STROMATOPOROIDEA

By Marius Lecompte

CONTENTS

© 2009 University of Kansas Paleontological Institute

INTRODUCTION

Stromatoporoids are an extinct group of organisms, exclusively colonial in mode of growth, which secreted a calcareous skeleton having the form of irregular rounded masses, relatively thin sheetlike expansions, and branched or unbranched subcylindrical structures. Some individual colonies exhibit thickness of more than 1 m. and width ranging to nearly 2 m. Others are small, with greatest dimensions less than 1 cm. Fossils recognized as belonging to the group are distributed from Cambrian to Cretaceous, but they are most abundant in some Silurian and Devonian formations, where they may be important reef-builders. Most stromatoporoids show a tendency to split in layers parallel to the surface of the colony, and they break less readily and evenly in directions transverse to these layers. The surface of some colonies is very smooth and devoid of visible markings, whereas that of others is characterized by presence of many small moundlike elevations. These monticules, called mamelons, may be regular or very irregular in distribution, and they may bear radially diverging small channels which subdivide outward.

Biological placement of the stromatoporoids is not firmly established, as indicated by the fact that various authors have suggested their assignment among algae, foraminiferal protozoans, sponges, hydrozoans, some other branch of the coelenterates, and even bryozoans. Conceivably, they represent an independent phylum of invertebrates, not known by students of living animals, but this seems unlikely. The consensus of specialists is that the stromatoporoids are coelenterates which may be segregated as an order of hydrozoans or treated as a class somewhat closely related to the hydrozoans. They are designated here as an order of the Hydrozoa.

MORPHOLOGY

GENERAL FEATURES OF THE SKELETON

FORM OF COLONIES

The skeletal form of stromatoporoid colonies is variable—massive, laminar (sheetlike), and dendroid (Fig. 86,*1-3*)—and as with corals, form of growth may be influenced by environment, although this is not always easy to determine. Some genera and species, nevertheless, are distinguished by their adoption of a massive growth habit or a laterally expanded laminar form. The dendroid colonies generally have been judged to belong to a special group unrelated to the others, some authors going so far as to exclude them from stromatoporoids altogether. The main reason for this somewhat strange interpretation is the presence in dendroid forms of a prominent axial canal, which is construed to be restricted to these dendroid colonies, but in fact it corresponds to structures very common in massive and laminar stromatoporoids; these are the axial canals of astrorhizae, to be described. As noted in the discussion of classification, almost every family of stromatoporoids contains one or more dendroid growth forms directly allied to a massive genus. Although the validity of generic distinction of some of these related forms is doubtful, they are provisionally recognized as separate.

Stromatoporoid colonies generally are free, but some form incrusting growths on other organisms or are intergrown zonally with them, especially where stromatoporoids occur with massive and laminar tabulate corals or less commonly with dendroid tabulates like *Trachypora* (Fig. 87). A more intimate sort of association is observed with the fasciculate tubular organism known since 1841 under the name of *Caunopora* Phillips, which really is a *Syringopora* (Fig. 88). Such intergrowth is found only in Paleozoic rocks to which this commensal tabulate is restricted; it has not the taxonomic value supposed by Bargatzky (1881) when he introduced the generic name *Diapora,* because it is found in various genera (as *Clathrodictyon, Stromatopora, Stromatoporella, Actinostroma,* and *Rosenella*).

SIZE

The size of colonies is a notably variable character, although it may have some bear-

© 2009 University of Kansas Paleontological Institute

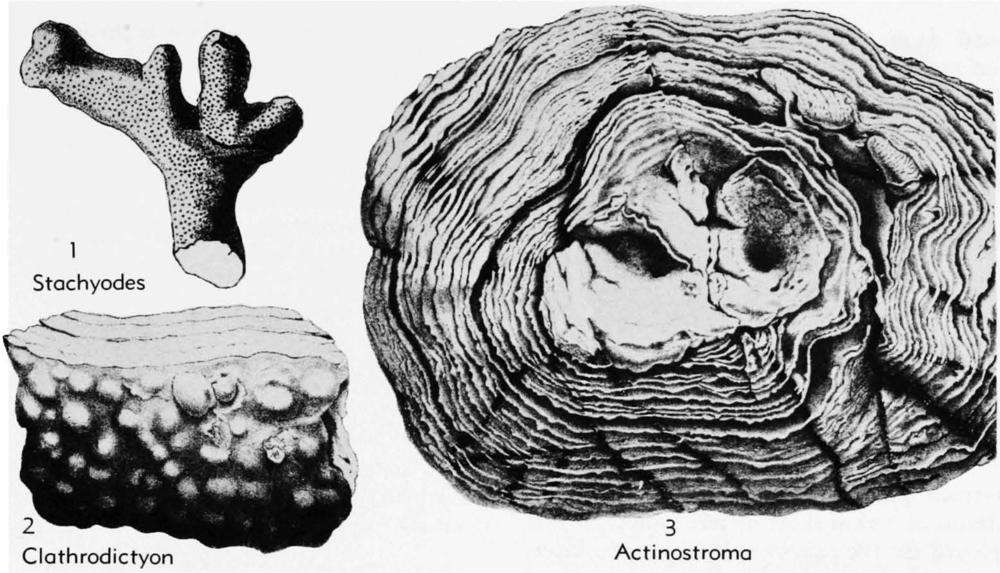


FIG. 86. Stromatoporoid colonies, showing some features of growth form and structure. *1, Stachyodes verticillata* (M'COY), Dev., Ger., a ramose form, ×1.5 (50*). *2, Clathrodictyon variolare* (ROSEN), Sil., Est., showing prominent mamelons on surface and latilaminae in section of colony, ×1 (50*). *3, Actinostrom clathratum* NICH., M.Dev., Eng., basal surface of colony showing many lamellae, ×0.5 (50*).

ing on definition of a species or even of a genus. For instance, *Actinostroma* is distinguished by commonness of colonies having unusually large size, whereas *Clathrodictyon* and *Stromatoporella* generally are represented by rather small laminar colonies. Mesozoic stromatoporoids generally are diminutive, as compared with Paleozoic forms.

SKELETAL STRUCTURE

CHIEF ELEMENTS

The underside of a colony, whether stalked or not, may be covered by an epitheca. The main mass of a colony consists typically of transverse elements, termed **lamellae** and vertical (radial) elements,

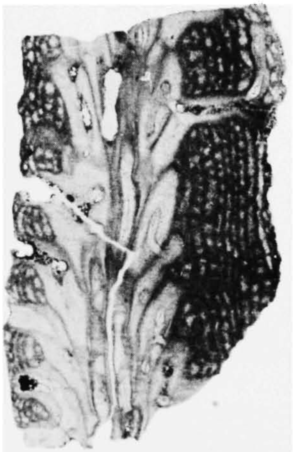


FIG. 87. Longitudinal section of *Trachypora circulipora* KAYSER, a tabulate coral, encrusted by *Stromatoporella* sp., M.Dev.(Givet.), Belg., ×6 (49*).

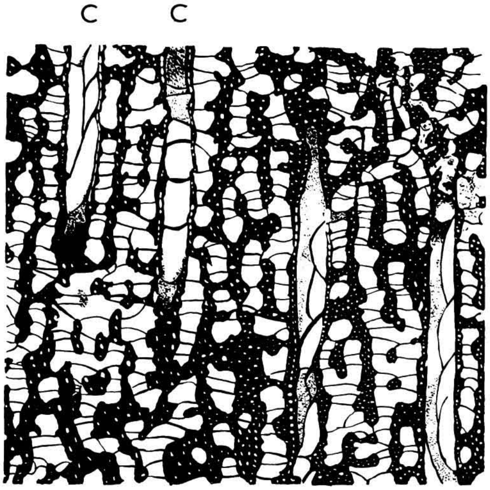


FIG. 88. Intimate intergrowth of a stromatoporoid (*Stromatopora hüpschii*) with the tabulate coral *Syringopora*, M.Dev., Ger., long. sec., ×12. Tubes of the coral, which generally have been described as *Caunopora*, are marked by "C" on the figure (49n).

© 2009 University of Kansas Paleontological Institute

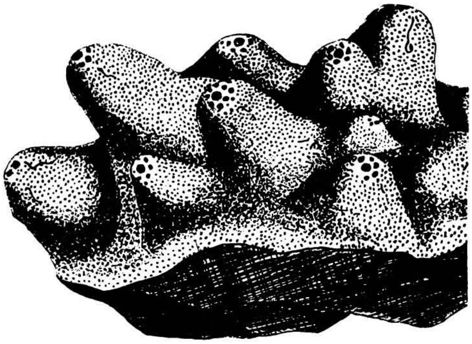


FIG. 89. Part of stromatoporoid colony (*Stromatopora polyostiolata,* M.Dev., Ger.) characterized by unusually prominent mamelons with openings of astrorhizal canals at their summits, ×1.5 (50*).

termed **pillars.** Lamella, which signifies a diminutive thin sheet or fine lamina, is employed for the microscopic transverse layers of stromatoporoids. The upper surface of various species belonging to different genera bears more or less prominent rounded or pointed elevations, termed **mamelons,** and at the center of these is the opening of an astrorhizal axial canal which trends subvertically downward from the surface (Fig. 89). The **astrorhizae,** which comprise star-shaped systems of outwardly branching canals, are clearly defined (Fig. 90) or not discernible, according to whether the surface corresponds to a stage within a lamella or between successive lamellae in building the colonial skeleton. In like manner and depending on the particular structure of the colonial skeleton **(coenosteum),** general ornamentation of the surface is tuberculate or reticulate.

The coenosteum of stromatoporoids is essentially trabecular in structure. In most forms, the skeletal elements consist of well-differentiated lamellae and pillars approximately perpendicular to each other (Fig. 91,*1*), but in some the skeleton has an open or close reticulate texture formed by undifferentiated elements (Fig. 91,*2*).

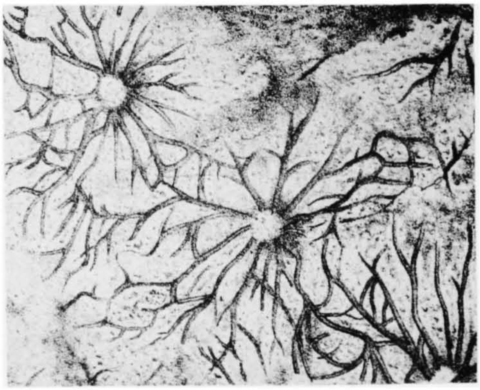


FIG. 90. Stellate pattern of surficial laterally extended branches of astrorhizal canals, seen on slightly weathered specimen of *Stromatoporella eifeliensis* (BARGATZKY), M.Dev., Ger., ×1 (50*).

LATILAMINAE

Vertical growth of some colonies proceeds in a periodic manner which results in building fairly regular, moderately thick composite sheets having lateral continuity. These layers, consisting of several individual lamellae, split apart readily along their interface contacts; they are termed latila-

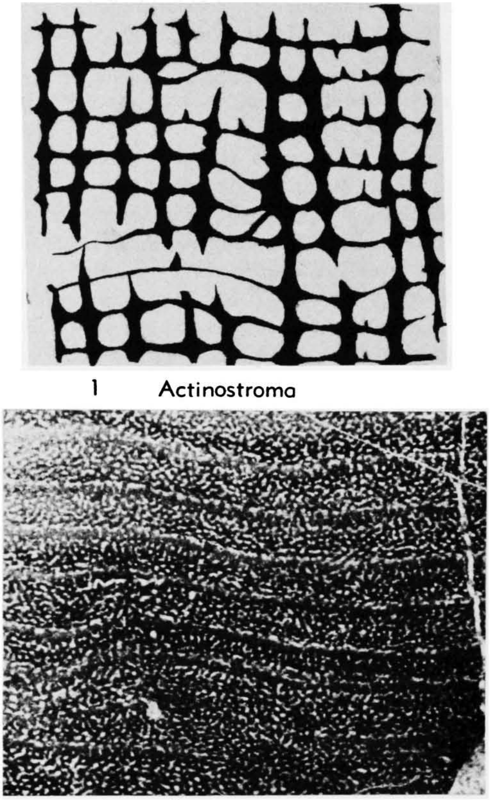
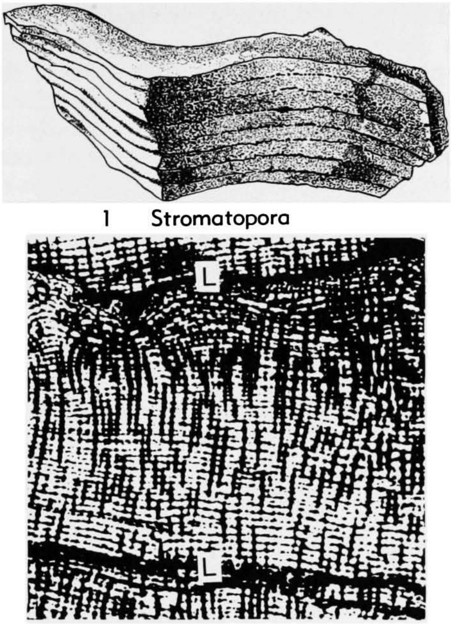


FIG. 91. Lamellae and pillars of stromatoporoid skeleton shown by longitudinal sections. *1, Actinostroma clathratum* NICH., Dev., Eng., ×18, with thin lamellae and relatively stout pillars (50). *2, Stromatopora concentrica* GOLDF., M.Dev., Belg., ×3, with less regular structure of pillars, ×3 (49*).

© 2009 University of Kansas Paleontological Institute



1 Stromatopora

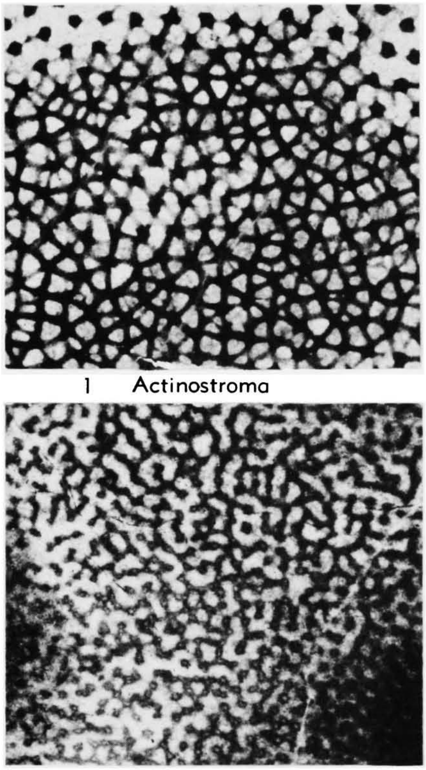
2 Actinostroma

FIG. 92. Latilaminae. *1,* Naturally fractured segment of colony of *Stromatopora concentrica* GOLDF., M. Dev., Ger., showing clearly marked thick layered structure denoting latilaminae, ×1 (50). *2,* Longitudinal section of *Actinostroma devonense* LECOMPTE, U.Dev., Belg., showing pillars and lamellae and indicating hiatus in growth between successive latilaminae (boundaries marked by "L"), ×3 (49n).

minae (Fig. 92,*1*). The presence of latilaminae is not confined to any particular species or genus, but they are best illustrated by some colonies of *Stromatopora concentrica.* Latilamination occurs in stromatoporoids composed of reticulate tissue, as well as in those having well-differentiated skeletal elements. Among the latter, vertical pillars generally are restricted to an individual latilamina, but it happens that some extend without interruption across boundaries of these layers. Boundaries between latilaminae may be marked by increased density or consolidation of the lamellae, by localized intensification of pigment, by a change in structure, such as replacement of reticulate tissue in the upper part of zones of *Stromatopora concentrica* by well-defined pillars or by greater development of astrorhizae at the base of zones.

A structure which sometimes is confused with this regular latilamination is an irregular zonation produced by more or less extensive interruptions in growth, such as are common in tabulate corals. These interruptions are indicated by changes in orientation of skeletal elements and astrorhizal systems, and not uncommonly also by intercalation of a thin layer of sediment (Fig. 92,*2*).

The origin of latilamination has not yet been explained precisely or satisfactorily. Generally, it is thought to denote periodic halts in growth, or alternating acceleration and retardation of growth. The very regular periodicity which characterizes it is not observed in all stromatoporoid colonies of a given deposit.



1 Actinostroma

2 Atelodictyon

FIG. 93. Meshes of lamellae as seen in tangential sections. *1, Actinostroma devonense* LECOMPTE, U. Dev., Belg., showing delicate rodlike horizontal elements enclosing subtriangular open spaces, somewhat resembling structure of a hexactinellid sponge, ×12 (49*). *2, Atelodictyon fallax* LECOMPTE, M. Dev., Belg., showing irregular vermiform pattern of openings in lamella, ×12 (49*).

© 2009 University of Kansas Paleontological Institute

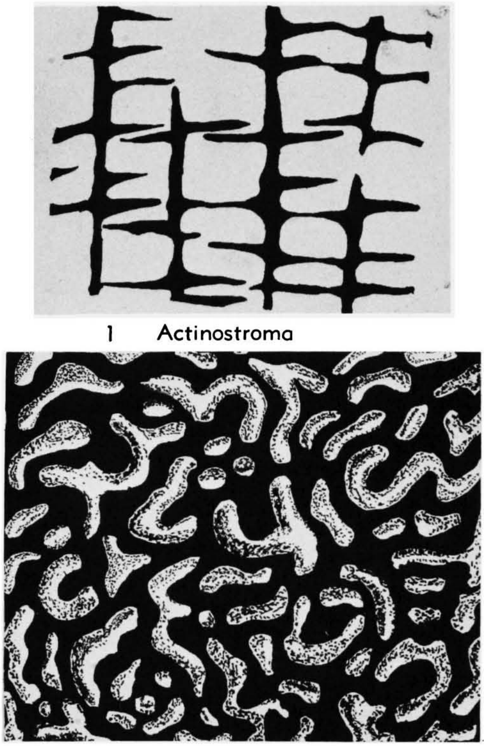


FIG. 94. Structure of lamellae and pillars. *1, Actinostroma intertextum* NICH., M.Sil., Eng., showing uneven spacing of lamellae, ×10 (52). *2, Clathrodictyon fastigiatum* NICH., Sil., Eng., tang. sec. in plane of lamella, ×30 (50).

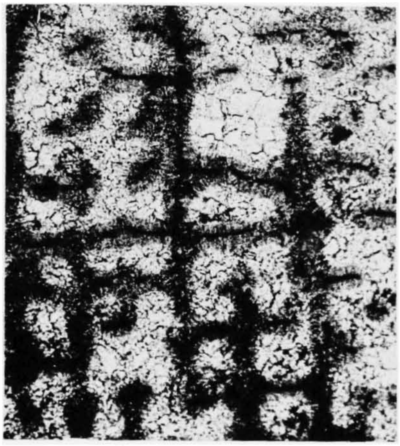
LAMELLAE

As compared with the layers termed latilaminae, the lamellae are very thin, for very many of them occur within a single latilamina; also, lamellae are evident in numerous species of stromatoporoids which lack latilamination. Each lamella consists of a calcareous fibrous network which intersects or impinges on pillars, or separates two contiguous stages of pillars. In genera such as *Actinostroma,* the meshes of the lamellar network have polygonal form resembling the arrangement of siliceous spicules of some hexactinellid sponges (Fig. 93,*1*); in others, the meshes are partly open on one or more sides, making a meandriform pattern as in *Atelodictyon* (Fig. 93,*2*), or a vermiculate design, as in *Clathrodictyon* (Fig. 94,*2*); by thickening, the network becomes a nearly continuous compact sheet which here and there is pierced by pores, as in *Stromatoporella.* Among some forms, especially of Silurian age, the meshes of the lamellae join the pillars at variable levels (Fig. 94,*1*), but in a large majority of species, the lamellae maintain nearly constant levels so as to define regular floors or platforms, arranged one above another (Fig. 91,*1*). In genera such as *Actinostroma, Atelodictyon,* and *Syringostroma,* the lamellae generally are very thin, but in *Hermatostroma, Stromatopora, Stromatoporella,* and others, they are relatively thick. An evolutionary trend toward thickening of lamellar structures seems to exist in some lines, as among Syringostromatidae, but variation in thickness may be influenced by ecologic factors or it may reflect specific differences.

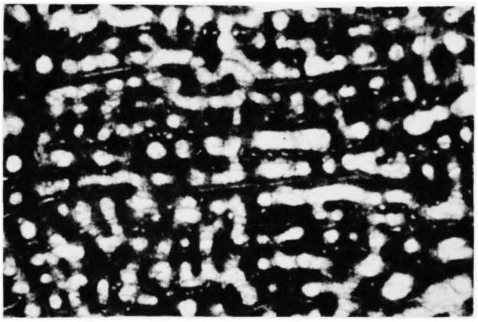
In many genera, lamellae disappear locally or generally. This gives rise to more or less uninterrupted tabular-bearing interpillar spaces extending vertically or sinuously through parts of a colony. Numerous authors have interpreted such structures incorrectly as zooidal tubes.

Lamellae are homogeneous in some genera (Fig. 92,*2*), but cross sections of them in others reveal a dark axial line which has led some authors to conclude that the lamellae are bipartite (Fig. 95,*1*,*2*). This axial line may be light, instead of dark, as a result of bleaching. TRIPP (1932) considers such structure to be a fundamental character, because it offers resemblance to some living athecate hydroids. The presumed bifoliate stromatoporoid lamellae are interpreted by him as the combined roof of one layer and floor of the next following layer, and this he terms the "closed type" *(Stromatoporella, Clathrodictyon).* Simple unipartite lamellae, interpreted as having had only a coenosarc cover, represent the so-called "open type" *(Actinostroma, Stromatopora, Parallelopora).* Distinction of these two types lacks the definiteness supposed by TRIPP, for axially divided lamellae occur in some specimens of *Actinostroma* and invariably are present in its Mesozoic descendants, *Actinostromaria* (Fig. 95,*1*). Moreover, proposed classification on this basis disregards important relationships indicated by other characters. The dark axis actually is a microstructural feature consisting of aligned centers of calcification,

© 2009 University of Kansas Paleontological Institute



1 Actinostromaria



2 Stromatoporella

FIG. 95. Structure of lamellae and pillars. *1, Actinostromaria stellata* CHALMAS, U.Cret.(Cenoman.), Fr., showing dense axial line in pillars and lamellae, long. sec., ×12 (49n). *2, Stromatoporella pertabulata* LECOMPTE, U.Dev.(Frasn.), Belg., long. sec. showing thin clear axial line in several lamellae, ×12 (49*).

and the term "primary lamella" frequently applied to it, like "secondary cover" for clear tissue enclosing it, manifestly lacks histological significance. The existence of an axial canal, as inferred by NICHOLSON (1886), is not supported by observation, for the dark axis does not represent a passageway filled by sediment but is a concentration of carbonaceous pigment within calcareous substance which is identical to the enclosing clear secretion.

PILLARS

The radial or vertical skeletal elements of the stromatoporoid coenosteum in many species are termed pillars. They are classed as continuous if they extend through a number of interlamellar spaces, or discontinuous pillars may falsely suggest existence of continuous pillars, as commonly in *Hermatostroma* and *Syringostroma,* but examination shows clearly that the pillars are interrupted by the lamellae (Fig. 96). Existence of an axial canal in the pillars, which has been reported in some genera, is as unfounded as that in lamellae; the annular appearance of pillars in tangential sections of some species (as *Stromatoporella*) is produced by invagination of a lamella in the plane of the section, for the lamellae may be bent sharply around extremities of the pillars.

RETICULATE TISSUE

Stromatoporoids classed as having reticulate coenosteal structure are distinguished by lack of well-differentiated lamellae and pillars, for the transverse and radial skeletal elements tend to be intergrown intimately. The reticulate tissue is of two types, one characterized by greater distinctness of transverse elements, and the other by dominance of the radial or vertical elements, but there are also intermediate forms which are not referable definitely to either type.

In the type species of *Clathrodictyon,* the transverse and radial elements join without break in continuity to form horizontally elongated vesicles having sufficient regularity of arrangement in successive layers to provide an appearance of lamellation (Fig. 97). This sort of structure, which may be called subreticulate, grades through an intermediate series into types having lamellae and pillars more and more sharply distinct but without loosening of their close bond-

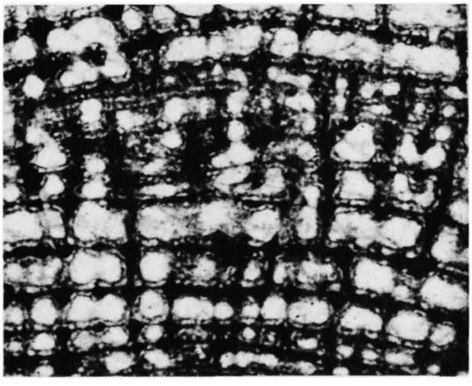


FIG. 96. Structure of lamellae and pillars. Longitudinal section of *Hermatostroma schlüteri* NICH. Dev., Ger., showing interruption of pillars by lamellae, ×12 (49n).

© 2009 University of Kansas Paleontological Institute

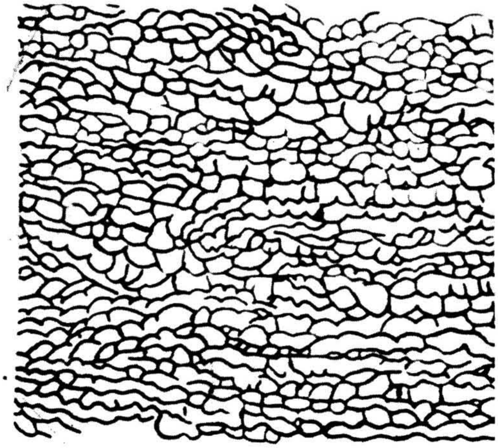


Fig. 97. Structure of lamellae and pillars. Pattern shown by longitudinal section of *Clathrodictyon vesiculosum* Nich. & Murie, M.Sil.(Clinton.), *Ohio,* ×15 (20).

ing together. Transverse sections of the vertical elements of specimens belonging to this group commonly exhibit a vermiculate appearance (Fig. 94,*2*). *Stromatopora,* and in lesser degree some forms of *Parallelopora,* show network meshes elongated vertically and more or less disarranged, so that lamellation is not discernible; chambers between the vertical elements are traversed by thin tabulae (Fig. 88). The reticulate tissue of these forms also is not strictly definable as a structural type distinct from that characterized by well-differentiated lamellae and pillars, for in *Stromatopora concentrica* the reticulate tissue develops typical pillars in upper parts of the latilaminae, and in other species of this genus, skeletal elements are clearly separate and mutually perpendicular.

Straight or curved thin oblique partitions in horizontal chambers are observed in all types of tissue. These partitions are interpreted as astrorhizal septa, because the extent of their occurrence is correlated with degree of ramification exhibited by astrorhizae.

Thickening of skeletal structures is so great in some colonies, that the chambers are considerably reduced in size and nearly closed. This is especially common in *Stromatoporella* and most pronounced in *S. obliterata.*

ASTRORHIZAE

Structural features. The most remarkable structures of the stromatoporoids are the features named astrorhizae by Carter (1880). At the surface of the coenosteum, an astrorhiza consists of a stellate system of furrows which lack walls of their own; the furrows spread radially from a circular opening which is located typically on the summit of a mamelon or less commonly on its flank and they tend to branch proceeding outwardly (Figs. 89, 90). A central opening seems to be lacking in the astrorhizae of some Silurian and Mesozoic species. Distally the furrows ramify into the normal network of the coenosteum and become confluent with neighboring systems (Fig. 98,*1a*); laterally also they communicate freely with chambers of the coenosteum. Among forms having interpillar tabulate chambers, these spring upward from lateral canals of astrorhizae, and they may join different levels of such canals (Figs. 98,*1b,2*). The whole structure of the coenosteum is in fact in close relation with the radiation and ramification of astrorhizal canals.

In many stromatoporoids, the astrorhizae are superposed exactly at each lamellar stage, so that the center of any astrorhizal system is occupied by a vertical canal extending from base to summit of the colony, or through one or more latilaminae, or through some lesser thickness (Fig. 98,*3*). In some species the astrorhizae are not superposed, but vary in placement from one growth stage of a colony to another; this irregularity seems to be much less common than has been supposed, however. Thus, reported lack of superposed astrorhizae in *Actinostroma* and use of this character as criterion for distinction of this genus from *Actinostromaria* are erroneous.

Approximate uniformity of spacing of astrorhizae on the surface of hemispherical colonies in spite of increase of this surface by growing is realized by subdivision of the astrorhizal systems in their upward growth (Fig. 99).

The diameter of the vertical canals and that of their radially outspreading branches are highly variable, as is also the rate of diminution in size of the canals away from astrorhizal centers; these measurements have value only for distinction of species. On the other hand, some genera are characterized by the very prominent develop-

© 2009 University of Kansas Paleontological Institute

ment of these structures and others by their delicate dimensions. This variation, combined with differently pronounced closeness of normal lamellation, explains the weak or strong contrast between astrorhizal structures and surrounding tissue as seen in vertical sections. Thus, the remarkably delicate astrorhizae of *Actinostroma* have escaped the notice of many observers; also, reported absence of astrorhizae in *Hermatostroma* is an error which may be ascribed to the near-matching in size of the astrorhizal canals and the coarse meshes of associated coenosteal tissue.

The occurrence of astrorhizae in dendroid stromatoporoids has not been perceived generally, and because of their presumed absence, Heinrich (1914) excluded this group from true stromatoporoids. Their existence, however, hardly admits doubt. Each colony has a single astrorhizal system consisting of a large axial canal and delicate branches which, as in massive stromatoporoids, are disposed parallel to the lamellation.

The ramifications of astrorhizal systems may be superposed during their vertical development, or they may alternate in position. Mamelons are invariably associated with the superposed type, either continuous-

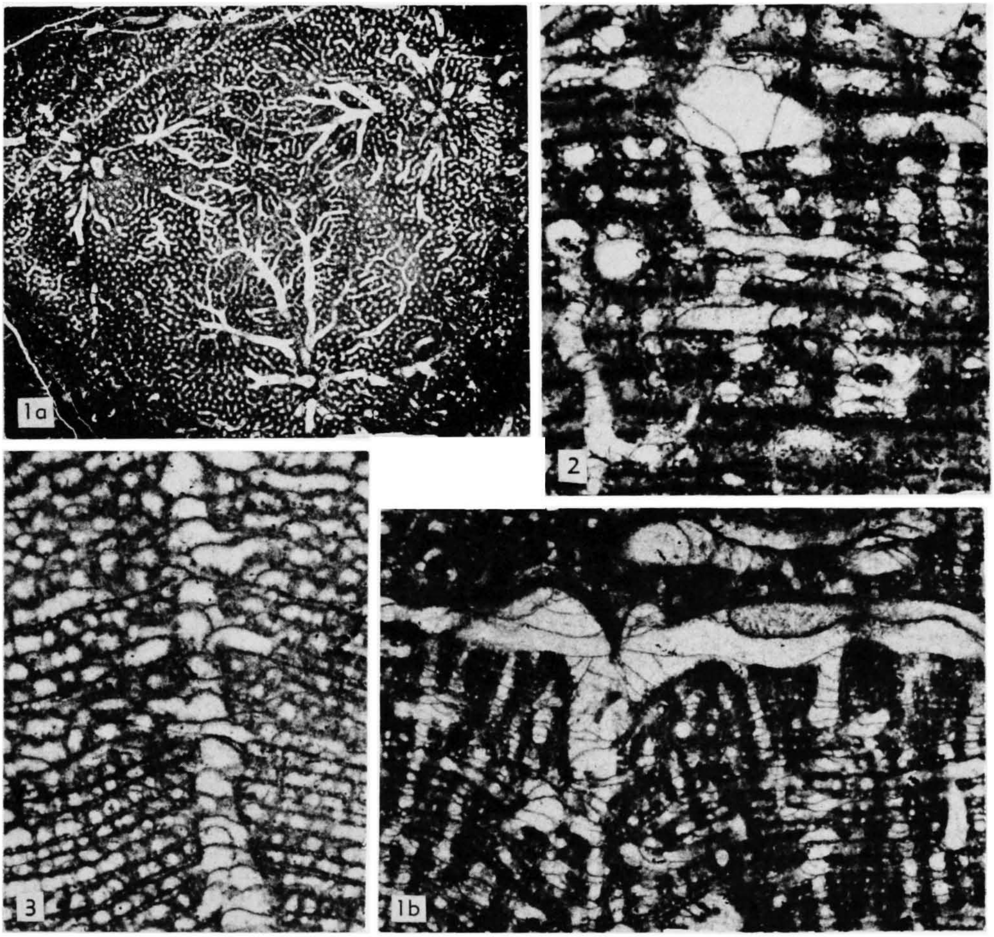


Fig. 98. Structure of astrorhizae. *1, Trupetostroma tenuilamellatum* Lecompte, U.Dev.(Frasn.), Belg.; *1a,* tang. sec. showing well-defined astrorhizal canals, ×3; *1b,* long. sec. through an astrorhiza showing tabulate vertical canals intersecting lateral canals, ×12 (49*). *2, T. thomasi arduennensis* Lecompte, M.Dev. (Givet.), Belg., long. sec. showing tabulate vertical canals enclosing horizontal ones between them ×12 (49*). *3, T. ruedemanni* Lecompte, U.Dev.(Frasn.), Belg., long. sec. through a vertical astrorhizal canal, ×12 (49*).

© 2009 University of Kansas Paleontological Institute

FIG. 99. Structure of astrorhizae. Longitudinal section of *Hermatostroma perseptatum* LECOMPTE, U. Dev.(Frasn.), Belg., showing subdivision of vertical astrorhizal canals that proceeds as colony develops, ×3 (49*).

ly or intermittently, but more or less rapid compensation in upward building of the surface characterizes the other type.

The axial canal and its branches are intersected obliquely by straight or curved tabulae (Fig. 98,*2,3*). These tabulae occur in all species, but exhibit a high degree of variability; generally they are more abundant in astrorhizae with canals of relatively large diameter. Their mode of origin and their function are unexplained.

Among Mesozoic stromatoporoids derived from *Parallelopora,* especially the Milleporellidae and Milleporidiidae, an important change occurs in attitude of the branching astrorhizal passageways. While these run in essentially horizontal position in Paleozoic forms, they tend in later types to become vertical. The Milleporellidae show star-shaped groups of the canals still present on horizontal surfaces but there is no axial canal, the center of the astrorhizal system being occupied by a close-packed bundle of canals which partly spread out radially at certain interlamellar levels, subdividing and passing into the tabulae-bearing vertical chambers (zooidal tubes of authors) between the pillars. Such structure is well shown by *Steinerella mecosola.* In *Milleporidium,* the branching astrorhizal systems have disappeared, the well-defined large tabulate tubes which replace them in the cortical zone passing downward into narrow tabulate chambers of normal type.

This progressive transformation of the astrorhizal systems parallels evolution of the pillars into vertical lamellae which tend to form enclosed tubes with close-spaced tabulae that take the place of vanished horizontal lamellae. Indeed, the general trend of stromatoporoid skeletal evolution seems to be a progressive development of tabulate vertical chambers.

Significance. The function of the stromatoporoid astrorhizal systems has not been determined. They cannot well be interpreted as equivalent to incurrent or excurrent canals of sponges, which are distributed irregularly and are unrelated to particular morphological features of the sponge skeleton. Among stromatoporoids, the secretion of coenosteal tissue was manifestly influenced by the features called astrorhizae, branches of which penetrate all of the skeletal meshwork in the manner of a hydrorhiza. Concordant with minute morphological details of the skeleton, they are seen to be particularly developed as a carpet at the base of latilaminae in Paleozoic forms and also next above a hiatus which defines a surface of necrosis. Their role is evidently one that contributes to building the colonial skeleton, therefore.

CARTER (1880), who first used the term "astrorhiza," interpreted these structures as stellate systems of stolons corresponding to the hydrorhyzae of *Hydractinia echinata,* and with this homology TRIPP (1929) agreed very nearly in showing close resemblance between astrorhizae and the spines of *Hydractinia.* NICHOLSON (1886) accepted the views of CARTER and extended comparison to the anastomosing branchwork of coenosarcal canals in the coenosteum of *Millepora.* He concluded that primary stolons of coenosarc occupied the axial canals and stolonal branches filled the astrorhizal furrows, but found no reason to think that any of the canals housed zooids. KÜHN (1939), on the contrary, has expressed judgment that the axial canals are the only structures recognizable as zooidal tubes, and more precisely, definable as emplacements of blastostyles.

The existence of zooidal tubes in stromatoporoid colonies has been a subject of much controversy. NICHOLSON asserted their occurrence in all stromatoporoids, pointing out that in the Actinostromatidae they are

© 2009 University of Kansas Paleontological Institute

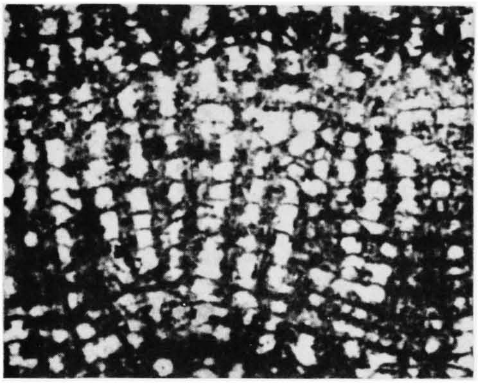


Fig. 100. Supposed zooidal tubes in stromatoporoids. Laterally directed passageways shown in the central part of this longitudinal section of *Parallelopora paucicanaliculata* Lecompte, M.Dev.(Givet.), Belg., seem not to be zooidal tubes, ×12 (49*).

represented by the normal, poorly differentiated interpillar spaces and that in the Stromatoporidae they consist of sporadic tabulae-bearing tubes. The presence of zooidal tubes is contested by Heinrich (1914), Tripp (1929), Yabe & Sugiyama (1930), Parks (1935), and Kühn (1939), although none offers explanation of the tabulate vertical chambers which especially characterize the Stromatoporidae and related forms. It is very difficult to interpret these chambers as zooidal tubes in forms such as the Devonian *Parallelopora paucicanaliculata* (Fig. 115) and the Mesozoic *Stromatoporellina* and *Steinerella,* in which all interpillar spaces bear tabulae. Vertical sections of these stromatoporoids show features strikingly similar to sections of *Hydractinia echinata* (Figs. 100, 101) and especially *H. circumvestiens,* as remarked by Nicholson. Between the spines of *Hydractinia* with their irregular large horizontal prolonga-

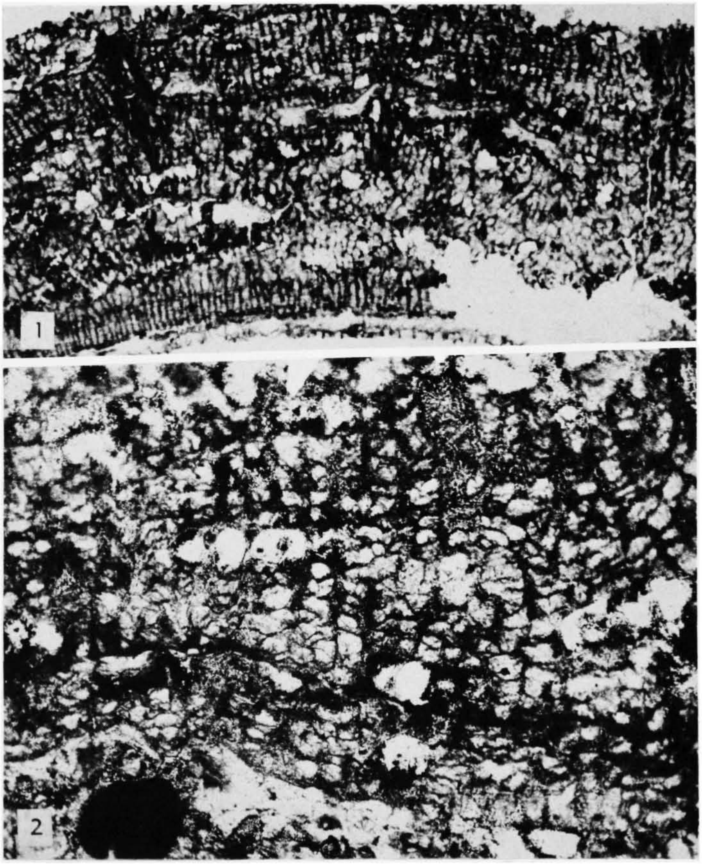


Fig. 101. Structure of modern hydrozoan, *Hydractinia echinata* (Fleming), North Sea, as shown by longitudinal sections; *1a,* ×3; *1b,* ×50 (49n).

© 2009 University of Kansas Paleontological Institute

tions which are strikingly like the branched astrorhizal systems of stromatoporoids, the entire coenosteum consists of parallel narrow vertical chambers traversed by close-spaced thin tabulae. In *H. echinata,* these chambers are mostly delimited by trabecular pillars but some are tubular. They connect with the large horizontal canals which become confluent with the furrows on flanks of the spines. At the surface they furnish passageway for hydranths or coenosarcal stolons, and at junctions of 2 or 3 of them, zooids grow upward. NICHOLSON states that in *H. circumvestiens* the vertical tubules, which he interprets as zooidal tubes, are most strongly developed.

MICROSTRUCTURE OF SKELETAL ELEMENTS

The microstructure of stromatoporoid skeletal elements has not yet been studied adequately. The most striking presently known feature is contrast between microstructure of the Paleozoic and Mesozoic forms. Skeletal elements of the latter are finely fibrous wherever observed, but among Paleozoic genera, this structure is found only in *Amphipora.*

PALEOZOIC FORMS

Two essential types of skeletal elements are recognized among Paleozoic stromatoporoids on the basis of microstructure: the *compact* type and the *cellular* or *vacuolar* type.

Compact type. The compact type is observed in the Actinostromatidae, Clathrodictyidae, and Labechiidae. The only structural feature of *Clathrodictyon* and some species of *Actinostroma* is occurrence of a dark axis in skeletal elements, which, as previously noted, has been interpreted erroneously as evidence of a bipartite construction of the lamellae and canaliculation of the pillars. The axis is recognizable even where pigment is lacking, for microcrystalline substance along this line is differently oriented, as shown by examination of thin sections under crossed nicols. A weakly fibrous structure indicated by some specimens may not be an original character, because some degree of recrystallization seems to affect most of these fossils. Such alternation probably accounts for a false cellular microstructure in certain examples of *Actinostroma,* which seems to be only granulation of the recrystallized calcite.

Cellular type. The cellular type of skeletal elements predominates in Paleozoic stromatoporoids. It prevails in the Stromatoporidae, Stromatoporellidae, and Syringostromatidae. The differentiation of subtypes of structure in this group, which has been attempted, such as regular porous, spongy, and irregular vacuolar, lacks value because these terms mostly reflect only conditions of preservation, the pores being enlarged progressively by alteration which transfers calcite from secreted fibrils to crystalline fillings of adjacent minute spaces. It happens that microstructure may not be recognizable at all, and this is especially common in *Stromatoporella.* Nevertheless, a certain systematic variation is observed: for instance, the cellules of the skeletal fiber are generally smaller, more regular, and better aligned in *Stromatoporella* than *Stromatopora* (Figs. 102,*3,4*). In the series *Syringostroma-Trupetostroma-Hermatostroma* of the Syringostromatidae, an evolutionary trend is seen in an increased regularity of the cellules, in their elongation, and in their alignment in single row along margins of the skeletal elements (Figs. 96; 102,*2*).

A tubular structure which has been recorded by NICHOLSON and others in various species (as *Stromatoporella granulata, S. eifeliensis, Parallelopora ostiolata, P. goldfussi, Stachyodes verticillata*) is nonexistent, for identification of it rests on misinterpretation of sections in one plane. Actually, these forms exhibit a microreticulate structure defined by a fine dark-pigmented meshwork as it is particularly clear in the type of *Parallelopora ostiolata* (Fig. 102,*1*), but according to state of preservation, this may appear as a fine longitudinal striation, as commonly in *Stachyodes.* No trace of a canal system filled by sediment is found; the pigment underlining the reticulation is purely carbonaceous and occurs in secreted calcium carbonate. This reticulate structure may result from an alteration which enlarges the original cellular alveoles at expense of surrounding fibrillar tissue. In any case, it is not confined to particular genera and within a single genus it may coexist with normal cellular structure, being ob-

© 2009 University of Kansas Paleontological Institute

served in forms other than those noted by NICHOLSON (such as *Stromatopora, Syringostroma, Trupetostroma, Hermatostroma*). In *H. beuthii* one may see marginal cellules enclosed by dark vertical and transverse fibers in a pattern exactly corresponding to that of the microreticulate structure of *Parallelopora ostiolata*.

Meshed-fiber type. A rather distinct type of skeletal microstructure not previously mentioned is found in the Paleozoic genus *Synthetostroma*. The lamellae of this form are composed of intricately intermingled fibers which, combined with interlamellar partitions, produce a complicated pattern in vertical sections.

MESOZOIC FORMS

Fibrous type. Except for *Dehornella* and *Ceraostroma*, which have a compact type of skeletal microstructure, Mesozoic stromatoporoids are characterized by fibrous structure. Two sorts have been distinguished by STEINER (1932) and YABE & SUGIYAMA (1935): one termed radial, consisting of fibers arranged perpendicularly to the axis of a skeletal element; and the other called fasciculate or "water-jet," comprising fiber

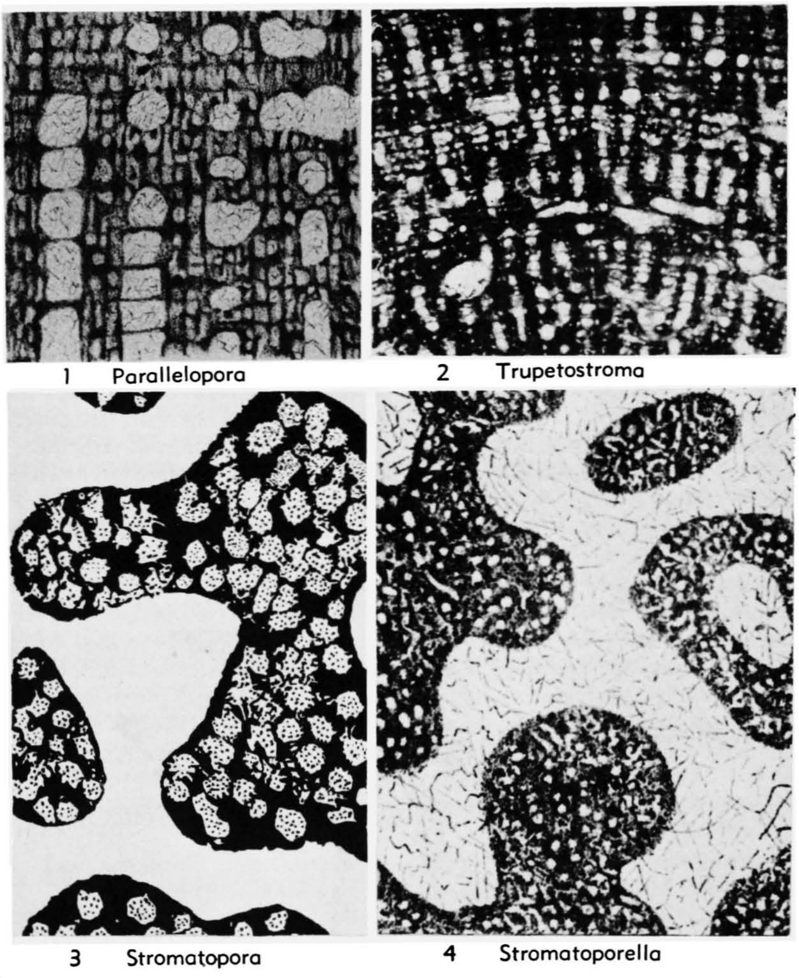


FIG. 102. Microstructure of stromatoporoids. *1, Parallelopora ostiolata* BARGATZKY, Dev., Ger., long. sec. showing microreticulate structure, ×48 (50*). *2, Trupetostroma tenuilamellatum* LECOMPTE, U.Dev. (Frasn.), Belg., long. sec. showing regularly arranged cellules, ×12 (49*). *3, Stromatopora carteri* NICH., M.Sil.(Wenlock.), Eng., tang. sec. showing closely spaced cellules in skeleton, ×48 (50). *4, Stromatoporella granulata* NICH., M.Dev.(Hamilton), N.Y., tang. sec. showing features resembling those of *3*, ×48 (50*).

© 2009 University of Kansas Paleontological Institute

bundles which open more or less shortly outward somewhat from the axis, with or without a central dark line. Actually, the arrangement of fibers is much more varied; the fibrosity may be complex, and in some, highly diffuse; and centers of calcification, generally marked by a concentration of dark pigment, may not be juxtaposed in continuous alignment along the axis but are quite dissociated, each with its own aureole of fibers.

Dehornella exhibits an aberrant sort of concretionary microcrystalline structure, for parts of skeletal elements, generally along the axis, show single extinction under crossed nicols. This structure is like that of *Ceraostroma* described by KÜHN (1926) and interpreted by him to denote a primitive chitinous composition, marking transition from calcareous hard parts of typical stromatoporoids to the chitinous hard parts of various living hydrozoans.

RELATIONSHIPS OF PALEOZOIC AND MESOZOIC TYPES

The contrasts, as well as some similarities, in the nature of skeletal microstructure observed in Paleozoic and Mesozoic stromatoporoids call for elucidation. STEINER'S (1932) hypothesis that the Paleozoic forms originally possessed a fibrous structure and that this has been lost by secondary alteration is difficult to conceive, especially as regards species which exhibit the cellular type of microstructure. It is hard to understand how recrystallization could produce such regularly arranged cells of nearly constant size in some genera, and how it could explain the evolutionary progression recognized in the family Syringostromatidae. The change in structure observed at the close of Paleozoic time must be interpreted as having subordinate taxonomic significance, because most of the Mesozoic genera manifestly belong in families which contain Paleozoic forms, and in all other characters they are closely similar or identical to older genera.

The classification and interrelations of microstructural characters are too little established by present knowledge to permit using them as a basis for taxonomy of the stromatoporoids. Most authors, in agreement with NICHOLSON, recognize microstructure as having value for defining genera, or less commonly, species. HEINRICH (1914), neglecting reservations expressed by NICHOLSON, made this the prime basis of general classification and, restricting the order very arbitrarily, divided Paleozoic genera into two families: Actinostromatidae, with homogeneous pillars; and Stromatoporidae, with porous or tubular structure. This too comprehensive grouping takes no account of textural characters and by associating distantly related forms lacks utility for study of phylogeny. According to STEINER, these 2 Paleozoic groups continue into the Mesozoic, characterized by new structural elements, the Actinostromatidae acquiring fibrous radial structure with a dark axis, and the Stromatoporidae assuming a fasciculate fibrous structure. This concept leads her to place *Siphostroma,* which has textural features indubitably close to the Stromatoporidae, in the Actinostromatidae, and to exclude from this family *Burgundia,* which is very close to *Clathrodictyon.* Moreover, a number of Mesozoic genera are too poorly described to provide information on microstructure. From all viewpoints, it is judged premature to undertake classification of the stromatoporoids on microstructural characters.

SYSTEMATIC POSITION OF STROMATOPOROIDS

Lack of definiteness in conclusions based on comparison of structural features of stromatoporoid hard parts and those of living organisms, supplemented by uncertainty as to the significance of astrorhizae, which are the most particular character of this group, has led authors to explore affinities with different main divisions of the invertebrates, especially Foraminifera among the Protozoa, the Porifera, and Hydrozoa among the Coelenterata.

RELATIONS TO FORAMINIFERA

Classification of stromatoporoids among Foraminifera has been advocated especially by HICKSON (1934) and PARKS (1935), basing opinions chiefly on certain resemblances of *Actinostroma* to the foraminifer *Gypsina*

© 2009 University of Kansas Paleontological Institute

plana. The arguments advanced relate only to secondary characters, however, or are not relevant, such as (1) analogy in appearance of reticulate structure seen in tangential sections, which is of little significance; (2) interpretation of coarse vertical astrorhizal canals of *Actinostroma* as passages for protrusion of pseudopodia; (3) explanation of lamellae in *Stromatoporella* as consequent on alignment of chambers, with pillar-supported interspaces serving only for separation of their rows; (4) existence of a basal layer of chambers different from others in the colony, corresponding to the microspheric or megalospheric proloculus of Foraminifera; (5) occurrence in some stromatoporoids of tubes called caunopores, assumed to represent one of the alternating generations observed among foraminifers; (6) variability in size, form, and arrangement of chambers, as observed both in stromatoporoids and Foraminifera. Lack of validity of most of these points is self-evident. For example, no reason is known for presumption that a certain layer of stromatoporoid chambers is equivalent to a foraminiferal proloculus; the so-called caunopore tubes are identified with reasonable certainty as belonging to tabulate corals; and variation in patterns of chambers in itself means nothing. How can the closed chambers of Foraminifera, compared with the open meshes of stromatoporoid tissue, signify taxonomic affinity? To imagine that the open meshes represent degeneration finds support in no observations, and it runs counter to what is known of evolutionary trends among stromatoporoids, in which the essentially trabecular skeletal tissue tends to a lamellar development with formation of closed tubes. Finally, the essentially spiral architectural plan of Foraminifera is wholly unknown in the stromatoporoids, and not to be found among them are foramina like those of *Gypsina*.

RELATIONS TO SPONGES

The hypothesis of affinity between Stromatoporoidea and Porifera has been supported by many, chiefly on the basis of analogy, plausible at first sight, between the astrorhizae of stromatoporoids and the water canals of sponges. HEINRICH (1914) and TWITCHELL (1929) especially held this view. An astrorhiza, for the authors, suggests an ingeniously modified rhagon type of sponge, but the astrorhizae are perfectly concordant with morphological peculiarities of the stromatoporoids, including a lamellar disposition, which is not observed in the Porifera. Actually, the coenosteum of stromatoporoids contains no space untouched by the highly ramified astrorhizal systems and (in some forms) by the tabulate inter-pillar spaces inrooted on these. Secretion of the skeleton is controlled so plainly and minutely by the astrorhizal structures that these cannot be interpreted as a simple system of water passageways.

The absence of spicules in the coenosteum of stromatoporoids is an impassable obstacle to classification with sponges, and this has not been overlooked by authors. TWITCHELL has drawn argument from a strange specimen of *Stromatopora centrota* which shows abundant broken skeletal elements, and these he regards as fragments of spicules. Judging from the published figures, this interpretation is highly dubious, and if correct, there is still need to determine whether the spicules really belong to the stromatoporoid or to a parasitic sponge. At all events, and contrary to TWITCHELL's assertion, the described specimen is very exceptional.

Some stromatoporoids having structure interpreted to represent a sponge in contracted state are recorded by TWITCHELL. The supposed contracted condition (as in a cited specimen of *Syringostroma densum*) exhibits none of the compensations of skeletal elements which should be found, and the observed structures are in perfect agreement with the recognized evolution of the family.

RELATIONS TO HYDROZOANS

Most authors have subscribed to views of CARTER (1877) in interpreting the stromatoporoids as ancestors of modern hydrozoans. Among these authors are STEINMANN (1878), NICHOLSON (1886), WAAGEN & WENTZEL (1887), DEHORNE (1920), KÜHN (1927, 1939), TRIPP (1929), and STEINER (1932). For reasons which follow, the view is also adopted here.

(1) The astrorhizae, which constitute so characteristic a peculiarity of the stromatoporoids, find satisfactory explanation only

© 2009 University of Kansas Paleontological Institute

according to this hypothesis. Unlike the canals of sponges, which are more or less complex systems deeply penetrating tissues in discordant manner, the astrorhizae are concordant with skeletal structure and control details of its development. An astrorhizal layer marks the beginning of new growth after an accidental hiatus or completion of a latilamina. The principal branches which ramify distally are joined laterally by a network of secondary canals extending to all chambers defined by the skeletal fibers. Such structures are closely similar to the hydrorhizae of the Hydrozoa. The evolution which astrorhizae undergo in Paleozoic and especially in Mesozoic time, leads to structures which diverge somewhat from observed features of the hydrorhizae, but nevertheless maintain resemblance to features shown by some species of *Hydractinia.*

(2) The existence of zooidal tubes, in part of the Stromatoporoidea at least, has been cited by Nicholson and others as a determining argument, if not sole one, for classifying these organisms as hydrozoans. Doubt that these tubes exist or firm denial of them has led some authors to reject the hypothesis of affinity between stromatoporoids and hydrozoans. This rejection of presumed affinities on such basis is not justified, however, for by no means all living hydrozoans possess zooidal tubes. Among stromatoporoids, it may well be that zooids could develop only on the superficial network of coenosarc, leaving no trace in hard parts of the coenosteum. As admitted by Nicholson, without doubt this was the case in the families Actinostromatidae and Clathrodictyidae, which are characterized by skeletal structure very closely similar to that of certain modern athecate hydroids.

The zooidal nature of the narrow vertical tabulate chambers of trabecular construction among Stromatoporidae, Stromatoporellidae, Syringostromatidae, and more or less tubular in Stromatoporidae, Milleporellidae, Milleporidiidae, has not been proved. This is difficult to understand, both in the Stromatoporellidae where these structures are so little developed and sporadic, and in certain species of *Parallelopora,* in the Stromatoporidae, and in the derived Mesozoic families where these structures comprise all tissue between the astrorhizae. But as already stated, some hydractinians have essentially comparable structures. Nicholson (1886, p. 68) has drawn attention to *Hydractinia circumvestiens* (Pliocene, England) which has a coenosteum traversed by many vermiform tubules, approximately vertical and parallel; these tubules are interrupted at various levels by irregular, horizontally disposed small chambers, which bend upward at nearly regular lateral intervals toward large pillars (spines) of cribriform texture that may be pierced by an axial canal. The tubules must have served for lodgement of zooids or for passage of coenosarcal stolons. Nicholson emphasized the close resemblance of this form with the Stromatoporidae rather than the Actinostromatidae. A vertical section of the chitinous skeleton of *H. echinata* (Fig. 101) shows a comparable structure, which also is strikingly like some species of *Parallelopora* and the Mesozoic Milleporellidae, although the closed tubes of the latter are less developed than in *H. circumvestiens.* New studies of the coenosarcal structure in relation to the more or less tubular coenosteum of *Hydractinia* are needed to throw light on skeletal changes observed in Paleozoic Stromatoporidae and their Mesozoic descendants. Without rejecting possible existence of zooidal tubes in the stromatoporoids, it seems preferable to designate the structures on which their presence is inferred, simply as vertical tabulate chambers; it is interesting to note that they are related closely to the astrorhizae.

(3) Stromatoporoids exhibit some peculiarities which are observed commonly among coelenterates but are unknown in the sponges or foraminifers. These include frequent interruptions in growth, latilaminar structure, and the tendency to build thick deposits of the sort characteristically associated with reefs.

EVOLUTION

The problem of distinguishing and tracing evolutionary trends in stromatoporoid skeletal structure is almost untouched, mainly because appropriate means for investiga-

© 2009 University of Kansas Paleontological Institute

tion have been lacking. Study of thin sections is insufficient because it permits observation of structures only at somewhat widely spaced planes. The method of progressive grinding and making peels or photomicrographs of polished surfaces at closely spaced intervals, has not yet been employed, and this alone seems to be available as a source of needed information. Some applications of this method which we have made to study of the skeleton have not been pursued far enough to permit definitive conclusions, but a few essential features may be indicated.

If attention is directed to families which persist into Mesozoic time, one may perceive plainly an evolutionary tendency toward disappearance of transverse lamellae with concurrent development of radial elements; the horizontal trabecular structures gradually are replaced by tabulae and finally these are the only transverse skeletal elements of the colony. The first step of this evolution appears in *Stromatoporella,* in which a few vertical chambers of moderate height traversed by tabulae are seen (Fig. 95,*2*). These structures are slightly better defined in the Syringostromatidae, even though genera of this family retain well-developed lamellae (Fig. 100). The tendency is emphasized in the Stromatoporidae, especially *Parallelopora,* which leads to the Milleporellidae and the Mesozoic Milleporidiidae. In the Middle Devonian (Givetian) *P. paucicanaliculata,* lamellation already approaches disappearance and all chambers between the pillars are intersected by tabulae (Fig. 100); these chambers have been described by many authors as zooidal tubes.

Increasing dominance of vertical elements and replacement of horizontal trabeculae by tabulae are associated with a tendency of the pillars to develop into vertical lamellae, which evolve progressively toward the form of closed tubes. The first stages of this must be sought in study of Paleozoic forms. Evolution shown by *Parallelopora paucicanaliculata* is already such that successive transversely ground surfaces show a practically continuous network and only rarely a few isolated pillars. The tendency is accelerated and more generalized in Mesozoic, even among Actinostromatidae. In *Actinostromaria* (Jur.-Cret.), the lamellation is still well marked but discontinuous in all species. Some forms, such as *A. salevensis* show by grinding a somewhat persistent network indicating a lamellar and tubular evolution of the vertical elements. The lamellae are not replaced by thin tabulae, but they exhibit important changes. Lamellae bend upward in the form of pillars and pillars turn outward into lamellae, so that relations of these two skeletal elements differ wholly from those of their ancestor *Actinostroma.*

Among the Stromatoporidae, these evolutionary tendencies which were already well defined in Paleozoic time, became accentuated in the Mesozoic. They reached their maximum in a descendant of *Parallelopora* called *Stromatoporellina* (Jur.), in which lamellation has disappeared almost entirely, tubulation of the coenosteum is advanced, and all vertical chambers are traversed by tabulae. This genus leads to the Milleporellidae (Jur.-Cret.), in which tubulation is accentuated and lamellae definitely have disappeared. The Milleporidiidae (Jur.-Cret.), derivatives of this family, include the end products of stromatoporoid evolution; they are characterized by perfectly developed tabulate tubes and in the cortical part of colonies larger and more cylindrical tubes seem to represent remains of differentiated astrorhizae. Moreover, skeletal evolution shown by the last-mentioned families is accompanied by a transformation of the astrorhizal system.

CLASSIFICATION

The various systems of classification proposed for the stromatoporoids reflect large uncertainties in assessing taxonomic value of the diverse morphological features of this group, often interpreted without consideration of phylogeny or notion of affinities with living hydrozoans. Particularly unsatisfactory are classifications which have been made on basis of Paleozoic forms alone. The work of chief contributors is noted chronologically.

WORK OF NICHOLSON

The essential starting point and most fundamental work on stromatoporoids consist of studies recorded by NICHOLSON

© 2009 University of Kansas Paleontological Institute

(1886). Based on penetrating knowledge of the morphology of these fossils, he divided stromatoporoid genera known to him in two main groups: (1) forms which he assigned to the family Actinostromatidae, characterized by absence of zooidal tubes; and (2) forms included in the Stromatoporidae and Labechiidae, provided with zooidal tubes. The first group was judged to be related rather closely to the hydractinians, whereas the second was interpreted to stand near hydrozoans of the "family Milleporidae" (now referred to the order Milleporina—not the family Milleporidiidae, composed of Mesozoic stromatoporoids). Although NICHOLSON's plan was accepted and developed by later workers such as DEHORNE (1920) and STEINER (1932), no good reason is seen for admitting passage from the Stromatoporidae and Labechiidae, characterized by single-type zooids, to the Milleporina, which have dimorphic zooids of coenosarcal type unknown in any stromatoporoid. Moreover, the skeletal structure of the Stromatoporidae and the families derived from it is much more like the partly tubular coenosteum of *Hydractinia* than colonial skeletons of *Millepora*. Summary of NICHOLSON's classification is given in the following table.

Nicholson's Classification of Stromatoporoids

Hydractinoidea. Forms without zooidal tubes, related to hydractinians; Actinostromatidae, Idiostromatidae.

Milleporoidea. Forms with zooidal tubes, related to milleporids; Stromatoporidae, Labechiidae.

STUDIES SINCE 1900

Chief contributions to understanding of the relationships to one another of the various kinds of discovered stromatoporoids and efforts to produce useful classification of them are contained in publications by HEINRICH, DEHORNE, KÜHN, TRIPP, STEINER, YABE & SUGIYAMA, and LECOMPTE. The conclusions of these investigators may be summarized and compared.

All Paleozoic genera were divided by HEINRICH (1914) into 2 families, defined on the basis of skeletal microstructure, but Mesozoic stromatoporoids were not considered. Defects of this treatment have been pointed out in the discussion of microstructure. Megascopic features of several Mesozoic genera clearly indicate assignment to the Actinostromatidae and Stromatoporidae, despite the fact that their microstructure differs from HEINRICH's diagnosis for these families, which follows.

Heinrich's Classification of Stromatoporoids

Actinostromatidae. Microstructure of skeletal elements homogeneous.

Stromatoporidae. Microstructure of skeletal elements porous or tubular.

Essential features of NICHOLSON's classification were adopted by DEHORNE (1920), but she added the family Burgundiidae, regarded as intermediate between Actinostromatidae and Stromatoporidae. The Burgundiidae seem too closely related to the Clathrodictyidae to permit acceptance of this classification; also DEHORNE's Stromatoporidae include Mesozoic forms (erroneously ascribed to *Stromatopora* and *Stromatoporella*) which clearly belong to other families. An outline of her classification follows.

Dehorne's Classification of Stromatoporoids

Actinostromatidae; Actinostromatinae, Clathrodictyinae.

Burgundiidae.

Stromatoporidae; Stromatoporinae, Stromatoporellinae.

A classification of the stromatoporoids was published by KÜHN (1927, 1939). Study of their evolutionary trends and phylogenetic relationships led to the conclusion that the Stromatoporidae are the ancestors of modern hydroids by descent through families named Disjectoporidae and Stromatoporinidae. The Disjectoporidae, however, include genera which do not seem to form a link between the Paleozoic Stromatoporidae and Mesozoic genera assigned by KÜHN to the Stromatoporinidae; the Disjectoporidae comprise a side branch. Also, because macrostructure of the Stromatoporidae and Stromatoporinidae is the same and because evolution of Mesozoic forms is exactly in line with that of Paleozoic genera, skeletal microstructure is not a valid criterion for separation of these families. KÜHN judged that the Actinostromatidae constitute beginning of an independent line which includes the Labechioidea, interpreted as an order. This seems unacceptable because the

© 2009 University of Kansas Paleontological Institute

Labechioidea have structural characters which are essentially the same as those of Stromatoporoidea. KÜHN's arrangement of divisions is indicated below.

Kühn's Classification of Stromatoporoids

Stromatoporoidea *(order), Cam.-Cret.*
  Actinostromatidae, *Cam.-Cret.* *Clathrodictyidae, Cam.-Perm.*
  Stromatoporidae, *Ord.-Perm.*—> Disjectoporidae, *Perm.* —>
    Stromatoporinidae, *Trias.-Cret.*—> Hydroidea *(order), Rec.*
Labechioidea (*order,* possibly derived from Actinostromatidae), *Ord.-Dev.*
Sphaeractinoidea (*order,* possibly derived from Disjectoporidae), *Jur.-Cret.*

According to TRIPP (1929), all stromatoporoids have characters closely approaching those of athecate hydroids (gymnoblasts), for the same two types of structures are found in both; the pronounced lamellar structure of the hydroid *Podocoryne* is matched by equivalents in the Clathrodictyidae, Stromatoporellidae, and Syringostromatidae, and the predominant continuous vertical skeletal elements of *Hydractinia* are seen also in the Actinostromatidae, Stromatoporidae, Milleporellidae, and Milleporidiidae. In addition, the partly tubular and tabulate skeleton of hydractinians and that of fossil forms can be cited as sign of relationship which needs elucidation. TRIPP made valuable contribution to the study of systematic relationships of the stromatoporoids, but his definition of groups, given below, is no improvement over that of HEINRICH.

Tripp's Classification of Stromatoporoids

GROUP 1. Closed-tissue forms, with bipartite lamellae.
  Skeletal fiber massive, as in *Clathrodictyon.*
  Skeletal fiber porous, as in *Stromatoporella.*
GROUP 2. Open-tissue forms, with simple lamellae.
  Skeletal fiber massive, as in *Actinostroma.*
  Skeletal fiber porous, as in *Stromatopora* and *Parallelopora.*

Important studies by STEINER (1932) led to the conclusion that phylogenetic relationships of the stromatoporoids were not determinable, and accordingly she sought to erect a classification based on structural characters and distinguished by lack of any morphological hiatus. Placement and subdivision of the stromatoporoids by STEINER, as outlined below, satisfactorily indicate relationships to living Tubularia on one hand and Hydrocoralla on the other.

