 [**O. vicarius*; OD] [=*Ophioleda* KOEHLER, 1906]. *Rec.*

Ophiothauma H. L. CLARK, 1938 [**O. heptactis*; OD]. *Rec.*

Ophiotholia LYMAN, 1880 [**O. supplicans*; OD]. *Rec.*

Ophiotoma LYMAN, 1883 [**Ophiotoma coriacea* LYMAN, 1883 (=**Ophiotoma bartletti* LYMAN, 1883); SD H. L. CLARK, 1915] [=*Ophiopora* VERRILL, 1899]. *Rec.*

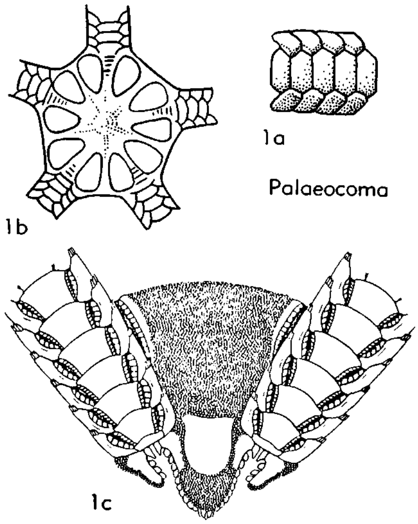


FIG. 86. Ophiodermatidae (p. *U*98).

Ophiotrema KOEHLER, 1896 [**O. alberti*; OD]. *Rec.*

Ophiurothamnus MATSUMOTO, 1917 [**Ophiomitra dicyla* H. L. CLARK, 1911; OD]. *Rec.*

Family HEMIEURYALIDAE Verrill, 1899

[=Ophiochondrinae VERRILL, 1899]

Disc and arm plates very stout. Vertebrae very stout, articulating as in Euryalina and arms coil in vertical plane. [Epizoic.] *?L.Jur.(Pliensbach.), Rec.*

Hemieuryale VON MARTENS, 1867 [**H. pustulata*; OD]. Dorsal arm plates completely divided, forming mosaic. Arm spines 3, short, flat. [A Jurassic species known only from isolated ossicles may belong here.] *?L.Jur.(Pliensbach.),* Switz.; *Rec.*

Ophiochondrus LYMAN, 1869 [**O. convolutus*; OD]. *Rec.*

Amphigyptis NIELSEN, 1933 [**A. perplexa*; OD] [=*?Ophiocyclus* H. L. CLARK, 1939]. *Rec.*

Ophiogyptis KOEHLER, 1905 [**O. nodosa*; OD]. *Rec.*

Ophioholcus H. L. CLARK, 1915 [**Sigsbeia sexradiata* KOEHLER, 1914; OD]. *Rec.*

Ophioleila A. H. CLARK, 1949 [**O. elegans*; OD]. *Rec.*

Ophiomoeris KOEHLER, 1904 [**Ophiomoeris spinosa* KOEHLER, 1904; SD H. L. CLARK, 1915] [=*Ophiurases* H. L. CLARK, 1911]. *Rec.*

Ophioplus VERRILL, 1899 [**Hemieuryale tuberculosa* LYMAN, 1833; OD]. *Rec.*

Quironia A. H. CLARK, 1934 [**Q. johnsoni*; OD]. *Rec.*

Sigsbeia LYMAN, 1878 [**S. murrhina*; OD]. Large supplementary plate present on either side of each

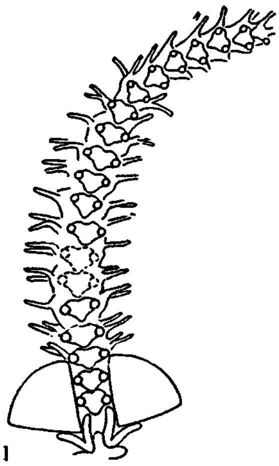


FIG. 87. Amphiuridae (p. U102).

dorsal arm plate; 2 genital clefts in each interradius. [Fossil doubtfully referred here.] *?Mio.*, Victoria; *Rec.*

Suborder GNATHOPHIURINA Matsumoto, 1915

[*nom. transl. et correct.* SPENCER & WRIGHT, herein (*ex* Gnathophiurida MATSUMOTO, 1915)]

