PART F

COELENTERATA

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CONTENTS

(F1)

INTRODUCTION

By Raymond C. Moore

As defined in this volume, the phylum Coelenterata comprises all of the so-called diploblastic lower invertebrates belonging to the Eumetazoa, that is, the numerically and structurally disparate groups named Cnidaria and Ctenophora. Excluded are the Porifera or sponges, which are classified as structurally distinct from Eumetazoa and designated as Parazoa. The coelenterates differ from other Eumetazoa, all of which have bilateral symmetry, in being characterized by primary radial or biradial symmetry derived from the larval stage and retained throughout ontogeny. Thus, the cnidarians and ctenophores taken together are definable as radiate forms or Radiata (Cuvier, 1816; *non* Lamarck, 1809), whereas remaining eumetazoans are the bilateral forms or Bilateria. Another distinction is that among the Radiata (or Coelenterata) no body cavities exist between the outer cell layer (ectoderm, epidermis) and inner cell layer (endoderm, gastrodermis), for these layers are in contact or connected by more or less structureless substance of jelly-like nature termed mesogloea; in most Bilateria, on the other hand, such spaces are developed and on account of this character they are often termed Coelomata.

The Cnidaria are distinguished mainly by possession of stinging capsules (nematocysts) and are characterized by ability to move their body parts muscularly. The Ctenophora lack nematocysts and retain the ciliary locomotion of the larval stage (planula) but are relatively advanced in having more definite organization of the digestive system and in development of an aboral sensory region. The common features and differences of the 2 groups are appropriately recognized by classifying them as subphyla of the phylum Coelenterata.

The contributors to this Part of the *Treatise* are not to be understood as committed individually to features of classification which have been adopted for the volume as a whole; this is my responsibility; but each author is granted the privilege of expressing his own views, and his conformance to the general plan of systematic organization of the text does not imply full endorsement necessarily. Some features of arrangement reflect effort on the part of the editor to make clearly and readily distinguishable the authorship of respective subdivisions, several of which do not coincide with ideal major segments adapted for placement in sequence conforming to zoological classification.

OUTLINE OF CLASSIFICATION

A tabular summary of main divisions recognized in the phylum Coelenterata is desirable near the beginning of the volume and because a number of departures from customary classification are introduced, these call for some explanation.

First, decision to include ctenophores with other radiate Eumetazoa in a single phylum called Coelenterata and division of this assemblage into 2 subphyla named Cnidaria and Ctenophora is based on considerations given in preceding paragraphs.

Next, the conclusion that the polypoid and medusoid types of organization, instead of representing a more or less unexplainable "alternation of generations," constitute the product of evolutionary differentiation in which the polypoid form is a persistent early-growth form and the medusoid a normal adult type of coelenterate leads to interpretation of the medusoids as initial types of Coelenterata. This is consonant with the paleontological record, which includes numerous Lower Cambrian and even some Precambrian medusoid fossils. Consequently, the simplicity of hydroid forms is not accepted as basis for placing them in first position among various types of coelenterates. Precedence is assigned to early medusoids.

Main Divisions of the Coelenterata

Cnidaria *(subphylum).* Precam.-Rec.
  Protomedusae *(class).* Precam.-Ord., ?Sil., ?Penn.
    Brooksellida *(order).* Precam.-Ord., ?Sil., ?Penn.
  Dipleurozoa *(class).* L.Cam.
    Dickinsoniida *(order).* L.Cam.
  Scyphozoa *(class).* Cam.-Rec.
    Scyphomedusae *(subclass).* ?L.Cam., U.Jur.-Rec.

Stauromedusida *(order)*. *Rec.*
Carybdeida. *?U.Jur., Rec.*
Coronatida. *?L.Cam., U.Jur.-Rec.*
Semaeostomatida. *?U.Jur., Rec.*
Lithorhizostomatida. *U.Jur.*
Rhizostomatida. *?U.Jur., Rec.*
?Scyphomedusae incertae sedis. *L.Cam.*
Conulata *(subclass)*. *Cam.-Trias.*
Conulariida *(order)*. *Cam.-Trias.*
Conchopeltina *(suborder)*. *M.Ord.*
Conulariina. *Cam.-Trias.*

Hydrozoa *(class)*. *Cam.-Rec.*
Trachylinida *(order)*. *?L.Cam., ?M.Jur., U.Jur.-Rec.*
Trachymedusina *(suborder)*. *?L.Cam., ?M.Jur., L.Cret.-Rec.*
Narcomedusina. *U.Jur.-Rec.*
Hydroida *(order)*. *Cam.-Rec.*
Gymnoblastina *(suborder)*. *?Trias.-?Cret., Eoc.-Rec.*
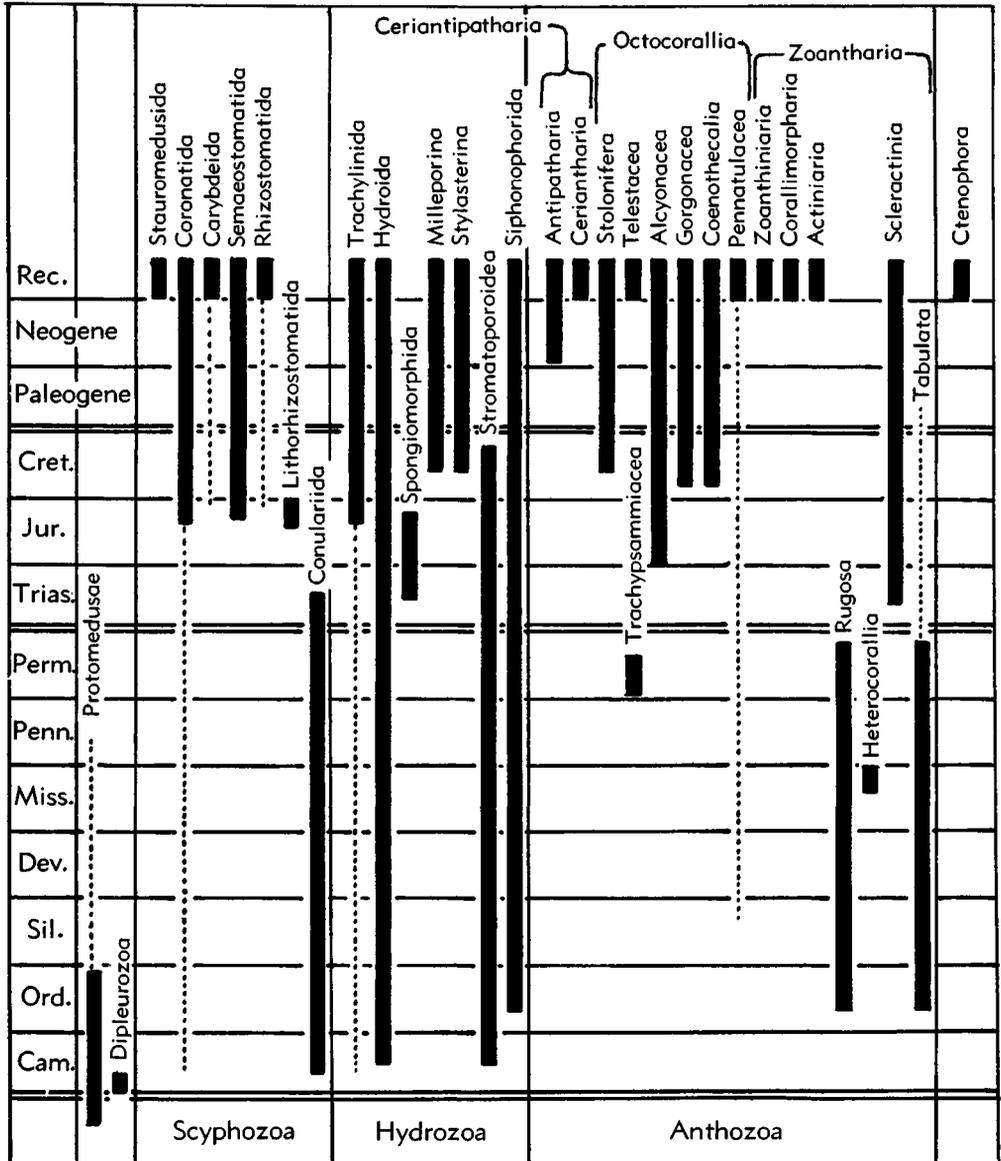Calyptoblastina. *Cam.-Rec.*
Spongiomorphida. *Trias.-Jur.*

FIG. 1. Geologic distribution of main divisions of Coelenterata (MOORE, n).

Milleporina. *U.Cret.-Rec.*
Stylasterina. *U.Cret.-Rec.*
Stromatoporoidea. *Cam.-Cret.*
Siphonophorida. *Ord.-Rec.*
  Calycophorina *(suborder)*. *Rec.*
  Physophorina. *Rec.*
  Rhizophysaliina. *Rec.*
  Chondrophorina. *Ord.-Rec.*
Anthozoa *(class)*. *M.Ord.-Rec.*
 Ceriantipatharia *(subclass)*. *Mio.-Rec.*
  Antipatharia *(order)*. *Mio.-Rec.*
  Ceriantharia. *Rec.*
Octocorallia *(subclass)*. *?Sil., Perm.-Rec.*
  Stolonifera *(order)*. *Cret.-Rec.*
  Telestacea. *Rec.*
  Alcyonacea. *L.Jur.-Rec.*
  Trachypsammiacea. *Perm.*
  Coenothecalia. *Cret.-Rec.*
  Gorgonacea. *Cret.-Rec.*
    Scleraxonia *(suborder)*. *Cret.-Rec.*
    Holaxonia. *Cret.-Rec.*
  Pennatulacea. *?Sil., Rec.*
    Sessiliflorae *(suborder)*. *?Sil., Rec.*
    Subselliflorae. *Cret.-Rec.*
    Incertae sedis. *Sil.-Cret.*
 Zoantharia *(subclass)*. *Ord.-Rec.*
  Zoanthiniaria *(order)*. *Rec.*
  Corallimorpharia. *Rec.*
  Actiniaria. *Rec.*
  Rugosa. *Ord.-Perm.*
    Streptelasmatina *(suborder)*. *Ord.-Perm.*
    Columnariina. *Ord.-Perm.*
    Cystiphyllina. *Ord.-Dev.*
  Heterocorallia *(order)*. *Carb.*
  Scleractinia. *M.Trias.-Rec.*
    Astrocoeniina *(suborder)*. *M.Trias.-Rec.*
    Fungiina. *M.Trias.-Rec.*
    Faviina. *M.Trias.-Rec.*
    Caryophylliina. *Jur.-Rec.*
    Dendrophylliina. *U.Cret.-Rec.*
  Tabulata *(order)*. *M.Ord.-Perm., ?Trias.-?Eoc.*
Ctenophora *(subphylum)*. *Rec.*

Geological distribution of the main divisions of coelenterates is shown graphically in Figure 1.

ACKNOWLEDGMENTS

CNIDARIA—GENERAL FEATURES

By Dorothy Hill and J. W. Wells

CONTENTS

To the ancients, outstanding features of the animals now collectively known as cnidarian coelenterates were their ability to sting and resemblance of their growth forms to those of plants, whence the names Acalephae, Cnidae, and later Zoophyta. Eighteenth-century workers noted their tentacles, whence were derived the terms "polyps" and Polypi (from their analogy with cuttlefish) or Radiata (from their evident radial symmetry). Early in the 19th century, their characteristic gastrovascular cavity (coelenteron) was seen to distinguish them from other radiate animals such as echinoderms, and hence the name Coelenterata was introduced. The Ctenophora, originally included in the Coelenterata, have been separated as a distinct phylum by many zoologists but here are classed as a subphylum.

NATURE OF CNIDARIA

The Cnidaria are free-swimming or sedentary animals, lacking definite head and centralized nervous system, and having fundamentally biradial structure, and a body wall of 2 layers of cells, an outer **ectoderm** and an inner **endoderm,** between which is a primarily structureless layer, the **mesogloea.** They are particularly characterized by **tentacles,** and stinging or adhesive bodies (**nematocysts,** Fig. 2). Within the body wall is a single cavity, the coelenteron, acting as a digestive tube with only a mouth opening, and complicated in some groups by partitions or canals. Digestion is partly intracellular; the nervous system consists of a diffuse network of cells (Fig. 3), and the muscular system is simple. In sexual reproduction the egg develops into an ovoid ciliated larva (**planula**), which usually becomes attached and grows into some type of polyp. Asexual reproduction is by various modes of budding. Cnidarians generally are regarded as representative of the primitive stock of metazoans characterized by acquired specializations.

The Cnidaria are remarkable for polymorphism, signifying the variety of form that a species may present. This includes 2 types, **polyp** and **medusa,** derivable one from the other. A polyp is sedentary, in shape an elongated cylinder attached to or resting on the substratum at the aboral end, with the mouth and tentacles at the free (oral) end. A medusa is a free-swimming, bowl-shaped animal with marginal tentacles, a very short oral-aboral axis, and great thickening of the mesogloea. Dominance of the types varies in the classes. Among Hydrozoa, both polypoid and medusoid forms may occur in the same species; the medusoid form preponderates in the Scyphomedusae, and the class Anthozoa is entirely polypoid (Fig. 4). Where both polypoid and medusoid forms occur in a species, the polyps reproduce only asexually, budding off medusae that reproduce sexually. The polyp may be regarded as a persistent larval stage and the medusa as the completely evolved cnidarian.

ORIGIN AND EVOLUTION OF CLASSES

The general evolutionary pattern of major groups of Coelenterata is speculative, for it is only hinted at in the structural series of living forms and has found little or no confirmation from the fossil record. The classical picture of the origin and evolution of

the phylum assumes (1) that the coelenterates are the nearest living representatives of the ancestral stock of all other metazoan groups and (2) that of the classes, the Hydrozoa are most primitive structurally and arose first. The more distant origin of the phylum is thought to lie in a ciliated polarized free-swimming bottom-feeder provided with ectoderm and endoderm, largely because all coelenterate groups possess a planula larval stage having these attributes. This hypothetical protocnidarian has been termed metagastraea. Further developments followed one or the other of 2 theoretical lines.
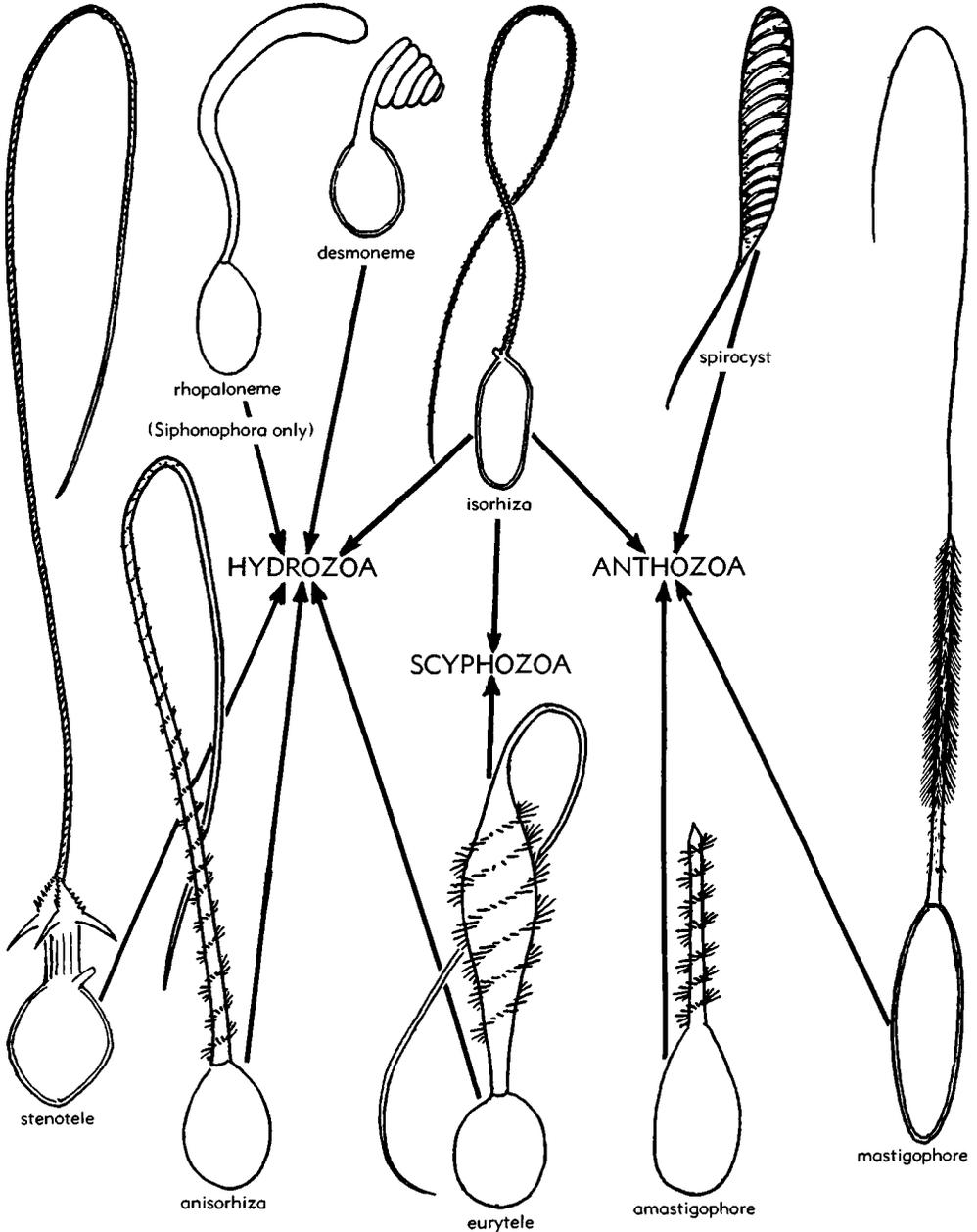
Fig. 2. Types of nematocysts and their occurrence in main groups of coelenterates (nematocysts much enlarged) (Hill & Wells, n).

One theory (Fig. 5*A*) postulates that attachment of the metagastraea at its aboral pole gave rise to a hydra-like polyp, from which hydroid colonies arose by asexual budding and that by development of polymorphism, some polyps became modified into medusae specialized for pelagic life and sexual reproduction.

Difficulties arise with this assumption, and many investigators consider more credible the hypothesis that ancestral coelenterates were primitive medusae derived from protocnidarians by development of tentacles and resembling the actinula larva of living Trachylinida (Fig. 5*C*). The hydrozoans could have arisen from such medusae if these first acquired the habit of asexual budding and then developed a prolonged attached stage as a polypoid colony that produced medusae by budding. This would account for the asexual nature of hydrozoan polypoids and the retention of a fully developed medusa stage, and it points to trachylines as the most primitive living coelenterates. The Scyphozoa (Scyphomedusae) could have originated from the same trachylinid actinula stage as the Hydrozoa by exploitation of the medusoid condition, in which the principal changes were develop-
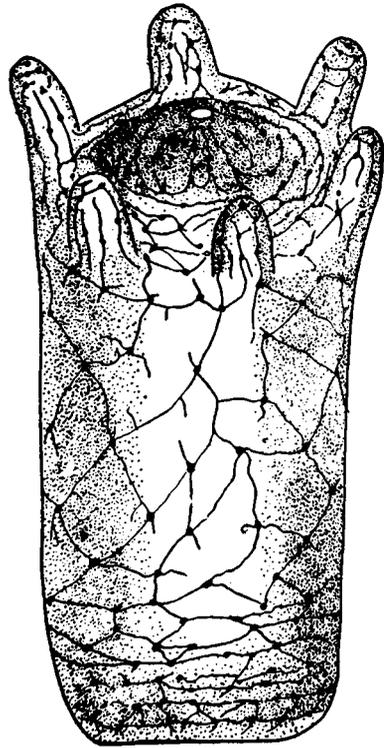
FIG. 3. Nervous system of *Hydra* (reticulate connection of nerve fibers doubtful) (HADZI).
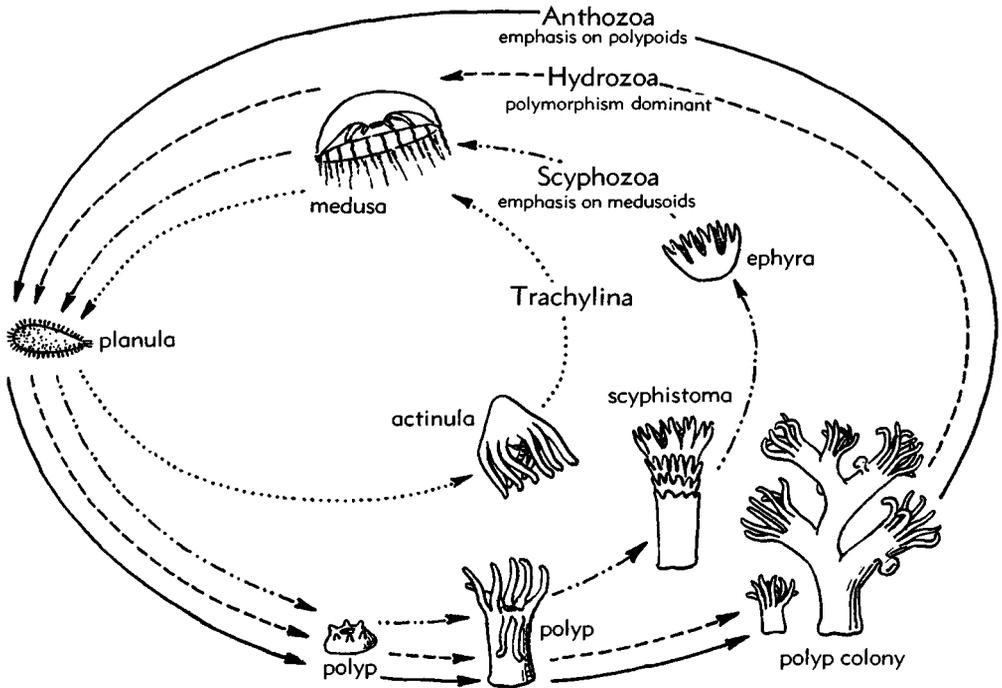
FIG. 4. Life cycles of main groups of coelenterates (HILL & WELLS, n).

ment of mesenteries associated with increase in size. In another direction from the trachylinid stem, emphasis on the polypoid stage, with increase in size and development of mesenteries, could have given rise to the Anthozoa, in which all traces of the medusa stage are absent, and the polypoid stage, originally a larval stage, dominates.

A different evolutionary scheme has been suggested by HADZI, who would derive the coelenterates from the rhabdocoele flatworms, an order of the class Turbellaria, phylum Platyhelminthes, more or less by retrogression (Fig. 4C). Several workers

have pointed out that there is no real difference in the structure of anemones and planarians as regards general body layers. On this plan, the anthozoans represent the primary group and first to evolve, the scyphozoans being derived from them, and hydrozoans constituting the most highly modified group. HADZI's hypothesis is open to the objection that if Anthozoa are considered to be the primary coelenterates, the derivation of medusae from them becomes unthinkable.

Unfortunately, although the paleontological record (Fig. 1) provides much information on evolution of some coelenterate orders
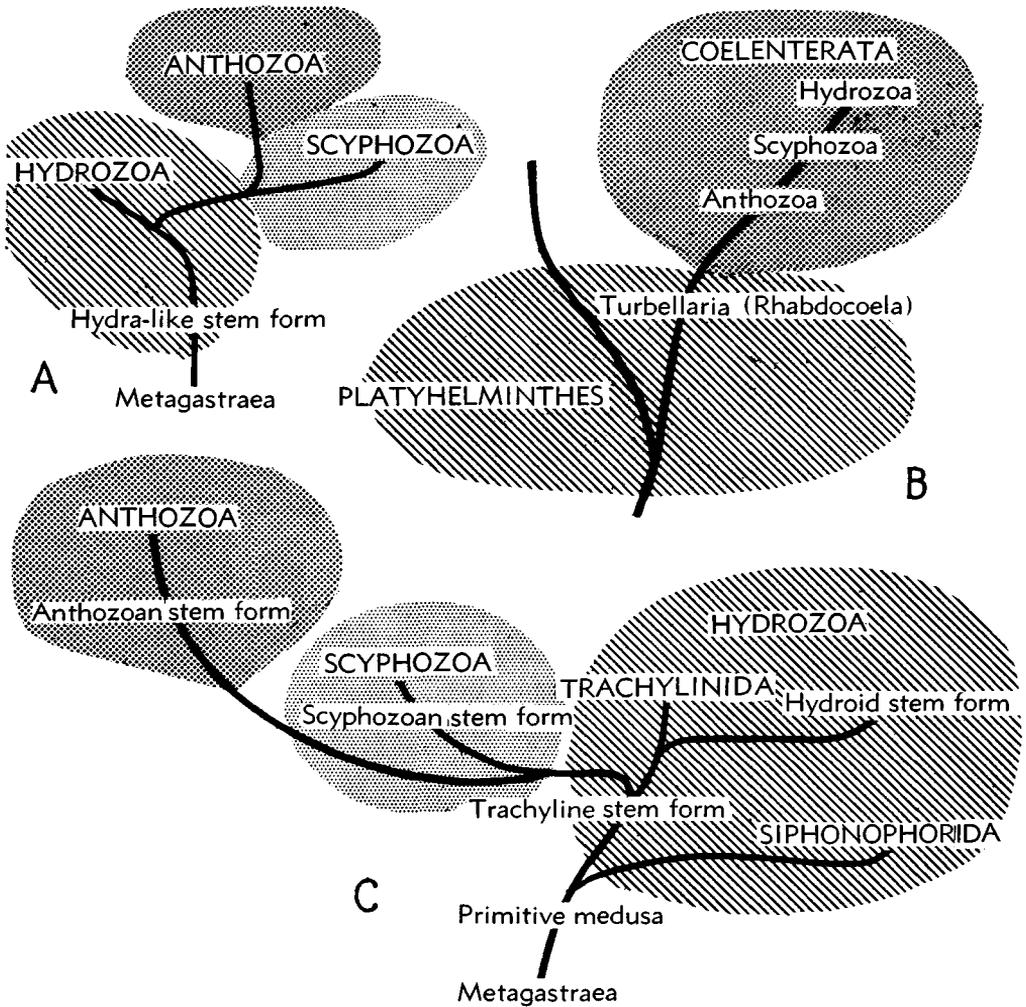
FIG. 5. Postulated phylogenetic relationship of main divisions of the coelenterates. *A*, Development through *Hydra*-like stem form with polymorphic differentiation of free-swimming medusae from attached polyps. *B*, Development through rhabdocoele flatworms, as postulated by HADZI. *C*, Development through primitive medusa and trachyline stem form (HILL & WELLS, n).

with skeletons, it provides no confirmation of any of these speculative lines of development of the great classes. As pointed out subsequently, separation of the classes of Cnidaria probably was completed in the unknown time before beginning of the Cambrian.

A skeleton, calcitic in some, aragonitic, horny or chitinophosphatic in others, has developed at different times in different coelenterate lines, each being a secondary development consequent on establishment of the polypoid stage and not necessarily indicating relationship. This sporadic appearance of a major structural type seems to characterize the coelenterates, among which it has occurred in about half of the main groups.

GEOLOGICAL IMPORTANCE

The living coelenterates are marine except for a few fresh-water hydroids, and fossils are known only from marine sediments. Although some soft-bodied forms are known from rare fossil impressions left in mud or sand, cnidarian fossils are dominantly the remains of groups with calcareous skeletons; many orders lacking skeletons are not known as fossils.

The oldest cnidarian recorded is a doubtful scyphomedusa from late Precambrian rocks of the Grand Canyon in Arizona; hydrozoans, scyphomedusae, and possibly anthozoans occur sporadically in Cambrian rocks; hydrozoan fossils, especially stromatoporoids, are more numerous in Paleozoic than in Mesozoic or Tertiary strata; Scyphomedusae are rare throughout; anthozoans became important in the Middle Ordovician, and have retained their importance into Recent time (Fig. 1).

Coelenterates live in all marine environments today, although, like most animals, they are more numerous on continental shelves than elsewhere. Forms with skeletons are sessile and benthonic but a few horny hydrozoans attach themselves to floating weed. Forms with calcareous skeletons seem on the whole to prefer a hard substratum, but forms with horny skeletons may attach themselves also on muddy bottoms. Calcareous anthozoans and hydro-

zoans in the past, as today, are the most important inhabitants of organic reef environments; many of them act and have acted as framework organisms; they are and have been more prolific in warm waters than in cold.

Phylum COELENTERATA Frey & Leuckart, 1847

[Originally included Porifera and Ctenophora] [=Zoophyta LINNÉ, 1758 (*partim*); Radiata LAMARCK, 1802 (*partim*); Actinozoa DE BLAINVILLE, 1831 (*partim*); Nematozoa BRONN, 1831; Nematophora HUXLEY, 1852 (*partim*), Coelentera LANKESTER, 1877; includes Cnidaria HAECKEL, 1881 (*non* Cnidaires M.EDW.-H., 1857); Cnidarea DELAGE & HÉROUARD, 1901; Enterocoela GRABAU, 1913 (*non* HUXLEY, 1875)]

Multicellular animals with biradial or radiobilateral symmetry; body wall with cells arranged in 2 layers (ectoderm and endoderm) connected by a structureless mesogloea containing cells chiefly of ectodermal origin; within the body wall is a single cavity (enteron) having a single opening (mouth) for ingestion and egestion and commonly being divided by radial folds and partitions; digestion partly intracellular; nervous system comprised of a network of cells; no respiratory, excretory, or circulatory systems. *Precam.-Rec.*

Subphylum CNIDARIA Hatschek, 1888

[Actinozoa DE BLAINVILLE, 1830; *non* Cnidaires MILNE-EDWARDS & HAIME, 1857 (=Anthozoa *hic*); *nec* Cnidaria VERRILL, 1865 (=Anthozoa *hic*); *nec* Cnidaria HAECKEL, 1881 (=Coelenterata *hic*)]

Mainly distinguished by possession of stinging capsules (nematocysts) and well-developed muscular action. Commonly with power of budding, by which either individuals or colonies may be formed; sexual reproduction typically producing an ovoid uniformly ciliated larva (planula); polymorphism characteristic, chief types being fixed cylindrical polyps and free cup-shaped medusae; some groups with endo- or exoskeleton of calcitic, aragonitic, horny or chitinophosphatic nature.[1] *Precam.(Algonk.)-Rec.*

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[1] Includes 3 main classes (Hydrozoa, Scyphozoa, Anthozoa) in addition to the 2 assemblages (Protomedusae, Dipleurozoa) designated by CASTER and HARRINGTON & MOORE as classes (p. F21, F24). The modern meaning of the term Scyphozoa is quite different from the original usage (GÖTTE, 1887), which embraced the Anthozoa and Ctenophora but consistent use during many decades for the acraspedote medusae supports retention of the name. As defined in the *Treatise*, the Scyphozoa include subclasses called Scyphomedusae and Conulata (p. F28).

MORPHOLOGY OF LIVING COELENTERATES

By Libbie H. Hyman

CONTENTS

CHARACTERISTICS OF COELENTERATES

The phylum Coelenterata, preferably termed Cnidaria after removal of the sponges and ctenophores, exemplifies a grade of animal structure characterized in two important ways, (1) in being composed of tissues not constituted into organs, and (2) in the arrangement of its parts on a radially symmetrical plan (Fig. 6). The body consists essentially of a solid wall inclosing a simple or more or less subdivided central cavity (coelenteron) that is closed at one end (aboral) and open by the mouth at the other end (oral). The wall is composed of an outer epithelium (ectoderm or epidermis), an inner epithelium (endoderm or gastrodermis) bounding the central cavity or cavities, and an intermediate tissue (mesogloea or mesenchyme) varying in thickness and construction. Other tissues present are a nervous network and strata of muscular fibers; these occur between the epithelia or at their bases.

The cnidarian body is constructed on the radial plan; that is, all parts are symmetric-ally arranged around the central oral-aboral axis, and any plane through the body that includes the whole of this axis will divide the body into halves that are identical with each other regardless of the direction of the plane. Radial symmetry is generally believed to be the original morphological plan of the phylum; it is altered to biradial and bilateral symmetry in many members of the class Anthozoa, but such alteration is commonly considered to be secondary (Fig. 7). In biradial symmetry the parts are arranged symmetrically not only with reference to the oral-aboral axis but also with reference to 2 planes at right angles to each other, arbitrarily called sagittal and transverse planes. The halves obtained by section through the oral-aboral axis and the sagittal plane are identical with each other but not identical with the halves obtained by section through the axis and the transverse plane although these are also identical with each other. In bilateral symmetry parts are arranged symmetrically with reference to one plane only, the median sagittal plane. A section along this plane in the anteroposterior axis will yield identical halves, and

this is not possible along any other plane of section. Symmetry observed in coelenterates is illustrated by diagrammatic transverse sections (Fig. 8).

Other prominent structural features of cnidarians are the tentacles and the nematocysts. The tentacles are long, slender, hollow or solid extensions of the wall that surround the oral end in one or more cycles. They are wanting in very few members of the phylum. The nematocysts or stinging capsules (not cells) are secreted bodies containing a coiled thread (actually a tube) that, under certain conditions of stimulation, is emitted to the exterior by turning inside out. Such everted threads penetrate prey and stupefy it by means of a toxic fluid of unknown nature emitted from the tip of the thread. All cnidarians are provided with nematocysts which are in fact diagnostic of the living members of the phylum.

The phylum illustrates to a marked degree the phenomenon of polymorphism,

Hydroid polyp in longitudinal section

Hydrozoan medusa in transverse section

Hydrozoan medusa
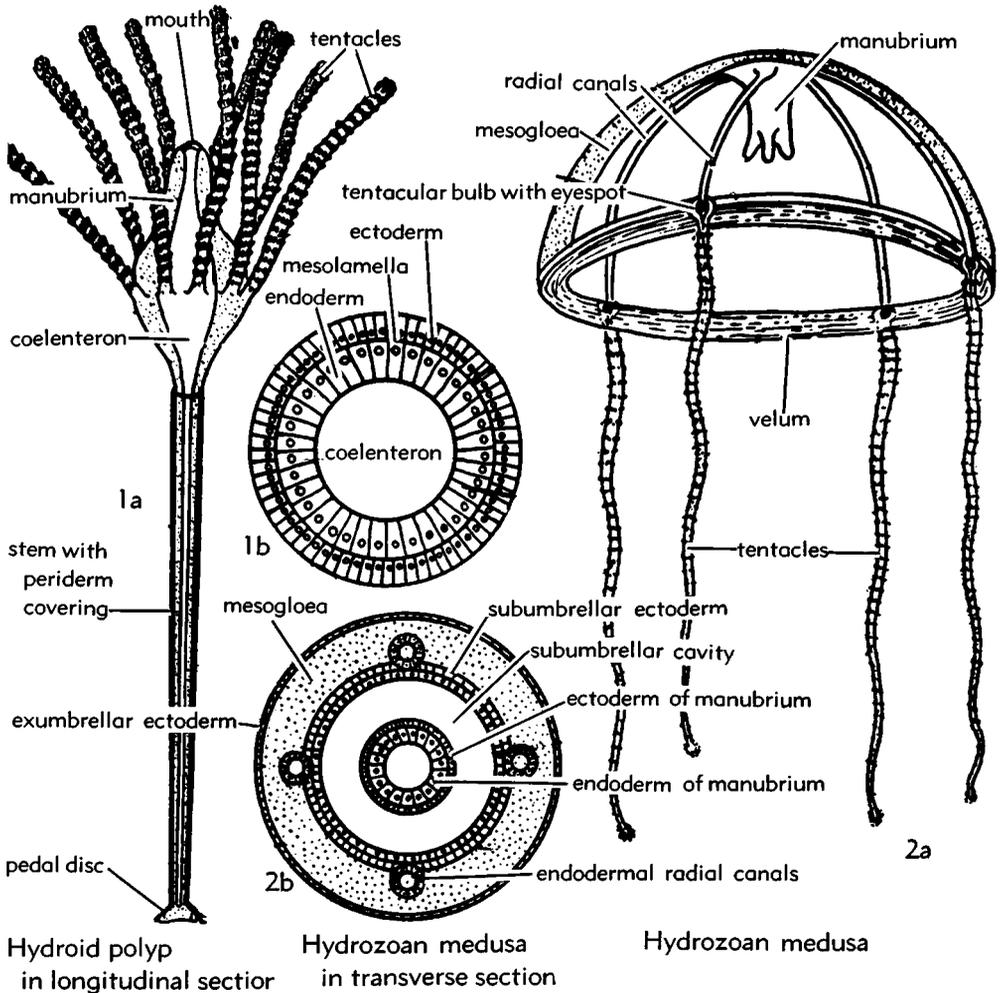
Fig. 6. Diagrams of coelenterate structure. *1*, Hydroid polyp; *1a*, partly in longitudinal section showing periderm-covered stalk with basal attachment and tentacle-encircled hydranth bearing the mouth and containing an undivided central digestive cavity (coelenteron); *1b*, transverse section through hydranth (much enlarged) showing cell layers. 2. Hydrozoan medusa; *2a*, somewhat oblique and partly sectional view of umbrella-shaped body with pendent tentacles, the mouth being located at end of a tubular extension (manubrium) at the summit of the vault on the concave surface; *2b*, transverse section above end of the manubrium. (Modified from L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York.)
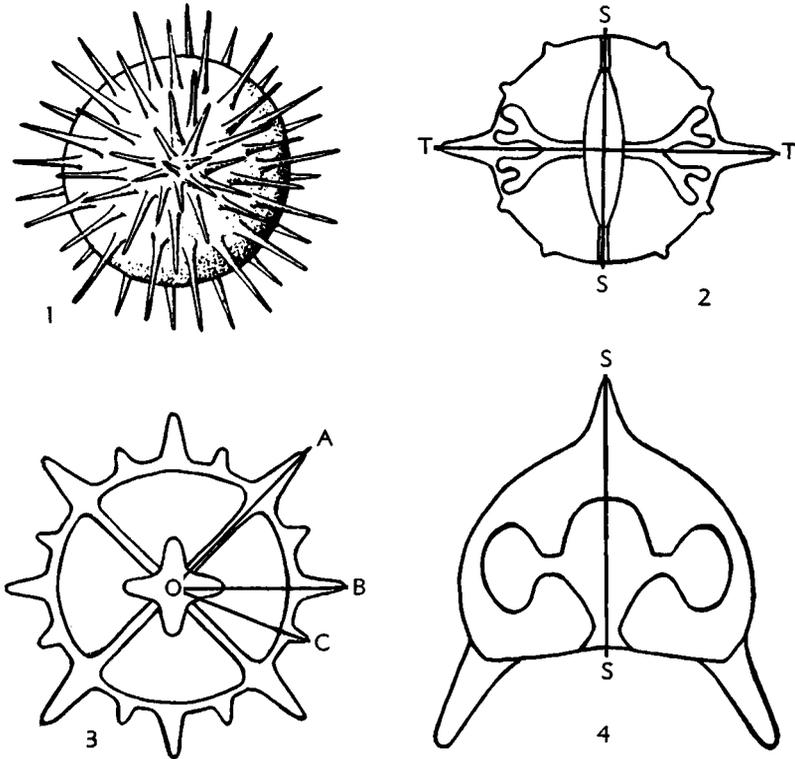
FIG. 7. Symmetry in invertebrate animals. *1*, Spherical symmetry. *2*, Biradial symmetry, characterized by lack of identity of halves produced by section along sagittal and transverse diameters. *3*, Radial symmetry of tetramerous type, characterized by identical nature of halves produced by section along any 2 diameters at right angles to each other. *4*, Bilateral symmetry, with differentiation of dorsal and ventral surfaces. *AO*, perradius; *BO*, interradius; *CO*, adradius; *SS*, sagittal axis; *TT*, transverse axis (modified from L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).

which is to say, that it expresses itself in a variety of morphologies that are, however, reducible to 2 plans, the polypoid and the medusoid. The polypoid cnidarian has a columnar form, attached at the aboral end, free at the oral end, which is directly encircled by tentacles (Fig. 6). The intermediate layer of the wall is relatively thin, varying from a thin cement to a stratum of connective tissue. The medusoid type, free-swimming, has the shape of a bowl or saucer with tentacles around the rim and mouth at the end of a tubular projection depending from the center of the concavity of the bowl (Fig. 6,*2a*). The intermediate layer is here very thick, composed of a gelatinous material, whence the common name of jellyfish applied to medusoids. The terms craspedote and acraspedote used with reference to medusae refer to the presence or absence of a circular muscular shelf extending inward from the bowl edge.

The polypoid type exhibits a high degree of asexual reproduction and tends to form colonies fixed to a substratum (Fig. 9). Such colonies require support and hence are provided with some sort of skeleton, either external or internal or both. The form and nature of this skeleton varies in the different groups of Cnidaria. The medusoid type is solitary, although a few forms are capable of budding off other medusae like themselves, and, being free-swimming, hence supported by the water, does not require and among living forms is not provided with any skeleton. Sexual reproduction commonly results in the formation of a swimming larva that in general settles and develops into some variant of the polypoid type. The medusoid type, when present in
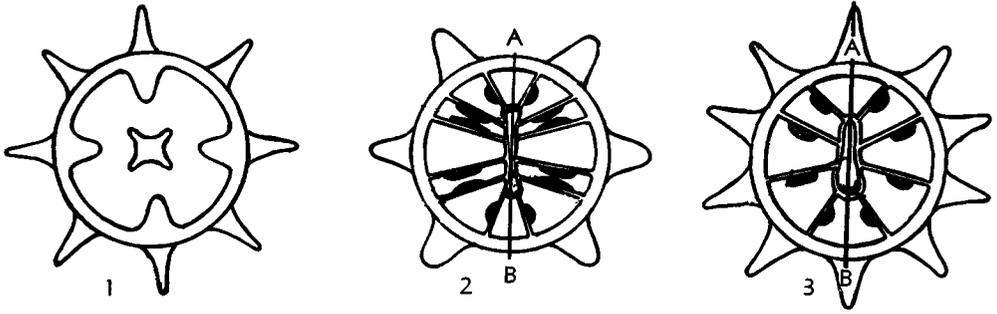
FIG. 8. Diagrammatic transverse sections of coelenterates illustrating symmetry. *1*, Hydrozoan or scyphozoan medusa, showing tetramerous radial symmetry. *2*, Anthozoan (anemone) showing hexamerous biradial symmetry. *3*, Anthozoan (octocoral) showing octamerous radiobilateral symmetry. *AB*, plane of bilateral symmetry (HYMAN).

the life cycle, arises by asexual budding from the polypoid.

The existing cnidarians are almost exclusively marine and widely distributed throughout the oceans, although most abundant on the continental shelves. The polypoid types are benthonic, with the exception of a few genuine pelagic forms besides others that habitually live attached to floating seaweeds. The medusoid types are pelagic, either neritic or oceanic, and some are limited to the deeper waters of the oceans.

CLASSIFICATION OF CNIDARIA

The Cnidaria (HATSCHEK, 1888) may be defined as radial, biradial, or radiobilateral Metazoa composed of tissues, without definite organs; parts organized around an oral-aboral axis, lacking cephalization; with one internal cavity, the coelenteron, simple or subdivided, closed aborally, open orally by the mouth surrounded (with few exceptions) by one or more circles of tentacles; with nematocysts as a defensive and food-capturing device; solitary or colonial, fixed or free-swimming; colonies produced by budding processes, generally provided with a skeleton; highly polymorphic, attached phases polypoid, free-swimming phases medusoid; sexual reproduction generally with a free larva that attaches to become a polypoid type; almost exclusively marine; ?Precambrian; Cambrian to Recent.

The Cnidaria are divided into 3 classes:[1] Hydrozoa, Scyphozoa, and Anthozoa.

The Hydrozoa are polymerous or tetra-

merous radially symmetrical cnidarians, that occur as polyps or medusae or both; coelenteron simple or branched but not provided with a stomodaeum, or with septal projections or with nematocyst-bearing structures; oral end of the polyp elongated into a manubrium; medusa of the craspedote type without rhopalia.