Steiner's Classification of Stromatoporoids

Tubularia.
Stromatoporoidea.
  Hydractinoidea; Ellipsactinidae, Actinostromatidae.
  Unnamed division; Siphostromatidae, Burgundiidae.
  Milleporoidea; Stromatoporidae, Milleporellidae.
Hydrocoralla.

Study of Mesozoic stromatoporoids by YABE & SUGIYAMA (1935) are basis for a classification of these forms in three families. As given below, this is incorporated in classification now adopted.

Yabe & Sugiyama's Classification of Stromatoporoids

Stromatoporidae. All skeletal elements generally trabecular, interspaces tabulate; with or without astrorhizae.
Milleporellidae. Vertical skeletal elements dominant over lamellar and tending to form closed tabulate tubes; astrorhizae weak or lacking.
Milleporidiidae. Vertical skeletal elements persistent, lamellar or tending to form closed tubes; tabulate interspaces include large ones of zooidal nature and small ones; horizontal elements lamellar, much reduced; no astrorhizae.

CLASSIFICATION ADOPTED IN TREATISE

Classification published in papers by LECOMPTE (1951, 1952) is adopted in the *Treatise.* As far as seems practicable in the state of present knowledge, this is defined by considerations of phylogeny and attention is given to features of skeletal structure, including microstructure in manner supplementing other characters. Division of the stromatoporoids in 2 main groups, as proposed by NICHOLSON and followed by others, cannot be maintained, for structures presumed to show relationship of these fossils with millepores do not exist. Also, oversimplified division in large groups based on microstructure, as in classifications by HEINRICH and TRIPP, is unnatural.

Analysis of older classifications and restudy of many genera have led to rejection of some proposed family units and different allocations of some genera. Thus, *Burgundia* is interpreted to belong to the Clathrodictyidae and the family Burgundiidae proposed by DEHORNE is not recognized; similarly

© 2009 University of Kansas Paleontological Institute

the Siphostromatidae of Steiner's classification is not accepted because *Siphostroma* seems clearly to belong to the Milleporellidae. *Ellipsactinia* and the Ellipsactiniidae are judged not to belong with the stromatoporoids, and *Sphaeractinia,* which Steiner included in this family, is assigned to the Actinostromatidae. The classification of Yabe & Sugiyama is adopted with only minor alterations for Mesozoic stromatoporoids; this includes recognition of the family Milleporidiidae, based on *Milleporidium,* which Steiner failed to distinguish from genera of the Milleporellidae.

The subcylindrical to dendroid colonies, which some authors (Heinrich, 1914; Kühn, 1939) have excluded from the Stromatoporoidea, call for discussion because of question about their relation to the massive and laminar types of growth. Nicholson (1886) grouped the 3 genera of dendroid form known to him in the family Idiostromatidae; of these, *Idiostroma* is here assigned to the Syringostromatidae, *Stachyodes* to the Stromatoporidae, and *Amphipora* to uncertain classificatory status. This distribution is in agreement with Ripper's (1937) conclusion that all or nearly all dendroid stromatoporoids belong to genera or at least to families composed mainly of massive forms. Dendroid (*) and massive (**) pairs having almost identical skeletal structure include **Actinostromarianina* (U. Jur.) and ***Actinostromaria* (Jur.-Cret.); **Dendrostroma* (Dev.) and ***Stromatoporella* (Sil.-Carb.); **Parksia* (U.Jur.) and ***Stromatopora* (Ord.-Perm.); **Stachyodes* (M.Dev.-U.Dev.) and ***Parallelopora* (Dev.-?Perm.); **Idiostroma* (Sil.-Dev.) and ***Hermatostroma* (Sil.-Dev.). The presence of a single large axial canal in dendroid colonies has served to mislead many authors; actually this is simply an astrorhizal axial canal from which branches extend into lamellar portions of the coenosteum precisely as in massive colonies. The family Aulaceridae includes Ordovician and Silurian genera of dendroid form, characterized by exceptionally large size of the axial canal and its division into bulbous chambers by strongly arched tabulae. Here belong *Beatricea* and seemingly also *Cryptophragmus.* They are classified among the stromatoporoids, even though their structural peculiarities and stratigraphic placement indicate that they are a very early, surprisingly divergent assemblage.

The families recognized in the *Treatise* section on Stromatoporoidea are listed below with record of their known stratigraphic distribution and statement of the number of genera included in each (shown by figures enclosed by parentheses).

Divisions of Stromatoporoidea

Stromatoporoidea *(order)* (67). *Cam.-Cret.*
  Actinostromatidae *(family)* (7). *Cam.-Cret.*
  Clathrodictyidae (6). *Cam.-Jur.*
  Stromatoporellidae (4). *Sil.-Carb., ?Trias.*
  Syringostromatidae (6). *Sil.-Jur.*
  Stromatoporidae (12). *Ord.-Cret.*
  Disjectoporidae (4). *Perm.-U.Trias.*
  Milleporellidae (4). *Jur.-Cret.*
  Milleporidiidae (2). *Jur.-Cret.*
  Labechiidae (10). *Ord.-Cret.*
  Aulaceridae (6). *Ord.-Sil.*
  Uncertain family (1). Sil.-Jur.

PALEOECOLOGY

Paleoecologic relationships of the stromatoporoids have been studied little, perhaps partly because taxonomy of the group is mostly unfamiliar to geologists and partly because these fossils are most abundant in calcareous rocks where observations of their occurrence are difficult.

The environments to which stromatoporoids seem best suited are about the same as those preferred by the corals. Both are adapted to reef building, but the stromatoporoids seem to tolerate a muddy bottom less well than many corals. Massive and globular colonies tend to occur in rather pure limestone, whereas laterally expanded sheet-like colonies commonly are found in impure limestones or in interstratified marly and clayey beds; in such a setting, interpreted to signify less shallow seas, rather rare laminar stromatoporoids are found associated with coralline bioherms in Devonian sections of the Ardennes region. Like the tabulate corals but in much smaller degree, the coenosteum of stromatoporoid colonies exhibits variations, especially in thickness of the skeletal elements, development of lamellae and pillars, and in spreading apart of these. This variability partly is an expression of local environment.

Paleozoic stromatoporoids contributed to

© 2009 University of Kansas Paleontological Institute

building reefs much more commonly than the Mesozoic forms. The Silurian and Devonian rocks of many regions contain numerous stromatoporoid-bearing bioherms and biostromes, some of which have considerable thickness and lateral extent. Remarkable are such masses in the Silurian of Gotland, attaining thickness of 10 to 20 m. and horizontal dimensions of several hundred meters; these are distributed in crinoidal limestones and marls. Locally, reef-like deposits consist exclusively of stromatoporoids, but generally tabulate corals and compound rugose corals are associated with them; also, algae of *Solenopora* type, especially *Pilotrix,* are intergrown with the coelenterate colonies and serve to bond fragments together (HADDING, 1941). Globular algae such as *Sphaerocodium* and *Spongiostroma* occur in beds below and above the reefs but not in them. The abundance of broken, more or less worn fragments of corroded stromatoporoid colonies and the presence of the algae are cited by HADDING as evidence of very shallow water, but as shown by the fine sediment associated in the reefs, evidently they were not formed close to a more or less rugged coast but in relatively quiet offshore waters, probably between 5 and 50 m. deep.

In Devonian strata of the Ardennes, bioherms and biostromes composed mainly or exclusively of stromatoporoids occur as lenticular bodies interfingering with surrounding calcareous sediment. Associated tetracorals, tabulates, and algae *(Sphaerocodium, Girvanella)* are quantitatively less important but individually of large size. Conversely, in reefs composed mainly of corals, invariably small, remains of stromatoporoids generally are absent, but if present, they are very thin laminar growths. Massive stromatoporoids of Devonian time were able to grow and build reefs in turbulent waters; corals living in this environment formed large colonies but below the zone of strong wave action their skeletons were small and flattened. Analysis of geologic sections containing reefs built by stromatoporoids, which brings to notice many disconformities, common occurrence of ripple marks, and local deposits of broken, worn reef organisms, indicates shallow-water environment.

Mesozoic stromatoporoids have very little importance as reef builders, even though they are associated locally with reef-formers such as the hexacorals, rudistid clams, and nerineids, and they occur commonly in oölitic limestones which denote a neritic, shallow-water environment. There are few algae, unless the Chaetetidae found in many places belong here at least partly. Chiefly important from paleoecological viewpoints seems to be the association of stromatoporoids with hexacorals.

SYSTEMATIC DESCRIPTIONS

Order STROMATOPOROIDEA Nicholson & Murie, 1878

Hydrozoans distinguished by a calcareous coenosteum basically of trabecular nature, generally with distinct transverse elements (lamellae) and vertical or radial elements (pillars) or with varied sorts of reticulate structure evolving lamellar elements that tended to become tubular; exclusively colonial, massive, sheetlike, or dendroid in growth. A characteristic structure possessed by all but a few genera is termed astrorhiza; it consists typically of a central canal directed normal to the surface and of laterally diverging, outwardly branching furrows on the surface or canals below the surface. Surface with or without tubercles (mamelons). *Cam.-Cret.*

Family ACTINOSTROMATIDAE Nicholson, 1886

[*nom. correct.* LECOMPTE, herein (*pro* Actinostromidae NICH., 1886)]

Colonies massive, flattened, or rarely dendroid. Coenosteum composed of well-differentiated trabecular skeletal elements; lamellae consisting of a hexactinellid network formed by processes joined at regular or irregular levels to more or less continuous vertical pillars. Astrorhizae narrow. Microstructure of skeletal elements massive or fibrous. *Cam.-Cret.*

Actinostroma NICHOLSON, 1886 [**A. clathratum*] [=?*Actinostromella* BOENKE, 1915; *Gerronostroma* YAVORSKY, 1931]. Skeletal elements essentially perpendicular to one another; lamellar network commonly formed by complex meshes connected at regular or variable levels to pillars. Skeletal

© 2009 University of Kansas Paleontological Institute

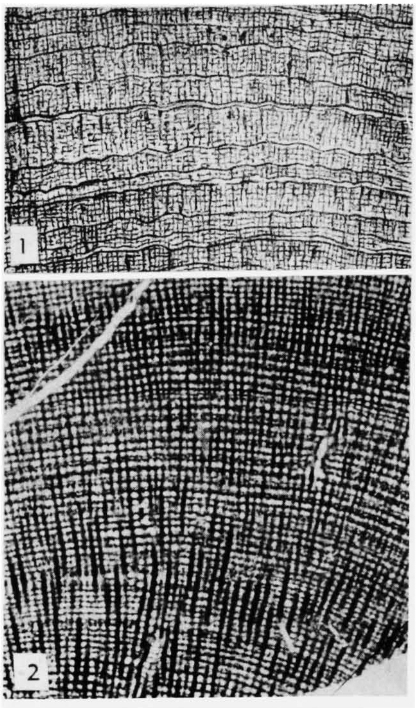


FIG. 103. Actinostromatidae. *1, Actinostroma astroites,* M.Sil., ×10. *2, A. devonense,* U.Dev., ×3.

fibers compact (20). *Cam.-L.Carb.,* cosmop. (This genus generally has been distinguished from *Actinostromaria* by its lack of superposed astrorhizae, but this character is not reliable, since they do occur in some species of *Actinostroma.* Mesozoic species assigned to *Actinostroma* actually belong to *Actinostromaria,* as shown by their fibrous skeletal structure.)——FIGS. 92,*2;* 93,*1;* 103,2. *A. devonense* LECOMPTE, U.Dev. (L.Frasn.), Belg.; long., tang., long. secs., ×3 (49).——FIGS. 86,*3;* 91,*1.* **A. clathratum,* M.Dev., Eng.; 86,*3,* exterior of base, ×0.5; 91,*1,* long. sec., ×12 (50*,50). ——FIG. 103,*1. A. astroites* ROSEN, M.Sil. (Wenlock.), Eng.; long. sec., ×10 (50*).——FIG. 94,*1. A. intertextum* NICH., M.Sil., Eng.; long. sec., ×10 (52).

Actinostromaria CHALMAS *in* DEHORNE, 1920 [**A. stellata*]. Coenosteum like that of *Actinostroma* but laminae very discontinuous and more delicate than pillars, which also may be interrupted; the lamellae constitute a simple, regular network, generally with quadrangular but also pentagonal meshes, all in the same plane and many opening on one or more sides so as to produce a meandriform pattern. Pillars commonly are formed by upward turning of lamellar processes. Astrorhizae highly branched, disposed in vertical systems formed by several canals arranged in bundles. Skeletal elements characterized by prominent dark axis surrounded by perpendicular crystalline fibers (7). *Jur.-Cret.,* Eu.-N.Am.-Afr.——FIGS. 95,*1;* 104,*3.* **A. stellata,* Cret. (Cenom.), Fr.; 95,*1,* long. sec., ×12; 104,*3a,b,* long and tang. secs. ×12 (49n all);——FIG. 104,*1. A. salevensis* DEHORNE, Cret., Fr.; tang sec., ×12 (49n).

Actinostromarianina LECOMPTE, 1952 [**Stromatopora milleporoides* DEHORNE, 1920]. A dendroid form with massive base and cylindrical branches: coenosteum as in *Actinostromaria,* pillars bending sharply from axis, occupied by a narrow astrorhizal canal, to meet surface perpendicularly. Astrorhizae feebly developed (18). *U.Jur.,* Eu.——FIG. 104,*4.* **A. milleporoides* (DEHORNE), U.Jur., Rumania; *4a,b,* long. secs. ×3, ×12 (49n).

Atelodictyon LECOMPTE, 1951 [**A. fallax*]. Coenosteum laminar or globular; pillars typically superposed, with appearance of continuity, but restricted in some to interlamellar spaces; lamellae in a subhexactinellid network, or showing in tangential section cellular to chainlike structure. Astrorhizae in vertical systems. Fibers compact. *M.Dev.,* Belg. (Superficially, coenosteum structure resembles that of forms commonly assigned to *Clathrodictyon,* which have pillars not subordinate to lamellae, however.)——FIGS. 93,*2;* 104,*2.* **A. fallax,* M. Dev.(Couvin.), Belg.; 93,*2,* tang. sec., ×12; 104, *2,* long. sec., ×12 (49*).

Pseudolabechia YABE & SIGUYAMA, 1930 [**P. granulata*]. Colonies laminar. Coenosteum like *Actinostroma,* but distinguished by horizontal lamellar processes not in regular superposed layers and in having vertical columns formed by considerably thickened, upward converging pillars, and marked on the upper surface by large tubercles. Astrorhizae lacking (46). *Ord.-Sil.,* Eu.-Asia.

?**Circopora** WAAGEN & WENTZEL, 1887 [**C. faveolata*], *Perm., Jur.,* Eu.-Asia.

?**Sphaeractinia** STEINMANN, 1878 [**S. diceratina*]. *Jur.-Cret.,* Eu. Imperfectly known, possibly synonym of *Actinostromaria.*

Family CLATHRODICTYIDAE Kühn, 1939

[*nom. correct.* LECOMPTE, herein (*pro* Clathrodictyonidae KÜHN, 1939)]

Coenosteum essentially composed of discontinuous pillars and lamellae intimately associated in manner forming subvesicular tissue, or in varying degrees differentiated. Astrorhizae present. Coenosteal elements compact or microcrystalline. *Cam.-Jur.*

Clathrodictyon NICHOLSON & MURIE, 1878 [**C. vesiculosum*] [=*Stictostroma* PARKS, 1936 (*partim*)]. Typically laminar but may be globular or massive, with skeletal elements poorly differentiated to distinct; pillars restricted to interlamellar

© 2009 University of Kansas Paleontological Institute

spaces, but closely associated with lamellae, which are the predominant structures; interlamellary septa may be abundant. Astrorhizae present or absent (22). *Cam.-Dev.*, cosmop., *Perm.*, Japan. As currently defined, this genus contains groups showing 2 sorts of structures: forms like the type species, with vesicular or subvesicular tissue lacking clear differentiation of pillars and lamellae (Fig. 97); and forms having well-defined lamellae and interlamellar pillars which may be bifurcate or hollow cone-shaped (Fig. 105,*2*). Some authors hold that one form merges with the other through progressive straightening of lamellae and separation of pillars, but the second group possibly is generically distinct.——Fig. 97. **C. vesiculosum*, L.Sil.(Clinton.), Ohio; long. sec., ×10 (50).——Fig. 105,*3*. *C. striatellum* Orb., M.Sil.(Wenlock), Eng.; long. sec., ×24 (50).——Fig. 105,*2*. *C. amygdaloides* Lecompte, M.Dev.(Couvin.), Belg.; long. sec. ×12 (49*). Also, Figs. 86,*2*; 94,*2*.

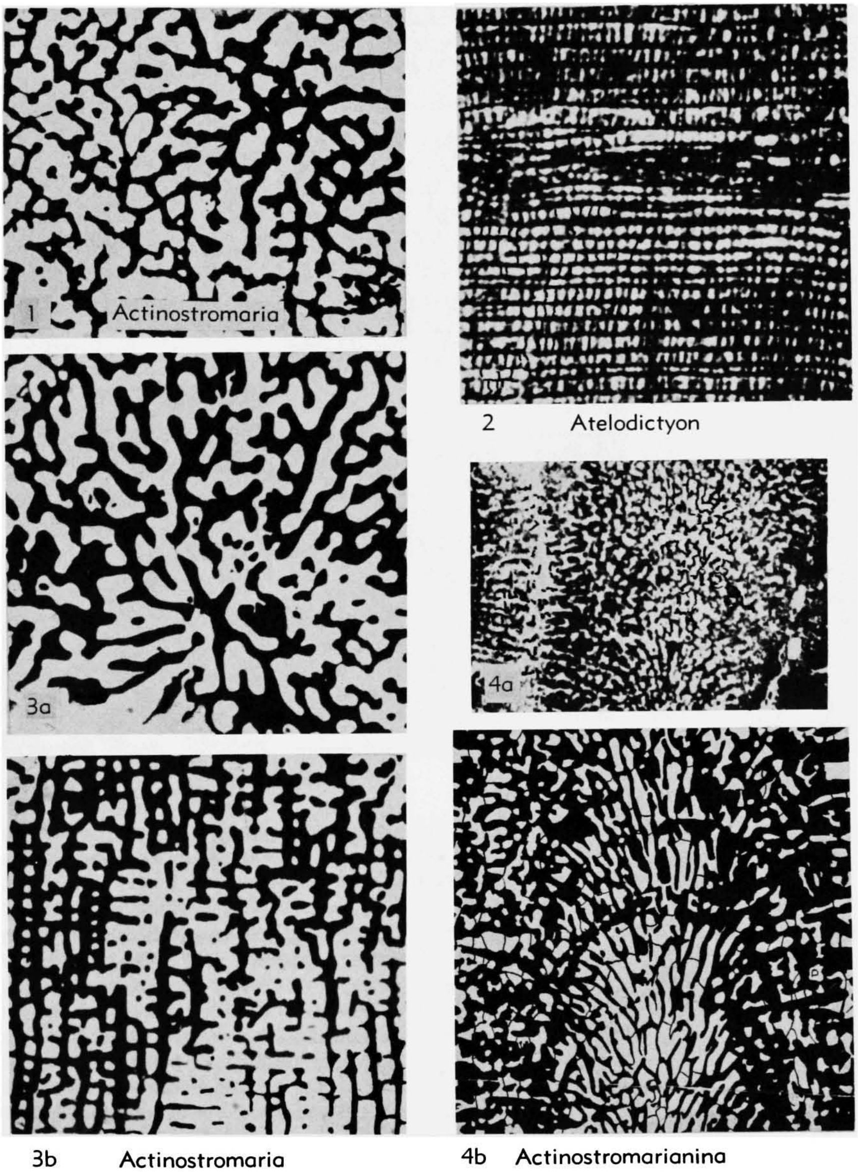


Fig. 104. Actinostromatidae. *1, A. salevensis,* Cret., ×12. *2, A. fallax,* M.Dev., ×12. *3a,b, A. stellata,* Cret., ×12. *4a,b, A. milleporoides,* U.Jur., ×3, ×12.

© 2009 University of Kansas Paleontological Institute

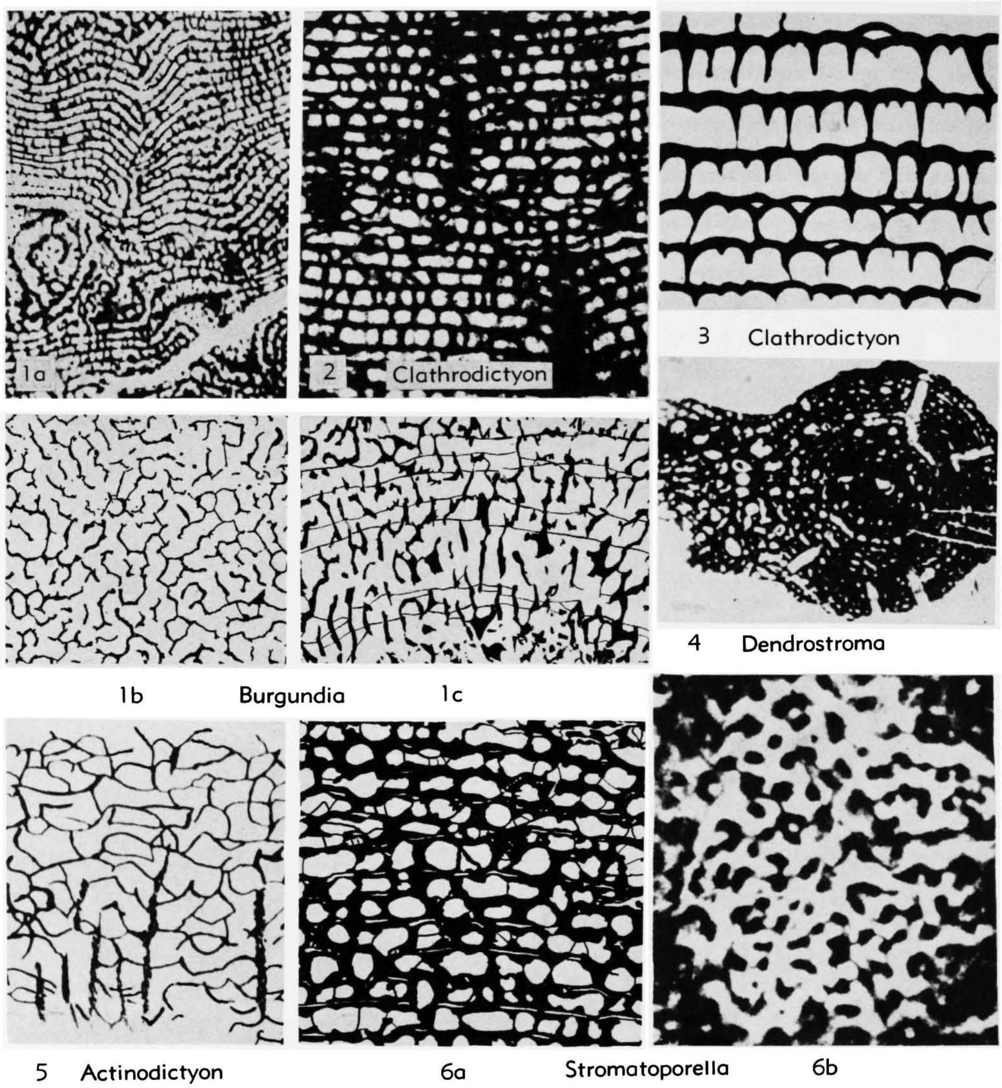


FIG. 105. Clathrodictyidae, Stromatoporellidae. *1a,b, B. trinorchii,* U.Jur., ×3, ×12. *2, C. amygdaloides,* M.Dev., ×12. *3, C. striatellum,* M.Sil., ×24. *4, D. oculatum,* Dev., ×3. *5, A. canadense,* M.Sil., ×10. *6a,b, S. granulata,* M.Dev., ×12.

Actinodictyon PARKS, 1909 [**A. canadense;* SD BASSLER, 1915]. Coenosteum composed of subvesicular tissue traversed by evenly spaced large spongy pillars (24). *M.Sil.-U.Dev.,* Eu.-N.Am.——FIG. 105,*5.* **A. canadense,* M.Sil., Hudson Bay; long. sec. ×10 (51).

Burgundia CHALMAS *in* DEHORNE, 1915 [**B. trinorchii*] [=?*Circoporella* HAYASAKA, 1917]. Growth form laminar, spheroidal, domed, or irregular, with surface marked by mamelons; predominant are well-defined continuous lamellae, more or less wavy and separated from one another in different specimens or parts of the same colony, or partly lenticular; pillars mostly short and straight, bifurcate at top or expanded at one or both extremities, restricted to a single interlamellar space; some pillars long and crooked, unbranched or branched to anastomosing, not restricted to a single interlamellar space; these two types may alternate zonally. Astrorhizae large, in vertical systems with branches abruptly terminated in interlamellar spaces. Lamellae in tangential sections show well-marked reticulate or meandriform structures. Skeletal elements compact, microcrystalline, or granular; a dark or clear filiform axis may be recognized in lamellae and rarely in pillars (6). *Jur.,* Eu.-Afr.-Asia. This

© 2009 University of Kansas Paleontological Institute

genus is closely allied to forms of *Clathrodictyon* having well-differentiated skeletal elements; it is distinguished by partly disordered, branched or anastomosed pillars extending through 2 or more lamellae. So-called zooidal tubes noted by some authors, which rarely occur in sections, seemingly are parts of astrorhizae.——Fig. 105,*1*. **B. trinorchii* U.Jur., Fr.; *1a,b,* long. and tang. secs., ×3; *1c,* long. sec., ×12 (49n).

Stylodictyon Nicholson & Murie, 1878 [**Syringopora columnaris* Nich., 1875]. Coenosteum very dense, formed of well-differentiated lamellae and interlamellar pillars traversed by nearly equidistant stout columns between which curved laminae occur in alternate open and close-spaced groups (22). *Dev.,* N.Am.-Russ.

?**Clavidictyon** Sugiyama, 1939 [**C. columnare*]. Colonies columnar, dendroid, or bundled; surface granulose; axial portion composed of reticulate tissue but peripheral part having well-defined lamellae joined by interlamellar pillars. Astrorhizae lacking (37). *M.Sil.,* Japan.

?**Pseudostylodictyon** Ozaki, 1938 [**P. poshanense*]. Columns much thicker and more widely spaced than in *Stylodictyon* and formed by bulging of lamellae only. Astrorhizae seem to be lacking (23). *Ord.,* China.

Family STROMATOPORELLIDAE Lecompte, 1951

Skeletal elements thick, well differentiated, comprising continuous, regularly spaced lamellae and discontinuous pillars confined to interlamellar spaces but superposed in some forms. Straight or tortuous vertical chambers bearing tabulae are poorly developed. Astrorhizae strong. Skeletal elements have porous microstructure. *Sil.-Carb., ?Trias.*

Stromatoporella Nicholson, 1886 [**Stromatopora granulata* Nich., 1873] [=?*Clathrocoilona* Yavorsky, 1931; *Stictostroma* Parks, 1936 *(partim)*]. Generally laminar, free, with basal epitheca, or encrusting; skeletal elements fairly well individualized and nearly equal in importance; pillars typically limited to interlamellar spaces, with tendency to superposition in some; vertical tabulated chambers few and short. Astrorhizal systems well developed, commonly associated with mamelons. Skeletal elements cellular (20). *Sil.-Carb.,* cosmop. None of the Mesozoic forms described under this name seemingly belong to the genus.——Fig. 105, *6*. **S. granulata* (Nich.), M.Dev.(Couvin.), Belg.; *6a,b,* long. and tang. secs., ×12 (49); also Fig. 102,*4*. Other species, Figs. 87, 90, 95,*2*.

Dendrostroma Lecompte, 1952 [**Idiostroma oculatum* Nicholson, 1886]. Dendroid colonies with coenosteum like that of *Stromatoporella,* with thick, well-differentiated pillars and lamellae, the pillars being limited to an interlamellar space. Large axial astrorhizal canal and its lateral branches intersected by partitions (17). *Dev.,* Eu.——Fig. 105,*4*. *D. oculatum* (Nich.), Dev., Ger.; long. sec., ×3 (49n).

Synthetostroma Lecompte, 1951 [**S. actinostromoides*]. Free or incrusting colonies. Much-folded lamellae of complex structure, with parallel or intertwined fibrils, and pillars limited to interlamellar spaces but superposed. Astrorhizae very strongly developed, intersected by numerous partitions (17). *M.Dev.,* Belg.——Fig. 106,*3*. **S. actinostromoides,* M.Dev.(Givetian), Belg.; long. sec., ×12 (49*).

?**Lithopora** Tornquist, 1900 [**L. koeneni*]. Structure like *Stromatoporella* but the sparse vertical chambers seemingly lack tabulae. Microstructure unknown. *M.Trias.,* Italy.

Family SYRINGOSTROMATIDAE Lecompte, 1951

[*nom. correct.* Lecompte, herein (*pro* Syringostromidae Lecompte, 1951)]

Well-differentiated continuous pillars and lamellae, thin in early forms but gradually thicker in later ones; vertical tabulated chambers more or less numerous and well developed. Microstructure cellular or reticulate in Paleozoic genera, uniformly in early forms but later tending to marginal localization; fibrous in Mesozoic forms. Skeletal elements with dark axis. *Sil.-Jur.*

Syringostroma Nicholson, 1875 [**S. densa;* SD Nich., 1886]. Free or incrusting colonies with coenosteum built of more or less continuous, strong pillars of straight or slightly sinuous form, and reticulate, generally thin, continuous lamellae which show axial lines. Vertical tabulated chambers slightly to well developed. Astrorhizae generally well developed. Skeletal fibers alveolar (19). *Sil.-Dev.,* Eu.-Asia-Austral.-N.Am.——Fig. 107,*2*. *S. centrotum* Girty, Sil., N.Y.; long. sec., ×10 (51*).——Fig. 106,*2*. *S. baccatum* Lecompte, M. Dev.(Givet.), Belg.; long. sec., ×12 (49*).

Hermatostroma Nicholson, 1886 [**H. schlüteri*]. Skeletal elements thick, subequal and mutually perpendicular; interlamellar chambers well delimited, typically rounded, and commonly divided by partitions; vertical tabulated chambers more or less numerous. Astrorhizae generally prominent. Skeletal elements with marginal cellular or canaliculo-cellular structure (20). *Sil.-Dev.,* cosmop.—— 107,*4*. **H. schlüteri.* M.Dev., Ger.; tang. sec., ×20 (49); also Fig. 96.——Fig. 99. *H. perseptatum* Lecompte, U.Dev.(L.Frasn.), Belg.; long. sec., ×3 (49*).

Idiostroma Winchell, 1867 [**I. caespitosum;* SD Bassler, 1915]. Dendroid or fasciculate colonies; pillars superposed and lamellae distinct; large

© 2009 University of Kansas Paleontological Institute

astrorhizal axial canal and lateral branches intersected by partitions; vertical chambers tabulated. Skeletal elements with cellular marginal structure (45). *Sil.-Dev.,,* N.Am.-Eu.-Asia-Austral.——FIG. 107,*3. I. roemeri* NICH., Dev., Ger.; transv. sec., ×3 (49*)

Syringostromina LECOMPTE, 1952 [**Stromatopora choffati* DEHORNE, 1920]. Moderately large, irregular subconcretionary colony with coenosteum as in *Syringostroma;* thin, closely spaced, continuous, parallel pillars are intersected by filiform, widely separated lamellae, between which the vertical chambers are divided by numerous, very thin tabulae; in tangential section, the lamellar system shows an extremely fine, complete or meandriform network. Astrorhizae very strongly developed, superposed, with scanty, irregular branches. Skeletal elements longitudinally striate or with trellis structure (18). *U.Jur.,* Eu.——FIG. 106,*4.* **S. choffati* (DEHORNE), U.Jur.(Lusit.), Port.; tang. and long. secs., ×12 (49n).

Trupetostroma PARKS, 1936 [**T. warreni*]. Compact lamellae pierced by circular pores corresponding to chambers and marking evolutionary tendency toward thickening; strong pillars superposed; vertical tabulated chambers very well developed, connected with astrorhizae. Cellules of skeletal elements tend toward marginal localization.

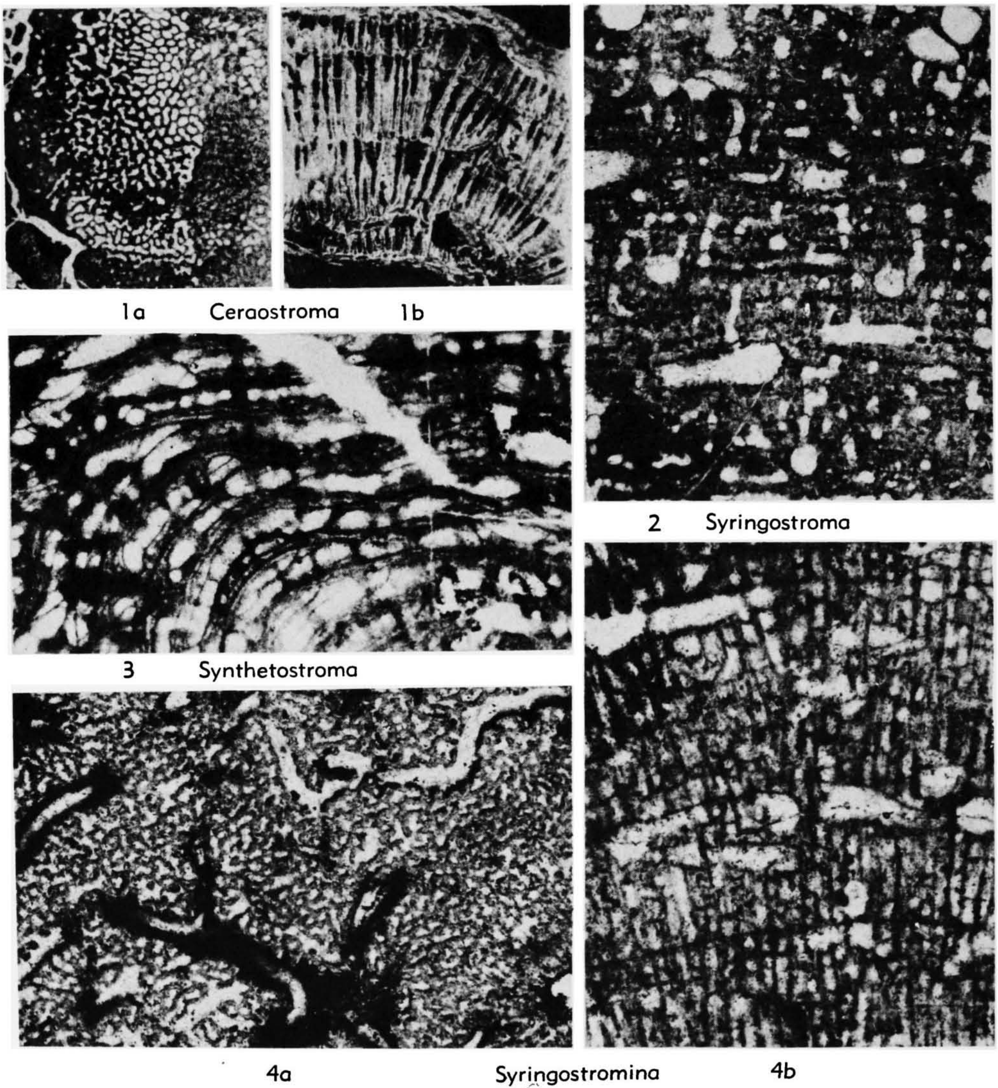
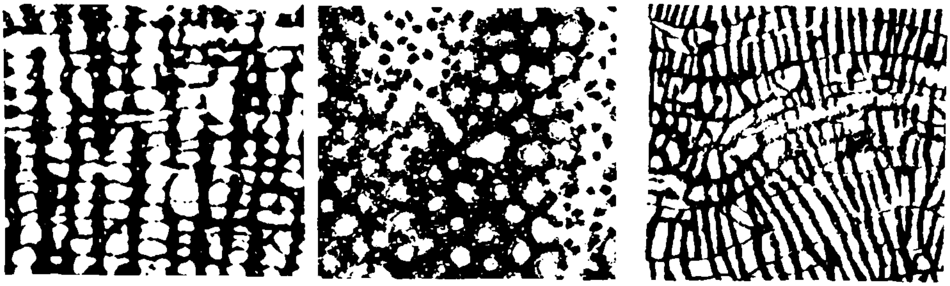
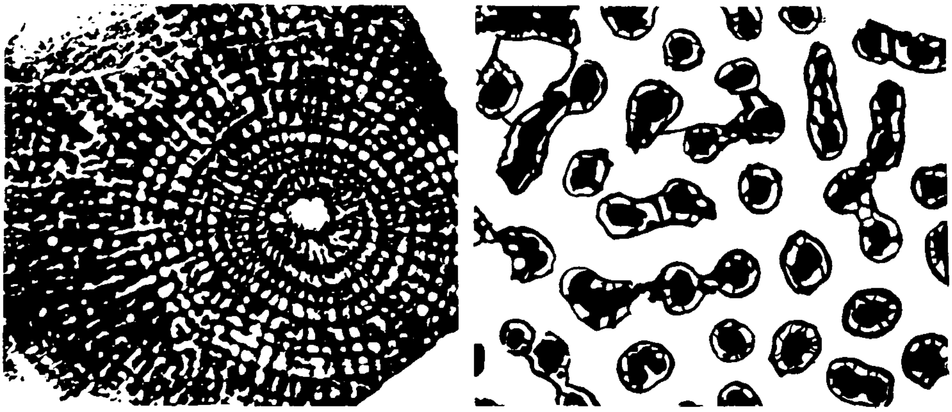


FIG. 106. Stromatoporellidae, Syringostromatidae. *1a,b, G. steinmanni,* U.Jur., ×2.8. *2, S. baccatum,* M.Dev., ×12. *3, S. actinostromoides,* M.Dev., ×12. *4a,b, S. choffati,* U.Jur., ×12.

© 2009 University of Kansas Paleontological Institute



1a Trupetostroma 1b 2 Syringostroma



3 Idiostroma 4 Hermatostroma

FIG. 107. Syringostromatidae. *1a,b, T. warreni,* Dev., ×10. *2, S. centrotum,* Sil., ×10. *3, I. roemeri,* Dev., ×3. *4, H. schlüteri,* M.Dev., ×20.

Astrorhizae prominent (27). *Dev.,* N.Am.-Eu.——FIG. 107,*1*. **T. warreni,* Dev., NW.Can.; *1a,b,* long. and tang. secs., ×10 (51*).——FIG. 98,*1*. *T. tenuilamellatum* LECOMPTE, U.Dev.(L.Frasn.), Belg.; *1a,b,* tang. and long. secs., ×3, ×12 (49*); also FIG. 102,*2*.——FIG. 98,*3*. *T. ruedemanni* LECOMPTE, U.Dev.(L.Frasn.), Belg.; long. sec., ×12 (49*).

?**Ceraostroma** KÜHN, 1926 [**C. steinmanni*]. Colony incrusting, skeleton probably chitinous originally and secondarily calcified. Continuous pillars and wide-spaced lamellae enclosing extended vertical chambers, which bear thin partitions. Astrorhizae well developed (13). *U.Jur.,* Eu.——FIG. 106,*1*. **C. steinmanni,* U.Jur.(Tithon.), Aus.; *1a,b,* long. and tang. secs., ×2.8 (48*).

Family STROMATOPORIDAE Nicholson, 1886

[=Coenostromidae WAAGEN & WENTZEL, 1887]

Colonial form massive, laminar, incrusting, or dendroid. Coenosteum has more or less open or close reticulate structure, lamellation tending to be lost in the reticulation of tissue or to be supplanted by pillars which in certain forms evolve in vertical lamellae. Vertical tabulated chambers numerous. Astrorhizae more or less well developed. Microstructure cellular or fibrous. *Ord.-Cret.*

Stromatopora GOLDF., 1826 [**S. concentrica*] [=*Coenostroma* WINCHELL, 1867; ?*Prisciturben* KUNTH, 1870; *Pachystroma* NICH. & MURIE, 1878; *Rosenia* WAAGEN & WENTZEL, 1887]. Growth massive or laminar, and in some, latilaminar. Coenosteum may be differentiated in strong vertical pillars and stout simple (not bifid) lamellae, but it shows a general tendency toward a closely reticulate structure with progressive loss of lamellation. Interpillar tabulated chambers present. Skeletal elements cellular. Astrorhizae more or less prominent (20). *Ord.-Perm.,* cosmop.——FIGS. 91,*2;* 108,*2*. **S. concentrica,* U.Dev.(L.Frasn.), Belg.; long. secs., ×3, ×12 (49*,49); also FIG. 92, *1*.——FIG. 109,*1*. *S. pachytexta* LECOMPTE, M.Dev., Ger.; long. sec., ×3 (49*). Other species, FIGS. 88, 89, 102,*3*.

Dehornella LECOMPTE, 1952 [**Stromatoporella hydractinoides* DEHORNE, 1918]. Small laminate incrusting form, entire surface covered by conical mamelons with opening of axial canal of stellate astrorhizae at summits; coenosteum beneath mame-

© 2009 University of Kansas Paleontological Institute

lons composed of continuous pillars, tortuous and very irregular in thickness, joined by uneven cross bars; between mamelons, continuous lamellae are fairly distinct and very irregular pillars are discontinuous and commonly restricted to an interlamellar space. Pillars cut transversely reveal a pig-

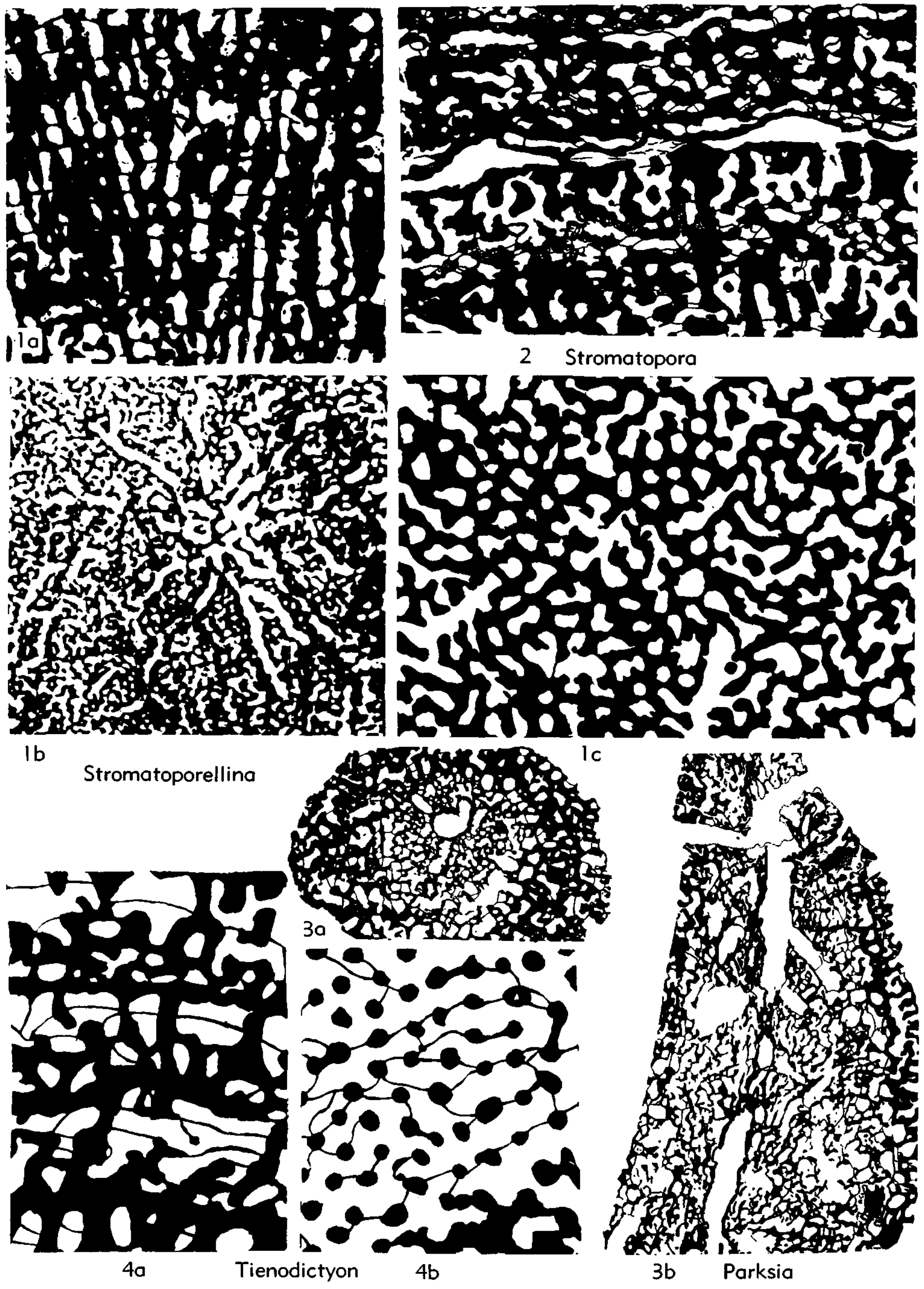


Fig. 108. Stromatoporidae. *1a-c, S. haugi,* U.Cret.; *1a,c,* ×12; *1b,* ×3. *2, S. concentrica,* M.Dev., ×12. *3a,b, P. douvillei,* U.Jur., ×6. *4a,b, T. zonatum,* Dev., ×12.

© 2009 University of Kansas Paleontological Institute

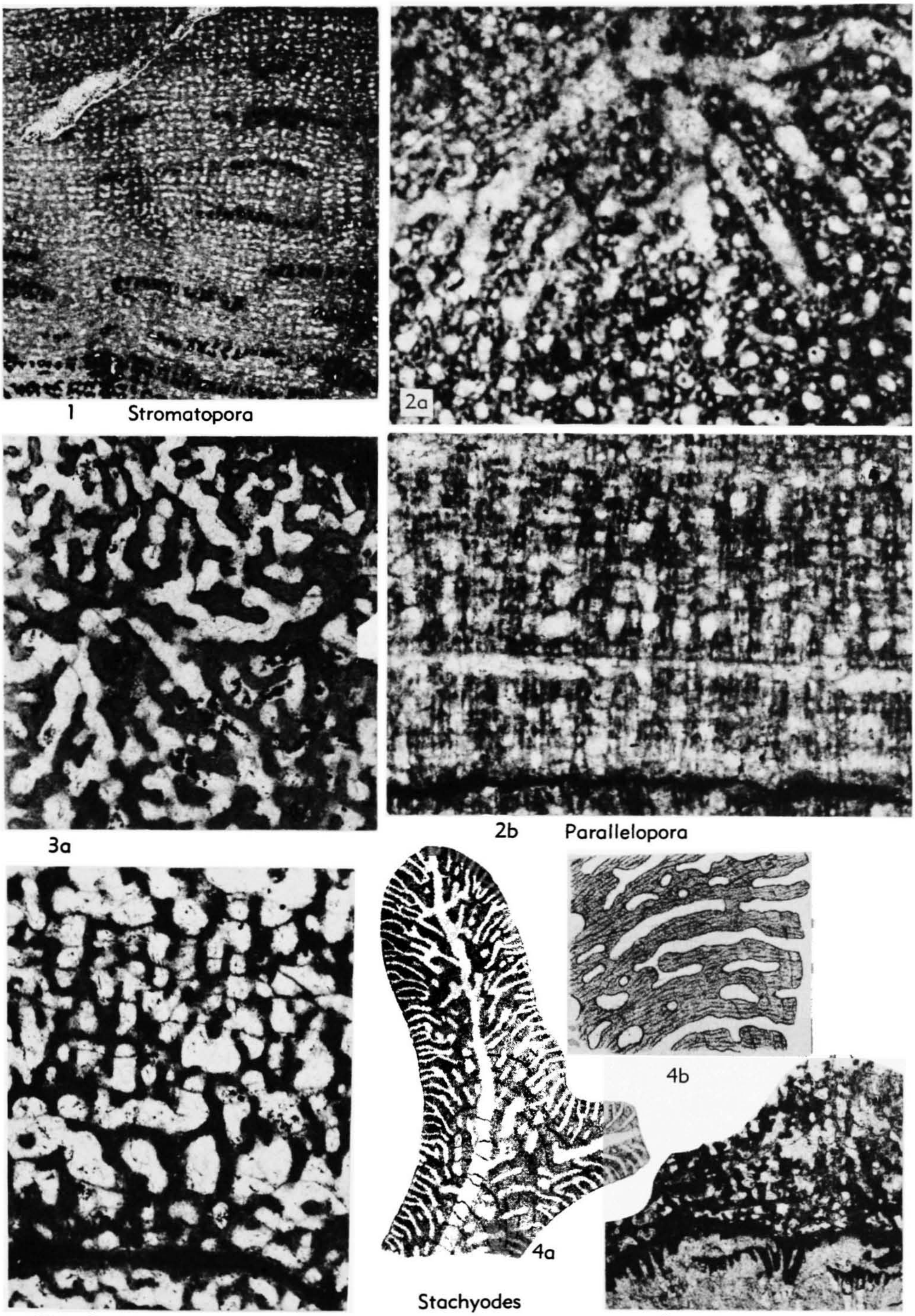


Fig. 109. Stromatoporidae. *1, S. pachytexta,* M.Dev., ×3. *2a,b, P. ostiolata,* M.Dev., ×20. *3a,b, S. choffati,* U.Jur., ×12. *4a,b, S. verticillata,* Dev., ×2, ×12. *5, D. hydractinoides,* U.Jur., ×6.

© 2009 University of Kansas Paleontological Institute

FIG. 110. Stromatoporidae. *Stachyodes radiata,* U. Dev., ×3.

mented core which undergoes extinction in polarized light, possibly indicating substitution of chitin (18). *U.Jur.,* SW.Eu.——FIG. 109,*5.* **D. hydractinoides,* U.Jur.(Lusitan.), Port.; long. sec., ×6 (49n).

Parallelopora BARGATZKY, 1881 [**P. ostiolata;* SD NICH., 1891]. Massive free colonies with loosely reticulate coenosteum, pillars predominating and lamellation tending to disappear; the stout, more or less continuous pillars are straight or tortuous, and they show tendency to develop in vertical lamellae evolving in closed tubes. All interpillar spaces bearing thin tabulae. Skeletal elements essentially cellular or in some reticulate. Astrorhizae strongly developed (1). *Dev.-?Perm.,* cosmop.——FIG. 109,*2.* **P. ostiolata,* M.Dev., Ger.; *2a,b,* tang. and long. secs., ×20 (49*); also FIG. 102,*1.*——FIG. 100. *P. paucicanaliculata* LECOMPTE, M.Dev. (Givet.), Belg.; long. sec., ×12 (49*).

Parksia LECOMPTE, 1952 [**Stromatopora douvillei* DEHORNE, 1918]. Delicate dendroid colonies with entirely reticulate coenosteum of *Stromatopora* type. Axial astrorhizal canals very large, with coarse lateral branches dipping obliquely and conformably to lamination. Microstructure fibrous, without pigmented dark axes; the fibers, which are longitudinally oriented at axis, bend toward periphery so as to produce wavy extinction under crossed nicols (18). *U.Jur.,* N.Afr.——FIG. 108,*3.* **P. douvillei* (DEHORNE), U.Jur., S.Tunisia; *3a,b,* transv. and long. secs., ×6 (49n).

Plassenia YABE & SUGIYAMA, 1931 [**P. alpina*]. Massive colonies with wavy, perforate lamellae and interlamellar spaces connected by lamellar or rarely columnar vertical partitions, the lamellar ones being irregularly folded and laterally variously joined to one another dividing the interlamellar spaces into numerous minute chambers elongated in various directions; extremely thin tabulae occur uncommonly. Vertical astrorhizae bear lateral branches at irregular intervals. Tangential sections show an irregular network with subcircular meshes, but more commonly elongated or curved in various directions. *U.Jur.,* Eu.

Stachyodes BARGATZKY, 1881 [**Stromatopora (Caunopora) verticillata* M'COY, 1851] [=*Sphaerostroma* GÜRICH, 1896]. Dendroid, fasciculate, or submassive colonies with compact or reticulate coenosteum more or less differentiated in distinct pillars especially in peripheral parts; lamellae filiform, intersecting all tissue. Large axial astrorhizal canals crossed by many straight, oblique, bent, or vesiculose tabulae; adventitious canals distributed, conformably to lamellation. Skeletal elements commonly showing fine longitudinal striae but probably essentially microreticulate (1). *M.Dev.-U.Dev.,* Eu.-Austral.——FIG. 109,*4.* **S. verticillata* (M'COY), Dev., Ger.; *4a,b,* long. sec., ×2, ×12 (50*). Also FIG. 86,*1.* ——FIG. 110. *S. radiata* LECOMPTE, U.Dev.(L.Frasn.), Belg.; long. sec., ×3 (49*).

Stromatoporellata BAKALOV, 1910 [**S. mammilaris*]. *U.Trias.,* Bulgaria.

Stromatoporellina KÜHN, 1927 [**Stromatoporella haugi* DEHORNE, 1917] [=*Epistromatopora, Parastromatopora* YABE & SUGIYAMA, 1935]. Massive mamelonate or branched colonies; coenosteum of *Parallelopora* type, with continuous subparallel pillars, straight or slightly bent, rarely trabecular, mostly lamellate and showing strong tendency to produce adjoined tubes, partly meandriform, of a single type crossed by thin regular tabulae. Astrorhizae well developed, with many tortuous branches, distally ramified; few horizontal canals appear in longitudinal sections. Skeletal elements lacking dark axis are composed of microcrystalline fibers in fine poorly defined bundles (14). *Jur.-Cret.,* Eu.-Afr.-Asia. (Since this form is allied to *Parallelopora,* rather than *Stromatoporella,* as presumed by KÜHN, the generic name is very ill chosen. *Stromatoporellina* embraces forms defined by YABE & SUGIYAMA [1935] as *Epistromatopora,* with granules concentrated in axes of skeletal elements, and *Parastromatopora,* with oblique fibers.)——FIG. 108,*1.* **S. haugi* (DEHORNE), U.Cret., Fr.; *1a,c,* long. and tang. secs., ×12; *1b,* tang. sec., ×3 (49n).

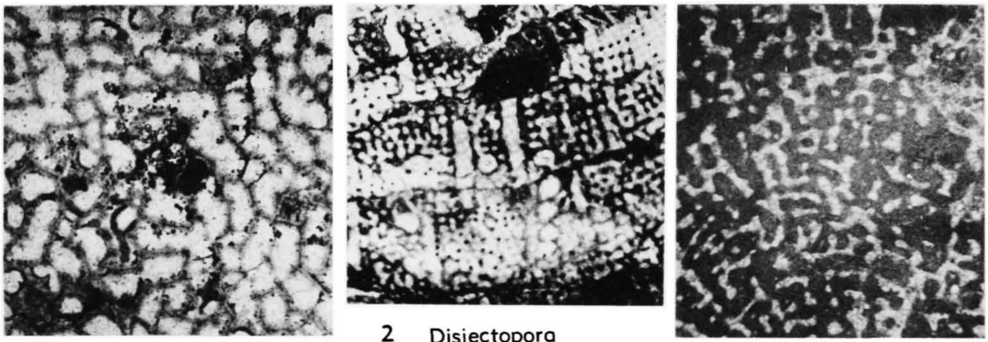
© 2009 University of Kansas Paleontological Institute

Stromatoporina Kühn, 1927 [**Stromatopora tornquisti* Deninger, 1906]. Coenosteum strongly latilaminar with structure like *Stromatopora*, lamellation remaining evident in the reticulation of tissue; pillars irregular, showing no tendency to form tubes; all intercolumnar spaces bearing thin tabulae. Astrorhizae present. Microstructure fibrous, fasciculate, or radial, without dark axis (14). *Trias.-Cret.*, Eu.-Asia. The type species not having been studied, description is based on Dehorne's (1920) species: *Stromatopora choffati, S. romanica,* and *S. arrabidensis.*——Fig. 109,*3. S. choffati* (Dehorne), U.Jur.(Lusitan.), Port.; *3a,b,* tang. and long. secs., ×12 (49n).

Stromatorhiza Bakalov, 1906 [**Thamnaraea? granulosa* Koby, 1888]. Coenosteum entirely reticulate, as in typical *Stromatopora,* but lacking tabular partitions and with homogeneous skeletal elements bearing a strong dark axis. *U.Jur.,* Eu.

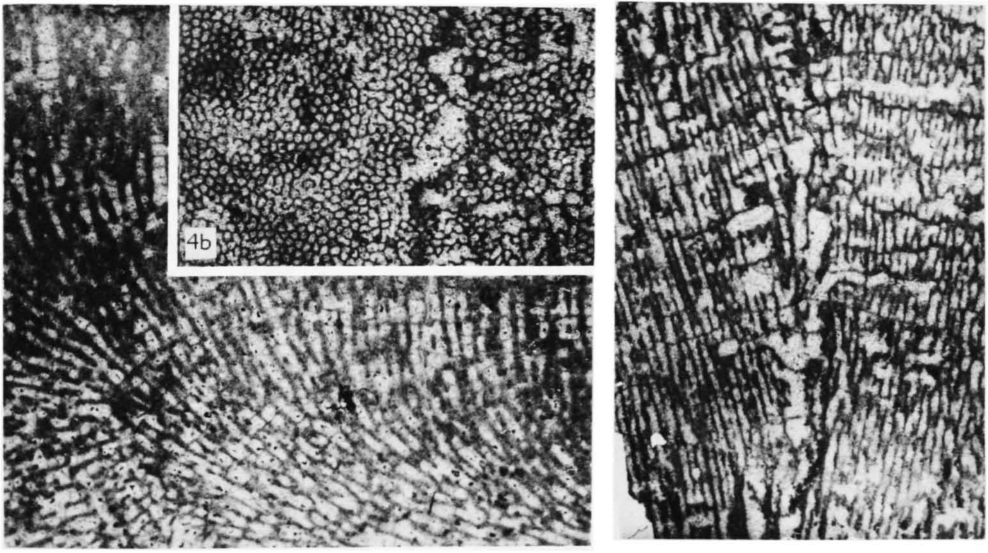
Tienodictyon Yabe & Sugiyama, 1941 [**T. zonatum*]. Colonies massive, with zonal structure and finely granulose surface; strong lamellae of fine trabecular structure separate the zones, which in lower parts consist of reticulate tissue with meshes partly intersected by tabulae, and in upper parts mainly comprise subvertical pillars joined to lamellae by their expanded ends and connected by thin partitions in lamellar disposition. Astrorhizae readily visible in longitudinal sections. *Dev.,* China.——Fig. 108,*4.* **T. zonatum; 4a,b,* long. and tang. secs., ×12 (55).

?**Stromatostroma** Bakalov, 1910 [**S. triasicum*]. *U.Trias.,* Bulgaria.


1 Siphostroma

2 Disjectopora

3 Balatonia



4a Milleporidium

5 Milleporella

Fig. 111. Disjectoporidae, Milleporellidae, Milleporidiidae. *1, S. arzieri,* L.Cret., ×12. *2, D. japonica,* M.Perm., ×50. *3, B. kochi,* U.Trias., ×7. *4, M. remesi,* U.Jur., ×12. *5a,b, M. adriatica,* L.Eoc., ×6.

© 2009 University of Kansas Paleontological Institute

Family DISJECTOPORIDAE Tornquist, 1901

Massive forms composed of regular or irregular trabecular tissue, traversed by strong, continuous vertical astrorhizae with tabulated canal and stellate, generally short branches. *Perm.-U.Trias.*

Disjectopora Waagen & Wentzel, 1887 [**D. milleporaeformis*]. Coenosteum composed of trabeculae forming a rectangular network. Astrorhizae with large axial canals, bearing tabulae, horizontal branches generally narrow (42). *Perm.-Trias.*, Asia.——Fig. 111,*2*. *D. japonica* Yabe & Sugiyama, M.Perm., Japan; long. sec., ×50 (55*).

Balatonia Vinassa, 1908 [**B. kochi*]. Spheroidal colony composed of vermiform elements, in central part arranged loosely in somewhat regular layers, but close and radially disposed toward periphery. Astrorhizae with straight axial tubes, invariably tabulate, and few branches, restricted to outer layers. *U.Trias.*, Eu.——Fig. 111,*3*. **B. kochi*, U. Trias., Hung.; long. sec., ×7 (54*).

Carta Stechow, 1921 [*pro Carterina* Waagen & Wentzel, 1887 (*non* Brady, 1884)] [**Carterina pyramidata* Waag.-W., 1887] [=*Arduorhiza* Waag.-W., 1889; *Carterinula* Strand, 1926]. Large massive coenosteum composed of an irregular network of trabeculae traversed in all directions by many continuous astrorhizae with strong axial canals and large branches irregularly ramified intersected by trabecular pseudosepta (33). *Perm.*, Asia.

Irregulatopora Waagen & Wentzel, 1887 [**I. undulata*]. Massive or laminate colonies, coenosteum composed of irregularly arranged trabeculae forming an irregular meshwork. Astrorhizae irregular, with trabecular tabulae (42). *Perm.*, Asia.

Family MILLEPORELLIDAE Yabe & Sugiyama, 1935

Massive or incrusting forms, coenosteum lacking lamellae; vertical elements partly or entirely lamellar, showing strong tendency to form closed tubes of uniform diameter, intersected by tabulae. Astrorhizae still very apparent are grouped in vertical bundles, extending radially sideward into coenosteal tissue; they are related to narrow vertical tabulate chambers. *Jur.-Cret.*

Milleporella Deninger, 1906 [**M. sardoa*] [=*Istriactis* Chalmas, 1883]. Subglobular colonies with mamelonate surface; trabecular or lamellar pillars tend to form incomplete or closed tubes joined by filiform cross pieces disposed in lamellar form; tangential sections show a fine fibrous network of regular polygonal meshes, mostly open in meandriform or hieroglyphic patterns. Astrorhizae in close vertical bundles, laterally digitate with uneven arrangement and extent; in tangential sections, they appear as stellate groups of twisted, branching, anastomosed passages which disappear in tissue without appreciable diminution in size. Structure microcrystalline (8). *Jur.-Cret.*, Eu.——Figs. 111,*5*; 112,*3*. *M. adriatica* (Chalmas), L.Eoc., Italy; long. and tang. secs., ×6 (49n).

Siphostroma Steiner, 1932 [**S. arzieri*]. Colony with wavy laminae; pillars generally continuous but locally interrupted and irregularly distributed, partly lamellar and tending to form tubes bearing thin, weakly convex tabulae; in expanded interspaces, pillars are absent, tabulae being replaced by subvesicular dissepiments; lamellar platforms few but thick or reduced to a single space or formed by bending of pillars. Tangential sections show a trabecular net of mostly open meshes intersected by irregular vague canal-like spaces, possibly astrorhizal. Pillars commonly have a dark axis with perpendicularly placed fiber bundles around it; locally, pillars are formed of clearly separate, superposed calcification centers and their fibrous aureoles. Tabulae consist of adjoined dark granules without fibrous covering (34). *L.Cret.*, Eu.—Figs. 111,*1*; 112,*4*. **S. arzieri*, L.Cret.(L. Valang.), Switz.; 111,*1*, long. sec., ×12; 112,*4a*, tang. sec., ×12; 112,*4b*, long. sec., ×82.5 (49n).

Steinerella Lecompte, 1952 [**Stromatopora mecosola* Steiner, 1932]. Coenosteum composed of parallel vertical elements, partly trabecular, mainly differentiated in lamellae which tend to form imperfectly or entirely closed tubes with thin tabulae. Astrorhizae very strong, grouped in vertical bundles which partly bend horizontally with upward and downward bifurcations that pass into narrow tabulate intercolumnar chambers; in tangential sections, they form stellate groups with axes marked by many large recurved tubes. Microstructure fibrous, fasciculate, without dark axes (18). *L.Cret.*, Eu.——Fig. 112,*1*. **S. mecosola*, L. Cret.(Neocom.), Switz.; *1a,b*, long. and tang. secs., ×6; *1c*, long. sec., ×12 (49n).——Fig. 112,*2*. *S. loxola* (Steiner), L.Cret.(M.Valang.), Switz.; *2a-c*, long. secs., ×12, ×12, ×55 (49n).

Tosastroma Yabe & Sugiyama, 1935 [**T. tokunagai*]. Like *Siphostroma* but having platforms developed intermittently at the same level (47). *U. Jur.*, Japan.

Family MILLEPORIDIIDAE Yabe & Sugiyama, 1935

Coenosteum entirely of tubular structure, lacking lamellation. Relatively large, uniform, tabulate tubes are distributed somewhat regularly among small ones comprising the bulk of tissue. Astrorhizae lacking. *Jur.-Cret.*

© 2009 University of Kansas Paleontological Institute

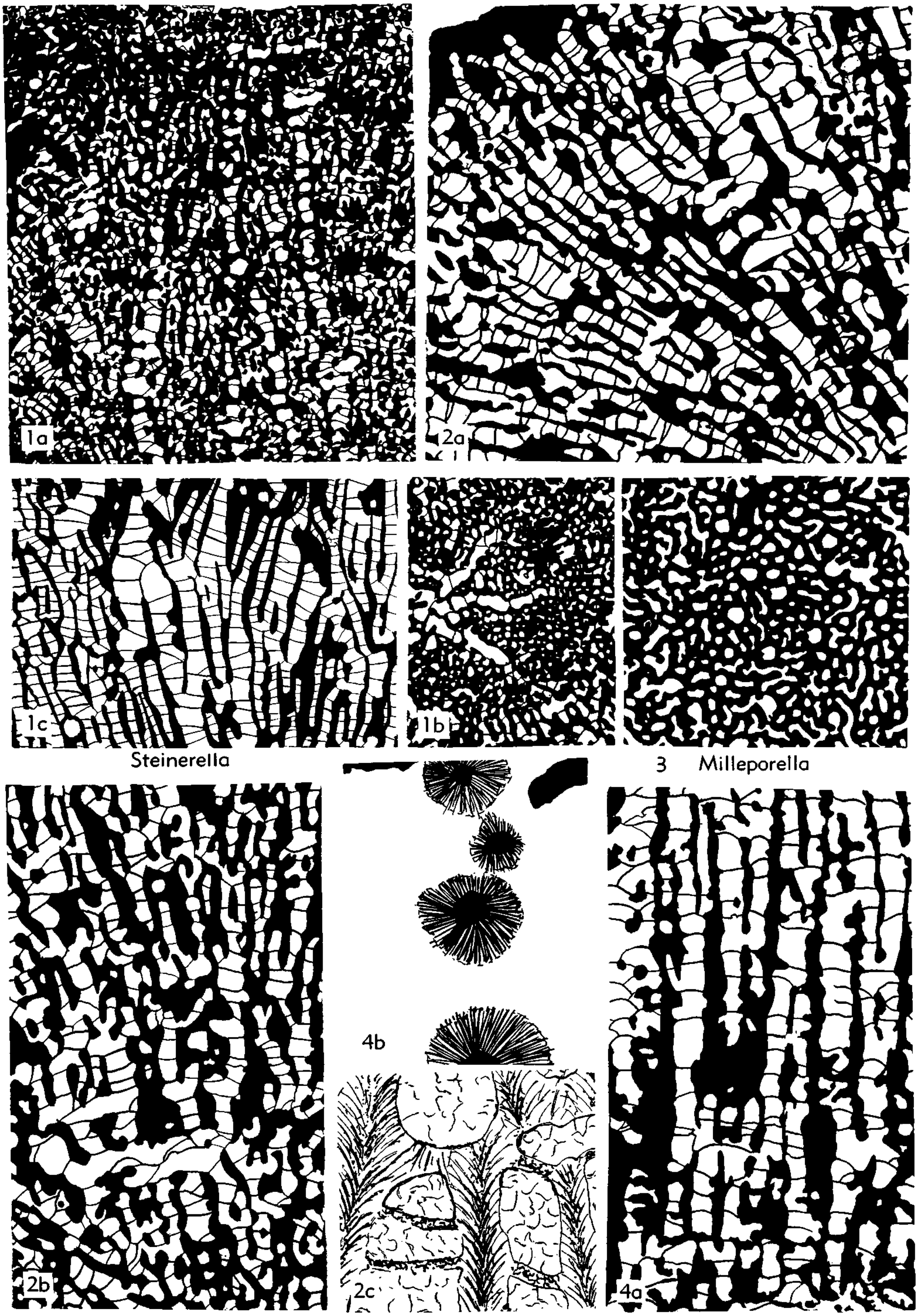


Fig. 112. Milleporellidae. *1a-c, S. mecosola,* L.Cret.; *1a,b,* ×6; *1c,* ×12. *2a-c, S. loxola,* L.Cret.; *2a,b,* ×12; *2c,* ×55. *3, M. remesi,* U.Jur., ×6. *4a,b, S. arzieri,* L.Cret., ×12, ×82.5.