Radial shield and genital plate articulating by conspicuous socket in former and large ball-like condyle on latter. Genital plates normally fixed firmly to vertebrae. Peristomial plates generally small and entire, rarely large or double. Oral frames normally with well-developed lateral wings. *?L.Jur., Rec.*

Family AMPHILEPIDIDAE Matsumoto, 1915

Arms long and slender, inserted ventrally below disc and not firmly fused with it. Vertebrae long and slender, commonly divided longitudinally by series of pores. Disc without granules or spines. *Rec.*

Amphilepis LJUNGMAN, 1866 [**Amphiura norvegica* LJUNGMAN, 1864; OD]. *Rec.*

Ophiochytra LYMAN, 1880 [**O. epigrus*; OD]. *Rec.*

Family OPHIACTIDAE Matsumoto, 1915

[*nom. transl.* FELL, 1960 (*ex* Ophiactinae MATSUMOTO, 1915)]

Arms slender, commonly constricted at nodes. Disc with granules or spinules. Jaws with lateral oral papillae separated by gap from dissimilar infradental papillae at apex. *Rec.*

Ophiactis LÜTKEN, 1856 [**O. krebsii* (=**Ophiolepis savignyi* MÜLLER & TROSCHEL, 1842); SD H. L. CLARK, 1915] [=*Amphiactis* MATSUMOTO, 1915]. *Rec.*

Hemipholis LYMAN, 1865 [**Ophiura elongata* SAY, 1825; OD]. *Rec.*

Ophiodaphne KOEHLER, 1931 [**O. materna*; OD]. *Rec.*

Ophiopholis MÜLLER & TROSCHEL, 1840 [**Ophiolepis scolopendrica* MÜLLER & TROSCHEL, 1840 (=**Asterias aculeatus* RETZIUS, 1783); SD H. L. CLARK, 1915]. *Rec.*

Ophiopus LJUNGMAN, 1866 [**O. arcticus*; OD] [=*Ophiaregma* SARS, 1872]. *Rec.*

Family AMPHIURIDAE Ljungman, 1867

Disc covered by fine imbricating scales or with minute spines or naked. Arms inserted ventrally in disc. Arm spines conical and stout. No dental papillae. Paired infradental papillae at apex of each jaw (10). *U.Cret.-Rec.*

Amphiura FORBES, 1843 [**A. chiajii*; SD VERRILL, 1899] [=*Hemilepis* LJUNGMAN, 1871]. Oral papillae not forming continuous row along jaw but having single infradental separated by gap from single outer papilla with internal one invisible above gap. Disc with fine, flat, imbricating scales. Tentacle scales 2. [Jurassic and Cretaceous fossils referred to this genus are all doubtful.] *Rec.*

Acrocnida GISLÉN, 1926 [**Asterias brachiata* MONTAGUE, 1804; OD] [=*Ophiocentrus* LJUNGMAN, 1867]. *Rec.*

Ailsaria FELL, 1962 [**Amphioplus echinulatus* MORTENSEN, 1940; OD]. *Rec.*

Amphiacantha MATSUMOTO, 1917 [**Amphioplus acanthinus* H. L. CLARK, 1911; OD]. *Rec.*

Amphichilus MATSUMOTO, 1917 [**A. trichoides*; OD]. *Rec.*

Amphichondrius NIELSEN, 1933 [**A. granulosus*; OD]. *Rec.*

Amphicontus HILL, 1940 [**A. minutus*; OD]. *Rec.*

Amphilimna VERRILL, 1899 [**Ophiocnida olivacea* LYMAN, 1869]. *Rec.*

Amphilycus MORTENSEN, 1933 [**A. androphorus*; OD]. *Rec.*

Amphinephthys FELL, 1962 [**Amphiura crossota* MURAKAMI, 1943; OD]. *Rec.*

Amphiocnida VERRILL, 1899 [**Ophiocnida putnami* LYMAN, 1871; OD]. *Rec.*

Amphiodia VERRILL, 1899 [**Amphiura pulchella* LYMAN, 1869; OD]. *Rec.*

Amphiomya H. L. CLARK, 1939 [**A. notabilis*; OD]. *Rec.*

Amphioncus H. L. CLARK, 1939 [**A. platydiscus*; OD]. *Rec.*

Amphipholis LJUNGMAN, 1866 [**A. januarii*

(=*Ophiolepis gracillima STIMPSON, 1852); OD]. *Rec.*

Amphioplus VERRILL, 1899 [*Amphiura tumida* LYMAN, 1899; OD]. Four or 5 oral papillae, outermost on adoral shield, small. Radial shields divergent. *Mio.*, Venezuela; *Rec.*