The Scyphozoa are solitary acraspedote tetramerous radially symmetrical medusae or medusa-like polypoids in which the coelenteron is subdivided in larva or adult into a central space and 4 interradial pockets by 4 projecting interradial septa; the coelenteron is armed with nematocyst-bearing tentacles (gastric filaments); the margin of the medusae bears sense organs (rhopalia) in the form of reduced and altered tentacles; the life cycle includes a polypoid larva that differs from a hydrozoan polyp in its tetramerous symmetry and subdivision of the coelenteron by 4 longitudinal septa and that develops directly into the adult medusae or gives off medusae by transverse fission.

The Anthozoa are exclusively polypoid cnidarians with hexamerous, octamerous, or polymerous biradial or radiobilateral symmetry; the oral end is expanded radially into an oral disc bearing hollow tentacles; a stomodaeum is present, usually provided with one or more siphonoglyphs; the coelenteron is more or less subdivided by endodermal septa some or all of which are fastened to the stomodaeum; parts of septa not fastened to the stomodaeum are edged with a cnidoglandular filament; all traces of a medusoid stage are absent; the members are solitary or colonial and commonly provided with skeletons.

[1] See classification given on p. F2-F4 for main divisions of Coelenterata which are recognized in this volume of the *Treatise*.—EDITOR.

HYDROZOA

MORPHOLOGICAL FEATURES

The Hydrozoa typically occur as radially symmetrical polypoid forms, either solitary or colonial, mostly the latter. The ordinary hydrozoan polyp consists of the attached **base,** the slender erect stem or **stalk,** and the elongated terminal expansion or **hydranth** that bears the mouth and tentacles. Colonies arise by formation of stem buds that grow out into branches and by basal outgrowths **(stolons)** that send up new stems; the latter develop terminal hydranths and repeat the budding and branching processes. These colonies are generally stiffened and protected by an external skeleton in the form of a chitinous tube. In the orders Milleporina and Stylasterina, however, the polyp colony occupies a massive calcareous exoskeleton permeated by the stems of the polyps in the form of tubes. The living part of a hydrozoan colony is hollow, containing a continuous coelenteron. Hydrozoan polyps show a good deal of polymorphism, often occurring in several types within the same colony.

Many hydrozoans also have a medusoid stage, budded off asexually to swim about as a free medusa. In such case the polypoid stage is wholly asexual and the medusa is the sexual form, producing sex cells that develop into the polypoid stage by way of a free larva, termed **planula.** However, the medusoid stage often shows more or less reduction or abortion, finally being reduced to an altered polyp **(gonozooid)** that produces the sex cells directly. In one group of Hydrozoa, the order Trachylina, on the contrary, the polyp stage is greatly reduced or absent and the free medusa dominates.

In the past, the hydrozoan life cycle that consists of an asexual polypoid phase budding off sexually reproducing medusae was regarded as typical and was interpreted as an alternation of asexual and sexual generations (metagenesis). It is more consistent with the facts about other invertebrate groups and a more physiological interpretation to regard the polypoid phase as a persistent juvenile stage that has continued to multiply asexually, whereas the medusoid phase is the definitive adult. It follows as a necessary corollary to this interpretation that

FIG. 9. Hydroid colony of calyptoblastic type *(Campanularia)*, illustrating sympodial growth (HYMAN).

the medusoid type is the original and primitive coelenterate.

DIVISIONS

The Hydrozoa are classified as follows:[1]

Order Hydroida, the hydroids. Polypoid generation well developed, solitary or colonial, mostly provided with a chitinous exoskeleton; with free medusae or aborted structures representing medusae present on the polypoids; medusae provided with ocelli or ectodermal statocysts or both.

Order Milleporina, the millepores. Hydroid colony occupying the surface layer of a massive calcareous exoskeleton with pores through which the polyps protrude; polyps dimorphic; protective polyps with capitate tentacles; with free but degenerated medusae, formed in special cavities.

Order Stylasterina. Similar to Milleporina, but protective polyps small, without tentacles; without free medusae; sex products formed on aborted medusae in special cavities.

[1] See footnote, p. F13.

Order Trachylina, the trachyline medusae. Hydrozoa with only the medusoid stage well developed; hydroid stage reduced or wanting; sense organs of medusae are statocysts and tentaculocysts with endodermal statoliths.

Order Siphonophora, the siphonophores. Hydrozoa existing as floating or free-swimming highly polymorphic colonies without skeleton, composed of an assortment of polypoid and medusoid individuals attached to a stem; without free medusae.

Order Chondrophora. Floating colonies consisting of polymorphic members attached to the underside of a disciform expansion; with free medusae.

SCYPHOZOA

MORPHOLOGICAL FEATURES

The Scyphozoa or Scyphomedusae are cnidarians primarily of the medusoid type which reaches a climax in this class. They have the same general appearance as the medusae of the Hydrozoa but are commonly much larger and of more complicated construction. Like the hydromedusae, the Scyphomedusae are based on a plan of tetramerous radial symmetry; that is, their main parts are arranged symmetrically in 4 or some multiple of 4 around the central oral-aboral axis of symmetry. This axis, therefore, falls at the intersection of 2 principal (but identical) planes of symmetry crossing at right angles. These 2 planes are those on which the mouth angles and gastric pockets lie. The 4 radii thus indicated are called **perradii** and the 4 radii halfway between them are termed **interradii;** when necessary, radii halfway between adjacent per- and interradii are referred to as **adradii.** There are obviously 4 perradii and interradii but 8 adradii. Section along the 4 perradii or the 4 interradii results in 4 morphologically identical quadrants; this is the essence of tetramerous symmetry.

The highly gelatinous body **(bell** or **umbrella)** varies in shape from a goblet or trumpet to a dome, bowl, or saucer; it bears tentacles on the margin at 4 or more radii or in indefinite number, further complicated assemblages of sensory organs called **rhopalia.** The bell margin is typically scalloped on the plan of 4 and the tentacles and rhopalia are definitely related to the scallops.

A rhopalium comprises an equilibratory organ (tentaculocyst), chemoreceptive sensory patches, and in some Scyphozoa eye spots. The scyphozoan bell lacks the velum characteristic of the hydrozoan medusa, that is, a circular muscular shelf extending inward from the bell margin, although a slight indication of this structure is present in some Scyphozoa. This difference leads to the names **craspedote medusae** and **acraspedote medusae** for hydro- and scyphomedusae, respectively.

From the center of concavity of the bell depends the beginning part of the digestive tract in the form of a quadrangular tube **(manubrium)** opening at its free end by the 4-cornered mouth. The mouth corners, commonly drawn out into frilly **oral lobes** or **arms,** define the perradii. The manubrium is lined with endoderm, not as earlier supposed with inturned ectoderm; hence, as in the Hydrozoa, a pharynx or stomodaeum is lacking in the Scyphozoa. The manubrium leads into the general coelenteron located in the substance of the bell; as characteristic of the Scyphozoa, in contrast with hydrozoan medusae, the coelenteron is subdivided into a central stomach and 4 gastric pockets located on the perradii produced by 4 partitions or septa projecting into the interior along the interradii. As a further characteristic of Scyphozoa, the free edges of the 4 partitions bear numerous tentacle-like projections, termed **gastric filaments,** that are armed with nematocysts and participate in the capture of prey. Definite gastric pockets and interradial partitions are lacking in adults of the higher orders of Scyphozoa, being confined to the larval stages, but gastric filaments are invariably present. From the periphery of the central stomach or its pockets gastrovascular canals, commonly much branched, are given off to the bell margin where a ring canal may or may not be present.

Another distinctive feature of the Scyphozoa, wanting in hydrozoan medusae, is the presence between the bell margin and the manubrium of a deep depression, the **subumbrellar funnel,** pushed into the partition in each interradius. This fundamental feature again is present in the adults of only the lower orders, being confined to the larval stage of the higher ones.

Strong muscles, running in circular and radial directions, are present; especially noticeable is the coronal muscle, a strong circular band on the subumbrellar side near the periphery. By its contractions the bell pulsates, enabling the medusa to swim and keep afloat. The nervous system consists of the usual plexus in the base of both epithelial layers, without cephalic concentration, but ganglionic concentrations of nervous tissue occur in connection with each rhopalium and these rhopalial ganglia are important in controlling activities of the animal.

REPRODUCTION

Adult Scyphozoa reproduce exclusively by the sexual method; the gonads are borne on the sides of the interradial partitions where present, or in the floor of the stomach periphery. The early larva (planula) attaches and develops into a polypoid type that reproduces extensively by asexual methods. It differs considerably from the hydroid polyp in having a trumpet-shaped body attached by an adhesive basal disc and 4 subumbrellar funnels and 4 interradial partitions. It is thus, like the adult, definitely tetramerous, unlike the hydrozoan polyp. Consequently, tetramerous radial symmetry is found to be fundamental to the class Scyphozoa. The scyphozoan polyp produces medusae by transverse fission of its summit; such juvenile medusae differ considerably from the adult in appearance and gradually develop the adult morphology.

OCCURRENCE AND CLASSIFICATION[1]

As the Scyphozoa are devoid of skeletal elements one would not expect any preservation as fossils. However, a few impressions left by them in favorable situations exist. The Scyphozoa are and always have been exclusively marine.

The Scyphozoa or Scyphomedusae are defined as acraspedote tetramerous medusae or medusa-like polypoids in which the coelenteron bears the gonads and gastric filaments armed with nematocysts; the coelenteron in adult or polypoid young is subdivided by 4 interradial partitions into a central space and 4 perradial pockets; the subumbrella is

indented by 4 interradial pits (subumbrellar funnels) sunk into the partitions when these are present; complicated marginal sense bodies (rhopalia) are present; life history includes a polypoid tetramerous young provided with interradial septa and subumbrellar funnels; this develops directly into the adult or gives off medusae by transverse fission. The class is divided into 4 orders:

Order Stauromedusae or Lucernariida. Adult as a solitary attached polypoid with goblet- or trumpet-shaped body, provided with interradial partitions, subumbrellar funnels, and 8 marginal groups of tentacles; not represented as fossils.

Order Carybdeida or Cubomedusae. Free medusae of cuboidal or quadrangular shape with 4 tentacles or groups of tentacles at the corners and 4 rhopalia between the corners; tentacles borne on a flattened bladelike base, the pedalium; with interradial gastrovascular septa and subumbrellar funnels.

Order Coronatae. Free medusae with scalloped bells, characterized by a circular coronal groove; tentacles borne singly on pedalia, alternating with rhopalia; with interradial partitions and subumbrellar funnels.

Order Semaeostomeae. Typical flat or saucer-like free medusae with generally 8 or 16 rhopalia borne in niches between the lappets; rhopalia alternating with one to many tentacles; mouth angles drawn out into long frilly lobes; interradial partitions, gastric pockets, and subumbrellar funnels wanting in the adult, but present in the polypoid young.

Order Rhizostomeae. Tentacles wanting; oral lobes branched into 8 thick gelatinous arms that obliterate the mouth and contain numerous small mouths; otherwise as in Semaeostomeae.

ANTHOZOA
MORPHOLOGICAL FEATURES

The Anthozoa are strictly polypoid cnidarians in which all trace of a medusoid stage has been lost from the ontogeny. The broad morphological alterations from the radial to the tetramerous type already seen at work in the hydrozoan medusa and in both hydroid and medusoid phases of the Scyphozoa are further evolved in the Anthozoa,

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[1] See footnote, p. F13, and p. F27-F66.

resulting in biradial and radiobilateral types of symmetry. Tetramerous symmetry easily passes into biradial symmetry. Whereas in tetramerous symmetry the 4 perradii have identical ends and planes along them divide the body into identical halves or quadrants, in biradial symmetry the 2 ends of one pair of perradii differ from the 2 ends of the other pair of perradii. Consequently, a plane along each pair of perradii will produce identical halves but those from one pair will not be identical with those from the other pair (Fig. 8). The 2 pairs of perradii are arbitrarily called **sagittal** and **transverse axes**. Bilateral symmetry is easily derived from either the tetramerous or the biradial type by the development of unlikeness along the sagittal axis.

The bilateral symmetry found in the Anthozoa is of the radiobilateral type, that is, it retains features of radial symmetry in the form of radiating partitions and hence is clearly an alteration of radial symmetry. It is therefore quite unlike the bilateral symmetry of the true bilateral animals which do not retain radial features, although presumably derived from a radial ancestor. Consequently HADZI's attempt to derive the Anthozoa from the flatworms appears poorly founded. The symmetry of the majority of the Anthozoa is best referred to as radiobilateral.

The anthozoan polyp differs in several ways from the hydrozoan polyp. It is relatively short and stout, with the oral end flattened into a disc bearing a central mouth encircled by one or more circlets of tentacles. As foreshadowed in the Scyphozoa, the coelenteron is no longer a simple cavity but is divided up into chambers by longitudinal partitions, the **septa** or **mesenteries**. The mouth leads into the coelenteron by way of an elongated pharynx or **stomodaeum** probably lined by inturned ectoderm. This opens freely below into the general coelenteron. Some of the septa just mentioned reach from body wall to pharynx, hence are termed perfect or complete septa; others that do not reach the pharynx are termed imperfect or incomplete. The free edges of all mesenteries are provided with a sinuous thickening called the septal **filament** armed with glands and nematocysts that reminds of the gastric filaments of the Scyphozoa. As all septa have free edges basal to the pharynx it is clear that all of the coelenteric chambers are in communication. The anthozoan pharynx commonly bears one or more **siphonoglyphs.** These are flagellated grooves by which water currents are directed into the interior. The presence of the siphonoglyphs defines the sagittal axis, and the mouth is also commonly elongated in this axis.

Another difference between the anthozoan and hydrozoan polyp is the much greater thickness of the intermediate layer between the 2 body epithelia in the former. This intermediate layer is invariably cellular and consists of some form of connective tissue. Thus, the standard concept of the coelenterates as 2-layered animals fails with regard to the Anthozoa and is best abandoned as of no comparative morphological value.

The anthozoan polyp may be solitary, in which case it is usually temporarily attached by a basal disc or other type of basal expansion. Most generally, however, anthozoans are colonial and the colonies are then supported by skeleton of varied nature, commonly developed strongly. Further, as in hydrozoan colonies, the polyps of anthozoan colonies are often di- or polymorphic.

The muscular system is mostly well developed, especially in the form of retractor muscles along the septa by which the body can be shortened quickly. The arrangement of these retractor muscles is of great systematic importance among the existing anthozoans. The nervous system takes the form of the usual network, not concentrated into anything resembling a center. The sex cells are produced along the septa and develop into a swimming larva of the planula type that settles and develops directly into a polypoid.

OCCURRENCE AND CLASSIFICATION[1]

The Anthozoa are exclusively marine and those with calcareous skeletons are well-preserved as fossils, furnishing, indeed, many types no longer in existence.

The Anthozoa are divisible into 2 great groups or subclasses, the Octocorallia with octamerous radiobilateral symmetry and the Zoantharia with various types of biradial or radiobilateral symmetry.

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[1] See footnote, p. F13, and chapters on Anthozoa.

SUBCLASS OCTOCORALLIA

The octocoral (or alcyonarian) polyp differs from all other anthozoan polyps in several respects. It is provided with 8 pinnate tentacles symmetrically arranged. The coelenteron is subdivided by 8 complete single septa that extend from the body wall to the pharynx into 8 chambers, each of which continues into a tentacle. The tentacles therefore alternate with the septa. The pharynx is provided with one siphonoglyph (or sulcus) and the side of the polyp that bears the siphonoglyph is arbitrarily termed ventral, or better sulcal. On its sulcal face, that is, the side toward the siphonoglyph, each septum bears a strong longitudinal muscle band, the retractor, by which the polyp can be contracted and its oral end drawn into the interior. The 8 symmetrically arranged tentacles and septa confer on the alcyonarian polyp a superficial appearance of octamerous radial symmetry (whence the name Octocorallia) but the presence of one siphonoglyph and the arrangement of the septal muscles modify this symmetry in the direction of bilaterality. There is but one plane of symmetry, that which bisects the siphonoglyph, leaving 4 septa in one half and 4 in the other.

Below the pharynx, the septa are free and gradually diminish in breadth to the polyp base, being finally reduced to mere ridges. Generally, only the 2 asulcal septa, that is, those opposite the siphonoglyph, reach the base. The free septal edge is thickened into a cord, the septal filament, mostly of digestive nature, but the filaments of the 2 asulcal septa differ from the other 6, being heavily flagellated and serving to create an upward current, whereas at the siphonoglyph the current runs inwards.

The existing octocorals are colonial. In simplest groups, the colony runs over a substratum in the form of single polyps erected from a stolon or mat. Most Octocorallia, however, occur as lobed or branching colonies in which only the oral part of the polyps protrudes; the basal parts are imbedded in a common flesh or coenenchyme and are connected with each other by gastrodermal (endodermal) tubes that permeate the coenenchyme. New polyps arise as a bulge from the gastrodermal tube, and this bulge then sprouts tentacles and forms a mouth and pharynx by epidermal invagination. The coenenchyme is covered externally with epidermis and within consists of a gelatinous mesenchyme containing amoeboid cells.

The polyps may be dimorphic, consisting of 2 sorts, the ordinary polyps or zooids and the siphonozooids. The latter are reduced in all structures except the siphonoglyph, which is strongly developed. The siphonozooids do not feed but serve to drive a water current through the colony.

The octocorallian (alcyonarian) colony is supported by skeleton which is generally a product of the cells of the mesenchyme, and is either calcareous or horny in nature. It may consist of separate calcareous spicules or of spicules fused by a calcareous cement or of amorphous calcareous substance or of calcareous spicules coated by or united by horn or of strands and lamellae of horn.

The nature of the skeleton more or less determines the different orders. Four of the 6 orders here recognized are represented by fossil remains, but in general the Octocorallia are not of paleontological importance.

Order Stolonifera. Polyps arising singly from a creeping base, not partly imbedded in a coenenchymal mass; may be provided with warty calcareous spicules secreted by the cells of the mesenchyme. The best-known member of this order is the red organ-pipe coral (*Tubipora*), in which each polyp is inclosed in a skeletal tube of fused calcareous spicules. The ensemble of these tubes resembles the pipes of a pipe-organ. The tubes are further united at intervals by transverse platforms. Curiously enough, *Tubipora* is not known as a fossil.

Order Telestacea. A small group, exemplified by *Telesto,* in which the colonies occur as simple or branched stems arising from a creeping base; not represented as fossils.

Order Alcyonacea. Comprises the fleshy types of octocorals, known as soft corals, in which the polyps are partly imbedded in a common massive or lobed coenenchyme. The skeleton consists of separate warty calcareous spicules secreted by the cells of the mesenchyme and commonly present in great profusion; these spicules are scantily represented as fossils.

Order Coenothecalia. Also a small group, represented by fossils and by one existing genus, the blue coral, *Heliopora,* with a

massive calcareous skeleton composed of fibers of aragonite fused into lamellae. The skeleton contains numerous blind tubes at right angles to the surface; these occur in 2 sizes, larger containing a polyp, and smaller containing gastrodermal tubes, united inside a thin superficial coenenchyme. As the colony grows, the living parts are pushed outward by the formation of transverse calcareous partitions and hence only the periphery of the mass is alive.

Order Gorgonacea. Conspicuous colonial animals of tropical and subtropical waters, including the sea whips, sea feathers, sea fans and other types collectively known as gorgonians or horny corals. Typically, the stems of gorgonians are supported by a horny axial rod which is covered over by a thin layer of coenenchyme containing the usual warty calcareous spicules and bearing the small or minute polyps. The red coral, *Corallium,* differs from other gorgonians in having a purely calcareous axis of cemented spicules. Gorgonian spicules may be preserved as fossils.

Order Pennatulacea. Fleshy colonies composed of the elongated body of the primary axial polyp and of numerous secondary polyps that spring laterally from the primary polyp. The coenenchyme as in other octocorals contains calcareous spicules that may be scantily preserved as fossils.

SUBCLASS ZOANTHARIA

This subclass includes all existing Anthozoa in which the number and arrangement of the septa and number and structure of the tentacles are otherwise than in the Octocorallia. The group is therefore more variable in morphology than is the subclass Octocorallia.

The cylindrical polyp is solitary or colonial and with or without a skeleton, here invariably an exoskeleton, secreted by the ectodermal surface of the animal. The oral end of the polyp forms an oral disc bearing hollow tentacles in one or more circlets or in radiating rows or differentiated into oral and marginal circlets. A well-developed pharynx is present, usually provided with 1 or 2 siphonoglyphs but in some zoantharians without them. The coelenteron is divided into compartments by septa, of which both the complete type reaching the pharynx and the incomplete type not reaching the pharynx are generally present. The septa are coupled, that is, in symmetrical correspondence on the 2 sides of the plane of symmetry that bisects the corners of the elongated mouth. In most individuals the septa are also paired, that is, occur in 2's close together. Thus we get the terms **exocoel** for the coelenteric chambers between pairs of septa and **endocoel** for the narrow chamber between the two members of a pair. Each septum is provided upon one face with a longitudinal retractor muscle and the arrangement of these retractors is of considerable importance among existing anthozoans. Usually the retractors of paired septa face each other, thus located on the side towards the endocoel, except for the pair of septa attached to a siphonoglyph where the retractors are on the exocoelic side. This fact distinguishes the septa of a siphonoglyph, which therefore are called directives. As in Octocorallia, the free edges of the septa are provided with filaments of glandular nature and also armed with nematocysts. Gonads are borne on the septa just back of the filaments.

The arrangement of the septa varies in the class but most commonly, as in anemones and stony corals, is hexamerous; that is, the pairs of septa occur in cycles of 6 or some multiple of 6. In a perfect hexamerous zoantharian, there are 2 siphonoglyphs, one at each end of the laterally flattened pharynx, 6 pairs of complete septa, that is, 2 pairs of directives, and 2 nondirective pairs (primaries) on each side; in the 6 exocoels between the complete pairs occur 6 incomplete pairs, also called secondaries; in the 12 exocoels so formed, 12 pairs of smaller incomplete septa, or tertiaries, and so on. As the animal grows, additional incomplete pairs arise. The hollow tentacles are related to the coelenteric chambers; typically there is one tentacle to each exocoel and one to each endocoel. Consequently the tentacles occur in the same cycles as the coelenteric chambers and increase in number with the formation of new septa.

Where 2 siphonoglyphs are present, the symmetry is of the hexamerous biradial type and the plane of symmetry is that which bisects the 2 siphonoglyphs. If but one siphonoglyph is present, the symmetry is radiobilateral.

The Zoantharia comprise 5 existing ord-

ers, of which one is provided with calcareous exoskeleton and hence of great paleontological significance.

Order Actiniaria. This order includes the sea anemones, familiar animals of the seashore, solitary polyps with a tentaculate oral end commonly of great beauty. As this group is devoid of skeleton it is not represented in fossil form.

Order Zoanthidea. A small group of mostly colonial forms, resembling small anemones, but differing from the latter decidedly in septal arrangement and other structural details. As the zoanthids lack skeleton they are of no paleontological importance.

Order Antipatharia. Also a small group, known as the black or thorny corals. They form slender branching plantlike colonies, having, like gorgonians, a hornlike skeletal axis covered with a thin coenenchyme bearing the small polyps. The type of skeleton is not readily preservable and hence this group has few fossil representatives.

Order Ceriantharia. The cerianthids appear like long cylindrical anemones but differ from these in having the tentacles differentiated into smaller oral and larger marginal sets and in an entirely different arrangement of septa all of which are perfect, reaching the pharynx. The soft body without skeleton is naturally not preservable in a fossil state.

Order Scleractinia. Zoantharians with hexamerous symmetry and calcareous hard parts; they are described in detail in a later section.

Extinct Orders. The extinct **Rugosa, Heterocorallia,** and **Tabulata,** are not discussed here because they are described in other sections of this volume.
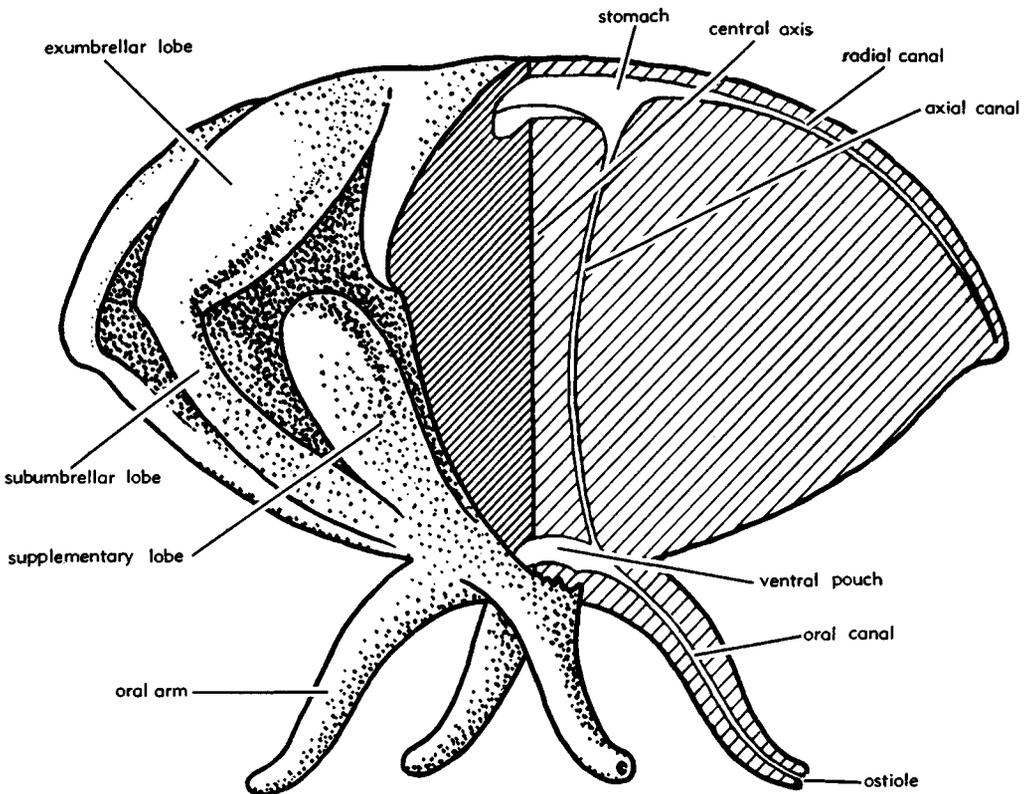

Fig. 10. Reconstruction of *Brooksella* showing morphology of external features and nature of internal structures (Harrington & Moore, n).

PROTOMEDUSAE

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

The class Protomedusae was introduced by Caster in 1945 to accommodate the peculiar Cambrian medusoid remains described by Walcott in 1896 under the names *Brooksella* and *Laotira,* referred by him to the class Scyphomedusae. These remains, preserved in cherty nodules 1 to 10 cm. in diameter—the famous "star cobbles" of the Middle Cambrian Conasauga shale of Coosa Valley, Alabama—show great variability in external shape. The simplest and most symmetrical specimens are subellipsoidal bodies displaying swollen, melon-like radial segments, sharply defined by deep radial grooves. The number of segments is highly variable, between 4 and 15 or more, and though some specimens display tetramerous symmetry, many others have an odd number of segments, 5 or 7 being common. The segments or lobes are usually irregular and those of the presumed upper or exumbrellar surface are typically wider than the corresponding ones of the lower surface. In addition, supplementary lobes are seen in many specimens, intercalated between the principals, usually inserted between the narrower subumbrellar segments. Walcott offered the plausible suggestion that the supplementary lobes acted as additional oral arms. Appendages interpreted as true oral arms, normally 4 or 5, are preserved on the subumbrellar side of a few specimens.

Walcott's reconstruction of the internal structure, based both on exfoliated specimens and polished sections, shows a central, disc-shaped aboral stomach giving rise to radial canals, one in each lobe, and to vertical axial canals connecting the stomach with a smaller, disc-shaped ventral cavity ("buccal stomach"). This cavity gives rise to radial canals, one in each oral arm, which appear to open to the exterior in a single ostiole at the distal extremity of the arms (Fig. 10). Gonads have not been recognized. Probably they were located in the central axis of the body below the aboral stomach.

The peculiar and highly variable lobation of the body, and particularly the presence of supplementary incomplete lobes, is a char-

acteristic of primary importance which distinguishes the class from all other Coelenterata. Such features as lack of marginal tentacles and absence of central mouth, which Walcott regarded as indicating a rhizostomatid alliance, were in all probability developed independently and have no phylogenetic significance.

The class Protomedusae seems restricted to the late Proterozoic and early Paleozoic. In addition to the Middle Cambrian forms originally described by Walcott, remains assignable to this class are now known from Algonkian rocks of Arizona, Upper Cambrian strata of Wyoming and Lower Ordovician beds of Sweden and France. A reference to *Laotira* sp. from the Pennsylvanian of Sinai Peninsula, Egypt, by Couyat & Fritel, has never been substantiated by figures or descriptions.

Class PROTOMEDUSAE Caster, 1945

Highly variable, primitive Coelenterata, with bodies swollen into radial pouches divided by deep sulci, commonly with incomplete supplementary lobes intercalated between principals; marginal sensory organs and tentacles absent; central stomach aboral, discoidal, giving rise to simple radial canals, one in each lobe, and to vertical axial canals connecting stomach with ventral cavity; ring canal absent; central mouth absent; oral arms 4 or ?5, each with mesial canal springing from ventral cavity and with ?single ostiole at distal end. *Precam.(Algonk.), M. Cam.-Ord., ?Penn.*

Order BROOKSELLIDA Harrington & Moore, nov.

Characters of class. *Precam.(Algonk.), M.Cam.-Ord., ?Penn.*

Family BROOKSELLIDAE Walcott, 1898

Body ellipsoidal to discoidal, deeply lobate with 4 to 15 or more irregular melon-like segments; exumbrellar lobes wide, fused at mid-field, continued ventrally on subum-
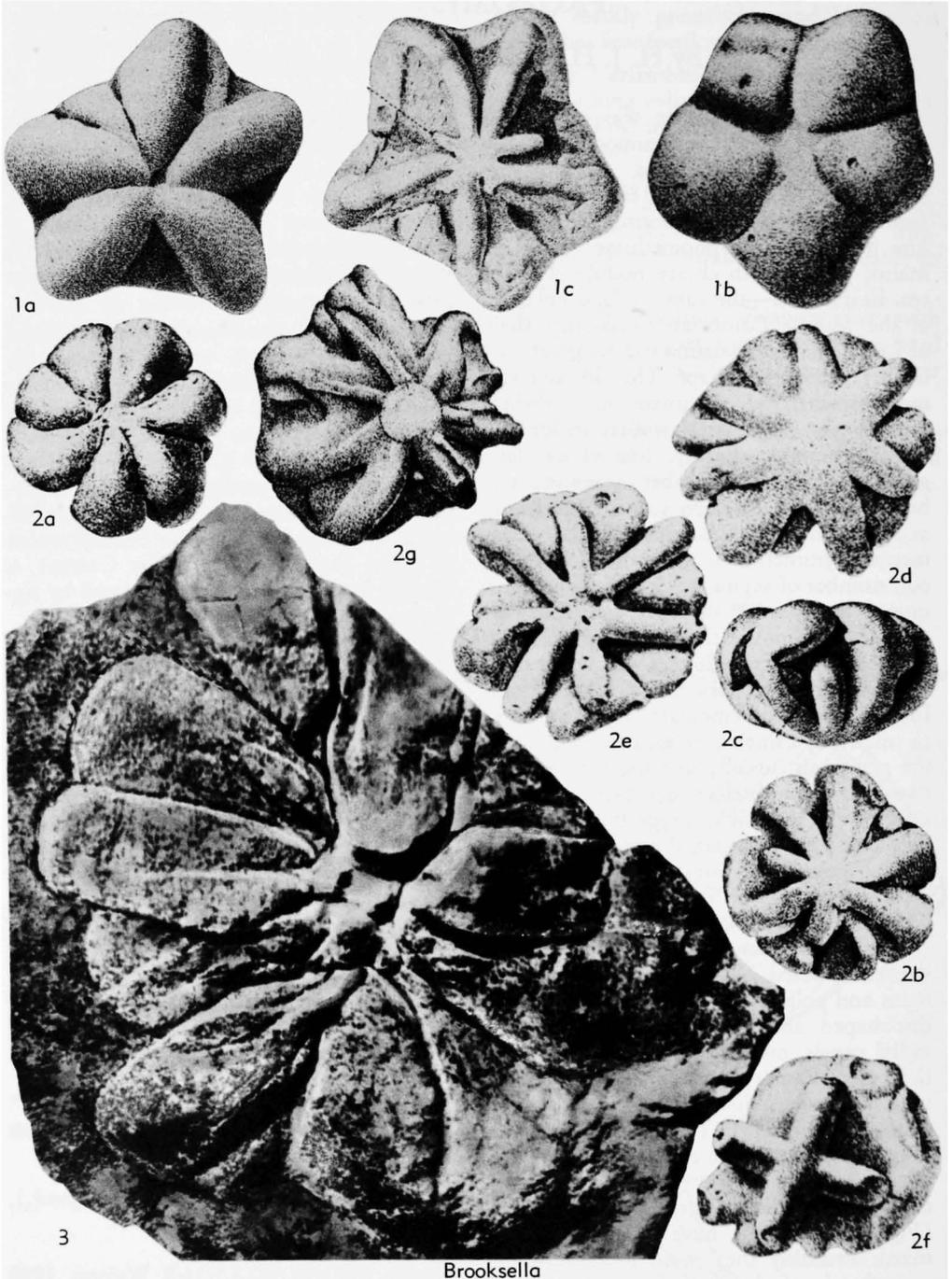
FIG. 11. Precambrian and Cambrian species of *Brooksella* from North America. *1, B. cambria*, M.Cam., Ala.; *1a,b*, exumbrellar views, ×1; *1c*, subumbrellar view, ×1 (WALCOTT). *2, B. alternata*, M. Cam., Ala.; *2a,d*, exumbrellar views; *2b,e-g*, subumbrellar views; *2c*, side view; all×1 (WALCOTT). *3, B. canyonensis*, Precam., Ariz.; holotype, ×1 (VAN GUNDY).

brella in narrow bands fused centrally; supplementary lobes, when present, seemingly fused internally along axial region of body. *Precam.(Algonk.), M.Cam.-Ord., ?Penn.*

Brooksella WALCOTT, 1896 [*nom. conserv.* proposed HARRINGTON & MOORE, 1955 (ICZN pend.)] [*B. alternata* (=*Laotira cambria* WALCOTT, 1896)] [?=*Staurophyton* MEUNIER, 1891 (**S. bagnolensis*), L.Ord., Fr.; *Laotira* WALCOTT, 1896]. Characters of family. *Precam.(Algonk.), M.Cam.-U.Cam.,* USA; *Ord.,* Swed.-?Fr.; *?Penn.,* Egypt.——FIG. 11,2. *B alternata,* M.Cam., Ala.; *2a-c,* exumbrellar, subumbrellar, and side views; *2d,e,* exumbrellar and subumbrellar views of another specimen; *2f,* oral arms of 3rd specimen; *2g,* subumbrellar view of 4th specimen; all ×1 (WALCOTT).——FIG. 11,1; 12,1. *B. cambria* (WALCOTT), M.Cam.-U.Cam., USA (type of *Laotira* (11,1, M. Cam., Ala.; 12,1, U.Cam., Wyo.); *11,1a,b,* exumbrellar views of 2 specimens, ×1; 11,1, subumbrellar view, ×1 (WALCOTT); 12,1, exumbrellar impression, ×0.65 (CASTER).——FIG. 12,2, ?*B. cambria* (WALCOTT), L.Ord., Fr. (type of *Staurophyton bagnolensis* MEUNIER); ×1 (MEUNIER)——FIG. 11,3. *B. canyonensis* BASSLER, Precam. (Algonk.), Ariz.; holotype, ×1 (VAN GUNDY).——FIG. 12,3. *B. silurica* (VON HUENE), Ord., Swed.; holotype, ×1 (VON HUENE).

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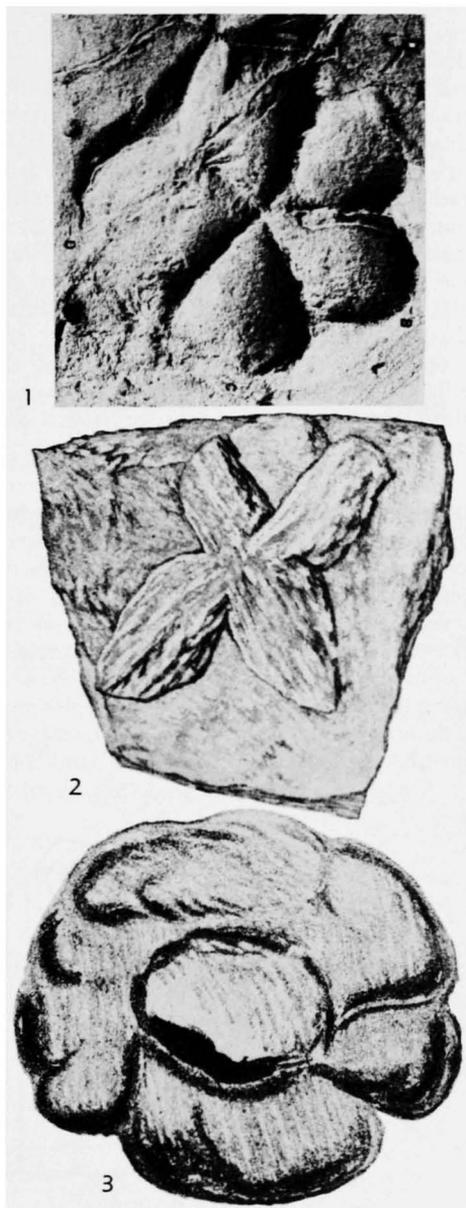
Brooksella

FIG. 12. Cambrian and Ordovician species of *Brooksella. 1, B. cambria,* U.Cam., Wyo.; exumbrellar impression, ×0.65 (CASTER). *2, ?B. cambria,* L. Ord., Fr.; exumbrellar view, ×1 (MEUNIER). *3, B. silurica,* Ord., Swed.; holotype, ×1 (VON HUENE).

DIPLEUROZOA

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

The class Dipleurozoa was introduced (1) to accommodate some very distinctive Lower Cambrian fossils from southern Australia described by Sprigg in 1947 under the generic name *Dickinsonia*. They are exceptionally neat impressions of small to medium-sized discoidal bodies of elliptical outline resembling a medusoid umbrella with radiating segments and marginal tentacles, but characterized by marked bilateral symmetry and differentiated extremities. A short median furrow along the main axis of the elliptical body gives off numerous simple, diverging lateral segments, shorter and more numerous at one extremity of the ellipse. The margin is scalloped into very short, rounded lappets, each bearing a simple tentacle (Fig. 13).

Sprigg suggested that the remains could represent a new and extinct class of Coelenterata or that, on account of their bilateral symmetry, they may belong in the Siphonophorida. Though bilateral symmetry is a common feature among the siphonophores, there is nothing to suggest that the remains under consideration represent the float or pneumatophore of a colonial coelenterate. The impressions indicate that the living animal had a consistent gelatinous body more or less homogeneous in structure, comparable to the bells of the medusae. One specimen shows what are here regarded as tentacles springing out from the marginal lappets; these structures were interpreted by Sprigg as chitinous radii, but their relation to the marginal lappets makes this view very implausible and strengthens the case for tentacles. These same relations—each tentacle springing out from the mesial part of a lappet make it highly improbable that they could represent submarginal dactylozooids of a colonial coelenterate comparable to the living genera *Velella* or *Porpita*.

Dipleurozoans seem to be restricted to the Lower Cambrian and are known exclusively from South Australia.

Class DIPLEUROZOA Harrington & Moore, 1955

Primitive, specialized Coelenterata with bell-shaped body of elliptical outline, displaying marked bilateral symmetry and differentiated extremities; median furrow along main axis of elliptical body giving off numerous flat, simple, diverging lateral segments separated by narrow grooves reaching periphery; margin scalloped into very short lappets, each bearing simple tentacle. *L.Cam.*
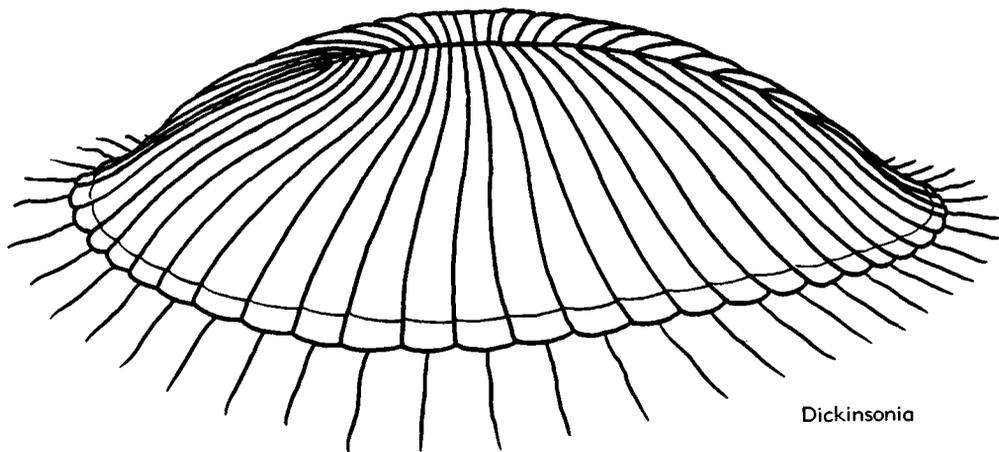
FIG. 13. *Dickinsonia spriggi* Harrington & Moore, oblique view (reconstr.) showing slightly scalloped margin with narrow lobes each bearing a short filiform tentacle. The bilateral symmetry and differentiation in character of the axial extremities are depicted, approx. ×1 (Harrington & Moore, n).

Order DICKINSONIIDA Harrington & Moore, 1955

Characters of class. *L.Cam.*

Family DICKINSONIIDAE Harrington & Moore, 1955

Body elliptical to ovoid in outline; median longitudinal furrow giving off 70 to 140

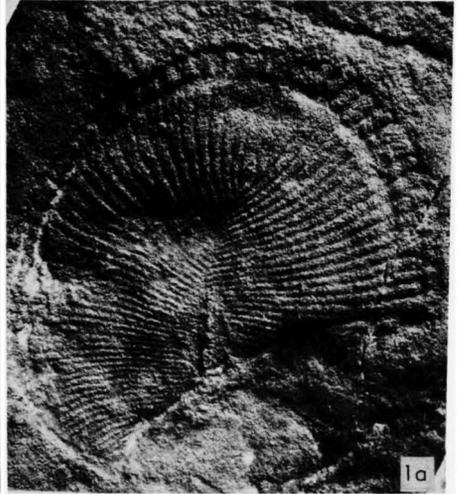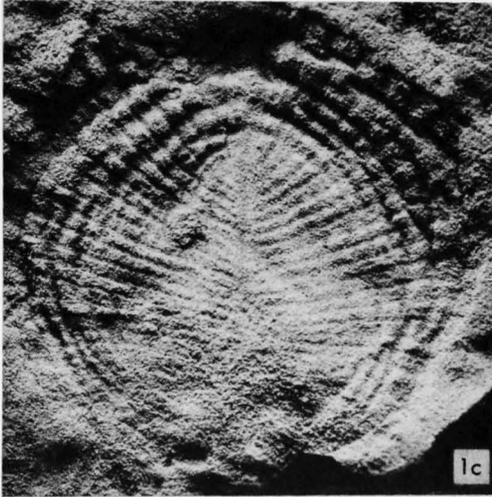Fig. 14. *Dickinsoni costata* Sprigg, from Lower Cambrian of South Australia; *1a*, ×1.25; *1b*, ×0.9; *1c*, ×1 (Sprigg).
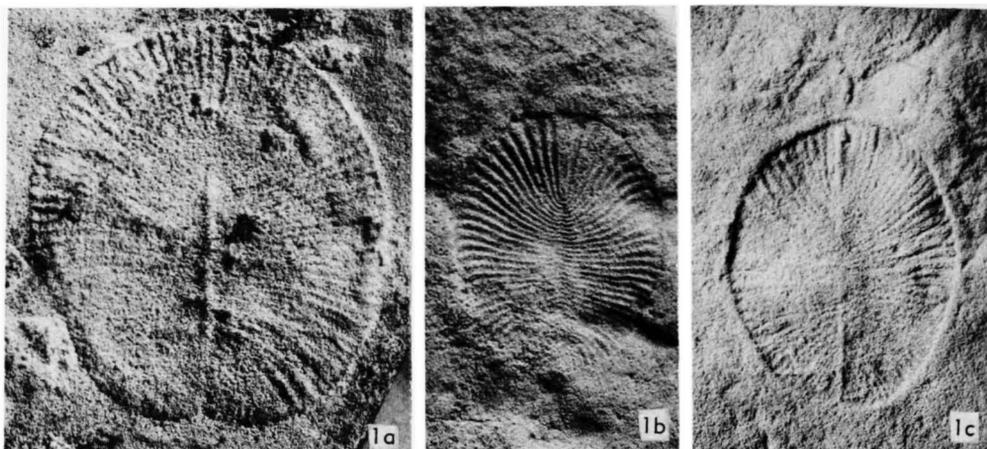
FIG. 15. *Dickinsonia minima* SPRIGG, from Lower Cambrian of South Australia; *1a*, ×0.8; *1b,c*, ×1 (SPRIGG).