© 2009 University of Kansas Paleontological Institute

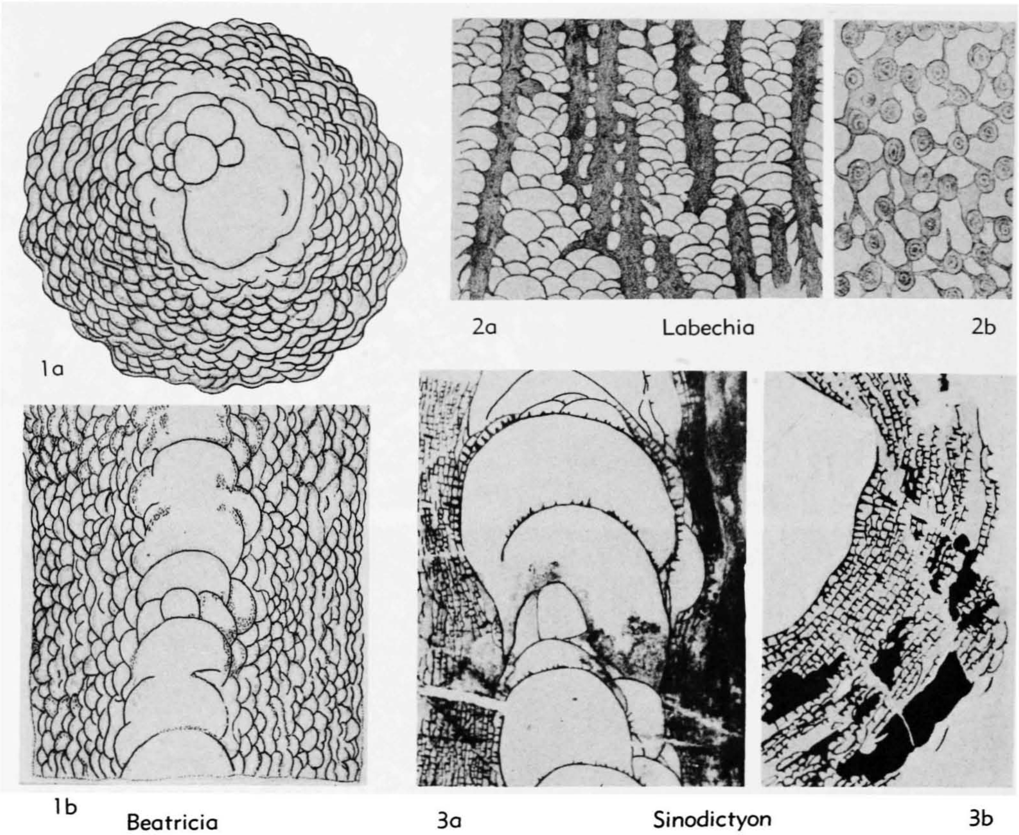


FIG. 113. Labechiidae, Aulaceridae. *1a,b, B. nodulosa,* U.Ord., ×2. *2a,b, L. conferta,* M.Sil., ×10, ×12. *3a,b, S. columnare,* Ord., ×4.

Milleporidium STEINMANN, 1903 [**M. remesi*]. Colonies dendroid. Large tabulate tubes, formed from small ones of the axial region, are located in the cortical region. The meandriform pattern of the network seen in transverse sections indicates that union in tubes formed by vertical elements is imperfect; irregular canal-like structures suggest astrorhizal structures, although these are lacking (36). *Jur.-Cret.,* Eu.-Afr.——FIG. 111,*4;* 112,*3.* **M. remesi,* U.Jur.(Tithon.), Aus.; 111,*4,* long. sec., ×12; 112,*3,* tang. sec., ×12 (both 49n).

Myrioporina KÜHN, 1939 [*pro Myriopora* VOLZ, 1904 (*non* REUSS, 1846)] [**Myriopora verbeeki* VOLZ, 1904]. Coenosteum composed of alternating layers of vermicular and rectilinear elements, the latter containing rounded tubes surrounded by a cyclic system of pores; pillars partly differentiated in tubes (16). *?U.Jur.,* Sumatra.

Family LABECHIIDAE Nicholson, 1885

Massive or laminar colonies with transverse skeletal elements typically composed of vesicular tissue, rarely of horizontal tabulae which invariably lack lamellar arrangement; vertical elements are laminae or strong radially disposed pillars, spiniform or continuous. Astrorhizae present rarely. *Ord.-Carb.*

Labechia M.EDW.-H., 1851 [**Monticularia conferta* LONSDALE, 1839]. Surface covered with tubercles, coalesced in some, making vermiform crests. Coenosteum composed of strong pillars with compact microstructure, joined by thin transverse plates which commonly form a vesicular tissue. Astrorhizae lacking. *Ord.-Carb.,* Eu.-Asia.-N.Am.——FIG. 113,*2.* **L. conferta* (LONSDALE), M.Sil.(Wenlock), Eng.; *2a,b,* long. and tang. secs., ×10, ×12 (50*).

Aulocerium PARKS, 1909 [**A. savagei*]. Coenosteum entirely composed of vesicular tissue, lacking pillars but pierced by vertical tubes containing strongly concave tabulae (24). *Sil.,* N.Am.——FIG. 114,*3.* **A. savagei,* M.Sil., Ill.; long. sec., ×10 (51).

Dermatostroma PARKS, 1910 [**Labechia papillata* JAMES, 1878]. Thin incrusting colonies covered by closely spaced papillae; coenosteum lacking pil-

© 2009 University of Kansas Paleontological Institute

lars, formed of thin leaves enclosing irregular chambers (24). *Ord.,* N.Am.

Labechiella Yabe & Sugiyama, 1930 [**Labechia serotina* Nicholson, 1890]. Like *Labechia* but pillars more regularly arranged and transverse elements nearly horizontal or slightly concave. Astrorhizae present (46). *Sil.-Dev.,* Eu.-Asia.——Fig. 114,*2*. **L. serotina* (Nich.), Dev., Eng.; long. sec., ×12 (50).

Lophiostroma Nicholson, 1890 [**Labechia? schmidti* Nich., 1890] [=*Chalazodes* Parks, 1908]. Colonies laminar, surface bearing prominent pointed or blunt mamelons; coenosteum formed by very wavy lamellae, with close-spaced conical elevations in position of the mamelons and forming pillars (20). *Sil.-?Perm.,* N.Am.-Eu.-Asia.

Ludictyon Ozaki, 1938 [**L. vesiculatum*]. Dendroid colonies composed of vesicles growing centrifugally; surface of vesicles covered by numerous very short pillars (23). *Ord.,* China.

Rosenella Nicholson, 1886 [**R. macrocystis*]. Massive or laminar growths largely composed of lenticular or cystose lamellae, which bear rudimentary spiniform pillars on their upper surface, not reaching to next higher lamina (20). *Sil.-L.Carb.,* N.Am.-Eu.-Asia.——Fig. 114,*4*. **R. macrocystis,* M.Sil.(Wenlock), Gotl.; long. sec., ×12 (50).

Rosenellina Raduguin, 1936 [**R. wellenformis*]. *L.Sil.,* Russ.

Stromatocerium Hall, 1847 [**S. rugosum*]. Like *Labechia* but with pillars replaced by vertical lamellae. *Ord.-?L.Carb.,* N.Am.-Eu.-Asia.

Stylostroma Gorsky, 1938 [**S. crassum*]. Irregu-

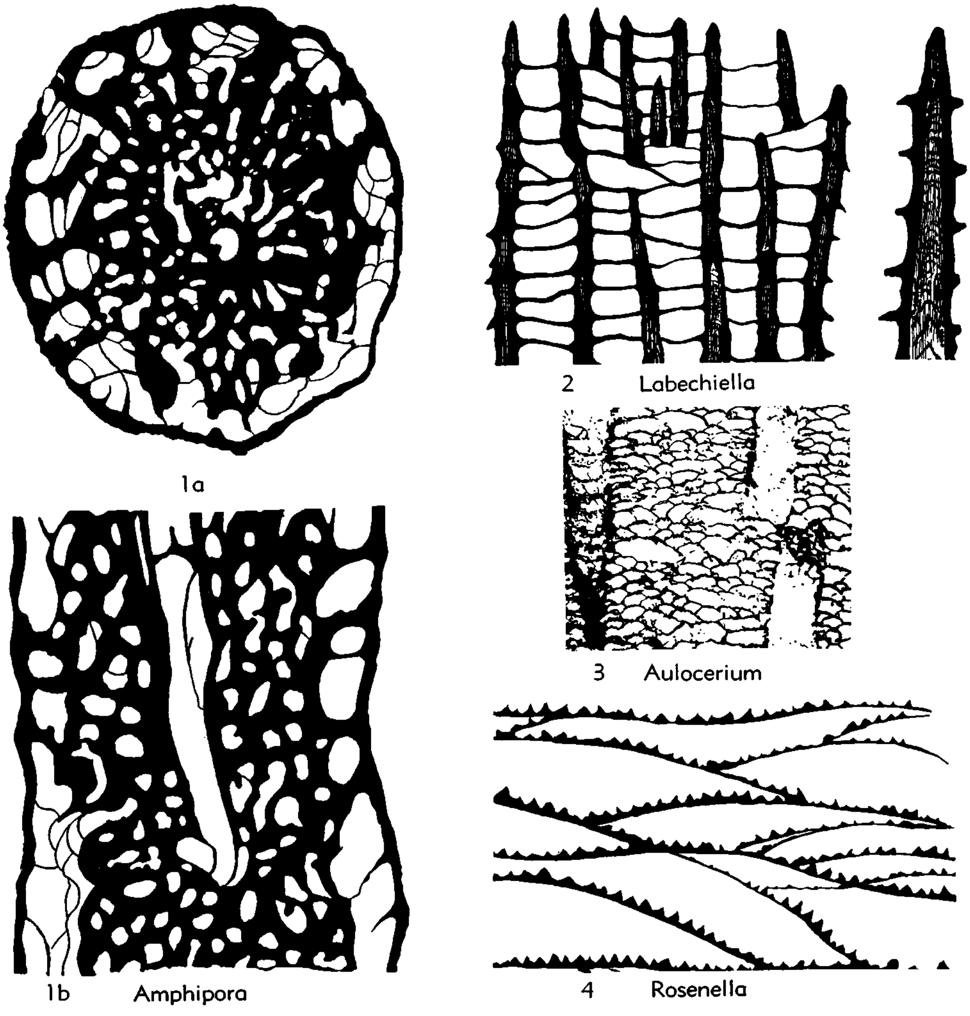


Fig. 114. Labechiidae, Incertae sedis. *1a,b, A. ramosa,* Dev., ×12. *2, L. serotina,* Dev., ×12. *3, A. savagei,* M.Sil., ×10. *4, R. macrocystis,* M.Sil., ×12.

© 2009 University of Kansas Paleontological Institute

larly hemispherical or laminate colonies with incomplete subvesicular lamellae strongly waved, intersected by stout pillars in fan-shaped arrangement. Possibly identical to *Labechia* (9). *U.Dev.-L.Carb.,* Russ.

Family AULACERIDAE Kühn, 1927

Branching colonies with a large axial canal divided into bulbous chambers by strongly arched tabulae, surrounded by vesicular tissue, with or without intersecting pillars or canals. *Ord.-Sil.*

Aulacera Plummer, 1843 [**Beatricea undulata* Billings, 1857]. Colonies distinguished from *Beatricea* only by lack of pillars and longitudinally folded surface. *U.Ord.-Sil.,* cosmop.

Beatricea Billings, 1857 [**B. nodulosa*]. Cylindrical unbranched colonies, surface wrinkled or covered with mamelons; a large axial canal is divided by strongly arched tabulae and surrounded by concentric vesicular tissue, generally prominent, and traversed in some forms by radially disposed pillars. *Ord.-Sil.,* N.Am.——Fig. 113,*1*. **B. nodulosa,* U.Ord., Ky.; *1a,b,* transv. and long. secs., ×2 (50).

Sinodictyon Yabe & Sugiyama, 1930 [**S. columnare*]. Fasciculate or laminar colonies with large axial canal divided into bulbous chambers by highly arched tabulae, bearing spines on their upper surface; peripheral zone composed of continuous closely spaced lamellae which are locally vesiculose and joined by short pillars or rarely by pillars extending through several layers (46). *Ord.,* Manchuria.——Fig. 113,*3*. **S. columnare; 3a,b,* long. and transv. secs., ×4 (55).

Thamnobeatricea Raymond, 1931 [**T. parallela*]. Like *Beatricea* but branching and with much reduced vesicular area (29). *M.Ord.,* N.Am.

?**Cryptophragmus** Raymond, 1914 [**C. antiquatum*]. Dendroid colonies with large wall-enclosed axial canal, divided into bulbous chambers by irregularly spaced, strongly arched partitions; inner side of canal wall bears a deposit of vesicular tissue. Peripheral tissue composed of thin, weakly separated calcareous leaves traversed by many radially disposed circular openings (28). *M.Ord.,* N.Am.

?**Cladophragmus** Raymond, 1931 [**C. bifurcatus*] (29). *M. Ord.,* N.Am.

Family INCERTAE SEDIS

Amphipora Schultz, 1883 [**Caunopora ramosa* Phillips, 1841]. Delicate dendroid colonies, with or without a large axial canal; thin rectilinear or vesiculose platforms may divide the canal or be lacking; coenosteum essentially reticulate, with more or less continuous pillars present in some, tending to form a marginal row of large vesicles; chambers with or without dissepiments. Skeletal elements generally bear a strong dark axis surrounded by radial fibers. *Sil.-Jur.,* Eu.-N.Am.-Afr.-Asia-Austral.——Fig. 114,*1*. **A. ramosa* (Phillips), Dev., Eng.; *1a,b,* transv. and long. secs., ×12 (50). Certain Mesozoic branching forms described as *Stromatopora douvillei* Dehorne belong to this genus; they lack an axial canal and marginal vesicles, closely resembling some Paleozoic stromatoporoids.

REFERENCES

Publications cited in the following list are judged to be most helpful in furnishing additional information concerning the stromatoporoids and in offering a guide to more extensive literature. The index numbers enclosed in parentheses in the column at left are employed in the text for identification of the publications.

Bargatzky, A.

(1) 1881, *Die Stromatoporen des rheinischen Devons:* Dissertation zur Erlagerung der Doctorwürde bei der hohen philosophischen Fakültät der rhein.-Friedr. Wilhelms Univ. zu Bonn, 78 p.

Boehnke, K.

(2) 1915, *Die Stromatoporen der nordischen Silurgeschiebe in Norddeutschland und in Holland:* Palaeontographica, Bd. 61, p. 147-190, pl. 16-18, fig. 1-35.

Carter, H. I.

(3) 1877, *On the close relationship of Hydractinia, Parkeria and Stromatopora:* Annals Mag. Nat. Hist. (London), ser. 4, v. 19, p. 44-76.

(4) 1879, *On the mode of growth of Stromatopora including the commensalism of Caunopora:* Same, ser. 5, v. 4, p. 101-106.

(5) 1880, *On Stromatopora dartingtonensis with tabulation in the larger branches of the Astrorhiza:* Same, ser. 5, v. 6, p. 339-347, pl. 18.

Dehorne, Y.

(6) 1915, *Sur un actinostromidé du Cénomanien:* Comptes rendus Acad. Sci. Paris, v. 161, p. 733-735.

(7) 1920, *Les Stromatoporoïdés des terrains secondaires:* Mém. explicatif carte geologique de France, 170 p., 17 pl., 31 fig.

Deninger, K.

(8) 1906, *Einige neue Tabulaten und Hydrozoen*

© 2009 University of Kansas Paleontological Institute

aus mesozoischen Ablagerungen: Neues Jahrb. Mineralogie, Paläontologie, Geologie: Bd. 1, p. 61-70, pl. 1-3.

Gorsky, I. I.

(9) 1938, *Some stromatoporoids from Palaeozoic beds of Novaya Zemlya:* Trans. Arctic Inst., v. 101, p. 14-31.

Heinrich, M.

(10) 1914, *Ueber den Bau und das System der Stromatoporoidea:* Neues Jahrb. Mineralogie, Paläontologie, Geologie, Abt. B, Centralbl. 1914, p. 732-736.

(11) 1914a, *Studien in den Riffkalken des rheinischen oberen Mitteldevons:* Dissertation zur Erlagerung der Doctorwürde bei der hohen philosophischen Fakültät der rhein.-Friedr. Wilhelms Univ. zu Bonn, 58 p., 3 pl.

Hickson, S. J.

(12) 1934, *On Gypsina plana and on the systematic position of the stromatoporoids:* Quart. Journ. Micr. Sci. London, v. 76, p. 433-480, pl. 26-27, fig. 1-13.

Kühn, O.

(13) 1926, *Eine neue Hydrozoen aus dem Stramberger Jura:* Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Bd. 135, p. 413-424.

(14) 1927, *Zur Systematik und Nomenklatur der Stromatoporen:* Neues Jahrb. Mineralogie, Paläontologie, Geologie, Abt. B, Centralbl. 1927, p. 546-551.

(15) 1928, *Fossilium Catalogus; I. Animalia, Pars 36, Hydrozoa:* (Berlin), 114 p.

(16) 1939, *Hydrozoa:* in SCHINDEWOLF, O. H., Handbuch der Paläozoologie, Bd. 2A, 68 p., 96 fig.

Lecompte, M.

(17) 1951-52, *Les stromatoporoïdes du Dévonien moyen et supérieur du bassin de Dinant:* Inst. Roy. Sci. Nat. Belg., pt. 1 (1951), mém. 116, p. 1-215, pl. 1-35; pt. 2 (1952), mém. 117, p. 216-359, pl. 36-70.

(18) 1952, *Revision des stromatoporoïdes mesozoïques des collections Dehorne et Steiner:* Inst. Roy. Sci. Nat. Belg., Bull. 28, no. 53, 39 p., 2 pl.

Nicholson, H. A.

(19) 1875, *Descriptions of Amorphozoa from the Silurian and Devonian formations:* Ohio Geol. Survey, v. 2 (Geol., Paleont., pt. 2), p. 245-255, pl. 24.

(20) 1886-92, *A monograph of the British stromatoporoids:* Palaeontograph. Soc. Mon. (London), 234 p., 29 pl.

(21) 1886-90, *On some new or imperfectly known species of stromatoporoids:* Annals Mag. Nat. Hist. (London), ser. 5, v. 17 (1886), p. 225-238, pl. 6-8; v. 18 (1886), p. 8-22, pl. 1-2; v. 19 (1887), p. 1-17, pl. 1-3; ser. 6, v. 7 (1890), p. 309-328, pl. 8-10.

——— & Murie, J.

(22) 1878, *On the minute structure of Stromatopora and its allies:* Jour. Linn. Soc. London, v. 14, p. 187-246, pl. 1-4, fig. 1-5.

Ozaki, K.

(23) 1938, *On some stromatoporoids from the Ordovician limestone of Shantung and South Manchuria:* Jour. Shanghai Sci. Inst., ser. 2, v. 2, p. 205-223, pl. 23-34.

Parks, W. A.

(24) 1907-10 [*Ordovician and Silurian stromatoporoids*]: Univ. Toronto Studies, Geol. Ser., no. 4 (1907), p. 137-172, pl. 1-6; no. 5 (1908), p. 175-240, pl. 7-15; no. 6 (1909), p. 243-292, pl. 16-20; no. 7 (1910), p. 295-344, pl. 21-25.

(25) 1933, *New species of stromatoporoids, sponges, and corals from the Silurian strata of Baie des Chaleurs:* Same, no. 33, 40 p., 8 pl.

(26) 1935, *Systematic position of the stromatoporoids:* Jour. Paleont., v. 9, p. 18-29, pl. 6-7.

(27) 1936, *Devonian stromatoporoids of North America:* Univ. Toronto Studies, Geol. Ser., no. 39, 125 p., 19 pl.

Raymond, P. E.

(28) 1914, *A Beatricea-like organism from the Middle Ordovician:* Can. Geol. Survey, Mus. Bull. 5, (Geol. Ser., no. 21), p. 1-18.

(29) 1931, *Notes on invertebrate fossils, with descriptions of new species:* Bull. Mus. Comp. Zool., Harvard College, Geol. Ser., v. 9, no. 9, p. 165-213, pl. 1-5.

Ripper, E. A.

(30) 1933-37, *The stromatoporoids of Lilydale limestone:* Proc. Roy. Soc. Vict., new ser., v. 45 (1933), p. 152-164, fig. 1-2; v. 49 (1937), p. 178-200, pl. 8-9, fig. 1-4.

(31) 1937, *On the stromatoporoids of the Buchan district, Victoria:* Same. v. 50, p. 11-38, pl. 2-5.

(32) 1938, *Notes on the Middle Palaeozoic stromatoporoid faunas of Victoria:* Same, v. 50, p. 221-243, fig. 1-4.

Stechow, E.

(33) 1921, *Neue Genera und Species von Hydrozoen und anderen Evertebraten:* Archiv Naturgesch., Abt. A, Bd. 87, p. 248-265.

Steiner, A.

(34) 1932, *Contribution à l'étude des stromatopores secondaires:* Bull. Lab. Géol. Univ. Lausanne, v. 50, 117 p., 14 pl.

Steinmann, G.

(35) 1878, *Ueber fossile Hydrozoen aus der Familie der Coryniden:* Palaeontographica, Bd. 25, p. 101-124.

(36) 1903, *"Milleporidium," eine Hydrocoralline aus dem Tithon von Stramberg:* Beitr.

© 2009 University of Kansas Paleontological Institute

Paläont. Geol. Oester.-Ungarns und Orients, Bd. 15, p. 1-8.

Sugiyama, T.

(37) 1939, *Geological and geographical distribution of stromatoporoids in Japan with notes on some interesting forms:* Jubilee Pub., Comm. 60th Birthday Prof. H. Yabe, v. 1, p. 328-456, pl. 1-2.

Tornquist, A.

(38) 1901, *Ueber mesozoische Stromatoporiden:* Sitzungsber. K. Preuss. Akad. Wiss. Berlin, Bd. 47, p. 1115-1123.

Tripp, K.

(39) 1929, *Untersuchungen über den Skelettbau von Hydractinien zu einer vergleichenden Betrachtung der Stromatoporen:* Neues Jahrb. Mineralogie, etc., Beil.-Band, Abt. B, Bd. 62, p. 467-508, pl. 21-30, fig. 1-45.

(40) 1932, *Die Baupläne der Stromatoporen:* Paläont. Zeitschr., Bd. 14, p. 277-293, fig. 1-22.

Twitchell, G. B.

(41) 1929, *The structure and relationships of the true stromatoporoids:* Am. Midl. Naturalist, v. 11, p. 270-307.

Waagen, Wilhelm

(42) 1887, *Salt-Range fossils, Part 7, Coelenterata, Amorphozoa, Protozoa:* Palaeont. Indica, ser. 13, v. 1, p. 925-998.

—— & Wentzel, Joseph

(43) 1886, *Salt-Range fossils, Part 6, Productus Limestone fossils, Coelenterata:* Palaeont. Indica, ser. 13, v. 1, p. 835-924.

Wentzel, Joseph

(44) 1890, *Ueber fossile Hydrocorallinen (Stromatopora und ihre Verwandten):* Lotos, v. 9, p. 1-24, pl. 1-3.

Winchell, Alexander

(45) 1887, *Stromatoporidae, their structure and zoological affinities:* Proc. Am. Assoc. Advanc. Sci. 15th Meet. (Buffalo), for 1886, p. 91-99.

Yabe, H. & Sugiyama, T.

(46) 1930, *On some Ordovician stromatoporoids from South Manchuria, North China and Chôsen (Corea), with notes on two European forms:* Sci. Rept. Tohoku Imp. Univ. (Sendai), ser. 2, v. 14, pt. 1, p. 47-62, pl. 1-7, fig. 1-5.

(47) 1935, *Jurassic stromatoporoids from Japan:* Same, ser. 2, v. 14, p. 135-191, pl. 1-32, fig. 1-32.

SOURCES OF ILLUSTRATIONS

Explanation of the use of index numbers for citing sources of illustrations is given in the Editorial Preface.

(48) **Kühn, O.**
(49) **Lecompte, Marius**
(50) **Nicholson, H. A.**
(51) **Parks, W. A.**
(52) **Ripper, E. A.**
(53) **Steiner, A.**
(54) **Vinassa de Regny, P. E.**
(55) **Yabe, H., & Sugiyama, T.**

© 2009 University of Kansas Paleontological Institute

SIPHONOPHORIDA

By H. J. Harrington and R. C. Moore

CONTENTS

MORPHOLOGY

The siphonophorids are highly specialized polymorphic hydrozoan colonies consisting of different kinds of modified medusoids and polypoids, which in association are adapted for a planktonic or nektonic existence at or near the surface of seas in all parts of the globe (Figs. 115-117). Many of them, like the Portuguese man-of-war *(Physalia)*, possess a float.

The polypoid individuals are classifiable in three categories: gastrozooids (siphons), dactylozooids (palpons), and gonozooids. (1) The **gastrozooids** are the only members of a colony capable of ingesting food. They have a polypoid form but are provided with only a single long hollow tentacle that commonly bears lateral contractile branches **(tentilla)** that terminate in a complex bunch of nematocysts. (2) The **dactylozooids** differ from gastrozooids in absence of a mouth and in having unbranched basal tentacles. Highly modified dactylozooids consist simply of a hollow tentacle-like body which may be associated with gonophores, being then termed **gonopalpons.** (3) The **gonozooids** or reproductive individuals may have polypoid form, resembling gastrozooids even to the extent of possessing a mouth, but they lack tentacles. Commonly they consist of branched stalks called **gonodendra,** which bear clusters of gonophores and may also have gonopalpons.

The medusoid individuals comprise 4 types: swimming bells (nectophores), bracts (hydrophyllia), gonophores, and floats (pneumatophores). (1) The **nectophores** have the form of a true medusa with velum, 4 radial canals, and a ring canal, but lacking mouth, tentacles, and sense organs. (2) The **hydrophyllia** are thick leaflike gelatinous bodies containing a simple or branched radial canal. (3) The **gonophores** are dioecious sexual members of the colony which may have a medusa-like form and in the Chondrophorina may be set free. (4) The **pneumatophores** are inverted bells consisting of an external exumbrellar wall and an internal subumbrellar wall (air sac), between which is a gastrovascular space that may be divided into chambers by transverse partitions.

All individuals of a colony are budded from a **stem (coenosarc)** which may be long and tubular or expanded radially into a disc fused to the wall of the float. The individuals typically are grouped in clusters **(cormidia),** each of which contains closely associated different kinds of medusoids and polypoids. In siphonophorids having a float and long stem, the upper part of the colony with nectophores is termed the **necto-**

© 2009 University of Kansas Paleontological Institute

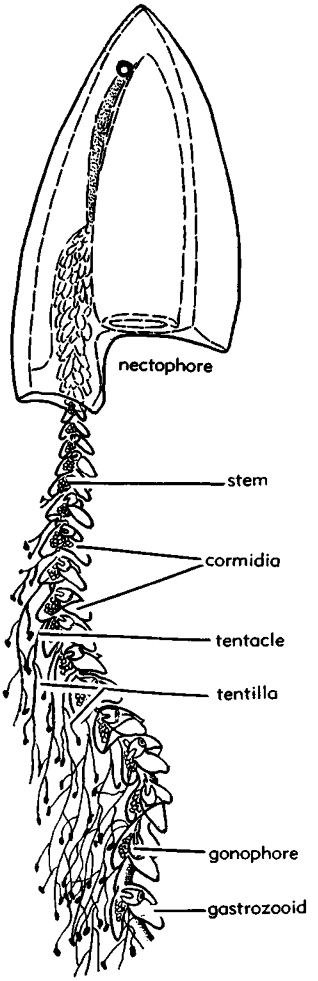


FIG. 115. Calycophorina: *Muggiaea,* Rec., showing swimming bell (nectophore) and trailing stem with cormidia, ×3.3 (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

some, and the lower part provided with cormidia is termed the **siphonosome** (Fig. 116).

DISTRIBUTION

Fossil siphonophorids are exceedingly rare. Only 5 genera are now recognized as included in this group, all belonging to the suborder Chondrophorina and all represented exclusively by the impression of their floats. Two of these, from the Devonian of New York and Germany, are classed among the Velellidae. The remaining 3 genera belong in the Porpitidae and range in age from Middle Ordovician to Late Devonian, being known from scarce remains found in North America, Australia, and Europe.

CLASSIFICATION

The number of known fossil genera in each category is recorded in the following tabulation.

Main Divisions of Siphonophorida

- Siphonophorida *(order)* (5). *M.Ord.-Rec.*
  - Calycophorina *(suborder). Rec.*
    - Sphaeronectidae. *Rec.*
    - Diphyidae. *Rec.*
    - Prayidae. *Rec.*
    - Hippopodiidae. *Rec.*
  - Physophorina *(suborder). Rec.*
    - Forskaliidae. *Rec.*
    - Agalmatidae. *Rec.*
    - Physophoridae. *Rec.*
    - Anthophysidae. *Rec.*
    - Rhodaliidae. *Rec.*
  - Rhizophysaliina *(suborder). Rec.*
    - Rhizophysidae. *Rec.*
    - Physaliidae. *Rec.*
  - Chondrophorina *(suborder)* (5). *M.Ord.-Rec.*
    - Velellidae (2). *U.Dev.-Rec.*
    - Porpitidae (3). *M.Ord.-Rec.*

Order SIPHONOPHORIDA Eschscholtz, 1829

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Siphonophora ESCH., 1829)]

Highly polymorphic, free-swimming or floating colonies composed of several types of polypoid and medusoid individuals attached to a stem or disc; polypoids without oral tentacles; medusoids never developing into complete medusae and rarely free. *M. Ord.-Rec.*

Siphonophorids are typical pelagic animals, inhabitants of the surface of the seas in all parts of the world, more abundant in warmer waters. A few forms live in moderate depths.

Suborder CALYCOPHORINA Leuckart, 1854

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Calycophorae LEUCK., 1854)]

Siphonophorida without float; summit of colony consisting of one or more nectophores. *Rec.* (Fig. 115).

Genera belonging to this suborder are classified in 4 families, none of which con-

© 2009 University of Kansas Paleontological Institute

tains known fossil representatives. They are: Sphaeronectidae Huxley, 1859, with only one nectophore; Diphyidae Eschscholtz, 1829, with 2, or temporarily 3 or 4 nectophores, the oldest definitive one differing from those subsequently formed in the presence of somatocyst; Prayidae Kölliker, 1853, with 2, or temporarily 3 or 4 nectophores, all structurally alike; and Hippopodiidae Kölliker, 1853, with many nectophores, all structurally alike. Many living genera, including *Sphaeronectes* Huxley, 1859; *Diphyes* Cuvier, 1817; *Praya, Galeolaria* de Blainville, 1834; *Hippopodius, Abyla* Quoy & Gaimard, 1827.

Suborder PHYSOPHORINA Eschscholtz, 1829

[*nom. correct.* Harrington & Moore, herein (*pro* Physophorae Esch., 1829)] [=Physonectae Haeckel, 1888]

Siphonophorida with apical float devoid of pore, succeeded by length of stem commonly divided into nectosome and siphonosome; forms with enlarged float have reduced or absent nectosome and cormidia crowded together beneath pneumatophore; cormidia forming large and complex groups comprising one or more dactylozooids each with unbranched tentacle, one gastrozooid with branched tentacle, one or more bracts and clusters of gonophores commonly on gonodendra with gonopalpons; cormidia never set free as eudoxids; gonophores never free-swimming. *Rec.* (Fig. 116).

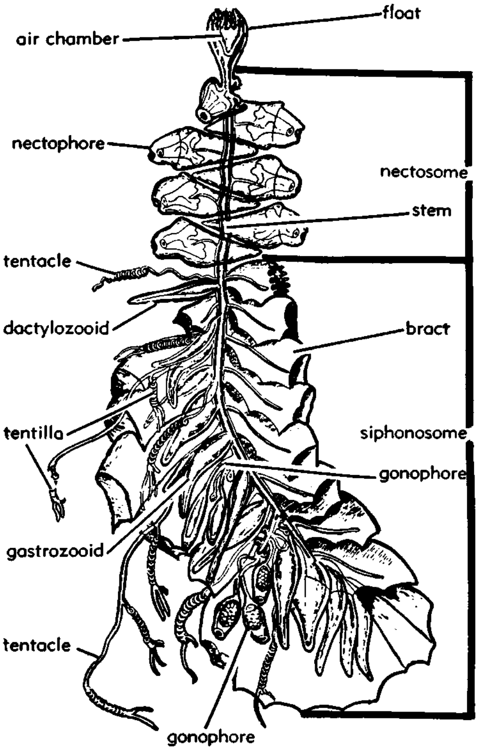


Fig. 116. Physophorina: *Agalma*, Rec., showing small apical float above stem with swimming bells (nectosome) (L. H. Hyman, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).

Genera belonging to this suborder are classified in 5 families, none of which contains known fossil representatives. These are: Forskaliidae Haeckel, 1888, with long stem, well-developed nectosome with elongated nectophores encircling coenosarc in many rows, and long tubular siphonosome; Agalmatidae (*nom. correct.* herein, *pro* Agalmidae) Brandt, 1935, with normal nectosome, normal or reduced siphonosome and nectophores in 2 alternating rows, closely pressed together; Physophoridae Eschscholtz, 1829, with enlarged float, much-shortened stem and crown of dactylozooids above siphonosome; Anthophysidae Brandt, 1835, with greatly enlarged float, nectophores absent and cormidia crowded together beneath float; and Rhodaliidae Haeckel, 1888, with bell-like evaginated portion of the float (aurophore) lying among a circle of nectophores and opposite zone of proliferation. Several living genera, including *Forskalia* Kölliker, 1853; *Agalma* Eschscholtz, 1825; *Stephanomia* Péron & Lesueur, 1807; *Rhodalia, Nectalia* Haeckel, 1888; *Physophora* Forskål, 1775; *Anthophysa* Brandt, 1835; *Dromalia* Bigelow, 1911.

Suborder RHIZOPHYSALIINA Chun, 1882

[*nom. correct.* Harrington & Moore, herein (*pro* Rhizophysaliae Chun, 1882)]

Siphonophorida with large hollow float, provided with apical pore; nectophores and bracts absent; cormidia simplified. *Rec.*

The genera of this suborder are classified in 2 families, none of which contains known fossil representatives. They are: Rhizophysidae Brandt, 1835, with oval float containing gas gland, succeeded by long and stout stem bearing succession of simple cor-

© 2009 University of Kansas Paleontological Institute

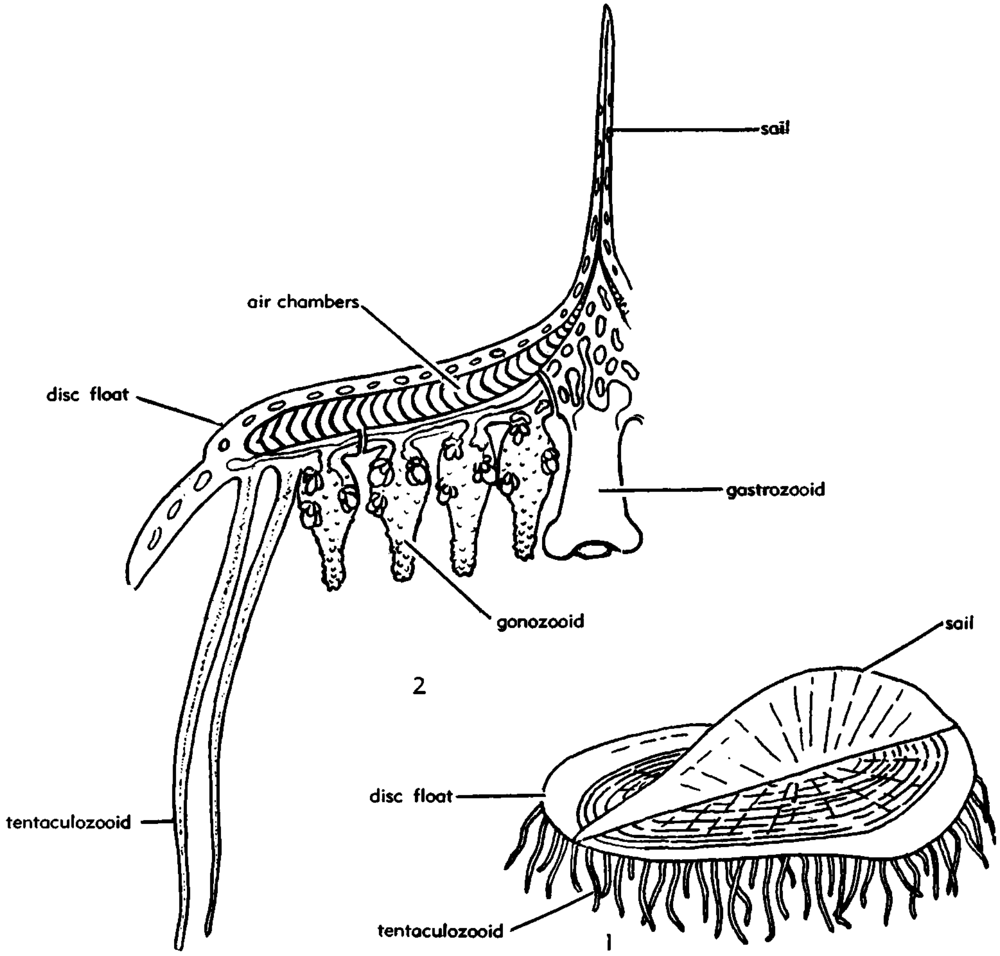


FIG. 117. Chondrophorina: *Velella,* a highly specialized modern siphonophorid with erect crest or sail; *1,* entire specimen; *2,* section across part of colony (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

midia, commonly composed of one or more gastrozooids with tentacle and one gonodendron bearing gonopalpons and clusters of gonophores; and Physaliidae BRANDT, 1835, with oval, crested, contractile float, and stem shortened to budding coenosarc on ventral surface of float from which there hang down several large and small dactylozooids with tentacles, bunches of gastrozooids without tentacles and many-branched gonodendra bearing gonopalpons, clusters of gonophores and special gelatinous zooids of unknown function. Few known genera, including *Rhizophysa* PÉRON & LESUEUR, 1807, *Epibula* HAECKEL, 1888, and *Physalia* LAMARCK, 1801.

Suborder CHONDROPHORINA
Chamisso & Eysenhardt, 1821

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Chondrophorae CHAMISSO-E., 1821)] [=Disconectae HAECKEL, 1888]

Siphonophorida with stem shortened to flat coenosarc forming firm rounded or oval disc together with float; float containing many concentric air chambers; underside of float with large central gastrozooid encircled by gonozooids with mouth, medusiform gonophores and marginal tentacle-like dactylozooids; gonophores freed as medusae (formerly regarded as separate genus named *Chrysomitra*). *M.Ord.-Rec.* (Fig. 117).

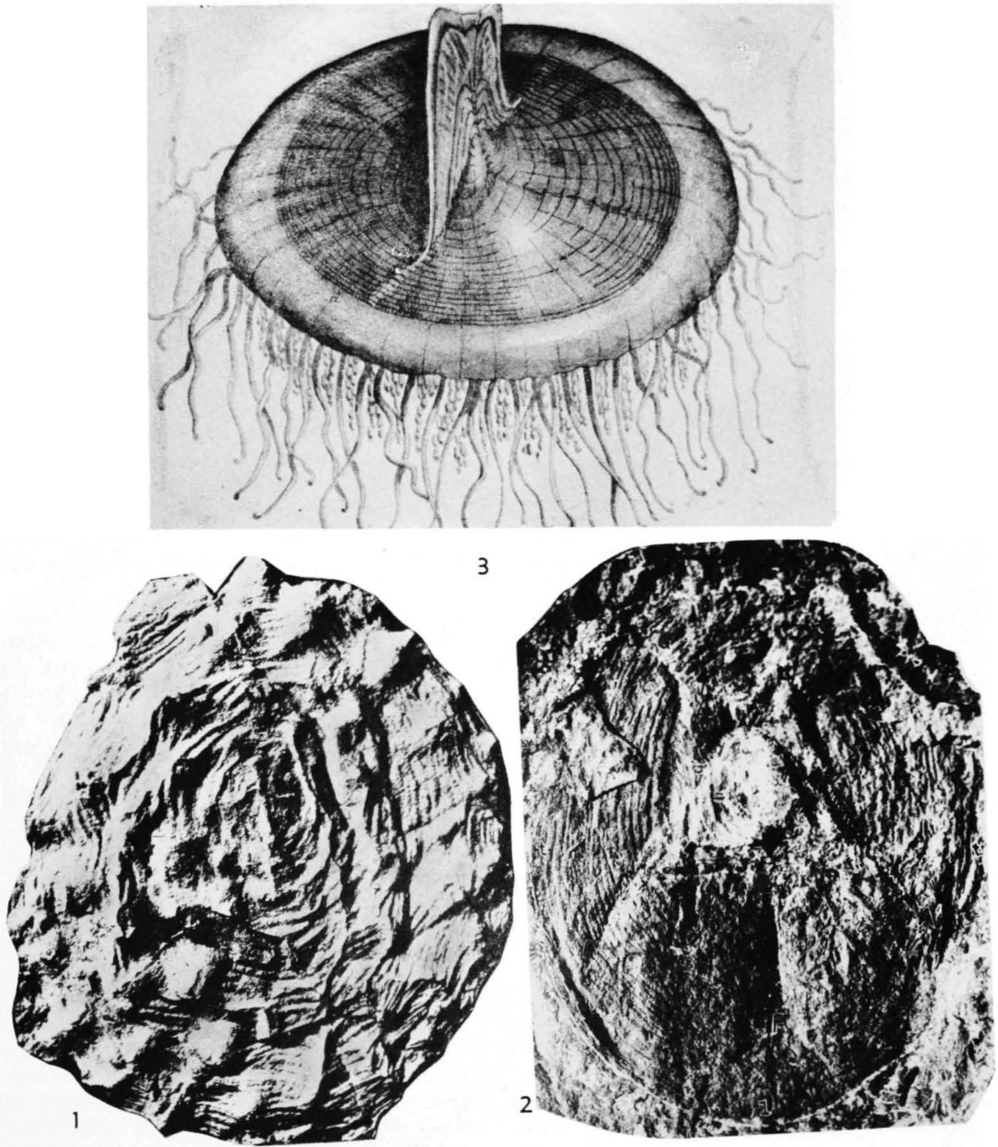
© 2009 University of Kansas Paleontological Institute

Family VELELLIDAE Brandt, 1835

Float with erect rounded crest; tentilla absent. *U.Dev.-Rec.*

Velella Lamarck, 1801 [**Medusa velella* Linné, 1758]. *Rec.* (Fig. 117). Only living genus.

Plectodiscus Ruedemann, 1916 [**P. molestus*]. Disc elliptical in outline and with compressed conical shape, external membrane ?chitinous; upper surface with numerous concentric sulci giving a corrugated appearance; radial knobs or bosses may be present, obscurely arranged in 3 or 4 cycles; central part of disc bearing diagonal keel, flattened against surface (indistinct in type species). Caster's detailed analysis of the remains shows that they are pneumatophores of a velellid siphonophorid. *U.Dev.*, N.Y.——Fig. 118,*1*. **P. molestus;* holotype, upper surface, ×0.6 (Ruedemann).——



Plectodiscus

Fig. 118. Chondrophorina: Upper Devonian fossils of velellid type from New York. *1, Plectodiscus molestus,* holotype, upper surface, ×0.6 (Ruedemann). *2,3, P. cortlandensis,* holotype, upper surface, and oblique view from above (reconstr.), ×0.6 (Caster).

© 2009 University of Kansas Paleontological Institute

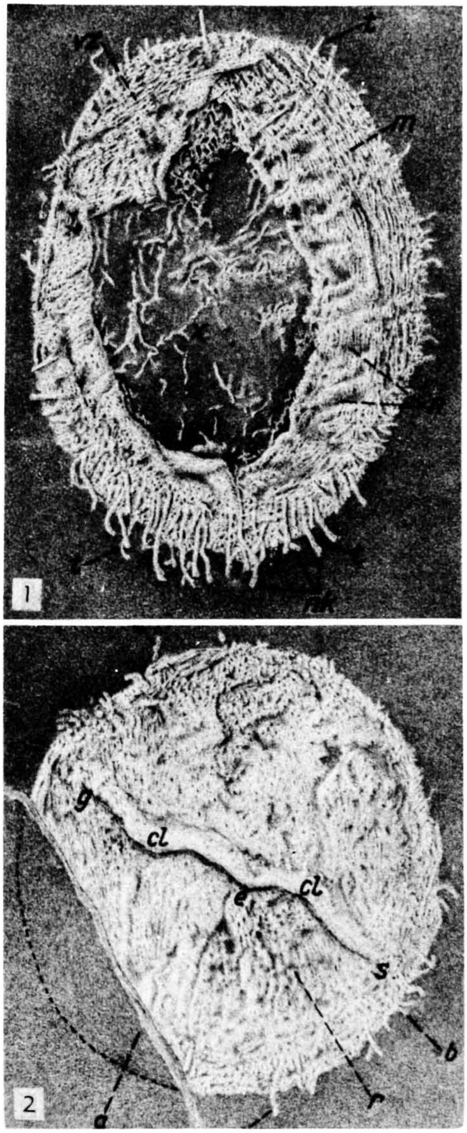


FIG. 119. Chondrophorina: *Paleonectris*, L.Dev. *1,2*, exumbrellar and subumbrellar views of 2 specimens, ×1 (RAUFF).

FIG. 118,*2,3*. *P. cortlandensis* CASTER; *2,3*, holotype, upper surface and oblique view from above (reconstr.), ×0.6 (CASTER).

Paleonectris RAUFF, 1939 [**P. discoidea*]. Body discoidal, of circular to elliptical outline; exumbrellar surface rugose, with obscure, irregular radial ornamentation (?radial muscular fibres) and thickened, smooth, sinuous band (?flattened "sail") crossing disc along a diameter; a few tentacles protrude for short distance beyond margin; subumbrella with numerous submarginal tentacles (?tentacle-like dactylozooids) having slightly thickened tips; one specimen, which seems to have lost all other elements, has a gaping hole in the center surrounded by irregular ring concentrically striated (?ring muscles); another specimen bears numerous numerous small, branched outgrowths (flattened against disc), regarded as gonostyles. Accepted here is RAUFF's view that the remains represent pneumatophores of a velellid siphonophore. *L.Dev.*, Ger.——FIG. 119,*1,2*. **P. discoidea; 1,2,* exumbrellar and subumbrellar views of 2 specimens, ×1 (RAUFF).

Family PORPITIDAE Brandt, 1835

[*non* Porpitidae MOORE & JEFFORDS, 1945 (*ex Porpites* SCHLOTHEIM, 1820, rugose coral)]

Corm high vaulted or flattened disclike, without crest or sails. *M.Ord.-Rec.*

Porpita LAMARCK, 1801 [**Medusa porpita* LINNÉ, 1758]. *Rec.* Other living genus: *Porpema* HAECKEL, 1888.

Discophyllum HALL, 1847 [**D. peltatum*]. Body discoidal, elliptical in outline; upper surface crossed by about 80 simple radiating bands of rounded surface, increasing in width toward periphery; interspaces narrower than bands, with fine median raised line; bands and interspaces crossed by numerous fine concentric lines. RUEDEMANN's interpretation of the remains as pneumatophores of a porpitid siphonophorid is very plausible. *M.Ord.*, N.Y.——FIG. 119,*1*. **D. peltatum; 1a,b,* holotype and paratype, ×1.15 (WALCOTT).

Palaeoscia CASTER, 1942 [**P. floweri*]. Thin, delicate disc (?chitinous in life) of circular outline; porelike depression at center from which 16 grooves (in 8 pairs) radiate for 1/7 the distance to periphery; very indistinct transverse lines between some radial grooves; remainder of disc with broad concentric corrugations. Accepted here is CASTER's view that the remains represent pneumatophores of the immature stage of a porpitid siphonophorid. *U.Ord.*, Ohio.——FIG. 119,*2*. **P. floweri; 2a,* holotype ×1.15; *2b,* paratype, ×2.8 (CASTER).

Paropsonema CLARKE, 1902 [**P. cryptophya*]. Body compressedly convex to discoidal, of circular outline; upper surface with 2 or 3 concentric cycles of 52 to 60 radial bands looking like knotted cords, separated by smooth, narrower bands bifurcating at inner boundary of each cycle; main radial bands bearing regular succession of concentric rows of pores; center of disc occupied by small circle from which fine lines radiate; tentacles (not preserved in type species) very numerous and delicate, some stronger than others and ?grooved (?hollow); lower surface marked by irregular folds and wrinkles. Both FUCHS and RUEDEMANN interpreted the remains as pneumato-

© 2009 University of Kansas Paleontological Institute

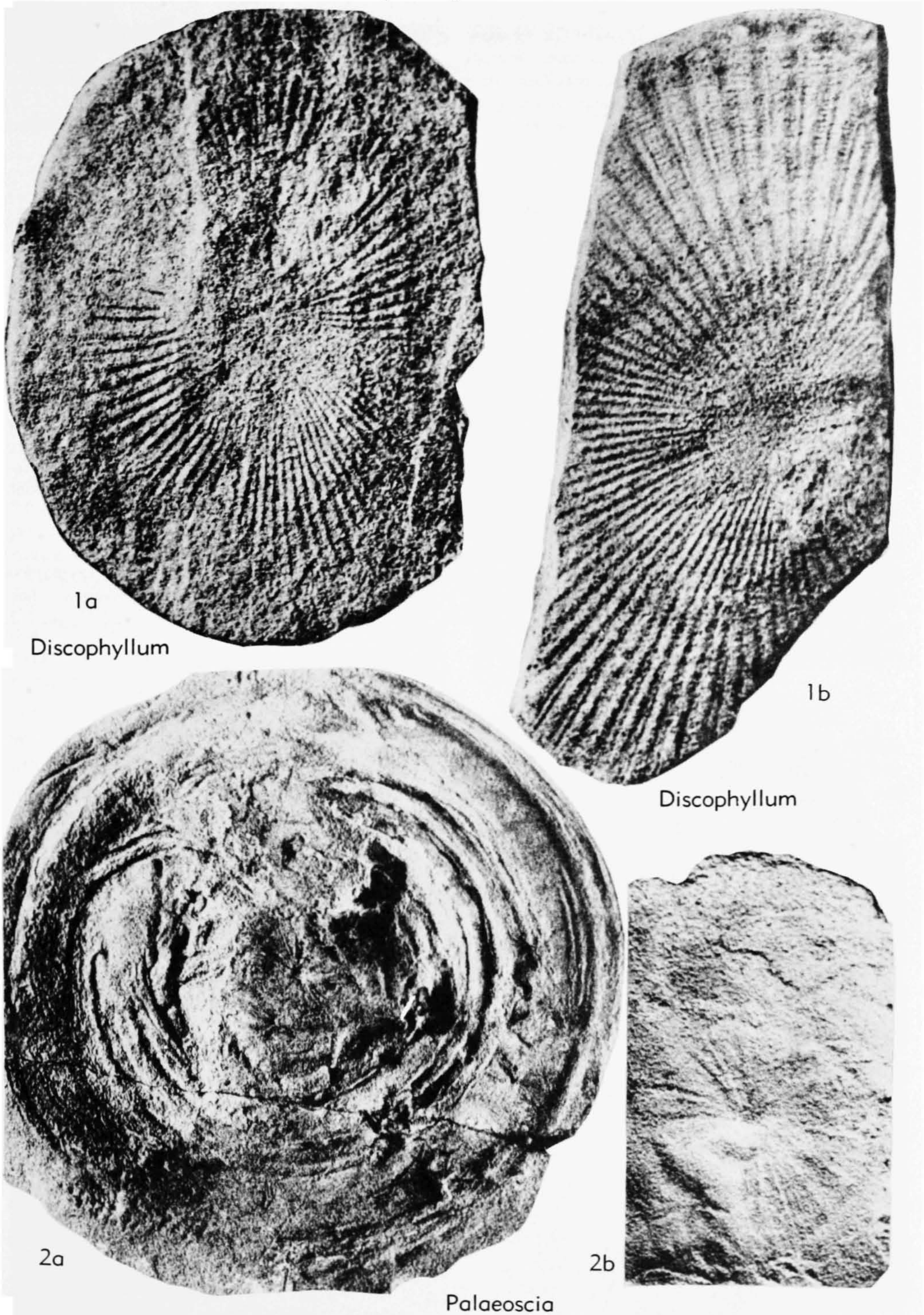


FIG. 120. Chondrophorina: Ordovician fossils from New York and Ohio. *1, Discophyllum peltatum,* M.Ord., N.Y.; *1a,b,* holotype and paratype, ×1.15 (WALCOTT). *2, Palaeoscia floweri,* U.Ord., Ohio; *2a,* holotype, ×115; *2b,* paratype, ×2.8 (CASTER).

© 2009 University of Kansas Paleontological Institute

phores of a porpitid siphonophorid. The ?hollow tentacles, preserved only in *P. mirabile* (CHAPMAN), originally referred to *Discophyllum*, may represent large dactylozooids similar to the marginal tentacle-like dactylozooids of *Porpita* and the smaller tentacles either gonopalpons or smaller feelers. *Sil.*, S.Austral.; *U.Dev.*, N.Y.——FIG. 121, *1,2*. **P. cryptophya*, U.Dev., N.Y.; *1*, lower surface, ×0.5 (CLARKE); *2*, upper surface of another specimen, ×0.5 (RUEDEMANN).——FIG. 121,*3*. *P. mirabile* (CHAPMAN), Sil., S.Austral.; holotype, upper surface, ×0.3 (CHAPMAN).

REFERENCES

Caster, Kenneth E.

(1) 1942, *Two new siphonophores from the paleozoic:* Paleontogr. Americana (Ithaca, N.Y.), v. 3, p. 56-90, pl. 1-2, fig. 1-6.

Chapman, F.

(2) 1926, *New or little known fossils in the National Museum. Pt. XXX: A Silurian jellyfish:* Roy. Soc. Victoria, Proc., v. 39, p. 13-17, pl. 1-2.

Clarke, John M.

(3) 1902, *Paropsonema cryptophya, a peculiar echinoderm from the intumescens zone (Portage beds) of western New York:* N.Y. State Mus., Bull. 39, v. 8, p. 172-178, pl. 5-9.

Hall, James

(4) 1847, *Corals of the Hudson River group:* Paleont. N.Y., v. 1, p. 247.

Kieslinger, A.

(5) 1924, *Medusae fossiles:* Fossilium Catalogus. I. Animalia, Pars 26, p. 1-20.

(6) 1939, *Scyphozoa:* in SCHINDEWOLF, O. H., Handb. d. Paläozoologie, Band 2A, Lief 5, p. A69-A109, fig. 1-42.

Rauff, H.

(7) 1939, *Paleonectris discoidea Rauff, eine siphonophoridae Meduse auf dem rheinischen Unterdevon nebst Bemerkungen zur umstrittnen Brooksella rhenana Kink.:* Palaeont. Zeitsch., Band 21, p. 194-213.

Ruedemann, Rudolf

(8) 1916, *Note on Paropsonema cryptophya Clarke and Discophyllum peltatum Hall:* N.Y. State Mus., Bull. 189, p. 22-27, pl. 1-2.

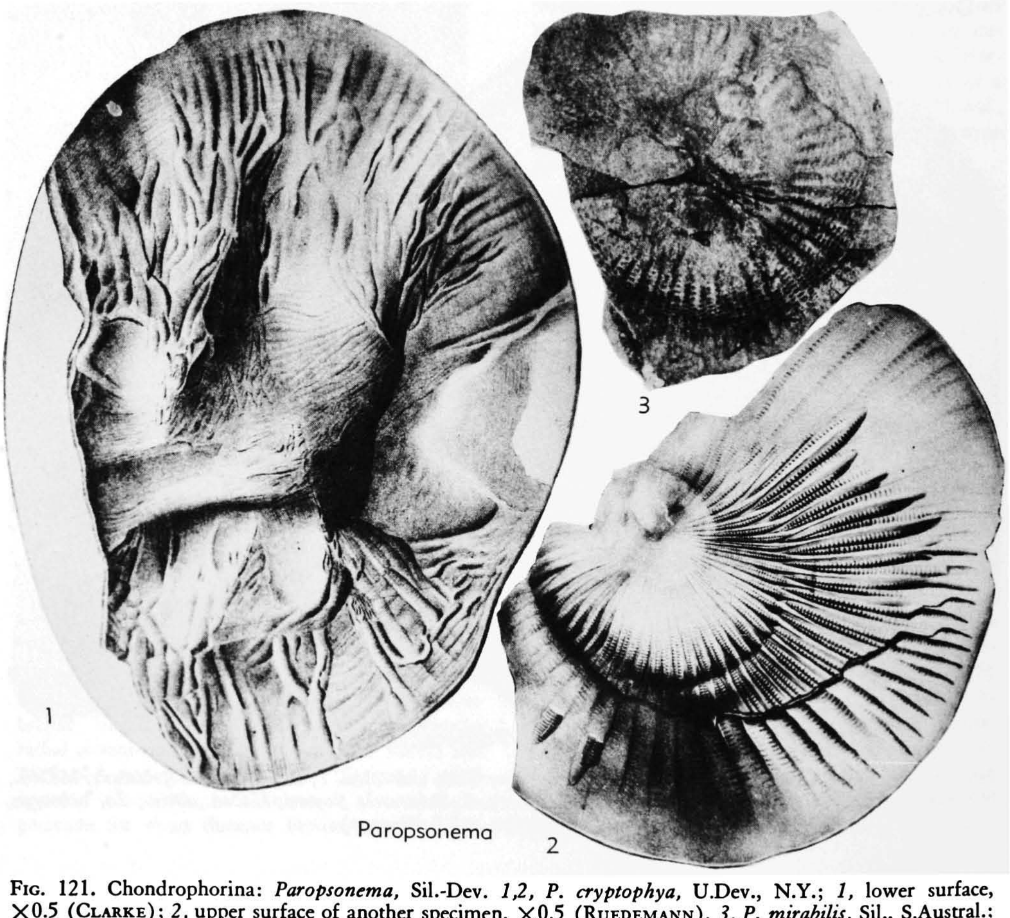


FIG. 121. Chondrophorina: *Paropsonema*, Sil.-Dev. *1,2*, *P. cryptophya*, U.Dev., N.Y.; *1*, lower surface, ×0.5 (CLARKE); *2*, upper surface of another specimen, ×0.5 (RUEDEMANN). *3*, *P. mirabilis*, Sil., S.Austral.: holotype, upper surface, ×0.3 (CHAPMAN).

© 2009 University of Kansas Paleontological Institute

MEDUSAE INCERTAE SEDIS AND UNRECOGNIZABLE FORMS

By H. J. Harrington and R. C. Moore

This section suffers acutely from the label "hypothetical," as it deals with the less distinct and more doubtful fossil records attributed to medusae. Some are, with a degree of probability that amounts to certainty, impressions left by such organisms, displaying enough distinctive features to deserve generic recognition but wanting in essential diagnostic characters to warrant their classification among the trachylinids, leptolinids, or scyphomedusae. These represent, therefore, "genera incertae sedis" within the medusoid assemblage. Others are less distinct medusoid impressions displaying such a paucity of relevant diagnostic features as to make impracticable any generic assignment. These represent "species incertae sedis," referred by their authors mostly to the "genera" *Medusites* and *Medusina,* which, however, have no status in coelenterate classification. *Medusites* Germar, 1825 [**M. capillaris*] [=*Lumbricaria* Goldfuss, 1826], was originally proposed for some problematic bodies now regarded as worm coprolites, having no resemblance to medusoid remains. *Medusina* Walcott, 1898 (type species *Spatangopsis costata* Torell, 1870; SD Caster, 1945), originally proposed "as a generic term to include all species of fossil medusae whose generic characters can not be determined"(!), is a synonym of *Spatangopsis* Torell, 1870 [**S. costata*]. Clearly, then, the medusoid forms referred to *Medusites* are incorrectly assigned to this genus and have no valid generic designation, while those referred to *Medusina,* none of which resembles *S. costata,* cannot be placed in *Spatangopsis,* and, therefore, also lack valid generic designation.

Lastly, a 3rd group comprises unrecognizable forms inadequately described or lacking cogent diagnostic characters, and forms which, though having a vague medusoid aspect, are now regarded as belonging to other organisms, animal or vegetal, or as inorganic impressions.

GENERA INCERTAE SEDIS

Cyclomedusa Sprigg, 1947 [**C. davidi*]. Margin circular, without notches, lappets or tentacles; ?exumbrella with prominent concentric grooves and

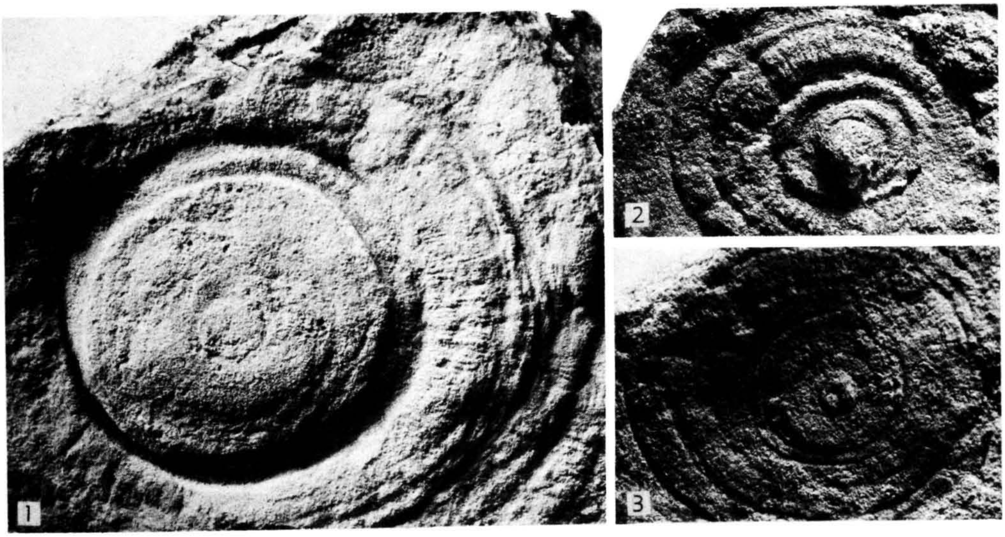


Fig. 122. *Cyclomedusa,* L.Cam., S.Austral. *1, C. gigantea,* holotype, ×0.95 (Sprigg). *2,3, C. davidi; 2,* holotype, ×1.3; *3,* another specimen, ×0.9 (Sprigg).

© 2009 University of Kansas Paleontological Institute

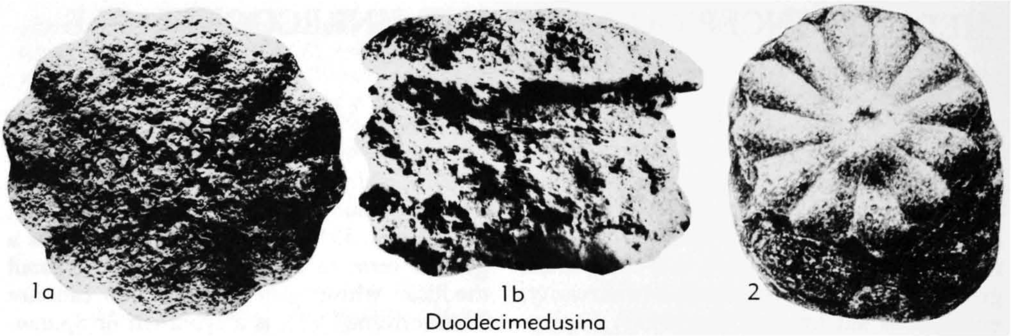


FIG. 123. *Duodecimedusina,* L.Dev., S.Am.; U.Penn., N.Am. *1, D. typica,* U.Penn., Kans.; *1a,b,* holotype, ?subumbrellar surface and side views showing pedestal, ×1 (KING). *2, D. ulrichi,* L.Dev., Bol.; ?subumbrellar surface and pedestal, ×1 (ULRICH).

rugae which may extend to margin, and very numerous, fine radial striae not continuous into mid-field, which may contain raised central knob; ?ring canal present. *L.Cam.,* S.Austral. Of the 3 species originally described by SPRIGG, *C. radiata* is here regarded as a synonym of *Tateana inflata* SPRIGG (=*Ediacaria flindersi* SPRIGG, p. F74). Whether the remaining 2 are also synonyms of *Ediacaria* is impossible to decide at present.——FIG. 122,*1. C. gigantea* SPRIGG; holotype, ×0.95 (SPRIGG).——FIG. 122,*2,3.* **C. davidi; 2,* holotype, ×1.3; *3,* another specimen, ×0.9 (SPRIGG).

Duodecimedusina KING, 1955 [**D. typica*]. Body subdiscoidal; lobes 12, regular, marked off by radial grooves disappearing at mid-field; margin cleft into 12 rounded lappets; mid-field smooth or with small central circular depression. [All observed specimens occur at summit of a cylindrical pedestal consisting of rock matrix (not part of fossil).] *L.Dev.* (Bol.), *U.Penn.* (USA).——FIG. 123,*1.* **D. typica,* Penn.(Missouri), Kans.; *1a,b,* holotype, ?subumbrellar and side view, ×1 (KING, in HARRINGTON & MOORE).——FIG. 123,*2. D. ulrichi* KING, L.Dev., Bol.; holotype, ?subumbrellar and side views, ×1 (ULRICH).

Madigania SPRIGG, 1949 [**M. annulata*]. Margin circular, without notches, lappets or tentacles; ?exumbrellar surface with numerous, conspicuous concentric grooves and rugae; radial striae absent; mid-field smooth or with raised central knob; ?ring canal present. *L.Cam.,* S.Austral.——FIG. 124. **M. annulata;* holotype, ×0.4 (SPRIGG).

Paramedusium GÜRICH, 1930 [**P. africanum*]. Body discoidal, of circular outline; ?upper surface with flat, very delicate radial ribs becoming coarser, irregular and anastomosing near periphery; 2 concentric grooves in distal 3rd of disc. *?Cam.,* SW. Afr.——FIG. 125. **P. africanum;* holotype, ×0.25 (KIESLINGER).

FIG. 124. *Madigania,* L.Cam., S. Austral.; *M. annulata,* holotype, ×0.4 (SPRIGG).

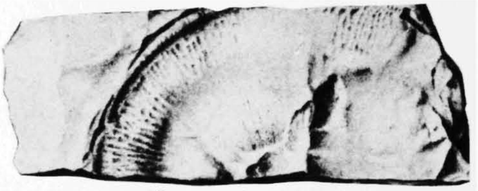


FIG. 125. *Paramedusium,* ?Cam., SW.Afr.; *P. africacum,* holotype, ×0.25 (KIESLINGER).

Peytoia WALCOTT, 1911 [**P. nathorsti*]. Umbrella with 32 lobes marked off by radial grooves, 4 large lobes 90° apart, 7 narrower, in each quadrant; outer extremities of lobes forming 32 short, round lappets; inner extremities with 2 short, broad points projecting inward into mid-field; mid-field subquadrate, inner extremities of large lobes at center of each side; tentacles and ring canal absent. *M.Cam.,* Can. WALCOTT interpreted the 3 known specimens as subumbrellar impressions and

© 2009 University of Kansas Paleontological Institute

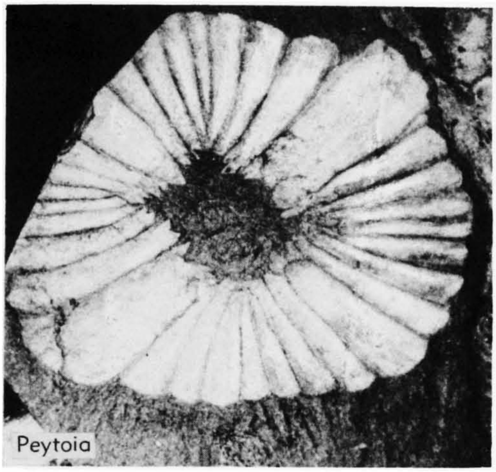


FIG. 126. *Peytoia,* M.Cam., Can.; *P. nathorsti,* holotype, probably an exumbrellar impression, ×1 (WALCOTT).

the mid-field as a central quadrate mouth, but the specimens are probably best regarded as exumbrellar impressions.——FIG. 126. **P. nathorsti;* holotype, ×1 (WALCOTT).