Anamphiura H. L. CLARK, 1939 [*A. valida*; OD]. *Rec.*

Ctenamphiura VERRILL, 1899 [*Amphiura maxima* LYMAN, 1879; OD]. *Rec.*

Diamphiodia FELL, 1962 [*Amphiura violacea* LÜTKEN, 1856; OD]. *Rec.*

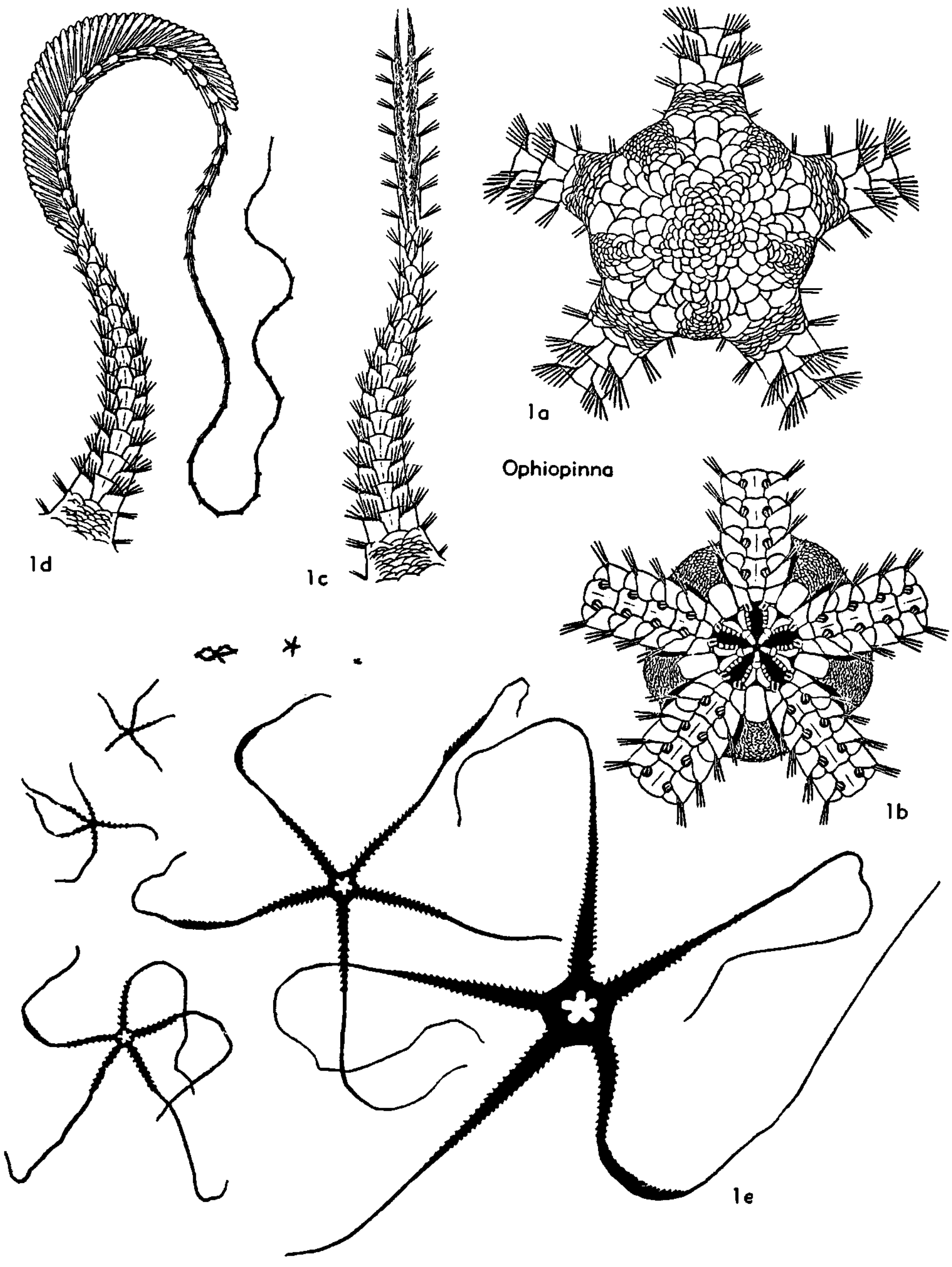


FIG. 88. *Ophiopinna elegans* (HELLER), U.Jur., Fr. (113) (p. *U*99).

Gymnodia FELL, 1962 [**Amphiodia tabogae* NIELSEN, 1932; OD]. *Rec.*

Icalia FELL, 1962 [**Amphiura denticulata* KOEHLER, 1896; OD]. *Rec.*

Monamphiura FELL, 1962 [**Amphiura alba* MORTENSEN, 1924; OD]. *Rec.*

Monopholis FELL, 1962 [**Amphiura vitax* KOEHLER, 1904; OD]. *Rec.*

Nannophiura MORTENSEN, 1933 [**N. lagani*; OD]. *Rec.*

Nullamphiura FELL, 1962 [**Amphiura psilopora* H. L. CLARK, 1911; OD]. Like *Amphiura* but no tentacle scales or only few rudimentary ones. *Cret.-Rec.*——FIG. 87,*1*. *N. felli* SKWARKO, Cenoman., Australia(Bathurst I.), oral view of arm, ×10 (129a).

Nullopholis FELL, 1962 [**Amphipholis nudipora* KOEHLER, 1944; OD]. *Rec.*

Ophiocentrus LJUNGMAN, 1867 [**O. aculeatus*; OD]. *Rec.*

Ophiocnida LYMAN, 1865 [**Ophiolepis hispida* LECONTE, 1851; SD VERRILL, 1899] [=*Ophiocnidella* LJUNGMAN, 1872]. Three or 4 subequal oral papillae. Disc with numerous scattered spines. *Pleist.*, Eng.; *Rec.*