FIG. 16. *Dickinsonia spriggi* HARRINGTON & MOORE, from Lower Cambrian of South Australia, holotype.

simple diverging lateral segments; segments at one extremity (?anterior) of elliptical body more numerous, narrower and less oblique than at opposite (?posterior) end. *L.Cam.*, S.Austral.

Dickinsonia SPRIGG, 1947 [*D. costata*]. Characters of family. *L.Cam.*, S.Austral.——FIG. 14,*1*. *D. costata*; *1a*, holotype, ×0.9; *1b*, another specimen, ×1.25; *1c*, 3rd specimen, ×1 (SPRIGG).——FIG. 15, *1. D. minima* SPRIGG; *1a*, holotype, ×0.8; *1b*, another specimen, ×1; *1c*, 3rd specimen, ×1 (SPRIGG).——FIG. 16. *D. spriggi* HARRINGTON & MOORE; holotype, ×1 (SPRIGG).

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SCYPHOZOA

By R. C. MOORE and H. J. HARRINGTON

CONTENTS

Class SCYPHOZOA Götte, 1887

[emend. HAECKEL, 1891, excluding Anthozoa, Ctenophora]

Mostly tetramerous (Fig. 17) free-swimming or attached Cnidaria lacking hard parts or protected by a thin chitinophosphatic periderm and typically characterized by presence of 4 interradial endodermal septa associated with longitudinal muscles of ectodermal origin and in some extinct forms with mineralized septa in this position. *Cam.-Rec.*

The Scyphozoa are exclusively marine coelenterates which include both attached (polypoid) and free-swimming (medusoid) forms. Among living representatives of the class, medusoids are overwhelmingly the more prominent, but fossils which here are assigned to the Scyphozoa mostly lack any obvious resemblance to modern free-swimming types. This generalization is dependent on revised classification that recognizes the widely distributed, not rare fossils called conulariids as belonging to the Scyphozoa, for otherwise the statement would be untrue and one could only say that the paleontological record of Scyphozoa is lamentably small. It becomes necessary to give reasons

for adding the long-extinct much-debated conulariids to the scyphozoans; also, the addition inevitably affects some names and their application.

During several decades zoologists have employed either or both of the names Scyphozoa and Scyphomedusae, introduced by HAECKEL (1891) and LANKESTER (1877), respectively, as applied to the so-called true

FIG. 17. Planes of symmetry in Scyphozoa. *1,2,* Subumbrellar views of a stauromedusid and a semaeostomatid showing position of perradial and interradial planes of symmetry; planes or lines halfway between these planes are termed adradial (modified from L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

jellyfishes, that is, the nonveiled (acraspedote) types. The older name, Acraspeda (GEGENBAUR, 1856), has not gained favor in spite of its appropriateness. In the classification adopted in the *Treatise,* the most generally accepted name, Scyphozoa, is recognized for the class and at the same time Scyphomedusae is employed in its customary taxonomic application but defined as a subclass. Another subclass named Conulata is introduced to contain extinct organisms which now are assigned position in the Scyphozoa; this subclass is divided into orders, one of which comprises the Conulariida. Diagnoses of the class and subclasses are given here as a basis of the discussion which follows; systematic descriptions of lower-rank divisions are reserved for sections devoted to Scyphomedusae and Conulata.

Subclass SCYPHOMEDUSAE Lankester, 1881

Mostly tetramerous medusae and medusalike polypoids, termed acraspedote because lacking true veil, although some possess a very similar structure (velarium); coelenteron in larva or adult partly divided by 4 interradial endodermal septa; except in a few groups, subumbrella indented by 4 deep ectoderm-lined funnels in position of the interradial septa and associated with longitudinal muscles of ectodermal origin; margin bearing reduced tentacles or rhopalia (tentaculocysts with endodermal statoliths); mesogloea cellular, containing fibers and loose amoeboid cells; polypoid larva (scyphistoma) with tetramerous symmetry defined by 4 septa dividing coelenteron, larva growing directly into adult or producing medusae by transverse fission. *Cam.-Rec.*

Subclass CONULATA Moore & Harrington, nov.

Mainly tetramerous cone-shaped to elongate pyramidal or subcylindrical organisms bearing a thin chitinophosphatic periderm which commonly bears transverse and longitudinal markings but may be smooth, some bearing an attachment disc at the pointed aboral extremity but in part probably living unattached; oral end may be protected by inward bent edges of periderm; oral margin with tentacles at least in some forms and probably in all. *M.Cam.-Trias.*
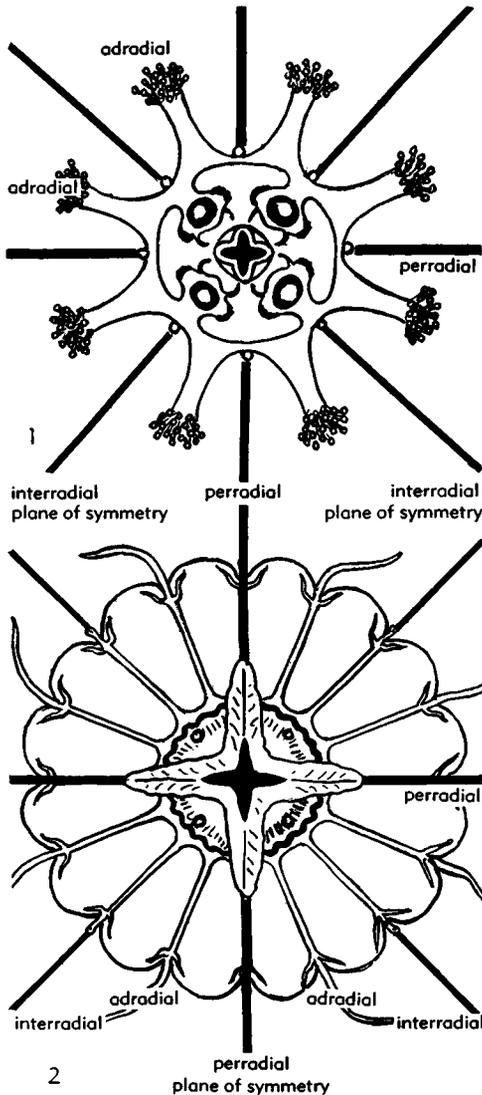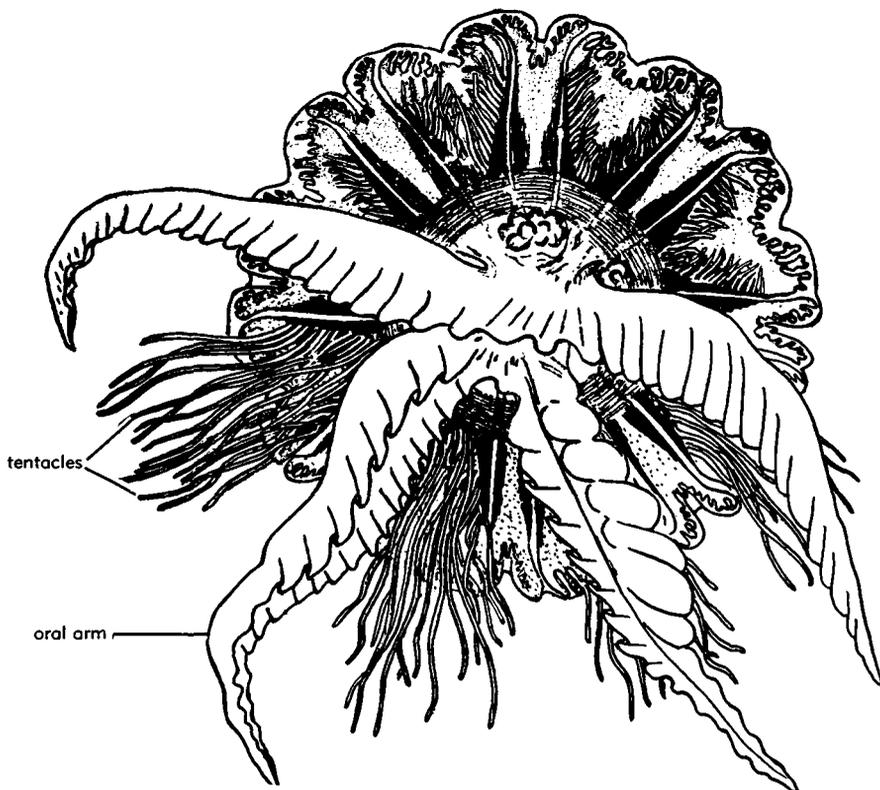
Fig. 18. Oblique view of subumbrellar surface of a modern scyphomedusan (*Cyanea,* order Samaeostomatida), showing prominent oral arms and areas of grouped tentacles; body parts are symmetrically repeated around the bell. *Cyanea arctica* attains a diameter of 2 m. or more, being distinguished as the largest known coelenterate (after L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

DISTINGUISHING CHARACTERS OF SCYPHOZOA

The outstanding feature of the Scyphozoa is strong development of tetrameral radial symmetry throughout life from larval to adult stages and in both polypoid and medusoid states. The body is divisible into identical quadrants by either of 2 sets of planes which intersect at right angles along the axis extending from center of the mouth to the aboral pole (Fig. 17). One set of such planes of symmetry can be placed so as to pass through the mouth arms or laterally outstretched angles and internally to divide each of 4 gastric pouches into halves; by definition these planes are termed perradial. The other set of planes of symmetry belongs halfway between the perradial planes so as to pass through inner angulations of the mouth and coincide with septa that bound the gastric pouches; these planes are designated as interradial. Any radial line or structure located halfway between adjacent perradial and interradial planes is called adradial but none of these define symmetry. In nearly all scyphozoans body parts are symmetrically repeated around the longitudinal axis in the number of 4 or multiples of 4 (Figs. 17, 18); a very few forms having scyphozoan attributes otherwise exhibit a hexameral plan and constitute exceptions.

BASIS FOR CLASSIFICATION

The recognition of divisions assigned rank of subclasses within the Scyphozoa, as indicated by the diagnoses just given, needs
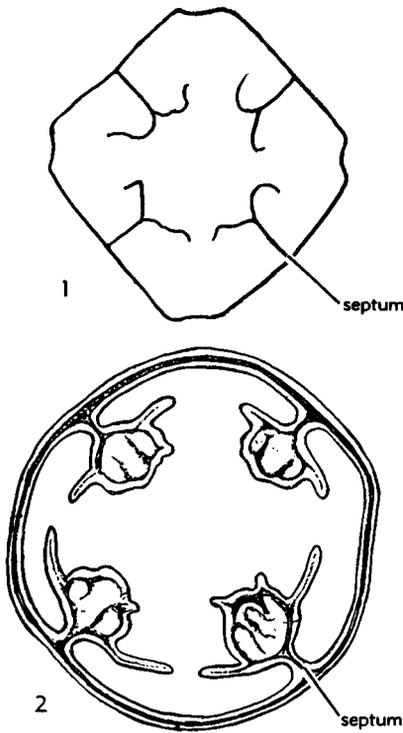
FIG. 19. Transverse sections of a Silurian conulate (*1, Eoconularia loculata,* ×15) and a modern scyphomedusan (*Craterolophus thetys,* ×1) showing similarity in development of bifurcate interradial septa formed of chitinophosphatic substance in the fossil but of soft tissue (endoderm) in living genera (KIDERLEN).

explanation. The conclusion that conulariids are coelenterates having closest affinities with scyphozoans is not new. KIDERLEN (1937) may be credited with marshaling most clearly the evidence of structural resemblances of conulariids and living scyphozoans which points to placement of both in proper phylogenetic relationships.

The Scyphomedusae, as defined to comprise living types of Scyphozoa and a very few extinct jellyfishes which have nearly identical structural features, are distinguished primarily by features of tetrameral symmetry which include partial compartmentation of the coelenteron by 4 interradially placed septa associated in some orders with deep funnel-shaped infolding of ectoderm in the oral region and development of longitudinal ectoderm-derived musculature that is so placed as to cause bifurcation of the septa. The scyphomedusan polypoid becomes anchored by a secretion

which hardens into a chitinous substance, although the free-swimming adult lacks chitinous external parts.

The Conulata are characterized by a chitinophosphatic thin periderm that covers and protects the soft parts. Excepting some forms which are considered to represent an antecedent evolutionary stage, they exhibit fundamental tetrameral symmetry and interradial septal structures which are interpreted as identical in relationship to ectodermal infolding and musculature observed in modern Scyphomedusae. This is illustrated.
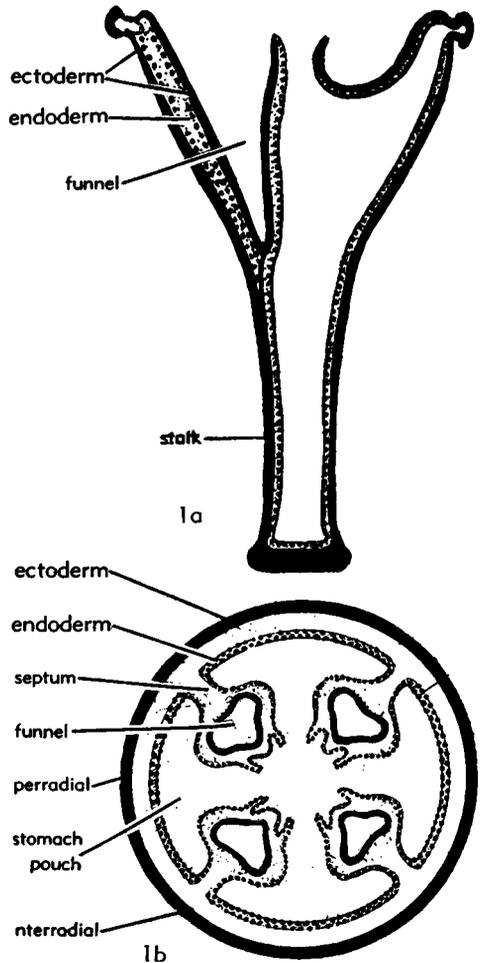

FIG. 20. Longitudinal and transverse sections of *Haliclystus* (Stauromedusida), Rec., showing ectoderm-lined funnels located in positions of the interradial septa; the longitudinal section is partly through an interradius (at left) and partly through a perradius (at right) (modified from L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

trated by transverse sections of representatives of the Conulata and Scyphomedusae (Fig. 19). The forked pattern of the septa that project into the interior of *Conularia loculata* exactly corresponds to the bifurcated septa of living scyphomedusans such as *Cratelolophus* and *Haliclystus* (Fig. 20, 1*b*).

COMPARISON OF SCYPHOME-
DUSAE AND CONULATA

The body form of polypoid scyphozoans ranges from slender subcylindrical through steep-sided conical or pyramidal shapes to trumpet-like and relatively low broadly flared types. The medusoid form may be goblet-shaped with length greater than width, broadly rounded, cuboid, or low saucer-shaped. Some Scyphozoa live in fixed position throughout life, being attached to seaweed or other foreign objects or the sea bottom by a chitinous secretion. Others are attached temporarily and able to re-attach the body to some support. A large majority of the living scyphozoans are free-swimming, movement being effected by muscular pulsations of peripheral parts of the jellyfish dome or bell.

MUSCULATURE

Musculature is almost wholly ectodermal. Especially noteworthy is the occurrence of longitudinal muscles that run along the interradial septa; these also are ectodermal and are associated in many living scyphozoans with very deep funnel-shaped infoldings of the ectoderm that extend from the surface near the mouth to vicinity of the aboral pole (Fig. 20). Similar longitudinal muscles are inferred to have characterized the Conulata, serving for inward pull on interradial edges of the periderm in order to close the aperture and, according to BOUČEK (1939), possibly functioning like the coronal muscles of modern Scyphomedusae for pulsatory swimming movements. Existence of such scyphozoan-type musculature in the Conulata rests on the wholly plausible but hardly provable interpretation of the median line and associated internal ridge or septum of conulariids as the place of longitudinal muscle attachment which was steadily shifted in adapertural direction during growth of the animal (Fig. 43).

The interradial position of the septa and their inwardly bifurcate form in many Scyphomedusae are matched by the interradial placement of peridermal septa in many Conulata, at least one fossil form (*Conularia*
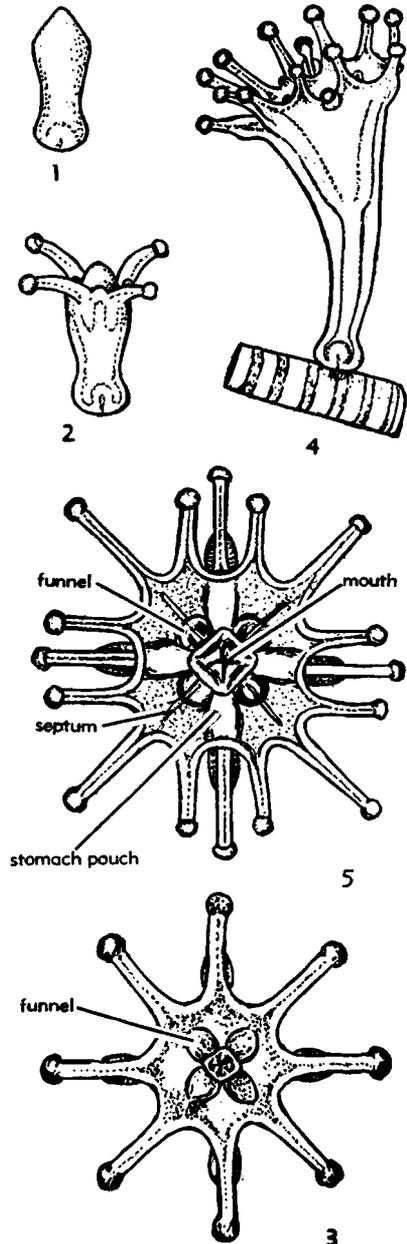

FIG. 21. Development of tentacles in ontogeny of a stauromedusid polyp (*Haliclystus*), showing (1-5) successive stages with 0, 4, 8, and 16 tentacles (after L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).

loculata) from Silurian rocks showing clearly marked inward bifurcations of these septa (Fig. 19,*1*). Taken in conjunction with other evidence, this similarity strongly supports classification of the Conulata among the Scyphozoa.

TENTACLES

Both Scyphomedusae and Conulata bear tentacles. In many genera of the scyphomedusans these are evident in larval or polypoid stages of growth (Fig. 21) but greatly reduced or lacking in adults; in others they are well developed throughout life, being either hollow or solid, strongly muscled and generally armed with abundant stinging cells (Fig. 18). In stauromedusid polyps, for example, at first 2 tentacles appear, then 4, 8, 16, and so on; the first 4 tentacles are developed in perradial position and the next 4 interradially (Fig. 21). Adult Stauromedusida may have hundreds of tentacles grouped on 8 adradial lobate extensions of the oral surface (Fig. 17,*1*). The occurrence of tentacles at the apertural margin in Conulata is hardly open to doubt, but traces of these are actually preserved, so far as known, only in some specimens of *Conchopeltis,* of Middle Ordovician age from New York (Fig. 22). Originally described as a gastropod, this form is proved by its clearly defined tetrameral symmetry and possession of

FIG. 22. *Conchopeltis alternata* WALCOTT, Middle Ordovician (Trenton), from Trenton Falls, N.Y., ×1.5, an unusually broad low conulariid with very thin periderm, apical view of specimen in Cornell University collections showing terminal parts of several tentacles that project beyond margin of the aperture. Another somewhat smaller specimen (not figured) also exhibits preservation of tentacles (J. W. WELLS photograph).
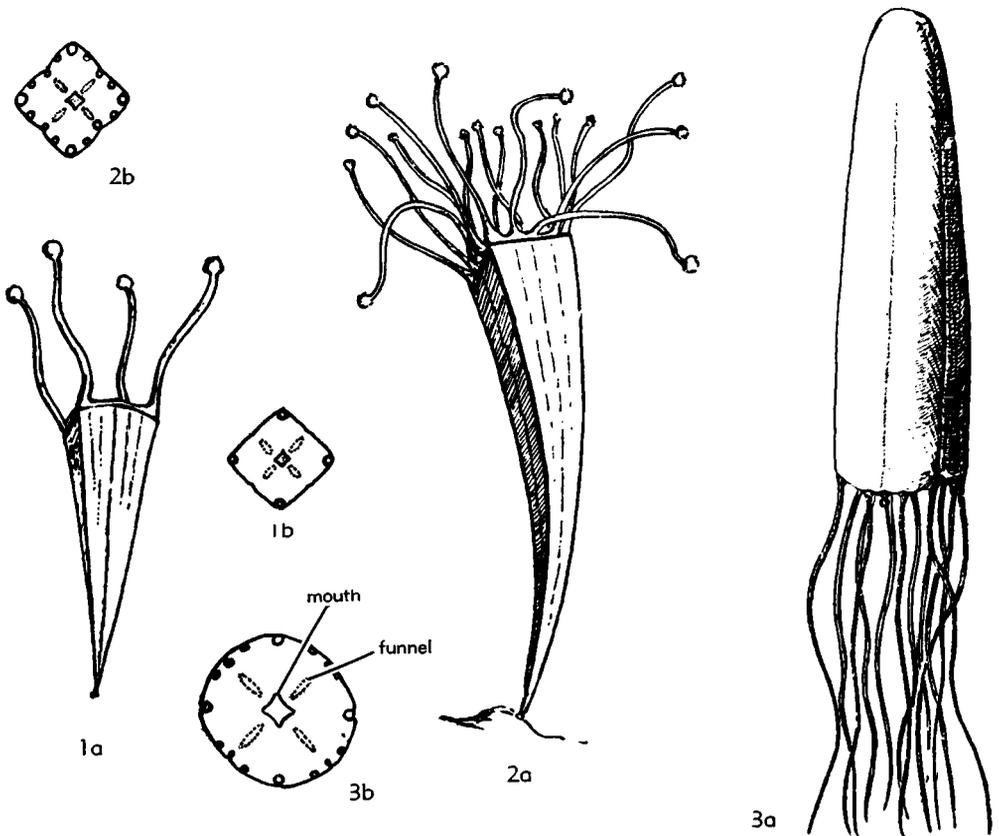
FIG. 23. Reconstructions of conulariids showing inferred number and location of tentacles, based on linear thickenings of the periderm interpreted to originate from attachment of tentacle muscles. *1a,b, Conularia cambria,* ×1, and *2a,b, Archaeoconularia fecunda,* ×0.7, are represented in attached position; *3a,b, Exoconularia consobrina,* ×0.7, is depicted as a free-swimming medusoid, its apical extremity sealed over by a transverse diaphragm (schott) (KIDERLEN).

peripheral tentacles to belong with the Scyphozoa. KIDERLEN (1937) has made reconstructions of tentacles arranged around the aperture of various types of Conulata, basing interpretation partly on peridermal traces such as longitudinal lines and furrows presumed to mark locations of tentacle muscle attachments; these reconstructions are very reasonable, especially in view of their correspondence to successive stages in tentacle development among modern Scyphomedusae (Fig. 23).

PERIDERM

The nature of the periderm of typical Conulata deserves attention. On first consideration, skeletal parts consisting predominantly of calcium phosphate seem utterly foreign to the Coelenterata, for all well-determined members of the phylum either lack hard parts entirely or only possess ability to secrete calcium carbonate or a chitinous substance. This consideration, however, is merely negative and not at all decisive. Modern stauromedusids may have a fixed attachment formed by chitin. The absence of phosphatic mineral salts associated with the chitin formed by some Scyphozoa and other kinds of living coelenterates does not rule out classification of extinct organisms as coelenterates merely because, like the Conulata, they are shown to be characterized by a chitinophosphatic covering. Definitive testimony must be of another sort. Accordingly, examination with open mind admits readily the possibility of recognizing a kind of coelenterate which differs from others in this character. It may be noted in
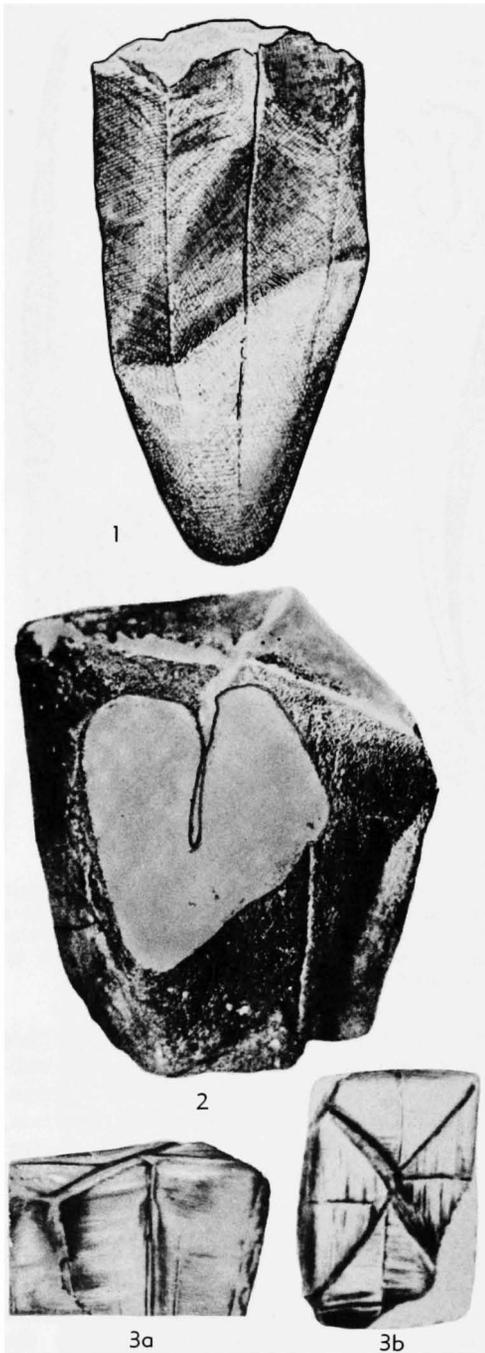
passing that statoliths secreted by living Scyphozoans are composed of calcium sulphate and calcium phosphate.

The chief observational features relating to the periderm of Conulata are its composition, extreme thinness, indication of original flexibility at least in areas adjacent to the aperture, evidence of its wholly ectodermal origin, variety of generally very fine external markings, nature of attachment and structural adaptation for freedom from attachment. Each of these will be reviewed briefly.

Composition. Study of the periderm of several species belonging to conulate genera as seen in thin sections or polished sections has established the presence of microscopic laminae parallel to the surface. They consist of chitin, chitinophosphatic substance of seemingly variable phosphatic content, and essentially pure calcium phosphate. The minerals phosphorite and kolophanite have been reported (BOUČEK & ULRICH, 1929). Published analyses of chemical composition show figures such as 66.6 and 70.9 per cent $CaPO_4$ for Ordovician species, and a recently made analysis of peridermal fragments from a Pennsylvanian conulariid indicates approximately 96 per cent $CaPO_4$ (indefiniteness being due to extremely minute quantity). Reddish to purplish brown, bluish gray, and white coloration of well-preserved specimens is interpreted to signify original pigment because the colors have been observed to show correlation with specific characters and to be independent of the matrix in which specimens occur.

Thinness. The periderm of individuals belonging to the Conulata is thin, in some species as little as 0.056 to 0.070 mm. in thickness. Averages of the minimal and maximal measurements of periderm thickness of 7 species (maxima including thickened areas at angles) are 0.23 and 0.37 mm., respectively, and the average represented by these figures is 0.30 mm. This thinness accords with use of the term periderm for the protective covering of Conulata, rather than exoskeleton or shell.

Flexibility. The flexibility of the conulate periderm is attested by the common occur-

rence of distorted but unbroken fossils. Some are merely flattened, whereas others show irregular indentations crossing the periderm without sign of associated fractures (Fig. 24,*1*). The inwardly bent apertural edges of many conulariids, some showing a complicated pattern of infolding along creases, furnish patent evidence of periderm flexibility in this region, for no specimens have been found that show sign of hingement or seam in positions of abrupt bending (Fig. 24,*2,3*). Furthermore, it is clear that the location of apertural inflections of the periderm must have shifted progressively away from the apex as growth added to length. Generally this growth seems to have been at nearly constant rate and although some specimens give indication (by irregularities in crowding of external features) of periodic halts or slower growth rates from time to time, none of these is associated with trace of localized prolonged periderm bending back and forth. Hence, it is safe to assert that in spite of the appearance of rigidity given by specimens having relatively coarse transverse ribs, the periderm of Conulata was flexible.

Ectodermal origin. The chitinophosphatic protective covering of conulariids was not secreted by endodermal layers of the body as might be possible if soft tissues extended over its outer surface. Rather, it was built from the outside inward and evidently, therefore, a product of secretion by ectodermal cells. Proof of this consists of the manner in which the exterior surface on any side of the conulariid furnished a place of attachment for inarticulate brachiopods, small edrioasteroids, other conulariids, and the like (Fig. 25). The nature of the scars clearly indicates that the host conulariid was alive when its periderm became a fixation site for other invertebrates, for the covering left behind by a dead conulariid would be incapable of localized distortion required to fit the shape of the attached organism. Thus, there is small room for doubt as to the truly external nature of the periderm. It follows that surface markings such as transverse ribs, tubercles, and like features are initial products of ectodermal secretion as growth in the apertural region proceeds, the smooth interior and inwardly built peridermal septa being the result of continued secretion by
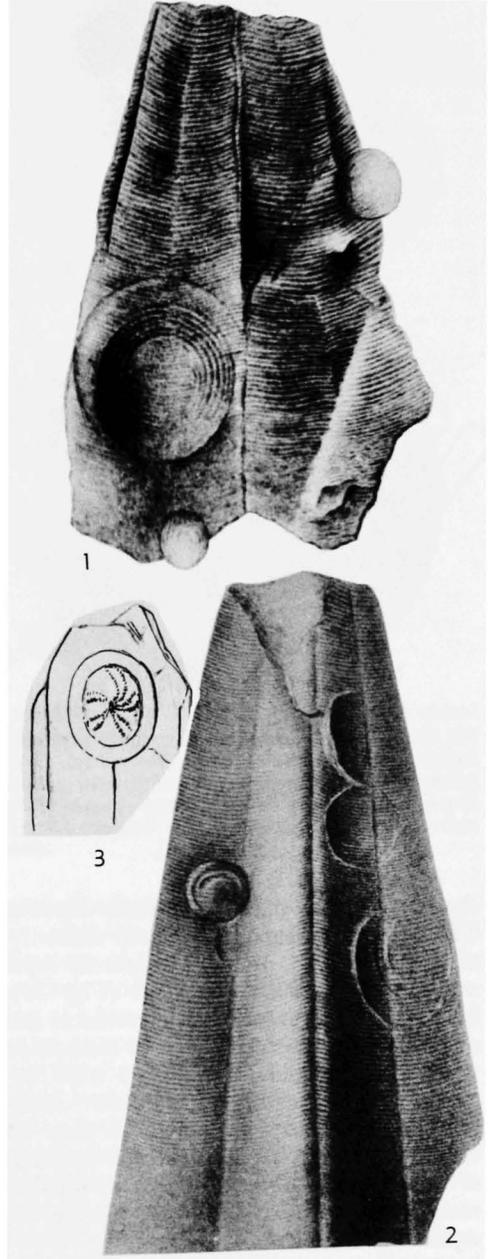
FIG. 25. Exterior of the conulate periderm as place of anchorage for other organisms. *1, Conularia continens*, M.Dev., N.Y., ×1; specimen with 2 small attached inarticulate brachiopod shells and scar left by a much larger inarticulate (HALL). *2, C. undulata*, M.Dev., N.Y., ×1; specimen also showing attachment scars on 2 faces (HALL). *3, Agelacrinites*, an edrioasteroid, on a specimen of *Exoconularia consobrina*, M.Ord., Czech., ×1 (BARRANDE).
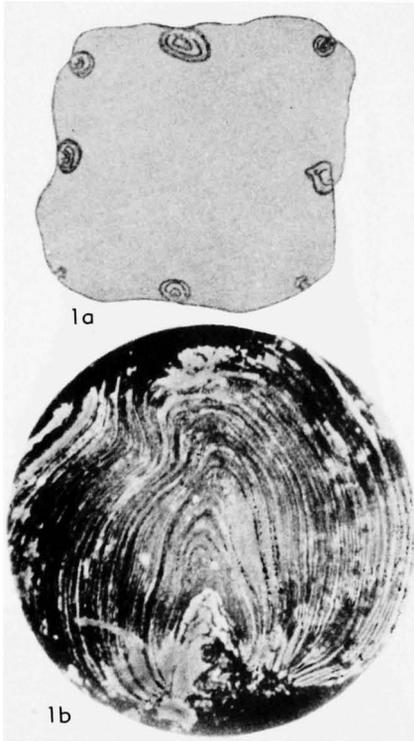
Fig. 26. Localized thickening of conulate periderm. *1a, Transverse section of Ctenoconularia* sp., Dev., S.Am.(Bol.), ×1, showing unusual inward growth of periderm at mid-line of faces and at corners; *1b*, one of these thickenings showing laminated structure, ×50 (Knod).

which may have fine radial striae on its lower or proximal surface and bear a pair of rings that define the margins or marginal impressions of an inner and outer inverted bowl above the disc (Fig. 28). The disc and bowls probably were not held in place by sucker-like action but by relatively firm cementation of the chitin to the substratum, thus paralleling the chitinous attachment of some modern stauromedusans which cannot move about after place of growth is determined by early fixation. The inverted bowls or cups of the conulariid attachment doubtless served a buttressing function.
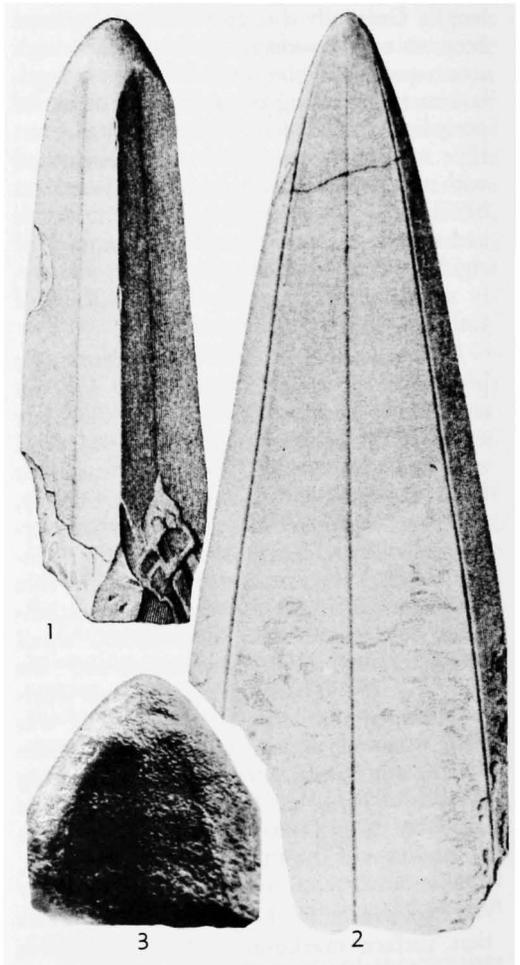
Fig. 27. Smoothly rounded proximal extremity of unattached conulariids. *1, Anaconularia anomala,* M.Ord., Czech., ×1 (Barrande). *2. Exoconularia consobrina,* M.Ord., Czech., ×1 (Barrande). *3, E. pyramidata,* U.Ord., Fr.(Normandy), ×1 (Kowalski).

the ectoderm of chitinophosphatic deposits. The laminated structure and local deflection of the laminae to join with internal septa accord with this interpretation (Fig. 26). The ectodermal nature of the periderm and septa has special significance in connection with the correlation of Conulata with Scyphomedusae, because a common distinguishing character of the latter is deep invagination of the ectoderm layer in positions of the 4 septa and development of ectodermal muscles that interrupt or divide the septa.

FIXATION

Discovery of numerous young conulariids in attached position and study of their mode of attachment (Ruedemann, 1898) throws interesting light on what was probably the prevailing mechanism for fixation of Conulata in early growth stages. This consists of a minute subcircular chitinophosphatic disc

FIG. 28. Attachment of conulariids. *1-7, Sphenothallus angustifolius,* M.Ord., N.Y.; *1,* adult with several young individuals fixed to its periderm, some clearly showing fixation discs but generally with only the linear thickenings at corners of their periderm preserved, ×2; *2-4,* fixation discs, 4 showing longitudinal section, ×10; *5,6,* juvenile individuals, *5* showing lappet-like distal prolongation of faces and *6* showing aperture closed by inbending of these lappets, ×8; *7,* holotype of *S. angustifolius* consisting of several individuals flattened to leaflike form, one (upper left) with attached young specimens, ×1 (all after RUEDEMANN).

UNATTACHED MODE OF LIFE

That many conulariids, if not most of them, were not attached during adult stages is indicated by the frequently observed occurrence of a rounded smooth apical end of mature-sized fossils. The smooth surface, convex toward the apex, is the exposed part of secondarily secreted periderm joined peripherally to the 4 side walls in the manner of a nautiloid septum (Fig. 27). Because longitudinal ridges or walls directed radially inward occur in some conulariids and are termed septa, the curved transverse peridermal structure is called diaphragm (*cloison,* Fr.; *Schott,* Ger.). The uniform adapical convexity of the diaphragm, its smooth confluence with the lateral walls, and common occurrence not far from the original apex indicate that secretion of a diphragm was not for the purpose of closing off an open end produced by accidental injury but a

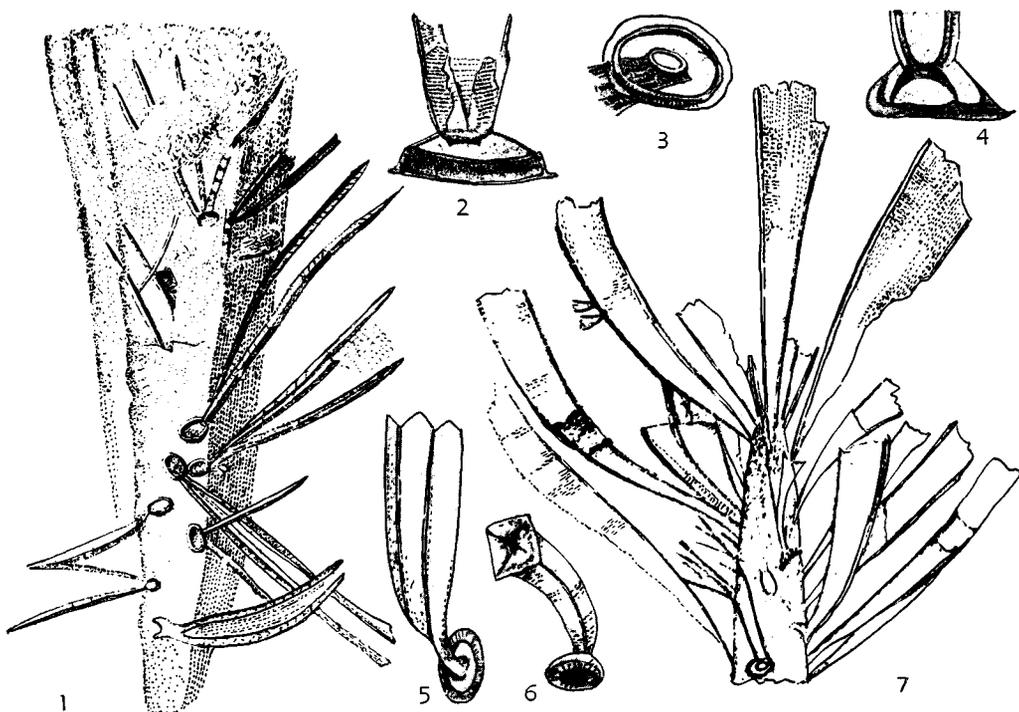normal adaptation for breaking free from an early-life anchorage (Figs. 24,*1;* 27). Fracture of the flexible, elastic periderm is unlikely and unless resorption and weakening of a band of the side walls were effected as an antecedent to breaking free and building the diaphragm, it is difficult to understand how the change from attached to free-living took place. In any case, no recorded observations support the conjecture that free-living conulariids lay inertly on the sea bottom, resting on any of their 4 sides; instead, it seems reasonable to postulate a free-swimming medusoid existence, as illustrated by a reconstruction drawn by KIDERLEN (1937) (Fig. 23, *3a*). The possibility of increased buoyancy by development of a small gas chamber next to the apical diaphragm is worthy of mention, although the thin periderm of the conulariids surely could be carried without much trouble by the animal in swimming.

In comprehensive view of the characters found to distinguish the conulariids and allied forms on the one hand and modern Scyphomedusae on the other, association of all them in the class Scyphozoa seems most appropriate. Accordingly, they are so classified here. Distinctions that serve to separate the Conulata from the Scyphomedusae are as far-reaching, however, as their resemblances are important. This is taken into account in defining each group as a subclass.

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SCYPHOMEDUSAE

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

CONTENTS

MORPHOLOGY

The Scyphomedusae are solitary, free-swimming animals consisting of a gelatinous bell either cuboidal or pyramidal, goblet,- trumpet-, dome-, bowl-, or saucer-shaped, typically displaying tetramerous symmetry, though in some cases arranged upon an hexameral plan. They range in size from a few to 50 cm. in diameter, but some species may attain dimensions of 2 m., being the largest known coelenterates.

The upper, aboral or convex side of the bell is termed **exumbrella;** the lower, oral or concave side is known as **subumbrella.** In the Coronatida, the exumbrellar surface is subdivided by a horizontal circular groove, the **coronal groove** (Fig. 30). The margin of the bell is usually scalloped into **lappets** and may bear a **velarium,** analogous to the velum of the hydrozoan medusae, but arising as an extension of the subumbrella. From the center of the subumbrella there hangs down a short, quadrangular tube, the **manubrium,** typically opened at its lower extremity in a 4-cornered **mouth.** The mouth angles are commonly drawn into short **oral lobes,** but in the Semaeostomatida they extend into long, curtain-like projections, called **oral arms** (Figs. 18, 33). In the Rhizostomatida the edges of the long, frilled, branched oral lobes, termed **mouth arms,** fuse so as to obliterate the mouth opening but contain instead hundreds or thousands of minute suctorial mouths or **ostioles.** The 4 corners of the mouth or the 4-branched mouth arms mark off the 2 main planes of tetramerous symmetry. The 4 umbrellar radii, placed 90° apart, upon which lie the 4 corners of the mouth, are termed **perradii;** the 4 radii at 45° position between the perradii are called **interradii;** and those located midway between these are called **adradii.**

The manubrium leads aborally into a gastric cavity which typically contains 4 soft-tissue partitions or **septa,** projecting along the interradii part way into the interior; these septa divide the cavity into a **central stomach** and 4 perradial **stomach pouches.** The free inner edge of the septa bear numerous tentacle-like **gastric filaments.** The septa are absent in the adult Semaeostomatida and Rhizostomatida, but commonly present in their scyphistoma larvae. The stomach pouches give rise to **radial canals,** which may be numerous and branched, leading to a **ring canal** running along the bell margin. In the orders Stauromedusida, Carybdeida and Coronatida, the subumbrellar surface bears 4 deep interradial, funnel-like pits, the **subumbrellar funnels,** which probably aid in respiration. In the Stauromedusida, Carybdeida and Coronatida, the **gonads** are borne on both sides of the gastric septa as elongated bodies projecting into the stomach pouches; the total number of gonads is 8, 2 in each pouch. In the Semaeostomatida and Rhizostomatida, which lack septa, the gonads (usually 4) occur in the floor of the gastric pouches.