Protolyella TORELL, 1870 [**P. princeps* (=*Medusites favosus* NATHORST, 1881)] [=*Hydromedusites* FRECH, 1897]. Body discoidal; margin subcircular; ?subumbrellar surface with large, circular, smooth central area and outer annular zone crossed by numerous radial grooves either simple, bifurcating, irregular and anastomosing or bearing "string-of-pearls" nodules (?gonads). *L.Cam.,* Swed.-S.Austral.-?USA.; *M.Cam.,* Czech. This "form genus" is here extended to cover the L.Cam. remains from S.Austral. described by SPRIGG under *Medusina;* the bifurcating radial striation of *"M." filamentus,* interpreted by SPRIGG as marginal tentacles, are here regarded as radial grooves of a specimen in which the impression of the periphery is not preserved. *Camptostroma resseri* RUEDEMANN, L.Cam., N.Y., very different from the type species *C. roddyi,* is also placed in this genus. KIESLINGER regarded it as a synonym of *Protolyella ("Medusina") bohemica,* but this seems too extreme a view.——FIG. 127,*6.* **P. princeps,* L.Cam., Swed.; holotype, ×1 (WALCOTT).——FIG. 127,*5. P. radiata* (LINNARSSON), L.Cam., Swed.; holotype, ×1 (WALCOTT).——FIG. 127,*1. P. asteroides* (SPRIGG), L.Cam., S.Austral., ×0.95 (SPRIGG).——FIG. 127,*2. P. mawsoni* (SPRIGG), L.Cam., S.Austral.; ×0.9 (SPRIGG).——FIG. 127, *7. P. filamenta* (SPRIGG), L.Cam., S.Austral.; holotype, ×1.3 (SPRIGG).——FIG. 127,*4. P. resseri*

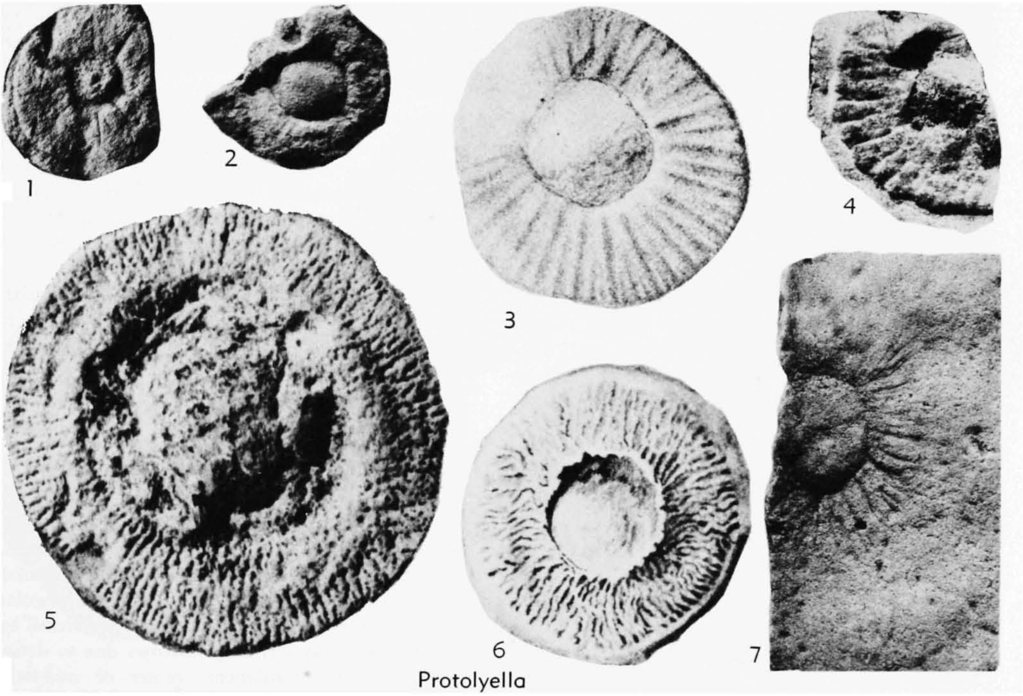


FIG. 127. *Protolyella,* Cam., Eu.-N.Am.-Austral. *1, P. asteroides,* L.Cam., Austral., ×0.95 (SPRIGG). *2, P. mawsoni,* L.Cam., Austral., ×0.9 (SPRIGG). *3, P. bohemica,* M.Cam., Czech., ×0.7 (WALCOTT). *4, P. resseri,* L.Cam., N.Y., ×0.5 (RUEDEMANN). *5, P. radiata,* L.Cam., Swed., ×1 (WALCOTT). *6, P. princeps,* L.Cam., Swed., ×1 (WALCOTT). *7, P. filamenta,* L.Cam., Austral., ×1.3 (SPRIGG).

© 2009 University of Kansas Paleontological Institute

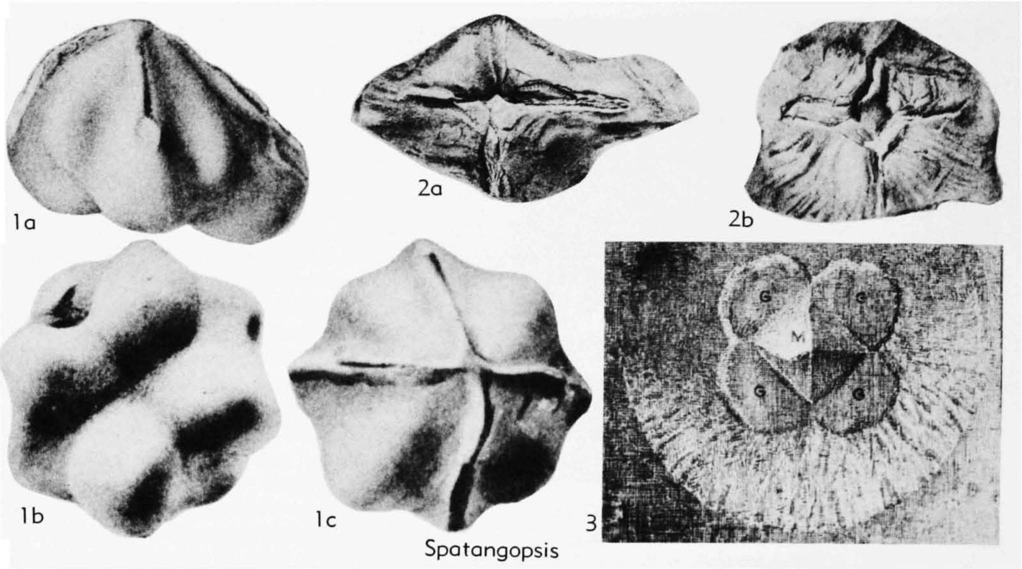


FIG. 128. *Spatangopsis costata,* L.Cam., Swed.; *1a-c,* steinkern, ×1; *2a,b,* subumbrellar impressions, ×0.5; *3,* same, another specimen, ×0.7 (WALCOTT).

(RUEDEMANN), L.Cam., N.Y.; holotype, ×0.5 (RUEDEMANN).——FIG. 127,*3. P. bohemica* (GORTANI), M.Cam., Czech.; holotype, ×0.7 (WALCOTT).

Spatangopsis TORELL, 1870 [**S. costata* (=*Agelacrinus lindströmi* LINNARSSON, 1871] [=*Medusina* WALCOTT, 1898 (obj., type species *Spatangopsis costata* TORELL, 1870; SD CASTER, 1945)]. Body discoidal; margin subcircular; exumbrella smooth; subumbrella with numerous radial grooves and large cruciform mouth. One specimen shows large semicircular interradial marking adjacent to mouth, regarded as gonads. Specimens considered as internal molds (steinkerns) of gastric cavity are pyramidal bodies with rounded base or with 4 to 5 rounded basal projections (?roof of gastric cavity), sides bounded by 4 to 5 sharp ridges meeting at apex and triangular areas between ridges flat or with elongated rounded projections (?casts of genital sacs). *L.Cam.,* Swed.——FIG. 128. **S. costata; 1a-c,* side, upper, and lower and side views of a gastric steinkern, ×1; *2a,b,* subumbrellar impressions, ×0.5; *3,* subumbrellar impression of another specimen showing supposed gonads, ×0.7 (all from WALCOTT).

SPECIES INCERTAE SEDIS

"Discophyllum plicatum" BARROIS, 1891. Body small, discoidal, of circular outline, with sharply marked small, circular, ?depressed central area and ?34 to ?40 simple radial ribs, exceptionally bifurcating, separated by narrower, shallow grooves; ribs with obscure, irregular transverse striae. *L.Ord.,* Fr. BARROIS identified the specimens with *Actinophyllum plicatum* PHILLIPS, L.Dev., Eng., regarded the genus as a synonym of *Discophyllum* HALL (here considered as a porpitid siphonophorid) and interpreted the remains as isolated metamers of *Anthomorpha* BORNEMANN (Archaeocyatha). STRAW opposed BARROIS's view, regarded *Actinophyllum* and *Discophyllum* as different genera, and held the French specimens to be specifically (?and generically) distinct from *A. plicatum.* As here interpreted, the French specimens do not seem to belong in either *Actinophyllum* or *Discophyllum;* though possibly medusoid, their relations cannot be established at present.——FIG. 129,*1a,b. "D. plicatum," 2,* specimens, ×1 (BARROIS).

"Medusina" atava POHLIG, 1892. Impression circular, with a broad, outer annular zone, concentrically striated, a narrow, smooth inner ring, and a large central mid-field with indistinct traces of 4 petalate lobes 90° apart and 4 smaller, subrhombic exsert lobes. *Perm.,* Ger.——FIG. 129,*3. "M." atava,* holotype, ×1 (WALCOTT).

"Medusina" boulangeri VAN STRAELEN, 1926. Known from a single ?exumbrellar impression. Umbrella convex; margin entire, circular, without tentacles; outer annular zone narrow, smooth, separated from large central zone by circular groove; large central area with ?30 irregular radiating grooves, some bifurcating, regarded by VAN STRAELEN as shrinkage furrows due to desiccation during entombment; center of mid-field damaged. *L.Carb.,* Belg.——FIG. 129,*6. "M." boulangeri; 6a,b,* holotype, side and ?exumbrellar views, ×0.25 (VAN STRAELEN).

"Medusina" eisfeldensis ADAM, 1950. Known from single specimen. Bell convex; mid-field about 1/3

© 2009 University of Kansas Paleontological Institute

the diameter of ?exumbrella, with central knob, indistinctly separated from outer annular zone bearing ?12 obscure radial lobes, vaguely defined by shallow radial sulci; margin scalloped into short, round lappets. *L.Trias.*, Ger.——FIG. 129,*4*. *"M." eisfeldensis*, holotype, ×0.5 (ADAM).

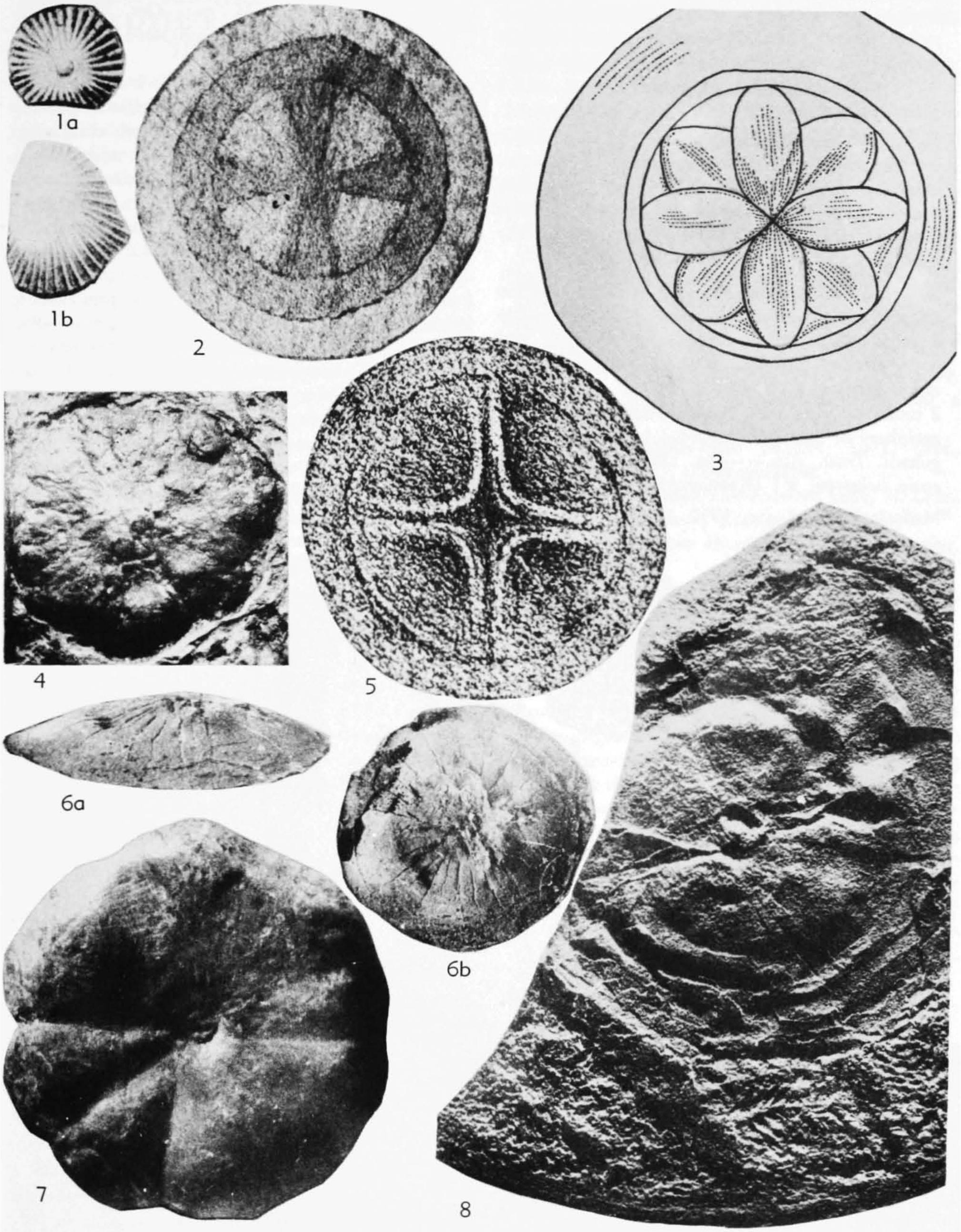


FIG. 129. Medusae species incertae sedis. *1, "Discophyllum plicatum,"* L.Ord., Fr., ×1 (BARROIS). *2, "Medusites bicinctus,"* U.Jur., Ger.; ×0.65 (HAECKEL). *3, "Medusina" atava*, Perm., Ger.; ×1 (WALCOTT). *4, "Medusina" eisfeldensis*, L.Trias., Ger.; ×0.5 (ADAM). *5, "Medusites" staurophorus*, U.Jur., Ger.; ×1 (HAECKEL). *6, "Medusina" boulangeri*, L.Carb., Belg.; ×0.25 (VAN STRAELEN). *7, "Medusina" liassica*, L.Jur., Ger.; ×0.8 (RÜGER-HAAS). *8. "Medusina" reiflingensis*, Trias., Aus.; ×1 (KIESLINGER).

© 2009 University of Kansas Paleontological Institute

"Medusina" liassica RÜGER-HAAS, 1925. Known from single specimen. ?Exumbrellar impression with small, buttonlike central knob encircled by shallow groove from which 10 shallow sulci radiate, giving rise to 10 subequal lobes ending at periphery in short, rounded lappets. *L.Jur.*, Ger.——FIG. 129,*7*. *"M." liassica;* holotype, ×0.8 (RÜGER-HAAS).

"Medusina" lincki HUNDT, 1940. ?Subumbrellar impressions 5 to 7 cm. in diameter; margin circular, entire; outer annular zone with 4 or 5 coarse concentric rugae; mid-field large, convex, with cruciform ?mouth. *U.Perm.*, Ger. Very poorly illustrated.

"Medusina" reiflingensis KIESLINGER, 1925. Known from single specimen. ?Subumbrellar impression circular, with narrow outer annular zone and large circular mid-field bearing several irregular radial grooves, small central circular marking and 2 broad protuberances, asymmetrically located near periphery of mid-field, regarded by KIESLINGER as gonads. *Trias.*, Aus.——FIG. 129,*8*. *"M." reiflingensis,* holotype, ×1 (KIESLINGER).

"Medusina" sp., ADAM, 1950. Known from single specimen. Small impression with large, smooth, concave mid-field and 16 raised, outer lobes, of elongate quadrangular shape, sharply separated by deep, broad grooves. *M.Trias.*, Ger. The poorly preserved specimen may be compared with *Lorenzinia gabelli.*

"Medusites" bicinctus HAECKEL, 1869. Known from single, obscure specimen. Subumbrellar impression circular, with entire margin, 2 smooth outer rings of subequal width, separated by circular groove, and large circular mid-field with indistinct center and 8 radial grooves marking off 8 radial lobes (4 larger 90° apart, one narrower in each quadrant). CASTER suggested that *"M." bicinctus* could represent an immature stage of *Rhizostomites admirandus,* but the specimen is too poorly preserved to draw any sound conclusion. *U.Jur.*, Ger.——FIG. 129,*2*. *"M." bicinctus,* holotype, ×0.65 (HAECKEL).

"Medusites" staurophorus HAECKEL, 1869. Known from single obscure specimen. Margin circular, entire; outer ring narrow, smooth; inner field large, circular, crossed by 4 hyperbolic low ridges marking off a central cruciform excavation (?mouth). *U.Jur.*, Ger.——FIG. 129,*5*. *"M." staurophorus,* holotype, ×1 (HAECKEL).

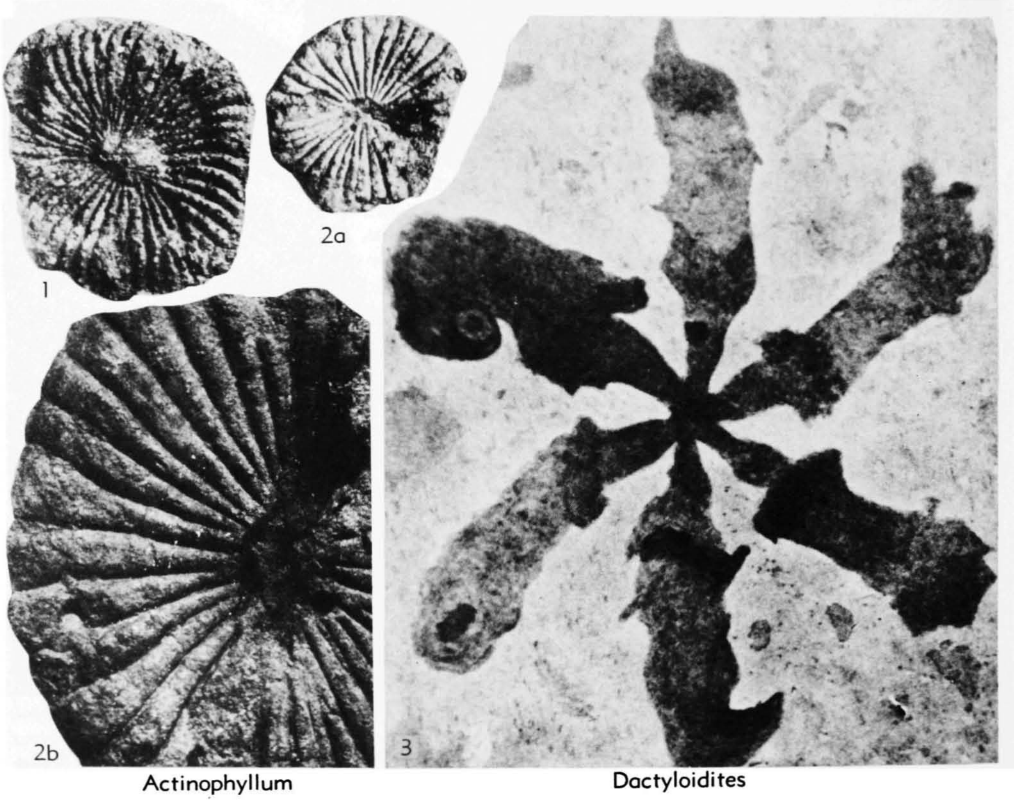


FIG. 130. *Actinophyllum* and *Dactyloidites*. *1*, *A. spinosum*, L.Dev., Eng.; ×2 (STRAW). *2*, *A. plicatum*, L. Dev., Eng.; *2a,b*, ×1, ×2.5 (STRAW). *3*, *D. asteroides*, L.Cam., N.Y.; ×1 (WALCOTT).

© 2009 University of Kansas Paleontological Institute

UNRECOGNIZABLE FORMS AND FORMS ATTRIBUTED TO MEDUSAE BUT NOW REGARDED AS BELONGING TO OTHER ORGANISMS OR AS INORGANIC

Actinophyllum Phillips, 1848 [**A. plicatum*]. Thin, nearly flat circular disc, with small, indistinct, ill-defined central area from which 36 to 56 ribs radiate to periphery; ribs flat, bifurcating near inner extremity and commonly again farther on; surface of ribs either smooth or with tiny spines arranged in alternating series along the middle; interspaces groovelike; ribs reaching margin and continuing on underside of body for half the distance toward center, where they curve upward and disappear leaving a large circular central opening through which internal surface of upper side is displayed. *L.Dev.(Downton.),* Eng. Phillips originally regarded this problematic form as a calcareous alga resembling the living *Acetabularia;* both M'Coy and Salter suggested its identity with *Spongarium* Milne-Edwards, 1839, U. Sil.(U.Ludlov.), Eng., but Straw showed that the 2 forms are different, *Spongarium* being almost paper thin, having one concave, smooth surface and the opposite convex and striated (not ribbed); Brodie regarded the form as a coral; Barrois argued its identity with *Discophyllum* Hall, 1847, M.Ord., N.Y., and regarded the fossils as metamers of *Anthomorpha* Bornemann (archaeocyathid); Straw opposed this view and went back to Phillips' idea; Kieslinger placed the form among the medusae incertae sedis. The weight of the evidence suggests that *Actinophyllum* is a calcareous alga.——Fig. 130,*1*. *A. spinosum* Straw; holotype, ×2 (Straw).——Fig. 130,*2*. **A. plicatum*; *2a,b,* holotype, ×1, ×2.5 (Straw).

Aequorfossa Neviani, 1925 [**A. farnesinae*]. *Plio.,* Italy. Known from single obscure impression consisting of 2 concentric circular grooves, regarded by Neviani as representing a leptolinid medusa (Aequoridae). Accepted here is the view of Sacco, who regarded the impression as inorganic.

Brooksella rhenana Kinkelin, 1903. *Dev.,* Ger. R. & E. Richter have shown that this impression belongs to *Pleurodictyum regulare* Maurer (coral).

Dactyloidites Hall, 1886 [**D. bulbosus* (=*Buthotrepis ? asteroides* Fitch, 1850)]. Starlike remains consisting of a thin carbonaceous film, having 4 to 7 radiating, widely separated lobes, typically expanded and bulbous near distal extremities. *L. Cam.,* N.Y., *?M.Cam.,* Vt. Fitch regarded the fossils as algae; Walcott placed them in the Brooksellidae (Protomedusae), a view accepted both by Kieslinger and Caster; Ruedemann reverted to Fitch's idea and suggested that they could represent remains of algae that lived attached to the sea bottom. The carbonaceous nature of the remains supports their algal origin and makes their medusoid affinities very implausible. ——Fig. 130,*3*. **D. asteroides* (Fitch), L.Cam., N.Y.; a typical specimen, ×1 (Walcott). *?D. edsoni* Ruedemann, 1934, M.Cam., Vt., possibly does not belong in this genus.

Medusichnites Matthew, 1891. No type. *Cam.,* Can. Inorganic markings and ?trails.

Medusites Germar, 1825 [**M. capillaris*] [=*Lumbricaria* Goldfuss, 1826]. *Paleoz.,* Ger. Not a medusoid; ?worm coprolites.

"Medusites" armoricanus Peneau, 1946. *L.Ord.,* Fr. Unrecognizable.

"Medusites" circularis Haeckel, 1869. *U.Jur.,* Ger. Unrecognizable.

"Medusites" cretaceus Kner, 1866. *Cret.,* Pol. Unrecognizable.

"Medusites" couffoni Peneau, 1946. *L.Ord.,* Fr. Unrecognizable.

"Medusites" dubius Peneau, 1946. *L.Ord.,* Fr. Problematic form of unknown affinities; not a medusoid.

"Medusites" helgolandicus Brandt, 1871. *Cret.,* Helgoland (Ger.). Unrecognizable.

"Medusites" latilobatus von Ammon, 1886. *?U.Cret.,* Ger. Not a medusoid; ?sponge.

"Medusites" porpitina Haeckel, 1869. *U.Jur.,* Ger. Unrecognizable.

Palaegina Haeckel, 1869 [**P. gigantea*]. *U.Jur.,* Ger. Cephalopod.

Papilionata Sprigg, 1947 [**P. eyrei*]. *L.Cam.,* S. Austral. Problematic form of unknown affinities; not a medusoid.

"Protoniobia" Sprigg, 1949 [**P. wadea*]. Known from single, very small impression consisting of a few prominent annular undulations with ring of tiny nodules near center; margin with 4 subcircular attached structures, of different size, arranged in incomplete hexagonal pattern, showing concentric sculpture similar to "parent" impression. *L.Cam.,* W.Austral. Sprigg regarded the impression as representing a leptolinid medusa (Anthomedusina) with 4 attached buds. Here interpreted as a concretion, inorganic.——Fig. 131. *"*P. wadea";* holotype, ×9 (Sprigg).

Trianisites Rafinesque, 1821 [**T. cliffordi*]. *Ord.,* Ky. Not a medusoid; ?algae.

Fig. 131. *"Protoniobia wadea,"* L.Cam., W.Austral.; ×9 (Sprigg).

© 2009 University of Kansas Paleontological Institute

REFERENCES

Adam, K.D.

(1) 1950, *Erster Medusen Nachweis in der Germanischen Trias:* Neues Jahrb. f. Min. etc., Mon. Band, Heft 11, p. 330-341, fig. 1-4.

Ammon, L. von

(2) 1886, *Über neue Exemplare von jurassischen Medusen:* Abhandl. Kgl. Bayer. Akad. Wiss., Math.-Nat. Kl., Band 15, p. 120-165, pl. 1-2, fig. 1-3.

Barrois, Charles

(3) 1891, *Memoir sur la faune du grès armoricain:* Soc. Geol. du Nord. de la France, Ann. 19, p. 134-237, pl. 1-5.

Brandt, A.

(4) 1871, *Über fossile Medusen:* Mem. Acad. Imp. Sci. St. Petersbourg (7), 16, no. 11, p. 1-18, pl. 1-3, fig. 1-2.

Fitch, Asa

(5) 1850, *Rocks and soils of Washington County (New York):* N.Y. State Agric. Soc., Trans., v. 9, p. 863.

Gortani, M.

(6) 1920, *Osservazzioni sulle impronte medusoidi del Flysch (Lorenzinia e Atollites):* Riv. ital. Paleont., anno 26, fasc, 3-4, p. 56-72, pl. 1-3.

Gürich, G.

(7) 1933, *Die Kuibis-Fossilien der Nama-formation von Sudwest-Afrika. Nachträge und Zusätze:* Paläont. Zeitschr., Band. 15, Heft. 2-3, p. 137-154, fig. 1.

Haeckel, Ernst

(8) 1869, *Über die fossilen Medusen der Jurazeit:* Zeitschr. f. wiss. Zoologie, Band 19, p. 554-561, pl. 42.

Hall, James

(9) 1886, *Note on some obscure organisms in the roofing slates of Washington County, N.Y.:* N.Y. State Mus., 39th Ann. Rept., p. 160, pl. 11.

Harrington, H. J. & Moore, R. C.

(10) 1955, *Kansas Pennsylvanian and other jellyfishes:* Kansas Geol. Survey, Bull. 114, pt. 5, p. 153-163, pl. 1-2.

Hundt, Rudolf

(11) 1940, *Eine Medusina aus dem Kieselschiefer des Ostthüringer Llandovery:* Zentralbl. f. Min. etc., Abt. B, p. 25-29, fig. 1-2.

(12) 1940, *Eine Meduse (Medusina lincki nov. sp.) des oberen Zechsteins Ostthüringens und ihr Einbettungsraum:* Beitr. geol. Thüringen, Band 6, Heft 1, p. 11-16, pl. 1.

Kieslinger, A.

(13) 1924, *Medusae fossiles:* Fossilium Catalogus. I. Animalia. Pars 26, p. 1-20.

(14) 1925, *Eine Meduse aus der alpinen Trias:* Neues Jahrb. f. Min. etc., Abt. B, Band 51, p. 494-502, pl. 1.

(15) 1939, *Scyphozoa:* in Schindewolf, O. H., Handb. d. Paläozoologie, Band 2A, Lief 5, p. A69-A109, fig. 1-42.

Kner, J.

(16) 1865, *Über eine Meduse in Feuerstein:* Sitzungsber. K. Akad. Wiss., Band. 52, p. 480.

Linnarsson, J. G. O.

(17) 1871, *Geognostiska och Paleontologiska Jakttagelser öfver Eophytonsandstenen i Vestergötland:* K. Svenska Vetenskapsakad. Handl., v. 9, no. 7, p. 1-16, pl. 1-2.

Nathorst, A. G.

(18) 1881, *Im aftryck af Medusor i Sveriges Kambriska Lager:* Same, v. 19, no. 1, p. 1-34, pl. 1-6.

(19) 1910, *Ein besonders instruktives Exemplar unter der Medusenabdrucken aus dem Kambrischen Sandstein bei Lugnås:* Sver. Geol. Undersök., Afhandl. (C), Aarsbok 3 (1909), no. 11, p. 1-7, pl. 1.

Neviani, Antonio

(20) 1925, *Di una nuova medusa fossile appartenente alle Aequoridae (Craspedote) rinvenuta nelle argille classiche della Farnesina presso Roma:* Atti Pont. Accad. Nuovi Lincei, tomo 78 (6), p. 148-156, fig. 1.

Peneau, J.

(21) 1946, *Étude sur l'ordovicien inférieur (arenigien = grès armoricain) et sa faune (specialement au Anjou):* Soc. Études Sci. Angers, B. an., 74-76, p. 39-94, 1 pl.

Phillips, John

(22) 1848, *Palaeontological appendix to Professor John Phillips' Memoir on the Malvern Hills compared with the Paleozoic districts of Abberley:* in Phillips, J., & Salter, J. W., Mem. Geol. Survey G.Brit., v. 2, pt. 1, p. 331-386, pl. 30.

Pohlig, H.

(23) 1892, *Altpermische Saurierfährten, Fische und Medusen:* Festschr. zum 70 Geburtst. Rudolf Leuckarts, Leipzig, p. 58-64, fig. 2, pl. 7.

Pompeckj, J. F.

(24) 1896, *Die Fauna des Cambriums von Tejrovic und Skrey in Böhmen:* Jahrb. k. k. geol. Reichsanst., Band 45 (1895), p. 501, pl. 14.

© 2009 University of Kansas Paleontological Institute

Ruedemann, Rudolf

(25) 1934, *Paleozoic plankton of North America:* Geol. Soc. Am., Mem. 2, 141 p., 26 pl., 6 fig.

Rüger, L., & Rüger-Haas, P.

(26) 1926, *Palaeosemaeostoma geryonides v. Huene sp., eine sessile Meduse aus dem Dogger von Wehingen in Württemberg und Medusina liasica nov. sp., eine coronatenähnliche Meduse aus dem mittleren Lias von Hechingen in Württemberg:* Sitzungsber. Heidelberg. Akad. Wiss., Math.-Nat. Kl., Jahrg. 1925, Abhandl. 15, p. 1-22, pl. 1-2.

Sprigg, R. G.

(27) 1947, *Early Cambrian(?) jellyfishes from the Flinders ranges, South Australia:* Roy. Soc. S.Australia, Trans., v. 71, pt. 2, p. 212-224, pl. 5-8.

(28) 1949, *Early Cambrian "jellyfishes" of Ediacara, South Australia, and Mt. John, Kimberley District, Western Australia:* Same, v. 73, pt. 1, p. 72-99, pl. 9-21.

Straw, S. H.

(29) 1926, *Some notes on the genus Actinophyllum:* Mem. & Proc. Manchester Lit. & Philos. Soc., v. 70, p. 133-139, 1 pl.

Torell, Otto

(30) 1870, *Petrifacta suecana formationis cambricaea:* Lunds Univ. Årsskrift 1869, pt. 2, no. 8, p. 1-14.

Ulrich, Arnold

(31) 1893, *Paleozoische Versteinerungen aus Bolivien:* Neues Jahrb. f. Min. etc., Abt. B, Band 8, p. 5-116, pl. 1-5.

Van Straelen, Victor

(32) 1926, *Sur les premiers restes de Meduses trouvés dans le calcaire carbonifère de Belgique:* Acad. Roy. Belgique, Bull., Cl. Sci., 5me. ser., v. 12, p. 952-956, 1 pl.

Walcott, Charles D.

(33) 1898, *Fossil Medusae:* U. S. Geol. Survey, Mon. 30, ix + 201 p., 47 pl.

(34) 1911, *Middle Cambrian holothurians and medusae:* Smithsonian Misc. Coll., v. 57, no. 3, p. 41-68, pl. 8-13.

Zelisko, J. V.

(35) 1937, *Einige Bemerkungen über das Vorkommen von frei schwimmenden Medusen in der kambrischen Formation:* Zentralbl. f. Min., etc., Abt. B, p. 205-208.

ANTHOZOA—GENERAL FEATURES

By J. W. WELLS and DOROTHY HILL

Anthozoans are exclusively polypoid, solitary or colonial, with no trace of a medusoid stage in their life cycles, but they retain the free-swimming planula larval stage. They are the only coelenterate group with a **stomodaeum,** a tube extending down from the mouth into the gastrovascular cavity. The stomodaeum may have 1 or 2 grooves **(siphonoglyphs)** lying in a so-called dorsoventral plane which is vertical with respect to the oral surface. The gastrovascular cavity is radially partitioned with respect to the oral-aboral axis by endodermal **mesenteries** extending inward from the inner surface of the column wall; and when these are attached in part to the stomodaeum they are said to be complete or perfect. The **tentacles** are invariably hollow and almost uniformly retractile. Some groups are characterized by a spicular or trabecular calcareous or horny skeleton **(corallum).**

Anthozoans are exclusively marine, and include a wide variety of common marine animals referred to as sea anemones, corals, soft corals, sea fans, sea pens, sea feathers, and so on.

KINDS OF ANTHOZOANS

The anthozoans are grouped in 3 subclasses: Ceriantipatharia, Octocorallia, and Zoantharia.

CERIANTIPATHARIA

The Ceriantipatharia include 2 orders: Antipatharia (colonial) and Ceriantharia (solitary). The colonies of the former are slender and branching, consisting of a horny skeletal axis covered by a thin coenosarc bearing polyps. Antipatharian polyps generally have only 6 simple tentacles, and 6, 10, or 12 complete mesenteries with very feeble musculature, 6 of which are considered primary, with 2 siphonoglyphs. Ceriantharian polyps lack any skeleton, and have 2 rings of tentacles. The numerous unpaired mesenteries are all complete, ar-

© 2009 University of Kansas Paleontological Institute

ranged in one cycle consisting of the 6 protocnemes in couples on either side of the single siphonoglyph, with many additional couples added serially and only in the dorsal intermesenterial space (Fig. 132,*c*). The **cerinula** larval stage of the ceriantharians resembles the antipatharian polyp, and both orders have 6 protocnemes in couples, of which the first-formed central transverse one is fertile. The subclass is virtually unknown in the fossil state.

OCTOCORALLIA

The Octocorallia are exclusively colonial in habit, with a calcareous spicular or horny (gorgonin) skeleton. The polyps have 8 pinnate tentacles and 8 complete mesenteries, which are directed ventrally from a directive pair said to be dorsal (Fig. 132,*d*). The subclass is known scatteringly by fossils from the Mesozoic onward.

ZOANTHARIA

The Zoantharia include solitary and colonial polyps, with calcareous trabecular skeletons in some orders. The polyps have simple or divided tentacles but never pinnate cyclically arranged ones and are especially distinguished by paired mesenteries. Basically there are 8 complete mesenteries and almost invariably 2 additional lateral couples, making a total of 6 pairs (Fig. 132, *e*), 2 of them being the dorsal and ventral directive pairs; generally additional cyclically arranged pairs are present. New mesenterial pairs are inserted according to several different plans (Fig. 132,*f,g,h*). The subclass is represented paleontologically from the Ordovician (or possibly earlier by a supposed anemone from the Cambrian) to the present day. It includes 6 orders separated largely on the presence or absence of a skeleton and by the mesenterial arrangement and development. These consist of the Zoanthiniaria, Rugosa, Heterocorallia, Corallimorpharia, Scleractinia, Actiniaria, and possibly the extinct Tabulata.

The Zoanthiniaria (zoanthids) are weakly colonial, anemone-like forms lacking a skeleton. The mesenteries are in a single cycle with 2 directive pairs, of which only the ventral one is complete, and new pairs of mesenteries beyond the first 6 are inserted only in the ventrolateral exocoeles on either side of the ventral directive pair (Fig. 132,*f*). They are unknown as fossils, but are believed by some to be representative of the most primitive zoantharians.

The Rugosa are an extinct group known only from Paleozoic rocks, and their relationships to other orders of the subclass are still speculative. The mesenterial arrangement and development can only be inferred from the mode of septal insertion, and this is capable of several interpretations. Many investigators are inclined to see closest affinities of the Rugosa in the Zoanthiniaria, from which they would differ only by having a calcareous exoskeleton and insertion of new septa (and mesenterial pairs) not only in exocoeles on either side of the cardinal septum (ventral mesenterial pair), as in the zoanthinarians, but also in spaces between the alar and counter-lateral septa (between lateral mesenterial pairs), that is, in 4 instead of 2 primary exocoeles (Fig. 132,*g*). Relationship to the endocoelactarian actiniarian anemones (Carlgren, 1918) and to the scleractinian corals has also been claimed (Schindewolf, 1942). The question is far from settled.

The Heterocorallia are a small, extinct Carboniferous group of doubtful affinities.

The orders Corallimorpharia, Scleractinia, and Actiniaria include the living sea anemones and corals, all of them lacking a skeleton except the Scleractinia, which are distinguished from the corallimorphs largely by this criterion. The mesenterial plan is practically identical in all and differs from that of the Zoanthiniaria and ?Rugosa in that the mesenterial pairs beyond the first cycle of 6 are inserted in dorsoventral order in all 6 primary exocoeles (hexactiniarian), rather than in 2 or 4 (Fig. 132,*h*), and in some groups septa may also develop in the endocoeles of the lateral pairs. The Scleractinia alone have a fossil record, from the Middle Triassic to Recent.

The Tabulata are a heterogeneous extinct Paleozoic group whose relations with other anthozoans are uncertain.

EVOLUTION

Three lines of anthozoan development are generally recognized: (1) ceriantipatharian, (2) octocorallian, and (3) zoantharian (Fig. 132).

© 2009 University of Kansas Paleontological Institute

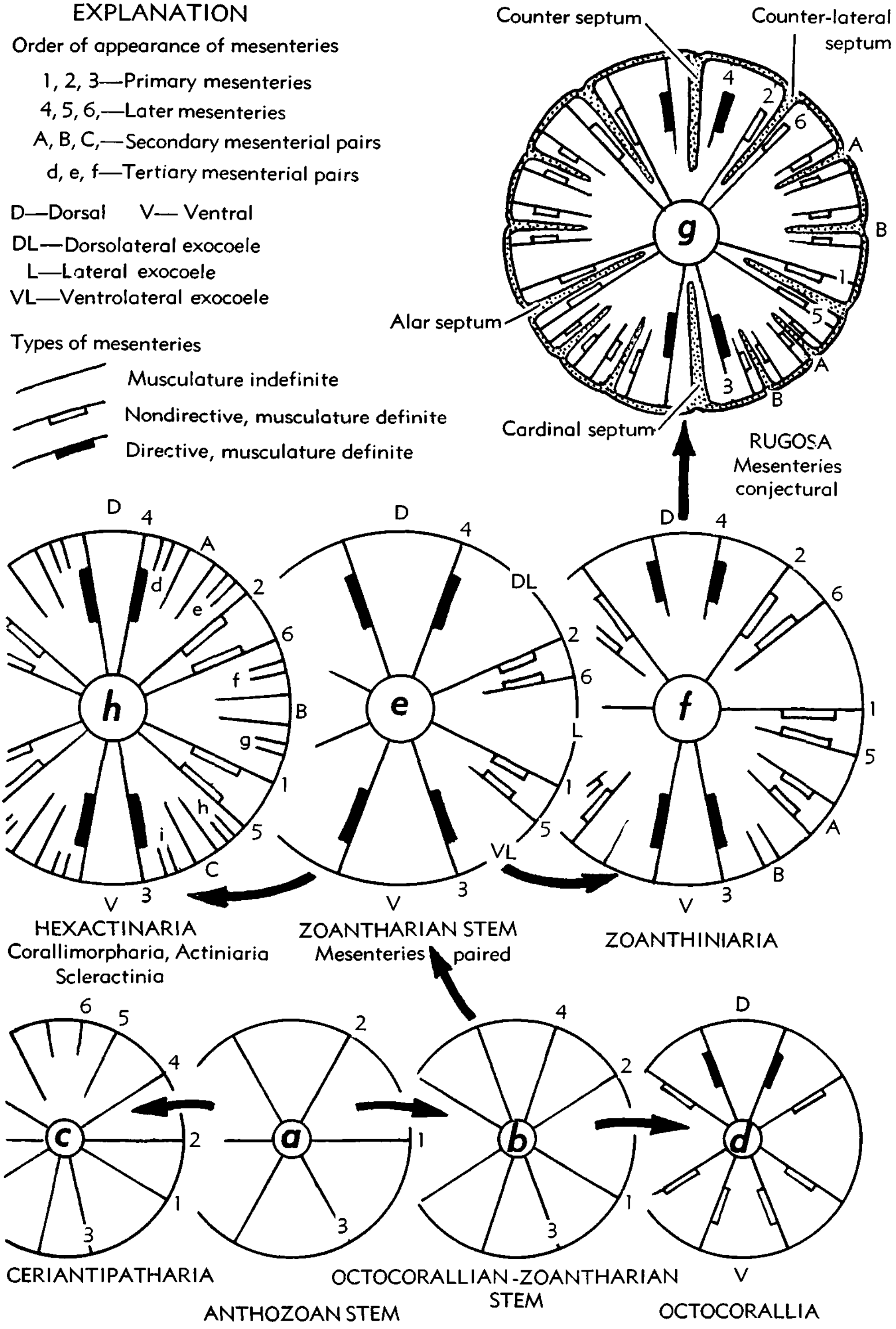


FIG. 132. Relations and mesenterial arrangements of principal anthozoan groups.

© 2009 University of Kansas Paleontological Institute

Antipatharians seems to represent a very old, primitive group related to the cerianthids. The cerinula larva of the latter is like the antipatharian polyp; both have simple tentacular and mesenterial arrangements and both have 6 mesenteries, of which the central transverse couple is largest. Cerianths diverge by development of additional couples in the dorsal intermesenterial space. The ancestral anthozoan type may have been a solitary polyp, something like the antipatharian polyp with 6 mesenteries in couples and 6 tentacles (Fig. 132,*a*), and by addition of a dorsal directive couple—the last to arise in ontogeny of the other groups—the basic octamerous plan of the other subclasses arose.

The ancestor of the octocorallian and zoantharian lines is considered by some to have been a skeletonless polyp with 8 mesenteries having very weakly developed musculature and 8 tentacles (Fig. 132,*b*), a form leading toward the Octocorallia. From the same stock perhaps arose the basic zoantharian type by the addition in the adult stage of all but the most primitive forms of 4 incomplete mesenteries for the total of 12 in 6 pairs (Fig. 132,*e*). Additional pairs beyond these, arising in the ventrolateral exocoeles, led to the zoanthiniarians (Fig. 132, *f*). The Rugosa may have been derived from these by the development of mesenterial pairs in the lateral as well as in the ventrolateral exocoeles (Fig. 132,*g*) and by appearance of an exoskeleton. The hexactiniarian corals and anemones (Corallimorpharia, Scleractinia, and Actiniaria) added mesenterial pairs in all 6 primary exocoeles, cyclically, in a dorsoventral order (Fig. 132, *h*). They are generally believed to have developed from another branch of the zoantharian stem, although some have tried to see the Rugosa as ancestral to the hexactiniarians, in a direct trend from insertion in 2 exocoeles (zoanthids) through insertion in 4 (rugosans) to insertion in all 6 (hexactiniarians).

Class ANTHOZOA Ehrenberg, 1834

[Less hydroids] [=Endoaria Rapp, 1829; Actinozoa de Blainville, 1830 *(partim)*; Actinoidea Dana, 1846; Corallaria Milne-Edwards & Haime, 1850; Oecioa Huxley, 1852; Coralliaria M.-Edw.-H., 1857 *(partim)*; Cnidaires M.Edw.-H., 1857; Actinoida Gosse, 1860; Polycyclia, Monocyclia *(partim)* Bronn, 1860; Coralligena Huxley, 1864; Cnidaria Verrill, 1865; Coralla Haeckel, 1866; Scyphopolypi, Scyphozoa *(partim)* Götte, 1887; Anthozoariae Delage & Hérouard, 1901]

Exclusively polypoid, solitary or colonial, mostly sedentary coelenterates. Oral end expanded as oral disc with centrally located mouth surrounded by peristome, around which are one or more rings of hollow tentacles. Stomodaeum strongly developed, leading from mouth into gastrovascular cavity, generally with 1 or 2 siphonoglyphs. Gastrovascular cavity biradially partitioned into compartments by complete or incomplete mesenteries, some of which bear endodermal gonads. Some groups characteristically with horny or calcareous spicular endoskeleton or calcareous exoskeleton. Exclusively marine. *Ord.-Rec.*

Representatives of this class are divided into three subclasses:

I. Mesenteries unpaired:
  A. Tentacles simple....Ceriantipatharia
  B. Tentacles pinnate............Octocorallia
II. Mesenteries paired..................Zoantharia

REFERENCES

Carlgren, O.

(1) 1918, *Die Mesenterienanordnung der Halcuriiden:* Lund Univ. Årsskr., Neue Folge, Avd. 2, v. 14, 37 p., 1 pl., 25 fig.

Clark, A. H.

(2) 1913, *Cambrian holothurians:* Am. Naturalist, v. 47, p. 488-507.

Delage, Y., & Hérouard, E.

(3) 1901, *Les Coelentérés:* in Delage & Herouard, Traité de zoologie concrète (Paris), tome 2, pt. 2, x+848 p., 72 pl., 1102 fig.

Dollfus, G.

(4) 1875, *Note sur les empreintes attribuable à un actinie (?Palaeactis vetula) dans les schistes cambriens des Moitiers-d'Allonne:* Soc. nat. Sci., nat.-math. Cherbourg, Mém. 9 (sér. 2), p. 224-232, pl. 3.

Hyman, L. H.

(5) 1940, *The invertebrates: Protozoa through Ctenophora:* McGraw-Hill (New York), xii + 726 p., 221 fig.

Kiesling, A.

(6) 1939, *Scyphozoa:* in Schindewolf, O. H., Handbuch der Paläozoologie, Borntraeger (Berlin), Band 2A, Lief. 5, p. A69-A109, fig. 1-42.

Pax, F.

(7) 1924, *Hexacorallia:* in Kükenthal's Handbuch der Zoologie, Band 1, p. 770-901, figs.

© 2009 University of Kansas Paleontological Institute

Ruedemann, Rudolf

(8) 1934, *Paleozoic plankton of North America:* Geol. Soc. America, Mem. 2, vii + 141 p., 26 pl., 6 fig.

Schindewolf, O. H.

(9) 1942, *Zur Kenntnis der Polycoelien und Plerophyllen; eine Studie über den Bau der "Tetrakorallen" und ihre Beziehung zu den Madreporarien:* Reichsamt Bodenforsch., Abh., Neue Folge, Heft 204, 324 p., 36 pl., 155 fig.

Walcott, C. D.

(10) 1911, *Middle Cambrian holothurians and medusae:* Smithson. Misc. Coll., v. 57, no. 3, p. 41-68, pl. 8-13.

CERIANTIPATHARIA

By J. W. Wells and Dorothy Hill

Subclass CERIANTIPATHARIA van Beneden, 1898

[=Hexacorallia Götte, 1902 (*non* Haeckel, 1866)]

Included here are 2 strongly divergent but related orders (1) Antipatharia, the "black corals," which are colonial forms characterized by a thorny skeletal axis of horny gorgonin, with small polyps having only 6 tentacles and 6 to 12 complete unpaired mesenteries, and (2) Ceriantharia, comprising relatively large solitary skeletonless anemone-like polyps with many tentacles arranged in 2 circles and an indefinite number of unpaired mesenteries. The larval stage of the ceriantharians resembles the antipatharian polyps, and both orders differ from other anthozoans in the very weak or indefinite musculature of the mesenteries and in the insertion of new mesenterial couples only in the dorsal intermesenterial space. *Mio.-Rec.*

Order ANTIPATHARIA Milne-Edwards & Haime, 1857

[=Antipathina Ehrenberg, 1834; Antipathidae Gray, 1840; Antipathacea Dana, 1846; Zoantharia cauliculata Milne-Edwards & Haime, 1850; Zoantharia sclérobasiques (Antipatharia) M.Edw.-H., 1857; Hexactina Bronn, 1860; Anticorallia Haeckel, 1896; Antipathidea Bourne, 1900]

Colonial, branching, with thorny horny axial skeleton surrounded by fleshy coenosarc bearing small polyps (Fig. 133,*2*). Polyps with 6 simple or 8 branched tentacles and 6, 10 or 12 complete coupled but unpaired mesenteries and having a single siphonoglyph. *Mio.-Rec.*

These corals are mostly non-reef dwellers and occur in depths of 1 to 1,900 fathoms. About 20 genera are known, only one of which has been found in the fossil state.

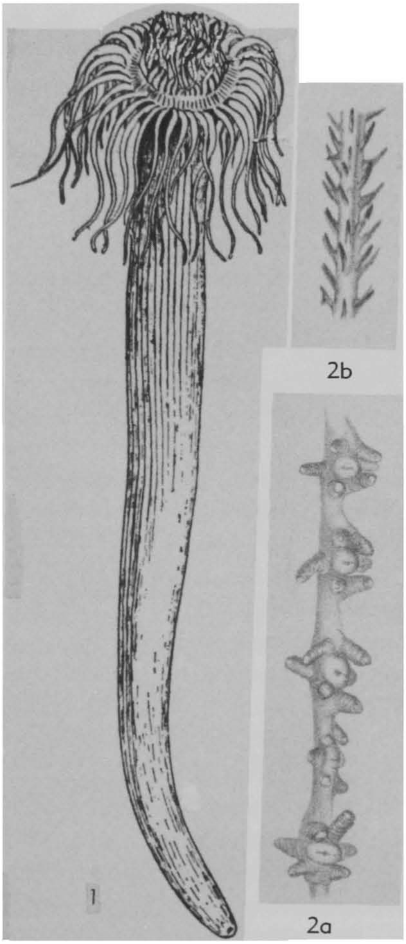


Fig. 133. Representatives of Ceriantipatharia. *1, Cerianthus* sp., Rec. (order Ceriantharia), ×1. *2, Antipathella subpinnata,* Rec., Medit., 135 fathoms; *2a,* polyps, ×5.5; *2b,* axis, ×26 (order Antipatharia) (*1,* L. H. Hyman, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York; *2,* after Brook).

© 2009 University of Kansas Paleontological Institute

Leiopathes HAIME, 1849 [**Antipathes glaberrima* ESPER, 1792]. *Mio.*, Italy; *Rec.*, Medit.

Order CERIANTHARIA Perrier, 1893

[=Cerianthidae MILNE-EDWARDS & HAIME, 1851; Paranemata BRONN, 1860; Tetractiniae LANKESTER, 1877; Heterocoralla HAACKE, 1879 (*non* Heterocorallia SCHINDEWOLF, 1941); Cerianthiae HERTWIG, 1882; Cerianthidea BOURNE, 1900]

Solitary, lacking skeleton. Column elongate, without pedal disc on aboral end. Oral disc with many simple tentacles arranged in 2 rings. Mesenteries complete, coupled but unpaired, in a single cycle. New couples added serially only in dorsal intermesenterial space. *Rec.*

A small group of semiburrowing anemones (Fig. 133,*1*), unknown in the fossil state, unless some vertical cavities in shales and sandstones are traces of cerianthid burrows.

OCTOCORALLIA[1]

By FREDERICK M. BAYER[2]

WITH SECTION ON TRACHYPSAMMIACEA

By EUGENIA MONTANARO-GALLITELLI

CONTENTS

---

[1] Published with permission of the Secretary of the Smithsonian Institution.

[2] Associate Curator, Division of Marine Invertebrates, U.S. National Museum.

© 2009 University of Kansas Paleontological Institute

INTRODUCTION

Although the octocorals are not extensively known in the fossil record, their remains have been discovered in deposits as old as the Cretaceous, with doubtful records back to the Silurian. Forms with a solid, calcified axis, such as various species of *Corallium, Isis, Primnoa* and related genera, are noticed more frequently than those that are less durably constructed. By far the largest number of species are of a more transient nature; their only calcified skeletal elements, in the form of minute spicules, are so small as readily to escape detection in the rocks should they not be dissolved before realizing their fossil destiny.

Spicules belonging to octocorals are found in modern marine sediments and occasionally have been observed as fossils. From the amount of calcareous material that octocorals are thought to contribute to reef deposits, it is reasonable to expect their spicules as fossils in larger numbers than actually have been reported. Very possibly the seemingly hopeless problem of identifying such isolated spicular remains has prompted many investigators to ignore them when observed in samples. Effort to identify some octocoral fragments is indeed hopeless, but accurate generic determination of others can be made on the basis of a single sclerite. Many genera have specialized spicules which are absolutely characteristic, but, unfortunately, most of them also have simple sclerite forms that could belong to any of a dozen genera classified in 2 or 3 orders. Since the spicules are apt to be dissociated, it is impossible to determine examples of generalized types. Specific identifications, depending upon the arrangement and combination of spicules, would be possible only with ideally well-preserved material.

None of the standard paleontological works gives more than a brief account of the octocorals, and the systematic treatments of the Recent forms, not written for paleontologists, are of use only to specialized systematists. The aim of this work is to present brief diagnoses of the important genera, both Recent and fossil, with illustrations of their characteristic skeletal elements, as a review of the diverse features of alcyonarian hard parts, for the use of paleontologists in the analysis of marine deposits, bottom sediments, and similar samples.

Previously published illustrations of most species figured in this section of the volume on coelenterates were not found to be adaptable for purposes of the *Treatise;* so new drawings have been prepared in nearly all instances. Furthermore, species chosen to illustrate the genera are not always the genotypes, sometimes because the genotype was thought not to portray the genus to best advantage, and sometimes simply because specimens of it were not available to me for illustration.

ACKNOWLEDGMENTS

I could not in good conscience present the following work without taking notice of the assistance so willingly given by friends and colleagues. The Editor, R. C. MOORE, has been most helpful and tolerant of seemingly inexcusable delays. I am grateful to F. A. CHACE, JR., for much good advice, especially in the field of nomenclature; to HELEN DUNCAN, JULIA GARDNER, J. BROOKES KNIGHT, ALFRED R. LOEBLICH, JR., and JOHN W. WELLS, for assistance of many kinds; to EUGENIA MONTANARO-

© 2009 University of Kansas Paleontological Institute

GALLITELLI for preparing the section on Trachypsammiacea, with which she is quite familiar; to IRA B. HANSEN, EDITH E. MORTENSEN, HARDING B. OWRE, and J. Q. TIERNEY for criticisms of the manuscript; and to L. B. ISHAM, staff illustrator of the Department of Geology of the U.S. National Museum, for much advice in regard to the figures. I also wish to thank the authorities of the Smithsonian Institution and my supervisors at the United States National Museum for permitting me to undertake what has proved to be an unreasonably time-consuming project.

MORPHOLOGY

Like other Anthozoa, members of the subclass Octocorallia are exclusively polypoid coelenterates. Unlike hydroids, they have a mouth invaginated to form a tubular **pharynx,** and a **gastrovascular cavity** radially partitioned by thin, noncalcareous septa, sometimes called **mesenteries** (Fig. 134). The **autozooids** are of a remarkably uniform type throughout the subclass. They have 8 pinnately branched **tentacles,** which alternate with 8 septa, all complete—i.e., with their upper ends extending from body wall to pharynx. The pharynx, which is a compressed tube, has along one of its narrower sides a strongly ciliated longitudinal tract known as the **siphonoglyph** (or sulcus), which maintains a circulation of water into the gastrovascular cavity. The side of the polyp bearing the siphonoglyph is referred to as "ventral" in older literature, but modern authors call it the **sulcal side** and the opposite the **asulcal.** Longitudinal retractor muscles are situated on the sulcal faces of the septa. The latter, attached along their centrifugal edges to the body wall, join with the **oral disc** above and with the pharynx along their distal inner edges, thus completely partitioning the upper part of the gastrovascular cavity into 8 blind sacs ending in the tentacles. Below the inner end of the pharynx the edges of the septa hang free and slope rapidly out toward the body wall, where they continue downward as 8 ridges, of which the asulcal pair extends farthest into the gastrovascular cavity. The free septal edges are thickened to form usually convoluted cords called **filaments,** of which the asulcal pair are longest and strongly ciliated. The remaining 6, lacking in some polyps, are shorter and densely glandular.

The type of individual just described is found in all orders of Octocorallia. In certain groups modified individuals may occur also, in which event the basic polyp type is called the autozooid. Modified polyps, called **siphonozooids,** with one rudimentary tentacle or none at all, may be present. In the Pennatulacea, the primary or axial polyp is given a special name, oözooid, and another type of nontentaculate polyp may be represented by the so-called mesozooid. These modified kinds of polyps have little importance from a paleontological standpoint, and accordingly a detailed account of their anatomy is omitted.

The regular octamerous symmetry of the octocorallian autozooid, so obvious externally, is shown by microanatomical investigation to have a basic bilaterality superimposed upon it by the presence of the single siphonoglyph, the modified asulcal pair of septal filaments, and the arrangement of the retractor muscles. By virtue of these features an autozooid may be divided longitudinally into identical halves through only one plane—that which divides the sulcal and the asulcal pairs of septa and consequently the siphonoglyph. Its symmetry is thus radiobilateral.

The upper portion of the autozooid, called **anthocodia** (Fig. 134), is usually retractile, either within the general coenenchymal mass or into the stiffened lower part of the polyp itself, called **anthostele.** In the former case, the polyps in contraction are visible as small pores or stellate apertures, whereas in the latter a distinct **calyx** (verruca) always remains visible as a hillock on the rind (Fig. 134). The tentacles are either folded over the oral disc or introverted into the gastrovascular cavity when the polyp withdraws.

In some instances (Stolonifera, Telestacea), the polyps spring from a basal sheetlike or bandlike stolon and stand as erect, branched or unbranched tubes with walls commonly supported by spicules, but usually the lower portions of the polyps are imbedded in a thick, gelatinous substance containing spicules, the **coenenchyme,** together

© 2009 University of Kansas Paleontological Institute

forming colonies of diverse architecture. The polyps occupy pits in the colonial coenenchyme, but unlike the stony corals, these pits are not marked by radial skeletal elements alternating in position with the septa; however, separate calcareous spicules may be so oriented around the base of the polyp and in its walls as to reflect its octamerous symmetry. The coenenchyme is penetrated by a complex system of tubules,

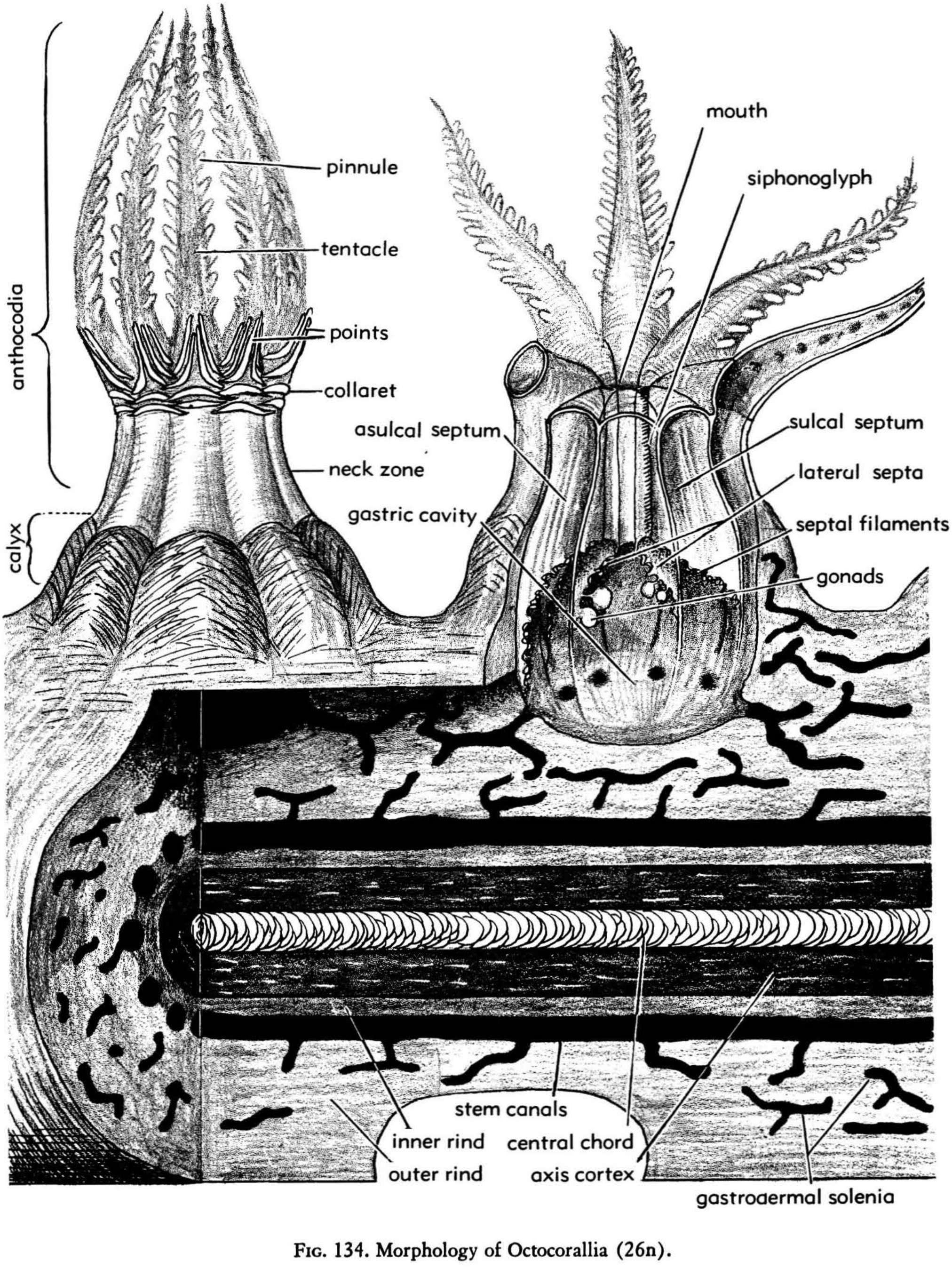


FIG. 134. Morphology of Octocorallia (26n).

© 2009 University of Kansas Paleontological Institute

the **solenia,** which are lined with gastrodermis and serve to interconnect neighboring polyps.

Commonly, sclerites are distributed in more or less symmetrical arrangement at the base of each tentacle and in the body wall between the septa. Below these tracts, the heavier spiculation of the anthostelar region may be symmetrically disposed, but in very many species this is not so.

In several octocorallian families the anthocodial spiculation is so arranged as to fold over the contracted tentacles and close the aperture of the anthostele like a lid, which commonly is recessed deeply within the calycinal orifice. In the Holaxonia, this structure has been utilized, especially by KÜKENTHAL and his students, to distinguish families (for example, Muriceidae, with operculum; Plexauridae and Acanthogorgiidae, both without operculum). The fact of the matter is that the spicules which make up an operculum are almost universally present and differ mainly in their degree of development. Thus it is impossible to distinguish between these families on a basis of the operculum alone, and keys making use of that feature are unreliable.

The opercula of paramuriceids, plexaurids, gorgoniids, and most other holaxonians consist of a few to many spindles arranged *en chevron* upon and immediately below the tentacle bases; the proximal spicules are ordinarily arranged transversely and form a ring (**collaret** or crown) around the polyp, upon which the 8 triangular spicular segments (points) rest (Fig. 134). These sclerites are chiefly interseptal in position. In some families, such as the Gorgoniidae and the Telestidae, there may also be some spicules in the body wall along the septa between any interseptal spicules that may be present. In Primnoidae with an operculum consisting of 8 platelike sclerites (all genera but *Primnoides*), the spicules are septally situated and therefore lie between the bases of the tentacles. This operculum, analogous to that of other families, is consequently homologous with the septal rods of telestids and gorgoniids, rather than with the functional opercular points of paramuriceids and plexaurids.

It is not only the arrangement of spicules upon the polyps that is of systematic importance, but also the size and form of the spicules, their distribution in various layers and zones of the coenenchyme, and in some groups even their color.

The basic spicule type, found in all orders (except Coenothecalia, which lack spicules), is the simple spindle, a monaxial rod which is more or less pointed at both ends. In the Pennatulacea they are usually 3-flanged and quite smooth, some being rather blunt. In other orders they are more or less strongly sculptured by spines, complicated warts, or other protuberances. If the spindles are relatively smooth, blunt and short, they may be referred to as rods, but if long, slender and sharp, as needles. Commonly they combine to form twins and cross-shaped deposits, and by various modifications produce scales, plates, thorn scales, clubs, capstans, dumbbells and other forms. Each of these may, in turn, be further specialized; such distinctive modifications will be discussed under the families and genera in which they occur.

Like other coelenterates, the Octocorallia consist of 2 epithelial layers—an outer epidermis derived from ectoderm, and an inner gastrodermis derived from endoderm—separated by a connective substance called the **mesogloea.** The latter is very thin in some places, such as the tentacles and septa, although elsewhere, as in the fleshy colonial tissue between the polyps, it is thick and usually packed with calcareous skeletal elements. The epidermis is a flat, cuboidal or columnar epithelium or syncytium, and consists of supporting, glandular and sensory elements in an outer stratum that generally secretes a thin cuticle, nervous cells in a middle stratum, and muscular cells (which may be imbedded in the mesogloea below) in the innermost stratum. Specialized stinging structures (**nematocysts**) are usually abundant in the surface stratum. The gastrodermis is constructed upon much the same plan but is more commonly found to be syncytial; nematocysts are restricted to the septal filaments. Intracellular symbiotic algae (**zooxanthellae**) are extremely abundant in many species.

The mesogloea is a jelly-like material containing amoeboid cells derived from the epidermis. Some of these become cnidoblasts, producing nematocysts, which ultimately

© 2009 University of Kansas Paleontological Institute

make their way to the outer surface. Others become scleroblasts, producing calcareous sclerites or a horny material, called **gorgonin,** which is a protein that has a lower sulphur content than true horn and commonly contains bromine and iodine united to tyrosin (11). In the anthocodia the mesogloea is thin and in many forms lacking spicules entirely; it constitutes the inner support for the septa, on the sulcal side of which it is raised into longitudinal plates where the retractor muscles are inserted.