Ophiomonas DJAKONOV, 1952 [**O. bathybia*; OD]. *Rec.*

Ophionema LÜTKEN, 1869 [**O. intricata*; OD]. *Rec.*

Ophionephthys LÜTKEN, 1869 [**O. limicola*; OD]. *Rec.*

Ophiophragmus LYMAN, 1865 [**Amphiura wurdemanii* LYMAN, 1860; SD H. L. CLARK, 1915] [=*Amphispina* NIELSEN, 1933]. *Rec.*

Ophiostigma LÜTKEN, 1856 [*O. *tenue*; OD] [=?*Amphistigma* H. L. CLARK, 1938]. *Rec.*

Pandelia FELL, 1962 [**Amphiura hinemoae* MORTENSEN, 1924; OD]. *Rec.*

Paracrocnida MORTENSEN, 1940 [**P. persica*; OD]. *Rec.*

Paramphiura KOEHLER, 1895 [**Ophiocoma punctata* FORBES, 1841; OD]. *Rec.*

Silax FELL, 1962 [**Aphiura verrilli* LYMAN, 1879; OD]. *Rec.*

Unioplus FELL, 1962 [**Amphioplus falcatus* MORTENSEN, 1933; OD]. *Rec.*

Family OPHIOTHRICIDAE Ljungman, 1866

Teeth stout, quadrangular, spiniform tooth papillae clustered at apex of each jaw. No oral papillae. *?L.Jur., Rec.*

Ophiothrix MÜLLER & TROSCHEL, 1840 [**Ophiura rosula* FLEMING, 1828 (=**Asterias pentaphylla* PENNANT, 1777); SD LYMAN, 1865] [=*Ophionyx* MÜLLER & TROSCHEL, 1840]. Both sides of disc with many plates, bearing spines; aboral surface granular. Radial shields small or partly concealed. Dorsal arm plates smooth. Arm spines 4 or more. *?L.Jur.(Sequan.)*, Fr.; *Rec.*