Tentacles and **sensory organs** arise from the bell margin, usually to the number of 4 or of some multiple thereof. The tentacles are borne either between sensory organs, in niches between lappets, on the lappets, or on the subumbrellar surface. Tentacles may be solid or hollow, single or in clusters, and may be very numerous; they are absent in the Rhizostomatida. In the Carybdeida and Coronatida they are borne on gelatinous basal expansions, the **pedalia.** The sensory organs or **rhopalia** are located either on the sides of the bell, on pedalia, or in niches between lappets; they are essentially tenta-culocysts acting as organs of equilibrium. In many genera they are provided with **ocelli,** sensitive to light. Nematocysts are abundantly distributed on the tentacles, oral lobes, oral arms, and mouth arms.

DISTRIBUTION

Twelve genera of fossil medusae are now assigned to the Scyphomedusae, but with 4 exceptions, the reference to this subclass is somewhat tentative and provisional. Two doubtful, very imperfectly known genera of uncertain family relationships have been described from the Lower Cambrian of South Australia. The remainder are mostly Upper Jurassic forms from Solnhofen, Germany, and species from Upper Cretaceous and Eocene strata of Italy, Albania, Poland, and Greece.

CLASSIFICATION

The number of fossil genera in each category is tabulated after the corresponding taxa. A question mark preceding a numeral (as ?9) indicates number of tentatively referred genera.

Main Divisions of Scyphomedusae

Scyphomedusae *(subclass)* (4+?9). *?L.Cam., U. Jur.-Rec.*
Stauromedusida *(order)*. *Rec.*
  Tesseranthidae. *Rec.*
  Eleutherocarpidae. *Rec.*
  Cleistocarpidae. *Rec.*
Carybdeida *(order)* (?1). *?U.Jur., Rec.*
  Carybdeidae (?1). *?U.Jur., Rec.*
Coronatida *(order)* (1+?4). *?L.Cam., U.Jur.-Rec.*
  Periphyllidae (1). *U.Jur.-Rec.*
    Periphyllinae. *Rec.*
    Paraphyllininae (1). *U.Jur.-Rec.*

Ephyridae. *Rec.*
Atorellidae. *Rec.*
Collaspididae (?4). *?L.Cam., ?U.Jur., ?U.Cret., ?Eoc., Rec.*
Semaeostomatida *(order)* (2). *?U.Jur., Rec.*
  Pelagiidae. *Rec.*
  Cyaneidae. *Rec.*
  Ulmariidae. *Rec.*
  ?Semaeostomitidae (1). *U.Jur.*
  ?Eulithotidae (1). *U.Jur.*
Lithorhizostomatida *(order)* (1). *U.Jur.*
  Rhizostomitidae (1). *U.Jur.*
Rhizostomatida *(order)* (?1). *?U.Jur., Rec.*
  Cassiopeidae. *Rec.*
  Cepheidae. *Rec.*
  Catostylidae. *Rec.*
  Leptobrachiidae (?1). *?U.Jur., Rec.*
  Rhizostomatidae. *Rec.*
  Archirhizidae. *Rec.*
?Scyphomedusae incertae sedis (2). *L.Cam.*

SYSTEMATIC DESCRIPTIONS

Subclass SCYPHOMEDUSAE Lankester, 1881

[=Acraspeda GEGENBAUR, 1856; Scyphozoa HAECKEL, 1891 (partim)]

A diagnosis of this subclass appears in a preceding section which states distinguishing features of the Scyphozoa and discusses division of the class into subclasses Conulata and Scyphomedusae (p. F27-F38). *?L. Cam., U.Jur.-Rec.*

Order STAUROMEDUSIDA Haeckel, 1880

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Stauromedusae HKL., 1880)] [=Lucernaridae JOHNSTON, 1847 (*partim*); Lucernaria CLARK, 1863]

Bell pyramidal-conical, flaring at oral end into broad concave subumbrella, tapering aborally into stalk, commonly attached to objects by aboral apex; margin usually with 8 adradial lobes bearing tentacles, commonly hollow, knobbed and in clusters; rhopalia absent or replaced by 8 anchors with ocelli or lithocysts; 4 long interradial septa; 4 large and deep subumbrellar funnels typically present; mouth cruciform, simple. *Rec.*

Genera belonging to this order are classified into 3 families, none of which contains known fossil representatives. They are: Tesseranthidae HAECKEL, 1880, pelagic, freeswimming medusae without lobes and with solid, nonknobbed tentacles; Eleutherocarpidae CLARK, 1863, sessile medusae with 4

simple perradial stomach pouches; and Cleistocarpidae CLARK, 1863, sessile medusae with 4 perradial stomach pouches divided into 2 spaces. Twelve genera known, including *Lucernaria* O.F.MÜLLER, 1776, and *Haliclystus* CLARK, 1863. Stauromedusida are inhabitants of cold seas; sessile forms found in bays and coastal waters.

Order CARYBDEIDA Claus, 1886

[*nom. correct.* MAYER, 1910 (*pro* Charybdeida CLAUS, 1886)] [=Marsupialidae L. AGASSIZ, 1862; Cubomedusae HAECKEL, 1880]

Bell cubical with interradial angles and perradial sides; margin without lappets; vel-
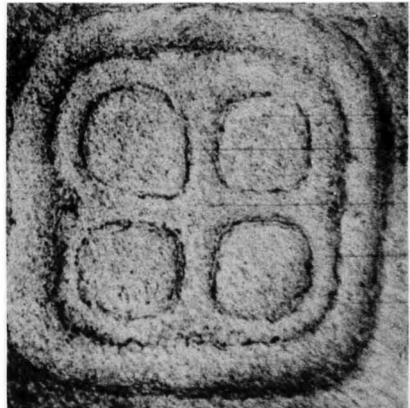

FIG. 29. Carybdeida: *Quadrimedusina quadrata,* Jur., Ger.; holotype, ×0.7 (HAECKEL).
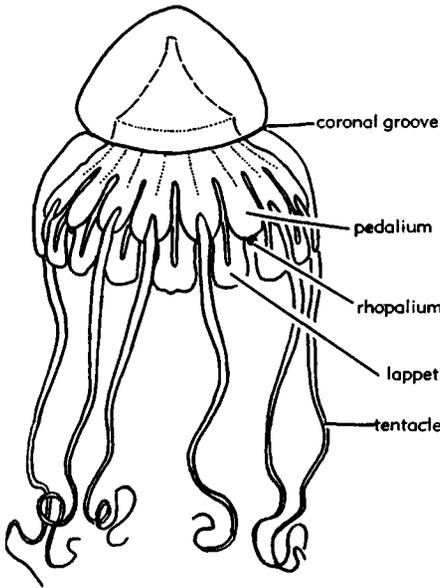
FIG. 30. Coronatida: *Periphylla hyacinthina,* one of the most common living members of the order, found in deep waters of all oceans. It has a purple bell with 16 lappets at the margin, 12 bearing tentacles (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

arium present; 4 interradial hollow tentacles, single or in clusters, bordered by spatuliform pedalia; 4 perradial knob-shaped rhopalia located within niches upon sides of bell; 4 interradial septa; subumbrellar funnels absent; mouth cruciform, simple; oral lobes very short. *?U.Jur., Rec.*

Inhabitants of the warmer waters of all present oceans, found mostly in the open sea but also swarming in harbors and bays.

Family CARYBDEIDAE Gegenbaur, 1856

Characters of order. *?U.Jur., Rec.*

Carybdea PÉRON & LESUEUR, 1809 [*C. marsupialis*]. *Rec.* Other living genera: *Procharybdis* HAECKEL, 1880; *Tamoya* F. MÜLLER, 1859; *Tripedalia* CONANT, 1897; *Chiropsalmus* L.AGASSIZ, 1862; *Chirodropus* HKL., 1880.

?Quadrimedusina HARRINGTON & MOORE, 1955 [*Medusites quadratus* HAECKEL, 1869]. Subumbrellar impression of square outline, with rounded angles; margin entire; submarginal groove present (?ring canal); central area with 4 radial grooves (?perradial canals) reaching submarginal groove at mid-distance between angles; resulting quadrants with single, large subcircular marking. *U.Jur.,* Ger.——FIG. 29. *Q. quadrata* (HAECKEL); holotype, ×0.7 (HAECKEL).

Order CORONATIDA Vanhöffen, 1892

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Coronatae VANHÖFFEN, 1892] [=Discomedusae HAECKEL, 1866 (*partim*); Coronata MAAS, 1903 (*non* JAEKEL, 1918)]

Bell conical, dome-shaped or discoidal; umbrella divided by horizontal coronal groove; margin cleft into lappets alternating with pedalia; 4 to 32 rhopalia and 4 to 32 solid tentacles borne by alternating pedalia; 4 subumbrellar funnels; mouth cruciform, simple; manubrium short. *?L.Cam., U.Jur.-Rec.*

Living forms are typical inhabitants of the deeper parts of the ocean but surface forms in warmer waters are also known (Fig. 30).

Family PERIPHYLLIDAE Claus, 1886

[=Peromedusae HAECKEL, 1880 (*partim*)]

Coronatida with 4 rhopalia, 4 or more lappets and 4 or more pedalia bearing tentacles. *U.Jur.-Rec.*

Subfamily PERIPHYLLINAE Claus, 1886

[*nom. transl.* BIGELOW, 1909 (*ex* Periphyllidae CLAUS, 1886)]

Rhopalia interradial; tentacles 4 to 28; lappets 8 to 32. *Rec.*

Periphylla STEENSTRUP, 1837 [*P. hyacinthina*]. *Rec.* Other living genera: *Pericolpa* HAECKEL, 1880; *Periphyllopsis* VANHÖFFEN, 1900; *Nauphontopsis* FEWKES, 1885.
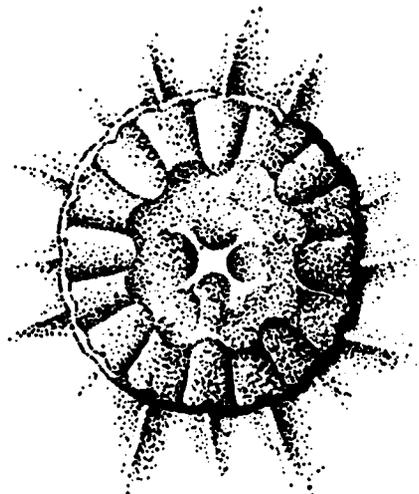
FIG. 31. Coronatida: *Epiphyllina distincta,* U.Jur., Ger.; holotype, ×3 (KIESLINGER).

Subfamily PARAPHYLLININAE Maas, 1903

[*nom. transl.* BIGELOW, 1909 (*ex* Paraphyllinidae MAAS, 1903)]

Rhopalia perradial; lappets 16; tentacles 12 (4 interradial, 8 adradial). *U.Jur.-Rec.*

Paraphyllina MAAS, 1903 [**P. intermedia*]. *Rec.* Only living genus.

Epiphyllina KIESLINGER, 1939 [*pro Paraphyllites* MAAS, 1906 (*non* HYATT, 1900)] [**Paraphyllites distinctus* MAAS, 1906]. Mid-field smooth; pedalia 16, wide, rhombic, alternating along periphery with 16 narrow crescentic lappets; tentacles 12, 4 carried by interradial, 8 by adradial pedalia. Differs from *Paraphyllina* in having 8 crescentic ad
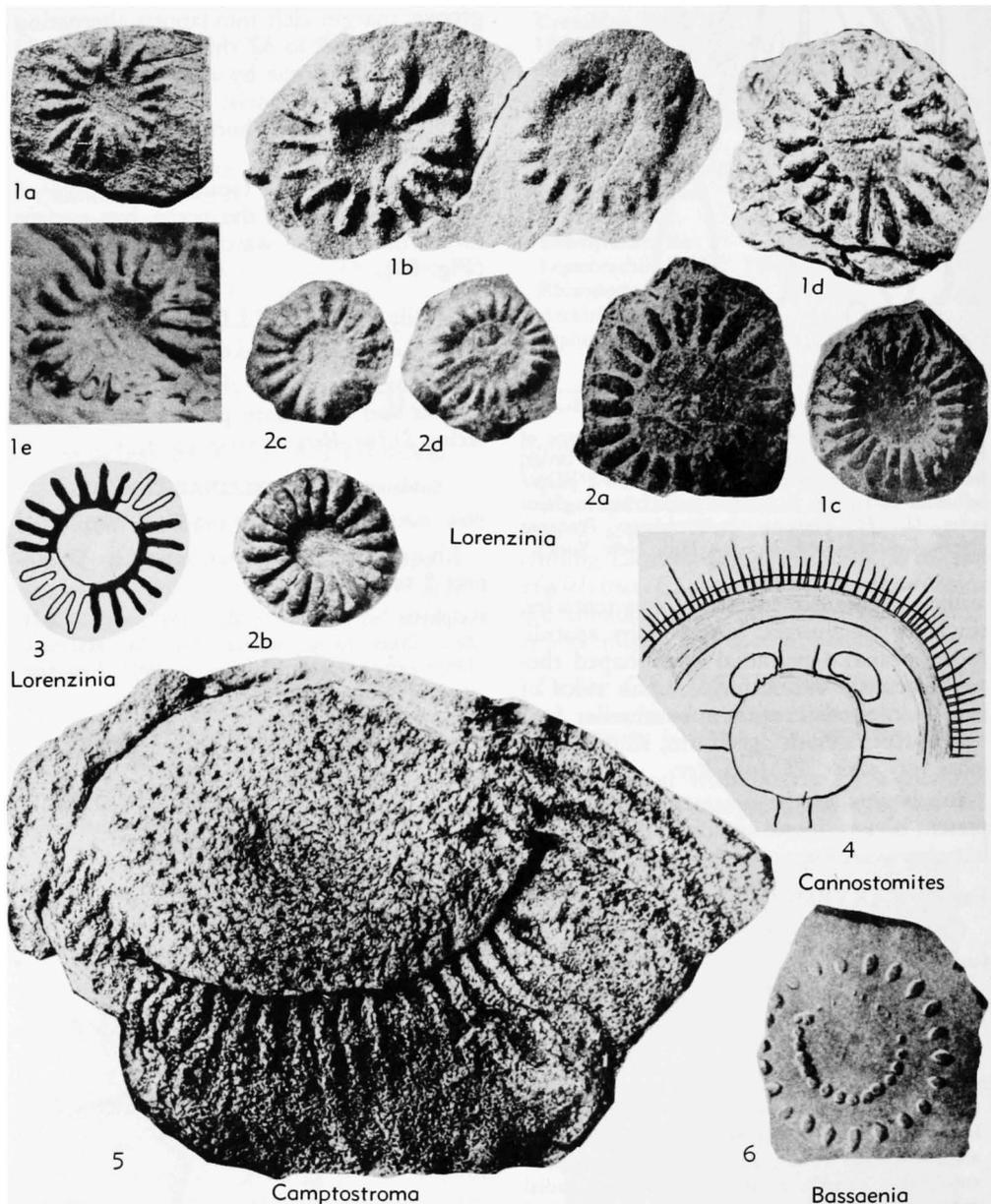
FIG. 32. Coronatida: L.Cam.-Eoc. fossil forms. *1, Lorenzinia apenninica,* ?Cret.-Eoc., Eu.; *1a,* holotype, ×1; *1b-e,* other specimens, all ×0.7 except *1c,* ×0.5 (GORTANI and others). *2, L. carpathica,* Eoc., Eu.; *2a,* holotype, ×0.5; *2b-2d,* other specimens, ×0.7, ×0.5 (ZUBER and others). *3, L. kulczynskii,* Eoc., Pol.; holotype, ×0.7 (KUZNIAN). *4, Cannostomites multicirratus,* U.Jur., Ger.; holotype, ×0.2 (KIESLINGER). *5, Camptostroma roddyi,* L.Cam., Pa.; holotype, ×1 (RUEDEMANN). *6, Bassaenia moreae,* U.Cret., Greece; holotype, ×0.5 (RENZ).

radial gonads placed 45° apart instead of grouped in pairs on both sides of the 4 interradii. *U.Jur., Ger.*——Fig. 31. **E. distincta* (Maas); holotype, ×3 (Kieslinger).

Family EPHYRIDAE Haeckel, 1880

[*ex Ephyra* Hkl., 1880 (=*Palephyra* Hkl., 1880)] [=Ephyri-dae+Linergidae Hkl., 1880; Ephyropsidae Claus, 1883]

Coronatida with 4 perradial and 4 interradial rhopalia; 8 or more tentacles and 16 or more lappets. *Rec.*

Although *Ephyropsites jurassicus* von Ammon, 1906, from Solnhofen, formerly was placed in this family, probably it is an exumbrellar impression of *Rhizostomites admirandus* (Lithorhizostomatida); accordingly, no fossil representatives of the family are now recognized.

Palephyra Haeckel, 1880 [**P. antigua*] [=*Ephyra, Zonephyra* Hkl., 1880]. *Rec.* Other living genera: Nausithoe Kölliker, 1853; Linuche Eschscholtz, 1829.

Family ATORELLIDAE Vanhöffen, 1902

Coronatida with 6 rhopalia. *Rec.*

Atorella Vanhöffen, 1902 [**A. subglobosa*]. *Rec.* Only known genus.

Family COLLASPIDIDAE Haeckel, 1880

[*nom. correct.* Harrington & Moore, herein (*pro* Collaspidae Hkl., 1880, *ex Collaspis* Hkl., 1880=*Atolla* Hkl., 1880); Haeckel's term Collaspidae was accepted as family name by Mayer, 1910, and having priority, is valid according to Copenhagen Decisions (1953)] [=Atollidae Bigelow, 1909]

Coronatida with more than 8 sense organs alternating with an equal number of tentacles; lappets twice as numerous as tentacles. *?L.Cam., ?U.Jur., ?U.Cret., ?Eoc., Rec.*

Atolla Haeckel, 1880 [**A. wyvillei*] [=*Collaspis* Hkl., 1880]. *Rec.* Only living genus.

?Lorenzinia Gabelli, 1900 [**L. apenninica*]. Body discoidal, convex; mid-field smooth, concave; margin with 16 to 24 prominent, outstretched, elongated subrectangular lobes (?pedalia), sharply separated from each other, raised at proximal end. *?Cret.,* Italy; *Eoc.,* Italy-Cyprus-Pol.-Albania. This problematic "form genus" may be a coronatid medusa. Abundant impressions with 11 to 13 irregular lobes, found associated together in some Eocene strata of Guipuzcoa, Spain, have been referred to *L. apenninica* but actually they belong to a different problematic organism which is not a medusoid.——Fig. 32,*1.* **L. apenninica,* Eoc., Eu.; *1a,* holotype, Italy, ×1 (Gortani); *1b,c,* other specimens from Italy, ×0.7, ×0.5; (*1b,* Simon-elli; *1c,* Agrisani; *1d,* specimen from Greece, ×0.7 (Mitzopoulos); *1e,* specimen from Cyprus, ×0.7 (Renz).——Fig. 32,*2.* *L. carpathica* (Zuber), Eoc., Eu.; *2a,* holotype. Pol., ×0.5 (Zuber); *2b,* an-

other specimen from Poland, ×0.7 (Kuzniar); *2c,d,* specimens from Albania, ×0.5 (Saxl).——Fig. 32,*3.* *L. kulczynskii* (Kuzniar), Eoc., Pol.; holotype, ×0.7 (Kuzniar).

?Bassaenia Renz, 1925 [**Lorenzinia (B.) moreae*]. Impressions consisting of an external ring of 22 separated, elliptical protuberances and an internal ring with an equal number of separated, smaller knobs in the radii of the larger ones. *U.Cret.,* Greece. (There is no apparent reason to regard this problematic form as a "subgenus" of *Lorenzinia,* as done both by Renz and Kieslinger. Its assignment to the Collaspididae is very questionable.)——Fig. 32,*6.* **B. moreae*; holotype, ×0.5 (Renz).

?Cannostomites Maas, 1902 [**C. multicirratus*]. Bell with strongly developed ring muscle; marginal lappets numerous (?136), somewhat irregular; tentacles relatively short, one at each notch between lappets; mid-field with large central ?stomach of circular outline, truncating 4 wide radial bands (?oral arms); quadrants between radial bands bearing reniform depression adjacent to ?stomach, regarded as gonads. Known by a single subumbrellar impression. *U.Jur.,* Ger.—Fig. 32,*4.* **C. multicirratus;* holotype, ×0.2 (Kieslinger).

?Camptostroma Ruedemann, 1933 [**C. roddyi*]. Body discoidal, outline elliptical due to distortion, upper side strongly convex, underside concave; upper side with large, circular, convex, rugose mid-field, separated by deep annular groove from outer ring of numerous (?52 to 60) moderately long, narrow radial lobes, commonly somewhat curved near distal extremity; lobes and underside with tiny rounded spots in a polygonal network of fine lines. Ruedemann interpreted the rugosity of the mid-field as due to a reticulate meshwork of tiny spicules surrounding round pores and monticules, and that of the lobes and underside as due to a polygonal network of small platelike spicules. Accordingly, he regarded the fossil as a colonial hydrozoan. Accepted here is the view of Kieslinger, who interpreted the rugosity as due to shrinkage of a gelatinous mass during dessication and placed the genus among the coronatids. *L.Cam.,* Pa.; *L.Ord.,* Ger.——Fig. 32.5 **C. roddyi,* L.Cam., Pa.; holotype, ×1 (Ruedemann). [Other species: *?C. germanicum* Hundt, L. Ord. (Tremadoc), Ger.; known from single, very obscure impression.]

Order SEMAEOSTOMATIDA L.Agassiz, 1862

[*nom. correct.* Harrington & Moore, herein (*pro* Semaeostomae L.Agassiz, 1862)] [=Semostomae Haeckel, 1880; Discomedusae Hkl., 1880 (*partim*); Semaeostomata Vanhöffen, 1888; Semaeostomae Maas, 1907]

Bell discoidal, without coronal furrow and without pedalia; margin cleft into lappets; tentacles hollow, arising from subumbrella, lappets or niches between lappets;
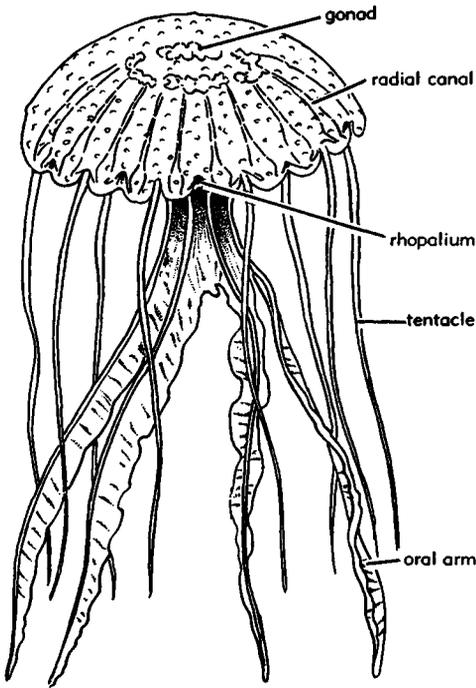
FIG. 33. Semaeostomatida: *Pelagia,* a leading modern representative which inhabits open oceans; oral arms long (L. H. HYMAN, *Invertebrata: Protozoa through Ctenophora,* McGraw-Hill, New York).

rhopalia typically 8 or 16, arising from niches between lappets; radial septa absent; mouth central, simple, with the 4 perradial angles developed into large gelatinous oral arms. *?U.Jur., Rec.*

Semaeostomatids are inhabitants of coastal waters of all oceans in all latitudes, commonly occurring in great numbers.

Family PELAGIIDAE Gegenbaur, 1856

Semaeostomatida with 8 or 16 rhopalia (4 perradial, 4 interradial, and when present, 8 adradial); 8 or more tentacles arising from niches between lappets; 16 to 64 lappets; simple lenticular stomach giving rise to completely separated, radiating pouches; ring canal absent; gonads occupying 4 interradial folds in wall of subumbrella; mouth cruciform. *Rec.*

Pelagia PÉRON & LESUEUR, 1809 [*Medusa noctiluca* FORSKÅL, 1775]. *Rec.*——FIG. 33. *Pelagia* sp. (HYMAN). Other living genera: Chrysaora PÉRON & LESUEUR, 1809; *Dactylometra* L.AGASSIZ, 1862; *Kuragea* KISHINOUYE, 1902; *Sanderia* GÖTTE, 1886.

Family CYANEIDAE L.Agassiz, 1862

Semaeostomatida with 8 or 16 rhopalia; tentacles in 8 or 16 clusters or arising diffusely in a wide annulus from subumbrella; stomach giving rise to radiating peripheral pouches and these to numerous branching nonanastomosing blind canals in lappets; ring canal absent; gonads in 4 complexly folded interradial outpocketings of wall of subumbrella; oral arms curtain-like. *Rec.*

Cyanea PÉRON & LESUEUR, 1809 [*Medusa capillata* LINNÉ, 1746]. *Rec.* (Fig. 18). Other living genera: *Desdemona* L.AGASSIZ, 1862; *Drymonema* HAECKEL, 1880; *Patera* LESSON, 1843.

Family ULMARIIDAE Haeckel, 1880

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Ulmaridae HAECKEL, 1877, *ex Ulmaris* HKL., 1880 =*Discomedusa* CLAUS, 1877); HAECKEL's term Ulmaridae was accepted as family name by MAYER, 1910, and having priority, is valid according to Copenhagen Decisions (1953)] [=Flosculidae + Ulmaridae HKL., 1880]

Semaeostomatida with 8 or 16 rhopalia; lappets 32 to 64; tentacles 24 to numerous; radial canals simple or branched, some anastomosing; ring canal present; gonads 4, interradial; oral arms curtain-like. *Rec.*

Discomedusa CLAUS, 1877 [*D. lobata*] [=*Ulmaris, Umbrosa* HAECKEL, 1880]. *Rec.* Several other living genera, including *Aurellia* PÉRON & LESUEUR, 1809, and *Phacellophora* BRANDT, 1835.

?Family SEMAEOSTOMITIDAE Harrington & Moore, nov.

[=Lithosemaeiden HAECKEL, 1874 (invalid vernacular name not based on generic name)]

Bell with numerous (?112) lappets and an equal number of tentacles; stomach giving rise to 4 perradial pouches; radial canals 16, simple (4 perradial, 4 interradial, 8 adradial); ring canal present; gonads 4, interradial; oral arms 4, very long. *U.Jur.*

Semaeostomites HAECKEL, 1874 [*S. zitteli*]. Tentacles simple, arising from niches between lappets; gonads large, centrifugal; 16 subtriangular adradial markings between distal ends of stomach pouches and gonads; mouth opening indistinct. Known from single specimen. *U.Jur.,* Ger.——FIG. 34. *S. zitteli;* holotype, ×1.2 (WALCOTT).

?Family EULITHOTIDAE Kieslinger, 1939

[=Eulithoten HAECKEL, 1869 (invalid vernacular name)]

Bell dome-shaped, with 16 lappets, 8 clusters of tentacles and 8 rhopalia; gonads 16; oral arms 4, short. *U.Jur.*

Eulithota HAECKEL, 1869 [*E. fasciculata* (=*Solnhofenistomites stechowi* KUHN, 1839, obj.)]
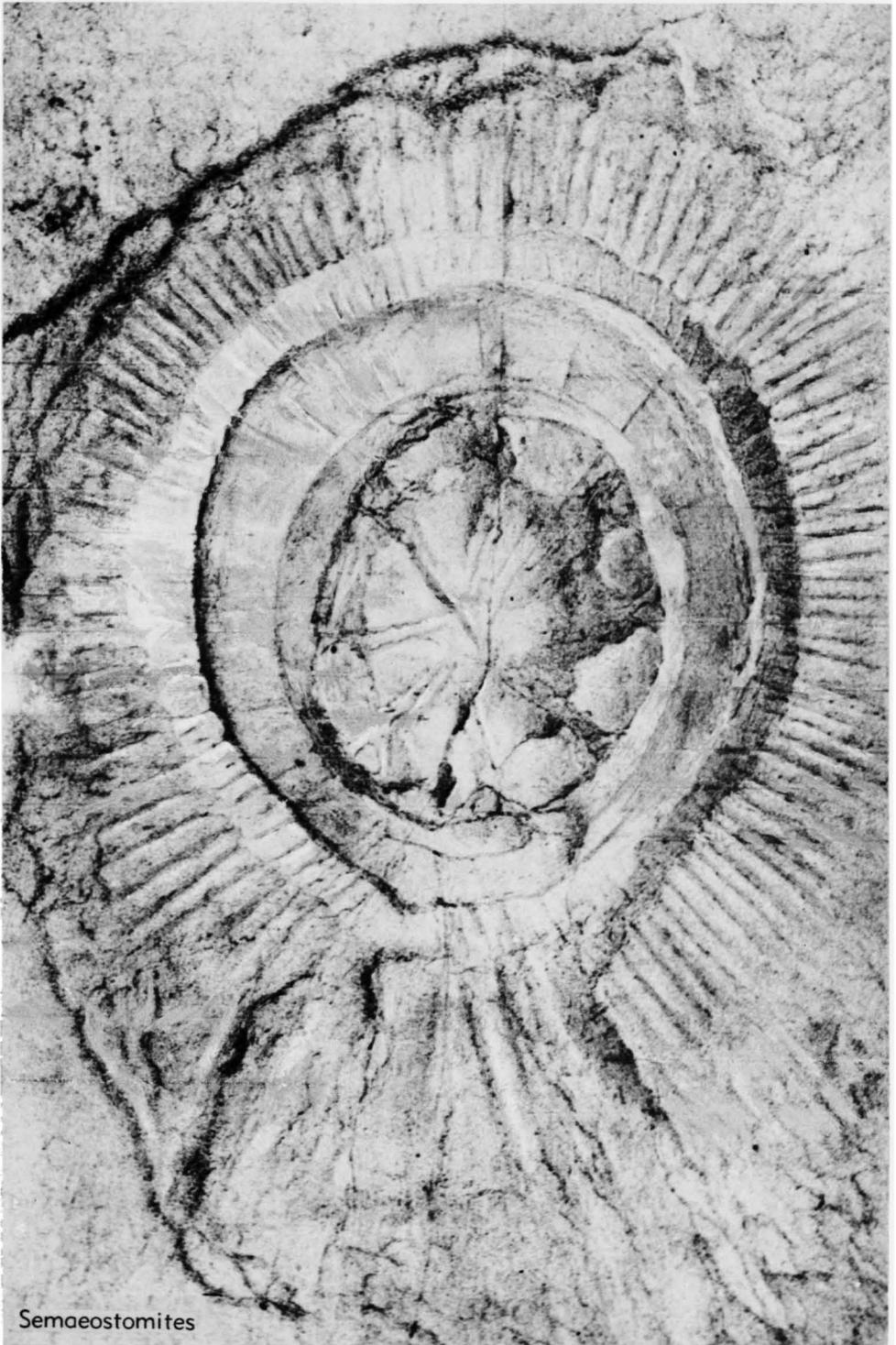
Semaeostomites

Fig. 34. Semaeostomatida: *Semaeostomites zitteli*, U.Jur., Ger.; holotype, ×1.2 (Walcott).

FIG. 35. Semaeostomatida: *Eulithota fasciculata,* subumbrellar surface (reconstr.), ×0.7 (HAECKEL).

[=*Solnhofenistomites* KUHN, 1938 (obj.)]. Tentacles in 8 clusters arising from niches between lappets; knob at base of each cluster interpreted as rhopalium; radial canals 16; gonads crescentic; mouth opening indistinct (?cruciform); faint indication of 4 simple, short oral arms. Known from single specimen. *U.Jur.,* Ger.——FIG. 35. *E. fasciculata;* subumbrellar surface (reconstr.), ×0.7 (HAECKEL).

Order LITHORHIZOSTOMATIDA von Ammon, 1886
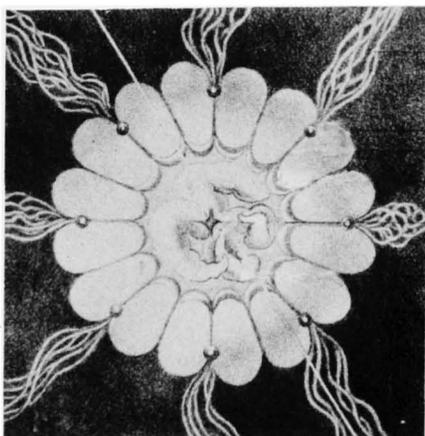
[*nom. transl. et correct.* HARRINGTON & MOORE, herein (*ex* Lithorhizostomeae VON AMMON, 1886)]

Bell dome-shaped, with 16 lappets, 8 cluslappets; rhopalia 8 (4 perradial, 4 interradial); tentacles short, ?ramified, in 8 clusters, arising from exumbrellar surface; pedalia absent; gonadic sacs 4, reniform to subtriangular, with individual opercula; ring canal present; ring muscle powerful; mouth cruciform, functional, with nonfunctional secondary branches; oral arms absent. *U.Jur.*

This order is introduced to accommodate the famous Solnhofen *Rhizostomites admirandus* which, since HAECKEL's original description, has commonly been referred to the order Rhizostomatida. The presence of a functional cruciform mouth (Fig. 36,2), absence of mouth arms and presence of 8 clusters of tentacles precludes reference to the Rhizostomatida without a drastic and unwarranted redefinition of this order. The clusters of tentacles, borne by the exumbrella, cannot be homologized with the tentaculiform extensions of the marginal lap-

pets of *Lobonema* MAYER, the only known rhizostomatid with such organs. None of the excellently preserved specimens shows traces of oral arms. Long mouth arms, however, are present in *Leptobrachites trigonobrachius,* known from a single laterally compressed specimen from Solnhofen and regarded by KIESLINGER as a crushed individual of *R. admirandus.* There is nothing, however, to support this view, as practically the only features that can be distinguished in the poorly preserved specimen are the mouth arms (8 according to HAECKEL, 5 according to BRANDT). None of the diagnostic characters of *R. admirandus* are displayed. CASTER suggested that *R. admirandus* could be a trachylinid medusa, interpreting as exumbrellar the impressions regarded by all other authors as subumbrellar. When all the Solnhofen material originally described as belonging to different genera and species but shown by KIESLINGER to be different "preservation aspects" of *R. admirandus* is taken into account, CASTER's ingenious interpretation does not resist a critical analysis.

Family RHIZOSTOMITIDAE Harrington & Moore, nov.

Characters of order. *U.Jur.*

Rhizostomites HAECKEL, 1866 [*R. admirandus (=R.? lithographicus* HKL., 1866; *Hexarhizites insignis* HKL., 1870; *Myogramma speciosum* MAAS, 1902; *M. speciosissimum* VON AMMON, 1908; *Ephyropsites jurassicus* VON AMMON, 1908] [=*Hexarhizites* HKL., 1870; *Myogramma* MAAS, 1902; *Ephyropsites* v. AMMON, 1908]. (1) SUBUMBRELLAR IMPRESSIONS OF SPECIMENS WITH RADIAL MUSCLES RELAXED (type of *Rhizostomites admirandus*). Mouth cruciform, functional (Fig. 36,2), each branch bifurcating into nonfunctional adradial grooves which give rise to 4 insert interradial lobes (forming an "iron-cross") and 4 exsert intercalary triangular perradial lobes; central portion of each lobe (insert and exsert) swollen into a low, rounded knob; oral arms absent; mouth area framed by rugose ring bearing 4 pads, one at distal end of each of the 4 interradial lobes; pads reniform to subtriangular, with inner concentric marking (?gonadic sacs and opercula); central area surrounded by annular zone, smooth adcentrally, concentrically striated along outer half, separated by sharply marked narrow band (?ring canal) from outer annular zone (ring muscle) which is concentrically striated; margin circular, cleft into 128 short, round lappets with 8 deeper perradial and interradial notches bearing small knobs regarded as rhopalia. (2) SUBUMBRELLAR

IMPRESSIONS OF SPECIMENS WITH RADIAL MUSCLES CONTRACTED (type of *Myogramma speciosum*). Differs from preceding in having pinnatisected marking (contracted radial muscles) in rings around mouth area; margin of bell contracted into 8-lobed rosette disclosing the tentacles borne by exumbrella. (3) EXUMBRELLAR IMPRESSION OF SPECIMENS WITH RADIAL MUSCLES RELAXED (type of *Ephyropsites jurassicus*). Central area circular, smooth, separated by sharp narrow ring from annular zone bearing 16 radial lobes (8 large, subtrapezoidal, 8 narrower, parallel-sided) marked off by fine raised striae and incompletely split by a less conspicuous radial line; each subtrapezoidal lobe bears a cluster of ?ramified tentacles located at ⅔ the distance from center of umbrella to periphery; each smaller lobe bears, at approximately same location, a short transverse stria from which springs outward a pair of short radial lines. (4) EXUMBRELLAR IMPRESSION OF SPECIMENS WITH RADIAL MUSCLES CONTRACTED (type of *Myogramma speciosissimum*). Differs from preceding in having pinnatisected radial markings ending at boundary of central area which is not sharply defined; the 16 principal radial striae continue onto this area for half the distance to center and gradually disappear leaving a central smooth mid-field. (5) *Hexarhizites insignis*, known from a single impression, is regarded as the subumbrellar surface (radial muscles relaxed) of an abnormal individual with 12 oral lobes. *U.Jur.*, Ger.——FIGS. 36-39. *R. admirandus;* 36,1, subumbrellar surface, radial muscles relaxed, ×0.28; 36,2, *ibid.*, another specimen, ×0.58 (both from BRANDT); 37, *ibid.*, a 3rd specimen, ×0.37 (WALCOTT); 38,1, *ibid.*, a 4th specimen, ×0.3; 39,2, *ibid.*, a 5th specimen, ×0.5
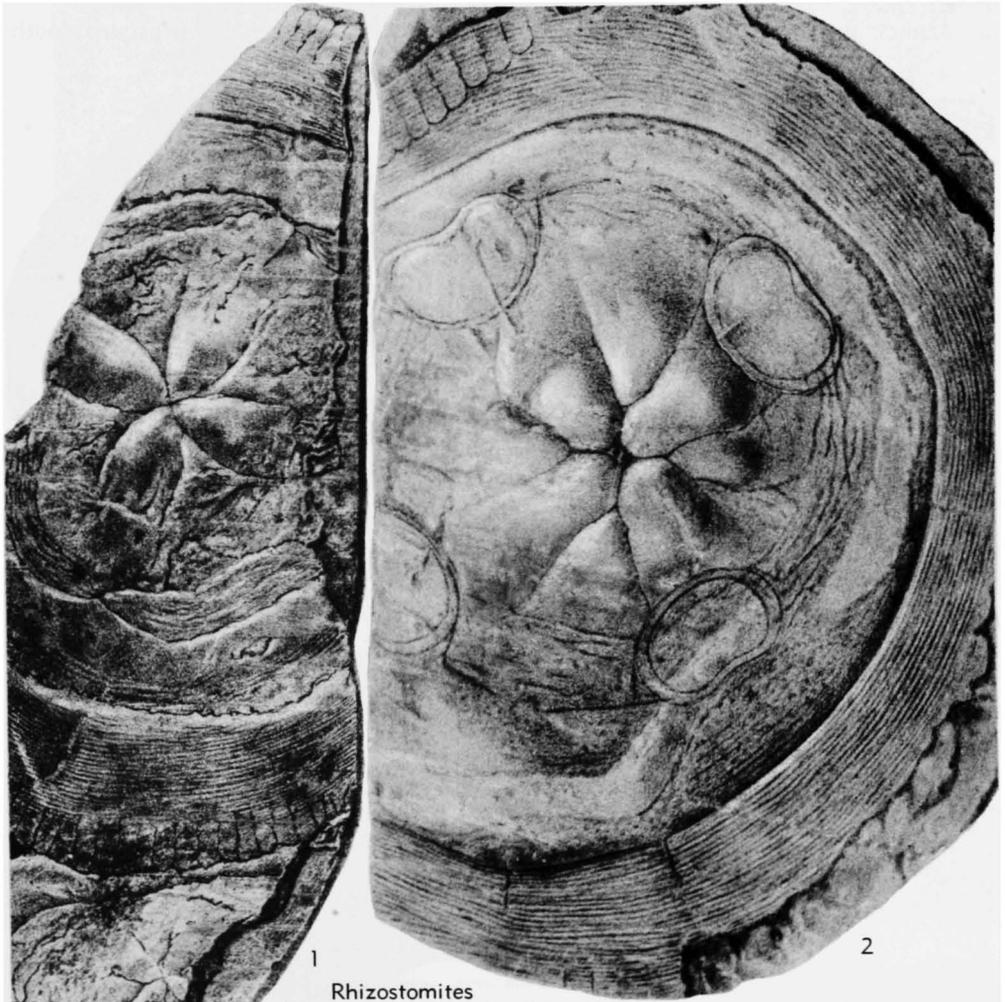

Rhizostomites

FIG. 36. Lithorhizostomatida: *Rhizostomites admirandus*, U.Jur., Ger.; *1,2*, specimens showing subumbrellar surface with radial muscles relaxed, ×0.28, ×0.52 (BRANDT).

both from von Ammon); 39,*1*, subumbrellar surface, radial muscles contracted ("*M. speciosum*"), ×0.33 (Maas); 38,*2*, exumbrellar surface, radial muscles relaxed ("*E. jurassicus*"), ×0.7; 38,*3*, exumbrellar surface, radial muscles contracted ("*M. speciosissimum*"), ×0.17 (both from von Ammon).

Order RHIZOSTOMATIDA Cuvier, 1799

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Rhizostomae CUVIER, 1799)] [=Rhizostomidae ESCHSCHOLTZ, 1829; Rhizostomeaea L.AGASSIZ, 1862; Rhizostomata VANHÖFFEN, 1888]

Bell dome-shaped or discoidal, without coronal furrow, without pedalia and without marginal tentacles (except in *Lobonema* MAYER, in which the lappets are prolonged in tentaculiform organs); margin cleft into 8 or more lappets; rhopalia 8 or more; central mouth absent; numerous ostioles borne upon 8 adradial, fleshy, branchlike mouth arms

which arise from center of subumbrella. ?U.Jur., Rec.

Rhizostomatids are inhabitants of tropical seas and the majority of genera confined to the warm waters of the Indo-Pacific region.

Family CASSIOPEIDAE Claus, 1883

[=Rhizostomata pinnata VANHÖFFEN, 1888; Arcadomyaria MAAS, 1903].

Rhizostomatida with 8 linear, pinnately or complexly branching mouth arms. *Rec.*

Cassiopea PÉRON & LESUEUR, 1809 [*Medusa andromeda* FORSKÅL, 1775] [=*Polyclonia* HAECKEL, 1880]. *Rec.* Other genus: *Toreuma* HKL., 1880.