The mesogloeal scleroblasts, which produce spicules, account for all of the skeletal elements of the coenenchyme and for certain axial structures. In the Gorgonacea, the axial structures are produced in 2 ways: (1) by more or less complete consolidation of spicules in the medullar region through the agency of horny or calcareous deposits (Scleraxonia); or (2) by the secretion of a horny, or calcareous and horny, central rod by the cells of a tubular upgrowth from the original basal plate of epidermis (Holaxonia). The latter is thus an external structure over which the colony is spread, as it were; whereas the former, made up of mesogloeal spicules and in many species penetrated by gastrodermal solenia, is an internal one. The axes of Scleraxonia and Holaxonia, although analogous in their supporting function, are produced in different ways and are not homologous.

It is characteristic of the Octocorallia that new polyps are asexually produced not by fission but by gemmation from the solenial system of the basal stolon or of the coenenchyme. The colonies so produced are of exceedingly diverse form. In one type, simple tubular polyps spring from a creeping stolonic ribbon or sheet (Fig. 135,*1*). There is rarely much development of mesogloea in the zooid walls, which lack solenial tubes and consequently do not produce daughter polyps. Most members of the Stolonifera follow this plan. In *Tubipora,* however, the spicules of the polyp walls fuse together inseparably and the numerous polyps, bound together by transverse, platform-like secondary stolons, eventually produce colonies of considerable mass. As the polyps ascend, they partition off the lower ends of their rigid tubes by double tabulae, consisting of a funnel-like lower part and an upper, lenticular cap, placed on a level with transverse platforms. The tubes are not filled in below and, for a time at least, living tissue remains within them. New polyps arise from the basal stolon and from the horizontal platforms (Fig. 135,*2*). In the Telestacea, in which the body walls of the polyps have become permeated by solenial tubes, new polyps may arise from the walls of older individuals, thus producing arborescent colonies of moderate size. The sequence of budding seems to be quite constant and forms the basis for separation of the several genera and species comprising the order. A schema of the ramification as seen in *Telesto* is given in Fig. 135,*3*, and the variation displayed by other genera is shown in Fig. 137, *1a,3a,4a*. In the order Alcyonacea, the mesogloea of the polyp walls has developed into a common colonial coenenchyme, in which the endoderm-lined gastric cavities of the polyps are imbedded, and through which ramifies a complex network of solenial tubes from which new polyps arise (Fig. 135,*4*). In certain families, the mesogloea separating the long, closely fascicled primary gastric cavities is more or less reduced and may contain few or no spicules. The resultant colonies are arborescent and, in some cases, closely approximate the appearance of gorgonaceans. In the latter order, however, the gastric cavities of all polyps are uniformly short. In the suborder Scleraxonia, they penetrate the branches only as deep as the medullar zone, into which a few gastrodermal canals may extend. In the Holaxonia, the medullar zone is not a densely spicular coenenchyme but instead a horny axis cylinder (with more or less calcareous matter) into which, of course, no solenia can penetrate (Fig. 135,*6*). In these forms, the cortical coenenchyme, now better termed rind, is comparatively thin and the colonies are usually much branched and arborescent in appearance. In some Scleraxonia, the medullar zone becomes thoroughly consolidated through fusion of the included spicules, and a distinct axis results. These always can be distinguished from the axes of holaxonians by their spicular structure, which is clearly revealed in thin section. In both Scleraxonia and Holaxonia the axis may be either continuous or divided into horny nodes and calcareous internodes. The horny nodes of

© 2009 University of Kansas Paleontological Institute

the articulate scleraxonians invariably contain numerous spicules imbedded in a spongy matrix of gorgonin, whereas those of the holaxonians are pure, translucent gorgonin.

The axis in all Holaxonia is made up of a basic **central chord** (Fig. 134) laid down at the growing branch tips by an axis epithelium, and a secondary cortical layer deposited around the central chord everywhere below the growing tip by an axis epithelium of a different character, which continues to increase the girth of the axis as long as the colony grows. The secondary thickening of the axis appears to be accomplished in 2 distinctly different ways. In the first, the secondary axis epithelium produces scales or fusiform bundles of horny gorgonin more or less completely permeated by calcareous matter, which are closely imbricated or otherwise tightly bound together in roughly concentric layers. In the second, the epithelium deposits columns, irregular prisms or rays of chiefly calcareous material radiating outward from the central chord. Each of the radial elements appears to be the work of a group of epithelial axoblasts acting as a unit.

These axial features, readily demonstrable in thin sections under polarized light, because of the orientation of the component calcareous fibers, may prove to be of diagnostic value for fossil material. The actual relationships of many gorgonacean fossils reported from the Cretaceous upward may well be clarified by a re-examination of their basic axis structure.

The members of 2 orders stand clearly apart from other octocorals in the structure of their colonies. These are the blue coral (Coenothecalia), which lacks spicules entirely but produces a massive calcareous skeleton similar to those of some hydrozoans; and the sea pens (Pennatulacea), which have evolved a highly specialized type of colony symmetrically developed around a long primary polyp which usually contains a supporting axial rod.

In the Coenothecalia the gastric cavities of the spiculeless polyps occupy the upper ends of tabulate tubes in a massive fibrocrystalline coenosteum. The tubes of the polyps are separated by numerous narrower tubes, also tabulate, occupied by caeca of the solenial system, which extend downward from the surface network.

In the Pennatulacea, the autozooids are symmetrically arranged around the primary oözooid, from whose walls they have budded, with radial orientation, in some, and bilateral in others. In the second instance they may be situated in longitudinal, oblique or transverse rows, and may be partly or wholly united into broad polyp leaves. The axial rod, which lies between the 4 longitudinal canals of the stalk and rhachis, is calcified in a radial pattern similar to that described above for certain holaxonian families.

MORPHOLOGICAL TERMS APPLIED TO OCTOCORALLIA

Many of the terms used in describing the morphological and anatomical features of octocorals are the same as those applied to other Anthozoa and to coelenterates in general. Among terms more closely associated with the Octocorallia some are derived from similarities with everyday objects, being thus readily understandable, but a few border on the ridiculous, especially when translated from one language to another.

GLOSSARY OF MORPHOLOGICAL TERMS

anthocodia. Upper, tentacular part of polyp which in many cases can be retracted within the rind or calycular structure (Fig. 134).

anthostele. Lower, thickened part of polyp's body wall into which the anthocodia may be withdrawn, commonly stiffened by spicules; may be equivalent to calyx.

asulcal. Side of polyp opposite siphonoglyph.

autozooid. Polyp with 8 well-developed tentacles and septa; only kind of polyp in monomorphic species and major type in dimorphic species.

axis. Central supporting structure of Gorgonacea and Pennatulacea; in the former, it may be spicular, consolidated or unconsolidated, or horny, with more or less nonspicular calcareous matter.

axis epithelium. Layer of cells derived from ectoderm that produces the axis of Holaxonia.

axoblast. Individual scleroblast of the axis epithelium.

balloon club. *See* spicule.

bark. Rind of holaxonian Gorgonacea.

bracket. *See* spicule.

buccal scale. *See* spicule.

calyx. Wartlike projecting anthostele (Fig. 134).

© 2009 University of Kansas Paleontological Institute

capstan. *See* spicule.

cell string. Nonlumenate strand of cells meandering through coenenchyme.

club. *See* spicule.

cnidoblast. Cell that produces nematocyst.

coenenchyme. Colonial spiculiferous mesogloea.

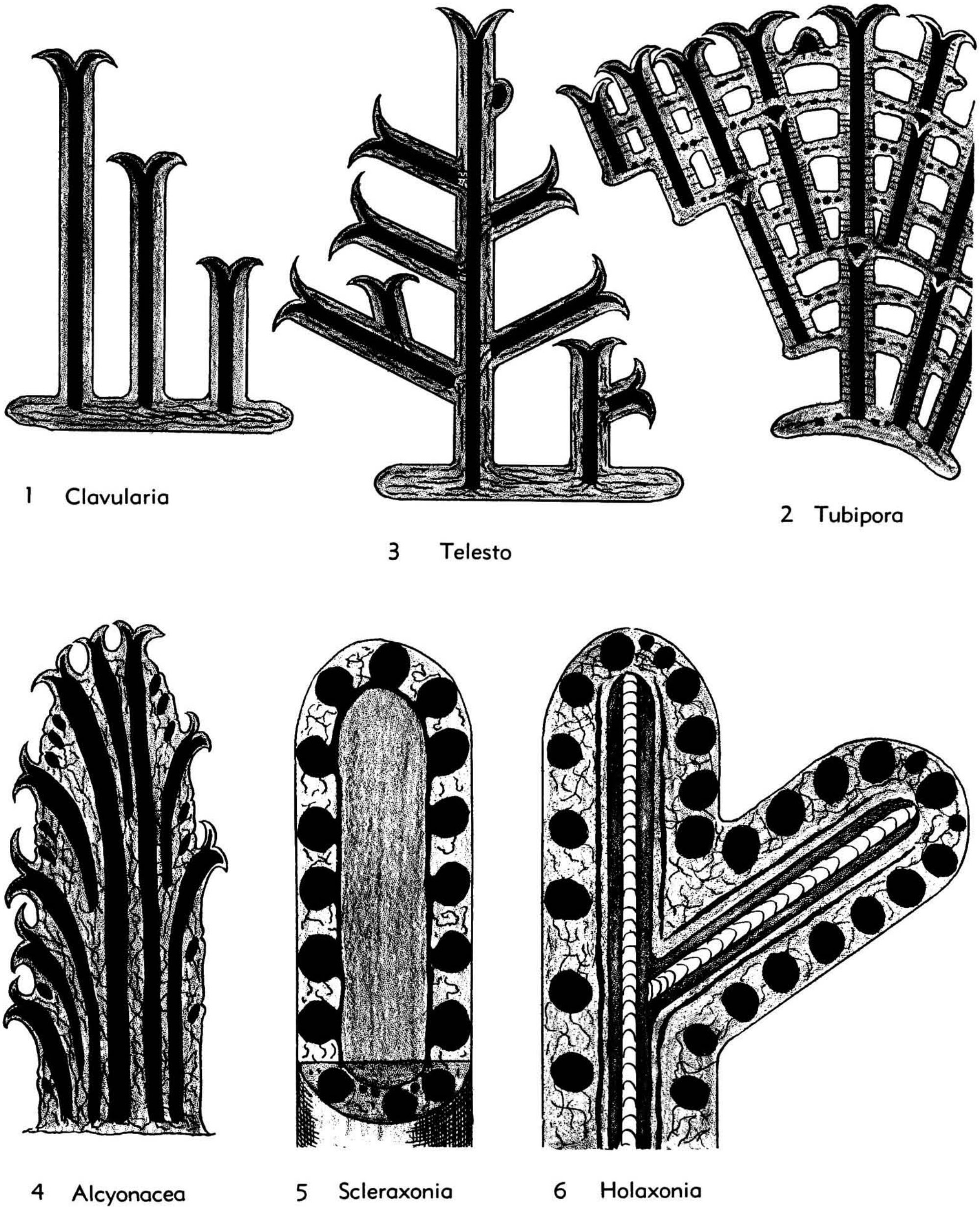
collaret. Transverse, subtentacular ring of spicules (Fig. 134).

cortex. Outer coenenchymal layer of gorgonaceans, especially Scleraxonia; outer, horny layer of holaxonian axis, as opposed to its medulla (central chord or core) (Fig. 134).

crown and points. Transverse collaret with superposed opercular rays.

disc spindle. *See* spicule.

double club. *See* spicule.



1 Clavularia

3 Telesto

2 Tubipora

4 Alcyonacea

5 Scleraxonia

6 Holaxonia

Fig. 135. Colony formation in Octocorallia (26n).

© 2009 University of Kansas Paleontological Institute

double wheel. *See* spicule.

filament. Thickened, convoluted edge of septum (mesentery); in Octocorallia, filaments of 2 septa opposite siphonoglyph are very long and heavily flagellated, whereas those of remaining 6 are shorter and glandular (Fig. 134).

gastrovascular cavity. Interior space of polyp radially partitioned by septa.

infrabasal scale. *See* spicule.

leaf club. *See* spicule.

loculus. Crescentic or lenticular calcified area or fiber-filled space in holaxonian axis (especially Plexauridae).

medulla. Central zone of scleraxonian stem; rarely, central chord of holaxonian axis.

mesentery. Soft septum.

mesogloea. Jelly-like substance separating the 2 cellular epithelial layers of coelenterates.

nematocyst. "Stinging cell" or "thread cell" formed within cnidoblasts.

operculum. Anthocodial spicular apparatus that more or less closes calyx or protects tentacles in contraction.

oral disc. Distal integument of polyp surrounding mouth, enclosed by ring of tentacles, forms roof over gastrovascular cavity.

pharynx. Tubular passageway between mouth and gastrovascular cavity.

pinnule. Digitate lateral branch of tentacle of octocoral polyps (Fig. 134).

plate. *See* spicule.

polyp. Individual of octocorallian colony (see autozooid).

polyp leaf. United proximal part of adjacent polyps that produces a leaflike expansion, from margin of which anthocodiae project; found in several genera of Pennatulacea and Ainigmaptilidae.

polypary. Colony as a whole.

pseudosepta. Spinelike or toothlike skeletal projections in calicles of Coenothecalia; bear no constant relationship with soft septa of polyps.

radiate. *See* spicule.

rind. Outer, spiculiferous coenenchyme of Holaxonia (Fig. 134).

scale. *See* spicule.

scaphoid. *See* spicule.

sclerite. Calcareous skeletal element of mesogloea, irrespective of form.

scleroblasts. Ectodermal cells of mesogloea that produce calcareous spicules.

septum. Thin radial noncalcareous partition (composed of soft tissue) dividing gastrovascular cavity of polyp (*see* mesentery).

siphonoglyph. Strongly ciliated groove extending down one side of pharynx (Fig. 134).

siphonozooid. Polyp with reduced tentacles or none, and commonly reduced septal filaments; usually much smaller than autozooids.

solenium. Canal lined with gastrodermis penetrating coenenchyme and interconnecting gastric cavities of the polyps (Fig. 134).

spicule. Calcareous skeletal element of mesogloea, irrespective of form; properly, a long, sharp sclerite. Specialized forms include:

balloon club. Spicule with practically smooth, spheroidal head (characteristic of *Eunicella*).

bracket. Same as scaphoid.

buccal scale. Thin flat plate just proximal to operculars (Calyptrophorinae).

capstan. Monaxial rod with 2 whorls of tubercles and terminal tufts.

club. Spicule enlarged at one end, may be strongly sculptured.

disc spindle. Derivative of capstan, with tubercles of 2 whorls fused into discs or wheels.

double club. Bispheroidal, 2-handled sclerite (*Corallium*).

double wheel. Disc spnidle.

infrabasal scale. In primnoids, sclerite situated between basal body scales and scales of rind.

leaf club. Spicule with head ornamented by foliate processes.

plate. Flat sclerite too thick to be called scale.

radiate. Sclerite with processes radiating in one plane (stellate), or in various planes in a more or less symmetrical order.

scale. Thin, flat or nearly flat sclerite.

scaphoid. Spindle more or less distinctly bent in form of a "C" and with warts of convex side reduced.

spindle. Straight or nearly straight monaxial spicule pointed at both ends.

thorn club. Clublike sclerite with processes of head sharp and spiny.

thorn scale. Tabular sclerite with central or marginal projecting process.

torch. Club with foliate processes of head strongly laciniate, resembling burning torch.

wart club. Clublike sclerite with only low, blunt protuberances ornamenting the head.

spindle. *See* spicule.

stolon. Creeping basal expansion, ribbon-like or membranous, from which polyps of Stolonifera and Telestacea arise.

sulcal. Side of polyp nearest siphonoglyph.

sulcus. *See* siphonoglyph.

supporting bundle. Sheaf of supporting spicules below anthocodia of nephthyid polyp.

thorn club. *See* spicule.

thorn scale. *See* spicule.

torch. *See* spicule.

verruca. Calyx; tubercle of sclerite.

wart club. *See* spicule.

zooid. In more recent literature in English, any individual of colony, irrespective of its morphological specializations, thus =polyp; in most German works, =siphonozooid.

© 2009 University of Kansas Paleontological Institute

BIOLOGY

NUTRITION

Many octocorals are largely holozoic in their nutrition, capturing small, planktonic organisms in large numbers. Small crustaceans and larval mollusks are frequently observed in the gastrovascular cavities of their polyps. The common purple or yellow sea whip, *Leptogorgia viminalis* (Pallas), of the southeastern coast of the United States, is often found to contain large numbers of lamellibranch larvae; where this gorgonian is common, as from Chesapeake Bay to northwest Florida, it must be able to decimate the populations of larval bivalves that pass among its branches.

On the other hand, a number of other octocorals, notably some Xeniidae and a species of *Clavularia,* have been found to live perfectly well without ever ingesting food; these species contain vast numbers of symbiotic algae, the zooxanthellae, in their gastrodermal layers. They thrive in the presence of adequate sunlight, even in filtered water. In the dark, however, they soon necrose and die, even if amply provided with food, which they seem completely unable to ingest (8). These species with abundant zooxanthellae in their tissues furthermore may have very few nematocysts (in some species I have found none at all) and greatly reduced digestive structures. Conversely, abundant nematocysts and well-developed digestive tissues are usually correlated with a small number or complete absence of zooxanthellae. Evidence as to whether the corals actually digest their zooxanthellae as food is inconclusive, but, in some at least, a sort of reciprocal interchange system has developed and the algae are not eaten. In these, the coelenterates seem able to utilize directly the photosynthetic products that the algae elaborate in excess of their own nutritional requirements, and the algae make use of some of the metabolic byproducts of the animal.

REPRODUCTION

Ordinarily it is the autozooids that are fertile, and the sexes are separate; but in some groups the siphonozooids contain the reproductive tissues, and in some, protogyny is usual.

The reproductive cells, which are derived from the endoderm, develop on the edges of the 6 septa away from the siphonoglyph, where they form conspicuous swellings. Ripe eggs commonly are connected to the septal edge only by a narrow stalk, and are covered by a layer of gastrodermis. The sex products may be discharged into the water, where fertilization and subsequent development take place, or the eggs may be retained after fertilization until late in the planula stage. There is no vestige of a medusoid generation.

ECOLOGY AND DISTRIBUTION

The Octocorallia are widely distributed organisms that occupy a great variety of ecological situations. Nevertheless, there are certain conditions, such as desiccation, heavy sedimentation, and reduced salinity, that they rarely tolerate to any extent. Some species, of course, are able to endure such conditions more or less regularly: the Alcyonacea of tropical Pacific reefs may be regularly exposed by the tides, and the common Atlantic *Leptogorgia viminalis* inhabits inshore waters that may be both muddy and brackish. As a rule, however, most species live below the low-tide mark, where they are safe from desiccation, occurring in clean water with a minimum of constant sedimentation. They extend around the world from Arctic to Antarctic, from the low-tide mark to the abysses. Most species are found on the continental shelf and slope, but a few descend to great depths. The deepest record for the subclass belongs to a pennatulacean, *Umbellula leptocaulis* Kölliker, which has been taken at 2,440 fathoms (4,440 m.). The isidid gorgonian, *Keratoisis profunda* (Wright), claims the deepest record for its order, at 2,300 fathoms (4,200 m.); and species of *Corallium* have been collected from depths down to 2,200 fathoms (4,000 m.) in the Atlantic and 1,314 fathoms (2,400 m.) in the Pacific.

Of the 7 orders, members of only one, the Pennatulacea, are regularly adapted for existence on a soft substrate. They have a

© 2009 University of Kansas Paleontological Institute

stalk, the lower end of which is dilatable, serving to anchor the colony in mud or sand. All other octocorals are typically fixed by a basal attachment to some solid object, although a few species have developed alternative adaptations for holding the colony in place. Notably, some alcyonaceans enclose a lump of mud in a basal expansion, and others produce rootlike, fleshy rhizoids, both effective solutions to the problem of fixation. The Telestidae characteristically form colonies that arise from creeping stolons, but individuals of certain species are able to live unattached on sandy bottoms. Associated with them are found gorgoniids and ellisellids that have made the same adjustment to their habitat. Other holaxonian gorgonaceans, for example certain genera of Isididae, have become adapted to a soft substrate by development of rootlike, calcareous processes in place of the usual incrusting, membranous attachment. Many Chrysogorgiidae and a few Primnoidae likewise can do so, or can attach by the conventional means to solid objects, as circumstances require.

The extent to which octocorals contribute to the formation of reef limestone is not known, but it is certain that they are prolific producers of calcium carbonate. At the Dry Tortugas, the spicule content of living colonies on the reef was estimated to average 5.38 tons per acre; with about 1/5 of the population being destroyed annually (based on a 5-year period), about one ton of calcareous material was made available per acre per year (5). Since this material is in the form of minute spicules, easily transported by currents or dissolved, probably no very high percentage of it actually becomes incorporated into the reef mass. On many tropical Pacific reefs the situation is much different. There, the luxuriant growth of gorgonaceans so characteristic of Caribbean reefs is greatly reduced and in most places completely lacking. The predominant octocorals of the reefs are massive alcyonaceans, which, having an even more densely spicular coenenchyme than the West Indian gorgonaceans, may actually become consolidated with the reef while the upper parts of the colonies are still living (6). No estimates have been made of the calcium carbonate production by the alcyonacean populations of these reefs, but it seems obvious that a higher percentage of it would actually be incorporated into the reef rock even though growth rate and productivity might be substantially lower. Some reefs in the tropical Pacific support a heavy growth of the blue coral, *Heliopora,* which can be a locally significant reef former.

SYMBIONTS AND COMMENSALS

As a result of their sedentary nature, octocorals have fallen victim to a considerable array of epizoic hangers-on, and a number of commensal, symbiotic and parasitic relationships have developed. Some of these associations are distinctly beneficial to the coral host, but most are not obviously so. How many of them are detrimental is difficult to say. The host can be killed, as usually happens when a colony of *Millepora* obtains a foothold on the accidentally exposed axis of a gorgonian. The hydrozoan by its rapid growth speedily pushes the living gorgonian substance farther and farther back until it occupies the entire axis and the gorgonian dies. Such occurrences are entirely fortuitous, however, depending upon the chance contact of a millepore larva in a settling mood with a suitably denuded axis. At any other time, the larva would continue on its way; at any other place on the gorgonian it might be captured and eaten, or at least prevented from settling. The millepore is not dependent upon the octocoral for support; it can form its colony independently elsewhere. In many other cases, however, the dependent partner indeed cannot live elsewhere. A complicated relationship has developed, as in the case of the ovulid gastropods, which seem completely dependent upon their alcyonarian hosts. The exact nature of this dependence is not known; the mollusk may feed directly upon the polyps without ever devouring enough of them to damage the colony, or it may only browse upon foreign materials that collect on the coral colony. In any event, alcyonarians infested with ovulid snails never seem to be unhealthy or damaged in any way. Another interesting mollusk-octocoral relationship is that between *Rapa* and *Sinularia.* The gastropods live imbedded deep in the fleshy tissue of the octocoral, with no direct means of communication with the outside; water

© 2009 University of Kansas Paleontological Institute

currents maintained by the polyps apparently suffice for their respiration, and their nutrition is probably derived in some way from host tissues.

Most, if not all, alcyonarian corals are infested with copepods of the peculiar family Lamippidae. In some cases, the commensals live in the gastrovascular cavities of the individual polyps, but in a great many others they inhabit the colonial gastrodermal canal system, which may be enlarged locally to accommodate them. Most of these copepods have degenerated into small, grublike creatures as a result of their confined habitat. Even more peculiar are the copepods apparently related to *Ophioika,* which have been found in the polyps of *Paramuricea* in the north Atlantic and of *Paracis* in the central Pacific. These are so modified as to bear little resemblance to conventional copepods. Some pycnogonids spend their youth in the polyps of *Chrysogorgia,* but details of their life history are unknown (22). These various arthropods betray their presence in the host only by localized galls or swellings, or by enlargement of individual polyps. Annelid commensals, however, frequently induce more conspicuous external modifications upon their hosts. They cause the polyps of primnoids to enlarge their lateral scales to form archways along the branches, in which the worms live. The polyps of acanthogorgiids, which have only slender fusiform sclerites, respond by sending out fleshy lobes that meet to form similar tunnels along the branches. In octocorals without projecting polyps, polychaetes may inhabit deep grooves in the coenenchyme, and in a few other species they live in the gastrodermal canal system.

Since it is impractical to mention here, even briefly, all of the associations in which alcyonarians are involved, I give below a systematic list of the principal organisms that have been observed to take part in such associations, together with their host corals.

Associations of Octocorallia with Other Organisms

Algae. ZOOXANTHELLAE: widespread in octocorals of warm, shallow waters.

Protozoa. FORAMINIFERA: commonly borne by telestids and other octocorals with an outer cuticle.

Porifera. Sponges may envelop colonies of *Telesto, Anthothela, Parisis* and other octocorals, which seem not to suffer as a result.

Coelenterata. HYDROZOA: *Hydrichthella epigorgia* STECHOW on *Anthoplexaura dimorpha* KÜK., *Millepora* on various Gorgonacea. ANTHOZOA: *Sagartia acanellae* on *Acanella arbuscula, Palythoa* sp. on *Corallium inutile, Parerythropodium coralloides* on *Eunicella verrucosa.*

Ctenophora. *Tjalfiella* and other Platyctenea on various octocorals (11).

Platyhelminthes. A polyclad was found clinging to branches of *Paracis orientalis* dredged in the Marshall Islands.

Brachiopoda. Unidentified species on *Chrysogorgia* (13).

Echinodermata. CRINOIDEA: comatulids often found clinging to gorgonaceans. OPHIUROIDEA: gorgonocephalid *Astrophyton muricatum* living entwined in branches of shallow-water gorgonaceans, especially *Antillogorgia,* in West Indian region; other gorgonocephalids and trichasterids occasionally discovered on branches of deeper-water gorgonaceans as *Schizostella* on *Swiftia* and *Muricea* (W.Indies); *Asteroschema* on *Narella* (Hawaii) and *Nicella* (W.Indies), *Astrogomphus* on *Thesea* (W.Indies), and many others.

Annelida. POLYCHAETA: *Leucodore* (=*Polydora*) in corallum of *Heliopora;* Polynoidae especially frequent upon Primnoidae, but found also on octocorals of other families, as *Harmothoë* on *Arthrogorgia, Narella, Thouarella* and *Corallium; Polyeunoa* on *Acanthogorgia* and *Thouarella; Polynoë* on *Anthomastus, Corallium, Acanthogorgia, Stenella, Acanella, Isidella* and *Pennatula;* Syllidae of the genera *Haplosyllis* and *Typosyllis* recovered from gastrodermal canals of every specimen examined of *Anthogorgia* (Indo-Pac.) and *Acanthacis* (W.Indies) (*fide* M. H. PETTIBONE).

Arthropoda. PYCNOGONIDA: *Ascorhynchus* sp. in polyps of *Chrysogorgia papillosa* (22). COPEPODA: Lamippidae in polyps and in gastrodermal canals of many octocorals; *Ophioika*-like forms in the gastrovascular cavities of *Paramuricea* (Atl.) and *Paracis* (Pac.). CIRRIPEDIA: lepadomorph barnacles sometimes found clinging to gorgonaceans; verrucomorph species observed on Telestidae; balanomorphs commonly forming galls on branches of gorgoniids or imbedding themselves in fleshy forms; Ascothoracica not uncommon on branches of Chrysogorgiidae. ISOPODA: Sphaeromidae found on rind of plexaurids and gorgoniids in W.Indies and Panama; Arcturidae on *Primnoella* in Antarctic. AMPHIPODA: caprellids sometimes found clinging in large numbers to colonies of Gorgoniidae. DECAPODA: anomurans *Orthochela* on *Eugorgia* and *Uroptychus* on *Calyptrophora* and *Chrysogorgia.*

Mollusca. APLACOPHORA: Solenogasters taken from branches of gorgonian corals. GASTROPODA: essentially entire family Ovulidae commensal on Alcyon-

© 2009 University of Kansas Paleontological Institute

acea and Gorgonacea; in W.Indies *Cyphoma* common on *Antillogorgia* and *Plexaura,* and *Simnia* upon *Leptogorgia* and *Gorgonia;* coralliophilid snail *Rapa* living imbedded in *Sinularia* (*fide* A. B. BRONSON); small dorid nudibranch common on living *Heliopora.* CEPHALOPODA: eggs of *Sepia* occasionally found attached to *Paramuricea placomus.*

Chordata. PISCES: egg-cases of small sharks attached to branches of gorgonians (13).

METHODS OF STUDY

It is practically impossible to outline methods of study for fossil Octocorallia. Perhaps it may suffice to describe techniques applicable to Recent forms, in order to indicate methods of getting at pertinent characters. From this foundation the paleontologist may then be able to erect a system of procedure appropriate to the material that confronts him.

When one consults a key to the orders of Octocorallia, such as that in DEICHMANN's monograph (7), it immediately becomes obvious that general macroscopical characters are of considerable value: whether or not the colony is solidly attached to a firm surface or only stuck in a muddy sea floor, and the way its component polyps are distributed upon it; whether there is a horny axis or not; whether the colonies are arborescent, lobate, or creeping; whether the gastrovascular cavities of the polyps are long (reaching to base of the colony) or short; whether the polyps are simple or produce branchlike daughters from their side walls; and whether the polyps are of one or more kinds. Many such characters can be observed directly and require no special techniques; some require dissection of fresh material to reveal structures that probably never could be fossilized; and a few require microscopic examination, as, for instance, the distribution of horny material in the coenenchyme.

In modern gorgonaceans the average diameter of the final branches is a useful character, for it seems to remain reasonably constant regardless of the total size of the colony. Also, in the terminal region the canal system and spiculation are not so likely to have suffered modifications attendant upon secondary growth. Therefore it is usually desirable to base conclusions on a study of this area rather than of older parts. As might be expected, in view of this fact, a small specimen is fully as satisfactory for study as a large one, and a fragment may supply all the information necessary for determination. Sad to relate, the same happy state of affairs does not obtain among the sea pens, of which a young specimen can be treacherously misleading, nor among the nephthyid alcyonaceans, in which the variations that occur from base to apex of the colony are important.

Color is usually quite fast in the Octocorallia, and where it is also constant it provides a useful character. In a few species the characteristic life color is due to pigmentation of the soft tissues and fades almost immediately when a specimen is placed in preservative. The greenish, brown, or yellowish coloration of many tropical reef-dwelling species is due to intracellular symbiotic algae, the zooxanthellae and zoochlorellae. The neontologist thus finds color to be of inconsistent value; the paleontologist, however, may find the persistent skeletal coloration of such things as tubipores (red) and heliopores (blue) of some use in the analysis of tropical reef deposits.

Of the 7 orders, the members of 3 (Pennatulacea, Gorgonacea, Trachypsammiacea) produce substantial, fossilizable axial structures. Those of the pennatulids are slender and rodlike, being known to the paleontologist under the generic name *Graphularia.* The axes of sea pens, in general, are quite uniform throughout the group and, to judge by Recent material, it is in most cases completely impossible to distinguish between species or even higher categories on external axial characters alone.

The axial structures of Gorgonacea can often be identified to family or genus with reasonable certainty. The jointed ones, belonging to the Melitodidae, Parisididae and Isididae, are recognizable at once and can be distinguished from one another by means of thin sections which reveal the spicular or nonspicular nature of the calcareous joints. In the Holaxonia, the structure of the central chord or medulla and its rela-

© 2009 University of Kansas Paleontological Institute

tionship to the cortical layer, and the concentric distribution of horny and calcareous substances are significant and must be investigated by sections also. Polarized light may reveal features indistinct or invisible in ordinary illumination, such as the orientation of the calcareous fibers in both axis and spicules.

In general, the calcareous spicules form the most important single character in the determination of octocorals. In certain families (Chrysogorgiidae, Primnoidae), the arrangement of sclerites on the polyps is as important as the shape of the spicules themselves, and in these the zooidal armature must always be studied intact on the polyps, as well as disassociated. In several other families, the organization of the zooidal armature must be considered, but this is somewhat less important than form of the coenenchymal spicules. No specimen of fossil octocoral in which the original arrangement of spicules has been preserved is known to me.

The isolated spicules recovered from marine deposits are probably best handled in a routine fashion as micropaleontological specimens. In order to study the spicules of Recent specimens it is necessary to free them from surrounding tissues. Traditionally, this is done by boiling a small fragment of the colony in a strong solution of caustic soda or potash, which is a cumbersome, messy, and potentially dangerous method. Far more practical is the use of sodium hypochlorite solution, which is readily obtainable as a laundry bleach under several trade names, or as a pharmaceutical. In some places, the commercial solution is known as "antiformin," in others as "Javelle water." It is quick, safe, and simple to use; for routine spicule examinations it is merely necessary to place a fragment of the coral on a slide, drop a small amount of "clorox" on it with a medicine dropper, and wait for a few moments. The bubbles that form can be removed by adding some water and removing excess fluid with bibulous paper. The preparation may then be covered with a glass coverslip and is ready for study. Should it be desirable to make a permanent spicule mount, the sample may be processed in a small vial to facilitate the repeated washings required to remove all traces of reagents. An alcoholic (or distilled water) suspension of spicules is pipetted onto a clean slide and allowed to dry. Any neutral mounting medium may be used, but some of the synthetic resins are better than balsam, which has a refractive index close to that of the spicules themselves.

If one wants to observe the arrangement of opercular elements, it is necessary only to dissect out the anthocodial region and place it in dilute clorox, which will act more slowly. As the tissues are dissolved they swell and become transparent, thus separating and clearly revealing the opercular spicules. Of course, the soft tissue is destroyed completely before long, so the preparation should be watched carefully under a stereoscopic microscope. If it is desirable to keep the spicular arrangement intact for a longer period, the polyp may be placed in a dilute solution of potassium hydroxide for a short time and then removed to water, whereupon the soft tissues swell, separating the spicules, and become transparent, rendering the arrangement of spicules clearly visible. With skill and some practice, such a preparation can be washed, dehydrated, and permanently mounted in balsam.

CLASSIFICATION

HISTORICAL SUMMARY

The classification of the octocorals can be divided historically into three periods: (1) the herbalistic, from ARISTOTLE to LINNÉ, during most of which corals were thought of and classified as plants and referred to in erudite polynomials; (2) the Linnean, from the 10th Edition of the *Systema* to KÖLLIKER's *Icones,* during which it became accepted that corals of all kinds were animals and the Linnean system of nomenclature became established, making possible a crude expression of relationships; and (3) the modern, from KÖLLIKER's *Icones* to the present, during which the relationships of various groups were investigated and systems of classification drawn up by the use of modern methods.

Little need be said about the pre-Linnean, herbalistic period of coral classification, save

© 2009 University of Kansas Paleontological Institute

that it is probably as old as civilization itself and that the octocorals, along with other coelenterates, were universally thought of as plants. Black corals (the axes of Antipatharia and Gorgonacea), precious coral *(Corallium rubrum)*, and the jointed white coral *(Isis hippuris)* were known to the ancients, who valued them for their magical, medicinal, and decorative properties. HICKSON (1924, *Introduction to the Study of Recent Corals,* Univ. Manchester) gives an extensive history of the commerce in these corals.

Descriptions and illustrations were, for the most part, poor. The earliest (but not the worst) illustration of a gorgonian that I know of appears in GESNER's *De Rerum Fossilium, Lapidum et Gemmarum,* 1565. The best are probably those in KNORR's *Deliciae Naturae Selectae.* Although the value of the skeletal spicules in the classification of octocorals was not discovered until a hundred years later, these structures were first figured in JOHN ELLIS' *Essay on the Natural History of the Corallines,* 1755.

The principal difference between the classification of alcyonarian corals during the years immediately preceding the 10th edition of LINNÉ's *Systema* and that of the hundred years following it is found in the expression of natural relationships made possible by Linnean nomenclature.

In organizing the corals for his *Systema Naturae,* LINNÉ brought together most of the species previously described and arranged them in 6 genera: *Tubipora, Madrepora, Isis, Gorgonia, Alcyonium,* and *Pennatula.* PALLAS (1766) and ESPER (1788-1830) recognized the same genera, with minor shifting of species and addition of others. New genera were added in profusion by LAMARCK (1801, 1816), LAMOUROUX (1812, 1816), EHRENBERG (1834), VALENCIENNES (1855), and MILNE-EDWARDS & HAIME (1857). LAMARCK (1801) began expanding the classification, dividing his order of radiates *(polypes à rayons)* into sections, the 2nd of which included the octocorals, distributed between 2 subdivisions. There was no grouping into families, and it is not likely that LAMARCK thought of any category in a familial sense. LAMOUROUX grouped the genera first into families, later into orders that did not differ, except in name, from his original families. It was EHRENBERG (1828, 1834) who first really elaborated on the classification of zoophytes, creating orders, tribes, and families within a "circle" Anthozoa. Unfortunately, his scheme was marred by its artificial duality, being divided into orders "Phytocorallia" and "Zoocorallia" each with identical tribes (e.g., Octactinia). The families of zoocorallian tribes were distinct from those of the phytocorallian tribes; e.g., the families Isidea and Gorgonina were phytocorallian Octactinia, whereas the Xenina, Tubiporina, Alcyonina, and Pennatulina were zoocorallian Octactinia. Although EHRENBERG was the first to penetrate deeper than superficial appearances and to use the characters of the polyps themselves in devising his classification, his artificial subdivision rendered the resulting system untenable. Therefore, DANA, MILNE-EDWARDS, and other subsequent workers reunited the parts of the Octactinia into a single taxonomic unit variously called Zoophytaria (DE BLAINVILLE), Alcyonaria (DANA), and Octocorallia (HAECKEL).

VALENCIENNES (1855) was apparently the first to recognize the value of the calcareous spicules in the classification of alcyonarian corals, but he failed to put his observations into actual practice. His *Extrait d'une Monographie de la Famille des Gorgonidées* was only an incomplete outline and served little purpose in advancing knowledge of relationships in the group. Thus it fell to KÖLLIKER to substantiate the suggestions of VALENCIENNES and put the classification of octocorals on a sounder basis through the publication of his *Icones histiologicae.* Subsequently, VERRILL, SAVILLE-KENT, E. P. WRIGHT, and THÉOPHILE STUDER adopted and expanded the spicular system introduced by KÖLLIKER.

The arrangement of the families and orders of Octocorallia, essentially as we now know it, emerged from the work of A. E. VERRILL, with improvements by HICKSON, KÜKENTHAL, and others. This system, as emended by HICKSON (1930), is basically employed herein. It is admittedly not perfect, and a re-examination of specimens and re-evaluation of characters is certain to bring about many changes. I have already modified the families of Scleraxonia, largely in accord with VERSEVELDT's researches on the

© 2009 University of Kansas Paleontological Institute

anatomy of several genera, and recognize a 7th order, Trachypsammiacea Montanaro-Gallitelli, which is established herein.

PHYLOGENY

In his chapter on geographical distribution of the Gorgonacea, Kükenthal (13) presents a phylogenetic tree of the group based partly upon inferences from his systematic data. Although voluminous and valuable, these data contain erroneous elements, which led Kükenthal to some conclusions that I believe untenable. Moreover, he neglected to reckon fully with paleontological evidence that several groups of octocorals have persisted with very little change through an appreciable part of geological time, and with the consequent implication that many not readily fossilizable octocorals may have existed as long. The distribution of certain modern genera, especially in the tropical American region where we are reasonably sure of Cenozoic paleogeography, furnishes evidence supporting the same point.

Kükenthal's supposition that the 2 species of *Erythropodium* recognized by him, because of their discontinuous distributions in the Atlantic and Indo-Pacific, represent the stocks from which the Atlantic and Indo-Pacific groups of briareids developed independently is quite untenable because its basic premise, that *E. caribbaeorum* and *E. marquesarum* are congeneric, is fallacious. These membranous forms were united in a single genus by Kükenthal in spite of their obvious differences, whereas *Iciligorgia* of the Caribbean is kept separate from *Semperina* and *Solenocaulon* of the Indo-Pacific in spite of their obvious strong similarities. It seems quite clear that the origin of Atlantic and Pacific groups of Scleraxonia antedates the geographical discontinuity of those areas, and that the 2 groups have common elements.

Hickson (10) has discussed evolution of the Pennatulacea, concluding that the group is derived from an *Anthomastus*-like alcyonacean ancestor. This inference is supported by the peculiar alcyonacean known as *Bathyalcyon,* apparently related to *Anthomastus.* In this odd genus, the colony consists of a monstrous primary autozooid, corresponding to the primary oözooid of the Pennatulacea, with many siphonozooids budding from the solenial system of its thickened outer wall. Although *Bathyalcyon* is an attached form, insofar as known specimens go, its relative, *Anthomastus,* may be either permanently attached to a hard substrate or anchored in a soft bottom by fleshy processes of the lower stalk.

Other workers have derived the sea pens from *Telesto*-like colonies in which secondary autozooids originate from the solenial system of the body wall of the primary polyp. Whatever its origin, the Pennatulacea is certainly a highly specialized group of octocorals.

The interrelationship of the various orders and the origin of the subclass from other Anthozoa may never be fully understood. If the tabulate Coenothecalia have phylogenetic affinity with any of the ancient Tabulata, *Heliopora* is a survivor of a very old lineage. But we will probably never know if any of the older tabulates are octocorals, and the tabulate structure of *Heliopora* may simply represent an independent solution to problems attendant upon upward growth and thus have no phylogenetic significance.

It is pertinent to remark that phylogenetic assumptions must be based on tangible morphological facts, on careful interpretation of geographical distributions, and on paleontological evidence. We must attain a much wider knowledge in these fields before a realistic phylogeny of the Octocorallia can be synthesized. We may never be sure of their origin. A remark by Kükenthal on this subject is apt: "Der Ursprung der Alcyonarien ist in Dunkel gehüllt, und auch die Paläontologie vermag uns nichts darüber auszusagen."

SUPRAGENERIC TAXONOMIC DIVISIONS

The subclass Octocorallia is divided into 7 orders. Of these, one (Pennatulacea) is sharply differentiated from the remaining 5, which are less clearly distinguished one from the other. An examination of extensive material indicates that many genera, as usually regarded, are unrealistically deployed within the existing families, some of which also fail of proper definition. In consequence, I have redefined some families and established or re-established others, and re-

© 2009 University of Kansas Paleontological Institute

assigned certain genera, to arrive at a systematic structure useful not only for the collections of the U. S. National Museum but also in further phylogenetic studies on octocorals.

The suprageneric divisions of the Anthozoa Octocorallia, as recognized herein, are listed in the following tabulation, which also records the known geologic range of each. The numbers enclosed in parentheses indicate totals of described genera considered as valid.

Suprageneric Divisions of Octocorallia

- Stolonifera *(order)*, polyps arising from a membranous or bandlike creeping stolon, without lateral budding; spicules when present mostly slender, rather spinous spindles (5). *Cret.-Rec.*
  - Cornulariidae (1). *Rec.*
  - Clavulariidae (3). *Cret.-Rec.*
  - Tubiporidae (1). *Rec.*
- Telestacea *(order)*, polyps arising from stolons but producing daughter polyps by lateral budding from solenial system; spicules slender and spinous or blunt and tuberculate, inseparably fused together in some (4). *Rec.*
  - Telestidae (3). *Rec.*
  - Pseudocladochonidae (1). *Rec.*
- Alcyonacea *(order)*, polyps proximally imbedded in fleshy, spiculiferous mesogloea, primary individuals extending from base of colony to its top; secondary individuals also extremely elongate; monomorphic or dimorphic (38). *L.Jur.-Rec.*
  - Xeniidae (7). *Rec.*
  - Alcyoniidae (13). *Rec.*
  - Astrospiculariidae (1). *Rec.*
- Nephtheidae (8). *L.Jur.-Rec.*
  - Siphonogorgiidae (6). *Rec.*
  - Viguieriotidae (3). *Rec.*
- Trachypsammiacea *(order)*, polyps surrounded by calcified coenenchymal vesiculae in radiating rays and short, interlocking longitudinal rows, arising from a central longitudinal canal system (1). *Perm.*
  - Trachypsammiidae (1). *Perm.*
- Coenothecalia *(order)*, massive calcareous skeleton made up of dimorphic, tubular, tabulate corallites comprising large autopores with pseudosepta, and small "siphonopores" (4). *Cret.-Rec.*
  - Helioporidae (3). *Cret.-Rec.*
  - Ceratoporellidae (1). *Rec.*
- Gorgonacea *(order)*, colonies branched treelike, but in some flagelliform, membranous or lobate, the polyps having uniformly short gastrovascular cavities; spicules of diverse form, sculptured with warts or spines (116; 5). *Cret.-Rec.*
  - Scleraxonia *(suborder)*, branches consisting of an inner medullar zone composed of horny material and calcareous spicules which may be inseparably fused, and an outer cortical zone with all spicules free, the polyps being imbedded in this zone; monomorphic or dimorphic (26). *Cret.-Rec.*
    - Briareidae (2). *Rec.*
    - Anthothelidae (11). *Rec.*
      - Anthothelinae (1).
      - Semperininae (3).
      - Spongiodermatinae (7).
    - Subergorgiidae (1). *Rec.*
    - Paragorgiidae (2). *Rec.*
    - Coralliidae (2). *Cret.-Rec.*
    - Melithaeidae (6). *Tert.-Rec.*
    - Parisididae (2). *Tert.-Rec.*
  - Holaxonia *(suborder)*, branches consisting of an inner axis of horny material which may have in it much calcareous matter but no true spicules (except Keroeididae, which have a chambered medulla unlike Scleraxonia), and a fleshy cortical zone containing spicules and the polyp cavities (90; 5). *Cret.-Rec.*
    - Keroeididae (1). *Rec.*
    - Acanthogorgiidae (3). *Rec.*
    - Paramuriceidae (25). *Rec.*
    - Plexauridae (12). *Rec.*
    - Gorgoniidae (8). *Rec.*
    - Ellisellidae (6). *Cret.-Rec.*
    - Ifalukellidae (2). *Rec.*
    - Chrysogorgiidae (7). *Rec.*
      - Lepidogorgiinae (1).
      - Chrysogorgiinae (5).
      - Chalcogorgiinae (1).
    - Primnoidae (13; 5). *Cret.-Rec.*
      - Primnoeidinae (1). *Rec.*
      - Primnoinae (7;5). *Cret.-Rec.*
      - Calyptrophorinae (3). *Rec.*
      - Callozostrinae (2). *Rec.*
    - Ainigmaptilidae (1). *Rec.*
    - Isididae (12). *Cret.-Rec.*
      - Keratoisidinae (4). *Rec.*
      - Mopseinae (3). *Eoc.-Rec.*
      - Muricellisidinae (1). *Rec.*
      - Isidinae (2). *Cret.-Rec.*
      - Incertae sedis (2). *Cret.*
- Pennatulacea *(order)*, free-living colonies consisting of primary oözooid with barren lower part that acts as a stalk and anchor, and upper part which produces secondary individuals singly, in groups, or fused together into bilaterally arranged leaflike processes. Spicules mostly smooth rods, bars or needles, commonly 3-flanged, or small plates or discs. Axial rod usually present (41). *?Sil., Rec.*
  - Sessiliflorae *(suborder)* (23). *?Sil., Rec.*
    - Veretillidae (5). *Rec.*
    - Echinoptilidae (2). *Rec.*
    - Renillidae (2). *?Sil., Rec.*
    - Kophobelemnidae (3). *Rec.*

© 2009 University of Kansas Paleontological Institute

Anthoptilidae (1). *Rec.*
Funiculinidae (1). *Rec.*
Protoptilidae (3). *Rec.*
Stachyptilidae (1). *Rec.*
Scleroptilidae (2). *Rec.*
Chunellidae (2). *Rec.*
Umbellulidae (1). *Rec.*

Subselliflorae *(suborder)* (13). *Cret.-Rec.*
  Virgulariidae (7). *Cret.-Rec.*
    Virgulariinae (6). *Tert.-Rec.*
    Balticininae (1). *?U.Cret., Rec.*
  Pennatulidae (3). *Rec.*
  Pteroeididae (3). *Tert.-Rec.*
Suborder and family uncertain (5). *Sil.-Cret.*

SYSTEMATIC DESCRIPTIONS

Subclass OCTOCORALLIA Haeckel, 1866

[=Octactinia EHRENBERG, 1828; Zoophytaria DE BLAINVILLE, 1834; Alcyonaria DANA, 1846]. The name Octocorallia is used in preference to prior terms because the 1st, Octactinia, implies relationship with Actiniaria, and was also part of EHRENBERG'S unusual dual classification; the 2nd, Zoophytaria, a relict of the botanical associations of these corals, has diverse connotations undesirable in modern usage; and the 3rd, Alcyonaria, although widely used, has been employed for the order Alcyonacea as well as for the subclass as a whole and thus leads to confusion.

Sedentary, colonial Anthozoa with polyps invariably bearing 8 tentacles, almost invariably pinnate; and 8 complete septa (mesenteries); pharynx with one "ventral" siphonoglyph. Skeletal structures usually consisting of calcareous spicules; in many, an axis of more or less calcified, hornlike substance is also present which may be in the form of fused spicules; rarely a massive, fibrocrystalline corallum. *?Sil., Rec.*

Order STOLONIFERA Hickson, 1883

Colonies composed of tall or short, cylindrical or blunt-conical polyps springing from a basal stolon which creeps upon solid objects; stolon ribbon-like, a reticulum of flat bands, or a thin flat sheet. Distal, tentacular part of polyps usually retractile within the stiffened proximal part (anthostele); connecting tubes or platforms may join adjacent polyps. New individuals budded only from stolon or connecting platforms, never from body wall of fully developed polyps. Spicules, when present, are usually slender, spinose rods; stolons and polyps usually invested with a horny external cuticle, which in some forms is the only skeletal structure. Colonies usually not conspicuous, although some may attain considerable size. *Cret.-Rec.*

The value of the horny cuticle in establishing limits of this order needs to be more thoroughly explored. Such a formation occurs in the Telestacea as well as in the Stolonifera, but in neither group are its extent, origin, and formation fully understood. A study of the internal anatomy and histology of both groups may throw light on their proper relationships.

At present, the only features safely utilizable for discrimination are structure of the individual polyps, general character of the stolon, and details of spiculation.

In the Stolonifera the polyps commonly have a well-defined proximal zone stiffened by densely packed spicules, into which the oral part, tentacles and all, may be retracted. The polyps arise from the stolon, which may be a meandering ribbon adhering to the substrate, a complex network of such ribbons, or a membranous sheet, but in none is there much thickening of the mesogloea. The anthostelar tubes of adjacent polyps may be connected by transverse tubes or platforms, which can give rise to new polyps just as the stolon itself is able to do, but daughter polyps are never budded off from primary individuals.

The form of the calcareous spicules is an indispensable character in classification of most stoloniferans. When present, the spicules are almost exclusively long, slender, and sharply thorny; they do not intrude the lower part of the gastric cavities. The arrangement of sclerites in and below the tentacles may be of significance.

TERMIER & TERMIER (23) include the Paleozoic families Syringoporidae MILNE-EDWARDS & HAIME (*Syringopora* GOLDFUSS, 1826), Syringoalcyonidae TERMIER-T. (*Syringoalcyon* TERMIER-T., 1945), and Auloporidae NICHOLSON (*Aulopora* GOLDF., 1826; *Cladochonus* M'COY, 1847; *Ceratopora* GRABAU, 1899; *Vermipora* HALL, 1874) in the Stolonifera. The skeleton in these forms has not been established to be spicular in nature nor to resemble in structure the calcareous skeletons of Recent octocorals. Most paleontologists refer the forms mentioned to the Tabulata, whose relation-

© 2009 University of Kansas Paleontological Institute

ships are obscure and probably diverse. OKULITCH (20) considers the Syringoporidae, Halysitidae, and Favositidae to be possible Paleozoic alcyonarians.

Family CORNULARIIDAE Dana, 1846

Small stoloniferans with completely separate polyps and no spicules; a delicate, horny cuticle invests stolons and anthosteles. *Rec.*

Cornularia LAMARCK, 1816 [**Tubularia cornucopiae* PALLAS, 1766; SD M.EDW.-H., 1850]. *Rec.*, Medit.-IndoPac.

Family CLAVULARIIDAE Hickson, 1894

Stoloniferans with small to large tubular polyps, armed with spicules which are usually separate but may be inseparably fused, and commonly (?invariably) also a horny cuticle. Spicules generally in the form of spinose spindles arranged longitudinally in body walls and more or less branched sclerites in stolons; tentacles may have spicules like those of polyp body, or small discs, or none at all. *Cret.-Rec.*

Of the 14 genera which HICKSON (10) refers to this family, only 2 seem clearly referable to it; the others fall either as synonyms of these 2 or out of the family altogether.

Clavularia DE BLAINVILLE, 1830 [**C. viridis* QUOY & GAIMARD; SD M.EDW.-H., 1850]. Polyps simple, arising from bandlike or membranous stolons; spicules including simple spinous spindles, rods, or clubs, and a few double forms. *Rec.*, Indo-Pac.-Atl.——FIG. 136,*1*. **C. viridis*, IndoPac.; *1a*, spindles of body wall (26n); *1b*, discs from tentacles (26n); *1c*, group of polyps (34).

Epiphaxum LONSDALE, 1850 [**E. auloporoides*]. Axis attached throughout, formed of solid fibers; visceral cavities seated in the axis and provided with 8 dentations or blunt lamellae; investing layer unknown. Possibly precursor of *Sarcodictyon*. *Cret.*, Eng.

Sarcodictyon FORBES, 1847 [**S. catenatum*]. Stolons form anastomosing network; anthosteles low and conical; spicules solidly fused together. Anthocodial armature of 8 triangular fields of spindles. *Rec.*, NE.Atl.-C.Pac.

Family TUBIPORIDAE Ehrenberg, 1828

[*nom. correct.* DANA, 1846 (*pro* Tubiporina EHR., 1828)]

Polyps long, forming rigid tubes by solid fusion of sclerites, tubes perforate, partitioned by peculiar double tabulae having funnel-shaped lower and lenticular upper element, nearly parallel, closely placed, joined by transverse platforms containing solenia; new polyps arising from stolons or from platforms, not from walls of old polyps. *Rec.*

For the time being, this family must be taken to include only a single genus with one rather variable species. Its alliance with *Pachyclavularia* and *Hicksonia* (=*Clavularia*) requires verification.

Tubipora LINNÉ, 1758 [**T. musica*]. *Rec.*, Indo-Pac.——FIG. 136,*2*. **T. musica*, Rec., CarolineI.; *2a*, part of corallum; *2b*, free and partly fused spicules of anthocodiae; *2c*, minute pharyngeal sclerites; *2d*, tentacular sclerites (26n).

Order TELESTACEA Hickson, 1930

Erect, branching colonies arising from bandlike, reticulate or membranous stolons; primary polyp produces daughters from its body wall; sclerites numerous, free, or partially or entirely fused to form rigid tubes; lower part of gastrovascular cavities may be filled in with spiculiferous intrusion tissue. *Rec.*

This order is comprised of 2 families clearly distinguished by their methods of colony formation: (1) Telestidae, which produce colonies by monopodial branching that results from lateral budding of very long axial polyps; and (2) Pseudocladochonidae, with sympodial colonies resulting from lateral budding of successive orders of subordinate polyps all of equal length. The external grooving of the outer wall, anthocodial armature, and structure of the lower part of the zooids are characters of importance in classification. The nature and extent of the external cuticle and cuticular lining of the coelentera are yet to be investigated in detail.

The members of this order are distinguished from stoloniferans by production of daughter polyps from the body wall of the axial or primary polyp, and from alcyonaceans by the absence of thick, spiculiferous mesogloea between the polyps.

Apparently, no Telestacea have been detected in the fossil record, although the species with fused sclerites are surely sturdy enough to allow of preservation. The branching of the Recent *Pseudocladochonus*, which has rigid, though delicate, body tubes, is strikingly like that of the Paleozoic fossil

© 2009 University of Kansas Paleontological Institute

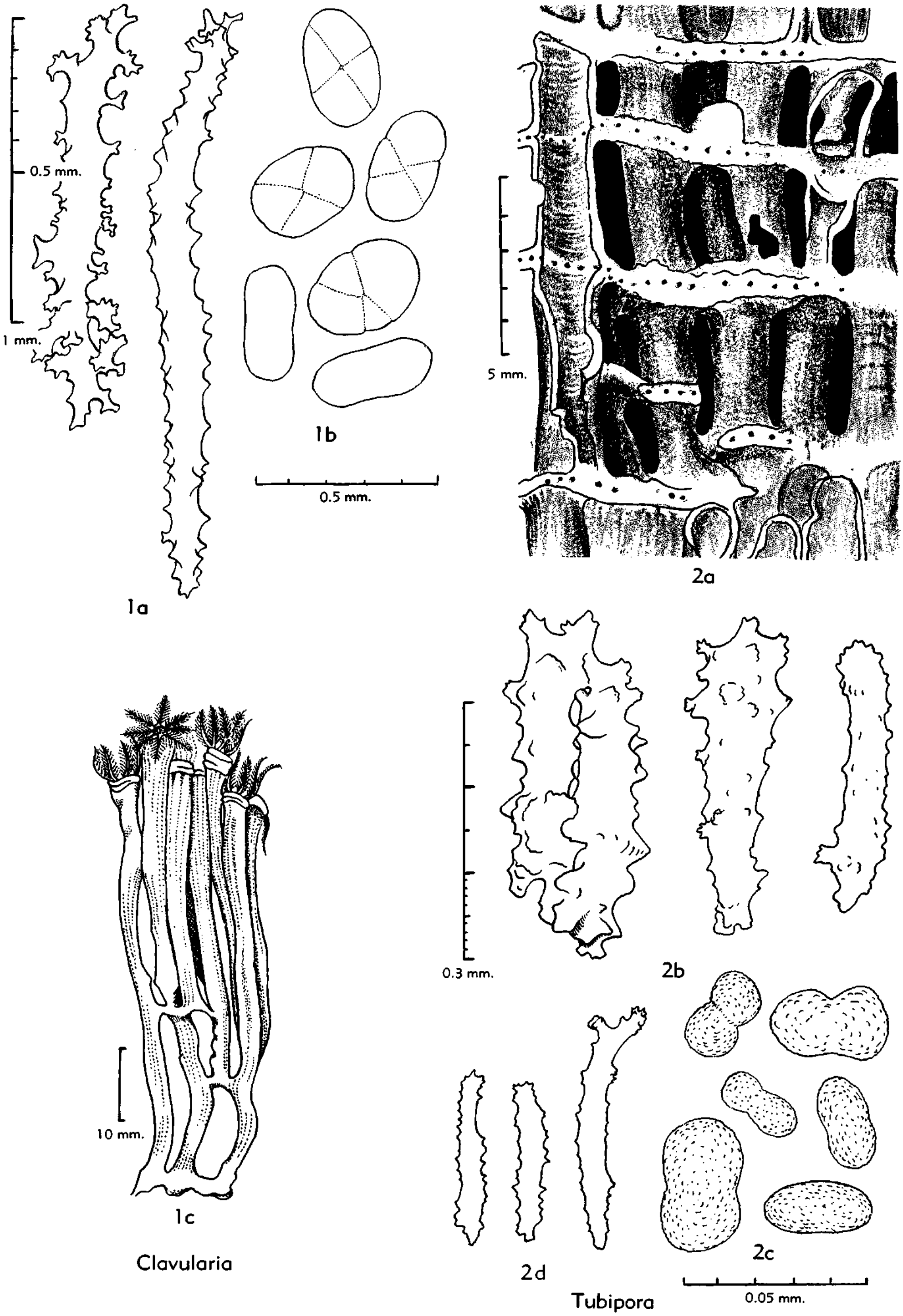


Fig. 136. Stolonifera (p. F184).

© 2009 University of Kansas Paleontological Institute

Cladochonus, but this feature seems to speak for homeomorphy rather than close phylogenetic relationship.

In modern seas, telestaceans occur widely from the low-tide line to 1,675 fathoms (3,180 m.).

Family TELESTIDAE Milne-Edwards & Haime, 1857

Colonies monopodial, with the primary polyp usually much taller than those of subordinate rank. *Rec.*

Telesto Lamouroux, 1812 [**T. aurantiaca;* SD M. Edw.-H., 1850]. Stolons reticulating or ribbonlike, producing tall axial polyps and shorter lateral polyps; lower parts of gastrovascular cavities not filled in with spiculiferous mesogloeal substance, and body walls not especially thickened. Sclerites long, spinose rods or blunt, coarsely tuberculate ovals, in some species fused solidly together, either in lower parts of polyps or throughout length of anthosteles. *Rec.,* Atl.-IndoPac.——Fig. 137,*2,5*. *T. sanguinea* Deichmann, Rec., Fla.; *2a,* small colony; *2b,* sclerites from body walls; *2c,* sclerites from anthocodiae; *5,* cross section of axial polyp near base, diagrammatic (26n).

Coelogorgia M.Edw.-H., 1857 [**C. palmosa*]. Colonies erect, arborescent, like *Telesto* but stolons not extensively developed, axial polyps very long and laterals very short; body wall of primary polyp greatly thickened by mesogloea perforated with solenia; gastrovascular cavities of axial polyps open to base, not filled in with spiculiferous intrusion tissue. Sclerites are tuberculate spindles and clubs. *Rec.,* Ind.O.——Fig. 137,*3,6*. **C. palmosa,* Rec., E.Afr.; *3a,* part of small colony; *3b,* spicules; *6,* cross section of axial polyp near base, diagrammatic (37).

Telestula Madsen, 1944 [**T. septentrionalis*]. Colonies like *Telesto* but smaller and less profusely branched; stolons bandlike; axial polyps long, sinuous, subordinates shorter; lower part of gastric cavities of both primary and secondary polyps filled in with spiculiferous intrusion tissue, leaving open only 8 canals. Sclerites of body wall usually blunt, coarsely tuberculate oval plates; those of intrusion tissue much-branched irregular forms more or less fused together. *Rec.,* Atl.-IndoPac.——Fig. 137, *1,7*. **T. septentrionalis,* Rec., Iceland; *1a,* small colony lacking secondary polyps (31); *1b,* spicules (31); *7,* cross section of polyp near base, diagrammatic (26n).

Family PSEUDOCLADOCHONIDAE Madsen, 1944

All polyps about equal in length, each giving rise near its distal end to one daughter at an acute angle (where branching occurs, 2 on opposite sides of parent polyp), thus forming zigzag, sympodial colonies; below point of origin of its daughter, each polyp is partially filled in with spiculiferous mesogloeal substance which leaves open 8 canals. *Rec.*

Pseudocladochonus Versluys, 1907 [**P. hicksoni*]. Spicules of body walls much branched, anastomosing, fused to form rigid but delicate tubes; spicules of mesogloeal intrusion tissue larger and less branched. *Rec.,* IndoPac.——Fig. 137,*4,8*. **P. hicksoni,* Rec., Japan; *4a,* part of a colony; *4b,* fused sclerites of body tube; *4c,* fused sclerites of intrusion tissue; *4d,* spicules from pinnules; *4e,* spicules from tentacle backs; *8,* cross section of polyp near base, diagrammatic (*4a-e,* 26n; *8,* 36).

Order ALCYONACEA Lamouroux, 1816

[*nom. transl.* Studer, 1887 (*ex* suborder Alyconacea Verrill, 1865; *nom. transl. et correct. ex* order Alcyoneae Lamx., 1816)] [Although the type genus of this order is *Alcyonium,* present rules do not require incorporation of the stem Alcyoni- in the ordinal name.]

Colonies thick and incrusting, lobate or erect and arborescent, consisting of very long polyps united in more or less extensively developed, usually spiculiferous coenenchyme. Primary polyps extend from base of the colony to the uppermost branches, secondary individuals arising from solenial system of primary polyp walls or of colonial coenenchyme. *L.Jur.-Rec.*

The development of colonial coenenchyme and the extremely long primary polyps distinguish this order from the Telestacea on the one hand and scleraxonian Gorgonacea on the other. The genera and species are recognizable only with difficulty in Recent material, and the indisputable determination of fossil material or isolated spicules seems beyond the realm of possibility.

The Alcyonacea embraces 6 families. In modern seas, representatives occur at all latitudes and in all depths from low tide to several hundred fathoms. Members of the family Alcyoniidae are the predominant reef-dwelling octocorals in the tropical Pacific, in contrast to the situation in the Atlantic, where gorgonaceans dominate the scene and no alcyonaceans at all are to be found in reef habitats. It is thus possible to assign virtually any large (up to 5 mm.), stout, spindle-shaped alcyonarian spicule

© 2009 University of Kansas Paleontological Institute

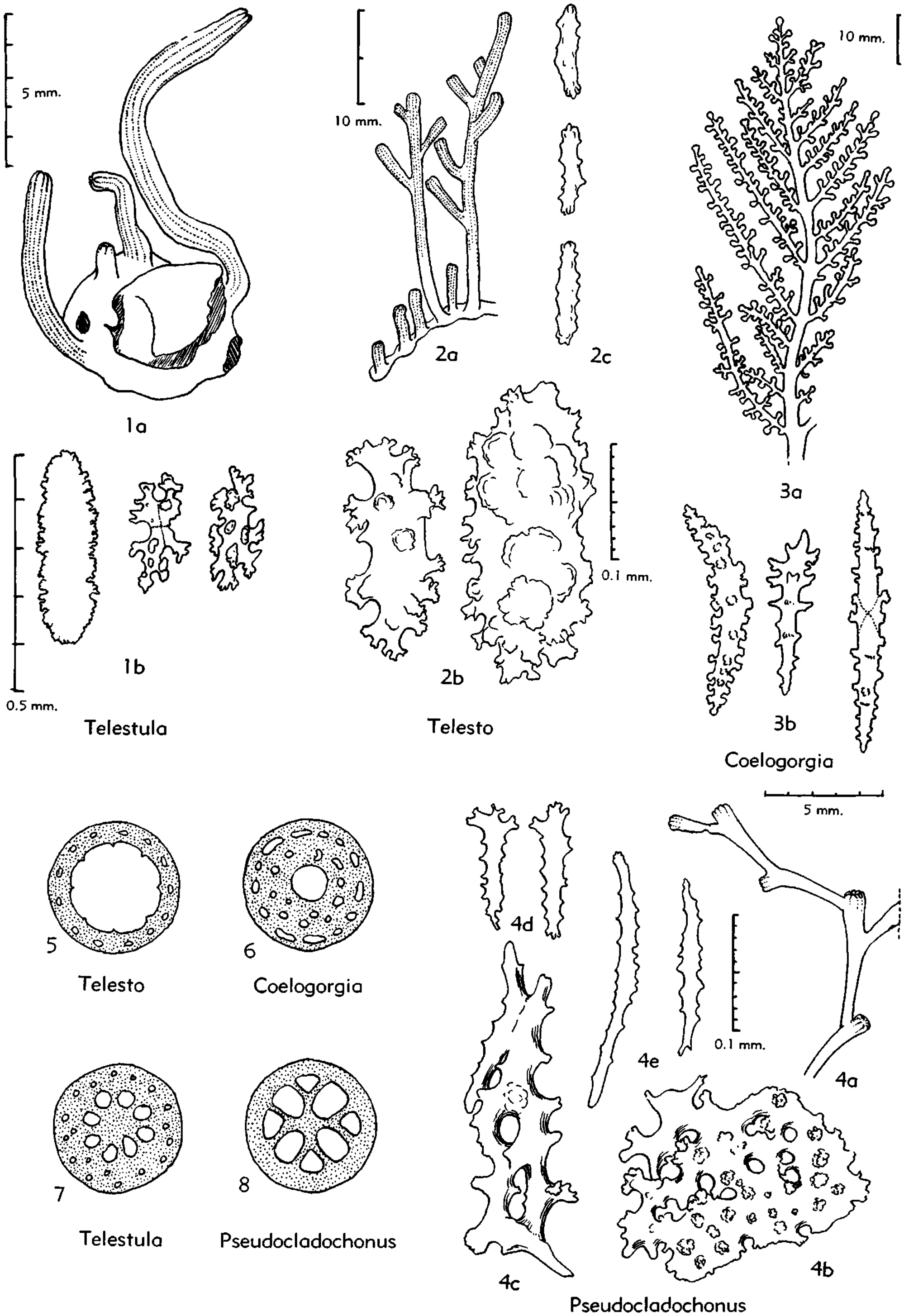


Fig. 137. Telestacea (p. F186).