Amphiophiothrix H. L. CLARK, 1946 [**Ophiothrix demessa* LYMAN, 1861; OD]. *Rec.*

Gymnolophus BROCK, 1888 [**Ophiothela holdsworthi* E. A. SMITH, 1878; OD]. *Rec.*

Lissophiothrix H. L. CLARK, 1938 [**L. delicata*; OD]. *Rec.*

Macrophiothrix H. L. CLARK, 1938 [**Ophiura longipeda* LAMARCK, 1816; OD] [=*Placophiothrix* H. L. CLARK, 1938]. *Rec.*

Ophioaethiops BROCK, 1888 [**O. unicolor*; OD] [=*Ophiohelix* KOEHLER, 1895]. *Rec.*

Ophiocnemis MÜLLER & TROSCHEL, 1842 [**Ophiura marmorata* LAMARCK, 1816; OD]. *Rec.*

Ophiogymna LJUNGMAN, 1866 [**O. elegans*; OD] [=*Ophiocampsis* DUNCAN, 1887]. *Rec.*

Ophiolophus MARKTANNER-TURNERETSCHER, 1887 [**O. novarae*; OD]. *Rec.*

Ophiomaza LYMAN, 1871 [**O. cacaotica*; OD] [=*Luetkenia* BROCK, 1888]. *Rec.*

Ophiopeltis DÜBEN & KOREN, 1846 [**O. securigera*; OD]. *Rec.*

Ophiophthirius DÖDERLEIN, 1898 [**O. actinometrae*; OD]. *Rec.*

Ophiopsammium LYMAN, 1874 [**O. semperi*; OD]. *Rec.*

Ophiopteron LUDWIG, 1888 [**O. elegans*; OD]. *Rec.*

Ophiosphaera BROCK, 1888 [**O. insignis*; OD]. *Rec.*

Ophiothela VERRILL, 1867 [**O. mirabilis*; OD] [=*Ophioteresis* BELL, 1892]. *Rec.*

Ophiotrichoides LUDWIG, 1882 [**O. lymani*; OD]. *Rec.*

GENERIC NAMES OF INDETERMINATE OR UNRECOGNIZABLE STATUS APPLIED TO FOSSIL OPHIUROIDEA

Acroura AGASSIZ, 1836 [**Ophiura prisca* MÜNSTER in GOLDFUSS, 1831; OD]. The holotype of the type-species is quite indeterminable and the genus must therefore be treated as *nom. dub. Trias.*, Ger.

Ataxaster JAEKEL, 1903 [**A. pygmaeus*; OD]. Undescribed ophiuroid. *Ord.*, Czech.

Ephipiellum LOMNICKI, 1899 [**E. symmetricum*; OD]. Unidentifiable ophiuroid vertebrae. *Mio.*, Pol.-Crimea.

Dolicharthra BERRY, 1938 [**D. bemelenica*; OD]. Based on isolated ossicles of several genera, including vertebrae that may belong to *Ophiomusium*. *U.Cret.(Maastricht.)*.

Ophiaxina MÜLLER, 1950 [**O. intercarinata*; OD]. Based on vertebrae only, which somewhat resemble those of *Ophiomyxa*. *U.Cret.(Campan.)*, Rügen.

Ophioma POMEL, 1887 [**Ophioma juliensis*; OD]. No description, only a figure of unidentifiable arm fragment. *Plio.*, Algeria.

Ophiotrigonum HESS, 1960 [**O. oxfordiense*; OD]. Disc not known. Arms sharply triangular in section. Dorsal and lateral arm plates smooth. Spines rudimentary. *M.Jur.(Oxford.)*, Switz.——FIG. 89, *1. *O. oxfordiense; 1a-d,* lat., dorsal, ventral views and cross section of arm, ×3 (Hess).

Ophiurella Agassiz, 1836 [**Ophiura speciosa* Münster in Goldfuss, 1831; OD]. Material is too poorly preserved for characters to be assessed. *M.Jur.-U.Jur.,* Ger.——Fig. 89,*2. *O. speciosa,* Kimmeridg.; oral surface, ×1 (111a).