Family CEPHEIDAE Claus, 1883

[=Chaunostomidae CLAUS, 1883; Rhizostomata dichotoma VANHÖFFEN, 1888; Radiomyaria MAAS, 1903]

Rhizostomatida with 8 separate mouth
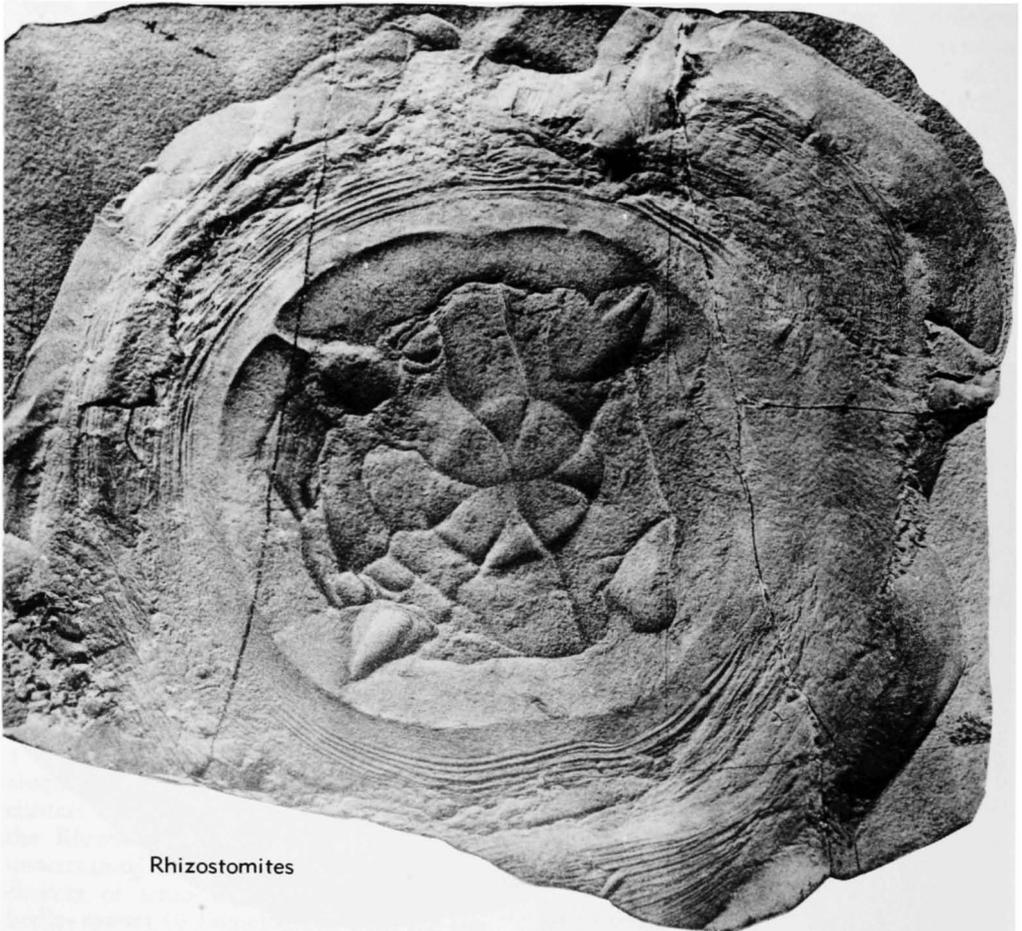
Rhizostomites

Fig. 37. Lithorhizostomatida: *Rhizostomites admirandus*, U.Jur., Ger.; subumbrellar surface, radial muscles relaxed (WALCOTT).

Rhizostomites

FIG. 38. Lithorhizostomatida: *Rhizostomites admirandus*, U.Jur., Ger.; *1*, subumbrellar surface, radial muscles relaxed; *2*, exumbrellar surface, radial muscles relaxed, ×0.7; *3*, exumbrellar surface, radial muscles contracted, ×0.17 (VON AMMON).

Rhizostomites

FIG. 39. Lithorhizostomatida: *Rhizostomites admirandus*, U.Jur., Ger.; *1*, subumbrellar surface, radial muscles contracted, ×0.33 (MAAS); *2*, subumbrellar surface, radial muscles relaxed, ×0.5 (VON AMMON).

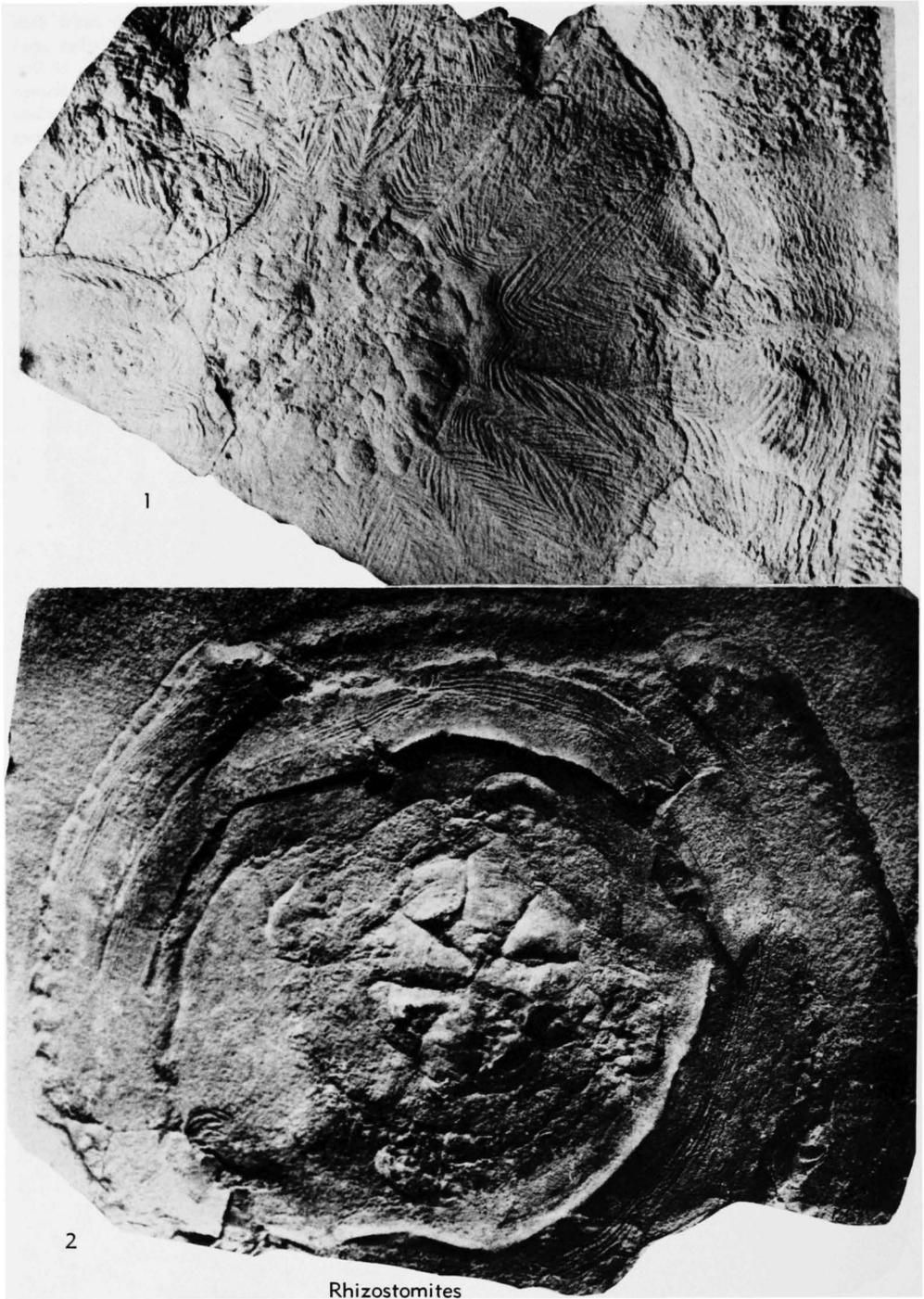arms the lower end of which give rise to 2 expanded leaflike side walls, the outer edges of which give rise to secondary branches and bear frilled ostioles; scapulets absent. *Rec.*

Cephea Péron & Lesueur, 1809 [*Medusa octostyla* Forskål, 1775] [=*Stylorhiza* Haeckel, 1880; *Netrostoma, Halipetasus* Schultze, 1898; *Microstylus, Perirhiza* Kishinouye, 1902]. *Rec.* Other living genera: *Polyrhiza, Cotylorhiza* L.Agassiz, 1862.

Family CATOSTYLIDAE Claus, 1883

[=Lychnorhizidae Claus, 1883; Rhizostomata triptera + R. trigona Vanhöffen, 1888; Rhizostomata triptera Maas, 1903]

Rhizostomatida in which the lower parts of the 8 separate mouth arms are 3-winged or Y-shaped in cross section, being expanded in a ventral and 2 dorsal lamellae; frilled ostioles borne upon the 3 lamellae; scapulets absent. *Rec.*

Catostylus L.Agassiz, 1862 [*C. mosaicus*] [=*Rhacopilus*, L.Agassiz, 1862; *Toxoclytus* L.Agassiz, 1863; *Crambessa* Haeckel, 1869; *Loborhiza* Vanhöffen, 1888]. *Rec.* Several other genera, including *Versura* Hkl., 1880; *Lychnorhiza* Hkl., 1890; *Lobonema* Mayer, 1910.

Family LEPTOBRACHIIDAE Claus, 1883

[=Rhizostomata lorifera Vanhöffen, 1888]

Rhizostomatida with very elongate, narrow, lashlike mouth arms; lower parts of arms 3-winged in cross section; ostioles developed upon and near the angles; upper parts of mouth arms very short and partially fused to arm disc by a series of arches spanning from one arm to another. *?U.Jur., Rec.*

Leptobrachia Brandt, 1838 [*Rhizostoma leptotus* Chamisso & Eysenhardt, 1821] [=*Leonura* Haeckel, 1880]. *Rec.* Other living genera: *Thysanostoma* L.Agassiz, 1862; *Lorifera* Hkl., 1880. ?**Leptobrachites** Haeckel, 1869 [*L. trigonobrachius* (=*Pelagiopsis leuckarti* Brandt, 1871, obj.)]. [=*Pelagiopsis* Brandt, 1871 (obj.)]. Based on single, obscure specimen from Solnhofen. Bell dome-shaped; margin cleft into lappets; pedalia and tentacles absent; mouth arms very long. According to Haeckel there are 48 lappets and 8 3-sided prismatic mouth arms. Brandt accepted only 10 lappets and 5 mouth arms. Von Ammon regarded the fossil as a laterally crushed specimen of *Rhizostomites admirandus*, a view opposed by Caster, *U.Jur.*, Ger.——Fig. 40. *L. trigonobrachius;* holotype, ×0.3 (Brandt).

Family RHIZOSTOMATIDAE Claus, 1883

[*nom. correct.* Harrington & Moore, herein (pro Rhizostomidae Claus, 1883)] [=Stomolophidae Claus, 1883; Rhizostomata scapulata Vanhöffen, 1888]

Rhizostomatida in which each of the 8 mouth arms bears a pair of wing-shaped outgrowths (scapulets) which arise from dorsal side of each arm near its point of origin from arm disc; frilled ostioles developed upon upper and outer sides of scapulets and upon lower parts of mouth arms. *Rec.*

Rhizostoma Cuvier, 1799 [*R. pulmo*] [=*Pilema* Haeckel, 1880]. *Rec.* Other living genera: *Eupilema, Rhopilema* Hkl., 1880; *Stomolophus* L. Agassiz, 1862.

Family ARCHIRHIZIDAE Haeckel, 1880

[=Rhizostomata simplicia Vanhöffen, 1888]

Rhizostomatida with 8 simple, separate, unbranched mouth arms; 16 radial canals give rise to side branches; ostioles without appendages, on ventral side of mouth arms. *Rec.* Family of doubtful validity because represented by 3 living genera seen only by Haeckel.

Archirhiza Haeckel, 1880 [*A. primordialis*]. *Rec.* Other living genera: *Haplorhiza, Cannorhiza* Hkl., 1880.

Leptobrachites

Fig. 40. Rhizostomatida: *Leptobrachites trigonobrachius,* U.Jur., Ger.; holotype, ×0.3 (Brandt).

?SCYPHOMEDUSAE INCERTAE SEDIS

Pseudorhopilema Sprigg, 1949 [*P. chapmani*]. Based on isolated impressions interpreted as subumbrellar mid-field. Mid-field slightly convex, with central groove giving rise to system of dichotomously branched primary, secondary and ?tertiary grooves, regarded as gastric canals at base of mouth arms. *L.Cam.*, S.Austral.——Fig. 41,*1.* *P. chapmani;* holotype ×0.7 (Sprigg).

Pseudorhizostomites SPRIGG, 1949 [**P. howchini*].
Based on isolated impressions interpreted by SPRIGG
as subumbrellar mid-field. Mid-field convex, with
cruciform grooves, each branching simply once;
slight suggestion of secondary dichotomous branch-
ing at end of one or more of 8 subradial grooves.
L.Cam., S.Austral.——FIG. 41,*3*. **P. howchini;*
holotype, ×0.7 (SPRIGG).——FIG. 41,*2*. *P.* sp.;
2a,b, ×0.9 (SPRIGG).

FIG. 41. Scyphomedusae incertae sedis: Lower Cam-
brian fossils from South Australia. *1, Pseudorho-
pilema chapmani;* holotype, ×0.7 (SPRIGG). *2,
Pseudorhizostomites* sp.; *2a,b,* specimens, ×0.9
(SPRIGG). *3, Pseudorhizostomites howchini;* holo-
type, ×0.7 (SPRIGG).

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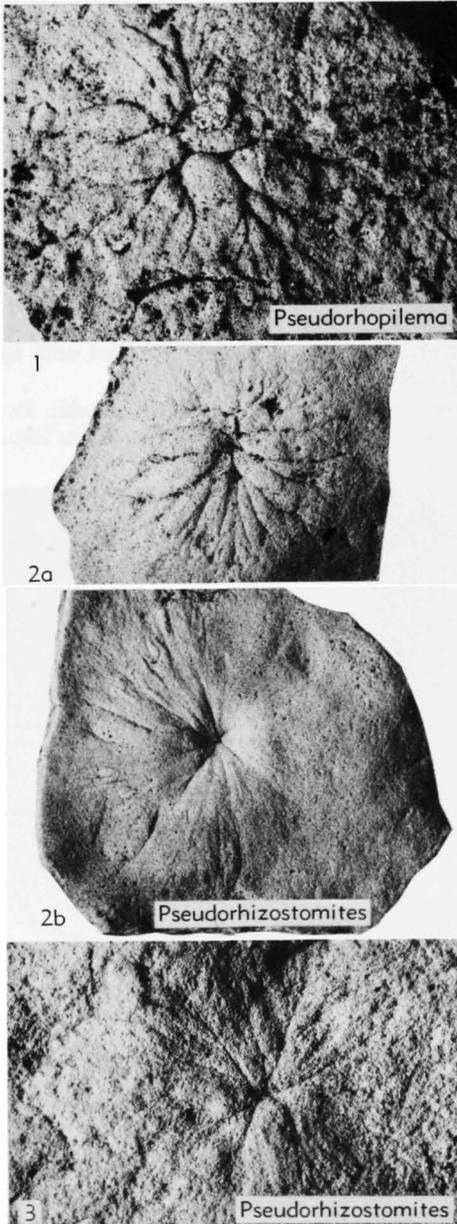p. 153-163, pl. 1-2.

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CONULATA

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

CONTENTS

A diagnosis of the subclass Conulata, accompanied by discussion of characters which are considered to support classification of this extinct group of invertebrates as a division of the Scyphozoa, has been given in the section entitled "Scyphozoa." Here, attention is directed to characters of the single order (Conulariida) that at present is assigned to the subclass. The conulariids are a varied but relatively stable assemblage having well-defined morphological attributes. We exclude from Conulata and also from Coelenterata fossils classed as belonging to the Serpulitidae, although KIDERLEN (1937) and some other authors have interpreted the chitinophosphatic, generally somewhat compressed elongate tubes with thickened longitudinal rods incorporated in the periderm as a simple type of early conulate, that is, close relative of the Conulariida. HOWELL (1949) has pointed out that *Serpulites* BLUMENBACH, 1803, introduced as a name for Mesozoic fossils found near Hanover, Germany, is clearly distinct from *Serpulites* in the sense used by MURCHISON (1839) for designation of Silurian fossils, this application of the name (erroneously attributed to MACLEAY) being ascribable

clearly to MURCHISON. For Paleozoic fossils which have been referred to *Serpulites* (as *S. angustifolius, S. gracilis*) HOWELL has published the new generic name *Tubelelloides*. This genus and the Middle Cambrian forms called *Urotheca* MATTHEW, 1899 (*non* COCTEAU & BIBRON, 1843), renamed *Tubulella* by HOWELL (1949), and various others (as *Coleoprion, Coleolus*, etc.), are considered to be worms and not at all suggestive of any known kinds of coelenterates. This conclusion certainly is acceptable in the light furnished by contemplation of such an attenuated threadlike form as *Tubulella flagellum* (MATTHEW) (see HOWELL, 1949, pl. 1, fig. 10).

Order CONULARIIDA Miller & Gurley, 1896

[*nom. correct.* MOORE, in MOORE, LALICKER & FISCHER, 1952 (*pro* Conularida MILLER & GURLEY, 1896)]

Characters of subclass. *M.Cam.-L.Trias.*

MORPHOLOGY

The periderm of conulariids typically has a steep-sided pyramidal form. From an attachment disc (*appareil fixateur, Haftscheibe*) (Fig. 27), the 4 sides or faces of the

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(*Explanation of Fig 42, continued from facing page.*)

surface, at right mold of opposite face on matrix, enlarged (17*). *8, Diconularia clavus*, M.Sil., Eng.; transverse rows of tubercles at corner, ×10 (29*). *9, Conularia cribristriata*, M.Dev., N.Y.; facial ornament, ×10 (20*). *10, C. continens*, M.Dev., N.Y.; facial ornament, ×10 (20*). *11, C. africana*, Dev., S.Am. (Bol.); middle part of face, ×5 (KNOD*). *12, Pseudoconularia dalecarliae*, Sil., Swed.; part of face, ×10 (21*). (Note: Inasmuch as conulariid specimens are illustrated both with apertural extremity directed upward and downward, presumably corresponding to orientations in attached and free-swimming conditions, respectively, no arbitrary orientation of figured specimens is adopted here and where the direction toward the aperture is not self-evident, this is indicated by an arrow.)
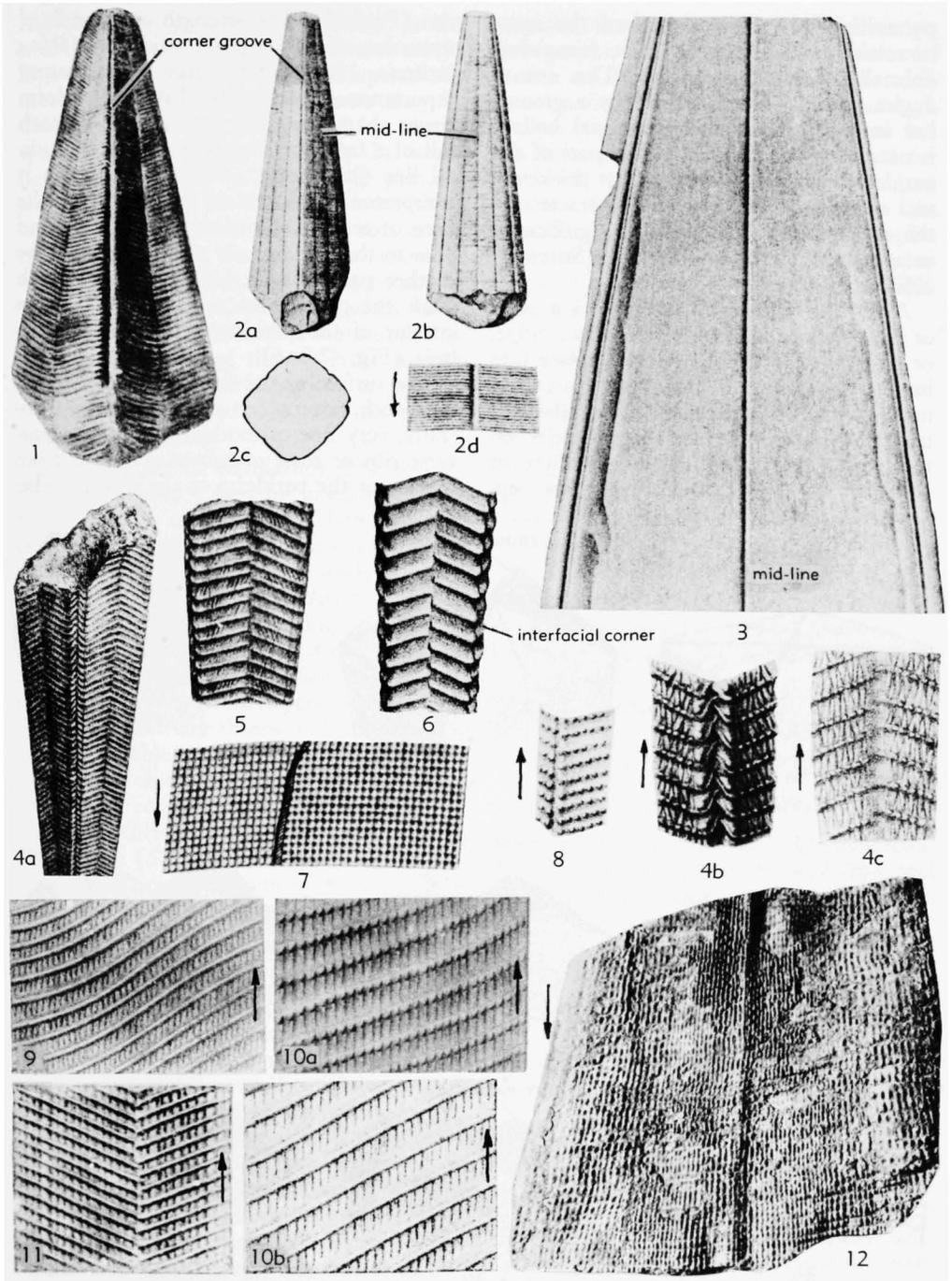
FIG. 42. Morphological features of Conulariida. *1, Paraconularia tubericosta,* L.Carb., Eng., ×1 (32*). *2, Archaeoconularia fecunda,* M.Ord., Czech.; *2a,b,* corner and facial views, ×1; *2c,* transverse section, ×1; *2d,* part of face, ×4 (17*). *3, A. insignis,* M.Ord., Czech.; part of face showing prominent mid-line and corner furrows, ×1 (17*). *4, Paraconularia warthi,* Perm., India; *4a,* corner view, ×1; *4b,c,* corner and mid-line of face, enlarged (33*). *5, P. tenuistriata,* Perm., India; face, ×1 (33*). *6, P.? laevigata,* Perm., India; face, ×1 (33*). *7, Exoconularia exquisita,* M.Ord., Czech.; facial ornament, part of left showing
(Continued on facing page.)

pyramidal form diverge toward the aperture with angles between them measuring normally about 90 degrees. The corner angles typically are furrowed by a groove, but in some genera this interfacial hollow is not developed (Fig. 42). This part of the periderm commonly is somewhat thickened and experience indicates that characters of the corner region have special significance in classification of conulariids (SINCLAIR, 1952).

Along the mid-line of each face is a more or less distinct longitudinal furrow, ridge, or pigmented line that divides the face into halves; this line is a prominent feature of many fossils, being accentuated by offsets in transverse ridges or rows of tubercles on the faces (Fig. 42,5,6) and by development internally of a longitudinal ridge or sep-

tum (Fig. 19). The strength and mode of expression of this facial mid-line (*ligne pariétale*, *Mittellinie*) has classificatory importance secondary to that of periderm corner characters. The central part of each half of a face may bear a distinct longitudinal line (lateral line, *Seitenlinie*) which is interpreted by KIDERLEN (1937) to be the trace of tentacular muscle attachment, and close to the mid-line on either side may be another pair of lines (*Nebenlinien*) which mark the position of septal ridges on the interior of the periderm, as in *Metaconularia* (Fig. 42,2a,b).

The surface of the faces somewhat rarely is smooth, except for cross wrinkles. Generally, very fine to moderately coarse transverse ribs or rows of tubercles extend from corners of the periderm to the mid-line, be-
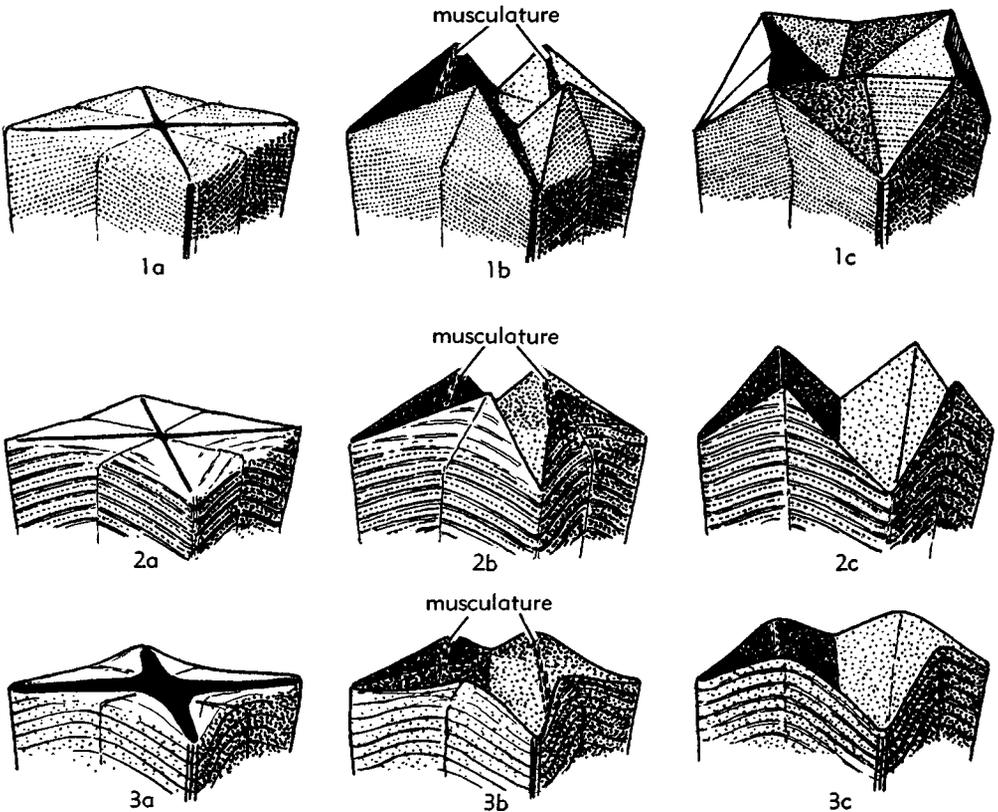

FIG. 43. Apertural region of conulariids showing types of closure by inward bending of the flexible periderm. *1a-c*, Plicated closure, characterized by evenness of apertural margin with sharp folds extending inward from corners, diagrams showing closed, partly open, and widely open positions. *2a-c*, Triangular lappet type of closure, distinguished by adapertural extensions of faces that fit neatly together when pulled inward, showing closed, partly open, and widely open positions. *3a-c*, Lobate lappet type, like *2a-c* except for shorter and marginally curved form of lappets. Inferred musculature for closing aperture is shown in *1b, 2b, 3b* (28n).

ing confluent or offset in position at the mid-line (Fig. 42). These transverse markings tend to slope or curve adaperturally more or less strongly. Interspaces may be devoid of markings or crossed by closely spaced barlike ridges; especially in forms having well-developed tubercles or pustules along the ribs or in transverse rows, these tend to be connected from row to row across the interspaces. In *Pseudoconularia,* accentuation of longitudinal arrangement of tubercles gives predominance of it over transverse features of surface sculpture (Fig. 42,*12*). Characters of the sculpture usually are reliable for discrimination of species, but they have subordinate value for differentiation of genera.

The aperture of conulariids may be partially or entirely closed by inward bending of distal parts of the faces. Three types of closure are distinguished, one consisting of plication of the transversely nearly straight apertural margin (Fig. 43,*1a-c*), and the others consisting of inbending of lappet-like triangular or semicircular extensions of the faces (Fig. 43,*2a-c, 3a-c*). Although many fossils show characters of apertural closure, the extreme thinness of this obviously very flexible part of the periderm, possibly more chitinous than phosphatic, may account for common lack of preservation.

A smoothly rounded, adapically convex diaphragm (*Schott, cloison*) constitutes the proximal extremity of some specimens which have broken free from an earlier attached location (Fig. 28).

CLASSIFICATION

Division of the Conulariida into at least 2 groups assigned rank as suborders is justified by present knowledge. These consist of nearly all described forms in one assemblage, here termed Conulariina, and *Conchopeltis* representing the other. This gives rise to highly disparate divisions, as must be recognized, yet distinction which sets *Conchopeltis* well removed from other conulariids seems necessary. Whether morphological characters of *Conulariella* are likewise different enough from those of common types of conulariids to call for placing it in a separate suborder is doubtful. The classification adopted here is essentially that proposed by SINCLAIR in 1952. Data

recorded in the systematic descriptions on stratigraphic and geographic distribution of genera are subject in varying degree to additions and corrections, because thorough study of specimens and the literature has not been possible in the time allotted for preparing this section. A summary of supra-generic divisions now recognized in the Conulata and the recorded stratigraphic range of each is given in the following tabulation. Numbers of genera defined at present are indicated.

Main Divisions of Conulata

Conulata *(subclass)* (20). *M.Cam.-L.Trias.*
 Conulariida *(order)* (20). *M.Cam.-L.Trias.*
  Conchopeltina *(suborder)* (1). *M.Ord.*
   Conchopeltidae (1). *M.Ord.*
  Conulariina *(suborder)* (19). *M.Cam.-L.Trias.*
   Conulariellidae (1). *M.Cam.-L.Ord.*
   Conulariidae (17). *U.Cam.-Perm.*
    Conulariinae (9). *U.Cam.-Perm.*
    Paraconulariinae (4). *M.Ord.-L.Perm.*
    Ctenoconulariinae (4). *M.Ord.-M.Dev., ?L. Miss.*
   Conulariopsidae (1). *L.Trias.*

Suborder CONCHOPELTINA Moore & Harrington, nov.

Broad low conical forms with strong tetrameral symmetry, periderm very thin and presumably consisting mainly of a chitinous substance (no calcium phosphatic mineralization observed); numerous tentacles along apertural margin which lacks any sign of inward bending to effect closure. *M.Ord.*

Family CONCHOPELTIDAE Moore & Harrington, nov.

Characters of suborder. *M.Ord.*

Conchopeltis WALCOTT, 1876 [**C. alternata*]. Faces gently convex with broadly lobate margins, separated laterally by wide and shallow interfacial furrows; width of cone approximately 3 times greater than height; surface of periderm marked by faint wavy growth lines concentric with margin and sharply defined fine radial striae. *M.Ord. (Trenton.),* N.Y., Minn.——FIGS. 22, 44. **C. alternata,* N.Y.; 22, specimen with tentacles preserved, Cornell Univ. coll., ×1.5 (34n); 44,*1a,c*, internal and external molds of holotype, ×0.9; 44,*1b*, side view of holotype, ×0.9 (23*).

Suborder CONULARIINA Miller & Gurley, 1896

[*nom. transl. et correct.* MOORE & HARRINGTON, herein (*ex* Conularida MILLER & GURLEY, 1896)]

Steeply pyramidal, generally 4-sided forms with thin chitinophosphatic periderm, faces bearing faint to strong transverse lirae or ribs more or less curved adaperturally and continuous or offset along mid-line of faces, which may be defined as a furrow or ridge or pigmented line or which is not evident
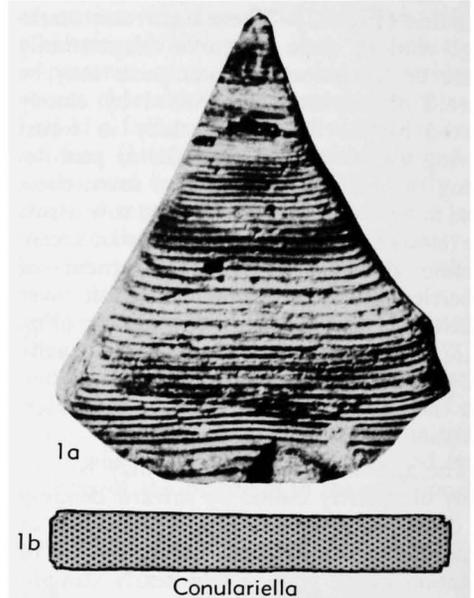

1a

1b

Conulariella

FIG. 45. Conulariina: Conulariellidae (p. F58).

at all; interfacial corners rounded or depressed in a more or less accentuated groove; apex with fixation disc, at least in well-preserved young specimens; aperture partly or entirely closable by inwardly bent edges of faces. *M.Cam.-Trias.*

Family CONULARIELLIDAE Kiderlen, 1937

Flattened trumpet-shaped forms with rectangular cross section having 2 opposite sides several times longer than others; aperture straight-sided, without sign of inward bending of faces; faces marked by transverse ribs that do not curve adaperturally; without mid-lines on faces or internal septa; interfacial corners grooved. *M.Cam.-L.Ord.*

Conulariella BOUČEK, 1928 (*Conularia robusta* BARRANDE, 1867). Differs from *Conularia* and other Conulariidae in rectilinear transverse ribs on faces and from several genera in absence of internal longitudinal ridges (septa). *M.Cam.-L. Ord.*, Eu.——FIG. 45,*1. *C. robusta* (BARRANDE), Czech.; *1a,b*, side and transv. sec., ×1 (*1a*, 18*; *1b*, 28n).

Family CONULARIIDAE Walcott, 1886

Steep-sided pyramidal forms, mostly with quadrangular cross section, faces generally marked by evident transverse lirae or ribs which are deflected adaperturally in crossing

1a

1b

1c

FIG. 44. Conchopeltina: Conchopeltidae (p. F57).

the face but longitudinal sculpture may dominate or the surface may be smooth except for small wrinkles; angles at corners typically thickened somewhat, with or without distinct furrow; mid-line of faces de-fined by narrow groove or ridge that in some genera corresponds to internal septa and it may be accompanied by 1 or 2 distinct longitudinal lines on either side, or mid-line may not be distinguishable as

1   Conularia

2

3b

3a

Conularia

4a

4b

4c

Mesoconularia

5a   Mesoconularia

5b

5c

Mesoconularia

6   Mesoconularia
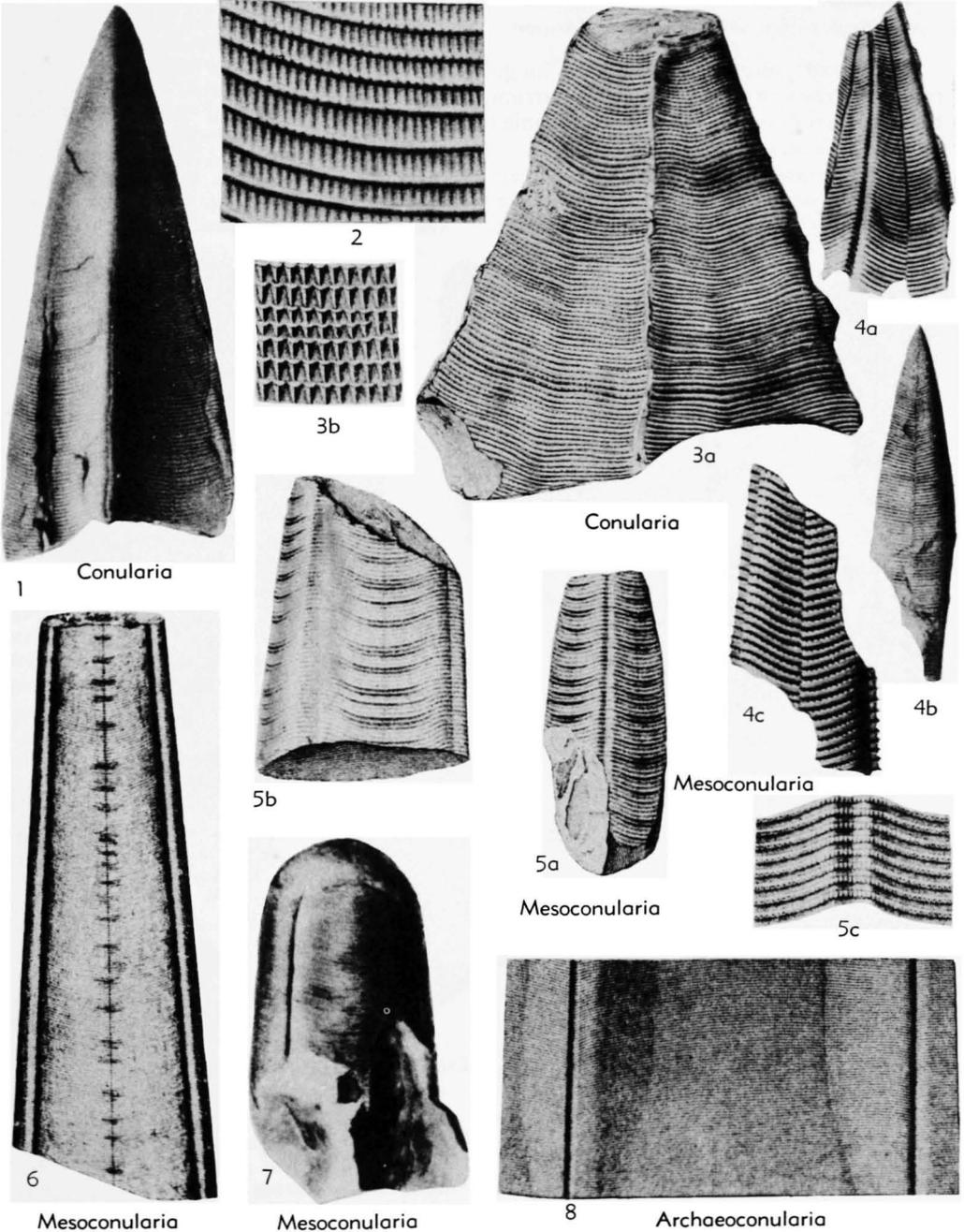
7   Mesoconularia

8   Archaeoconularia

Fig. 46. Conulariina: Conulariidae (p. F60-F61).

morphological feature; aperture closable by inward bending of facial periderm and apical extremity may consist of smoothly rounded diaphragm (*Schott*). *U.Cam.-Perm.*

Subfamily CONULARIINAE Walcott, 1886

[*nom. transl.* SINCLAIR, 1952 (*ex* Conulariidae WALCOTT, 1886)]

Corners of periderm indented by longitudinal furrow which does not interrupt transverse sculpture and is not accompanied by distinct thickening. *U.Cam.-Perm.*

Conularia SOWERBY, 1821 [**C. quadrisulcata* (=*C. sowerbyi* DE BLAINVILLE, 1825; *C. cancellata* SANDBERGER, 1847) (*non C. quadrisulcata* SLATER,

1907=*C. tubericosta* SANDB., 1847)] [=*Plectoconularia* BOUČEK, 1939 (obj.)]. Transverse ribs well defined, closely spaced, finely tuberculate, with interspaces crossed by bars or striae; facial mid-line not marked surficially by groove or ridge nor produced internally as septal ridge. *U.Cam.-Perm.*, world-wide.——FIG. 23,*1a,b, C. cambria* WALCOTT, U.Cam., N.Am.; reconstr., ×1 (22*).——FIGS. 25, *1; 42,10. C. continens* HALL, M.Dev., N.Y.; 25,*1*, specimen with attached inarticulate brachiopods and attachment scars, ×1 (20*); 42,*10*, facial ornament, ×10 (20*).——FIG. 25,*2. C. undulata* CONRAD, M.Dev., N.Y.; specimen with attachment scars of brachiopods, ×1 (20*).——FIG. 42,*9. C. cribristriata* HALL, M.Dev., N.Y.; facial ornament, ×10 (20*).——FIGS. 42,*11; 46,1. C. africana* SALTER, Dev., S.Am.(Bol.-Brazil); 42,*11*, facial orna-
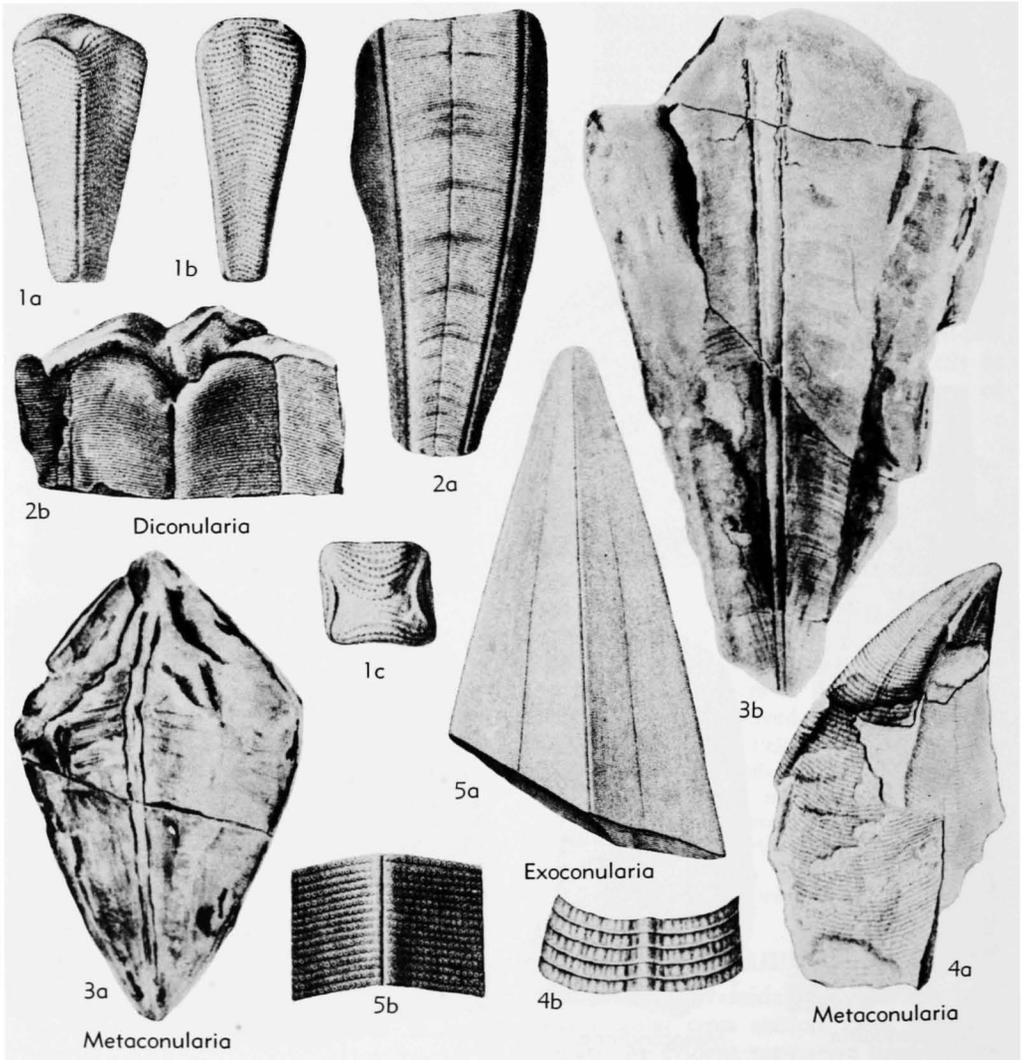

1a   1b

2b   Diconularia

2a

1c

3b

3a   Metaconularia

5a   Exoconularia

5b

4b

4a   Metaconularia

FIG. 47. Colunariina: Conulariidae (p. F61).

ment, ×5 (Knod*); 46,*1*, side view, ×1 (19*).
——Fig. 46,*3*. *C. niagarensis* Hall, M.Sil., Ind.; *3a*,
side view of mold, ×1; *3b*, surface ornament, en-
larged (20*).——Fig. 46,*2*. *C. congregata* Hall, U.
Dev., N.Y.; surface ornament, ×10 (20*).

Archaeoconularia Bouček, 1939 [*Conularia in-
signis* Barrande, 1867]. Small to medium-sized,
periderm very thin, faces with prominent median
groove and adapertural part extended as acute
triangular lappet that may be bent inward for
closure of aperture; surface marked by fine trans-
verse threads gently arched adaperturally and
crossed by faint longitudinal striae; apical dia-
phragm observed in some species. *L.Ord.-Sil.*, Eu.-
N.Am.——Figs. 42,*3*; 46,*8*. *A. insignis* (Bar-
rande), Ord., Czech.; 42,*3*, type, ×1; 46,*8*, part
of face, ×2 (17*).——Fig. 24,*3a,b*. *A. slateri*
(Reed), U.Ord.(Ashgill.), Scot.; *3a,b*, side and
apertural views showing closure by infolded peri-
derm, ×1 (29*).——Figs. 23,*2a,b*; 42,*2a-d*. *A. fe-
cunda* (Barrande), Ord., Czech.; 23,*2a,b*, reconstr.,
×0.7 (22*); 42,*2a-c*, side views and transv. sec.,
×1; 42,*2d*, part of face, ×4 (17*).