© 2009 University of Kansas Paleontological Institute

from tropical Indo-Pacific reef sediments to the family Alcyoniidae.

Family ALCYONIIDAE Lamouroux, 1812

[*nom. correct.* May, 1899 (*pro* Alcyonidae Dana, 1846; *nom. correct. pro* family Alcyoneae Lamx., 1812)]

Fleshy or membranous Alcyonacea with mostly spindle-like spicules, some with clubs, crosses, and multiradiate spicules but none with small biscuit-like platelets exclusively. Mostly dimorphic. *Rec.*

A large proportion of the many described genera inevitably fall into synonymy. The following list is neither complete nor critical. The valid type designations have, in the main, never been determined; of those given here, only the monotypes, original designations, and a few subsequent designations should be considered final.

Alcyonium Linné, 1758 [**A. digitatum;* SD M. Edw.-H., 1850] [=*Lobularia* Lamarck, 1816]. *Rec.*, Atl.——Fig. 138,*4*. **A. digitatum*, Rec., N.Atl.; spicules (26n).

Acrophytum Hickson, 1900 [**A. claviger*]. *Rec.* S.Afr.

Anthomastus Verrill, 1878 [**A. grandiflorus*]. *Rec.*——Fig. 138,*1*. **A. grandiflorus; 1a,* spicule of inner stalk (26n); *1b,* surface spicules (26n); *1c,* colony (35).

Bathyalcyon Versluys, 1906 [**B. robustum*]. Single giant autozooid partially retractile within a colonial calyx containing numerous siphonozooids. Spicules similar to those of *Anthomastus*. *Rec.*, Pac.

Carotalcyon Utinomi, 1952 [**C. sagamianum*]. *Rec.*, Japan.

Cereopsida Strand, 1928 [*pro Cereopsis* Kent, 1870 (*non* Latham, 1801)] [**Cereopsis bocagii* Kent, 1870]. *Rec.*, E.Atl.

Lobophytum Marenzeller, 1886 [**L. crassum;* SD Moser, 1919]. *Rec.*, IndoPac.——Fig. 138,*6*. **L. crassum*, Marshall I.; spicule (26n).

Nidalia Gray, 1835 [**N. occidentalis*]. *Rec.*——Fig. 138,*5*. **N. occidentalis*, Rec., Fla.; *5a,* spicule in outline; *5b,* tip of same at higher magnification to show tubercles (26n).

Nidaliopsis Kükenthal, 1906 [**N. pygmaea*]. *Rec.*, W.Afr.

Sarcophyton Lesson, 1834 [**S. lobulatum;* SD M. Edw.-H., 1850]. *Rec.*, IndoPac.——Fig. 138,*2*. *S. trocheliophorum* Marenzeller, Marshall I.; *2a,* clubs of capitulum surface; *2b,* spindle of stalk (26n).

Sinularia May, 1898 [**S. brassica*]. *Rec.*, Indo-Pac.

Sphaerella Gray, 1869 [**Alcyonium tuberculosum* Quoy & Gaimard] [=*Lobularia* Ehrenberg (*non* Lamarck); *Cladiella* Gray; *Microspicularia* Macfayden] (4). *Rec.*, IndoPac.——Fig. 138,*3*. *S. krempfi* Hickson, Marshall I.; spicules (26n).

Family ASTROSPICULARIIDAE Utinomi, 1951

Fleshy, monomorphic Alcyonacea of bushy habit with sterile stalks and polypiferous terminal lobes, polyps of uniform size, tentacles without pinnules; armature of spicules continued from rind; coenenchyme fleshy, honeycombed with chambers containing several stellate spicules each; solenia penetrating mesogloea between spicule chambers.

Astrospicularia Utinomi, 1951 [**A. laurae*]. *Rec.*, Formosa.

Family NEPHTHEIDAE Gray, 1862

[*nom. correct.* Utinomi, 1954 (*pro* Nepthyadae Gray, 1862)]

Arborescent or lobular colonies with sterile stalks, polyps placed singly or in clusters at tips of ultimate branches. Spiculation usually dense but sparse in some; spicules strongly sculptured spindles, capstans and clubs, in some genera reaching a length of several mm. *L.Jur.-Rec.*

Nephthea Audouin, 1826 [**N. chabrolii;* SD M. Edw.-H., 1850]. *L.Jur.*(Eu.)-*Rec.* (RedSea-Indo-Pac.).

Dendronephthya Kükenthal, 1905 [**Nephthya savignyi* Ehrenberg, 1834; SD Utinomi, 1954]. *Rec.*, RedSea-IndoPac.

Eunephthya Verrill, 1869 [**Nephthya thyrsoidea* Verrill, 1865]. *Rec.*, N.Atl.-S.Afr.-Pac.

Gersemia Marenzeller, 1877 [=?*Eunephythya* Verrill, 1869 (*fide* Madsen, 1944)]

Lemnalia Gray, 1868 [**L. jukesii*]. *Rec.*, RedSea-IndoPac.

Litophyton Forskål, 1775 [**L. arboreum;* SD Kükenthal, 1903] [=*Ammothea* Lamarck, 1816]. *Rec.*, RedSea-IndoPac.

Neospongodes Kükenthal, 1903 [**N. atlantica;* SD Deichmann, 1936]. *Rec.*, W.Atl.

Stereonephthya Kükenthal, 1905 [**S. papyracea;* SD Utinomi, 1954]. *Rec.*, W.Pac.

Family SIPHONOGORGIIDAE Kölliker, 1874

Tall slender arborescent colonies, with polyps retractile into low calyces; coenenchyme separating long gastrovascular canals in stem is packed with spicules and forms rigid walls. *Rec.*

Siphonogorgia Kölliker, 1874 [**S. godeffroyi*]. *Rec.*, Indo-Pac.

Agaricoides Simpson, 1905 [**A. alcocki*]. *Rec.*, Ceylon.

Cactogorgia Simpson, 1907. *Rec.*, Ind.O.

Paranephthya Studer, 1887 [**P. capitulifera* Wright & Studer, 1889; SM Wright-S., 1889]. *Rec.*, Philip.

© 2009 University of Kansas Paleontological Institute

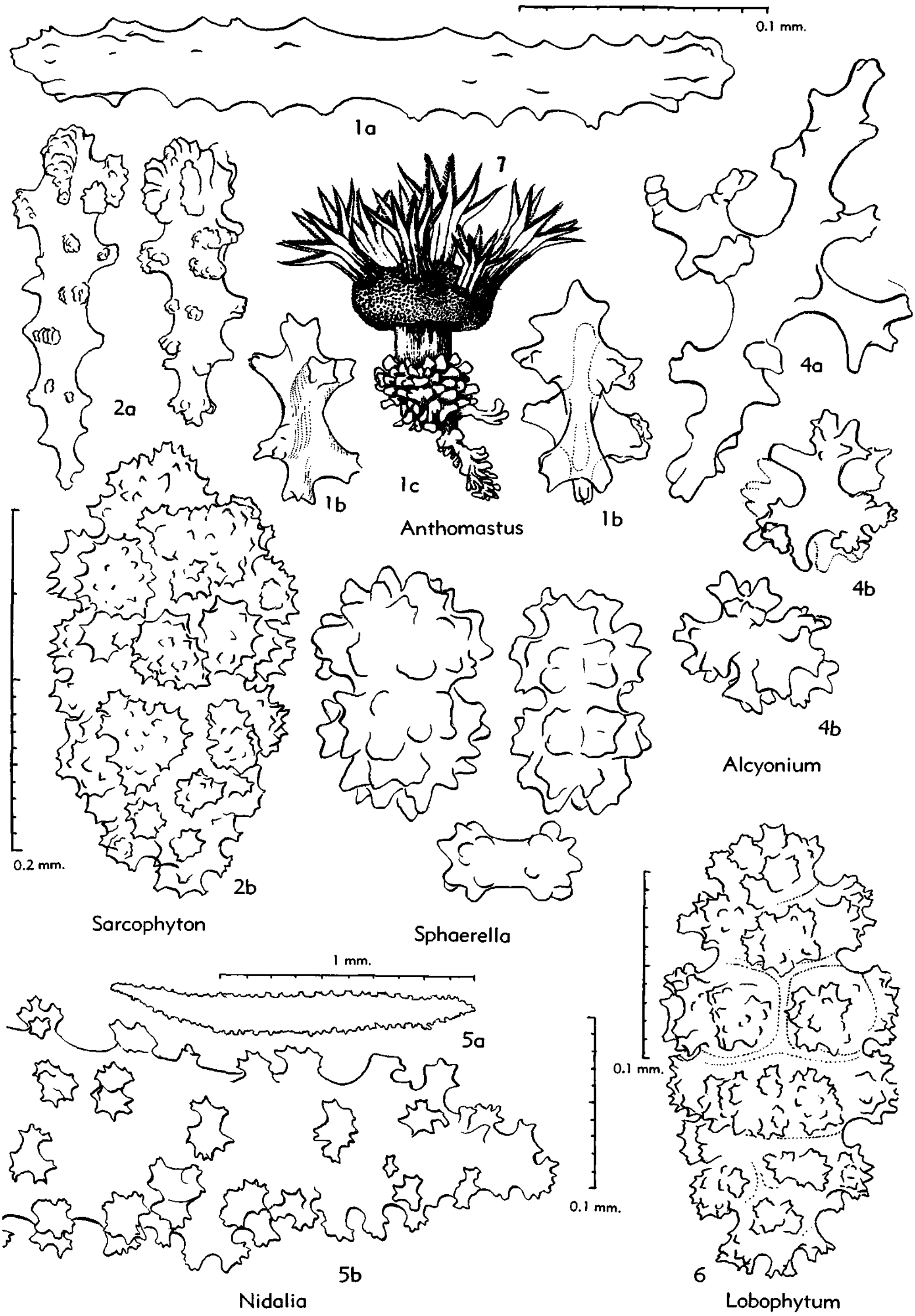


Fig. 138. Alcyonacea: Alcyoniidae (p. F188).

© 2009 University of Kansas Paleontological Institute

Scleronephthya Studer, 1887 [**S. pustulosa* Wright & Studer, 1889; SM Wright-S., 1889]. *Rec.*, Philip.

Stereacanthia Thomson & Henderson, 1906 [**S. indica*]. *Rec.*, AndamanI.

Family VIGUIERIOTIDAE Bayer, 1954

Alcyonacea with polyps united in groups, distally free and bearing lateral polyps, proximally fused into common trunk within which the upper free, finger-like processes may be retracted. Spicules in the form of spindles. *Rec.*

Viguieriotes Bayer, 1954 [*pro Fascicularia* Viguier, 1888 (*non* Lamarck, 1816; *nec* Lyell, 1839; *nec* Dybowski, 1873)] [**Fascicularia radicans* (=*Paralcyonium edwardsii* de Lacaze-Duthiers, 1888)]. *Rec.*, Algeria.

Paralcyonium M.Edw.-H., 1850 [**Alcyonidia elegans* M.Edw., 1835]. *Rec.*, Algeria.

Studeriotes Thomson & Simpson, 1909 [**Studeria mirabilis* Thomson, 1908]. *Rec.*, AndamanI.

Family XENIIDAE Ehrenberg, 1828

[*nom. correct.* May, 1899 (*pro* Xenidae Verrill, 1866, *pro* Xenina Ehr., 1828)]

Polyps soft, fleshy, nonretractile; sclerites minute, biscuit-shaped (8). Some authors have treated the family as a distinct order. *Rec.*

Xenia Lamarck, 1816 [**X. umbellata;* SD M.Edw.-H., 1850]. *Rec.*, RedSea-IndoPac.

Anthelia Lamarck, 1816 [**A. glauca*]. *Rec.*, Red Sea-IndoPac.

Ceratocaulon Jungersen, 1892 [**C. wandeli*]. *Rec.*, NorwegianSea-Antarct.

Cespitularia M.Edw.-H., 1850 [**Cornularia multipinnata* Quoy & Gaimard]. *Rec.*, IndoPac.

Efflatounaria Gohar, 1939 [**E. tottoni*]. *Rec.*, Austral.

Heteroxenia Kölliker, 1874 [**H. elisabethae*]. *Rec.*, RedSea-IndoPac.

Sympodium Ehrenberg, 1834 [**S. fuliginosum;* SD M.Edw.-H., 1850 (but see Gohar, 8)]. *Rec.*, RedSea-IndoPac.

TRACHYPSAMMIACEA

By Eugenia Montanaro-Gallitelli[1]

Order TRACHYPSAMMIACEA Montanaro-Gallitelli, nov.

Corallum dendroid, with medullar canal system which gives rise to new corallites; skeletal structures of cortical region oriented radially. *Perm.*

Family TRACHYPSAMMIIDAE Gerth, 1921

[*nom. correct.* Lecompte, 1952 (*pro* Trachypsammidae Gerth, 1921]

Characters of order. *Perm.*

Although the medullar system can in general be compared with that of the Octocorallia, identity of *Trachypsammia*[2] with known forms is not possible because of its combination of a central, medullar canal system, extramedullar, radial coenenchyme, and origin of new corallites from the central medullar canal.

The first description of this unique form was given by Gerth (1921), based upon specimens from the Upper Permian of Timor. He recognized its peculiarity and referred it to the Tabulata, near the Pachyporinae, albeit with some trepidation because of the structure of the extramedullary skeleton and the external sculpture, which he compared with the coenenchyme and sculpture of Tertiary and living Scleractinia of the families Oculinidae, Eupsammiidae, and Dendrophylliidae. Gerth admitted also the possibility that the trachypsammiids could be referred to the Octocorallia, according to some authors, closely related to the Tabulata.

The structure and systematic position of this fossil were discussed subsequently by Hehenwarter, who excluded any connection with the Pachyporidae, emphasized possible relationship with the Octocorallia as already suggested by Gerth, and related *Trachypsammia* to the Gorgonacea. Recent investigations by Montanaro-Gallitelli (16) on topotypes of the original species and on a new species, *T. mediterranea* Mont.-Gall., have permitted a revision of structural interpretations and an effort to verify the relationship with Octocorallia. An affinity with fossil colonial forms like *Thamnopora* is definitely and obviously ruled out.

Although the medullar system can be compared generally with that of the Octocorallia, identity of *Trachpysammia* with known forms is not possible because of its combination of a central medullar canal sys-

---

[1] Istituto di Geología e Paleontología, Università, Modena, Italia.

[2] Classed in Tabulata by Hill & Stumm (p. F469).

© 2009 University of Kansas Paleontological Institute

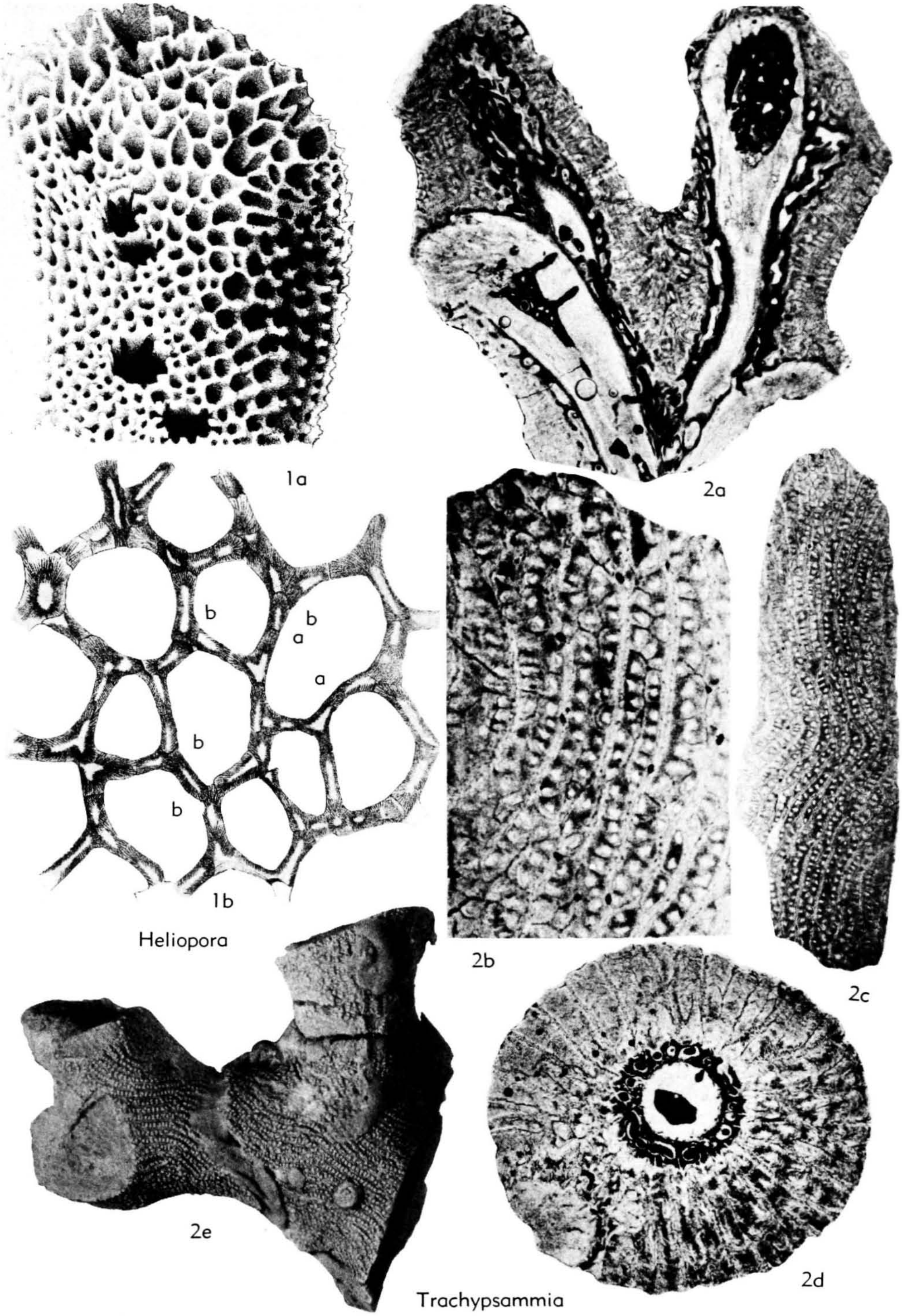


Fig. 139. Trachypsammiacea, Coenothecalia (p. F192-F194).

© 2009 University of Kansas Paleontological Institute

tem, extramedullar radial coenenchyme, and origin of new corallites from the central medullar canal.

Relationship to the Gorgonacea (e.g., *Gorgonia*), as suggested by HEHENWARTER, is not possible because of the existence of a strongly developed mesoskeleton and the great difference in structure and development of the medullar region, which in *Gorgonia* is an ectodermal product consisting of succeeding cupuliform, overlapping lamellae, concentric layers more or less calcified, or irregular sclerodermites radially oriented in the center and surrounded by secondary calcification arranged either radially or longitudinally.

In comparison with other types of modern Octocorallia, *Trachypsammia* clearly differs from Stolonifera (e.g., *Tubipora*) that have parallel corallites connected only by horizontal, stolonic platforms. However, a similarity can be drawn with certain forms of Telestacea and Alcyonacea, in which young corallites originate at various levels from solenia of the vertical corallite walls of the parent. *Trachypsammia* could be considered, in regard to the medullar system, as an archaic precursor of this structural plan, having a single primary basal polyp, a single central medullar structure with one large central cavity (therefore different from forms like *Briareum*). Some octocorals possess intriguing structural similarities to *Trachypsammia*. It is important to note that Gorgonacea such as *Isis hippuris* LINNÉ and *Corallium rubrum* (LINNÉ) present a singularly analogous radial arrangement of sclerodermites in the calcareous axis. These differ from *Trachypsammia* by the absence of the central canal system and the exclusion of corallites from the axial skeleton, but these can be found in the gorgonacean genus *Tripalea* (=*Suberia, partim*) (with unconsolidated skeleton) which, moreover, has a very open, vesicular cortex that may show traces of radial arrangement. A comparison of the radial, extramedullar coenenchymatic system with any known coenenchymatic structure of Alcyonacea is extremely problematic and remains an open question. On the other hand, similarity between the radiate structures of *Trachypsammia* with the coenenchymatic structures of the Dendrophylliidae and Eupsammiidae, as suggested by GERTH, fails entirely of homological documentation.

Trachypsammia[1] GERTH, 1921 [**T. dendroides*]. *External characters:* Corallum compound, dendroid, adherent by a broadly cuneiform base. External sculpture of minute tubercles in single or double files, separated by thin ridges axially or sinuously directed, increasing in number and anastomosing in some, chiefly in the vicinity of the corallites. Calyces minute, generally in 2 opposite longitudinal series, less commonly scattered sparsely; slightly projecting, with coronal tubercles and with wall subdivided into 24 to 28 sectors, simulating septal striae. *Structure of coenenchyme:* Medullar region formed of a system of sinuous, labyrinthine canals with frequent anastomoses and ramification (Fig. 139,*2a,d*). Corallites originating in the canalicular region as an axial calcareous process in the fossil skeleton, inserted in the canal system, part of which becomes peripheral to them; one or more canals penetrating also the developing skeleton and forming the axial cavity of a new corallite, which bends centrifugally as it elongates, the central cavity becoming funnel-shaped, and the calcareous column being subdivided into a series of 24 to 28 radial sectors ("septal ridges" of GERTH and HEHENWARTER). In the mature stage the peripheral canals are arranged in a single series around the calicular margin. *Extramedullar tissue:* Transverse, axial and tangential thin sections demonstrate (1) a system of vertical, concentric thin lamellae ("interradial bridges" of HEHENWARTER), which are finely and regularly vesicular (Fig. 139,*2d*) and produce the external sculpture of winding files of tubercles (Fig. 139,*2e*); (2) a system of 28 to 50 longitudinal septum-like lamellae that cross the concentric system, undulating mostly in a vertical direction, and not rarely anastomosing as shown in tangential section (Fig. 139,*2b*); (3) a reticulate system of minute dark points (?pores) on each side of the lamellae, visible at even low power (×5) in both tangential and cross sections; (4) a system of relatively few, large cortical lumina irregularly disposed on the sides of the vertical, radial lamellae. *Dimensions:* fragmentary colonies measure 1.5 to 6 cm. in height, 0.5 to 2.0 cm. in diameter. *U. Perm.*, Timor-Italy.——FIG. 139,*2*. *T. mediterranea* MONT.-GALL., Sicily; *2a*, axial section of branch tips, ×4; *2b*, tangential section, ×12; *2c*, same, ×4; *2d*, transverse section, ×7; *2e*, fragment of colony, ×3 (*2a-d*, 32; *2e*, 28).

(End of section by MONTANARO-GALLITELLI)

Order COENOTHECALIA Bourne, 1895

Octocorals without spicules but produc-

---

[1] Classed in Tabulata by HILL & STUMM (p. F469).

© 2009 University of Kansas Paleontological Institute

ing a massive skeleton of fibrocrystalline aragonite. Corallum penetrated by wide tubes occupied by the polyps and narrow tubes containing blind downgrowths of the solenial system; both kinds of tubes regularly tabulate. Calicles with pseudosepta varying in number, not corresponding with the 8 soft septa. *Cret.-Rec.*

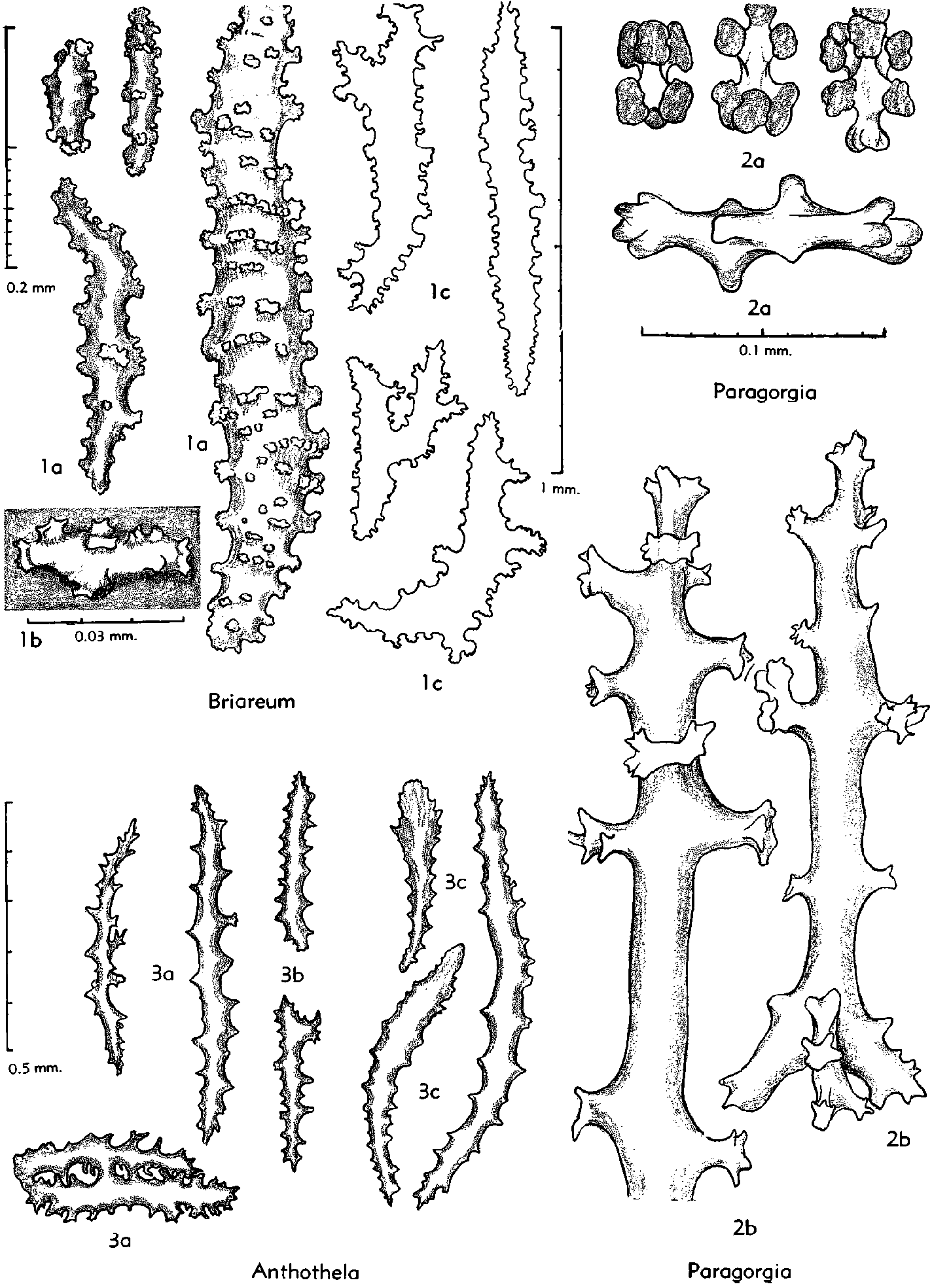


Fig. 140. Gorgonacea: Briareidae, Anthothelidae, Paragorgiidae (p. F194, F197).

© 2009 University of Kansas Paleontological Institute

A number of fossil genera have at one time or another been placed in this order. Most, however, seem not referable to the Octocorallia and have been removed.

Family HELIOPORIDAE Moseley, 1876

Heliopora DE BLAINVILLE, 1830 [**Millepora coerulea* PALLAS, 1766]. Corallum bright blue in color, massive, vertical, commonly lobate plates with 10 to 16 (usually 15) pseudosepta; an important reef-former in some areas. *Rec.*, IndoPac.——FIG. 139, *1*. **H. coerulea; 1a,* tip of corallum, ×6 (33); *1b,* tangential section of growing edge of corallum; (*a,* junctions of adjacent triradiate figures; *b,* junctions of 3 calcareous lamellae to form triradiate figure) (27).

Octotremacis GREGORY, 1900 [**Polysolenia hochstetteri* REUSS, 1866]. Large, well-developed pseudosepta, 8 in each calicle, in 2 cycles. *Mio.*, Java.

Polytremacis D'ORBIGNY, 1849 [**P. bulbosa*]. Pseudosepta strong, reaching almost to center of calyces, 8 to 20 in number. *U.Cret.-L.Tert.*, Eu.

Family CERATOPORELLIDAE Hickson, 1912

Colonies forming a massive skeleton of crystalline calcium carbonate, in which a few slender spicules are imbedded; no tabulae, tubes closing below by continuous growth of thecal walls; pores monomorphic, small. *Rec.*

Ceratoporella HICKSON, 1912 [**Ceratopora nicholsonii* HICKSON, 1911]. *Rec.*, Cuba.

Order GORGONACEA Lamouroux, 1816

[*nom. transl.* STUDER, 1887 (*ex* suborder Gorgonacea VERRILL, 1866; *nom. transl. et correct. ex* order Gorgonieae LAMX., 1816)] [Although the type genus of this order is *Gorgonia,* present rules do not require incorporation of the stem Gorgoni- in the ordinal name; furthermore, the fact that the originally published ordinal name does incorporate this stem is not a compelling reason for changing Gorgonacea to Gorgoniacea.]

Octocorals with uniformly short gastrovascular cavities; chiefly arborescent, rarely lobate or incrusting colonies producing more or less specialized axial structures, either as a distinct central axis of horny or calcareous material, or both, or as a central medullar zone of calcareous sclerites which are loosely or inseparably bound together by horny or calcareous matter. *Cret.-Rec.*

Suborder SCLERAXONIA Studer, 1887

[=Pseudaxonia (*partim*) VON KOCH, 1878]

Gorgonaceans with central axis, medullar zone or inner layer containing spicules bound together more or less solidly either by horny or calcareous material; outer layer of coenenchyme (cortex) containing proximal portions of gastrovascular chambers of the polyps, endodermal canals and solenia; cortical spicules free and commonly of a different sort from those in medullar region; axial cylinder or medulla may contain canals and solenia but polyp cavities do not penetrate it and it has no cross-chambered central chord. *Cret.-Rec.*

Family BRIAREIDAE J. E. Gray, 1859

Monomorphic Scleraxonia with continuous medulla containing separable spicules, perforated by gastrodermal canals all the way to branch tips, not separated from cortex by a ring of boundary canals. *Rec.*

Briareum DE BLAINVILLE, 1830 [**Briareum gorgonoideum* (=**Alcyonium asbestinum* PALLAS, 1766)]. Sclerites basically spindles with irregular tubercles, very large and sinuous or branched in medulla; white and purple in color. *Rec.*, W.Indies. ——FIG. 140,*1*. **B. asbestinum,* Fla.; *1a,* spicules of cortex; *1b,* sculptural detail of same; *1c,* spicules of medulla in outline (26n).

Solenopodium KÜKENTHAL, 1916 [**Erythropodium stechei;* SD KÜKENTHAL, 1916]. Sclerites like those of *Briareum* but more slender, with tubercles displaying strong tendency toward alignment in regular transverse belts; sclerites of cortex colorless, those of medulla chiefly violet. *Rec.*, RedSea-Malay Arch.-Oceania.

Family ANTHOTHELIDAE Broch, 1916

Monomorphic Scleraxonia with medulla surrounded by longitudinal boundary canals which separate it from cortex; medulla only rarely perforated by gastrodermal solenia in smaller branches and then not extensively as in lower parts of colony. *Rec.*

Subfamily ANTHOTHELINAE Broch, 1916

Cortical sclerites elongate and pointed, anthocodial spindles bent and commonly strongly clubbed; polyps occupying projecting, cylindrical calyces. *Rec.*

Anthothela VERRILL, 1879 [**Briareum grandiflorum* SARS, 1856]. Slender, tortuous, commonly anastomosing branches; no main stems developed. *Rec.*, Atl.-IndoPac.——FIG. 140,*3*. **A. grandiflora,* Grand Banks; *3a,* spicules of medulla; *3b,* spicules of cortex; *3c,* spicules of anthocodia (26n).

© 2009 University of Kansas Paleontological Institute

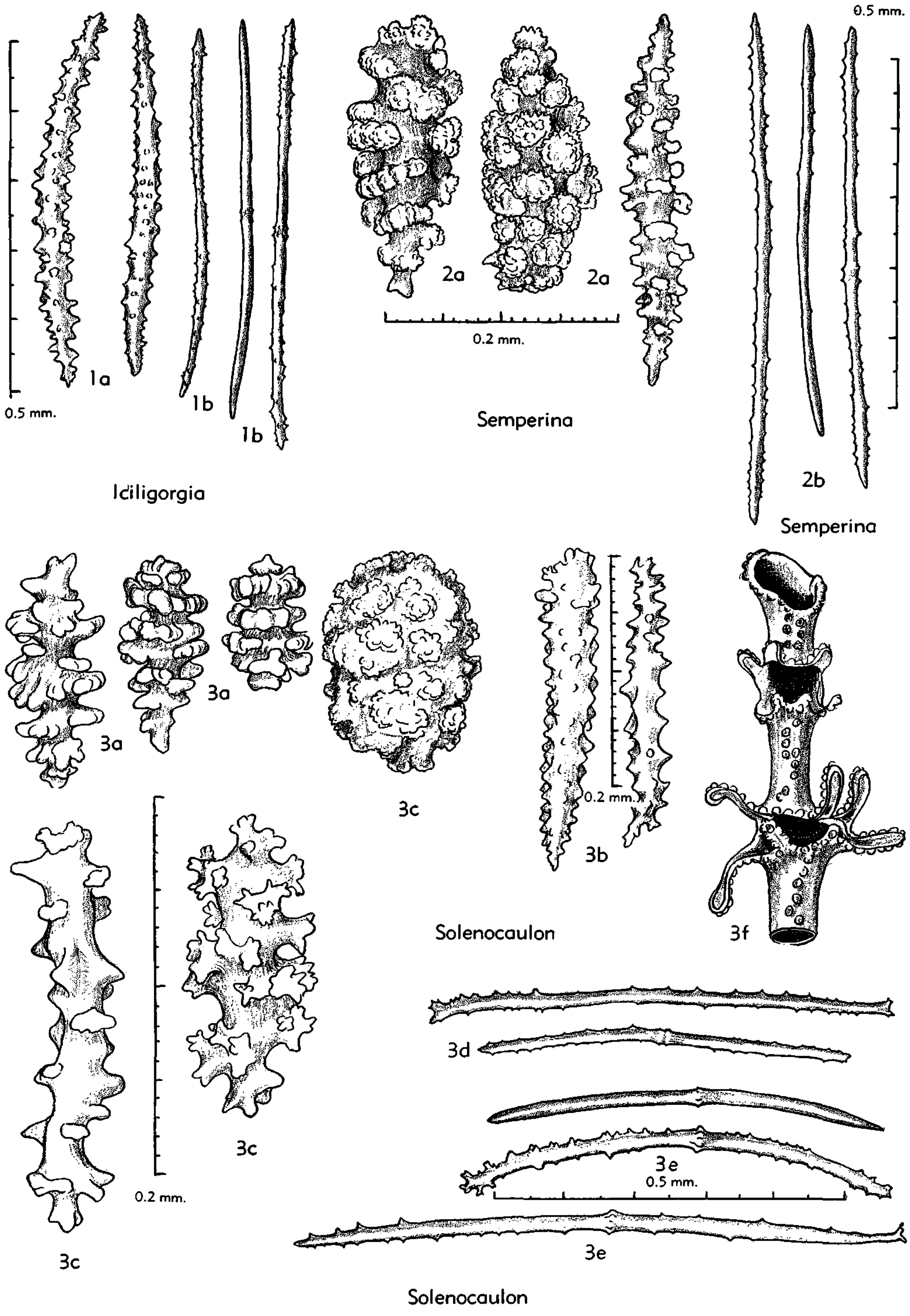


Fig. 141. Gorgonacea: Anthothelidae (p. F196).

© 2009 University of Kansas Paleontological Institute

Subfamily SEMPERININAE Aurivillius, 1931

[*nom. transl.* Bayer, herein (*ex* Semperinidae Aurivillius, 1931)]

Axial sclerites consisting of long, slender needles; cortical sclerites including thorny or tuberculate spindles but no radiate forms; polyps occupying hemispherical calyces. *Rec.*

Semperina Kölliker, 1870 [**S. rubra*]. Zooids leaving one face of colony free; branches slightly flattened, tips clavate and commonly fistulose; spindles of cortex elongate-fusiform, openly tuberculated; axial needles finely prickly. *Rec.*, IndoPac.——Fig. 141,*2*. *S. brunnea* Nutting, Ind. O.; *2a*, cortical sclerites; *2b*, medullar needles (26n).

Iciligorgia Duchassaing, 1870 [**I. schrammi*]. Polyps in 2 longitudinal series along opposite edge of branches; twig tips commonly fistulose, cortical spicules spinous bent spindles; axial spicules slender needles, usually thorny, some smooth. *Rec.*, trop.W.Atl.——Fig. 141,*1*. **I. schrammi*, Fla.; *1a*, cortical spicules; *1b*, medullar spicules (26n).

Solenocaulon Gray, 1862 [**S. tortuosum*]. Polyps chiefly on small twigs, which may be clavate and terminally fistulose; main stem expanded, gutterlike or closed and tubular; stalk solid, some spatulate below; cortical sclerites consisting of capstans and coarsely tuberculated spindles, with a few spinose rods; medullar sclerites including many very slender needles, all spinose in branchlets, few completely smooth in stalk. *Rec.*, IndoPac.——Fig. 141,*3*. *S. sterroklonium* Germanos, Philip.; *3a,b*, spicules of branch cortex; *3c*, spicules of stalk cortex; *3d*, spicules of branch medulla; *3e*, spicules of stalk medulla; *3f*, tip of tubular stem (26n).

Subfamily SPONGIODERMATINAE Aurivillius, 1931

[*nom. transl.* Bayer, herein (*ex* Spongiodermatidae Aurivillius, 1931)]

Medullar sclerites consisting of stout rods, commonly with strong spines or branching processes, cortical sclerites including capstans or radiate forms. *Rec.*

Spongioderma Kölliker, 1870 [**Solanderia verrucosa* Möbius, 1861]. Spicules of cortex mostly 4-, 5- and 6-radiates, coarser than those of *Titanideum;* 2 rings of longitudinal canals. *Rec.*, S.Afr.

Alertigorgia Kükenthal, 1908 [**Iciligorgia orientalis* Ridley, 1884] [=*Machaerigorgia* Kükenthal, 1916 (obj.)]. Colonies with long, flat branches, zooids fully retractile and aligned biserially along narrow edges; cortical spicules short oval bodies with closely and irregularly placed tubercles, longer spindles with smaller warts less closely placed, and intermediate forms; spicules of medulla mostly spinous rods, with a few tuberculate forms like those of cortex. *Rec.*, IndoPac.

Callipodium Verrill, 1869 [**C. pacificum*]. Incrusting species in form of broad bands or sheets; spicules including short belted spindles, 3- and 6-radiates, those of inner zone commonly fused together in a solid layer next to substratum; red or yellow; placed in this family because of spicular characters. *Rec.*, W.Mexico-Panama.——Fig. 142, *2*. **C. pacificum*, Panama; *2a*, cortical sclerites; *2b*, part of the fused basement layer (26n).

Diodogorgia Kükenthal, 1919 [**D. ceratosa*]. Spicules of cortex mostly small 6-radiates in anthosteles, coarsely warted spindles in rind; stout rods with sparse processes predominant in medulla; with double ring of longitudinal canals. *Rec.*, trop. W.Atl.——Fig. 143,*1*. **D. ceratosa*, Carib.; *1a*, rod from medulla; *1b*, cortical spindle; *1c*, longer spindle of inner cortex; *1d*, radiates from polyp walls (26n).

Erythropodium Kölliker, 1865 [**Xaenia caribaeorum* Duchassaing & Michelotti, 1860]. Spicules 4- and 6-radiates, those of cortical zone colorless, of medullar region red; discontinuous layer of fused sclerites next to substratum; membranous form placed here because of spicular characters. *Rec.*, trop.W.Atl.——Fig. 142,*3*. **E. caribaeorum*, Fla.; *3a*, colorless cortical sclerites; *3b*, red medullar sclerites (26n).

Titanideum Verrill, 1863 [**Gorgonia suberosa* Ellis & Solander, 1786 (*non* Pallas, 1766) (=*Solanderia frauenfeldtii* Kölliker, 1865)]. Spicules of cortex chiefly pink or red 4- and 5-radiates; of medulla, colorless branched rods; double ring of longitudinal canals, one immediately surrounding medulla, other dividing cortex into thin outer and thick inner layer. *Rec.*, SE. USA.——Fig. 142,*1*. **T. frauenfeldtii*, N.Car., *1a*, radiate spicules or cortex; *1b*, medullar spicules (26n).

Tripalea Bayer, 1955 [**Suberia clavaria* Studer, 1878]. Spicules of cortex short capstans in thin outer layer, warted and spinous spindles in spongy inner layer; medulla with rods branched at ends; one ring of boundary canals. *Rec.*, E.S.Am.——Fig. 143,*3*. **T. clavaria*, Arg.; *3a*, spicules of inner cortex; *3b*, of outer cortex; *3c*, of medulla (26n).

Family SUBERGORGIIDAE Gray, 1859

[*nom. correct.* Bayer, herein (*pro* Subergorgiadae, Gray, 1859)]

Arborescent, monomorphic, with medullar region containing spicules partially fused together to form a well-differentiated axis set off from cortex by ring of longitudinal boundary canals of which 2 may be larger than others; no solenia or central chord in medulla; cortical sclerites include short capstans and longer spindles with transverse belts of tubercles, irregularly tuberculated spindles, and disc spindles ("double wheels"); medullar sclerites mostly long,

© 2009 University of Kansas Paleontological Institute

sinuous, commonly branching and anastomosing, without spines or warts; a few shorter rods, smooth except for tiny terminal cluster of tubercles at each end. *Rec.*

Subergorgia Gray, 1857 [**Gorgonia suberosa* Pallas, 1766]. *Rec.,* includes some monstrous sea fans of E.Indies-Oceania.——Fig. 143,*2*. *S. mollis* (Nutting), Rec., MarshallI.; *2a,* disc-spindles, and *2b,* belted spindles of cortex; *2c,* sclerites of medulla (26n).

Family PARAGORGIIDAE Kükenthal, 1916

[*nom. transl.* Aurivillius, 1931 (*ex* Paragorgiinae Kükenthal, 1916)]

Like Briareidae except polyps dimorphic. *Rec.*

Paragorgia M.Edw.-H., 1857 [**Alcyonium arboreum* Linné, 1758]. Massive, treelike colonies with thick branches; sclerites of cortex small 6-, 7- and 8-radiate capstans; in medulla, long rods with branching processes, derived from capstan type. *Rec.,* Arct.-Atl.-Pac.——Fig. 140,*2*. **P. arborea,* Grand Banks; *2a,* cortical capstans and rod; *2b,* long medullar sclerites (26n).

Sibogagorgia Stiasny, 1937 [**S. weberi* (=**Suberia köllikeri* Nutting, 1911, *non* Studer, 1879)]. Spicules similar to those of *Paragorgia;* boundary canals present. *Rec.,* E.Indies.

Family CORALLIIDAE Lamouroux, 1812

[*nom. correct.* Gray, 1857 (*pro* Corallieae, Lamx., 1812)]

Dimorphic, with treelike or bushy form and hard unjointed axis consisting of in-

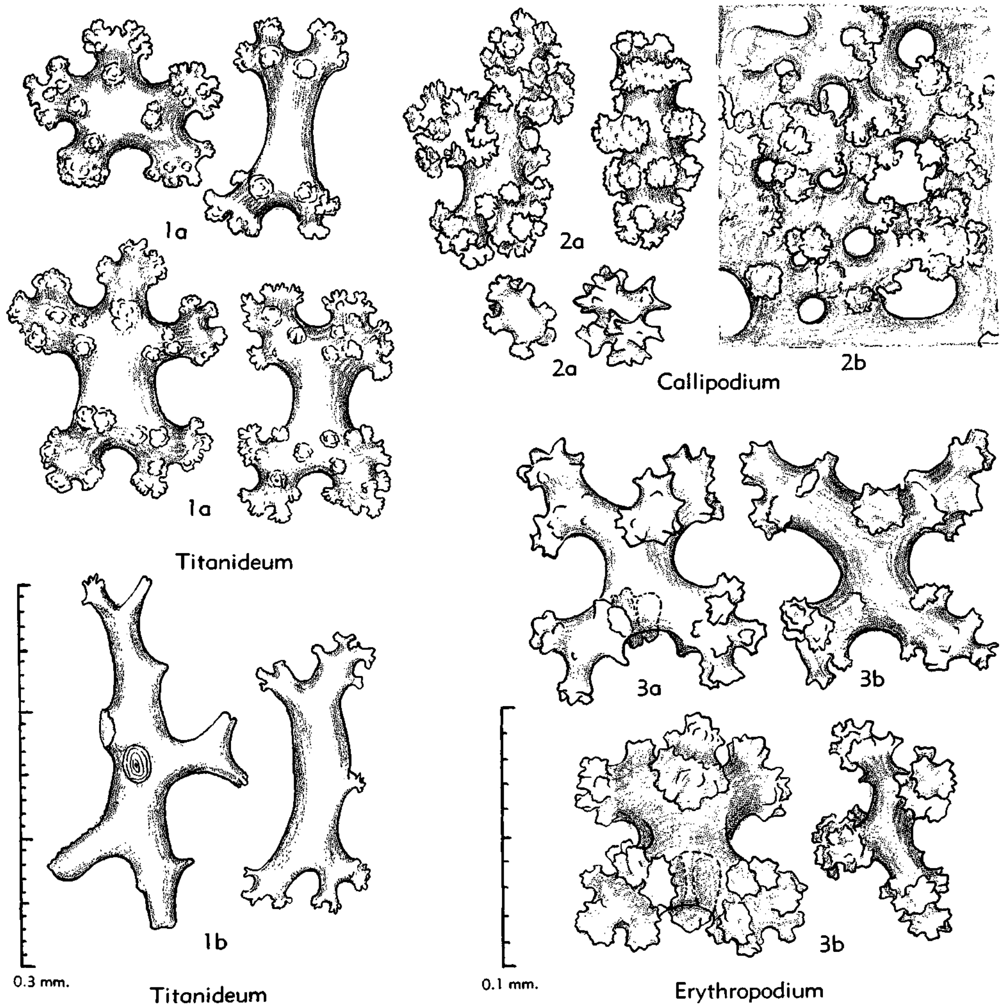


Fig. 142. Gorgonacea: Anthothelidae (p. F196).

© 2009 University of Kansas Paleontological Institute

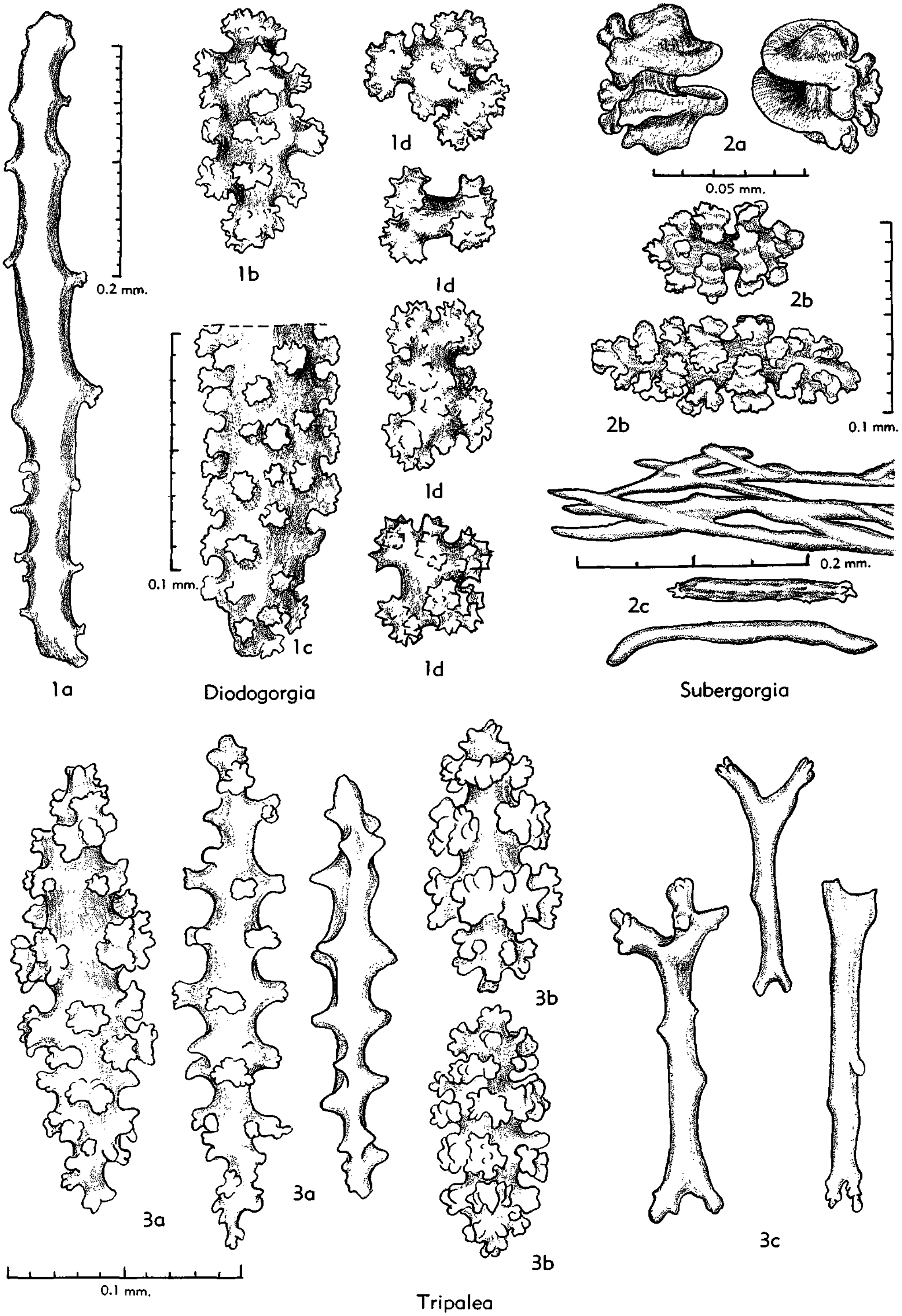


FIG. 143. Gorgonacea: Anthothelidae, Subergorgiidae (p. F196-F197).

© 2009 University of Kansas Paleontological Institute

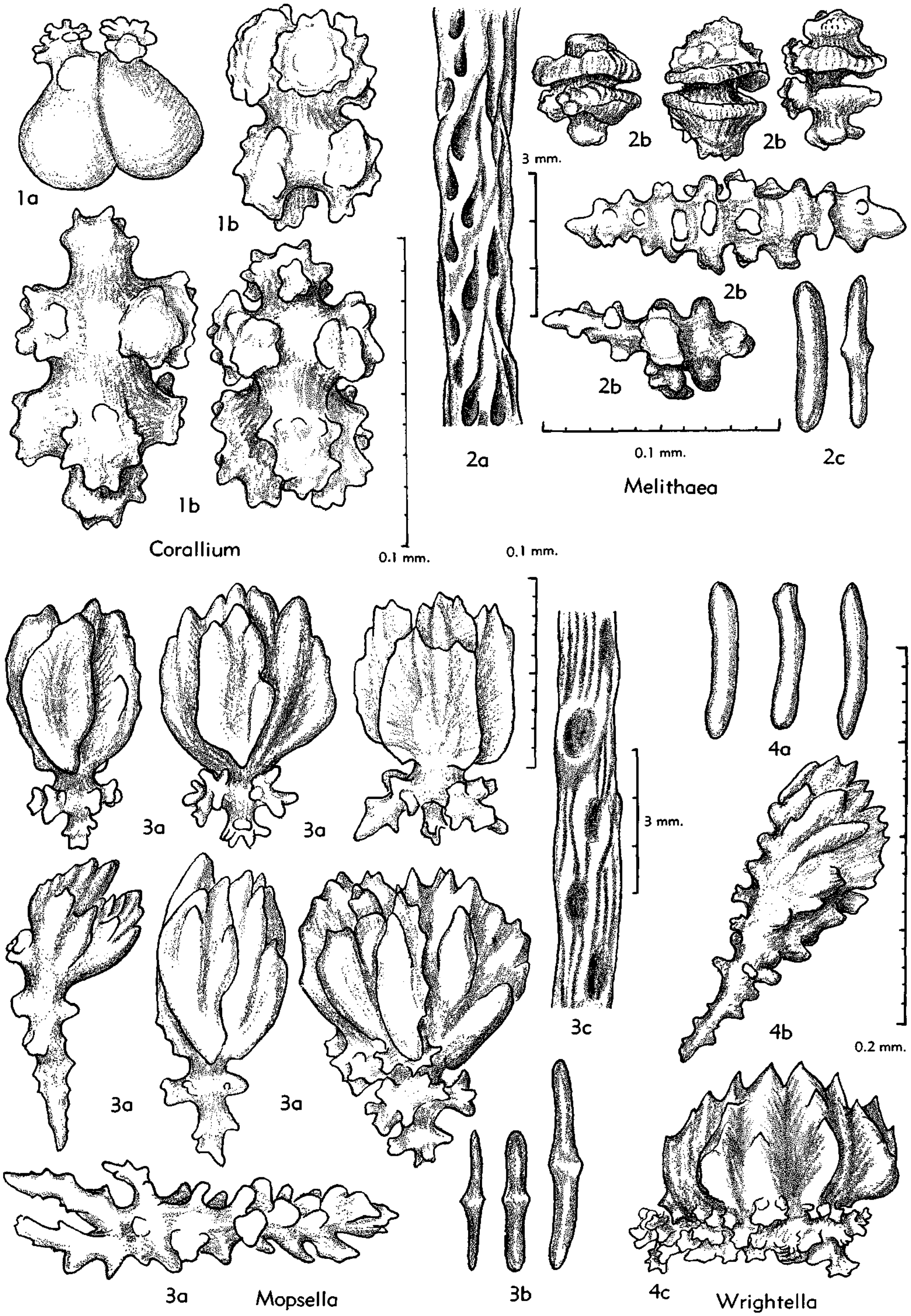


Fig. 144. Gorgonacea: Coralliidae, Melithaeidae (p. F200).

© 2009 University of Kansas Paleontological Institute

dividual sclerites solidly fused by interstitial calcareous material; polyps occurring on all sides, on one face and laterally, or biserially, and invariably forming distinct calyces; zooids very small, distributed between and upon polyp calyces; rind of varying thickness, containing small 6-, 7- and 8-radiate capstans and commonly abundant double clubs or in some species thorny spindles, or broad plates beset with thorns on outer surface; predominantly pink or red, some yellow or white. *Cret.-Rec.*

Corallium Cuvier, 1798 [**Madrepora rubra* Linné, 1758; SM Lamarck, 1801]. Cortical sclerites including capstans, in some species exclusively, in others with crosses, spindles and highly characteristic double clubs. *Cret.-Rec.,* E.Atl.-Medit.-Ind. O.-E. Indies-Philip.-Japan-Hawaii-L.Calif.——Fig. 144,*1*. *C. borneënse* Bayer, Rec., N.Borneo; *1a,* double club; *1b,* radiate spicules (26n).

Pleurocoralloides Moroff, 1902 [**P. formosum*]. Like *Corallium* but cortical sclerites comprising large spindles and plates instead of capstans and double clubs. *Rec.,* Japan.

Family MELITHAEIDAE Gray, 1870

[=Melitodidae Wright & Studer, 1889 (*partim*)]

Arborescent, monomorphic, with axis composed of alternating hard internodes of inseparably fused calcareous spicules and soft nodes of spongy, spiculiferous horny material; branches arising usually from horny nodes; cortical sclerites strongly sculptured spindles and clubs of various kinds; axial spicules smooth rods, commonly with median transverse raised belt. *Tert.-Rec.*

Melithaea M.Edw.-H., 1857 [*pro Melitaea* Lamouroux, 1812 (*non* Péron & Lesueur, 1810)] [**Isis ocracea* Linné, 1758] [=*Melitodes* Verrill, 1864 (obj.)]. Spicules of cortex very diverse in form, including warty spindles, clubs and disc-spindles, but no predominance of any one kind; axial internodes frequently with sculpture of anastomosing grooves and ridges. *Tert.-Rec.,* RedS.-IndoPac.——Fig. 144,*2*. **M. ocracea,* Rec., FijiI.; *2a,* axial internode; *2b,* spicules of cortex; *2c,* rods from axial node (26n).

Acabaria Gray, 1859 [**A. divaricata*]. Cortical sclerites chiefly long spindles; some species with a few clubs and capstans; axial internodes frequently with sculpture of parallel grooves and ridges. *Rec.,* RedS.-Ind.O.-Japan-Austral.-Oceania.——Fig. 145,*1*. *A. crosslandi* Stiasny; *1a,* spicules of cortex; *1b,* rods of axial nodes; *1c,* surface detail of internode (26n).

Clathraria Gray, 1859 [**C. rubrinodis*]. Cortical spicules including spindles, thorny and leafy clubs; internodes solid, with sculpture of both pits and parallel grooves and ridges. *Rec.,* IndoPac.

Melitella Gray, 1859 [**M. elongata;* SD Hickson, 1937]. Cortical spicules predominantly of peculiar, birotulate type. *Rec.,* IndoPac.

Mopsella Gray, 1857 [**Isis dichotoma* Pallas, 1766]. Colonies erect and flabellate, commonly retiform, some bushy; cortical spicules characteristically including very numerous foliate clubs, some resembling flower buds, others recalling a torch with flame blown aslant; axial internodes with shallow pits and a few grooves. *Rec.,* Indo-Pac.——Fig. 144,*3*. *M. aurantia* (Esper), Philip.; *3a,* clubs and spindle from cortex; *3b,* rods of axial nodes; *3c,* axial internode (26n).

Wrightella Gray, 1870 [**Isis coccinea* Ellis & Solander, 1786; SD Kükenthal, 1908]. Cortex with surface layer of leafy globes packed closely together. *Rec.,* IndoPac.——Fig. 144,*4*. **W. coccinea,* Mauritius; *4a,* rods of axial nodes; *4b,* club, and *4c,* leaf-globe of cortex (26n).

Family PARISIDIDAE Aurivillius, 1931

[=Trinelladae Gray, 1870]

Arborescent, monomorphic, like Melithaeidae but internodal sclerites tuberculate, nodal sclerites lobate rods, cortical sclerites coarse plates, and ramification proceeds from calcareous internodes. *Tert.-Rec.*

Parisis Verrill, 1864 [**P. fruticosa*]. Large rigid colonies branched in one plane. *Tert.*(Italy-India)-*Rec.* (IndoPac.).——Fig. 145,*2*. **P. fruticosa,* Rec., Sulu Sea; *2a,* cortical sclerites; *2b,* detail of tubercle of large plate from cortex; *2c,* lobate rods of axial nodes; *2d,* part of axis, decorticated; *2e,* end view of internode; *2f,* surface detail of internode (26n).

?**Skleranthelia** Studer, 1878 [**S. musiva*]. Membranous or stoloniferous forms placed in this family (probably incorrectly) because of spicular similarity. *Rec.,* E.Atl. (no other record of Parisididae in Atl.).

Suborder HOLAXONIA Studer, 1887

[=Axifera von Koch, 1878]

Gorgonacea with distinct central axis made up of horny material alone or of horny material more or less heavily permeated with calcareous substance, continuous or with alternating horny and calcareous joints. *Cret.-Rec.*

Calcareous material of the peripheral zone of the axis is in nonspicular form, with single exception of the Keroeididae, a small family in which it takes the form of smooth, glassy, elongated, pointed scales or rods, the axis having a definite chambered central

© 2009 University of Kansas Paleontological Institute

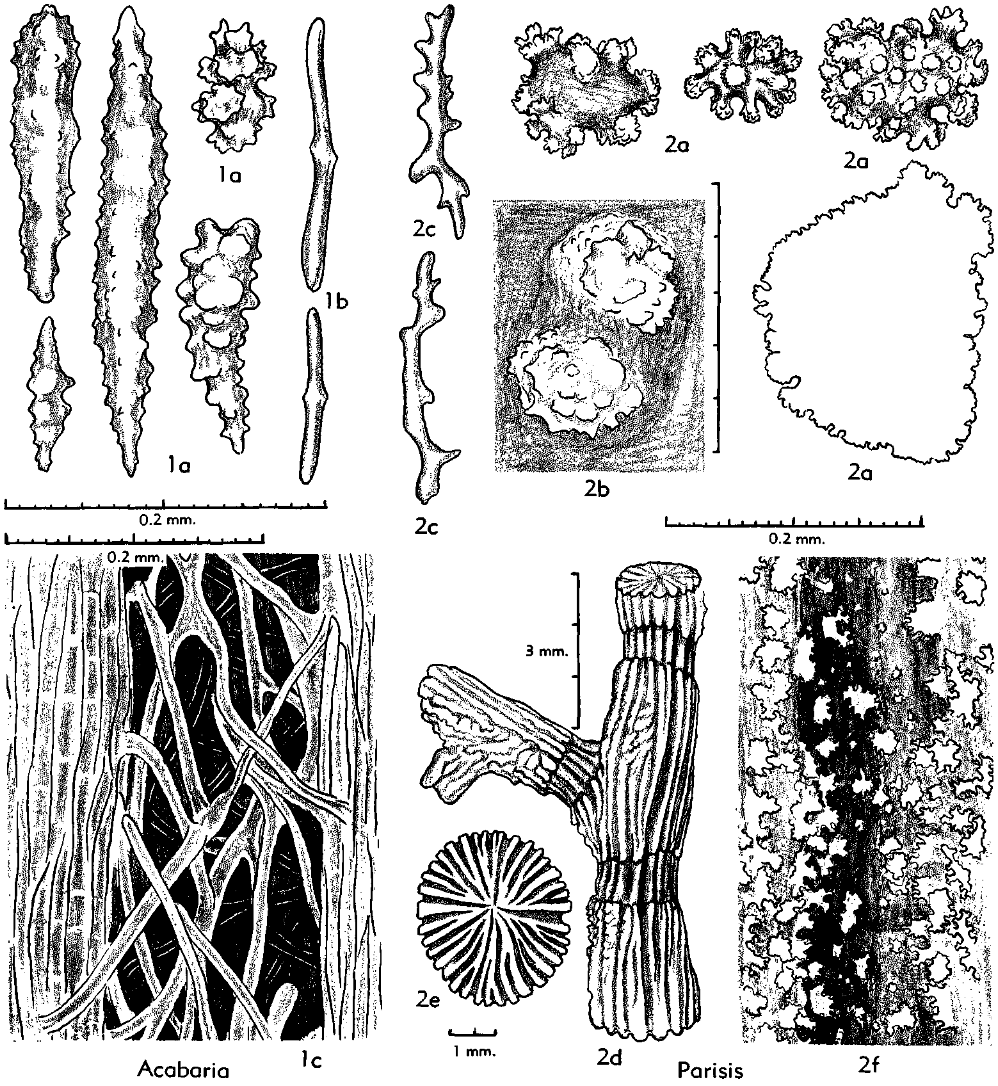


Fig. 145. Gorgonacea: Melithaeidae, Parisididae (p. F200).

chord, which disinguishes it from the Subergorgiidae, which have similar axial spicules.

Family KEROEIDIDAE K. Kinoshita, 1910

[=Suberogorgidae Studer, 1887 *(partim)*]

Axis with chambered central chord surrounded by peripheral zone of smooth, elongated, pointed scales or rods which are not solidly fused together; coenenchymal cortex (rind) with large fusiform or plate-like, roughly warted spicules; anthocodiae with strong spiculation; color, red to white. *Rec.*

This family, with its chambered, central axial chord, well-defined axis epithelium, and spicular axis cortex, bridges the gap between the Subergorgiidae in the Scleraxonia on one side and the primitive families of the Holaxonia on the other. In spite of the outer, spicular layer of its axis, it must be referred to the Holaxonia.

Keroeides Studer, 1887 [**K. koreni* Wright &

© 2009 University of Kansas Paleontological Institute

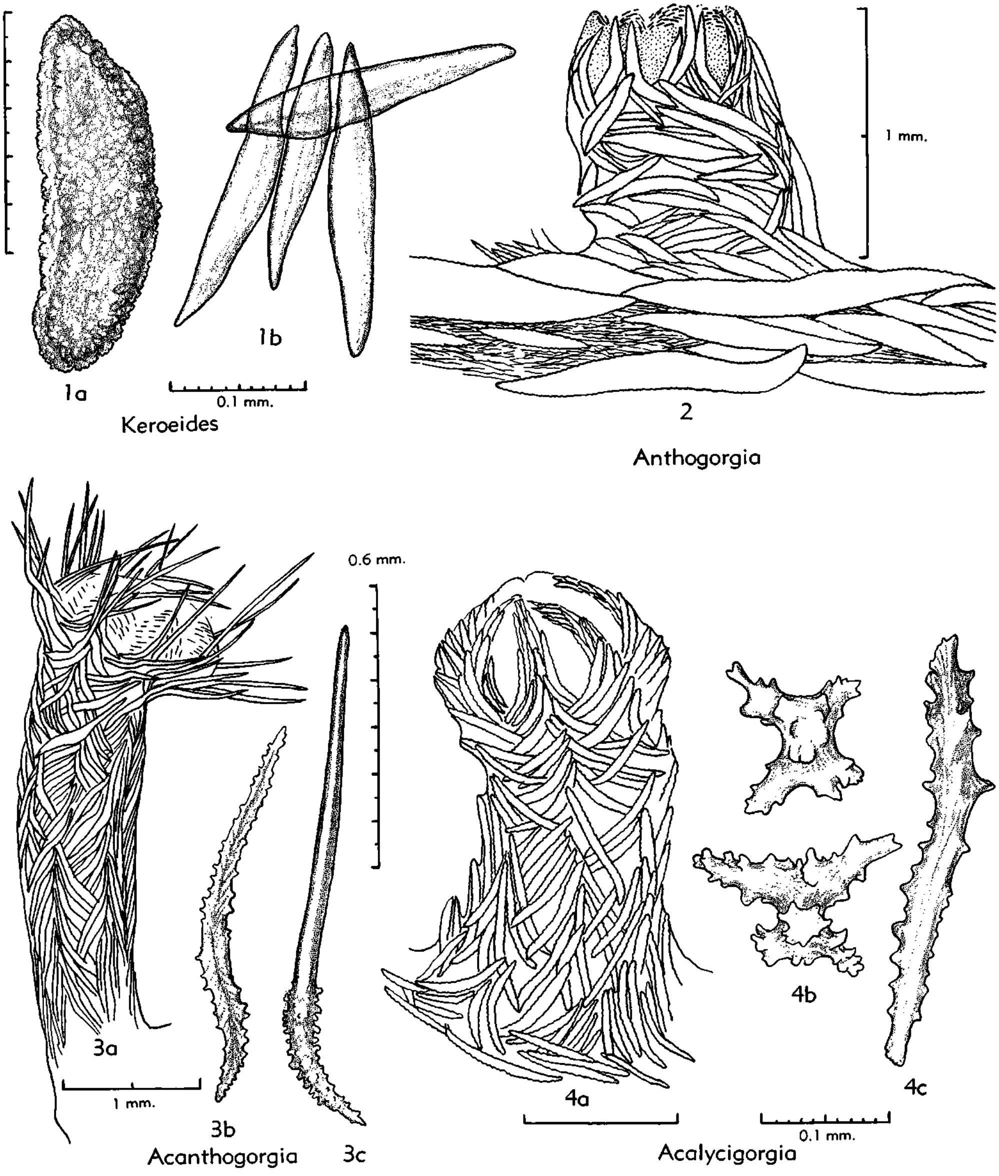


FIG. 146. Gorgonacea: Keroeididae, Acanthogorgiidae (p. F202-F203).

STUDER, 1889; SM WRIGHT-S., 1889]. *Rec.*, Indo-Pac. (Andamans-Hawaii; Japan-New Brit.)-Atl. (Guadalupe).——FIG. 146,*1*. **K. koreni*, Marshall I.; *1a*, coarse spindle of rind; *1b*, spicules of axis (26n).