Ophiuriocoma Valette, 1929 [**O. mazenoti*; OD]. Description insufficient for affinities to be decided. *L.Jur.(Aalen.),* Fr.

Platyarthra Berry, 1938 [**P. jekerica*; OD]. Based on ossicles of several genera, including lateral arm plates perhaps belonging to *Ophiomusium. U.Cret. (Maastricht.),* Neth.

Pseudaspidura Kolosváry, 1941 [**P. hungarica*; OD]. Unidentifiable. *Oligo.,* Hung.

Schizospondylus Müller, 1950 [**S. jasmundiana*; OD]. Based on vertebrae only, which are similar to those of *Ophiocamax. U.Cret.(Campan.),* Rügen.

Transspondylus Müller, 1950 [**T. bubnoffi*; OD]. Based on unidentifiable vertebrae. *U.Cret. (Campan.),* Rügen.

Xenura Schöndorf, 1938 [**X. kobuldi*; OD]. Unrecognizable. *Dev.,* Ger.

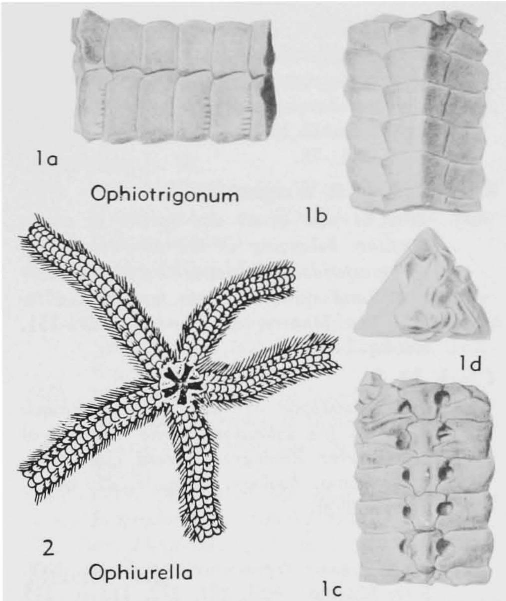


Fig. 89. *Ophiotrigonum* and *Ophiurella*; *1a-d, Ophiotrigonum oxfordiense* Hess, U.Jur., Switz. (113) (p. *U*102); *2, Ophiurella speciosa* (Münster), U.Jur., Ger. (113) (p. *U*102-*U*103).

GENERIC NAMES OF INDETERMINATE OR UNRECOGNIZABLE STATUS APPLIED TO FOSSIL ASTEROZOA

Asteriatites von Schlotheim, 1813 [=*Asteriacites* von Schlotheim, 1820; *lapsus*]. The name was first published (p. 68, *non* p. 109, for a foraminifer), with three included species, names for which apparently were based on nonbinominal names in Knorr, since the only description was an indication to Knorr's figures. These are of Solenhofen fossils (U.Jur., Kimmeridg.) all crinoids *(Saccocoma)* except for a single ophiuroid; the figures on the plate are not separately identified in Schlotheim's indication. In 1820 Schlotheim published *Asteriacites* with a single included species, *A. ophiurus,* which is an unidentifiable ophiuroid from the "Muschelkalk." If, as Neave maintains, *Asteriacites*, 1820, is a *lapsus* for *Asteriatites,* 1813, the type-species must be found among the 1813 species, if any of their names are available. Although Schlotheim's indications to Knorr's figures are in puzzling form, it seems that at least two of the names could be fixed among the crinoids and could therefore be treated as available from 1813. One of them, *pennatus,* was attributed by Schlotheim in 1820 to *Ophiurites,* with again an indication to Knorr's figures. It seems best to place *Asteriaties* Schlotheim, 1813 [=*Asteriacites* Schlotheim, 1820; *lapsus*] as a *nom. dub.* in the synonymy of *Saccocoma* Agassiz, 1836.

Stereoaster Foerste, 1919 [**S. squamatus*; OD]. Not asterozoan. *Sil.,* Ohio.

Trichotaster T. Wright, 1873 [**T. plumiformis*; OD] [=*Trochitaster* Woodward, 1874; *lapsus*]. Specimen not traced. Probably not asterozoan. *Sil.,* Eng.

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