Mesoconularia Bouček, 1939 [*Conularia fragilis*
Barrande, 1867]. Faces showing more or less dis-
tinct mid-line but no secondary longitudinal lines,
transverse ribs distinct. *L.Dev.-Penn.*, Eu.-Afr.-N.
Am.-S.Am.——Fig. 46,*5*. *M. fragilis* (Barrande),
L.Dev., Czech.; *5a,b*, side views of 2 specimens,
×1; *5c*, part showing corner groove and trans-
verse ribs, enlarged (17*).——Fig. 46,*4*. *M.
ulrichana* (Clarke), Dev., Brazil(Parana); ×1
(19*).——Fig. 46,*6*. *M. roeperi* (Miller & Gur-
ley), Penn., Pa.; ×0.7 (27*).——Fig. 46,*7*. *M.
globosa* (Slater), L.Carb., Eng.; specimen with
apical diaphragm, ×1 (32*).

Diconularia Sinclair, 1952 [*Conularia micronema*
Meek, 1871]. Corners simple, with furrow or not
furrowed; faces bearing close-spaced transverse
ribs marked by prominent subcircular pustules;
mid-line more or less defined on surface and gen-
erally associated with low septal ridge on inner
side of periderm. *M.Ord.-Penn.*, N.Am.-Eu.——
Fig. 47,*2*. *D. micronema* (Meek), L.Miss., Ohio.;
2a, holotype, ×1; *2b*, another specimen with peri-
derm infolded for closure of aperture, ×2 (26*).
——Figs 42,*8*; 47,*1*. *D. clavus* (Reed), M.Sil.,
Eng.,; 42,*8*, ornamentation, ×10; 47,*1a,b*, corner
and side views, ×1; 47,*1c*, aperture showing in-
wardly bent rounded lappets, ×1 (all 29*).

Metaconularia Foerste, 1928 [*Conularia aspersa*
Lindström, 1884]. Corners with rather incon-
spicuous shallow furrow; periderm of faces very
thin, surface marked by nearly horizontal trans-
verse rows of minute granules which also may be
aligned vertically; mid-line of faces inconstantly
marked by faint groove or not defined externally,
on inner side enclosed by a pair of well-developed
septal ridges which in compressed specimens may
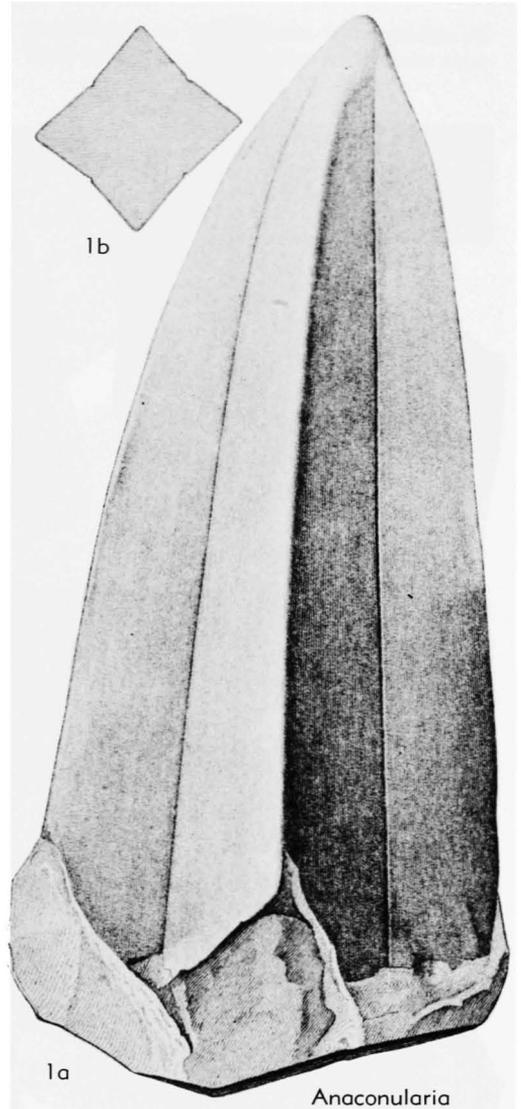distort outer surface so as to produce longitudinal

FIG. 48. Conulariina: Conulariidae (p. F62).

linear elevations; aperture closed by extensions of
facial periderm in form of triangular lappets. *M.
Ord.-U.Sil.*, Eu.-N.Am.——Fig. 47,*3*. *M. aspersa*
(Lind.), U.Sil.(Ludlov.), Eng.; *3a*, aperture closed
by triangular lappets, ×1; *3b*, side of another lar-
ger specimen, ×1 (32*).——Fig. 47,*4*. *M. soli-
taria* (Barrande), M.Ord., Czech.; *4a,b*, flattened
specimen, ×1, and detail of surface, enlarged
(17*).

Exoconularia Sinclair, 1952 [*Conularia exquisita*
Barrande, 1867]. Faces with accessory longitudi-
nal lines varying in position in different species,
surface bearing transverse rows of pustules. *L.Ord.-
U.Ord.*, Eu.-N.Am.——Fig. 42,*7*; 47,*5*. *E. ex-
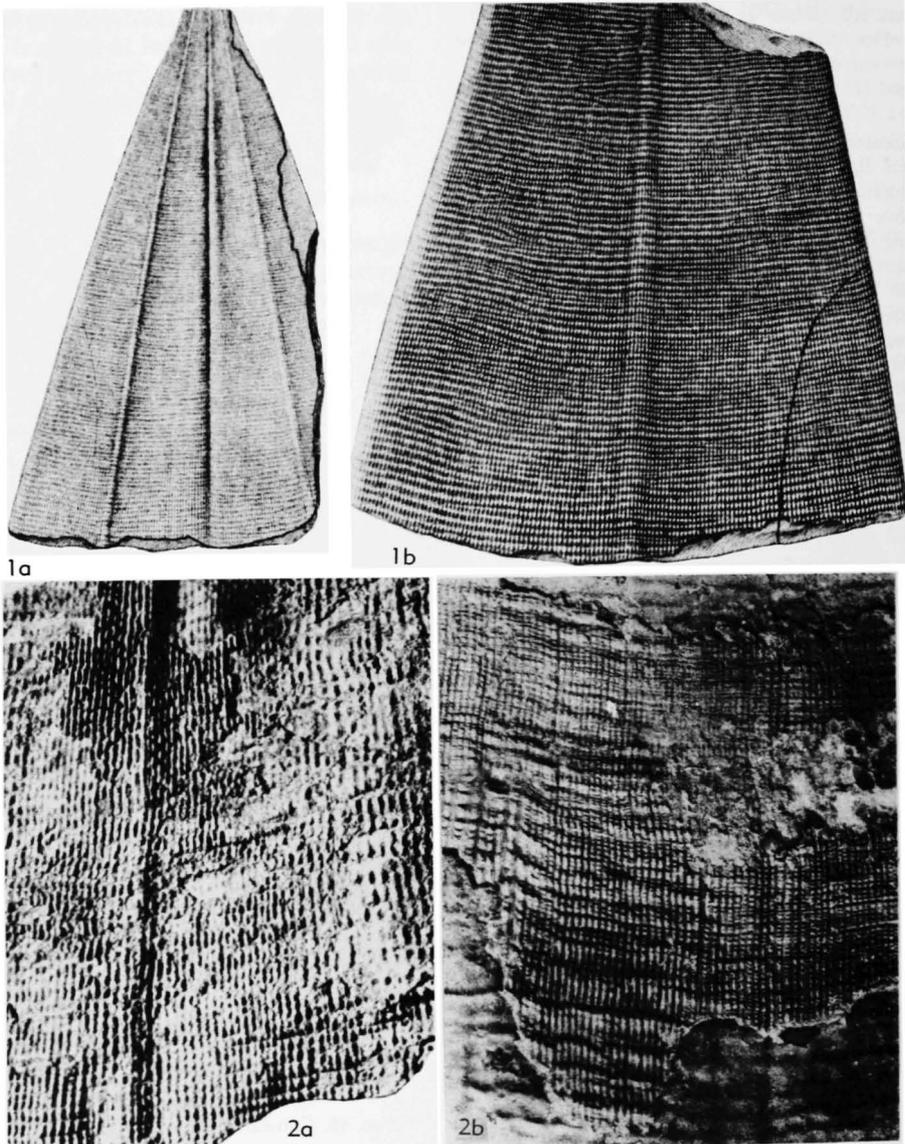
Pseudoconularia

Fig. 49. Conulariina: Conulariidae (p. F63-F64).

quisita (BARRANDE), M.Ord., Czech.; 42,7, orna-
ment, enlarged; 47,5a,b, side view, ×1, and part
of surface showing rows of tubercles, enlarged
(17*).——FIGS. 24,1; 28,3. E. pyramidata
(HOENINGHAUS), M.Ord., Czech.; 24,1, distorted
but unbroken specimen indicating flexibility of
periderm, ×0.7 (22); 28,3, specimen with
schott, ×1 (25).——FIGS. 23,3; 24,2; 25,3. E.
consobrina (BARRANDE), M.Ord.-U.Ord., Czech.-
Fr.; 23,3, reconstr. of free-swimming medusoid
adult, ×0.7 (22*); 24,2, apertural region with

oblique section showing infolded periderm, ×1
(25*); 25,3, part of surface with attached edrioas-
teroid (Agelacrinites), ×0.75 (22*).
Anaconularia SINCLAIR, 1952 [*Conularia anomala
BARRANDE, 1867]. Corners without trace of fur-
rows, being elevated in rounded or sharp ridge.
M.Ord., Eu.——FIGS. 28,1; 48,1. A. anomala
(BARRANDE), M.Ord., Czech.; 48,1a,b, side view
and transv. sec., ×1 (17*). 28,1, specimen with
schott, ×1 (17*).
Palaenigma WALCOTT, 1886 [*pro Tetradium

SCHMIDT, 1874 (*non* DANA, 1846)] [*Tetradium wrangeli* SCHMIDT, 1874]. *L.Ord., Eu.*

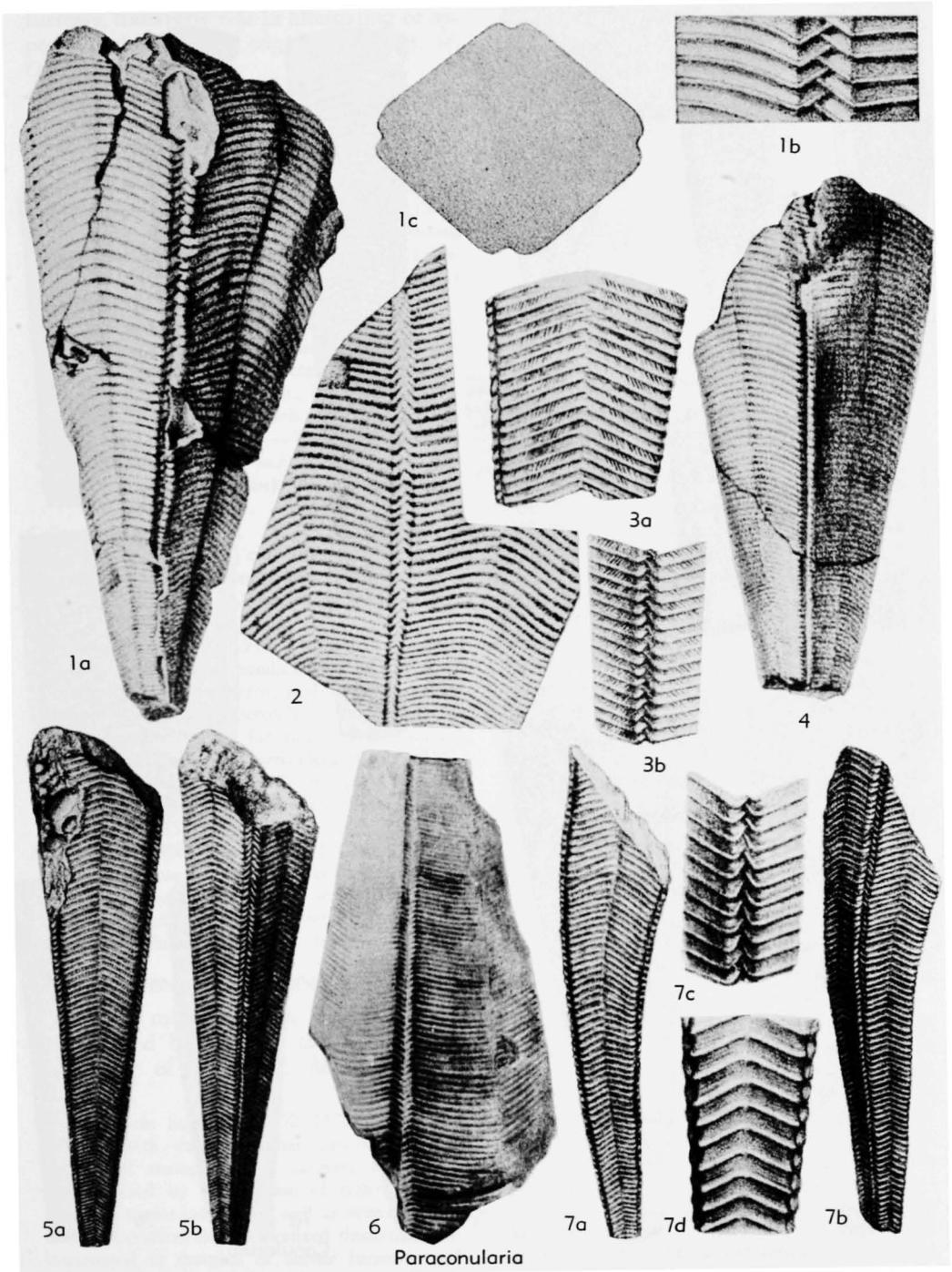*sima* BARRANDE, 1867]. Faces with mid-line defined by low but distinct ridge but without acces-

FIG. 50. Conulariina: Conulariidae (p. F65).

ing of closely spaced longitudinal rows of vertically elongate tubercles. *Sil.*, Eu.-N.Am.——Fig. 49,1. *P. grandissima* (Barrande), Czech.; *1a,b,* side view of 2 specimens, ×1 (17*).——Fig. 49,2. *P. dalecarliae* Hessland, Swed.; *2a,b,* part of surface, ×15, ×10 (21*).
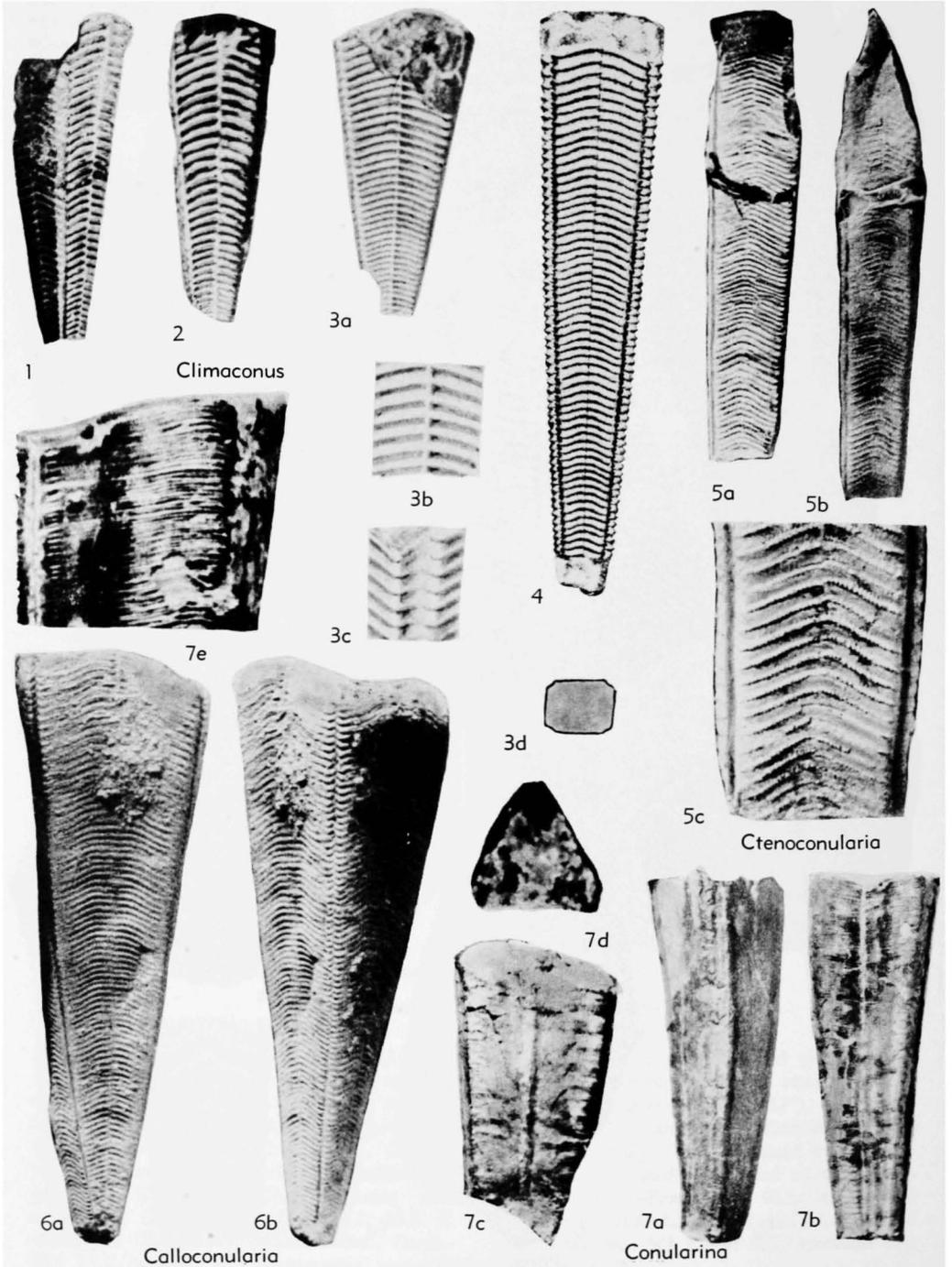

Fig. 51. Conulariina: Conulariidae (p. F65).

Subfamily PARACONULARIINAE Sinclair, 1952

Corners of periderm sharply inflected, with surface sculpture interrupted at corner furrows, transverse ribs in alternating or opposed positions along edges of furrows. *M. Ord.-L.Perm.*

Paraconularia SINCLAIR, 1940 [*Conularia inaequicostata* DEKONINCK, 1883]. Transverse ribs moderately strong, faintly tuberculate, abruptly bent adaperturally at their terminations on edges of corner furrows; mid-line on faces indicated only by slight deflection of ribs along it. *M.Sil.-L.Carb.,* Eu.-N.Am.——FIG. 50,*1.* *P. inaequicostata* (KON.), L.Carb(Tournais.), Belg.; *1a-c,* ×1 and enlarged (24*).——FIG. 50,*2.* *P. blairi* (MILLER & GURLEY), L.Miss.(Kinderhook.), Mo.; ×1ˉ (27*).——FIG. 50,*6.* *P. tubericosta* (SANDBERGER), L.Carb., Eng.; ×1 (form identified by SLATER as *Conularia quadrisulcata*) (SLATER).——FIG. 50,*3.* *P. tenuistriata* (M'COY), Perm., India; ×1 (33*). ——FIG. 50,*4.* *P. irregularis* (KON.), L.Carb. (Visé.), Belg.; ×1 (24*).——FIG. 50,*5.* *P. worthi* (WAAGEN), Perm., India; *5a,b,* ×1 (33*).——FIG. 50,*7.* *P. laevigata* (MORRIS), Perm., India; *7a,b,* ×1; *7c,d,* enlarged (33*).

Calloconularia SINCLAIR, 1952 [*C. strimplei*]. Transverse ribs low and crowded, joined by longitudinal bars in interspaces. *Penn.,* N.Am.—— FIG. 51,*6.* *C. strimplei,* U.Penn.(Missourian), Okla.; *6a,b,* ×1 (31*).

Eoconularia SINCLAIR, 1943 [*Conularia loculata* WIMAN, 1894]. Rather small, corner furrows with slightly thickened periderm; mid-line of faces not strongly marked but internally a thin distally bifurcate septum reaches far into interior; surface smooth except for cross wrinkles. *M.Ord.-M.Sil.,* Eu.-N.Am.——FIG. 19,*1.* *E. loculata* (WIMAN), M.Sil., Gotl.; transv. sec. showing bifurcate interradial septa, ×15 (35*).

Neoconularia SUGIYAMA, 1942 [*Conularia rectangularis* HAYASAKA, 1920]. Faces flat and smooth except for transverse irregular wrinkles, without sign of mid-line; cross section rectangular (known only from steinkerns). *L.Perm.,* Japan.

Subfamily CTENOCONULARIINAE Sinclair, 1952

Corners more or less furrowed and strengthened by internal carinae or other thickening of periderm. *M.Ord.-M.Dev., ?L.Miss.*

Ctenoconularia SINCLAIR, 1952 [*C. obex*]. Very slender, with shallow corner furrows marking position of strong internal carinae; mid-line of faces marked by interruption of transverse ribs, which comprise internal as well as external elevations of periderm due to localized thickening, ribs interrupted at margins of corner furrows, with pustulose crests but unlike *Conularia s.s.,* inter-
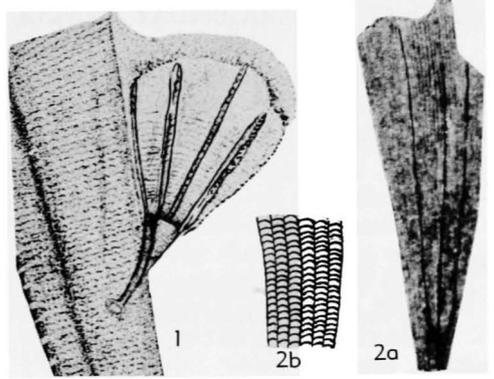

FIG. 52. *Sphenothallus angustifolius* (p. F65).

spaces lack cross bars. *M.Ord.-M.Dev., ?L.Miss.* ——FIG. 51,*5.* *C. obex,* M.Ord.(Blackriveran), Minn.; *5a,c,* ×2.5; *5b,* ×7 (41*).——FIG. 51, *4. ?C. greenei* (MILLER & GURLEY). L.Miss.(Keokuk), Ind.; ×1 (27).

Climaconus SINCLAIR, 1952 [*Conularia quadrata* WALCOTT, 1879]. Small forms with square to rectangular cross sections; faces with strong smooth transverse ribs that along mid-line meet in opposed or alternating position, mid-line appears externally as ridge with adaperturally diminished height in each interspace and having straight or zigzag appearance, not associated with internal septal ridge; corner furrows may have transverse wrinkles. *M.Ord.-U.Ord.,* N.Am.-Eu.——FIG. 51, *2.* *C. quadratus* (WALCOTT), M.Ord., N.Y.; ×2 (31*).——FIG. 51,*1.* *C. batteryensis* (TWENHOFEL), U.Ord., Que.; ×2 (31*).——FIG. 51,*3.* *C. bottnicus* (HOLM), M.Ord., Swed.; *3a,d,* ×1.5; *3b,c,* ×3 (31*).

Conularina SINCLAIR, 1942 [*Conularia triangulata* RAYMOND, 1905]. Slender; faces with mid-line expressed as low ridge flanked by shallow depressions that form low ridges internally; transverse section triangular or quadrangular; surface marked by fine transverse striae crossed commonly by fine oblique folds near shoulders of corner furrows. *M.Ord.,* N.Am.——FIG. 51,*7.* *C. triangulata* (RAYMOND), Vt.; *7a-d,* ×2; *7e,* ×7.5 (31*).

Sphenothallus HALL, 1847 [*S. angustifolius;* SD MOORE & HARRINGTON, herein (=*Conularia gracile* HALL, 1847)] [=*Hallotheca* BOUČEK, 1936 (obj.); *Glyptoconularia* SINCLAIR, 1952 (type, *Conularia gracilis* HALL, 1847)]. Corners strengthened by pronounced thickening of periderm and faces with mid-line produced inward as carina; surface with longitudinal ornamentation. *M.Ord.,* N.Am.—— FIG. 27,*7;* 52,*1,2.* *S. angustifolius,* N.Y.; 27,*7,* holotype, ×1; 52,*1,* young individual attached to adult, ×2 (30*); 52,*2a,b,* holotype of *Conularia gracilis,* ×1, and ornament, enlarged (20*).

Family CONULARIOPSIDAE Sugiyama, 1942

Corners of pyramid raised, lacking furrows; faces marked by coarse sinuous longitudinal ridges and by widely spaced transverse folds which may be adventitious. *L. Trias.*

Conulariopsis SUGIYAMA, 1942 [**C. quadrata*]. Characters of family. *L. Trias.,* Japan.

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HYDROZOA—GENERAL FEATURES

By Dorothy Hill and J. W. Wells

GENERAL NATURE AND TYPES OF HYDROZOA

Hydrozoans are either polymorphic, with both polypoid and medusoid forms, or monomorphic and medusoid. Their symmetry is tetramerous or polymerous and radial—any 2 diameters at right angles dividing the animal into similar halves. Their coelenteron is without a stomodaeum or gullet, and it is not divided by projecting ridges or partitions. The mesogloea does not contain cells that have wandered in from either ectoderm or endoderm. Tentacles may be hollow or solid and sex cells ripen in the ectoderm. The oral end of the polyp is elongated, and characteristic of the hydrozoan medusoid is the **velum** or shelf on the inner rim of the umbrella. Exoskeletons occur in some orders and these are either horny or calcareous.

The class may be divided into 7 orders (Trachylinida, Hydroida, Spongiomorphida, Milleporina, Stylasterina, Stromatoporoidea, Siphonophorida) which differ in degree of polymorphism and relative importance of the polypoid and medusoid generations. The trachylinids, regarded by some as the most primitive, are medusae, which as a whole lack a polypoid generation; if one is present, it is minute and attached. The siphonophorids, like the trachylinids, never develop a skeleton but they exhibit marked polymorphism. Because of the diversity of modified medusoid or polypoid individuals of several kinds which compose the swimming or floating siphonophorid colonies, they are regarded commonly as the most specialized group of hydrozoans, although some zoologists consider the polypoid and medusoid kinds to be below the grade of individuals and thus interpret the siphonophorids as the most primitive coelenterates.

Among hydroids the polypoid generation is dominant and usually colonial; the polyps may bud off free medusae, or there may be structures resembling abortive medusae. In the milleporines and stylasterines, which secrete calcareous skeletons, the polypoid colonies have 2 kinds of retractile polyps, whereas the very small medusae perish after a few hours of life during which sex cells are shed. The stromatoporoids and spongiomorphids are extinct orders, but they also seem to have comprised colonies of polyps.

The graptolites, which formerly often were classed as an extinct group of hydrozoans, now are considered to be hemichordates allied to the living pterobranchs.

Hydrozoans with calcareous skeletons are invariably sessile benthonic forms, which seem to flourish better in warm than cold waters. Milleporines and stylasterines are common in Tertiary and Recent reef environments, and the stromatoporoids were characteristic of many Paleozoic and Mesozoic organic reefs. Siphonophores and trachylines are floaters and swimmers, as are the medusoid generations of other orders. The hydroids, being dominantly polypoid, are mostly sessile, and are either benthonic or attached to floating weeds. Most are colonial; a few, such as *Hydra,* are solitary. The latter genus and a few medusoid hydroids are unusual in that they live in fresh water.

Class HYDROZOA Owen, 1843

[Originally included hydroids only; extended by Huxley, 1859, to include siphonophores and trachylines but not milleporines] [=Anoecia Huxley, 1852; Ectocarpen O.Hertwig & R.Hertwig, 1879 (*sine* Ctenophora); Aphacellae Lendenfeld, 1884; Hydromedusae Zittel, 1900 (*non* Vogt, 1851); Hydrozoaria Delage & Hérouard, 1901]

Coelenterates with tetrameral or polymeral radial symmetry; polymorphic, with both polypoid and medusoid forms, or exclusively medusoid; enteron without stomodaeum or nematocysts, and not divided by projecting ridges and partitions; mesogloea noncellular; sex cells ripening in the epidermis; oral end of polyp elongated into a hydranth; medusae almost invariably with velum; exoskeleton, if present, generally chitinous, rarely calcareous. *L.Cam.,-Rec.*

TRACHYLINIDA

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

CONTENTS

The hydrozoan medusae are all morphologically alike, but important differences in their ontogenetic development divide them into 2 natural groups, the Trachylinida and the medusae of the Hydroida. The trachylinids are characterized by a reduction or absence of the polypoid generation, having typically a planula-actinula-medusa life history. In many genera the tentacles of the actinula larva become those of the medusa, and as the bell margin continues to grow after the tentacles have become fully developed, they are "left behind," deeply rooted in the jelly-like mesogloea and springing from the exumbrellar surface of the bell. Though the trachylinids and the medusae of the Hydroida have sense organs structurally similar, the lithocysts of the former contain endodermal lithocytes and statoliths and are, therefore, not comparable with the ectodermal sense organs of the latter. The trachylinids are best regarded as medusiform actinulae which are not homologous with the medusae of the Hydroida, having attained independently a medusiform appearance. Their ontogenetic development indicates that they are the most primitive of living coelenterates.

MORPHOLOGY

The trachylinid medusae are solitary, free-swimming animals of small to moderate size, consisting of a gelatinous bell similar to that of the Scyphomedusae (Fig. 53).

As in that subclass, the upper side of the body is termed **exumbrella,** while the lower side is termed **subumbrella.** The margin of the bell may be either circular or scalloped into **lappets.** An extension of both the exumbrella and the subumbrella, known as **velum,** forms a muscular annular band partly closing the subumbrellar concavity. From the center of the subumbrella there hangs down a cylindrical or quadrangular tube, the **manubrium,** which in some genera may be found at the end of a long projection of the subumbrella, called **pseudomanubrium,** containing extensions of the radial canals. The manubrium opens at its lower extremity into a **mouth** and leads aborally into a central gastric cavity or **stomach.** The manubrium is absent in the Narcomedusina where the mouth opens directly into the capacious stomach. The gastric cavity is typically outpocketed into 4, 8, or 16 radial **stomach pouches.** These give rise to **radial canals,** commonly 4, 6, or 8, leading into a circular **ring canal** running along the margin of the bell which, in its turn, may give rise to numerous **blind centripetal canals** extending toward the summit of the bell. In some genera, however, the ring canal is absent and the radial canals have blind distal ends. The **gonads** occur either in folds or pendent sacs beneath the radial canals or in the floor of the stomach pouches.
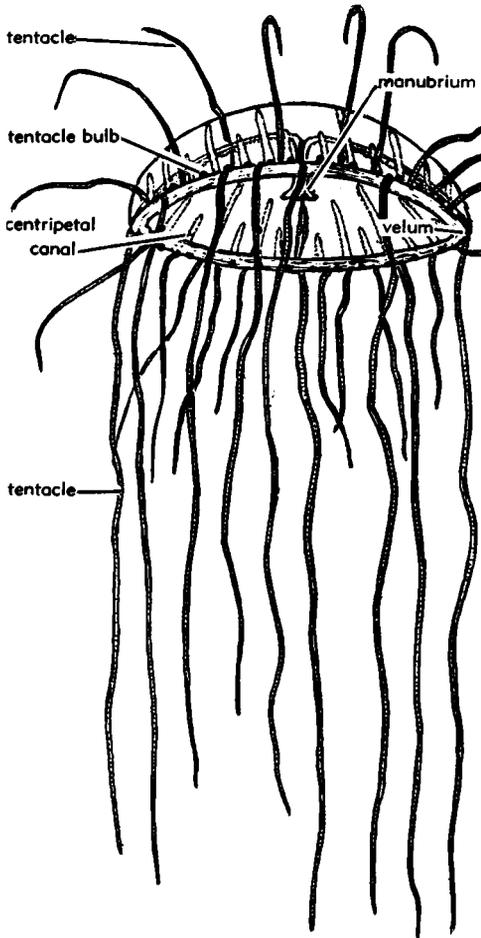
FIG. 53. A living trachylinid, *Olindias*, of the suborder Trachymedusina, showing inverted bowl-shaped form and extended manubrium (pseudomanubrium) at the center of the under (subumbrellar) surface. In addition to long pendent tentacles distributed around the margin, relatively stiff shorter ones project upward (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).

The **tentacles,** of the same or greater number than the radial canals, commonly spring from the exumbrellar surface and may bear **adhesive discs** near their tips. The endodermal core of the tentacles normally continue into the jelly as **tentacular roots,** and the ectoderm of their inner faces may extend on the exumbrella to the bell margin forming thick bands, the **peronia,** which divide the margin into lappets. The **otoporpae** are tracts similar to the peronia, located on the exumbrellar side above the lithocysts. Ocelli

are generally absent but **lithocysts** (organs of equilibrium) of endodermal origin are commonly present, located between the **tentacle bases** and of the same or greater number than the radial canals. **Nematocysts** (nettling or stinging organs) are abundantly distributed on the tentacles, peronia, otoporpae, bell margin and, in certain forms, in streaks ascending the exumbrella.

The radial canals, tentacles, sense organs, gonads, and other structures are typically arranged upon a plan of tetramerous symmetry. The 4 main radii, corresponding to the 4 basic radial canals and tentacles, are termed **perradii;** the 4 radii at 45° position between the perradii are called **interradii;** those located midway between perradii and interradii are known as **adradii.**

DISTRIBUTION

Very few fossil records of unquestionable trachylinid medusae are known. These belong in the genus *Kirklandia* from the Lower Cretaceous of Texas and Germany. In addition, 7 genera are now tentatively placed in this order, 5 of them having uncertain family relationships. With the exception of a Lower Cambrian form from South Australia, they are European genera ranging in age from Middle Jurassic to Early Cretaceous.

CLASSIFICATION

The number of fossil genera in each of the following categories is tabulated after the corresponding taxa. A question mark preceding a numeral (as ?7) indicates number of genera tentatively classified.

Main Divisions of Trachylinida

Trachylinida *(order)* (1+?7). *?L.Cam., ?M.Jur., U.Jur.-Rec.*
  Trachymedusina *(suborder)* (1+?1). *?L.Cam., ?M.Jur., U.Jur.-Rec.*
    Olindiadidae. *Rec.*
    Petasidae. *Rec.*
    Limnocnididae. *Rec.*
    Pectyllididae. *Rec.*
    Kirklandiidae (1). *?M.Jur., L.Cret.*
    Trachynematidae (?1). *?L.Cam., Rec.*
    Geryoniidae. *Rec.*
  Narcomedusina *(suborder)* (?1). *?U.Jur., Rec.*
    Solmariidae. *Rec.*
    Cuninidae (?1). *Rec.*
    Aeginidae. *Rec.*
  ?Trachylinida incertae sedis (5). *L.Cam.-L.Cret.*

SYSTEMATIC DESCRIPTIONS

Order TRACHYLINIDA Haeckel, 1877

[*nom. correct.* PEARSE, 1936 (*pro* Trachylinae HKL., 1877)]

Hydrozoid medusae having sense organs consisting of statocysts and tentaculocysts of ectodermal origin; tentacles usually inserted above bell margin, springing from exumbrellar surface; with reduced or absent polypoid generation, commonly developing from actinula larvae either directly or by budding. *?L.Cam., ?M.Jur., U.Jur.-Rec.*

Living trachilinids are inhabitants of the open ocean of world-wide distribution, more frequent in warmer seas than in cold waters. Exceptions are 2 fresh-water genera (Fig. 53).

Suborder TRACHYMEDUSINA Haeckel, 1866

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Trachymedusae HKL., 1866)] [=Trachomedusae HKL., 1879]

Margin of bell entire, not cleft into lappets; radial canals 4, 6, or 8; gonads commonly developed upon radial canals; tentacles usually solid. *?L.Cam., ?M.Jur., L. Cret.-Rec.*

Family OLINDIADIDAE Haeckel, 1879

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Olindiadae HKL., 1879)]

Some or all tentacles projecting from sides of bell above margin, not grouped in clusters, with adhesive discs; gonads linear, saclike or folded upon the 4 or 6 radial canals. *Rec.*

Olindias F.MÜLLER, 1861 [**O. sambaquiensis*]. *Rec.*——FIG. 53. *O.* sp., Bermuda (HYMAN). Several other living genera.

Family PETASIDAE Haeckel, 1879

Tentacles without adhesive disc; radial canals 4; gonads linear or saclike; lips 4. *Rec.*

Petasus HAECKEL, 1879 [**P. atavus*]. *Rec.* Several other living genera, including the fresh-water *Craspedacusta* LANKESTER, 1880.

Family LIMNOCNIDIDAE Mayer, 1910

Tentacles numerous, hollow, not in clusters, without adhesive disc; lithocysts numerous, on exumbrellar side of velum; radial canals 4 or 6; gonads diffuse in ectoderm of stomach wall; mouth round. *Rec.*

Limnocnida GÜNTHER, 1893 [**L. tanganjicae*]. *Rec.* Only known genus (fresh-water).

Family PECTYLLIDIDAE Haeckel, 1879

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Pectillidae HKL., 1879)] [*ex* Pectyllis HKL., 1879 (=*Ptychogastria* ALLMAN, 1878)] [=Ptychogastridae MAYER, 1910]

Numerous more or less isolated clusters of tentacles, some with adhesive disc; numerous free lithocysts; radial canals 8; stomach 8-lobed; lips 4. *Rec.*

Ptychogastria ALLMAN, 1878 [**P. polaris* (=*Pectyllis arctica* HAECKEL, 1879)] [=*Pectyllis, Pectiss, Pectanthis* HKL., 1879]. *Rec.* Only known genus.

Family KIRKLANDIIDAE Caster, 1945

Subumbrellar mid-field lobate, typically with 8 adradial sulci bifurcating near periphery, originating 4 perradial and 4 interradial large, petalate insert lobes (stomach pouches) and 8 adradial, smaller, triangular exsert lobes; radial canals 8 (4 perradial, 4 interradial), each with bulging outpocketing genital sac containing paired gonads; mouth quadrate, functional; manubrium very short; oral arms absent; peripheral area imperfectly known; ?tentacles ?8, rodlike, covered with ovate pustules (?nettling structures); exumbrellar mid-field typically with 8 radiating shallow sulci. *?M.Jur., L.Cret.*

Kirklandia CASTER, 1945 [**K. texana*]. Characters of family. *?M.Jur.*, Ger., *L.Cret.*, USA.——FIG. 54,1. **K. texana*, L.Cret., Tex.; *1a*, holotype, subumbrellar surface; *1b*, paratype, subumbrellar surface; *1c*, subumbrellar surface of another specimen; *1d*, paratype, exumbrellar surface; *1e*, side view of another specimen; all ×0.75; *1f*, ?nettling structures of tentacle, ×3.5 (CASTER).——FIG. 55. *?Kirklandia* sp., M.Jur., Ger.; *1*, subumbrellar surface; *2*, *ibid.*, another specimen, both ×1 (LÖRCHER).

Family TRACHYNEMATIDAE Gegenbaur, 1856

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Trachynemidae GEGEN., 1856)] [*ex* Trachynema GEGEN., 1856 (=*Rhopalonema* GEGEN., 1856)] [=Aglauridae HAECKEL, 1879]

Tentacles without adhesive disc; radial canals 8, simple; ring canal simple. *?L. Cam., Rec.*

Rhopalonema GEGENBAUR, 1856 [**R. velatum* (=*Trachynema ciliatum* GEGEN., 1856)] [=*Trachynema* GEGEN., 1856; *Calyptra* LEUCKART, 1856]. *Rec.* Numerous living genera.

?Beltanella SPRIGG, 1947 [**B. gilesi*]. Exumbrellar impression circular; outer ring (?velum) con-

centrically striated, narrow; inner field (?stomach) large, circular, with 2 central concentric grooves (?oral structures); intermediate annular zone crossed by 4 paired grooves 90° apart (?radial canals), with 2 evenly spaced circular markings in each quadrant (?gonads); ring canal and tentacles absent. *L.Cam.*, S.Austral. SPRIGG compared the only known impression with the living genus *Rhopalonema.*——FIG. 56. **B. gilesi; 1a,* reconstruction of umbrella with section removed, ×0.5; *1b,* diagrammatic sketch of subumbrellar surface, ×0.55 (SPRIGG); *2,* holotype, ×0.55 (SPRIGG).

Family GERYONIIDAE Eschscholtz, 1829

Radial canals 4 or 6; gonads flat, expanded, leaflike; stomach upon gelatinous peduncle; ring canal giving rise to blindly ending centripetal canals. *Rec.*

Geryonia PÉRON & LESUEUR, 1809 [**G. proboscidalis*]. *Rec.* Other living genus: *Liriope* LESSON, 1843.

Suborder NARCOMEDUSINA Haeckel, 1879

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Narcomedusae HKL., 1879)]
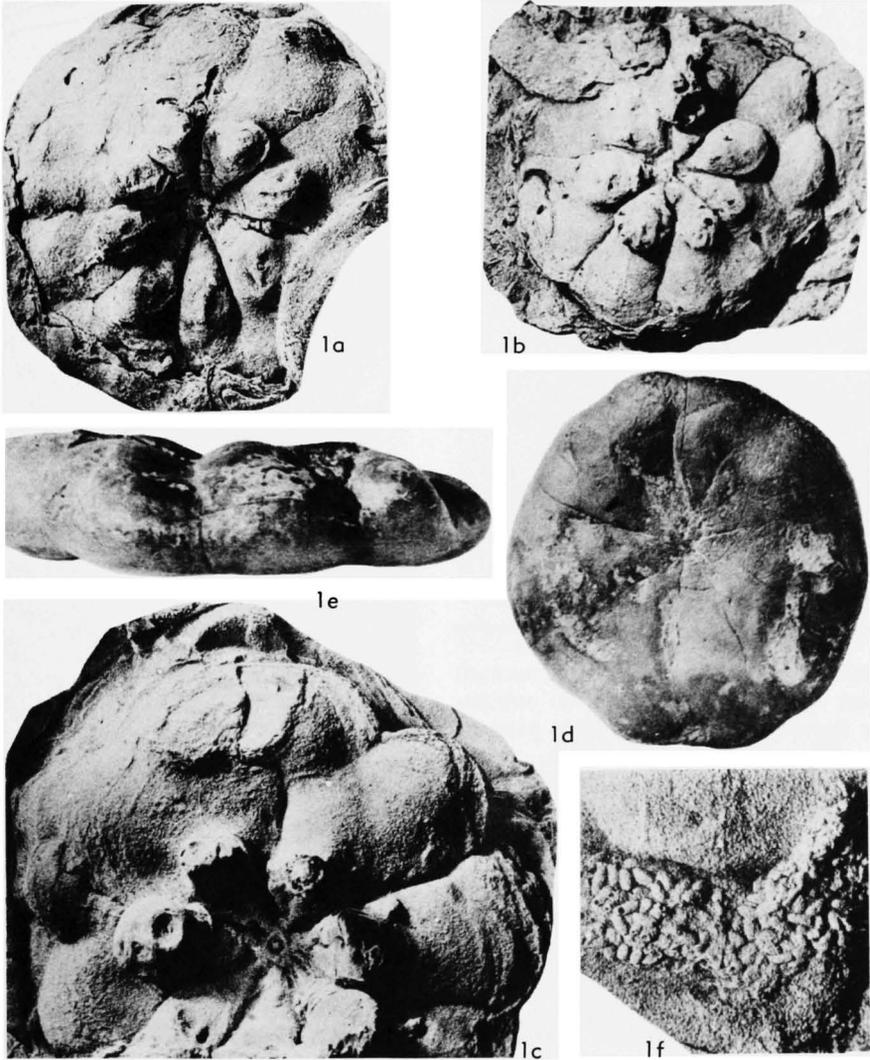
Kirklandia

FIG. 54. Trachymedusinaa: *Kirklandia texana*, L.Cret., Tex.; *1a-e,* ×0.75; *1f,* ×3.5 (CASTER).
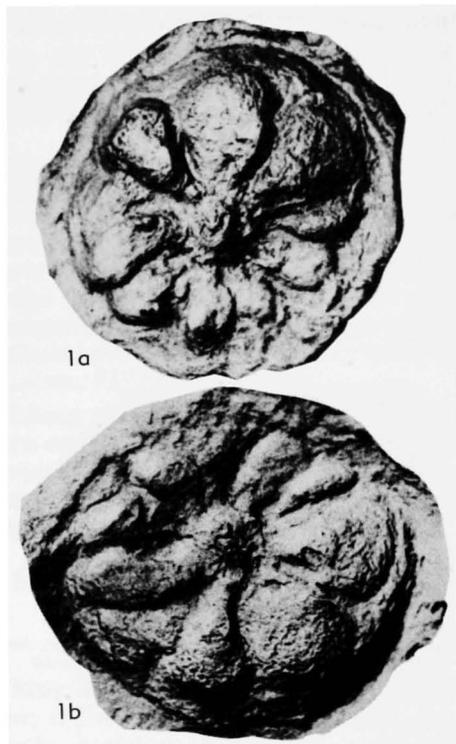
FIG. 55. Trachymedusina: *?Kirklandia* sp., M.Jur. Ger.; subumbrellar side of 2 specimens, ×1 (LÖRCHER).