Family ACANTHOGORGIIDAE Gray, 1859

[*nom. correct.* KÜKENTHAL & GORZAWSKI, 1908 (*pro* Acanthogorgiadae GRAY, 1859)]

Axis purely horny, with wide, chambered central chord; rind thin, polyps not retractile, forming prominent, cylindrical calyces with spicules arranged in 8 *en chevron* fields; calycular spicules continuous with those of tentacular crown, without any intervening spicule-free neck zone or transverse collaret and consequently no clear division between anthocodia and anthostele; spicules fusiform but in stem rind may be radiate. *Rec.*

© 2009 University of Kansas Paleontological Institute

Species of this family inhabit moderate to considerable depths; various species of *Acanthogorgia* occur in all seas, some thriving in very cold waters. The genera *Anthogorgia* and *Calicorgorgia* are limited to the Indo-Pacific region, so far as now known.

Acanthogorgia GRAY, 1857 [**A. hirsuta* (?=*A. aspera* POURTALÈS, 1867)] [=*Paracanthogorgia* STIASNY, 1943]. Calyces tall and cylindrical, with crown of strongly projecting spinous spindles in tentacle bases; stem rind with spindles or in some with radiates. [Species with rough projecting spines have been separated by STIASNY (1943, 1947) as a distinct genus, *Paracanthogorgia,* which at present cannot be maintained.] *Rec.,* IndoPac.-Atl.——FIG. 146,*3*. *A. aspera* POURTALÈS, W.Atl. (off Ga.); *3a,* calyx; *3b,* bent spindle of calyx wall; *3c,* spinous crown spicule (26n).

Acalycigorgia KÜKENTHAL, 1908 [**A. grandiflora* KÜKENTHAL & GORZAWSKI, 1908; SD KÜKENTHAL & GORZAWSKI, 1908]. Calyces similar to those of *Acanthogorgia* but without the crown of strongly projecting spines. *Rec.,* IndoPac.——FIG. 146,*4*. *A. ceylonensis* (THOMSON & HENDERSON), Timor; *4a,* calyx; *4b,* radiates from stem rind; *4c,* spindles from calyx wall (26n).

Anthogorgia VERRILL, 1868 [**Muricea divaricata* VERRILL, 1865]. Calyces cylindrical, spicules converging *en chevron* as 8 marginal points, beneath which they may be transverse or disposed irregularly. *Rec.,* IndoPac.——FIG. 146,*2*. *A bocki* AURIVILLIUS, 1931, Japan; part of a branch with one calyx (26n).

Family PARAMURICEIDAE Bayer, nov.

Axis horny, with wide, chambered central chord; rind thin, or in some moderately thick, polyps retractile within protruding calyces by virtue of a neck zone with few or no spicules; anthocodial armature of strong points of *en chevron* spicules usually resting on a transverse collaret; coenenchymal sclerites spindles only in some but commonly modified strongly as thorn scales or having other forms, ordinarily best-dedeveloped in or near calyces. *Rec.*

The establishment of this family is necessitated by removal of the genus *Muricea* from this assemblage, formerly called Muriceidae (DUCHASSAING & MICHELOTTI, 1864), which forms a reasonably homogeneous group. It occurs at moderate to considerable depths in all seas.

Paramuricea KÖLLIKER, 1865 [**Gorgonia placomus* LINNÉ, 1758; SD VERRILL, 1883]. Characteristic sclerites are thorn scales with lobed or laciniated edges and a stout outer projection, some long and spinelike, others short and blunt. *Rec.,* Atl.-Medit.-IndoPac.——FIG. 147,*1*. **P. placomus,* Grand Banks; *1a,* contracted polyp in its calyx; *1b,* spicules of inner rind; *1c,* calycular thorn scales (26n).

Acanthacis DEICHMANN, 1936 [**A. scabra*]. Colonies irregularly branched in one plane; rind spicules in one layer, stout spindles or plates; calyces low, armed with stout thorn scales. *Rec.,* W.Indies.——FIG. 148,*1*. *A. austera* DEICHMANN, Porto Rico; *1a,* calyx with surrounding thorn scales; *1b,* thorn scales, isolated (26n).

Anthomuricea STUDER, 1887 [**A. argentea* WRIGHT & STUDER, 1889; SD NUTTING, 1910]. No thorn scales; outer rind with blunt spindles sculptured with rounded, simple warts; inner rind with small, bent rods. Calyces tall, cylindrical, biserial or on all sides, armature in 8 double rows, *en chevron;* opercular spicules in converging rows, commonly including clublike spindles. *Rec.,* Japan-Hawaii-MalayArch.-Patagonia.——FIG. 149,*2*. *A. tenuispina* NUTTING, Hawaii; *2a,* spicules of outer rind; *2b,* of inner rind (26n).

Bebryce PHILIPPI, 1842 [**B. mollis*]. Characteristic sclerites are stellate plates with central boss, which make up inner layer of rind spicules, and smaller, rosette-like bodies, which lie closely packed in surface layer and become asymmetrical toward calycular margins where they project as spinous processes, commonly branched. *Rec.,* Medit.-IndoPac.-Atl.——FIG. 150,*4*. *B. cinerea* DEICHMANN, Fla.; *4a,* sclerites of calycular margin; *4b,* rosette of rind surface; *4c,* stellate plate of inner rind (26n).

Calicogorgia THOMSON & HENDERSON, 1906 [**C. investigatoris;* SD KÜKENTHAL, 1924].

Cyclomuricea NUTTING, 1908 [**C. flabellata*]. Small, fanlike colonies branched in one plane. Calyces shelflike, directed toward one face of colony; anthocodiae not retractile but with narrow neck zone that is inconspicuous in contraction. Rind sclerites clubs and spindles irregularly and asymmetrically sculptured with foliate tubercles; anthocodial spicules resembling flat tentacular rods of Gorgoniidae. *Rec.*——FIG. 149,*3*. **C. flabellata,* Hawaii; *3a,* contracted polyp; *3b,* rind sclerites; *3c,* tentacular rods (26n).

Discogorgia KÜKENTHAL, 1919 [**Placogorgia campanulifera* NUTTING, 1901]. Characteristic sclerites are discoidal or ovoidal plates with more or less lobate edges and sculpture of complicated tubercles; spindles may occur also in some, plates of calycular margin are thorn scales; inner rind contains various radiate forms. *Rec.,* IndoPac.——FIG. 147, *2*. *D. dendritica* (NUTTING), Celebes; *2a,* calycular thorn scales; *2b,* large plate from outer rind; *2c,* radiates from inner rind (26n).

?**Echinogorgia** KÖLLIKER, 1865 [**E. pseudosasappo* (=**Gorgonia sasappo reticulata* ESPER, 1791)]. Characteristic sclerites are leafy clubs, but simple

© 2009 University of Kansas Paleontological Institute

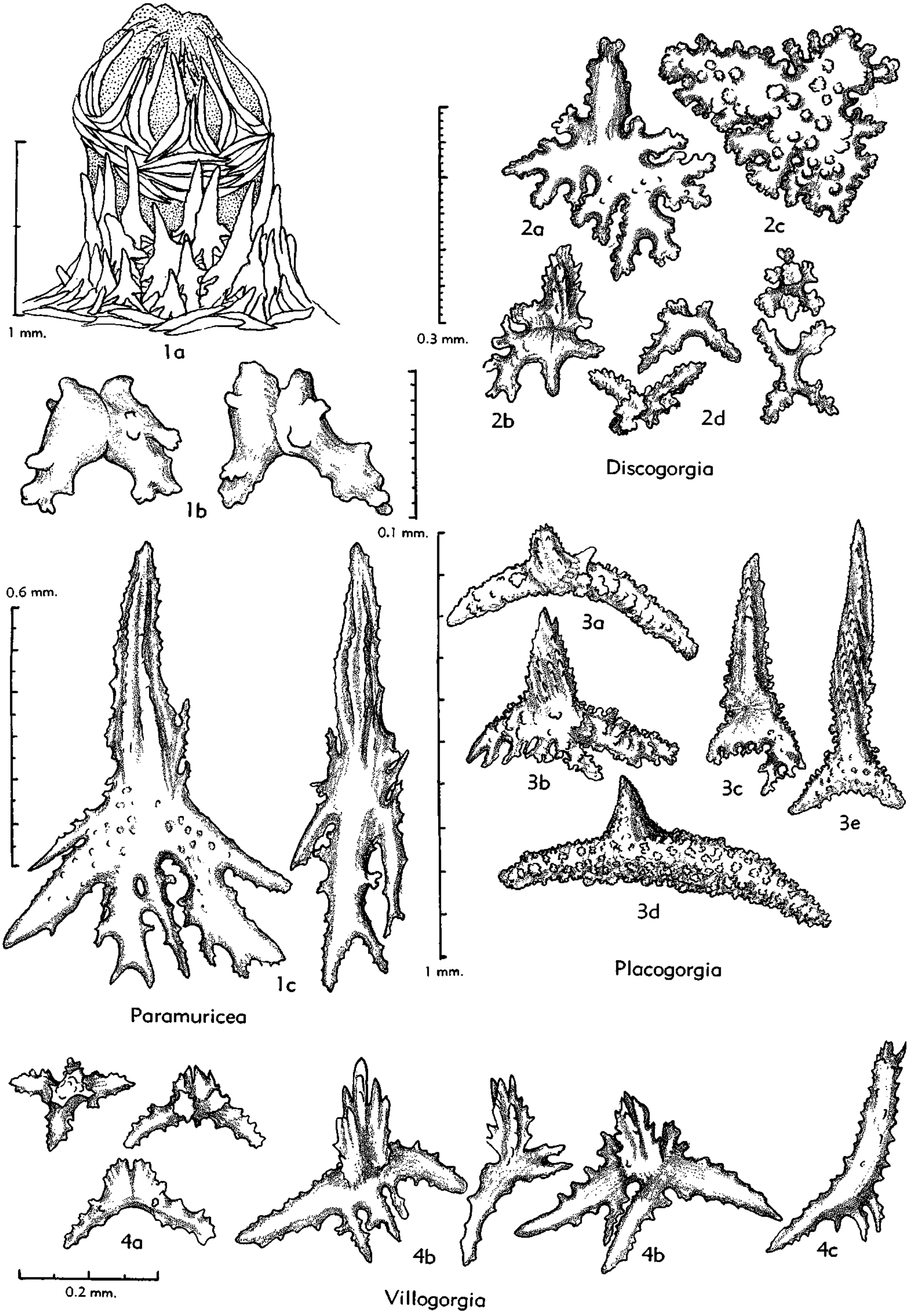
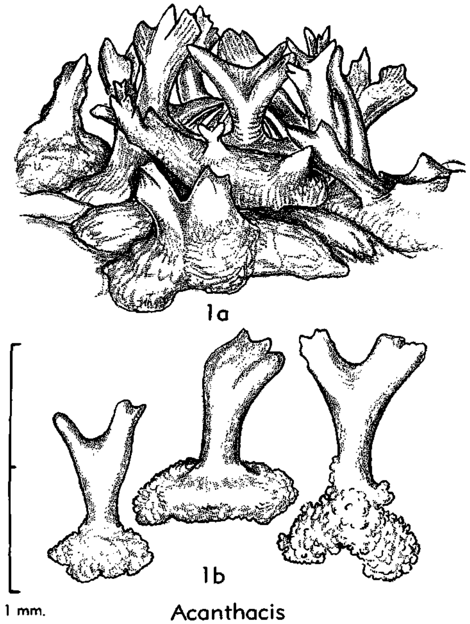
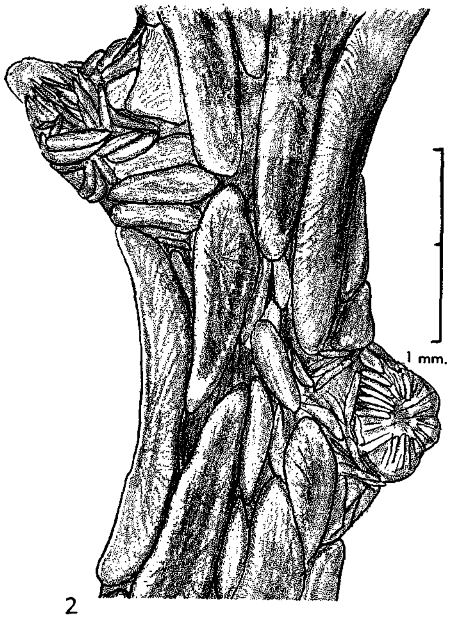


FIG. 147. Gorgonacea: Paramuriceidae (p. F203-F210).

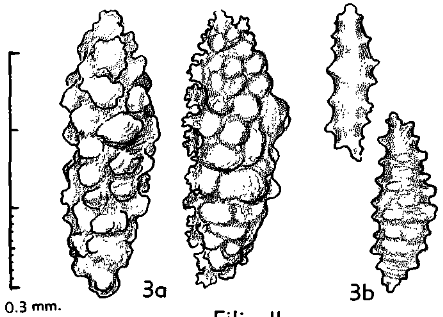
© 2009 University of Kansas Paleontological Institute



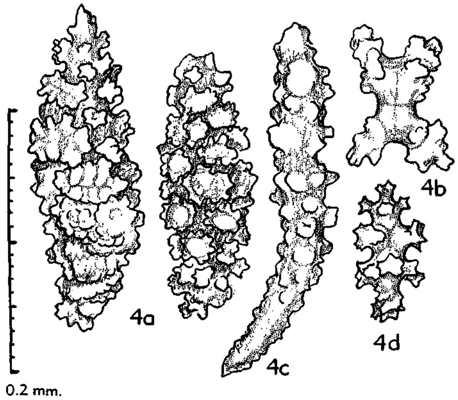
Acanthacis



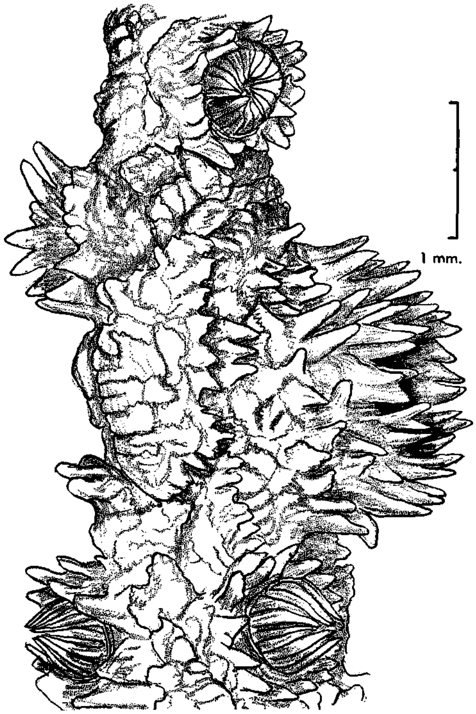
Scleracis



Filigella



Heterogorgia



Paracis

Fig. 148. Gorgonacea: Paramuriceidae (p. F203-F206).

© 2009 University of Kansas Paleontological Institute

spindles, commonly large and some with high external processes, may also be present at rind surface; rind moderately thick, calyces low and crowded. [This genus may belong in Plexauridae, for it seems close to, if not identical with, *Plexauroides.*] *Rec.,* IndoPac.——Fig. 150,*3*. *E. flexilis* Thomson & Simpson, 1909; *3a,* leaf clubs of calyces; *3b,* sclerites of inner rind (26n).

Echinomuricea Verrill, 1869 [**Nephthya coccinea* Stimpson, 1855]. Characteristic sclerites are thorn scales with stout, simple spine projecting from branched or lobed basal plate; spindles with or without strong outer processes may be present. Colonies usually branched in one plane and may be reticulate. [?Not separable from *Lissogorgia.*] *Rec.,* IndoPac.-Atl.——Fig. 150,*2*. *E. coronalis* Germanos, Celebes; *2a,* thorn scales; *2b,* quadriradiate (26n).

Filigella Gray, 1868 [**F. gracilis*]. Slender, unbranched or weakly branched colonies that may be attached to solid objects by basal disc or lie free on soft bottom. Spicules fusiform, some clavate, commonly stout and with coarse tubercles on outer surface. *Rec.,* IndoPac.-Calif.——Fig. 148,*3*. *F. mitsukurii* K. Kinoshita, Japan; *3a,* spicules from rind surface; *3b,* from deeper rind (26n).

Filigorgia Stiasny, 1937 [**F. riodouroi*]. Similar to *Filigella* but large coenenchymal spindles with tubercles of outer surface tall and spinelike; possibly identical with *Swiftia. Rec.,* W.Afr.

Heterogorgia Verrill, 1868 [**H. verrucosa;* SD Nutting, 1910]. Rind sclerites chiefly irregularly warted spindles, smaller capstans, and a few crosses; anthocodiae with strong armature of stout, bent spindles. *Rec.,* trop.E.Pac.——Fig. 148,*4*. *H. papillosa* Verrill, L.Calif.; *4a,* spindles of rind; *4b,* quadriradiate; *4c,* bent spindle from opercular radius; *4d,* capstan (26n).

Hypnogorgia Duchassaing & Michelotti, 1864 [**H. pendula*]. Tall, flexible colonies branched in one plane in a loose pinnate manner. Calyces bracket-like, topped by tall opercula composed of long rods, biserial on branches. Spicules long, simple spindles or rods. *Rec.,* W.Indies.

Lepidomuricea Kükenthal, 1919 [**Acanthomuricea ramosa* Thomson & Henderson, 1906] [*non Lepidomuricea* Verrill, 1922 (=*Paramuricea* Kölliker)].

Lissogorgia Verrill, 1864 [**Antipathes flabellum* Verrill (*non* Esper, 1791) =*Lissogorgia eubrandella* Bayer, *nom. nov.*] [=*Eubrandella* Deichmann, 1936 (obj.)]. Colonies flabellate, reticulate. Cortical sclerites including large stellate thorn scales with single, projecting spine, and spindles. *Rec.,* ?Fla.

Menacella Gray, 1870 [**M. reticularis*]. Colonies flabellate and reticulate; rind sclerites including spindles with crenulate or foliate tubercles. *Rec.,* MalayArch.

Muriceides Studer, 1887 [**M. fragilis* Wright & Studer, 1889; SM Wright-S., 1889]. Colonies scantily branched in one plane. Spicules comprising spindles with spinous sculpture, some differentiated as thorn scales. *Rec.,* IndoPac.-E.Atl.

Muricella Verrill, 1869 [**Lissogorgia flexuosa* Verrill, 1866; SD Nutting, 1910]. Colonies branching in one plane, some anastomosing. Calyces prominent, their sclerites usually forming 8 marginal points. Spicules of rind in 2 distinct layers, mostly spindles, some clubs or discoidal forms. Tentacular operculum distinct. *Rec.,* IndoPac.——Fig. 149,*1*. *M. abnormalis* Nutting, Japan; part of branch with calyces (26n).

Paracis Kükenthal, 1919 [**Acis orientalis* Ridley, 1882]. Colonies usually but not invariably branched in one plane. Calyces distinct, distributed generally or leaving one face of colony free. Rind sclerites in form of large spindles, plates or scales, some with spines. *Rec.,* IndoPac.——Fig. 148,*5*. **P. orientalis,* MarshallI.; part of branch with calyces, large one parasitized by a copepod (26n).

Placogorgia Studer, 1887 [**P. atlantica* Wright & Studer, 1889; SM Wright-S., 1889] [=*Pseudothesea* Kükenthal, 1919]. Colonies branched in one plane. Calyces low, on all sides, armed with thorn scales. Rind with large spindles having strong spines on their outer surfaces. *Rec.,* Atl.-IndoPac. ——Fig. 147,*3*. *P. tenuis* Deichmann, W.Indies; *3a-c,* variously developed thorn scales; *3d,* spinous spindle of rind; *3e,* crutch-shaped central spicule of opercular radius (26n).

Scleracis Kükenthal, 1919 [**S. pumila* (=**Acis guadalupensis* Duchassaing & Michelotti, 1860)]. Colonies branched in one plane, lateral and dichotomous combined. Calyces biserial, alternating. Rind sclerites in 2 layers; in outer, chiefly large warted spindles, somewhat flattened and commonly bent; in inner, mostly straight sparsely warted spindles. *Rec.,* W.Atl.——Fig. 148,*2*. **S. guadalupensis,* Cuba; part of branch with 2 calyces (26n).

Swiftia Duchassaing & Michelotti, 1864 [**Gorgonia exserta* Ellis & Solander, 1786 (*non Thesea exserta* Duch.-M., 1860)] [=*Stenogorgia* Verrill, 1883; *Platycaulos* Wright & Studer, 1889; *Allogorgia* Verrill, 1928]. Colonies with lax branching, chiefly in one plane; polyps scattered or biserial, forming prominent conical calyces, anthocodiae commonly exsert. Rind thin, outer layer filled with spinous rods, spindles, and capstans; inner layer mostly restricted to areas between longitudinal canals, containing only small capstans. Tentacles with stout rods. *Rec.,* IndoPac.-Atl.——Fig. 149,*4*. **S. exserta,* Fla.; *4a,* spindle from tentacles; *4b,* from calyx; *4c,* from outer rind; *4d,* capstans of outer rind; *4e,* small capstans from inner rind between stem canals (26n).

Thesea Duchassaing & Michelotti, 1860 [**T. exserta* Duch-M. (*non Gorgonia exserta* Ellis & Solander, 1786) (=*Thesea guadalupensis* Duch.-M., 1864)]. Colonies usually branched in one plane, branches slender to rather stout; calyces distinct, with 8 marginal teeth formed of simple

© 2009 University of Kansas Paleontological Institute

spindles. Sclerites of rind in 2 layers, outer containing large, spheroidal or platelike bodies with outer faces commonly undulated, inner layer including warted spindles. *Rec.*, W.Atl.——FIG. 149, *5*. *T. grandiflora* DEICHMANN, Barbados; *5a*, spicules of outer rind; *5b*, of inner (26n).

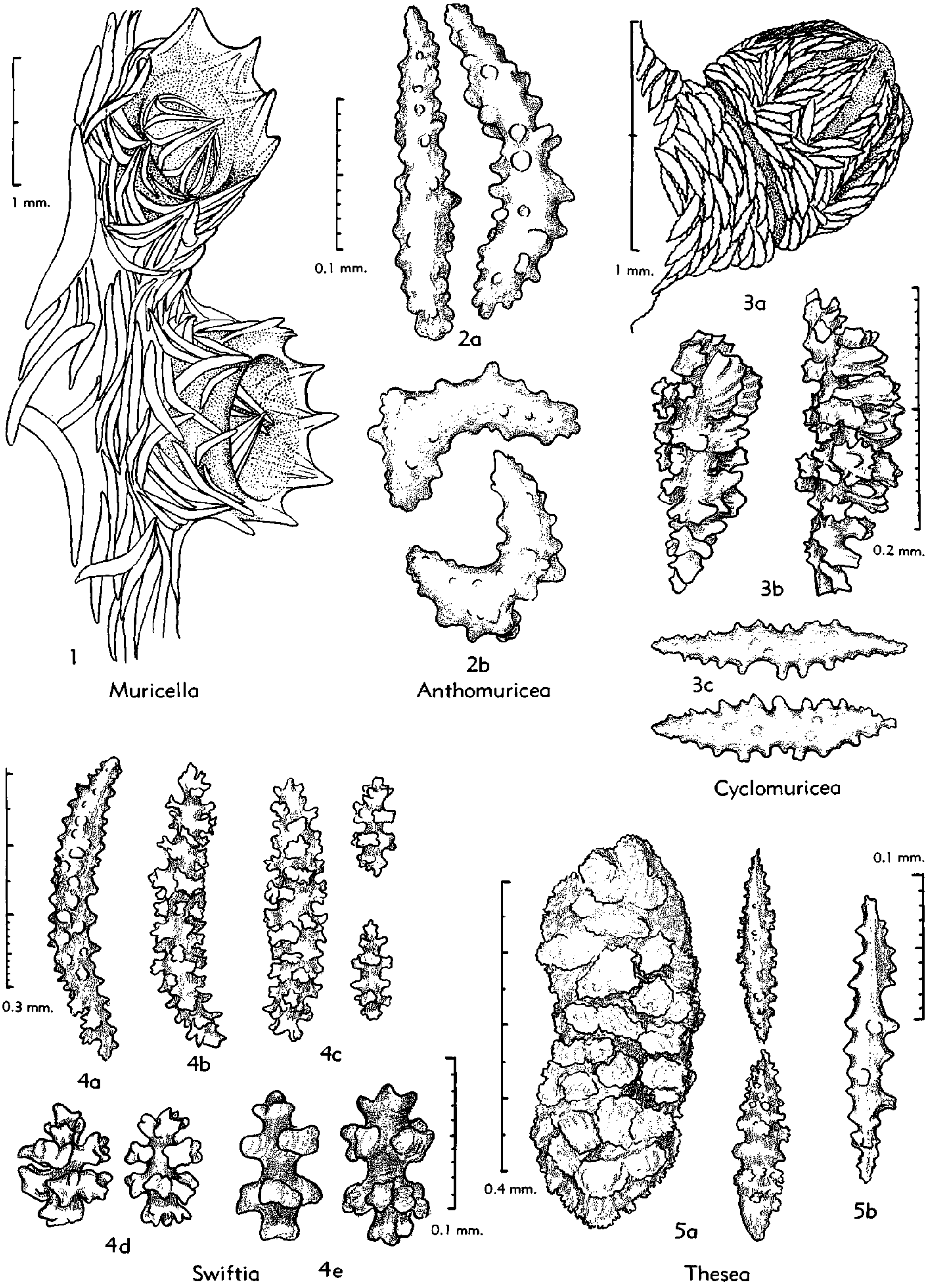


FIG. 149. Gorgonacea: Paramuriceidae (p. F203-F207).

© 2009 University of Kansas Paleontological Institute

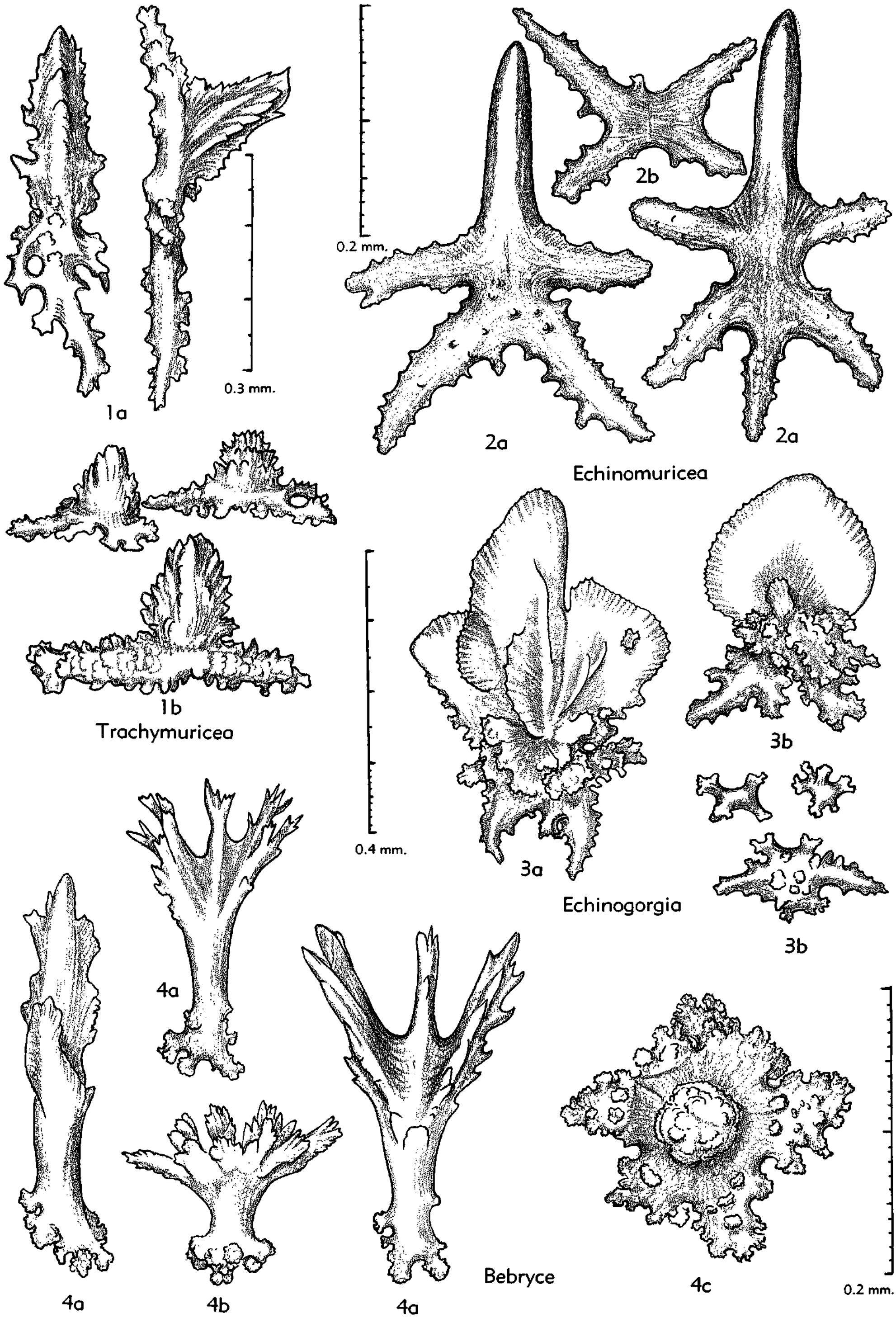


FIG. 150. Gorgonacea: Paramuriceidae (p. F203-F210).

© 2009 University of Kansas Paleontological Institute

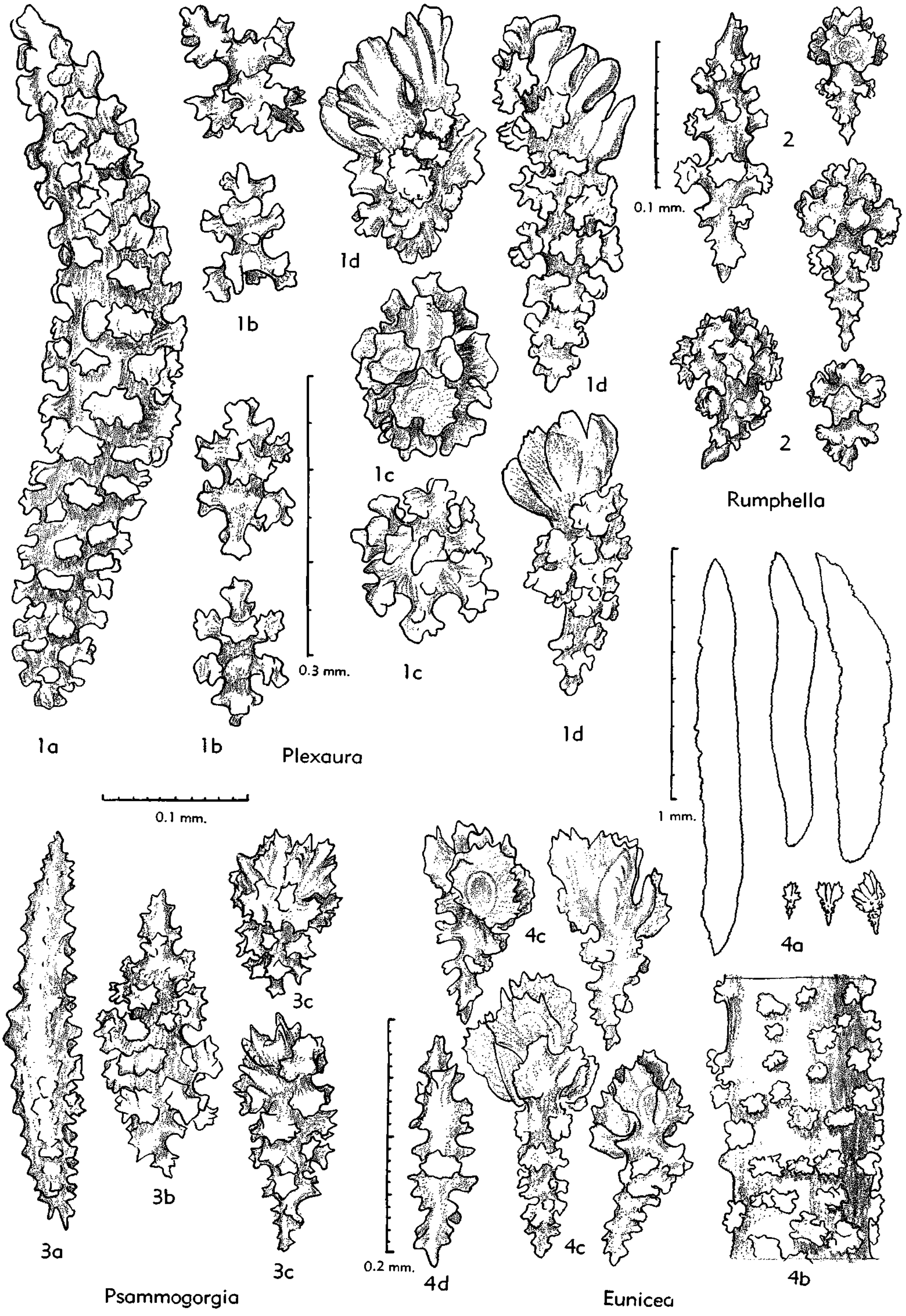


FIG. 151. Gorgonacea: Plexauridae (p. F210-F212).

© 2009 University of Kansas Paleontological Institute

Trachymuricea Deichmann, 1936 [**Acanthogorgia hirta* Pourtalès, 1867]. Small colonies with large, conical calyces and strong opercula of converging rows of spindles above a high collaret. Rind sclerites are spinous rods with rough projecting process; calycular thorn scales with strong, laciniated projection. *Rec.*, W.Atl.——Fig. 150,*1*. **T. hirta*, Fla.; *1a*, calycular thorn scales; *1b*, spicules of outer rind (26n).

Villogorgia Duchassaing & Michelotti, 1860 [**V. nigrescens*] [=*Brandella* Gray, 1869; *Perisceles* Studer, 1887; *Acamptogorgia* Wright & Studer, 1889; *Paracamptogorgia* Kükenthal, 1919]. Colonies branched in one plane; calyces prominent, operculum strong, collaret well-developed. Rind sclerites including specialized thorn scales with spinous, digitate or foliate process. *Rec.*, Atl.-Medit.-IndoPac.——Fig. 147,*4*. **V. nigrescens*, Fla.; *4a*, spicules of stem rind; *4b*, of calyces; *4c*, bent spindle of opercular radius (26n).

Family PLEXAURIDAE Gray, 1859

Colonies of very diverse form but generally with thick branches arising laterally, dichotomously or in some pinnately. Polyps completely retractile or forming distinct calyces into which anthocodiae can be withdrawn. Axis with wide, chambered central chord and peripheral zone of loculated horny material usually containing nonspicular calcareous matter, commonly with tendency toward heavy calcification of base in old colonies. Rind thick, perforated by system of longitudinal canals surrounding axis, which delimits outer and inner (axial sheath) layer of cortex that generally differs in spiculation. Sclerites usually including some form of club, but some with spindles only, oval bodies, or large quadriradiates. *Rec.*

Plexaura Lamouroux, 1812 [**Gorgonia homomalla* Esper, 1792; SD Verrill, 1912] [=*Plexauropsis* Verrill, 1907] Stout, treelike colonies with thick branches, bushy but commonly tending to spread in one plane. Rind thick, polyps fully retractile; without prominent calyces. Outer layer of spicules mostly spindles and clubs, colorless or purple; inner layer with spiny spindles, mostly purple, some colorless; in some species also short, multiradiate bodies. *Rec.*, trop.W.Atl.——Fig. 151,*1*. **P. homomalla*, W.Indies; *1a*, superficial spindle; *1b*, 6-, 7-, and 8-radiates of inner rind; *1c*, multiradiate oval bodies of inner rind; *1d*, superficial clubs (26n).

Anthoplexaura Kükenthal, 1908 [**A. dimorpha*]. Bushy colonies with large, completely unarmed polyps retractile within prominent calyces. Rind with oval spindles sculptured with tall irregularly placed warts and small capstans with tubercles in transverse belts; red. *Rec.*, Japan.

Eunicea Lamouroux, 1816 [**E. mammosa;* SD Bayer, 1955]. Stout, thick-branched, arborescent colonies resembling *Plexaura* but generally with prominent tubular or shelflike calyces; polyps with anthocodial crown and points. Outer layer of rind containing numerous small clubs, commonly foliate, mostly colorless; deeper parts of outer rind with warty spindles, mostly purple; inner rind with colorless and purple spinous spindles. *Rec.*, trop.W.Atl.——Fig. 151,*4*. **E. mammosa*, Bahamas; *4a*, clubs and spindles of outer rind in outline, showing relative sizes; *4b*, sculptural detail of large spindle; *4c*, surface clubs in detail; *4d*, purple spindle of inner rind (26n).

Eunicella Verrill, 1869 [**Gorgonia verrucosa* Pallas, 1766]. Colonies branched scantily or moderately in one plane; calyces prominent or not. Rind with surface layer of characteristic balloon clubs and deeper layer of belted spindles. *Rec.*, Atl.-Medit.-IndoPac.——Fig. 152,*3*. **E. verrucosa*, Spain; *3a*, spindles of inner rind; *3b*, balloon clubs of surface layer (26n).

Euplexaura Verrill, 1865 [**E. capensis*]. Erect colonies branched in one plane, arising from spreading base that bears polyps and commonly short stems also; polyps fully retractile. Rind with superficial layer of oval, coarsely warted sclerites, and deeper layer of capstans. *Rec.*, IndoPac.——Fig. 153,*2*. *E. erecta* Kükenthal, Japan; *2a*, bent spindle from collaret; *2b*, coarse ovoids from rind (26n).

Hicksonella Nutting, 1910 [*non* Simpson, 1910] [**H. princeps*] [=*Rhabdoplexaura* Kükenthal, 1919 (obj.)]. Thick-branched arborescent colonies; polyps retractile into low calyces. Spiculation of capstans commonly modified as clubs and large rods. *Rec.*, IndoPac.——Fig. 152,*4*. **H. princeps*, Japan; *4a*, large rod; *4b*, capstans; *4c*, spindle; *4d*, clubs (26n).

Muricea Lamouroux, 1821 [**M. spicifera*]. Arborescent colonies richly branched, commonly tending to remain in one plane; branches moderately to very thick, with close-set, prickly, tubular or shelflike calyces on all sides. Sclerites usually fusiform, with strong outer or terminal spines or both; rarely some irregular forms. *Rec.*, trop.W.Atl.-E.Pac.——152,*1* **M. spicifera*, W.Indies; *1a*, outlines of large spindles; *1b-c*, spinous spindles at higher power; *1d*, sculptural detail of *1b* (26n).

Muriceopsis Aurivillius, 1931 [**Gorgonia tuberculata* Esper, 1791]. Colonies low, shrublike and irregularly branched, or taller and pinnate; calyces low but usually distinct, with small lower lip. Spicules of outer rind mostly foliate clubs and stout spindles with foliate processes on one side. Inner rind contains symmetrically sculptured spindles, usually bright purple. *Rec.*, trop.W.Atl.——

© 2009 University of Kansas Paleontological Institute

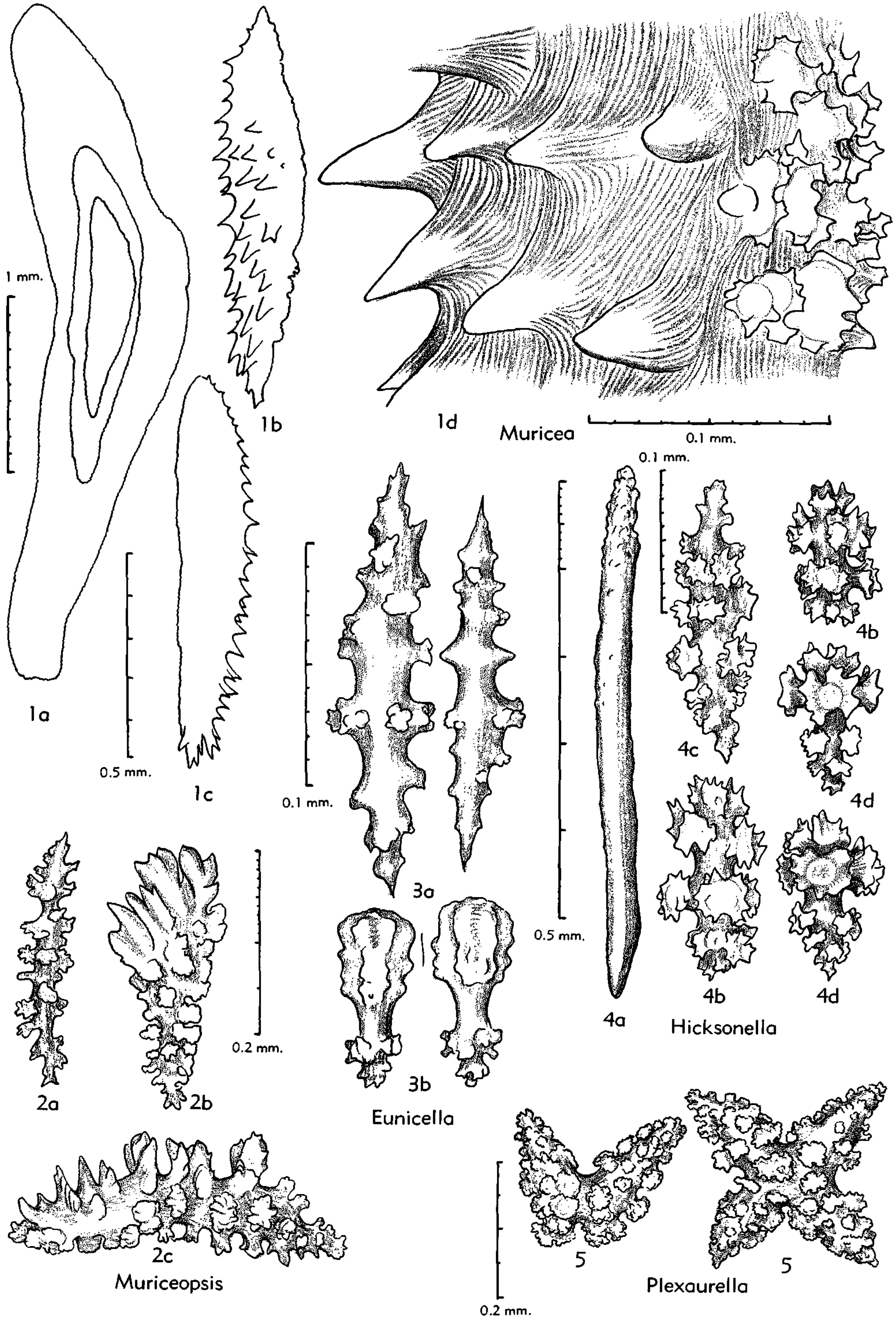


FIG. 152. Gorgonacea: Plexauridae (p. F210-F212).

© 2009 University of Kansas Paleontological Institute

FIG. 152,*2*. *M. flavida* STIASNY, VirginI.; *2a*, purple spindle of inner rind; *2b*, surface club; *2c*, asymmetrical foliate spindle of outer rind (26n).

Paraplexaura KÜKENTHAL, 1909 [**Plexauroides asper* MOROFF, 1902; SD KÜKENTHAL, 1917]. Branching mostly in one plane; polyps forming distinct calyces on all sides. Rind thick, containing warty and leafy clubs, commonly with very coarse heads, some developed into platelike forms; inner rind with fusiform and radiate sclerites. *Rec.*, IndoPac.——FIG. 153,*1*. **P. asper,* Japan; leaf clubs and coarse plate (26n).

Plexaurella VALENCIENNES, 1855 [**Gorgonia dichotoma* ESPER, 1791]. Erect, dichotomously branched colonies with thick, stiff branches; polyps on all sides, fully retractile, with only raised margins at most, none with prominent calyces. Characteristic sclerites are quadriradiates; simple spindles may be present. *Rec.*, trop.W.Atl.——FIG. 152,*5*. **P. dichotoma,* W.Indies; spicules (26n).

Psammogorgia VERRILL, 1868 [**Echinogorgia arbuscula* VERRILL, 1866]. Colonies low, bushy, irregularly branched dichotomously; polyps on all sides, calyces low or absent. Rind rather thick, with spindles and aculeate wart clubs; spicules red. *Rec.*, W.Mexico-Panama.——FIG. 151,*3*. **P. arbuscula,* Costa Rica; spicules (26n).

Rumphella BAYER, 1955 [**Plexaura aggregata* NUTTING, 1910]. Erect, bushy colonies with thick, sinuous or nearly straight branches; axis dark, with abundant calcareous deposits, especially near base which is much thickened and stony in old specimens; polyps on all sides, calyces low or absent. Rind spicules as warty spindles, with superficial layer of small wart clubs having whorl of 3 warts as a head. *Rec.*, E.Indies-Oceania.——FIG. 151,*2*. *R. antipathes,* Rec., GilbertI.; spicules (26n).

Family GORGONIIDAE Lamouroux, 1812

[*nom. correct.* JOHNSON, 1862 (*pro* Gorgonidae *auctt.; nom. correct. pro* family Gorgonieae LAMX., 1812)]

Axis purely horny with narrow but distinct chambered central chord and cortex little loculated, if at all; polyps fully retractile, some forming low calyces, scattered or biserially disposed. Rind moderately thick, packed with spindles and capstans with regular belts of tubercles, in certain genera modified into disc spindles, scaphoids, or unilaterally spined forms; anthocodial armature weak, in form of crown composed of flat rodlets with scalloped edges, or lacking entirely. Colonies of diverse form, from unbranched to pinnate, closely reticulate or foliate. *Rec.*

A number of species of "*Gorgonia*" are recorded as fossils by early authors but these records are almost certainly erroneous. For a few such references see G. FISCHER DE WALDHEIM, *Bibliographia Palaeonthologica Animalium Systematica* (1834).

The genus of fossils called *Plumalina* HALL, 1858, has been placed in this family by some authors (J. S. WILLIAMS, 24), but it has more resemblance to certain delicate plumose hydroids and probably belongs to that group.

Websteria M.EDW.-H., 1850, also was assigned tentatively by its authors to the Gorgoniidae, but probably it does not belong here.

Gorgonia LINNÉ, 1758 [**G. flabellum;* SD VERRILL, 1868] [=*Rhipidigorgia* VALENCIENNES, 1855 (obj.)]. Spicules in form of strong scaphoids and symmetrical spindles. Branches in one plane, closely anastomosing. *Rec.*, W.Indies.——FIG. 153,*3*. **G. flabellum,* Nassau; *3a*, scaphoid; *3b*, spindle (26n).

Antillogorgia BAYER, 1951 [**Gorgonia acerosa* PALLAS, 1766]. Spicules are slender scaphoids and symmetrical spindles. Branches closely pinnate, not anastomosing. *Rec.*, W.Indies.——FIG. 153,*8*. **A. acerosa,* Key West; *8a*, scaphoids; *8b*, spindle (26n).

Eugorgia VERRILL, 1868 [**Leptogorgia ampla* VERRILL, 1864]. Spicules chiefly disc spindles; ordinary spindles present in small numbers in some species. Branching lateral, in one plane or bushy. *Rec.*, Calif.-Peru.——FIG. 153,*4*. **E. ampla,* Acapulco; *4a*, disc spindles in side, end and oblique views; *4b*, spindle (26n).

Leptogorgia M.EDW.-H., 1857 [**Gorgonia viminalis* PALLAS, 1766; SD VERRILL, 1868]. Spicules are spindles, shorter ones with warts of one side fused like those of disc spindles; long ones symmetrical or with warts on one side simple and conical, elsewhere compound. Colonies little-branched, slender, and whiplike. *Rec.*, W.Atl.——FIG. 153,*7*. **L. viminalis,* W.Fla.; *7a*, short, almost disc spindle, and top view of one disc; *7b*, spindle (26n).

Lophogorgia M.EDW.-H., 1857 [**Gorgonia palma* PALLAS, 1766]. Spicules exclusively symmetrical spindles without unilateral fusion of warts to form discs; anthocodial armature of flattened rods may be present. Branches long and slender, or short and pinnately arranged, in one plane or bushy. *Rec.*, Atl.-Medit.-IndoPac.——FIG. 153,*5*. **L. palma,* S.Afr.; *5a*, spindles of rind; *5b*, rods from crown (26n).

Pacifigorgia BAYER, 1951 [**Gorgonia stenobrochis* VALENCIENNES, 1846]. Spicules as in *Lophogorgia*, commonly long and pointed. Branches in one plane and closely anastomosed to form netlike fans. *Rec.*, GulfCalif.-Panama-Brazil.

Phycogorgia M.EDW.-H., 1850 [**Gorgonia fucata*

© 2009 University of Kansas Paleontological Institute

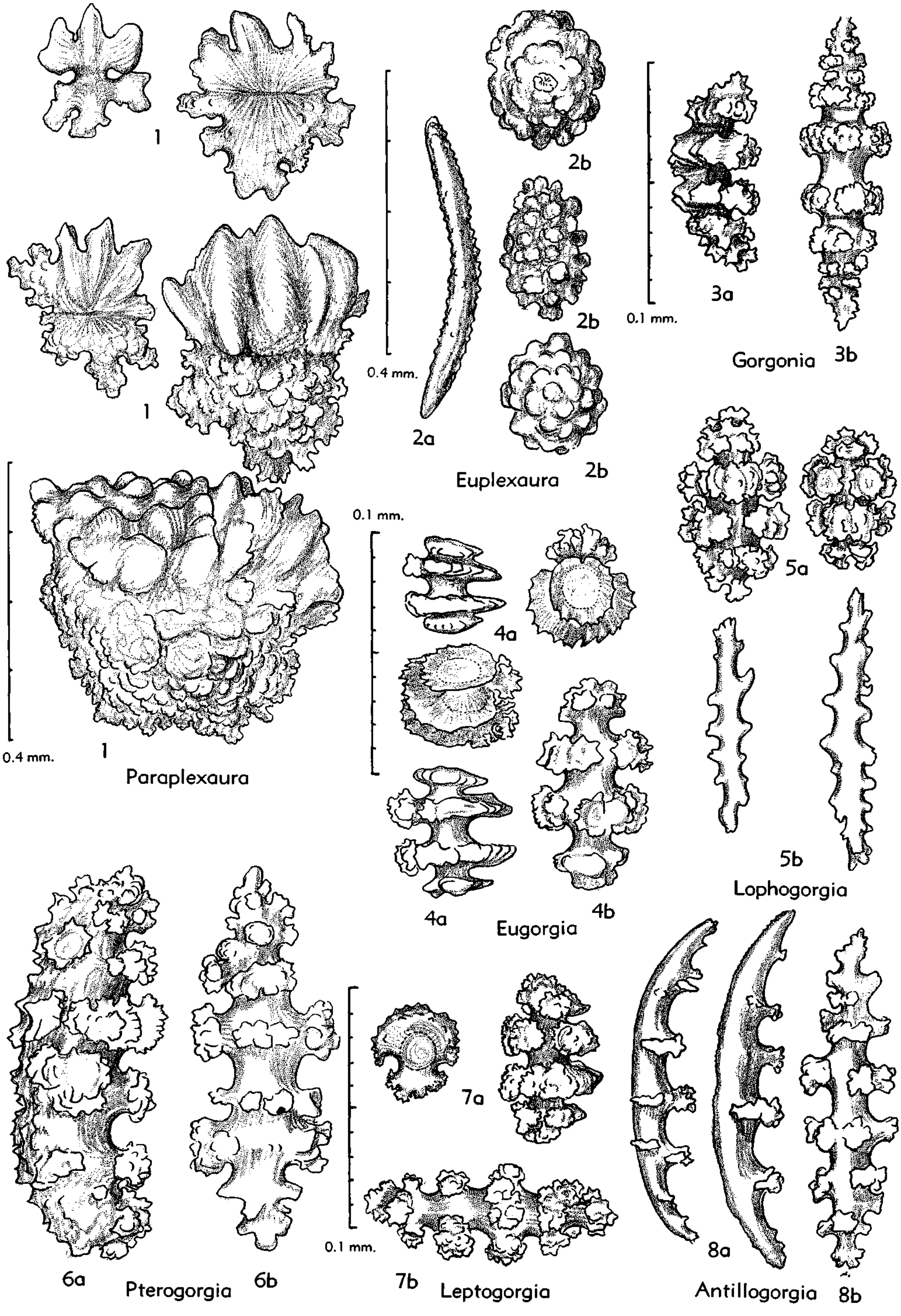


FIG. 153. Gorgonacea: Plexauridae, Gorgoniidae (p. F210-F214).

© 2009 University of Kansas Paleontological Institute

VALENCIENNES, 1846] Spicules exclusively short, blunt, symmetrical capstans. Branches flattened into broad fronds, with lamellar axis. *Rec.*, Mazatlan-Chile.

Phyllogorgia M.EDW.-H.,, 1850 [**Gorgonia dilatata* ESPER, 1806]. Spicules including scaphoids as well as spindles. Branches flattened into broad fronds, with loosely reticulating axis. *Rec.*, Brazil.

Pterogorgia EHRENBERG, 1834 [**Gorgonia anceps* PALLAS, 1766; SD M.EDW.-H., 1850] [=*Xiphigorgia* M.EDW.-H., 1857 (obj.)]. Spicules are very coarse spindles and scaphoids. Ramification lax, branches rather long; polyps bi- or triserial, retracting into thin, raised coenenchymal flanges. *Rec.*, W.Indies.——FIG. 153,6. **P. anceps*, Curaçao; *6a*, scaphoid; *6b*, spindle (26n).

Family ELLISELLIDAE Gray, 1859

[*nom. correct.* BAYER, 1955 (*pro* Elliselladae GRAY, 1859)]

Axis strongly calcified, made up of concentric layers not markedly undulating, central chord not soft and chambered; calcareous material deposited in irregular radial sectors (4). Colonies unbranched, loosely branched, or forming broad, flat fans with or without anastomoses. Spicules small (0.05-0.15 mm.), of characteristic dumbbell shape, some modified into clubs, and longer double spindles, all regularly sculptured with strong, hemispherical tubercles. *Cret.-Rec.*

Ellisella GRAY, 1858 [**Gorgonia elongata* PALLAS, 1766; SD NUTTING, 1910] [=*Scirpearia* KÖLLIKER, 1865, and later authors (*non* CUVIER, 1817, 1830); *Viminella* GRAY, 1870]. Colonies simple or with few long, whiplike branches; calyces biserial or in lateral tracts, usually prominent. Spicules including double spindles approaching 0.2 mm. in length concentrated in calyces, and double heads or dumbbells half as long or less, chiefly in general cortex. *Rec.*, Atl.-Medit.-RedS.-IndoPac.——FIG. 154,4. *E. funiculina* (DUCHASSAING & MICHELOTTI), Rec., GulfMexico; dumbbells from calyces and spindles from rind (26n).

Ctenocella VALENCIENNES, 1855 [**Gorgonia pectinata* PALLAS, 1766]. Branching characteristically lyrate. Spicules chiefly stout double heads. *Rec.*, IndoPac.——FIG. 154,5. **C. pectinata*, Torres Straits; *5a*, colony (30); *5b*, spicules (26n).

Junceella VALENCIENNES, 1855 [**Gorgonia juncea* PALLAS, 1766; SD NUTTING, 1910]. Colonies simple or dichotomously branched, calyces usually distinct and biserially disposed, some generally scattered. Characteristic sclerites are flattened clubs in outer cortex and dumbbells with strong, conical warts in thin axial sheath layer. *?Eoc., Rec.*, IndoPac.——FIG. 154,*2*; 158,*2*. **J. juncea*, Rec., Philip.; 154,*2a*, dumbbell from axial sheath zone; 154,*2b*, face and edge view of cortical club; 158,*2a*, axis in transverse, 158,*2b* in longitudinal section (left margin of *2b* follows edge of central chord), as seen in polarized light (all 26n).

Nicella GRAY, 1870 [**N. mauritiana* (=**Scirpearia dichotoma* GRAY, 1859)]. Colonies ramified in one plane, branches usually slender and cylindrical; polyps biserial, with hemispherical calyces. Rind with inner layer of double spindles up to twice length of dumbbells of outer layer. *Rec.*, IndoPac.-Atl.——FIG. 154,*3*. *N. guadalupensis* DUCHASSAING & MICHELOTTI, Barbados; spicules (26n).

Riisea DUCHASSAING & MICHELOTTI, 1860 [**R. paniculata*]. Colonies finely divided, with numerous very slender branchlets arranged on main branches in alternating pinnate fashion; core of axis excentric; calyces prominent, clavate, placed at ends of short twigs and along upper side of branchlets. Spiculation much as in *Nicella*, with dumbbells in rind and long, tapered spindles (longer ones flattened) in calyces. *Rec.*, trop.W.Atl.——FIG. 155, *2;* 158,*3*. **R. paniculata*, Porto Rico; 155,*2a*, rods of calyces; 155,*2b*, dumbbells of rind; 155,*2c*, branchlet, 158,*3a,b*, axis in transverse and long. sect. (light zone along left edge of *3b* is axial core), as seen in polarized light (all 26n).

Toeplitzella DEICHMANN, 1936 [**Junceella laevis* VERRILL, 1866]. Like *Ellisella* but no long double spindles. *Rec.*, IndoPac.

Verrucella M.EDW.-H., 1857 [**Gorgonia flexuosa* LAMARCK, 1816 (=**Gorgonia umbraculum* ELLIS & SOLANDER, 1786); SD BAYER, 1955]. Colonies flabellate, some reticulate, branches slender; polyps with distinct verruciform calyces. Rind containing slender double heads and somewhat longer double spindles; twin or triplet forms producing crosses or stars may be more or less numerous. *Cret.(Dan.)-Rec.*, Eu.-RedS.-IndoPac.——FIG. 154,*1*. *V. delicatula* (NUTTING), *Rec.*, Philip.; spicules (26n).

Family IFALUKELLIDAE Bayer, 1955

Arborescent, with strongly calcified axis made up of gently undulating concentric lamellae, calcareous material not oriented in radial sectors, central chord not soft and cross-chambered. Sclerites minute (less than 0.1 mm. in length), flattened oval biscuit-shaped, or double discs, with irregular surfaces, very similar to spicules of *Xenia* and polyps of *Tubipora*. *Rec.*

Ifalukella BAYER, 1955 [**I. yanii*]. Colonies densely bushy, not pinnate; axis spirally ridged, arising from massive calcareous base onto which ridges extend as high, calcareous crests with lobed, in many places strongly laciniated, edges that may give rise to small twigs, which here and there develop into full-sized colonies. Spicules extremely

© 2009 University of Kansas Paleontological Institute

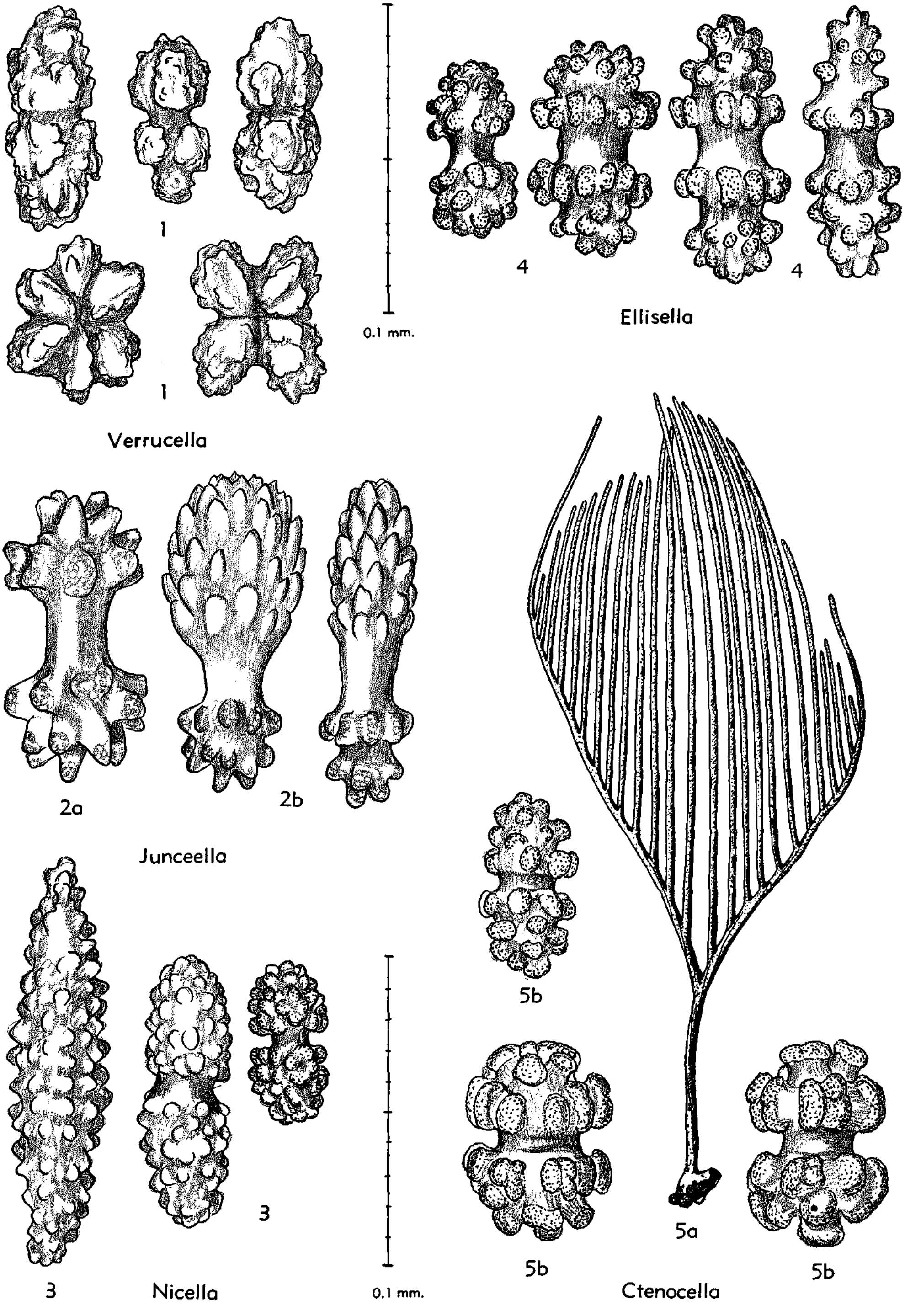


FIG. 154. Gorgonacea: Ellisellidae (p. F214).

© 2009 University of Kansas Paleontological Institute

scarce, those present being mostly oval rods with some twin forms. Zooxanthellae extraordinarily numerous. Distribution unknown, but type species is frequent at Ifaluk Atoll (Carolines), where it is the one abundant reef-dwelling gorgonian, inhabiting reef fronts beyond surge-channels in 15 or 20 feet of water; apparently quite restricted ecologically. Its peculiar, calcareous base should be easy to recognize if found in reef limestones, and might be a good paleoecological indicator. *Rec.* ——FIG. 156,*2*. **I. yanii; 2a,* spicules (circle represents relative size of zooxanthellae); *2b,* calcareous colonial base (26).

Plumigorgia NUTTING, 1910 [**P. hydroides*]. Colonies delicate, flexible, pinnately branched, arising from calcareous base. Polyps forming calyces or wholly retractile into general coenenchyme. Spicules numerous. *Rec.,* SuluArch.-ChinaS.——FIG. 156,*1*. **P. hydroides;* spicules (26).

Family CHRYSOGORGIIDAE Verrill, 1883

Axis highly calcified, continuous, glossy, iridescent or metallic, made up of smooth concentric lamellae (Fig. 158,*1*), rarely undulating; calcareous matter not oriented in radial sectors; branching may not occur, but more frequently does so in a very regular order, uniserial, spiral or dichotomous. Sclerites are basically rods, commonly sharp and needle-like or flattened and becoming scale- or platelike. The oval or elongate scales of the Chrysogorgiidae show in polarized light brilliant interference colors, concentrically arranged (Fig. 158,6), but never a cruciform pattern radiating out from the center. Base may be either a large, branched, calcareous root or a small disc, former being adapted for life on soft bottoms and latter for attachment to rocks or other solid material. *Rec.*

Subfamily LEPIDOGORGIINAE Versluys, 1902

Colonies unbranched; polyps uniserial, without operculum of 8 plates. *Rec.*

Radicipes STEARNS, 1883 [**R. pleurocristatus*] [=*Lepidogorgia* VERRILL, 1884]. Sclerites of polyps mostly fusiform rods; of rind, variable but commonly consisting of small scales. Roots subdivide dichotomously, forming long zigzag processes by dominance of alternate branches of succeeding dichotomies. *Rec.,* Atl.-IndoPac.—FIG. 156,*3*. **R. pleurocristatus,* Japan; *3a,* sclerites; *3b,* sculptural detail of spicule; *3c,* part of branch with calyces; *3d,* the rootlike colonial base (26n).

Subfamily CHRYSOGORGIINAE Verrill, 1883

Colonies with main stem giving rise to branches, which may be either simple or further branched. Polyps with rods or scales but no specialized operculum of 8 plates. *Rec.*

Chrysogorgia DUCHASSAING & MICHELOTTI, 1864 [**C. desbonni*]. Colonies erect, sympodial, branches arranged in a spiral and dichotomously subdivided in one plane or in alternating planes at right angles to each other. *Rec.,* Atl.-IndoPac.——FIG. 155,*3;* 158,*6*. *C. elegans* VERRILL, W.Atl.; 155,*3a,* colonies (25); 155,*3b,* spicules (26n); 158,6, scale in polarized light.

Iridogorgia VERRILL, 1883 [**I. pourtalesii*]. Colonies monopodial, main trunk coiled in upright spiral with simple branchlets arising from its outer side in single series. *Rec.,* W.Atl.-Hawaii.——FIG. 157,*4,* **I. pourtalesii,* Dominica; colony (25).

Metallogorgia VERSLUYS, 1902 [**Dasygorgia melanotrichos* WRIGHT & STUDER, 1889]. Colonies monopodial, straight main trunk distally giving off strong lateral branches, which profusely subdivide in a dichotomous pattern. *Rec.,* IndoPac.-Atl.——FIG. 158,*1*. **M. melanotrichos;* axis in thin section, in polarized light; *1a,* cross; *1b,* longitudinal.

Pleurogorgia VERSLUYS, 1902 [**P. plana*]. Main branches with simple branchlets uniserially placed along one side; polyps chiefly on branchlets, uniserial. Sclerites are spindles and very irregular bodies. *Rec.,* IndoPac.——FIG. 157,*5*. **P. plana,* Moluccas; spicules and branching pattern (36).

Trichogorgia HICKSON, 1905 [**T. flexilis*]. Colonies branched mostly in a plane, some with long terminal branches; calyces thickly set on all sides. *Rec.,* S.Afr.-W.Atl.

Subfamily CHALCOGORGIINAE Bayer, 1949

Colonies unbranched, zooids biserial. Sclerites of rind are medially constricted scales, those of zooids irregularly lobed plates, 8 triangular plates forming a distinct operculum. *Rec.*

Chalcogorgia BAYER, 1949 [**C. pellucida*]. *Rec.*——FIG. 155,*1*. **C. pellucida,* Cuba; *1a,* part of stem; *1b,* single calyx; *1c,* colonial base; *1d,* calycular scales; *1e,* opercular scale; *1f,* accessory rods lying between opercular scales (26).