Margin of bell scalloped by peronia; gonads borne in floor of stomach. *?U.Jur., Rec.*

Family SOLMARIIDAE Haeckel, 1879

[*nom. correct.* HARRINGTON & MOORE, herein (*pro* Solmaridae HKL., 1879)] [=Peganthidae HAECKEL, 1879]

Stomach circular, simple, without stomach pouches; saccules may arise from subumbrellar floor of stomach; all other parts of gastrovascular system lacking. *Rec.*

Solmaris HAECKEL, 1879 [**S. godeffroyi*]. *Rec.* Other living genus: *Pegantha* HKL., 1879.

Family CUNINIDAE Broch, 1929

Central stomach giving rise to simple, undivided pouches; marginal scallops, peronia and tentacles of same number (8 or more) as pouches. *?U.Jur., Rec.*

Cunina ESCHSCHOLTZ, 1829 [**C. globosa*]. *Rec.* Other living genera: *Solmissus, Cunoctantha* HAECKEL, 1879.
?Acalepha BEYRICH, 1849 [**A. deperdita*] [=*Craspedonites* HAECKEL, 1865 (obj.); *Trachynemites* HKL., 1869 (obj.)]. Subumbrellar im-

pression with 2 smooth concentric outer rings, inner rosette with 8 radial segments and central circular area; oral arms absent; tentacles ?absent. HAECKEL interpreted the central area as stomach and mouth, the groove along the periphery of rosette as ring canal, the internal outer ring as the umbrellar margin and the external ring as a furrow in the matrix. BRANDT regarded the 2 outer rings as annular folds in the umbrella developed during entombment and the inner structure as a central stomach of circular outline giving rise to 8 undivided stomach pouches. MAYER accepted
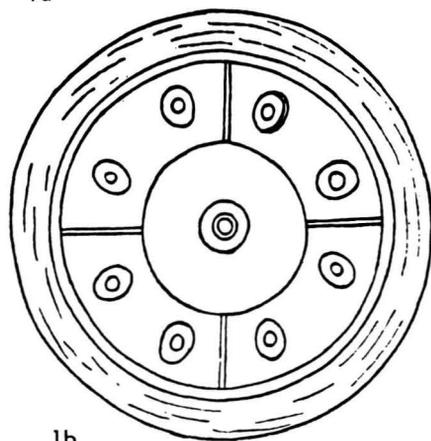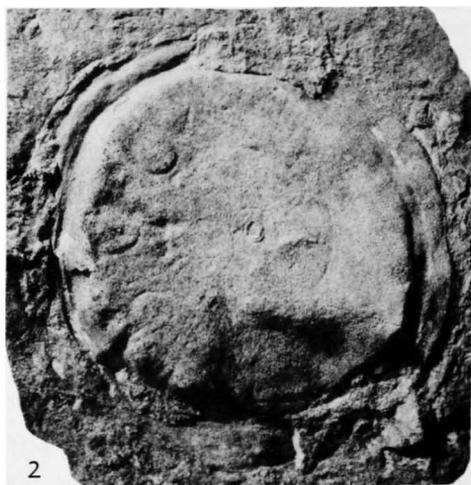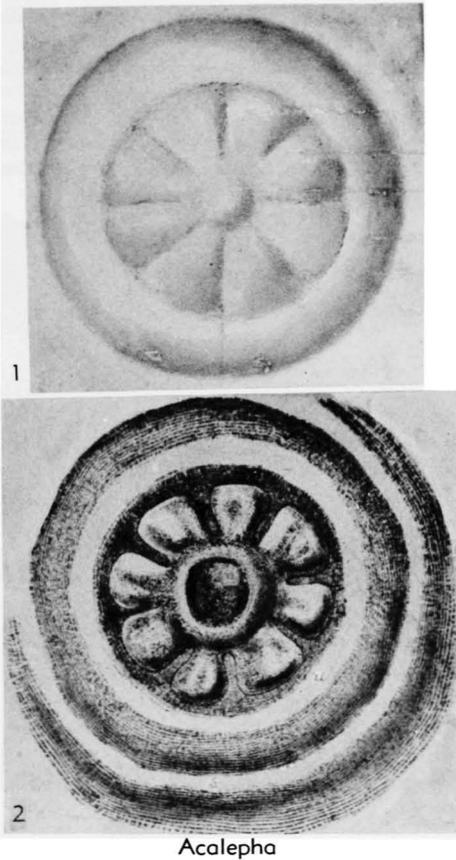

Beltanella

FIG. 56. Trachymedusina: *Beltanella gilesi*, L.Cam., S.Austral.; *1*, section and subumbrellar side (reconstr.); *2*, holotype, ×0.55 (SPRIGG).

Acalepha

FIG. 57. Narcomedusina: *Acalepha deperdita*, U.Jur., Ger.; 2 specimens, ×0.7, ×0.25 (HAECKEL, WAL-COTT).

lobes. HAECKEL interpreted the central area as stomach and mouth surrounded by 8 gonads (inner lobes), the radial grooves marking off the 8 outer lobes as radial canals, the periphery of the outer lobes as the subumbrellar margin cleft into 8 lappets and bearing a ring canal, the internal outer ring as a fold of the umbrella developed during entombment, and the external ring as a furrow in the matrix. Accepted here is the view of CASTER, who regarded the 8 larger lobes as stomach pouches separated by narrow sulci (not radial canals), bearing genital sacs (inner lobes). *U.Jur.*, Ger.——FIG. 58. **A. antiquus* (HAECKEL); holotype, ×0.375 (HAECKEL).

Atollites MAAS, 1902 [**A. zitteli*]. Body discoidal, of circular outline; mid-field with small, circular, smooth depression (?mouth), encircled by slightly convex annular zone crossed by 12 to 14 raised,
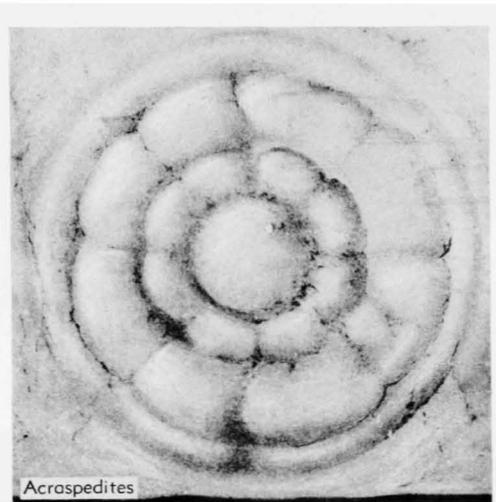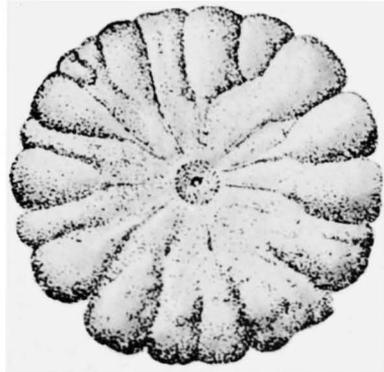

Acraspedites

FIG. 58. Incertae sedis: *Acraspedites antiquus*, U.Jur., Ger.; holotype, ×0.375 (HAECKEL).

BRANDT's interpretation and compared the fossils with the living genus *Cunoctantha*. *U.Jur.*, Ger. -——FIG. 57. **A. deperdita; 1*, plaster impression, according to HAECKEL, ×0.7 (HAECKEL); *2*, plaster impression of a different specimen, according to BRANDT, ×0.25 (WALCOTT).

Family AEGINIDAE Haeckel, 1879

[=Cunanthidae HKL., 1879]

Central stomach giving rise to bifurcate pouches; 2 or 4 pouches between successive tentacles. *Rec.*

Aegina ESCHSCHOLTZ, 1829 [**A. citrea*]. *Rec.* Several living genera, including *Aeginopsis* BRANDT, 1836, and *Solmundella* HAECKEL, 1879.

?TRACHYLINIDA INCERTAE SEDIS

Acraspedites HAECKEL, 1869 [**Medusites antiquus* HKL., 1865]. Subumbrellar impression with 2 smooth, concentric outer rings, large circular central area and 2 intermediate rings with 8 radial


Atollites

FIG. 59. Incertae sedis: *Atollites zitteli*, L.Cret., Ger.; holotype, ×1.5 (KIESLINGER).

narrow radial bands (?radial canals); external
zone with 12 to 14 pyriform lobes, wider and
thicker at periphery, sharply separated by deep
radial sulci, some partly split by supplementary
radial grooves. Both MAAS and KIESLINGER re-
garded *Atollites* as a collaspidid scyphomedusa. As
here interpreted, the remains represent the central
subumbrellar area of a trachylinid medusa dis-
playing 12 to 14 radial canals bearing centrifugal
genital sacs. *L.Cret.*, Ger.——FIG. 59. **A. zitteli;*
holotype, ×1.5 (MAAS).

Ediacaria SPRIGG, 1947 [**E. flindersi (=Tateana
inflata* SPRIGG, 1949; *Cyclomedusa radiata* SPRIGG,
1949] [=*Tateana* SPRIGG, 1949]. (1) SUBUM-
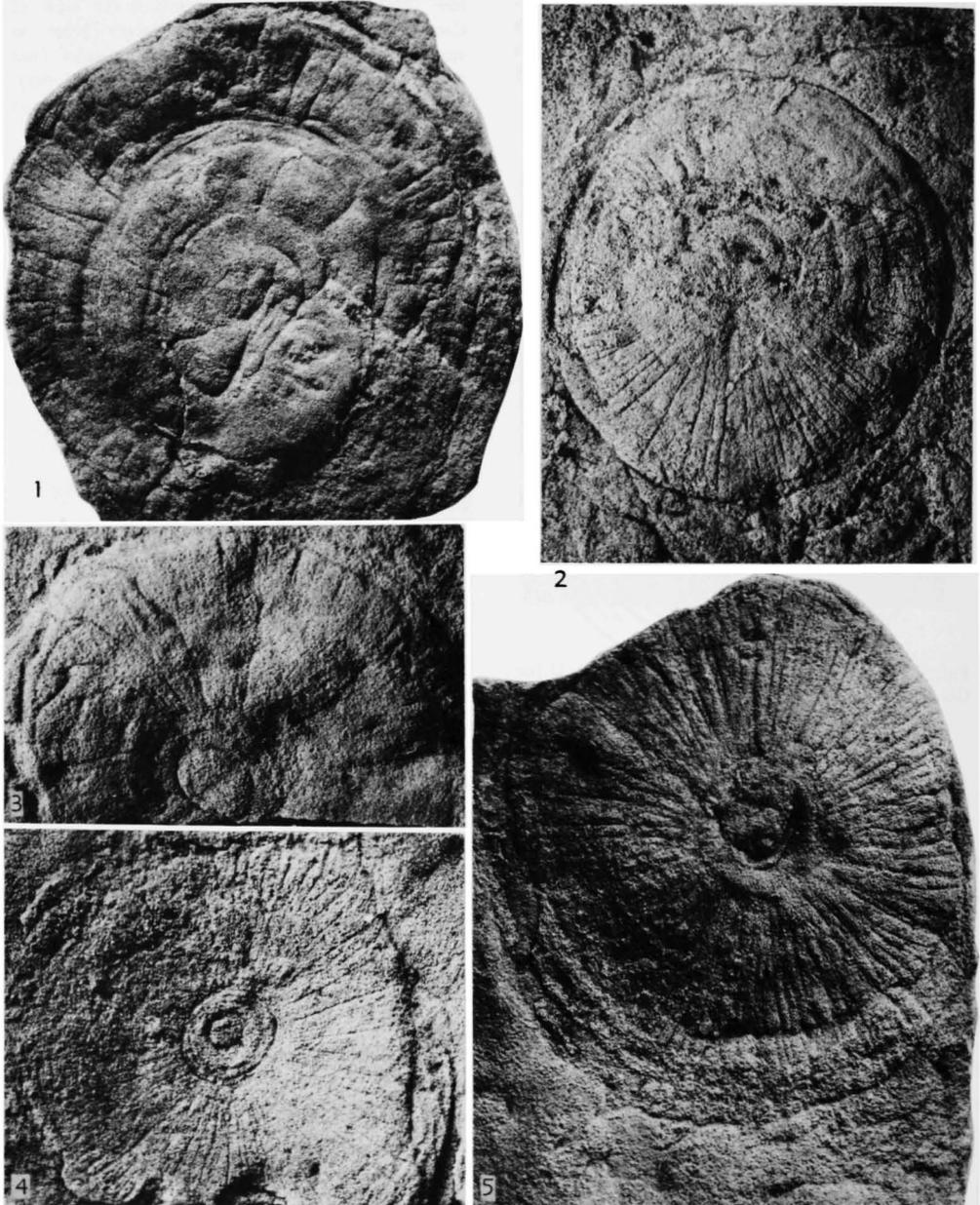
Ediacaria

FIG. 60. Incertae sedis: *Ediacaria flindersi*, L.Cam., S.Austral.; *1*, holotype, ×0.7; *2-5*, exumbrellar im-
pressions of other specimens assigned to other genera and species by SPRIGG but here referred to *E.
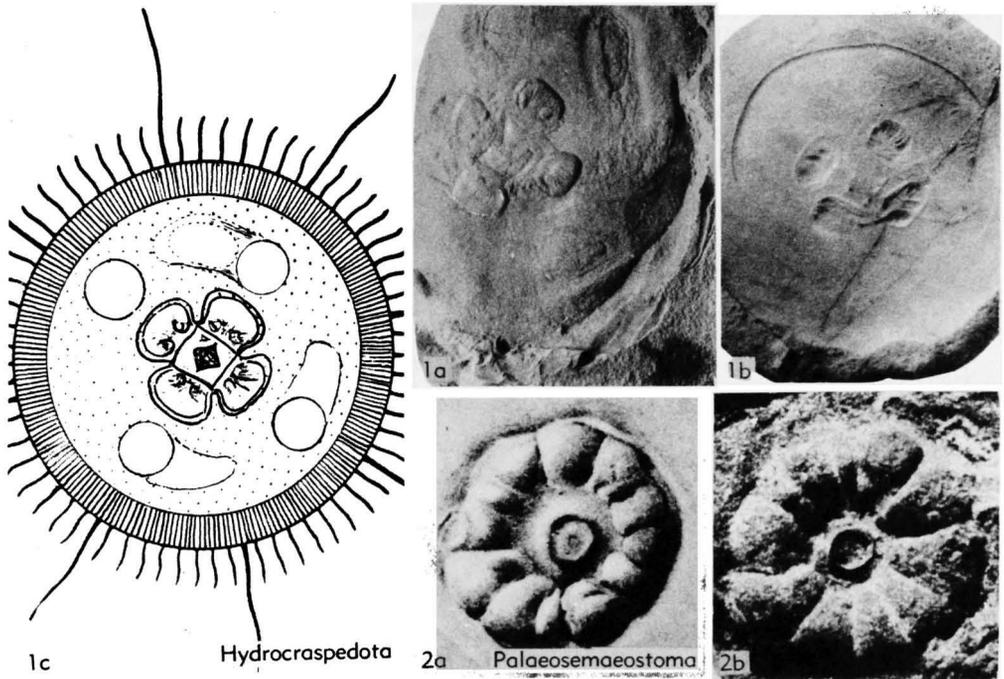flindersi*, ×8.1, ×8.3, ×1.1, ×1.3 (SPRIGG).

Fig. 61. Incertae sedis: Jurassic trachylinids. *1, Hydrocraspedota mayri*, U.Jur., Ger.; *1a,b*, holotype and young specimen, ×0.35; *1c*, subumbrellar surface and tentacles (reconstr.), ×0.25 (KOLB). 2, *Palaeosemaeostoma geryonides*, M.Jur., Ger.; holotype and another specimen, ×1, ×0.5 (VON HUENE, KIESLINGER).

BRELLAR IMPRESSION (type of *E. flindersi*). Circular; margin ?entire, without notches; outer annular zone with numerous radial grooves, irregularly distributed, of unequal length and depth, some bifurcating centripetally, crossed by few irregular concentric rugae; intermediate annular zone somewhat inflated, with few, indistinct radial grooves; imperfectly separated from central midfield by annular groove; mid-field with ?ring of ?8 small circular knobs (only 4 displayed) and asymmetrical triangular lobe attached to center and spreading outward. (2) EXUMBRELLAR IMPRESSION (type of *Tateana inflata* and of *Cyclomedusa radiata*). Circular, with circular central area (?stomach) marked by one or several concentric grooves and wide outer ring with numerous radial grooves, irregularly distributed and increasing in number toward periphery by implantation and bifurcation, crossed by several coarse concentric rugae. SPRIGG interpreted the radial grooves as radial canals, the outermost concentric ruga as epimarginal ring canal, the triangular lobe in the subumbrellar midfield as a flattened manubrium, and the small circular knobs as outpocketing genital sacs. As here interpreted, the outer annular zone of the subumbrellar surface represents the impression of a velum with numerous radial shrinkage furrows due to desiccation during entombment, the ?8

central knobs are regarded as centripetal gonads (?located upon radial canals, traces of which may be represented by the radial grooves of the intermediate zone), and the triangular lobe as the impression of a flattened, campanulate manubrium. *Tateana inflata* and *Cyclomedusa radiata* are here regarded as exumbrellar impressions of *Ediacaria flindersi*. L.Cam., S.Austral.——FIG. 60. *E. flindersi; 1*, holotype, ×0.7; *2*, exumbrellar impression (type of *Tateana inflata*), ×8.1; *3*, another exumbrellar impression (type of *T. inflata*), ×8.3; *4*, exumbrellar impression (type of *Cyclomedusa radiata*), ×1.1; *5*, another exumbrellar impression (type of *C. radiata*), ×1.3 (SPRIGG).

Hydrocraspedota KOLB, 1951 [*H. mayri*]. Margin circular, entire; velum narrow, with 600 to 800 fine radial striae (?impressions of statocysts); gonads 4, elliptical, perradial, centrifugal (observed only in adult specimens); mid-field with central quadrate mouth, short manubrium and 4 perradial reniform impressions of mouth tentacles, each with whirl-like bunch of raised striae at both ends; marginal tentacles ?not preserved. KOLB compared the impressions with the living freshwater genus *Craspedacusta*. U.Jur., Ger.——FIG. 61,1. *H. mayri; 1a*, holotype, mature individual, ×0.3; *1b*, young individual, ×0.35; *1c*, reconstructions of subumbrellar surface, mature individual, ×0.25 (KOLB).

Palaeosemaeostoma Rüger, 1933 [*pro Medusa* Wagner, 1932 (*non* Linné, 1758)] [**Medusina geryonides* von Huene, 1901 (=*Medusa gorgonoides* Wagner, 1932)]. Body depressedly convex; ?subumbrellar surface with rosette of 11 or 12 pillowy sectors sharply defined by deep, narrow grooves; center of disc with depressed circular (?mouth) area encircled by sharp, raised narrow collar; lobation extending around border of disc; ?exumbrellar side with central hollow stem. *M.Jur.*, Ger.——Fig. 61,*2.* **P. geryonides* (v.Huene); *2a,* holotype, ×1 (von Huene); *2b,* another specimen, ×0.5 (Kieslinger).

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MEDUSAE OF THE HYDROIDA

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

CONTENTS

The medusae of the Hydroida obviously do not constitute a separate order of Coelenterata, as they represent the completely evolved, sexual generation sprung by budding from the asexual polyps. However, the hydroid generation from which many medusae presumably came has not been definitely identified. Moreover, the hydroid and medusoid generations may evolve independently in such manner that very similar medusae are budded from quite different hydroid types and vice versa. These difficulties make it necessary to use a special classification for the medusae of the Hydroida side by side with that developed for the hydroids, and it must be apparent that the medusoid classification becomes imperative and unavoidable when the corresponding polyps are unknown. The alternative would be to classify such medusae as incertae sedis within the Hydroida until their polyps are identified, but it must be obvious that in this case the fossil medusae would remain forever in such a category.

MORPHOLOGY

The medusae of the Hydroida are morphologically similar to the trachylinids, consisting of a gelatinous bell typically dome-, bowl-, or saucer-shaped (Fig. 62). As in the trachylinids, the upper side of the bell is termed **exumbrella**, the lower side being known as **subumbrella**. The margin of the bell is always circular and unscalloped. A **velum** is typically present, as well as a **manubrium**, which in some genera is found
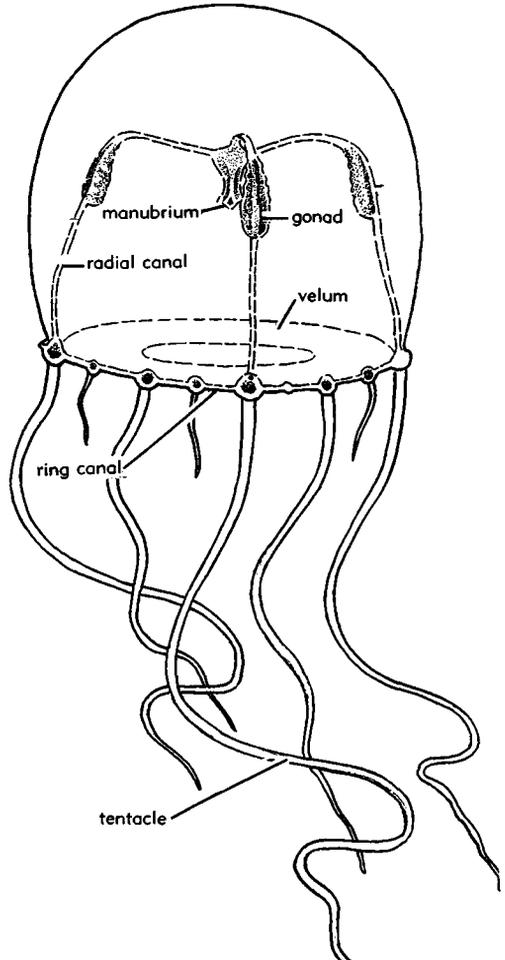

Fig. 62. Calyptoblastina: *Thaumantias maeotica,* Rec., ×5 (Mayer).

at the end of a long **pseudomanubrium.** As in the trachylinids, the manubrium opens at its lower end in a **mouth** and leads aborally into a central gastric cavity or **stomach.** The stomach gives rise to **radial canals,** typically 4 or some multiple thereof, leading into a circular **ring canal** running along the margin of the bell. The **gonads** are found either encircling the manubrium or upon the radial canals.

The bell margin bears **tentacles,** typically 4 or some multiple thereof. In some genera they are very numerous, while in others only 2, 1, or none are developed. The **tentacle bases** commonly bear **ocelli** sensitive to light, and the subumbrellar side of the velar base may bear **statocysts** (sense organs of equilibrium) of ectodermal origin. **Nematocysts** are abundantly distributed on the manubrium, bell margin, exumbrella, and tentacles.

The medusae of the Hydroida usually display marked tetramerous symmetry. The terms **perradii, interradii,** and **adradii** are used in the same sense as applied to the Trachylinida.

DISTRIBUTION

Fossil medusae of the Hydroida seem exceedingly rare. None has been unquestionably identified as belonging in this order and only 2 forms, one from the Lower Cambrian of South Australia, the other from the Upper Pennsylvanian of Nebraska, are here tentatively classified as such.

CLASSIFICATION

The medusae of the Hydroida have received collective designations which, of course, have no status in coelenterate classifications, being synonyms of other widely used terms. The name Hydromedusae, employed by MAYER in 1910, as well as the

older names Cryptocarpae ESCHSCHOLTZ, 1829, Gymnopthalmae FORBES, 1848, and Craspedota GEGENBAUR, 1856, are comprehensive designations covering all the non-scyphozoan medusae and, therefore, include the Trachylinida, here classed separately. The more restricted term Leptolinae HAECKEL, 1879, on the other hand, is exactly equivalent to the order Hydroida and the 2 recognized suborders of Leptolinae (Anthomedusae HAECKEL, 1879, and Leptomedusae HAECKEL, 1866) are the exact counterparts of the suborders Gymnoblastina and Calyptoblastina, respectively, of the Hydroida. Clearly, then, both classifications are equivalent down to the level of suborders, and it is only in the taxa of family and lesser rank that important differences appear. It is debatable which of the 2 parallel classifications should be regarded as the natural one and receive preference, but the fact that the medusoid classification applies to completely evolved sexual forms while the hydroid classification is based on asexual polyps regarded as persistent larval stages, suggests that the former deserves the priority currently given to the latter.

The number of known fossil genera in each category is recorded after the corresponding taxa. The question mark (as ?2) indicates tentative classification.

Main Divisions of Hydroid Medusae

Hydroida (Leptolinida) *(order)* (?2). *L.Cam.,*   *?Penn., Rec.*
  Gymnoblastina (Anthomedusina) *(suborder)* (?1).   *?Penn., Rec.*
   Sarsiidae. *Rec.*
   Cladonematidae. *Rec.*
   Oceaniidae (?1). *?Penn., Rec.*
  Calyptoblastina (Leptomedusina) *(suborder)* (?1).   *?L.Cam., Rec.*
   Thaumantiadidae (?1). *?L.Cam., Rec.*
   Eucopidae. *Rec.*
   Aequoreidae. *Rec.*

SYSTEMATIC DESCRIPTIONS

Medusae of the Order HYDROIDA

[=Leptolinae HAECKEL, 1879]

Veiled medusae developed through alternation of generations from Gymnoblastina or Calyptoblastina hydroids; tentacles grow outward from bell margin after bell has de-

veloped; ocelli and otocysts, when present, of ectodermal origin. *?L.Cam., ?Penn., Rec.*

The medusae of the Hydroida are inhabitants of coastal waters, rarely seen in the open ocean far from land, for they cannot maintain themselves in situations unsuited to the growth of their hydroids.

Medusae of the Suborder GYMNOBLASTINA

[=Oceanidae Gegenbaur, 1856 (*partim*); Anthomedusae Haeckel, 1879]

Medusae with gonads in the ectoderm of the manubrium; marginal otocysts and sensory clubs absent. *?Penn., Rec.*

Family SARSIIDAE Forbes, 1848

[*nom. correct.* Harrington & Moore, herein (*pro* Sarsiadae Forbes, 1848)] [=Codomidae Haeckel, 1879]

Gonads ringlike, encircling the manubrium; radial canals 4 to 6, simple; tentacles simple; mouth without oral tentacles and without prominent lips. *Rec.*

Sarsia Lesson, 1843 [*S. tubulosa*]. *Rec.* Numerous other genera.

Family CLADONEMATIDAE Gegenbaur, 1856

[*nom. correct.* Harrington & Moore, herein (*pro* Cladonemidae Gegenbaur, 1856)]

Marginal tentacles feathered or branched; radial canals 4 or more, simple or branched;

FIG. 63. Gymnoblastina: *Crucimedusina walcotti,* U.Penn., Nebr.; *1a,b,* subumbrellar and exumbrellar sides of holotype, ×0.34 (Barbour).

gonads ringlike, encircling stomach or segregated upon interradial and adradial sides of manubrium or developed in brood pouch above stomach. *Rec.*

Cladonema Dujardin, 1843 [*C. radiatum*]. *Rec.* Several other living genera.

Family OCEANIIDAE Eschscholtz, 1829

Marginal tentacles single or in clusters; simple; gonads 4 or 4 pairs, isolated upon interradial or adradial sides of stomach; mouth with 4 lips. *?Penn., Rec.*

Oceania Péron & Lesueur, 1809 (*sensu* Kölliker, 1853) [*O. armata* Kölliker, 1853]. *Rec.* Numerous other genera.

?Crucimedusina Harrington & Moore, 1955 [*Medusina walcotti*, Barbour, 1914]. Bell pyramidal-conical; subumbrella slightly concave, quadrangular in outline, with interradial rounded angles and perradial concave sides; mouth cruciform, large; exumbrella pyramidal-conical, with 4 rounded ridges meeting at apex and 4 slightly concave sides; surface marked by concentric rugae. *U.Penn.,* Nebr. The fossils may be compared with the living genus *Bougainvillia* Lesson, 1836.——Fig. 63. *C. walcotti* (Barbour); *2a,b,* holotype, subumbrellar and exumbrellar views, ×34 (Barbour).

Medusae of the Suborder CALYPTOBLASTINA

[=Leptomedusae Haeckel, 1866]

Medusae with gonads upon radial canals; lithocysts, when present, of ectodermal origin. *?L.Cam., Rec.*

Family THAUMANTIADIDAE Gegenbaur, 1856

[*nom. correct.* Harrington & Moore, herein (*pro* Thaumantiadae Gegenbaur, 1856)] [=Cannotidae Haeckel, 1879]

Lithocysts present; gonads upon or extending outward over radial canals, not confined exclusively within walls of stomach. *?L.Cam., Rec.*

Thaumantias Eschscholtz, 1829 (*sensu* Mayer, 1910) [*Laodicea cellularia* A.Agassiz, 1865]. *Rec.* ——Fig. 62. *T. maeotica,* Rec.; ×5 (Mayer). Numerous other genera.

?Protodipleurosoma Sprigg, 1949 [*P. wardi*]. Exumbrellar impression circular; outer ring (?velum) concentrically striated, wide; mid-field large, circular, with ovoid, unevenly constricted lobate central area (?stomach) and irregularly developed radial grooves (?radial canals) branched nondichotomously; primary grooves strong, reaching submarginal groove (?ring canal), giving rise to shorter grooves by branching near base. *L.Cam.,*
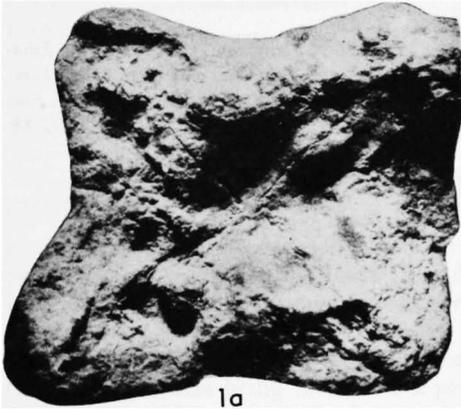
FIG. 64. Calyptoblastina: *Protodipleurosoma wardi,* L.Cam., S.Austral.; holotype, ×0.8 (SPRIGG).

S.Austral. SPRIGG compared the fossil with the living genus *Dipleurosoma* BOECK, 1866.——FIG. 64. **P. wardi;* holotype, ×0.8 (SPRIGG).

Family EUCOPIDAE Gegenbaur, 1856

Lithocysts present; radial canals less than 8; gonads developed upon radial canals. *Rec.*

Eucope GEGENBAUR, 1856 (*non* L.AGASSIZ, 1862) [**Thaumantias globosa* FORBES, 1848]. *Rec.* Numerous other genera.

Family AEQUOREIDAE Eschscholtz, 1829

Otocysts present; radial canals 8 or more. *Rec.*

Aequorea PÉRON & LESUEUR, 1809 [**A. forskalea*]. *Rec.* Several other genera.

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HYDROIDA AND SPONGIOMORPHIDA

By Dorothy Hill and J. W. Wells

CONTENTS

HYDROIDA

MORPHOLOGY

The solitary hydroid polyp, divisible into the attached base, stalk, and main body region or **hydranth,** is attached either by a **pedal disc** or by rootlike holdfasts (Fig. 6). In colonial forms, stolons or rhizomes extended over the substratum, as either a branching or anastomosing tangle, the anchoring **hydrorhiza** being fused into a peridermal mat with peridermal spines projecting up among the polyp bases; from this arises either the **hydrocaulus** (or main stalk) (Figs. 9, 65) of an arborescent colony, or the subequal single stalks **(caulomes)** of a matlike colony. The hydrocaulus is usually simple but may be fascicled (polysiphonic) (Fig. 66), that is, covered by stolons from the hydrorhizae or by branches from below. Four types of budding occur: (1) **hydrorhizal,** in which polyps spring singly from stolons of the hydrorhiza or mat or from a group of parallel stolons projecting vertically as a bundle (rhizocaulome); (2) **monopodial with terminal hydranths** (Fig. 67), giving rise in many gymnoblasts to racemose branching in which the stems of all buds

have a growing point just below the terminal hydranth for production of one new hydranth; (3) **monopodial with terminal growing points** (Fig. 68), in higher calyptoblasts with tip of the hydrocaulus and of each branch a growing point, just behind which new zooids appear; and (4) **sympodial** (Fig. 69), the hydranth stems in lower calyptoblasts having no growth zone, each successive bud overlapping its parent hydranth so as to produce **cymose branching.**

Stolons, caulomes, and hydrocaulus of many forms are enclosed in a chitinous or in some forms a calcareous **periderm** transversely wrinkled near branching points. This is the only part known fossilized. In tubularian gymnoblasts, the periderm does not cover any part of the hydranth or gonads (Fig. 6,*1a*), but in calyptoblasts, a chitinous cuplike **hydrotheca** (Fig. 70) may protect the hydranth and a gonotheca the gonads; where protective zooids of different size and shape from the hydranths are developed, **dactylothecae,** usually much smaller than the hydrothecae, form over them. These thecae are marked off from the stems by a constriction or **shelf** (diaphragm) of periderm. The hydrothecae may be sessile and

may be closed by a lid (**operculum**) with one to 4 parts.

The medusoids of the Hydroida are small animals without periderm and therefore unlikely to be found as fossils. They differ from the Scyphozoa but resemble the siphonophores and trachylines in having a velum or inner shelf around the rim of the umbrella· They are solitary and free-swimming, with form of a gelatinous bowl- or bell-shaped umbrella from whose rim and concave subumbrellar surface the principal parts depend (Fig. 6, 2a). Most of them
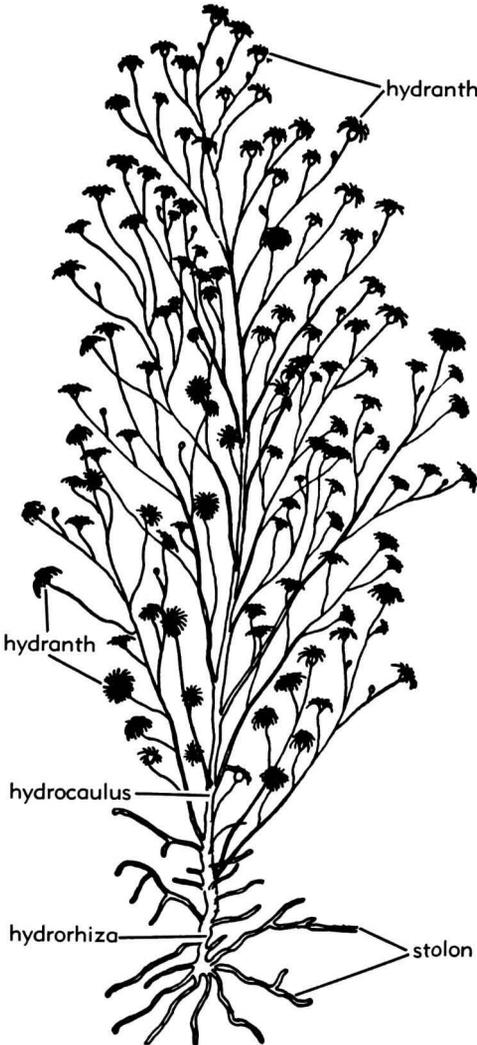

Fig. 65. A gymnoblastic hydroid colony, *Eudendrium*, showing monopodial growth with terminal hydranths (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).
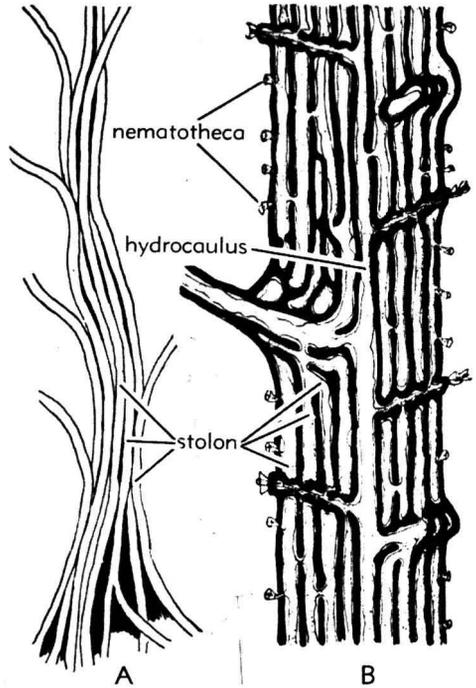

Fig. 66. Structures in hydroid colony growth. *A, Eudendrium*, with simple type of fascicled stem composed of parallel stolons. *B, Plumularia*, with complicated type of fascicled stem, with true hydrocaulus in center encircled by stolons (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).

have perfect tetrameral radial symmetry. From the center of the subumbrellar surface hangs the **manubrium,** which is a cylindrical or quadrangular tube opening directly into the gastrovascular cavity and bearing the mouth. The manubrium commonly is surrounded by a ring of tentacles heavily loaded with nematocysts at their outer ends. The gastrovascular cavity contracts into 4 **radial canals** (in some forms, into 6 or 8 radial canals), which radiate to the margin and open into a ring or **marginal canal.** The margin is unscalloped and bears most of the tentacles and sense organs, the tentacles being usually in multiples of 4. The base of each tentacle is commonly enlarged into an **ocellar bulb,** bearing an ocellus or other sensory patches such as **statocysts.**

DISTRIBUTION

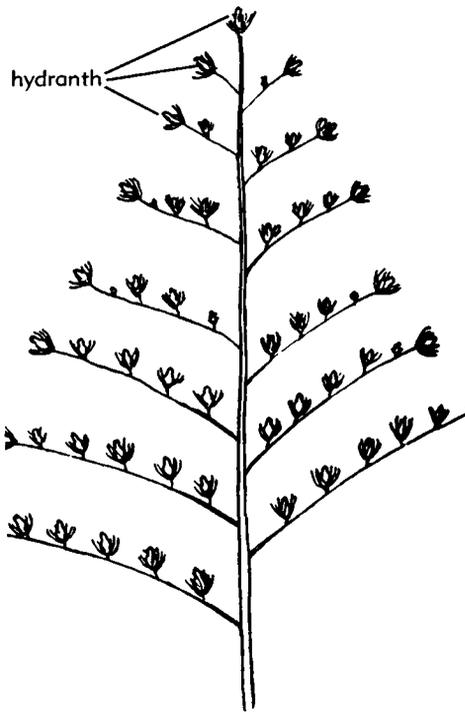Living hydroids are almost exclusively marine, occurring typically in littoral and

FIG. 67. Monopodial type of hydroid colony with terminal hydranths, *Pennaria* (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).

shallow offshore waters, but some, like the plumularians, go down to depths of 550 fathoms or more. Most prefer a hard substratum but some are adapted to soft bottoms, and many of these are found down to 2,750 fathoms. The colony form is susceptible to environmental changes. The group is most abundant in temperate and cold zones. The hydroid medusae are typically pelagic and planktonic animals of the shore and shallow seas. All are strictly carnivorous. Only a few of the many families are known as fossils.

Gymnoblastine hydroids are known doubtfully from Jurassic strata of the Mediterranean region and certainly from the Cretaceous and Tertiary of Europe. Fossils assigned to this suborder are also found in Lower Cambrian rocks of Australia. Calyptoblastines are recorded from the Middle Cambrian and Lower Ordovician of Victoria, Upper Cambrian of Texas, Middle Ordovician of Virginia and New York, and

Middle Devonian of Michigan, as well as from Mesozoic and Tertiary rocks.

Order HYDROIDA Johnston, 1836

[=Sertulariens AUDOUIN & M.-EDWARDS in LAMARCK, 1828; Exoarier RAPP, 1829 *(partim)*; Nudibrachiata FARRE, 1837; Polypiaria GRAY, 1840; Hydrozoa OWEN, 1843; Hydroidea DANA, 1846; Hydraria M.EDW.-H., 1850; Diplomorpha CARUS, 1863 *(partim)*]

Polypoid generation dominant, the few solitary species nude; colonial genera with exoskeleton generally horny, weakly calcareous in some; budding off free medusae or with structures resembling abortive medusae. Medusae velate, with ocelli and ectodermal statocysts. *Cam.-Rec.*

The order includes 3 suborders: Eleutheroblastina, Gymnoblastina, and Calyptoblastina, all defined by ALLMAN, 1871; of these the few Eleutheroblastina are solitary, naked forms (*Hydra*) and are not found fossil.
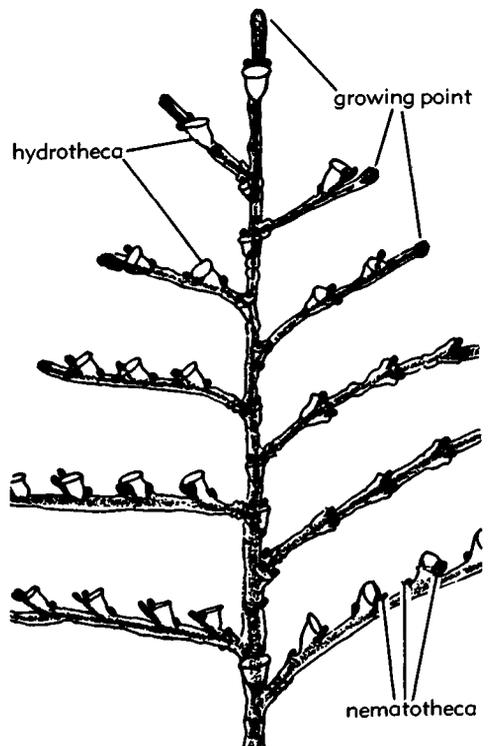

FIG. 68. Monopodial type of hydroid colony with terminal growing points, *Plumularia* (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora*, McGraw-Hill, New York).
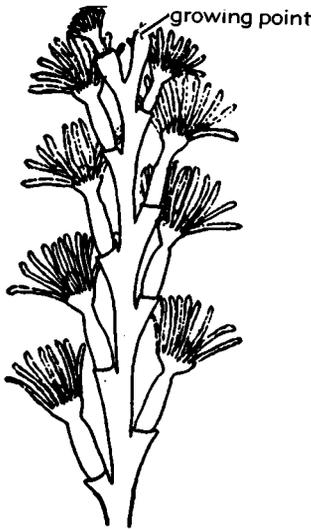
FIG. 69. Branch end of *Halecium* showing sympodial growth (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

Suborder GYMNOBLASTINA Allman, 1871

[=Tubularina EHR., 1834; Athecata HINCKS, 1868; Anthomedusae HKL., 1896]

Colonial; hydranths without hydrothecae; gonophores naked; exoskeleton of hydrorhizae and caulomes horny, or in some calcareous. Free medusae tall, bell-like, with ocelli but lacking statocysts; gonads borne on the manubrium. ?*Trias., ?Jur., ?Cret., Eoc.-Rec.*

Family HYDRACTINIIDAE Agassiz, 1862

[*nom. correct.* HINCKS, 1868 (*ex* Hydractinidae AGASSIZ, 1862)] [Incl. ?Syringosphaeridae DUNCAN, 1879 (as order); ?Heterastrididae FRECH, 1890; ?Ellipsactinidae POLJAK, 1936; ?Heterastridiidae KÜHN, 1939]

Encrusting, caulomes rising from a chitinous or calcareous mat of tangled hydrorhizae with periderm; caulomes in vertical tubes in the peridermal mat. ?*Trias., ?Jur., ?Cret., Eoc.-Rec.*

Hydractinia BENEDEN (1841, *genus caelebs*), 1844 [**Alcyonium echinatum* FLEMING, 1828] [=*Echinochorium* HASSALL, 1841; *Synhydra* QUATREFAGES, 1843; *Synhydre* BENEDEN, 1844; *Hydractinea* ALLMAN, 1864; ?*Kerunia* MAYER-EYMAR, 1899 (symbiotic with hermit crab); *Cyclactinia, Poractinia* VINASSA, 1901; ?*Hydrocorella, Janaria, Hydrissa* STECHOW, 1921; ?*Hydroconophora, Hydrokerion* GREGORY, 1931]. Periderm horny or calcareous; encrusting mat laminated and with spines projecting upward among the polyp bases so as to leave pores in the mat; commonly encrusting gastropod shells. ?*Jur.-?Cret.,* Eu.; *Eoc.*-

Rec.——FIG. 71,*1. H. echinata* (FLEMING), Rec., Eu.; *1a,* colony on shell occupied by hermit crab, ×1; *1b,c,* transv. secs. of chitinous spine protruding from base of colony, near base and summit of spine (chitin oblique shaded), ×50; *1d,* long. sec. of spine showing proximal part of hydranths developed from coenosarc covering spine, ×37.5 (ALLMAN); *1e,* long. sec. of part of base, ×30 (9).