Family PRIMNOIDAE Gray, 1857

[*nom. correct.* VERRILL, 1868 (*pro* Primnoadae GRAY, 1857)]

Axis strongly calcified, unjointed, made up of undulated concentric layers (Fig. 158,*4*), core not a soft, chambered central chord, base a calcareous disc, rarely a branched, rhizoidal structure. Colonies usually profusely branched, rarely flagelliform; polyps

© 2009 University of Kansas Paleontological Institute

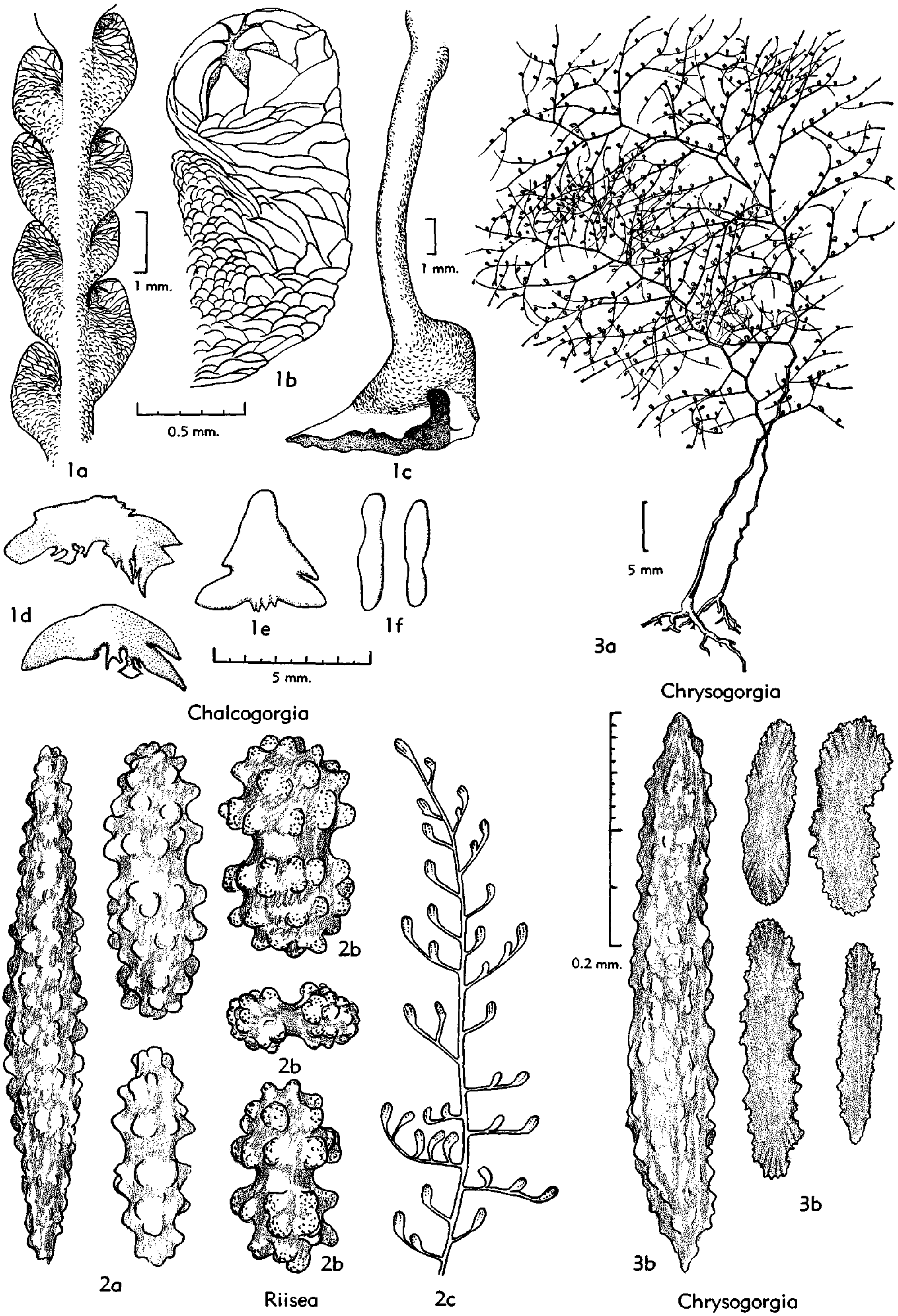


FIG. 155. Gorgonacea: Ellisellidae, Chrysogorgiidae (p. F214-F216).

© 2009 University of Kansas Paleontological Institute

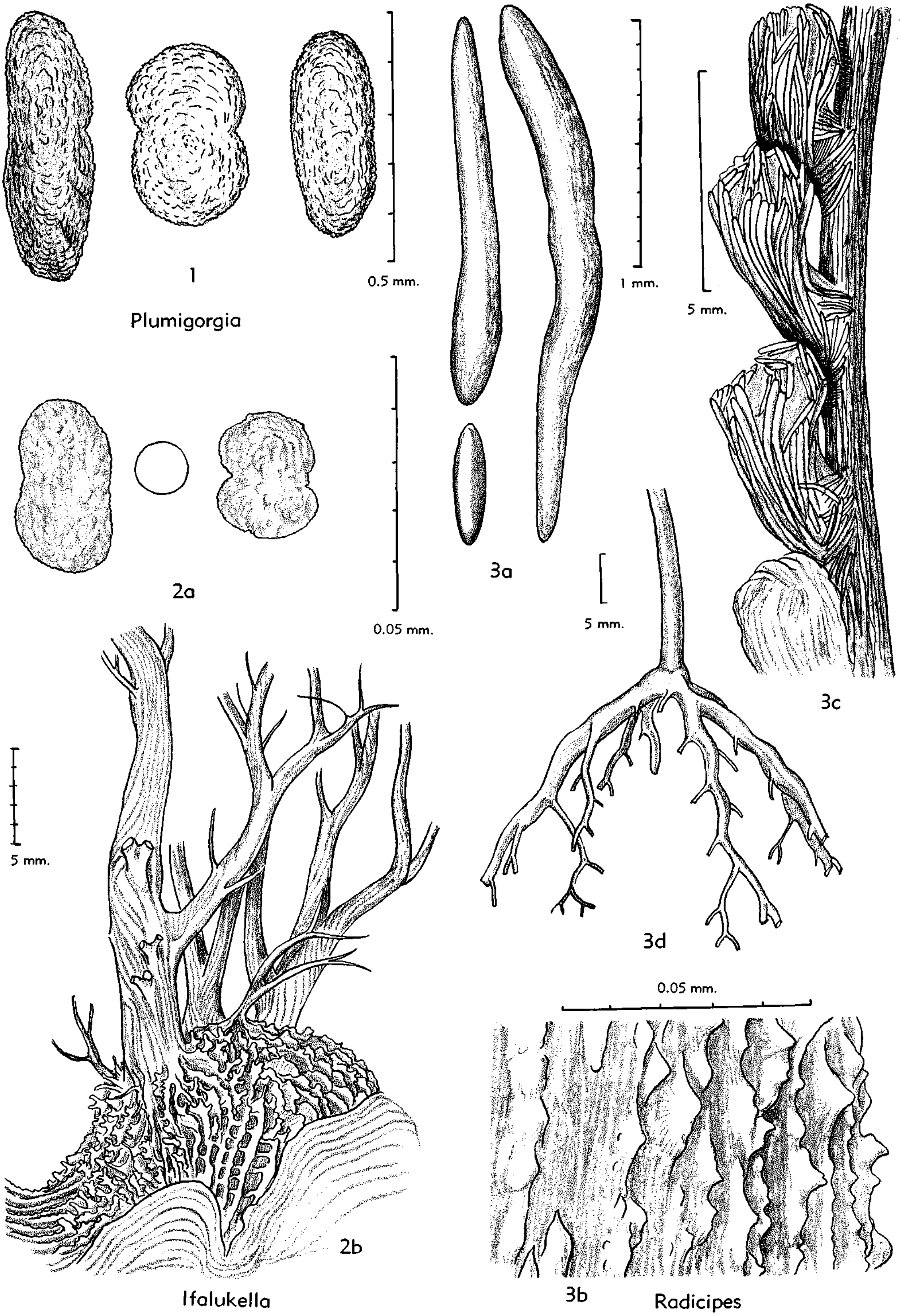


FIG. 156. Gorgonacea: Ifalukellidae, Chrysogorgiidae (p. F214-F216).

© 2009 University of Kansas Paleontological Institute

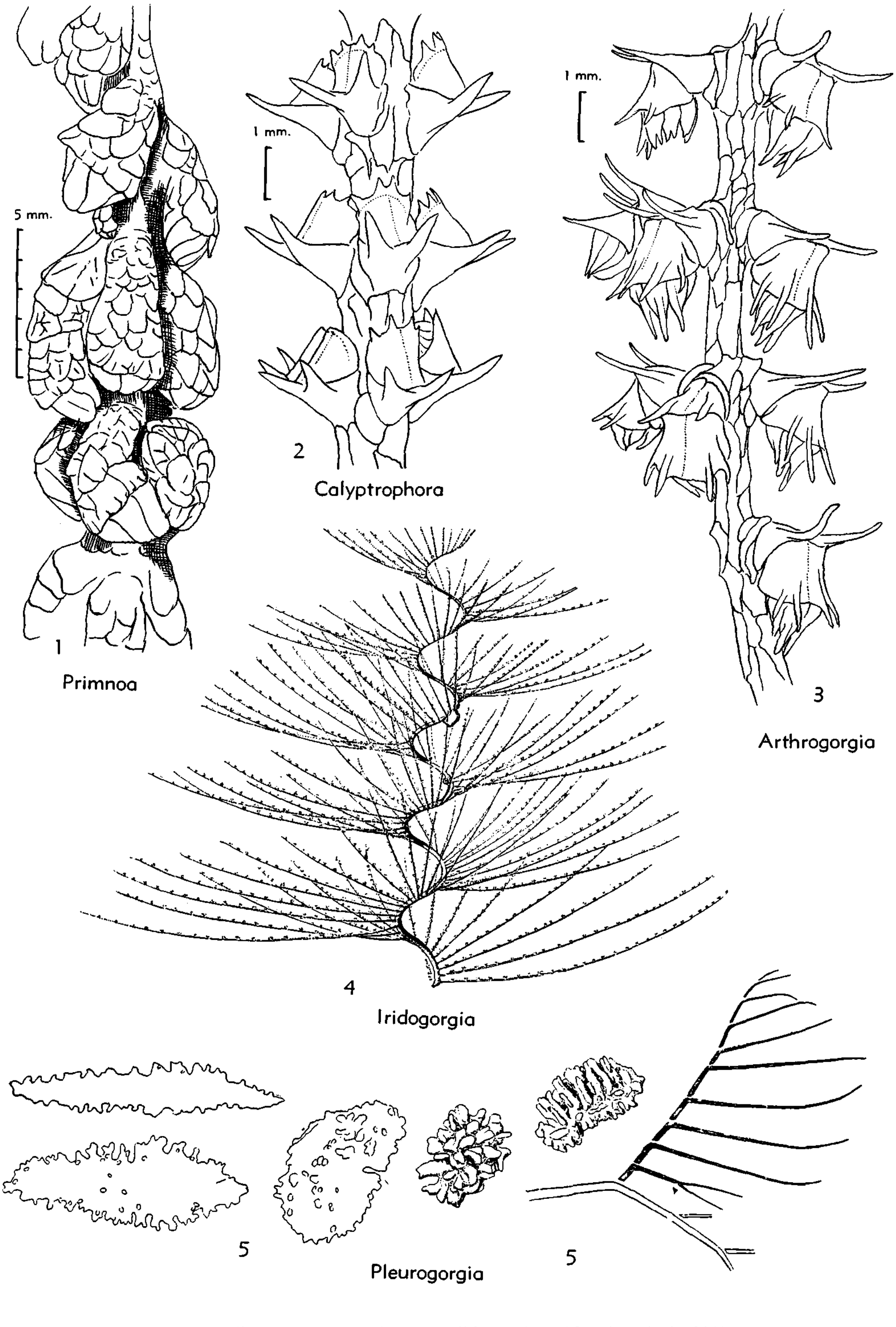


Fig. 157. Gorgonacea: Chrysogorgiidae, Primnoidae (p. F216-F222).

© 2009 University of Kansas Paleontological Institute

single, in pairs, or regular whorls, heavily armored with calcareous scales (Fig. 158,*5*) and permanently exsert; in contraction tentacles are infolded and protected by 8 triangular scales making up a distinct operculum, below which scales of polyp body are aligned in 8 rows, some of which may be reduced or missing on adaxial side; rarely (1 sp.) scales not regularly arranged and operculum undifferentiated. In rind, a layer of plates or scales, commonly elongate, some with an inner layer of stellate spicules. *Cret.-Rec.*

The scalelike sclerites of the Primnoidae can always be distinguished by the cruciform pattern of extinction that they show in polarized light (dark field) (Fig. 158,*5*, *Primnoella*). The scales of chrysogorgiids, isidids and pennatulids never show such a pattern.

Subfamily PRIMNOEIDINAE Studer, 1887

Polyps without differentiated operculum, body scales not in rows. *Rec.*

Primnoeides Studer, 1887 [**Primnoides sertularoides* Wright & Studer, 1889; SM Wright-S., 1889]. *Rec.*, Ind.O.

Subfamily PRIMNOINAE Gray, 1857

[*nom. transl.* Studer, 1887 (*ex* Primnoidae *nom. correct.* Verrill, 1868, *pro* Primnoadae Gray, 1857)]

Polyps with well-differentiated operculum, body scales in 8 complete or incomplete rows, some of which may be missing. *Cret.-Rec.*

Primnoa Lamouroux, 1812 [**Gorgonia lepadifera* Linné, 1767 (=**Gorgonia reseda* Pallas, 1766)]. Colonies treelike, dichotomously branched, commonly very large; axis densely calcareous; polyps thickly distributed all around twigs and branches, irregularly oriented but commonly facing downward, especially at twig tips; polyps large (up to 5 mm. long) with 8 opercular and 8 marginal scales, but body scale rows reduced; adaxial surface of polyps without scales. Rind sclerites are scales. *U.Cret.-Rec.*, Arct.——Fig. 157,*1*. **P. reseda* (Pallas), *Rec.*, Grand Banks; part of branch with polyps (26n).

Callogorgia Gray, 1858 [**Gorgonia verticillata* Pallas, 1766]. Colonies usually pinnately branched, some dichotomously, mostly in one plane; axis longitudinally striated, commonly iridescent; polyps in regular whorls, bent inward; adaxial rows of body scales reduced; spicules usually elaborately sculptured externally; cortical sclerites thick and pebble-like or more elongate. *Rec.*, Atl.-Medit.-IndoPac.-Arct.-Antarct.——Fig. 158,*4*; 159,*2*. **C. verticillata*, W.Indies; 158,*4*, cross section of axis in polarized light; 159,*2*, part of branch with 3 whorls of polyps (26n).

?**Eogorgia** Hickson, 1938 [**E. sullivani*]. Stout, straight primnoid axis assigned by Hickson to Scleraxonia; not definitely assignable to any subfamily but its size suggests Primnoinae. *Eoc. (Jackson.)*, Miss.

Plumarella Gray, 1870 [**Gorgonia penna* Lamarck, 1815]. Branching in one plane, pinnate, closely so in many; polyps biserial, alternate or rarely opposite, never in whorls. All 8 rows of body scales present, adaxials of some with fewer scales. Cortical sclerites of some species scales or warty radiates in lower parts of colony and inner rind. *Rec.*, Atl.-Medit.-IndoPac.——Fig. 159,*7*. **P. pourtalesii* (Verrill), Fla.; part of branch with polyps (26n).

Primnoella Gray, 1858 [**Primnoa australasiae* Gray, 1849]. Colonies branched sparingly or not at all, stems long and whiplike; polyps in whorls, closely appressed to stem. Opercular scales more or less overreached by marginals; abaxial rows of body scales well developed, adaxials reduced or wanting. Superficial sclerites of rind are scales; commonly an inner layer with small, warty sclerites is present. *Rec.*, Atl.-IndoPac.-Arct.-Antarct.——Fig. 158,*5*; 159,*1*. *P. polita* Deichmann, W. Indies; 158,*5*, scale in polarized light; 159,*1*, part of stem with whorls of polyps (26n).

Pseudoplumarella Kükenthal, 1915 [**Plumarella thetis* Thomson & Mackinnon, 1911]. Similar to *Plumarella*, but polyps may be in whorls. Opercular scales 8, but marginals fewer than 8; fewer than 8 rows of body scales. *Rec.*, Indo-Austral.

Thouarella Gray, 1870 [**Primnoa antarctica* Valenciennes, 1846]. Main stem producing short, slender branches all around, like bottle-brush. Marginal scales overreach operculars; rows of body scales commonly reduced. *Rec.*

T. (Thouarella) [=*Parathouarella* Kükenthal, 1915]. Polyps irregularly distributed. Marginal scales with foliate process. *Rec.*

T. (Euthouarella) Kükenthal, 1915 [**Plumarella hilgendorfi* Studer, 1878; SD Bayer, herein]. Polyps in pairs or whorls of 3 to 4. Marginal scales with median spine. *Rec.*, IndoPac.——Fig. 159,*3*. **T.* (*E.*) *hilgendorfi*, Philip.; part of branch with polyps (26n).

T. (Epithouarella) Kükenthal, 1915 [**Thouarella crenelata* Kükenthal, 1907; SD Bayer, herein]. Polyps closely placed all around branches, but not in whorls. Marginal scales without projecting spine; body scales dentate. *Rec.*, Antarct.

Subfamily CALYPTROPHORINAE Gray, 1870

[*nom. transl. et correct.* Studer, 1887 (*ex* Calyptrophoradae Gray, 1870)]

Polyps with operculum well differentiated; large body scales reduced to 2 or 3 pairs of plates curved to encircle zooid; adaxial marginal scales retained in some as "adaxial buccal scales." *Rec.*

© 2009 University of Kansas Paleontological Institute

Calyptrophora Gray, 1866 [**C. japonica*]. Two pairs of large body scales meeting or nearly meeting adaxially so as to encircle polyp, in some inseparably fused ring-wise; only one pair of infrabasal scales connecting body scales to those of rind; never any vestigial adaxial buccal scales. Branching dichotomous or unilateral pinnate, commonly in one plane, in some flabellate. *Rec.*, Atl.-IndoPac.——Fig. 157,*2*. **C. japonica*, Japan; branch with 3 whorls of polyps (26n).

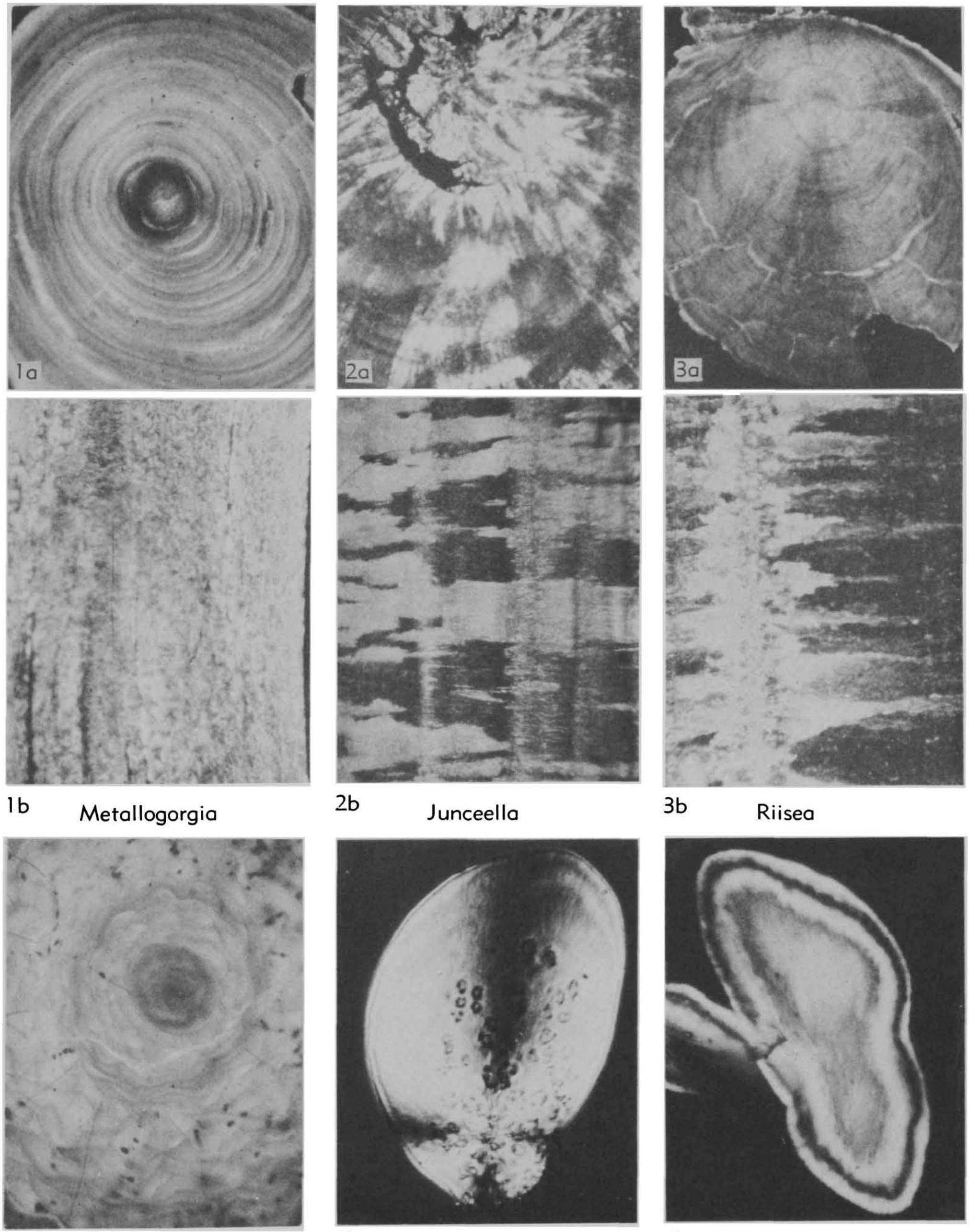


Fig. 158. Gorgonacea: Ellisellidae, Chrysogorgiidae, Primnoidae (p. F214-F220).

© 2009 University of Kansas Paleontological Institute

Arthrogorgia Kükenthal, 1908 [**A. membranacea* (=**Calyptrophora ijimai* Kinoshita, 1907)]. Like *Calyptrophora* but more than one pair of infrabasal scales and some vestigial adaxial buccals present. Branching pinnate or dichotomous. *Rec.*, NW. Pac.——Fig. 157,*3*. **A. ijimai,* Japan; part of branch with whorls of polyps (26n).

Narella Gray, 1870 [**Primnoa regularis* Duchassaing & Michelotti, 1860] [=*Stachyodes, Calypterinus* Studer, 1887]. Three or 4 pairs of large body scales partially encircling polyp but rarely meeting adaxially; adaxial buccal scales commonly present. Branching pinnate, dichotomous, or trichotomous. *Rec.*, Atl.-IndoPac.-Antarct.——Fig. 159, *5*. **N. regularis,* W.Indies; part of branch with 3 whorls of polyps (26n).

Subfamily CALLOZOSTRINAE Studer, 1887

Polyps with operculum well differentiated; polyps in whorls, erect, not bent inward toward stem. *Rec.*

Callozostron Wright, 1885 [**C. mirabile*]. Polyps in close-set whorls of at least 8. Marginal scales with long, projecting spines. *Rec.*, Antarct.

Candidella Bayer, 1954 [*pro Stenella* Gray, 1870 (*non* Gray, 1866)] [**Primnoa imbricata* J. Y. Johnson, 1862]. Polyps in widely spaced whorls of up to 5.

C. (Candidella). Marginal scales 4. *Rec.*, Atl.-IndoPac.——Fig. 159,*4b*. **C. (C.) imbricata,* W. Indies; part of branch with 3 whorls of polyps (26n).

C. (Parastenella) Versluys, 1906 [**Stenella doederleini* Wright & Studer, 1889; SD Bayer, herein]. Marginal scales 8. *Rec.*, IndoPac.——Fig. 159,*4a*. **C. (P.) doederleini,* Japan; part of branch with 3 whorls of polyps (26n).

Family AINIGMAPTILIDAE Carlgren, 1943

[*nom. correct.* Bayer, 1950 (*pro* Ainigmaptilonidae Carlgren, 1943)]

Axis strongly calcified; polyps borne on expanded, unsupported, simple or branched polyp leaves. Spicules are thin scales; operculum of 8 scales. *Rec.*

Ainigmaptilon Dean, 1926 [**A. haswelli*] [=*Lycurus* Molander, 1929]. Several specimens of various species are provided with expanded funnel-like base, apparently adapted for anchoring colony by enclosing a lump of mud. *Rec.*, Antarct. ——Fig. 159,*6*. *A. edisto* Bayer; *6a,* polyp leaf; *6b,* isolated polyp; *6c,* body scales; *6d,* opercular scale (26).

Family ISIDIDAE Lamouroux, 1812

[*nom. correct.* Kükenthal, 1915 (*pro* Isideae Lamx., 1812)]

Axis composed of alternating purely horny nodes and nonspicular calcareous internodes; base may be either a rootlike calcareous structure for anchoring colony in soft bottom or a basal disc for attachment to hard objects. *Cret.-Rec.*

Subfamily KERATOISIDINAE Gray, 1870

[*nom. transl. et correct.* Bayer, herein (*ex* Keratoisidae Gray, 1870)] [=Ceratoisidinae Studer, 1887]

Polyps nonretractile, with spindles, needles or rods placed along septa. *Rec.*

Keratoisis Wright, 1869 [**K. grayi*]. Colonies with branching from calcareous internodes, some unbranched; internodes hollow or solid. Polyps cylindrical, irregularly disposed but with tendency toward biserial arrangement; distal part of polyp body with 8 longitudinal rows of spindles and needles, some projecting beyond tentacles; stellate forms in pharynx. *Rec.*, Atl.-IndoPac.——Fig. 160, *1*. *K. ornata* Verrill, Grand Banks; section of stem with node, and internode with branch; short, horny node at base of branch is not an invariable feature (26n).

Acanella Gray, 1870 [**Mopsea arbusculum* Johnson, 1862]. Colonies bushy, branched in whorls from horny nodes. Spicules of calyces are mostly spindles and some flattened blunt rods, with fine prickles or low warts. *Rec.*, Atl.-IndoPac.——Fig. 160,*3*. **A. arbuscula,* Grand Banks; *3a,* entire colony (25); *3b,* tip of branch with terminal polyp (26n); *3c,* node with one branch (26n).

Isidella Gray, 1857 [**Isis elongata* Esper, 1788]. Colonies branched from nodes dichotomously and in one plane; internodes hollow. Calycular sclerites mostly rodlets which do not project. *Rec.*, E. Atl.-Medit.

Lepidisis Verrill, 1883 [**L. caryophyllia;* SD Kükenthal, 1915]. Colonies simple or sparsely branched from nodes; internodes hollow. Calycular sclerites projecting needles and elongate scales. *Rec.*, Atl.-?IndoPac.——Fig. 160,*2*. **L. carophyllia,* NW.Atl.; *2a,* polyp; *2b,* colonial base; *2c,* scales, and *2d,* rods from calyces (26n).

Subfamily MOPSEINAE Gray, 1870

[*nom. transl. et correct.* Wright & Studer, 1889 (*pro* Mopseadae Gray, 1870)]

Polyps nonretractile, with transversely arranged platelike sclerites; branching from internodes. *Eoc.-Rec.*

Mopsea Lamouroux, 1816 [**Isis dichotoma* Linné, 1758; SD M.Edw.-H., 1850]. Colonies branched pinnately or dichotomously in one plane. *Eoc.-Rec.*, MalayArch.-Austral.-Antarct.——Fig. 161,*3*. *M. elongata* Roule, Rec., Antarct.; 2 internodes (26n).

Peltastisis Nutting, 1910 [**P. uniserialis*]. Colonies unbranched; polyps with operculum of 8 plates. *Rec.*, MalayArch.

Primnoisis Studer, 1887 [**Isis antarctica* Studer, 1878; SD Kükenthal, 1915]. Colonies branched on all sides bottle-brush fashion. *Rec.*, Antarct.-

© 2009 University of Kansas Paleontological Institute

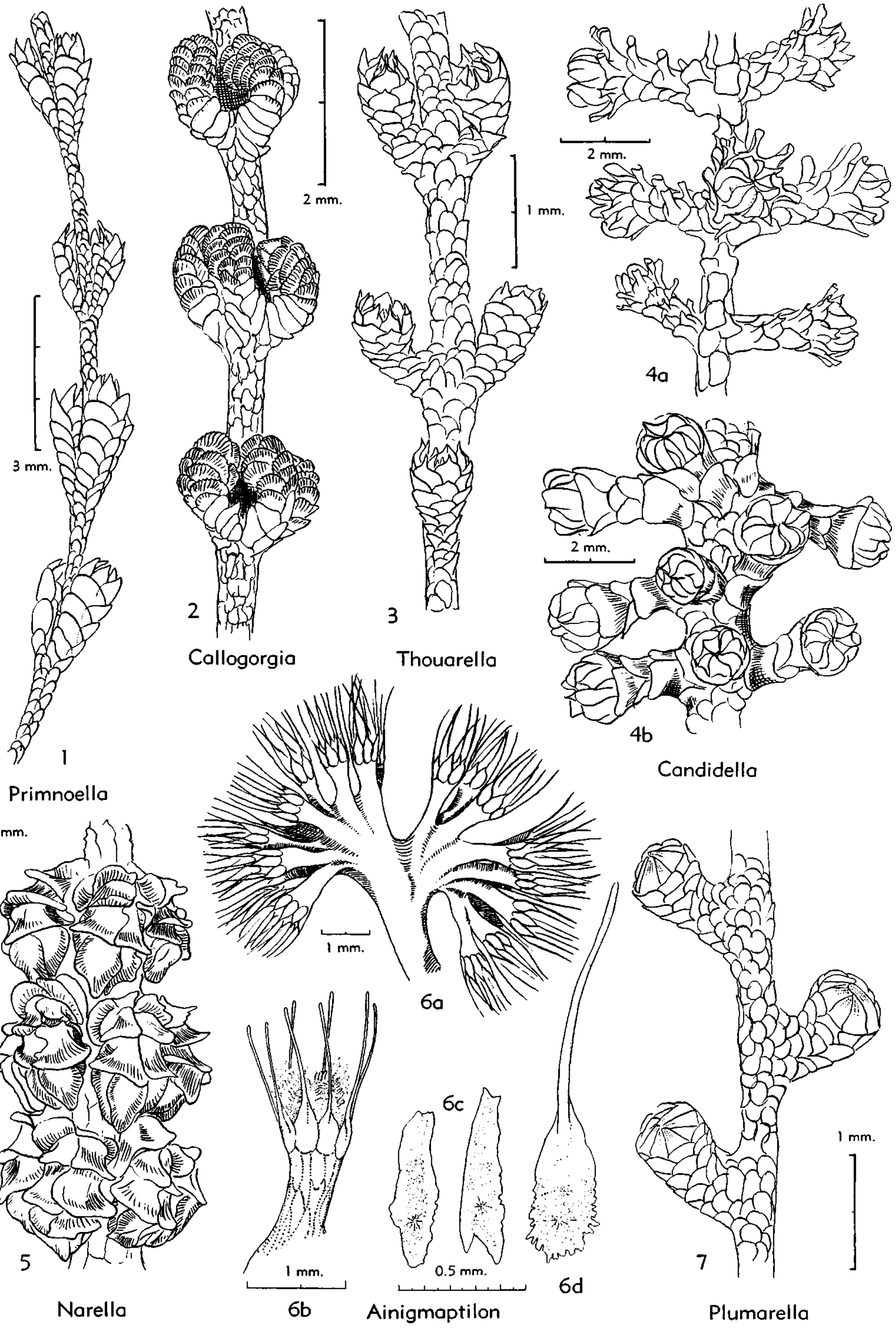


Fig. 159. Gorgonacea: Primnoidae, Ainigmaptilidae (p. F220-F222).

© 2009 University of Kansas Paleontological Institute

Subantarct.-S.Afr.-Arg.——FIG. 161,*2*. **P. antarctica,* Marguerite Bay; *2a,* sclerites; *2b,* part of branch partially decorticated to show ramification of axial internode (26n).

Subfamily MURICELLISIDINAE Kükenthal, 1915

Anthocodiae rectractile within distinctly separated calyces, armed with strongly thorned spindles. Branching from internodes, which are hollow. *Rec.,* Japan.

Muricellisis KÜKENTHAL, 1915 [**M. echinata*]. *Rec.,* Japan.

Subfamily ISIDINAE Lamouroux, 1812

[*nom. transl.* STUDER, 1887 (*ex* Isididae *nom. correct.* KÖLLIKER, 1865, *pro* Isideae LAMX., 1812)]

Anthocodiae fully or partially retractile within coenenchyme, armed with small rods having transverse girdles of tubercles, and various radiate forms. *Rec.*

Isis LINNÉ, 1758 [**I. hippuris;* SD M.EDW.-H., 1850]. Branching from internodes; colonies bushy, with thick rind into which polyps are fully retractile. [Various fossil species attributed to this genus almost certainly do not belong here.] *Rec.,* IndoPac.——FIG. 161,*1*. **I. hippuris,* Philip.; *1a,* spicules; *1b,* decorticated axis (26n).

Chelidonisis STUDER, 1890 [**C. aurantiaca*]. Branching from internodes, dichotomous, in one plane. Rind thin, polyps retractile into hemispherical verruciform calyces. *Rec.,* Atl.-S.Afr.

Subfamily UNCERTAIN

Axogaster LONSDALE, 1850 [**A. cretacea*]. Base branched, creeping, rootlike. Calcareous internodes with calycular pits having fewer than 12 pseudosepta; branching from internodes. *Cret.,* Eng.

Moltkia STEENSTRUP, 1846 [**M. isis*]. Colonies spread roughly in a plane, dichotomously branched, anastomosing. Nodes overgrown by the calcareous internodes, completely enclosed. Axis pitted by calyces and sculptured by beaded longitudinal striae which may continue into calycular pits. *U.Cret. (Dan.),* Denm.

Order PENNATULACEA Verrill, 1865

[*nom. transl.* KÖLLIKER, 1880, as order Pennatulida (*ex* suborder Pennatulacea VERRILL, 1865); *nom. correct.* STUDER, 1887, as order Pennatulacea]

Colonial octocorals unbranched, not firmly attached, consisting of a primary polyp (oözooid) that elongates to produce a barren, proximal stalk, which anchors colony in mud, and a polypiferous distal rhachis from which secondary polyps spring, either directly or from ridgelike or broadly expanded polyp leaves. Gastric cavity of primary polyp divided into 2 primary and 2 secondary longitudinal canals by fleshy partitions at center of which a more or less calcified horny axis usually is produced. Secondary polyps invariably of at least 2 kinds. Spicules in form of smooth or 3-flanged rods or needles, rarely tuberculated; or small scales or plates which, in polarized light, behave optically like plates of Chrysogorgiidae. Axes of pennatulids formed of irregular, prismatic columns of calcareous material radiating outward from axis core, which seems to contain a higher proportion of organic matter, thus resembling closely axes of ellisellid Gorgonacea. *?Sil., Rec.*

Classification of the sea pens depends upon arrangement of the autozooids and siphonozooids, distribution and form of the calcareous spicules, and other features ordinarily not preserved in fossils. External characters of the axis are so variable as to be useless except in a most general way. Consequently, the "species" of *Graphularia,* established on such characters, are of very questionable standing. The differences in patterns of calcification may, however, afford a new means of evaluating these fossils, and need to be more thoroughly investigated.

A number of presumed botanical fossils have recently been assigned to the Renillidae, and it is probable that still more need reinterpretation.

Molds interpreted as fossil pennatulids have lately been reported from both East and West Indian Tertiary deposits (3), and similar remains have been noted in European strata.

Suborder SESSILIFLORAE Kükenthal, 1915

Sea pens with polyps standing separately and arising directly from rhachis without being united near their bases by ridgelike or leaflike structures (12). *?Sil., Rec.*

Family VERETILLIDAE Herklots, 1858

[*nom. correct.* GRAY, 1870 (*pro* Veretilloides HERKLOTS, 1858)]

Stout, commonly clavate colonies without trace of bilaterality; polyps fully retractile, no calyces. Spicules of various types, none 3-flanged. *Rec.*

Veretillum CUVIER, 1798 [**Pennatula cynomorium*

© 2009 University of Kansas Paleontological Institute

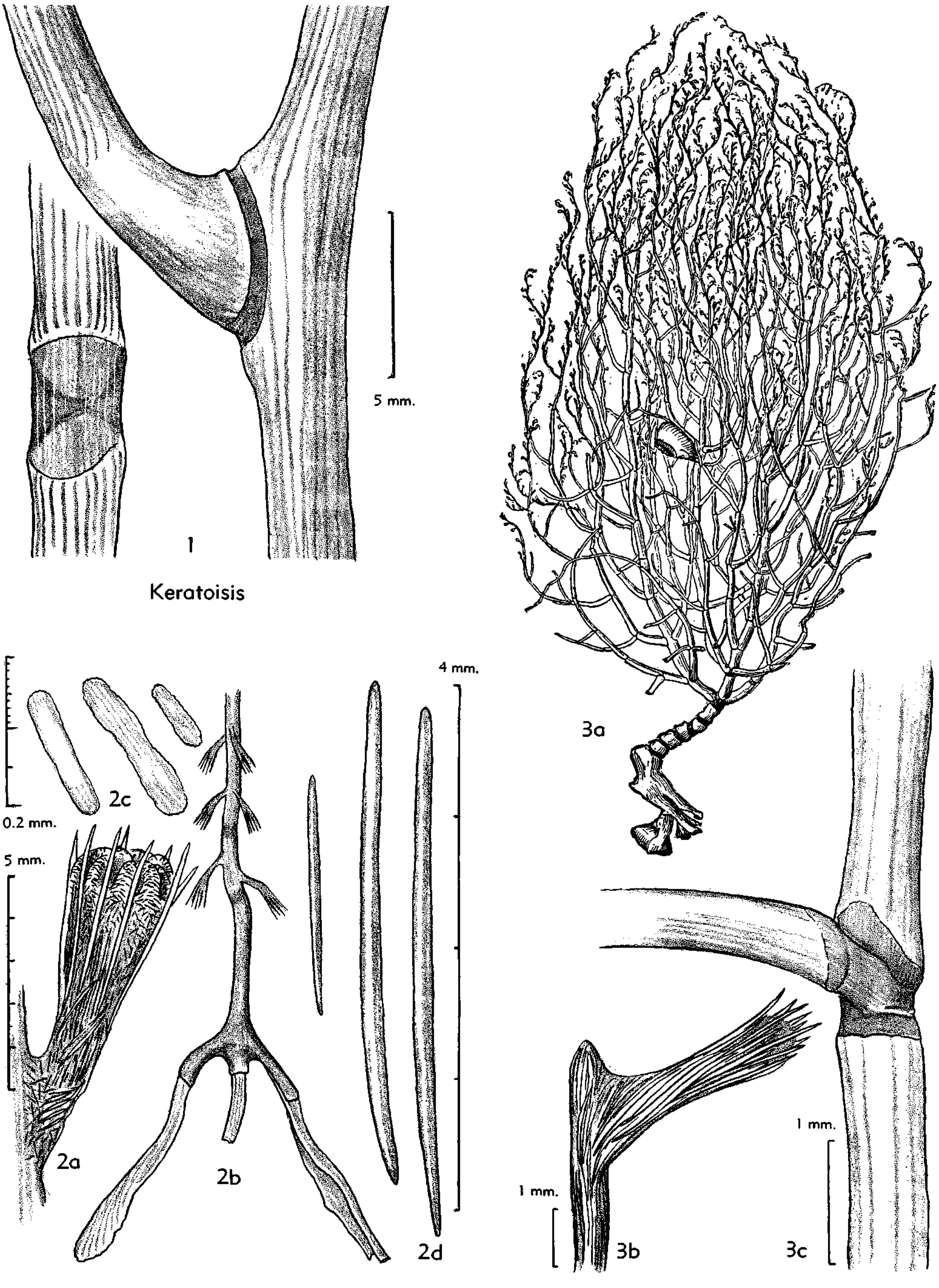


FIG. 160. Gorgonacea, Isididae (p. F222).

© 2009 University of Kansas Paleontological Institute

Pallas, 1766; SD M.Edw.-H., 1850]. Spicules are minute oval constricted plates in polyps as well as in rhachis and stalk. *Rec.,* W.Afr.-S.Eu.

Cavernularia M.Edw.-H., 1850 [**C. obesa*]. Spicules consisting of oval or elongated rods. *Rec.,* W.Afr.-Medit.-IndoPac.

Cavernulina Kükenthal & Broch, 1911 [**C. cylindrica*]. Spicules are rods with bilobed ends. *Rec.,* Ind.O.

Lituaria M.Edw.-H., 1850 [**Pennatula phalloides* Pallas, 1766]. Spicules are plates, commonly with terminal denticles. *Rec.,* IndoPac.

Policella Gray, 1870 [**P. australis*]. Spicules are minute, oval bodies in interior of stalk, and small, biscuit-shaped platelets in outer layer; spicules absent in polyps. *Rec.,* IndoPac.

Family ECHINOPTILIDAE Hubrecht, 1885

Colonies cylindrical, bent, lacking axis, with polyps radially disposed but in some showing traces of bilateral orientation; polyps standing in transverse rows, with calyces. Spicules are 3-flanged rods. *Rec.*

Echinoptilum Hubrecht, 1885 [**E. mackintoshi*]. *Rec.,* Ind.O.

Actinoptilon Kükenthal, 1910 [**A. molle*]. *Rec.,* S.Afr.

Family RENILLIDAE Gray, 1860

[*nom. correct.* Gray, 1870 (*pro* Renilleae Gray, 1860)]

Sea pens with slender stalk and oval or reniform foliate rhachis bearing polyps on upper surface only; no axis. Spicules are 3-flanged rods which may be more or less platelike. *?Sil., Rec.*

Renilla Lamarck, 1816 [**Renilla americana* (=**Pennatula reniformis* Pallas, 1766)]. *Rec.,* W.Atl.-E.Pac.——Fig. 162,*4*. **R. reniformis,* S. Car.; colony (26n).

?**Alectorurus** Schimper, 1869 [*non* Gloger, 1842]. *Sil.*

?**Cancellophycus** Saporta, 1872 [**Taonurus liasinus* Fischer-Ooster, 1858] [=*?Taonurus*]. Colonies flattened, in form of broad, undulating spiral blade, some with accessory blades; spiral may encompass several turns or may be quite lax, blade being formed of successive more or less concentric and arcuate imbricating lamellae joined together at close intervals by oblique cross trabeculae, altogether producing a reticulate structure with meshes consisting of sigmoid lozenges thought to have contained gastric cavities of the individual polyps. In section, the lamellae are seen to contain calcite needles (15 to 40 microns in diameter and about 1 mm. in length), trifoliate in cross section and practically identical with the spicules of various pennatulids (1). *Jur.-Cret.*

?**Spirophyton** Hall, 1863 [**S. typum*] [=*?Taonurus*]. *Sil.*

?**Taonurus** Fischer-Ooster, 1858 [**Fucoides brianteus* Villa]. *Cret.*

Family KOPHOBELEMNIDAE Gray, 1860

[*nom. correct.* Kükenthal, 1915 (*pro* Kophobelemnonieae Gray, 1860)]

Sea pens with polyps bilaterally oriented on rhachis but with some tendency to radial symmetry; colonies clavate, with axis. *Rec.*

Kophobelemnon Asbjörnsen, 1856 [**K. mülleri* (=**Pennatula stellifera* O. F. Müller, 1776)]. Elongate, clavate colonies with large autozooids, which do not form calyces. Spicules are prismatic rods, shorter ones commonly distinctly tuberculated. Axis slender, rounded quadrangular. *Rec.,* Atl.-Medit.-IndoPac.——Fig. 162,*2*. **K. stelliferum,* Grand Banks; *2a,* spicules (26n); *2b,* entire colony (35).

Mesobelemnon Gravier, 1907 [**M. gracile*]. Similar to *Kophobelemnon* but spicules are small bone-shaped rods. Axis rounded in section. *Rec.,* Red Sea.

Sclerobelemnon Kölliker, 1872 [**S. schmeltzei*]. Similar to *Kophobelemnon* but spicules are small plates, smooth or with serrate ends. *Rec.,* IndoPac.

Family ANTHOPTILIDAE Kölliker, 1880

Bilateral sea pens with polyps in transverse or somewhat diagonal rows on 2 sides of rhachis. Sclerites absent except for minute oval bodies in interior of stalk. Axis round or quadrangular with rounded angles. *Rec.*

Anthoptilum Kölliker, 1880 [**Virgularia grandiflora* Verrill]. *Rec.,* Atl.-IndoPac.

Family FUNICULINIDAE Gray, 1860

[*nom. correct.* Gray, 1870 (*pro* Funiculineae Gray, 1860)]

Colonies elongate, slender; autozooids rather small, arranged laterally and ventrally on rhachis, producing distinct calyces with 8 marginal teeth; siphonozooids infrequent. Spicules are prismatic needles. Axis quadrangular. *Rec.*

Funiculina Lamarck, 1816 [**Pennatula quadrangularis* Pallas, 1766; SD M.Edw.-H., 1850]. *Rec.,* Atl.-IndoPac.

Family PROTOPTILIDAE Kölliker, 1872

[*nom. correct.* Kölliker, 1880 (*pro* Protoptileae Kölliker, 1872)]

Bilateral sea pens with autozooids longitudinally arranged in one or more lateral rows. Spicules 3-flanged. Axis stout, rounded. *Rec.*

© 2009 University of Kansas Paleontological Institute

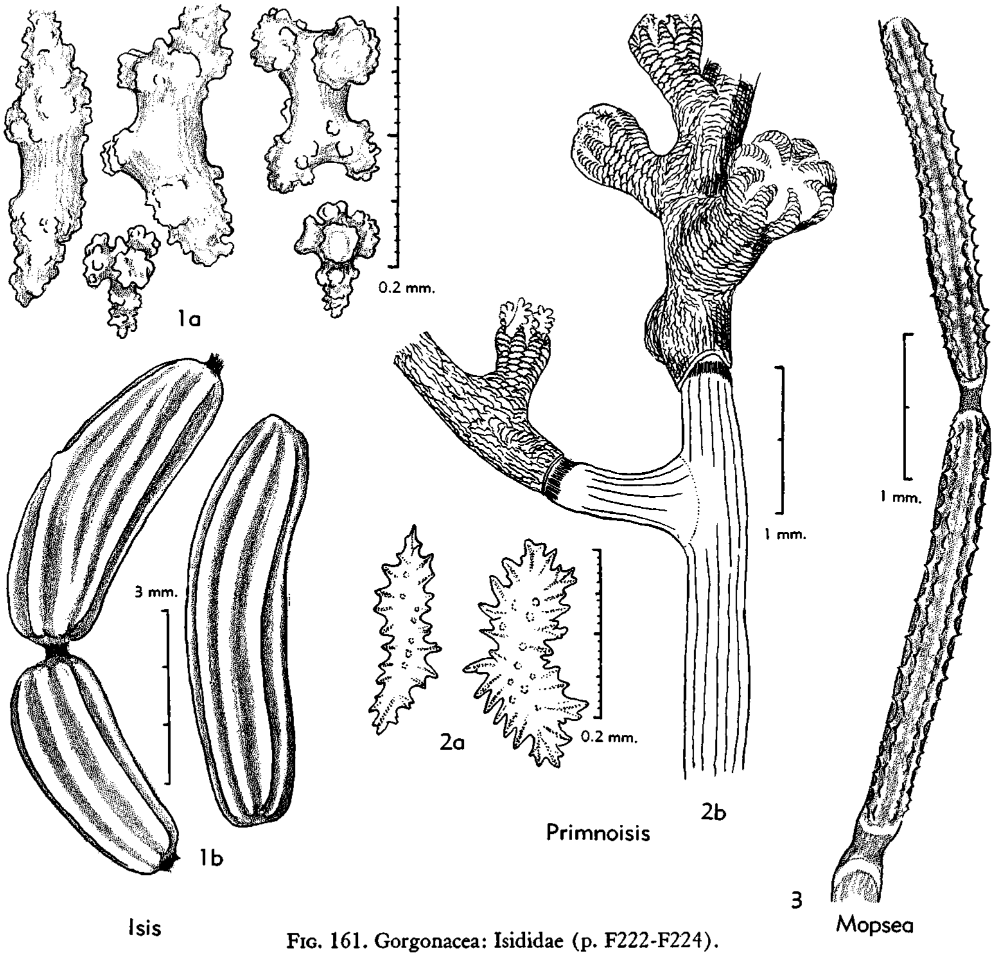


FIG. 161. Gorgonacea: Isididae (p. F222-F224).

Protoptilum KÖLLIKER, 1872 [**P. carpenteri;* SD KÜKENTHAL, 1915]. *Rec.,* N.Atl.-Indo.O.

Distichoptilum VERRILL, 1882 [**D. gracile*]. *Rec.,* Atl.-Pac.

Helicoptilum NUTTING, 1912 [**H. rigidum*]. *Rec.,* Japan.

Family STACHYPTILIDAE Kölliker, 1880

Bilateral colonies with autozooids arranged laterally in transverse rows but not in longitudinal rows also. Autozooids and siphonozooids with well-developed, scale-like calyces. Spicules are 3-flanged needles. *Rec.*

Stachyptilum KÖLLIKER, 1880 [**S. macleari*]. *Rec.,* trop.Pac.

Family SCLEROPTILIDAE Jungersen, 1904

Rhachis elongate, bearing autozooids closely arranged in indistinct whorls; dorsal track free of autozooids; siphonozooids scattered between autozooids. *Rec.*

Scleroptilum KÖLLIKER, 1880 [**S. grandiflorum;* SD BAYER, herein]. With 3-flanged spindles. *Rec.,* Atl.-N.Pac.-Ind.O.

Calibelemnon NUTTING, 1908 [**C. symmetricum*= *Protocaulon indicum* THOMSON & HENDERSON, 1906]. No spicules. Axis quadrangular. *Rec.,* Ind. O.-Hawaii.

Family CHUNELLIDAE Kükenthal, 1902

Rhachis extremely slender; autozooids in widely separated whorls; small siphonozooids on lateral tracts of rhachis, larger ones within autozooid whorls. Axis apparently quadrangular. *Rec.*

Chunella KÜKENTHAL, 1902 [**C. gracillima*]. Ter-

© 2009 University of Kansas Paleontological Institute

minal autozooid rudimentary or absent. *Rec.*, E. Afr.

Amphiacme KÜKENTHAL, 1903 [**Amphianthus abyssorum* KÜKENTHAL, 1902]. Terminal autozooid well developed, asymmetrical. *Rec.*, E.Afr.

Family UMBELLULIDAE Lindahl, 1874

[*nom. correct.* KÖLLIKER, 1880 (*pro* Umbelluleae LINDAHL, 1874)]

Rhachis slender, elongate, bearing at its apex an umbelliform tuft of large autozooids; siphonozooids situated among autozooids and in groups or rows on barren parts of rhachis. Spicules are 3-flanged needles in polyp walls, rhachis and stalk rind, and small oval bodies in deep layers of stalk. Axis round or quadrangular. *Rec.*

Umbellula CUVIER, 1798 [**Isis encrinus* LINNÉ, 1758]. *Rec.*, cosmop., deep-sea.——FIG. 162,*3*. *U. güntheri* KÖLLIKER, 1880, W.Indies; small colony, about ×1 (25).

Suborder SUBSELLIFLORAE Kükenthal, 1915

Polyps united by their bases, situated in rows on lateral swellings or foliate polyp leaves. *Cret.-Rec.*

Family VIRGULARIIDAE Verrill, 1868

[*nom. correct.* JUNGERSEN, 1904 (*pro* Virgularidae VERRILL, 1868)]

Bilateral, with slender rhachis; autozooids situated in transverse rows and united together by their bases, rhachis beneath them raised into lateral swellings or small leaves. Spicules present as prismatic needles, small biscuit-shaped plates, or entirely absent. Axis stout. *Cret.-Rec.*

Subfamily VIRGULARIINAE Verrill, 1868

[*nom. transl. et correct.* KÜKENTHAL & BROCH, 1911 (*ex* Virgularidae VERRILL, 1868)]

Autozooids form low to prominent polyp leaves. *Cret.-Rec.*

Virgularia LAMARCK, 1816 [**Pennatula mirabilis* MÜLLER, 1776; SD M.EDW.-H., 1850]. Long, slender colonies with lateral rows of low polyp leaves separated by dorsal track and in some also by ventral groove; autozooids retractile; siphonozooids between or on polyp leaves and along dorsal track. Spicules absent except for small, oval platelets in interior of stalk. Axis stout, projecting apically. *Cret.-Rec.*, nearly cosmop.——FIG. 162,*6*. *V. presbytes* BAYER; *6a*, dorsal, lateral, and ventral views of part of rhachis with fully developed polyp leaves (Rec., GulfMexico) (26); *6b*, mold of ventral side of colony (Wilcox.-Claiborn., Trinidad) (29).

Acanthoptilum KÖLLIKER, 1870 [**A. pourtalesii;* SD KÜKENTHAL, 1915]. *Rec.*

Graphularia M.EDW.-H., 1850 [**G. wetherelli*]. Axial rods slightly compressed, narrower sides flattened or slightly concave; central core wide; cortical zone consisting of long, irregular, calcareous radii extending from core to periphery, perforated by radial tubules extending outward from central core. These axes correspond closely in structure with those of modern *Stylatula,* with which they may be congeneric (4). *Eoc.*(London Clay), Eng.

Scytaliopsis GRAVIER, 1906 [**S. djiboutiensis*]. *Rec.*

Scytalium HERKLOTS, 1858 [**S. sarsi*]. *Rec.*

Stylatula VERRILL, 1864 [**S. elongata;* SD KÜKENTHAL, 1915 (?=*Virgularia elongata* GABB, 1863)]. Polyp leaves supported by radiating spicules. *Rec.*, Atl.-E.Pac.

Subfamily BALTICININAE Gray, 1870

[*nom. transl.* BAYER, herein (*ex* Balticinidae GRAY, 1870)] [=Pavonariinae KÜKENTHAL & BROCH, 1911]

Autozooids stand in oblique rows surrounded by ridges or folds of rhachis. *?U. Cret.(Senon.), Rec.*

Balticina GRAY, 1870 [**Virgularia finmarchica* SARS, 1851] [=*Pavonaria* KÖLLIKER, 1869 (*non* SCHWEIGGER, 1820)]. *?U.Cret.(Senon.), Rec.*, N. Atl.-IndoPac.

Family PENNATULIDAE Ehrenberg, 1828

[*nom. correct.* DANA, 1846 (*pro* family Pennatulina EHRENBERG, 1828)]

Bilateral sea pens with well-developed polyp leaves bearing one or more marginal rows of autozooids, which have calyces with marginal teeth formed by spicules; siphonozooids on rhachis, not on leaves. Spicules as minute oval bodies, plates, rods, and prismatic needles. *Rec.*

Pennatula LINNÉ, 1758 [**P. phosphorea;* SD KÜKENTHAL, 1915]. Calyces usually with 8 marginal teeth; spicules as prismatic rods and needles, inconspicuously 3-flanged in stalk, where plates occur also. *Rec.*, cosmop.——FIG. 162,*1*. *P. aculeata* DANIELSSEN, Mass.; *1a*, colony from the side (35); *1b*, spicules (26n).

Leioptilus GRAY, 1860 [**Pennatula fimbriata* HERKLOTS, 1858]. *Rec.*

Ptilosarcus GRAY, 1860 [**Sarcoptilus (Ptilosarcus) gurneyi;* SD BAYER, herein]. Calyces with only 1 or 2 teeth; large plates in interior of stalk. *Rec.*, off W.N.Am.

Family PTEROEIDIDAE Kölliker, 1880

Bilateral sea pens like Pennatulidae but polyp leaves supported by rays of stout

© 2009 University of Kansas Paleontological Institute

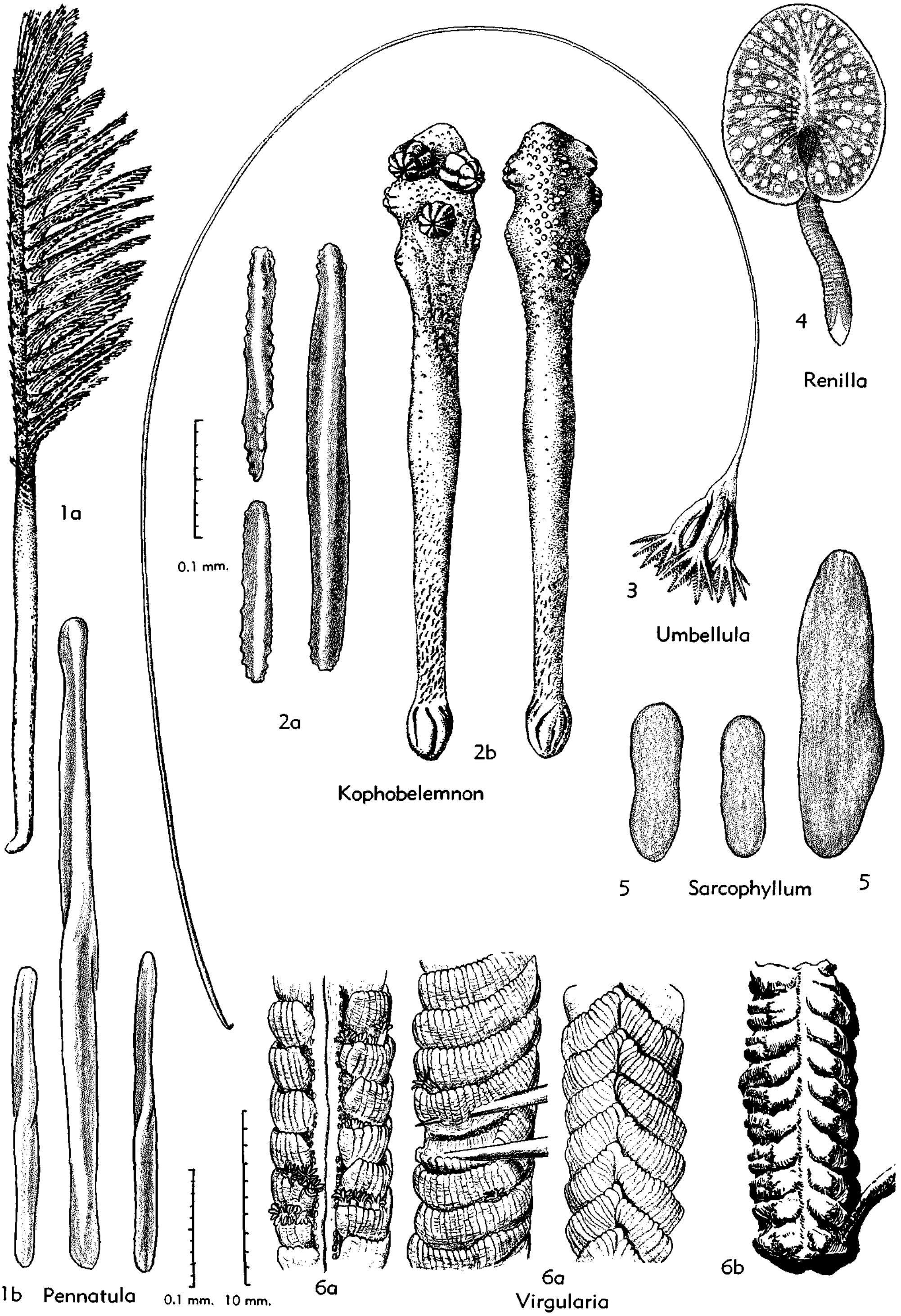


FIG. 162. Pennatulacea (p. F226-F230) (for *Sarcophyllum* read *Sarcoptilus*, p. F230).

© 2009 University of Kansas Paleontological Institute

spicules; autozooid calyces not formed by spicules; spicules not 3-flanged. *Tert.-Rec.*

Pteroeides Herklots, 1858 [**Penna grisea* Bohadsch, 1761 (=*Pennatula spinosa* Ellis, 1764; *Pteroeides spinosum* Herklots, 1858); SD Kükenthal, 1915]. Polyp leaves lack accessory leaves. *Tert.*(Sumatra)-*Rec.*(E.Atl.-Medit.-IndoPac.).

Sarcoptilus Gray, 1848 [**S. grandis*] [=*Sarcophyllum* Kölliker, 1860]. Supporting rays absent, but spicules as rods and plates, never prismatic. *Rec.*, Austral.-N.Z.——Fig. 162,*5*. **S. grandis;* spicules (26n).

Struthiopteron Broch, 1910 [**Pteroeides caledonicum* Kölliker, 1869]. Leaves with supporting rays and accessory leaves along dorsal track. *Rec.*, NewCaledonia-Amboina.

Suborder and Family UNCERTAIN

Glyptosceptron Boehm, 1890. *U.Cret.(Senon.)*, Bavaria.

Palaeosceptron Cocchi, 1870. *U.Cret.*

Pennatulites Cocchi, 1870. *U.Cret.(Senon.).*

Prographularia Frech, 1890. Like *Graphularia,* but longitudinally striated and with symmetrical pair of deep grooves. *Trias.*

Protovirgularia M'Coy, 1850. *Sil.*

REFERENCES

Publications cited in the following list are judged to be helpful in furnishing additional information concerning the octocorals and in offering a guide to more extensive literature. The index numbers enclosed in parentheses in the column at left are employed in the text for identification of the publications.

Alloiteau, James

(1) 1952, *Sous-classe des Alcyonaria:* in Piveteau, Jean, Traité de Paléontologie, Masson (Paris), tome 1, p. 408-417, 3 figs.

Bayer, F. M.

(2) 1953, *Zoogeography and evolution in the octocorallian family Gorgoniidae:* Bull. Marine Sci. Gulf and Caribbean, v. 3, no. 2, p. 100-119, fig. 1-5.

(3) 1955, *Remarkably preserved fossil sea-pens and their recent counterparts*: Jour. Washington Acad. Sci., v. 45, p. 294-300, fig. 1-2.

(4) 1955, *Contributions to the nomenclature, systematics and morphology of the Octocorallia:* Proc. U.S. Natl. Mus., v. 105, p. 207-220, pl. 1-8.

Cary, L. R.

(5) 1918, *The Gorgonaceae as a factor in the formation of coral reefs:* Carnegie Inst. Washington, Pub. 213, p. 341-362, pl. 100-105.

(6) 1931, *Studies on the coral reef of Tutuila, American Samoa, with especial reference to the Alcyonaria:* Papers from Tortugas Lab., Carnegie Inst. Washington, v. 27, no. 3, p. 53-98, pl. 1-7, fig. 1-14, table 1-14, map 1.

Deichmann, Elisabeth

(7) 1936, *The Alcyonaria of the western part of the Atlantic Ocean:* Mem. Mus. Comp. Zool. Harvard, v. 53, p. 1-317, pl. 1-37.

Gohar, H. A. F.

(8) 1940, *Studies on the Xeniidae of the Red Sea:* Pub. Marine Biol. Sta. Ghardaqa (Red Sea), no. 2, p. 25-118, pl. 1-7.

Hickson, S. J.

(9) 1916, *The Pennatulacea of the Siboga Expedition:* Siboga-Exped. (Leiden) Mon. 14, x+265 p., 10 pl., 45 text-fig., 1 chart.

(10) 1930, *On the classification of the Alcyonaria:* Proc. Zool. Soc. London, 1930, pt. 1, p. 229-252, fig. 1-2.

Hyman, L. H.

(11) 1940, *The Invertebrates: Protozoa through Ctenophora:* McGraw-Hall (New York), xii+726 p., 221 fig.

Kükenthal, Willy

(12) 1915, *Pennatularia:* Das Tierreich, Lief. 43, xv+132 p., 126 fig.

(13) 1919, *Gorgonaria:* Wissenschaft. Ergebn. deutsch. Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899, Band 13, pt. 2, p. i-viii+1-646+i-vi+647-946, pl. 30-89, fig. 1-319.

(14) 1924, *Gorgonaria:* Das Tierreich, Lief. 47, xxviii+478 p., 209 fig.

Milne-Edwards, Henri, & Haime, Jules

(15) 1850, *A monograph of the British fossil corals. Pt. 1, Introduction; corals from the Tertiary and Cretaceous formations:* Palaeontographical Soc., London, lxxxv+71 p., 11 pl.

Montanaro-Gallitelli, Eugenia

(16) 1955, *Il Permiano del Sosio e i suoi coralli:* Palaeontographia Italica, tomo 49, p. 1-98, pl. 1-10, figs. 1-10.

Nielsen, K. B.

(17) 1913, *Moltkia isis, Steenstrup og andre Octocorallia fra Danmarks Kridttidsaflejringer:* Mindeskrift for Japetus Steenstrup, pt. 18, p. 1-20, pl. 1-4, fig. 1-2.

(18) 1917, *Heliopora incrustans nov. sp., with a survey of the Octocorallia in the deposits of the Danian in Denmark:* Meddelelser fra

© 2009 University of Kansas Paleontological Institute

Dansk geologisk Forening, v. 5, pt. 8, p. 1-13, fig. 1-17.

(19) 1925, *Nogle nye Octocoraller fra Danienet:* Same, v. 6, pt. 28, p. 1-6, fig. 1-3.

Okulitch, V. J.

(20) 1936, *On the genera Heliolites, Tetradium, and Chaetetes:* Am. Jour. Sci., ser. 5, v. 32, p. 361-379, fig. 1.

Počta, Philipp

(21) 1885, *Über fossile Kalkelemente der Alcyoniden und Holothuriden und verwandte recente Formen:* Sitzungsber. Kaiserlichen Akad. Wissenschaft. (math.-naturw. Cl.), Band 92, no. 1, p. 7-12, pl. 1.

Stock, J. H.

(22) 1953, *Contributions to the knowledge of the pycnogonid fauna of the East Indian Archipelago:* Biol. Results of Snellius Exped., XVII, Temminckia, v. 9, p. 276-313, fig. 1-18.

Termier, Geneviève & Termier, Henri

(23) 1950, *Foraminifères, Spongiaires et Coelentérés. Invertébrés de l'Ère Primaire, fasc. 1:* Paléontologie Marocaine, II. Morocco, Service Géol., Notes et Mémoires, no. 73, p. 1-218, pl. 1-51.

Williams, James Steele

(24) 1943, *Stratigraphy and fauna of the Louisiana limestone of Missouri:* U. S. Geol. Survey Prof. Paper 203, iv+133 p., 9 pl.

SOURCES OF ILLUSTRATIONS

Explanation of the use of index numbers for citing sources of illustrations is given in the Editorial Preface.

(25) **Agassiz, Alexander**
(26) **Bayer, F. M.**
(27) **Bourne, G. C.**
(28) **Cooper, G. A.**
(29) **Hogue, R. E.**
(30) **Kükenthal, Willy**
(31) **Madsen, F. J.**
(32) **Montanaro-Gallitelli, Eugenia**
(33) **Moseley, H. N.**
(34) **Thomson, J. A., & Dean, L. M. I.**
(35) **Verrill, A. E.**
(36) **Versluys, Jan**
(37) **Wright, E. P., & Studer, Théophile**

ZOANTHARIA—GENERAL FEATURES

By J. W. Wells and Dorothy Hill

Subclass ZOANTHARIA de Blainville, 1830

[=Helianthoïda Latreille, 1825; Zoantha Blainv., 1834; Zoocorallia polyactinia, Phytocorallia polyactinia, Phytocorallia dodecactinia Ehrenberg, 1834; Anthozoa helianthoida Johnston, 1837 (*partim*); Actinaria Dana, 1846; Hexacorallia, Tetracorallia Haeckel, 1866; Hexactiniae Schneider & Rötteken, 1871; Hexacoralla + Rugosa Nicholson in Lankester, 1877; Zoanthactiniaria + Rugosa van Beneden, 1898; Actinanthida Delage & Hérouard, 1901; Dodecacorallia Carlgren, 1908]

Solitary and colonial anthozoans, with or without calcareous trabecular exoskeleton, characterized by coupled and paired mesenteries, and by insertion of new pairs of mesenteries, generally after the first 6, in 2 (ventrolateral), 4 (lateral and ventrolateral), or all 6 primary exocoeles. *Ord.-Rec.*

Representatives of the Zoantharia are divided into orders according to arrangement of their mesenteries and corresponding septa if a skeleton is present.

Classification of Zoantharia

1. Septa inserted only within "bifurcated" outer ends of 4 original septa (cardinal, counter, and alars) Heterocorallia
2. Mesenterial pairs, after first 6, inserted only in ventrolateral exocoeles ....Zoanthiniaria
3. Septa inserted in 4 spaces: between cardinal and alar septa, and between alar and counter-lateral septa (?mesenterial pairs inserted in lateral and ventrolateral exocoeles) ....Rugosa
4. Mesenterial pairs (and septa) inserted in dorsolateral, lateral, and ventrolateral exocoeles ....Hexactiniaria
   - A. One tentacle over each exocoele and entocoele; exoskeleton
     - i. Absent ....Actiniaria
     - ii. Present ....Scleractinia
   - B. More than one tentacle over each exocoele and entocoele; skeleton absent ....Corallimorpharia

© 2009 University of Kansas Paleontological Institute