?Cycloporidium PARONA, 1909 [**C. tubiforme*]. *U. Cret. (Cenom.),* Italy.

?Ellipsactinia STEINMANN, 1878 [**E. ellipsoidea*]. Hemispherical or elliptical; thick, finely tuberculate laminae with few, irregular connections. *Trias.-Cret.,* Eu.-Afr.——FIG. 71,*2. *E. ellipsoidea,* U.Jur., Aus.; *2a,* part of surface, ×8; *2b,c,* median sec. ×1, ×10 (14).

?Heterastridium REUSS, 1865 [**H. conglobatum;* SD DIENER, 1921] [=*Stoliczkaria, Syringosphaera* DUNCAN, 1878]. Spherical or nodular, commonly with minute cephalopod shell as nucleus; laminae and pillars finely perforate, the perforations of successive laminae lying above one another, forming fine, radial unwalled tubules (?dactylopores); with large radial cylindrical unwalled, discontinuous tubes (?gastropores, ?gonopores); without tabulae; surface tuberculations markedly stellate with skeletal tissue below them much thickened but not astrorhizal. GERTH has suggested that these forms were pelagic. *Trias.,* Eu.-Asia-Timor.—— FIG. 72. [**H. conglobatum*] [=*H. pachystylum*
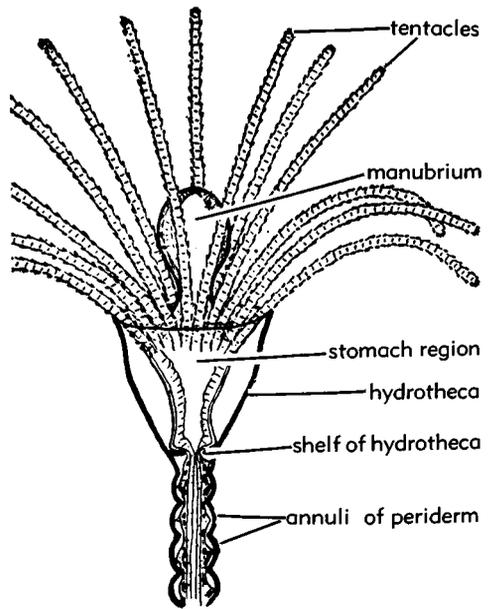

FIG. 70. Calyptoblastine hydranth, *Obelia,* with single filiform circlet of tentacles (L. H. HYMAN, *Invertebrates: Protozoa through Ctenophora,* McGraw-Hill, New York).

FRECH], *U.Trias.*, Aus.; *a,b*, transv. and long secs., ×5 (STEINMANN).
?**Philippinactinia** YABE & SUGIYAMA, 1939 [*P.

hasimotoi]. *Oligo.*, Philip.
?**Stromactinia** VINASSA, 1901 [*S. triassica*]. *U. Trias.*, Carpath.
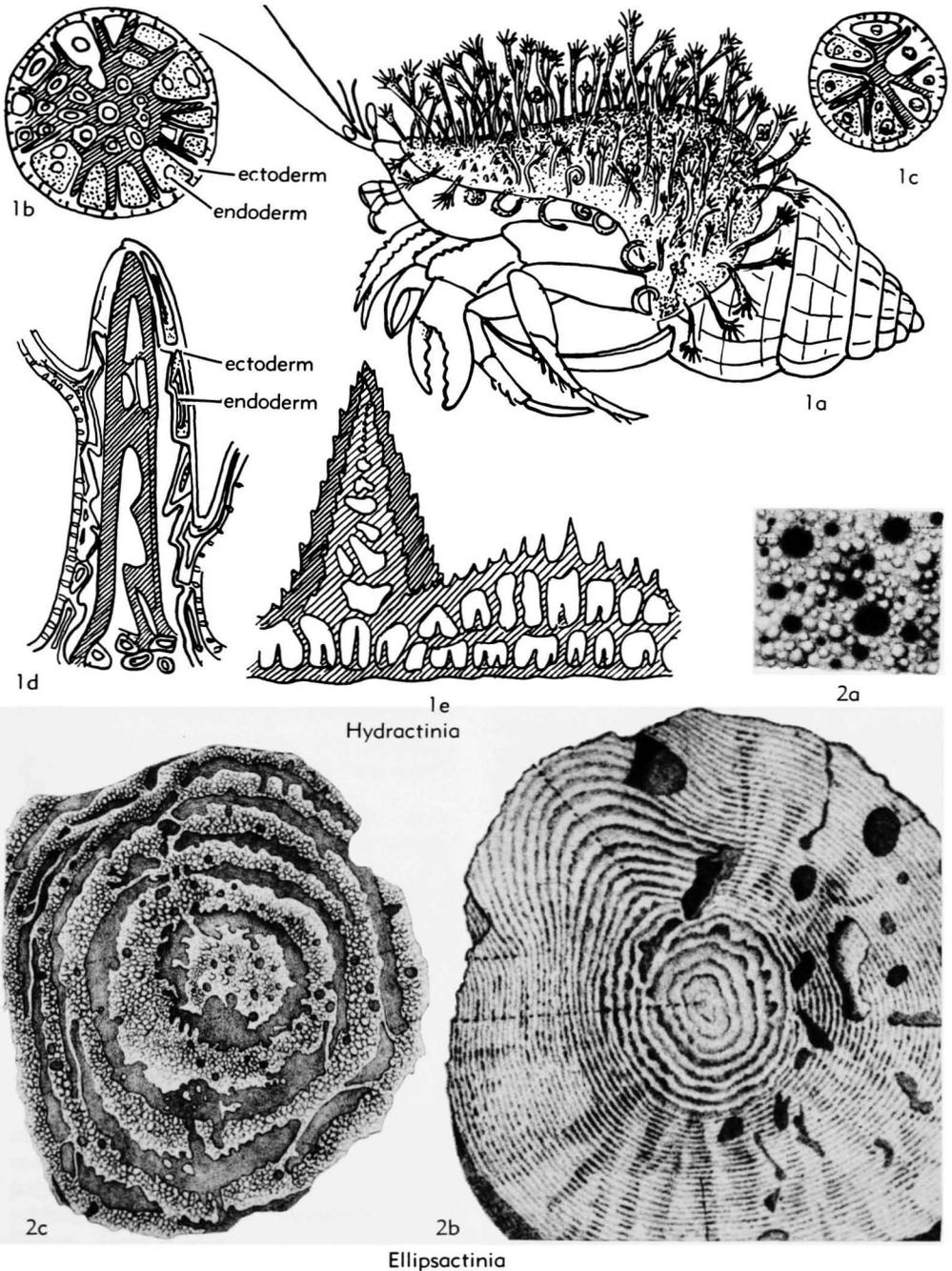

Hydractinia

Ellipsactinia

FIG. 71. Hydractiniidae. *1a-e, H. echinata*, Rec., showing living colony, ×1, and sections of chitinous skeleton, enlarged. *2a-c, E. ellipsoidea*, U.Jur., surface enlarged, and sections.
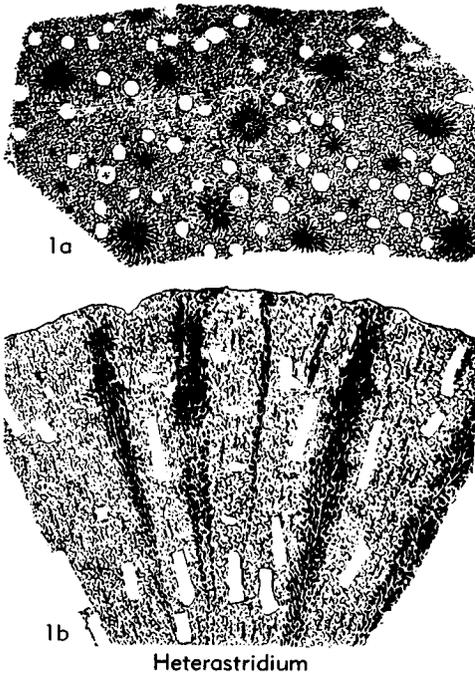
FIG. 72. Hydractiniidae. *1a,b, H. pachystylum,* U. Trias., sections, ×5.

ANTHOMEDUSAE

The medusoid generations of Gymnoblastina, many of which are not correlated reliably with known polypoids, are collectively designated Anthomedusae. The fossil record of the group is treated in sections of this volume entitled "Medusae of the hydroids" and "Medusae incertae sedis and unrecognizable forms."

Suborder CALYPTOBLASTINA
Allman, 1871

[=Sertulariadae FLEMING, 1828; Sertularina EHR., 1834; Thecaphora HINCKS, 1868; Leptomedusae HAECKEL, 1866 (often used for calyptoblastean medusae)]

Hydranths provided with hydrothecae; gonophores enclosed in gonothecae; enclosing periderm may be chitinous; free medusae bowl- or saucer-shaped, usually with statocysts and gonads borne on radial canals. *Cam.-Rec.*

Several fossil forms have been described that may pertain to this suborder, but they cannot safely be referred to any living family.

Family UNCERTAIN

Archaeocryptolaria CHAPMAN, 1919 [*A. skeatsi; SD D. THOMAS, herein]. Hydrocaulus slender, more or less erect or slightly flexuous. Hydrothecae cylindrical or elongate-conical, narrowing very slightly toward base; adnate or attached to hydrocaulus for some distance; aperture circular, lip slightly everted. Periderm chitinous, coarsely wrinkled or scaly. Gonothecae elongate pyriform and incurved to axis. *M.Cam.,* Vict.-Tasm.; *U. Cam.,* Tex.; *M.Ord.,* Va.——FIG. 73,3. *A. skeatsi;* M.Cam., Austral., ×2.5 (10).

Archaeolafoea CHAPMAN, 1919 [*A. longicornis]. Hydrocaulus slender, flexuous, with few lateral branches. Hydrothecae long conical, narrowing slightly toward base, apertures circular; borne equally on sides of hydrocaulus and branches at angles of 15 to 50 degrees. Periderm transversely wrinkled. Gonothecae small, elongate pyriform. *M.Cam.,* Vict.-Tasm.-N.Y.; *U.Cam. (Lancefield.),* Vict., Ord., N.Y.——FIG. 73,1. *A. longicornis, M.Cam.,* Vict.-Tasm.; *1a,* colony, ×2.5; *1b,* gonotheca, ×12.5 (10).

Protohalecium CHAPMAN & THOMAS, 1936 [*P. hallianum]. Hydrocaulus short, repeatedly branching, with shallow hydrothecae on stalks. *M.Cam.,* Vict.-Tasm.

Sphenoecium CHAPMAN & THOMAS, 1936 [*Sphenothallus filicoides* CHAPMAN, 1917; SD D. THOMAS, herein]. Hydrocaulus with short stipe or pedicle with wedge-shaped hydrothecae arranged radially or serially. *M.Cam.,* Vict.-Tasm.

Palaeokylix EISENACK, 1932 [*P. chitinosus]. Slender chitinous pipes with irregular swellings; simply
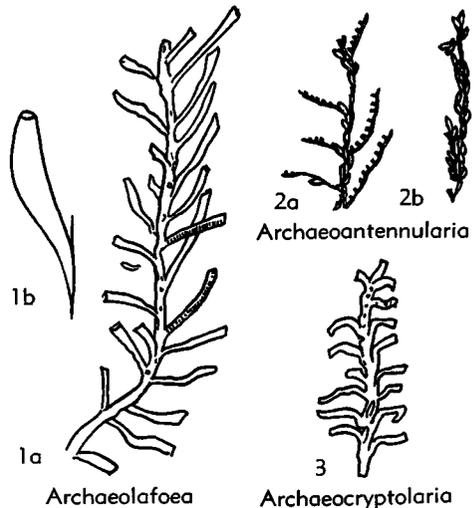

FIG. 73. Calyptoblastina. *1a,b, A. longicornis,* M. Cam., colony, ×2.5, and gonotheca, ×12.5. *2a,b, A. byersi,* M.Dev., ×2. *3, A. skeatsi,* M.Cam., ×2.5.

1b · 1a
Spongiomorpha

2c

2b

2a
Heptastylis

3a 3d 3c 3b
Stromatomorpha
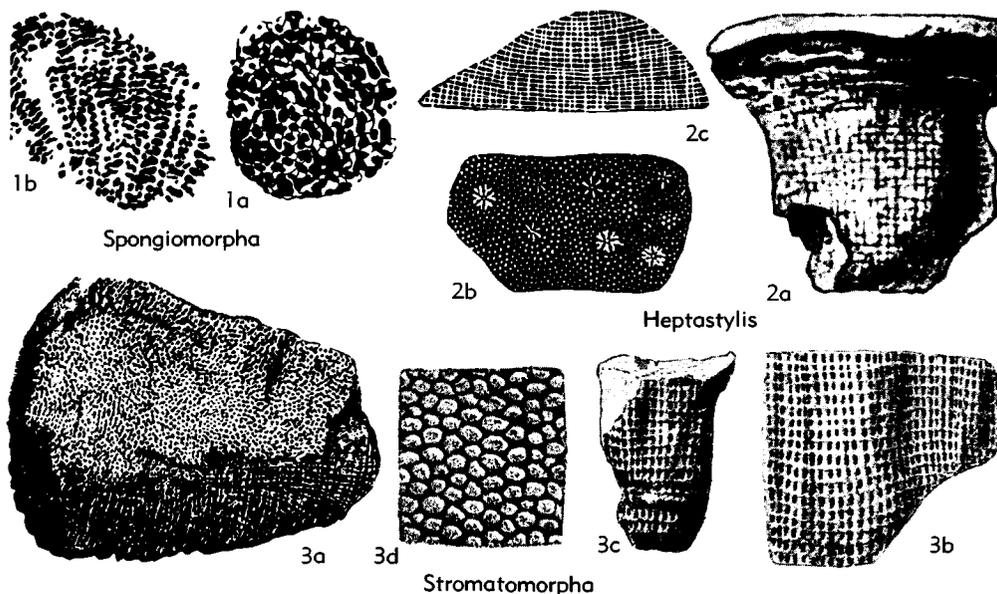
Fig. 74. Spongiomorphidae. *1a,b, S. acyclica,* Trias., sections, ×4. *2a-c, H. stromatoporoides,* Trias., exterior, ×2, and secs., ×4. *3a-d, S. stylifera,* Trias.; *3a,* ×1; *3b,c,* ×2; *3d,* ×6.

branching, ending in short wide theca (6). *Ord., Balt.*

Palaeotuba EISENACK, 1934 [*P. polycephala*]. Hydrocaulus dichotomously branching, branches widening gradually to terminal thecae (6). *Ord., Balt.*

Cylindrotheca EISENACK, 1934 [*C. profunda*]. Hydrocaulus simply branched, with long cylindrical theca (6). *Sil., Czech.*

Mesokylix EISENACK, 1935 [*M. hydra*]. Hydrocaulus branched, thecae shallow, wide terminal cups (6). *M.Jur., Ger.*

Archaeoantennularia DECKER, 1952 [*A. byersi*]. Branches radiating in all directions from central axis, which consists in part of large gonangia and in part of hydrothecae. *M.Dev., Mich.*——FIG. 73, 2. *A. byersi;* ×2 (11).

?**Kristinella** RICHTERS, 1913 [*K. monilifera*]. *Cret., Ger.*

LEPTOMEDUSAE

The term Leptomedusae refers to the medusoid generations of Calyptoblastina, many of which are not correlated with their polypoid generation. Tentatively classed with Leptomedusae is *Protodipleurosoma* SPRIGG, from Lower Cambrian rocks of South Australia. Reference to this and other medusoid fossils is contained in sections of Part F entitled "Medusae of the hydroids"

and "Medusae incertae sedis and unrecognizable forms."

SPONGIOMORPHIDA
MORPHOLOGY

The spongiomorphs seem to be more closely allied to the stromatoporoids than to any other group. When first described, they were referred to the scleractinian corals on account of the apparent grouping of 6 vertical pillars (?trabeculae) about a 7th. They possess none of the real characters of anthozoan skeletons, however, whereas all their characteristic features are found within the Hydrozoa. Thus, their vertical pillars and concentric retiform laminae are found in the hydractinians and stromatoporoids, and they lack the ?gastropores of the sphaeractiniids and possess ?astrorhizal structures not found in the hydractinians. They might be referred to the Stromatoporoidea, although the regular astrorhizal structures are somewhat more specialized than in that group. They are characteristic of the Triassic, particularly of warm waters of the Tethys. They have also been recorded from the Jurassic of Japan and northern Africa.

Order SPONGIOMORPHIDA Alloiteau, 1952

Stromatoporoid-like hydrozoans in which stellate ?astrorhizal vertical tubules may develop from the radial grouping of 6 vertical pillars about a 7th. *Trias.-Jur.*

Family SPONGIOMORPHIDAE Frech, 1890

Massive, radial pillars dominant, united by annular thickenings or by horizontal bars, which may merge to form concentric but perforate laminae; latilaminae not developed; 6 pillars may be grouped starwise as a vertical, tubular, astrorhizal space around a 7th; tabulae may be developed. *Trias.-Jur.*

Spongiomorpha Frech, 1890 [*S. acyclica; SD Diener, 1921] [=Heptastylopsis Frech, 1890]. Horizontal bars not merged to form concentric laminae; tabulae numerous. *Trias.*, Eu.-Asia-N. Am.-N.Afr.——Fig. 74,1. *S. acyclica, Eu.; 1a,b, tang. and radial secs., ×4 (12).

Heptastylis Frech, 1890 [*H. stromatoporoides]. Horizontal bars merged to form well-developed concentric laminae; no tabulae; with stellate ?astrorhizal groupings of pillars. *Trias.*, Eu.-N. Am.; *Jur.*, Japan-N.Afr.——Fig. 74,2. *H. stromatoporoides, Trias., Eu.; 2a, exterior of side, ×2; 2b,c, tang. and radial secs., ×4 (12).

Stromatomorpha Frech, 1890 [*S. stylifera; SD Diener, 1921] [=Cylicopsis LeMaitre, 1935]. Vertical pillars thickened ringwise at regular intervals, the rings of neighboring pillars united by porous concentric laminae. *Trias.*, Eu.-N.Am.; *Jur.*, Asia-N.Afr.——Fig. 74,3. *S. stylifera, Trias., Eu.; 3a, exterior, ×1; 3b,c, radial surfaces, ×2; 3d, transv. sec., ×6 (12).

GENERA OF UNCERTAIN SYSTEMATIC POSITION

Delheidia Dollfuss, 1898 [*Tubipora proxima]. *Oligo.*, Belg.

Graptogeitonia Ruedemann, 1934 [*G. adherens]. *Ord.*, N.Y.

Jillua Krumbeck, 1913 [*J. tubifera]. Encrusting hydrorhiza of unknown hydrozoan. *U.Trias.*, E. Indies.

Lovčenipora Giattini, 1903 [*L. vinassai]. *U. Trias.-Jur.*, Eurasia.

Plumalina Hall, 1858 [*Filicites? plumaria Hall, 1843]. *U.Dev.(Senecan)*, N.Y.

Rhizostromella Parona, 1909 [*R. appenina]. *U. Cret.(Cenom.)*, Italy.

Roseoporella Spriestersbach, 1935 [*R. rhenana]. *Dev.*, Ger.

Stoliczkiella Carter, 1888 [*S. theobaldi]. *?Cret.*, Karakorum.

Tarrichnium Wanner, 1938 [*T. balanocrini]. Traces of hydrorhizae of unknown hydrozoans in crinoid columns. *Mio.*, E.Indies.

GENERIC NAMES REFERRED TO HYDROZOA BUT BELONGING TO OTHER GROUPS

Aphrostoma Gürich, 1906 (alga or stromatolite), *L.Carb.*, Belg.

Aprutinopora Parona, 1909 (bryozoan), *Cret.*, Italy.

Bradyzoum Kühn, 1939 (Foraminifera) [=Bradya Stache, 1873 (non Boek, 1873)]. *U.Cret.*, Eu.

Chondrostroma Gürich, 1906 (alga or stromatolite), *L.Carb.*, Belg.

Cladocoropsis Felix, 1907 (alga), *U.Jur.*, Jugoslavia.

Corynoides Nicholson, 1867 (graptolite), *Sil.*, Scot.

Cylindrohyphasma Steinmann, 1878 (?sponge), *M.Carb.*, Moscow.

Malacostroma Gürich, 1906 (alga or stromatolite), *L.Carb.*, Belg.

Marinduqueia Yabe & Sugiyama, 1939 (?sponge), *Eoc.*, Philip.

Millarella Carter, 1888 (?Parkeria), *U.Cret.*,Eng.

Palaeocoryne Duncan & Jenkyns, 1869 (bryozoan), *Miss.*, Scot.

Parastroma Douvillé, 1927 (rudistid), *U.Cret.*, Cuba.

Parkeria Carpenter, 1870 (Foraminifera), *Cret.*, Eng.

Porosphaera Steinmann, 1878 (sponge), *Cret.*, Eu.

Ptychostroma Gürich, 1906 (alga or stromatolite), *L.Carb.*, Belg.

Spongiostroma Gürich, 1906 (alga or stromatolite), *L.Carb.*, Belg.

Thalamospongia d'Orbigny, 1850 (probably sponge) [=Thalamosmilia de Fromentel, 1860; Thalaminia Steinmann, 1878; Thalamina Waagen & Wentzel, 1887]. *Jur.-L.Cret.*, Fr.

Thaumatostroma Weissermel, 1926 (stromatolite), *Eoc.*, SW.Afr.

Websteria M.Edw.-H., 1850 (bryozoan), *Eoc.*, Eng.

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(1) 1871-72, *A monograph of the gymnoblastic or tubularian hydroids:* Roy. Soc. (London), xxii+450 p., 23 pl., 77 fig.

Chapman, Frederick, & Thomas, D. E.
(2) 1936, *The Cambrian hydroids of the Heathcote and Monegeeta districts:* Proc. Roy. Soc. Vict., v. 48, p. 193-212, pl. 14-17.

Frech, F.
(3) 1890, *Die Korallenfauna der Trias, 1. Die Korallen der juvavischen Triasprovinz:* Palaeontographica, Bd. 37, 116 p., 21 pl.

Gerth, H.
(4) 1915, *Die Heterastridien von Timor:* Paläont. von Timor, Lief. 2, Abt. 4, p. 61-69, pl. 42.

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LeMaitre, Dorothée
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SOURCES OF ILLUSTRATIONS

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

(8) Carter, H. J.
(10) Chapman, Frederick
(11) Decker, C. E.
(12) Frech, F.
(13) Hill, Dorothy, & Wells, J. W.
(14) Steinmann, G.

MILLEPORINA AND STYLASTERINA

By Hilbrand Boschma[1]

CONTENTS

INTRODUCTION

The Milleporina and Stylasterina, which now are recognized as groups of hydrozoans that secrete a calcareous skeleton, were classified among scleractinian Anthozoa before the structure of their soft parts became known. The affinity of *Millepora* with hydroids was first demonstrated by Agassiz (1) in 1858 and similarly that of the stylasterines by Moseley (30, 31) about 20 years later. For a long time the 2 groups were considered to be so closely allied as to warrant classifying them together in an order called Hydrocorallina but Hickson (18, 19) defined the Milleporina (1901) and Stylasterina (1906) as independent orders distinct from other hydrozoans. The structure of the soft parts, however, indicates that each may find a place among the hydroids. Thus, Broch's (8) classification of the Hydroida assigns the groups with a calcareous skeleton to the suborder Athecatae, arranging the Milleporidae into the section Capitata containing forms with short capitate tentacles that bear a terminal knob, and the Stylasteridae into the section Filifera containing forms with elongate tapering filiform tentacles. Both divisions include numerous families that lack calcareous hard parts. Recent tendency is to recognize the Hydroida, Milleporina, and Stylasterina as separate orders of hydrozoan polyps (23).

The Milleporina differ from the Stylasterina not only in shape of the tentacles but also in the manner of their sexual reproduction, for milleporines produce free-swimming medusae, whereas sexual individuals of the stylasterines are reduced to gonophores.

According to current definition, the Milleporina incorporate 2 family assemblages that probably are not at all closely allied; these are the Milleporidae and Axoporidae. In

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[1] The author is much indebted to Raymond C. Moore for editorial assistance in preparing this chapter.
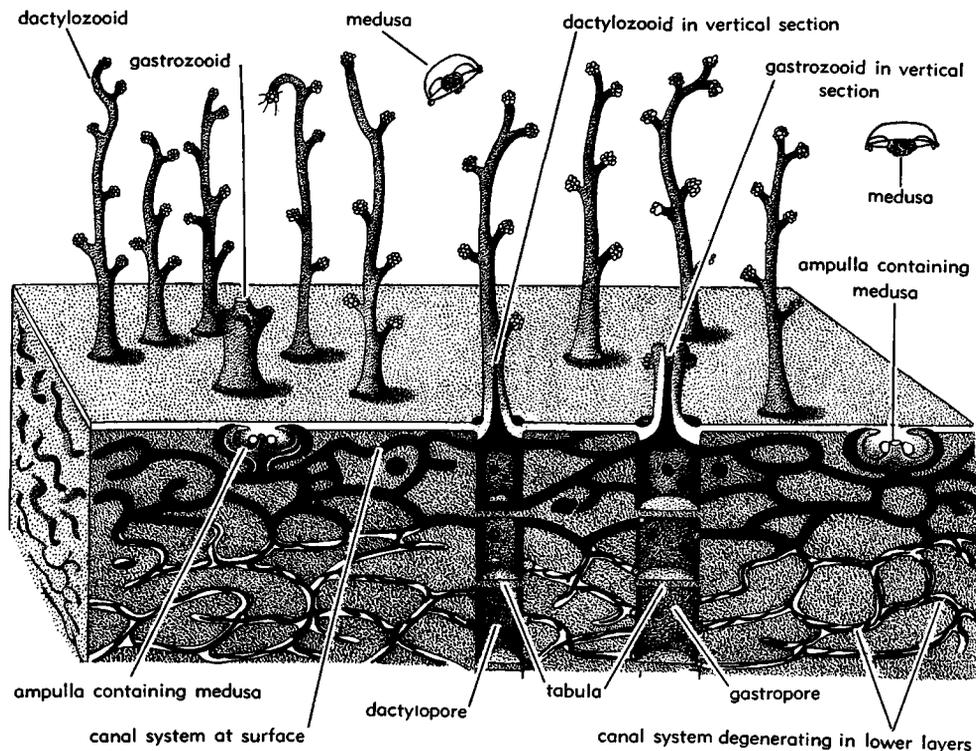
FIG. 75. Diagrammatic sketch of part of a *Millepora* colony showing soft parts and structure of hard parts, enlarged (41 mod.).

1939, KÜHN (26) included 4 genera (*Millepora, Milleaster, Axopora, Diamantopora*) in the Milleporidae, no other family being then recognized. The dimorphic polyps of *Millepora* are enclosed in tubular cavities of the colonial skeleton, which are differentiated as gastropores and dactylopores, both lacking axial structures. *Milleaster* seems not to be significantly different. The genus *Axopora* is characterized by the occurrence of gastropores that bear an axial column (gastrostyle) and by absence of dactylopores. The presence of gastrostyles is a feature suggesting the Stylasterina, but genera of this order have both gastropores and dactylopores. The structure of *Diamantopora* and *Axoporella* resembles that of *Axopora*. These genera comprise a group that probably deserves the rank · of a separate order, distinct from both the Milleporina and Stylasterina, but for the present they are classed as a family (Axoporidae) of the Milleporina (5, 6).

MILLEPORINA

Order MILLEPORINA Hickson, 1901

Gastrozooids short, cylindrical, with 4 short tentacles; dactylozooids elongate, with 5 to 7 tentacles; tentacles capitate; sexual generation of free-swimming medusae. *U. Cret.-Rec.*

MORPHOLOGICAL FEATURES
SOFT PARTS

Recent species of the genus *Millepora* are the only available forms for description of the soft parts of Milleporina. These show that the living part of colonies (coenosarc) is restricted to superficial layers where gas-
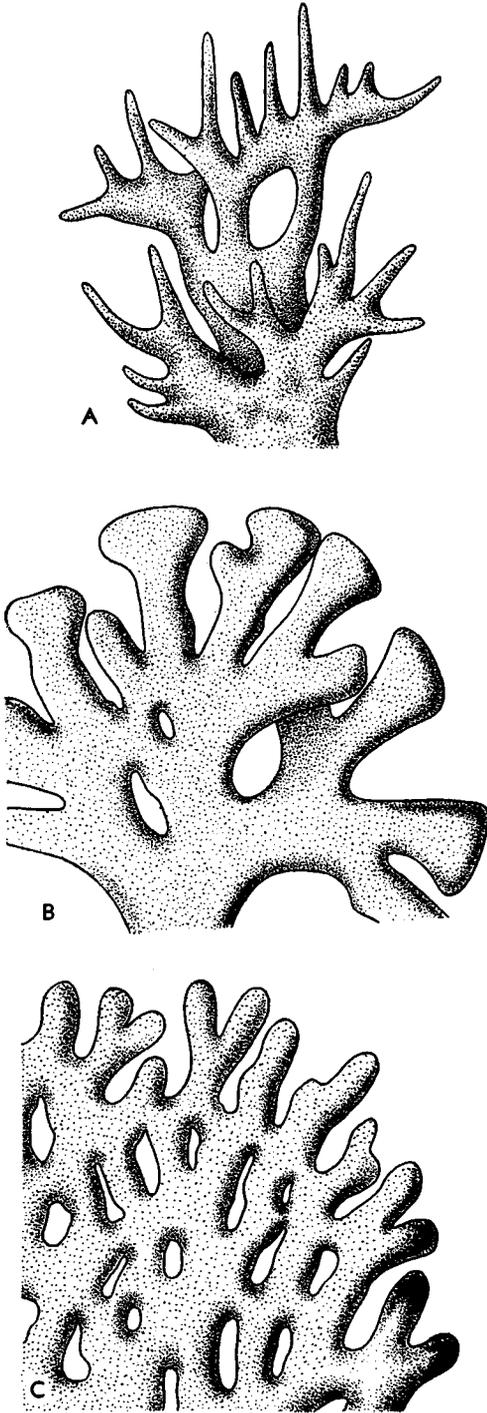
tropores and dactylopores have formed their most recent tabulae (Fig. 75). In this area an intricate meshwork of minute canals occupies small pores that extend between trabeculae of the skeleton, tissue of the canal system being alive near the surface of the colony but degenerating in layers below the most recently secreted tabulae.

Two kinds of polyps occur in tubular openings perpendicularly to the surface of a colony, **gastrozooids** lodged in relatively large cavities termed gastropores, and **dactylozooids** situated in somewhat narrower tubes called dactylopores (Fig. 75 shows hardly perceptible difference in width of gastropores and dactylopores). Both types of polyps connect with the **canal system** at their bases. The gastrozooids are short cylindrical polyps provided with 4 capitate tentacles (round knob at tip) that surround a short conical hypostome with central circular mouth. The dactylozooids are arranged in circular rows with 5 to 7 individuals around a gastrozooid, forming what is termed a **cyclosystem.** Where the polyps are unusually crowded, arrangement in cyclosystems becomes obscured and only the presence of numerous small pores (dactylopores) associated with fewer large pores (gastropores) can be discerned. The dactylozooids are long slender mouthless polyps, which bear 5 to 7 short capitate tentacles. The sexual individuals occur in the upper part of special pores (**ampullae**) consisting of rounded cavities in which sexual generation produces small medusae that eventually become free-swimming. These are hydromedusae of reduced structure, for they lack velum, tentacles, and radial canals. The sexual cells develop on the manubrium, which is a tubular projection of the mouth.

HARD PARTS

Colonies of *Millepora* commonly build large variously shaped calcareous structures, which are upstanding where growth conditions are favorable but laterally extended incrustations where the environment is unfavorable. Some species secrete broad solid plates, whereas others produce branching forms with pointed or rounded tips (Figs. 76*A,C*) or laterally compressed broad tips (Fig. 76*B*), all branching mostly in a single plane to form fan-shaped colonies.

FIG. 76. Growth forms of *Millepora* illustrated by distal parts of colonies belonging to Recent species: *A, M. alcicornis* LINNÉ, W. Indies; *B, M. tenera* BOSCHMA, Molluccas; *C, M. dichotoma* FORSKÅL, Red Sea; all ×1 (35n).

The surface of the calcareous skeleton shows numerous small subcircular or irregularly polygonal openings of **gastropores** surrounded by the slightly smaller apertures of **dactylopores** of similar shape (Fig. 77,*1b*). The outline of these pores locally is definitely stellate in colonies of various species (Fig. 77,*1a*). Gastropores and dactylopores may be arranged in cyclosystems, as described previously, or such a pattern may not be evident. The **coenosteum** between the pores appears very finely porous because of the very minute cavities between trabeculae composing the skeleton, as well shown in sections (Fig. 77,*1c*).

The rounded cavities occupied by ampullae are rare in *Millepora,* although they are known in many different species (2, 3). Generally these openings are greater in width than height and are covered by part of the skeleton that rises slightly above surrounding areas of the surface. The reticulate mass of trabeculae overlying an ampulla has a characteristic shape in each species. Colonies of *Millepora* are dioecious, for the relatively small male ampullae and slightly larger female ampullae are confined to different colonies.

The genus *Milleaster* incrusts gastropod shells or grows in subramose colonies (Fig. 77,*2*). Relatively large subrounded pores (gastropores) confluent with the surface are surrounded by more numerous smaller stellate orifices (dactylopores) located at the summit of tubercle-like elevations and by many minute rounded openings (cavities between trabeculae) that lack raised margins. In at least one species (*M. interglacialis* RICHARDS), however, the stellate pores are not elevated.
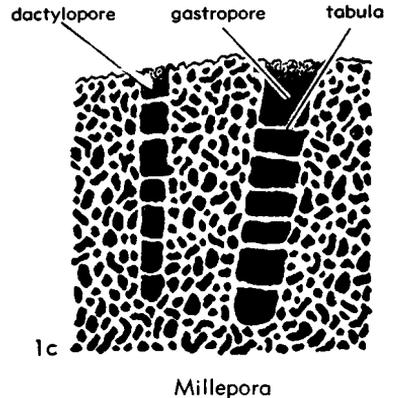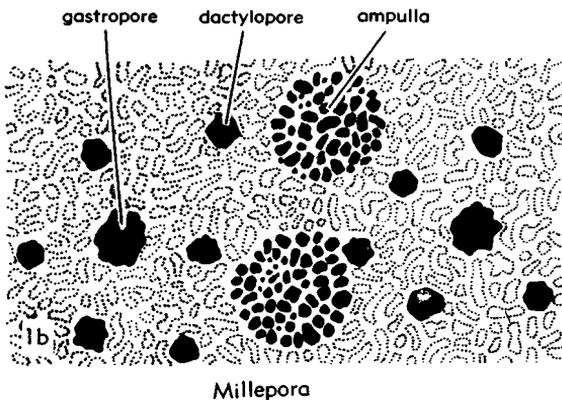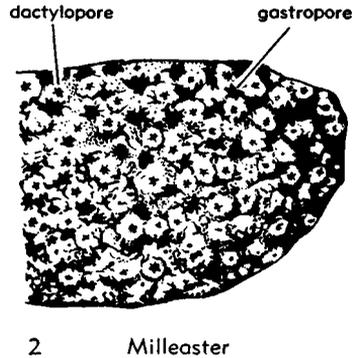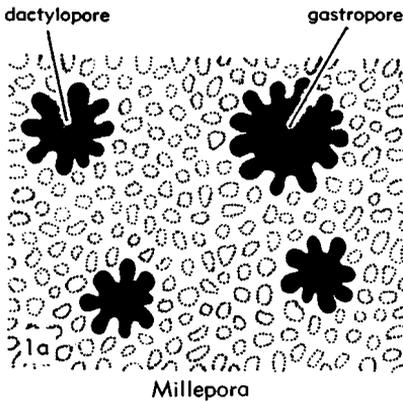

FIG. 77. Milleporidae. *1a, M. complanata,* Rec., ×36. *1b,c, M. tenera,* Rec., ×20. *2, M. incrustans,* Mio., ×8.

The skeleton of *Axopora* contains only one kind of pores, seemingly gastropores, which are regularly distributed circular or somewhat polygonal openings (Fig. 78,*1b*). The central part of these pores contains a longitudinally grooved pillar (gastrostyle), which seems to be built by several firmly united parallel rods (Figs. 78,*1b,2*).

In *Diamantopora,* the style is described as solid, without longitudinal grooves (Fig. 78,*4*), and in *Axoporella* it bears numerous small spines, like those of the gastrostyles in Stylasterina (Fig. 78,*3*).

OCCURRENCE

Modern species of *Millepora* are found commonly on coral reefs, generally at depths not exceeding 30 m., which seems to be correlated with dependence of the colonies on symbiotic unicellular algae (zooxanthellae) that need light for their processes of assimilation.

Among many fossils assigned to *Millepora,* HICKSON (17) judges that few really belong to the genus. BOSCHMA (5) concludes that *M. tornquisti* BOSCHMA [=*M. cylindrica* TORNQUIST (*non* REUSS)], from Eocene rocks of Madagascar, can be recognized al-. most surely as a species of *Millepora,* and the reported occurrence (34) of *M. alcicornis* LINNÉ in Pleistocene deposits of the Canal Zone can be accepted. Possibly the form described as *M. parva* NIELSEN, from the Danian at Faxe, Denmark, also belongs to the genus, but this is not certain.

SYSTEMATIC DESCRIPTIONS

Family MILLEPORIDAE Fleming, 1828

[*nom. correct.* AGASSIZ, 1858 (*pro* Milleporadae FLEMING, 1828)]

Colonial skeleton with gastropores associated with smaller more numerous dactylopores; gastrostyles and dactylostyles lacking. *U.Cret.-Rec.*

Millepora LINNÉ, 1758 [*M. alcicornis;* SD M.EDW.-H., 1850] [=*Palmipora* BLAINV., 1830]. Colony arborescent, composed of upstanding plates, or incrusting. Gastropores and dactylopores circular to irregularly polygonal at orifices, exceptionally stellate; walls not extended above surface; 5 to 7 dactylopores commonly arranged around each gastropore forming indistinct cyclosystems. Ampullae in the coenosteum forming little or no bulge at the surface, covered by somewhat loose-textured plates. *U.Cret.(Dan.)-Rec.*——FIG. 77, *1b,c. M. tenera* BOSCHMA, Rec.; *1b,* surface of specimen from C.Pac.(Yap) showing 2 cyclosystems and 2 ampullae, ×20; *1c,* long. sec. of specimen from E.Indies, ×20 (35*).——FIG. 77,*1a. M. complanata* LAMARCK, Rec., W.Indies; surface showing stellate pores, ×36 (35*).

Milleaster ULR., 1904 [*M. incrustans*]. Colony incrusting, some with a few short branches. Gastropores with irregularly circular apertures, walls not raised above surface; dactylopores with star-shaped orifices on summits of papillae; cyclosystems not evident. Ampullae unknown. *Mio.-Pleisto.*——FIG. 77,*2. *M. incrustans,* Mio., Md.; surface, ×8 (35*).

Family AXOPORIDAE Boschma, 1951

Gastropores with distinct gastrostyle, dactylopores lacking. *Eoc.-Oligo.*

Axopora M.EDW.-H., 1850 [*Geodia pyriformis* MICH., 1847]. Colony incrusting, forming lumpy protuberances or arborescent. Gastropores with circular opening; gastrostyles longitudinally grooved. Ampullae unknown. *Eoc.-Oligo.*——FIG. 78,*1a,b. A. solanderi* (DEFR.), Eoc., Fr.; *1a,* colony, ×1; *1b,* surface, ×20 (*1a,* 38; *1b,* 35*).——FIG. 78,*2. A. michelini* DUNCAN, Oligo., Eng.; long. sec. of gastropore, enlarged (37).

Diamantopora WEISSERMEL, 1913 [*D. lotzi*]. Like *Axopora* but gastropores with irregularly polygonal apertures and gastrostyles without longitudinal grooves. *Eoc.*——FIG. 78,*4. *D. lotzi,* Eoc., S.Afr.; transv. sec. showing gastropores and canals of coenosteum (black), and gastrostyles and trabeculae (white), ×20 (35*).

Axoporella BOSCHMA, 1954 [*A. kolosváryi*]. Like *Axopora* but gastrostyles bearing many small spines. *Eoc.*——FIG. 78,*3. *A. kolosváryi,* Eoc., Hung.; gastrostyle fragments, ×100 (35*).

GENERA ERRONEOUSLY ASSIGNED TO MILLEPORINA

Arachnopora WOODS, 1878.
Millestroma GREGORY, 1898.
Milleporidium STEINM., 1903.
Promillepora DEHORNE, 1920.
Thaumatostroma WEISSERMEL, 1926.

STYLASTERINA

Order STYLASTERINA Hickson & England, 1905

Gastrozooids short cylindrical, with filiform tentacles or lacking tentacles; dactylozooids small finger-shaped, without tentacles; sexual generation by gonophores that remain attached to colony. *U.Cret.-Rec.*

MORPHOLOGICAL FEATURES
COLONIAL FORM

The shape of stylasterine colonies exhibits great differences. Some species are incrusting, others subramose with short lumpy branches, and still others have an arborescent form with very many slender branches. Some colonies are bushy, with branches extending in all directions, and many are fan-shaped, with branches disposed chiefly or wholly in a single plane. In these last-mentioned flabelliform colonies, slight differences in the nature of the opposite nearly flat surfaces serve to distinguish one as anterior (generally somewhat concave) and the other as posterior (mostly gently convex). In some genera cyclosystems are confined to the anterior surface of the colony and in others they tend to be more numerous on this surface. The ampullae occur in greater number on the posterior surface and in some species they are restricted to this surface. An irregularly bushy shape characterizes some colonies in which a polychaete worm occupies a tube formed by thin layers of the stylasterine skeleton; nearly all known specimens of *Conopora* display these features, but a few colonies that lack an associated worm have a fairly regular flabelliform shape.

SOFT PARTS

The coenosarc generally extends more deeply below the surface of stylasterine genera than in *Millepora*. It consists chiefly of a complicated network of canals that connect with the gastrozooids, dactylozooids, and ampullae. The canals have a membranous wall consisting of an outer (ectoderm) layer
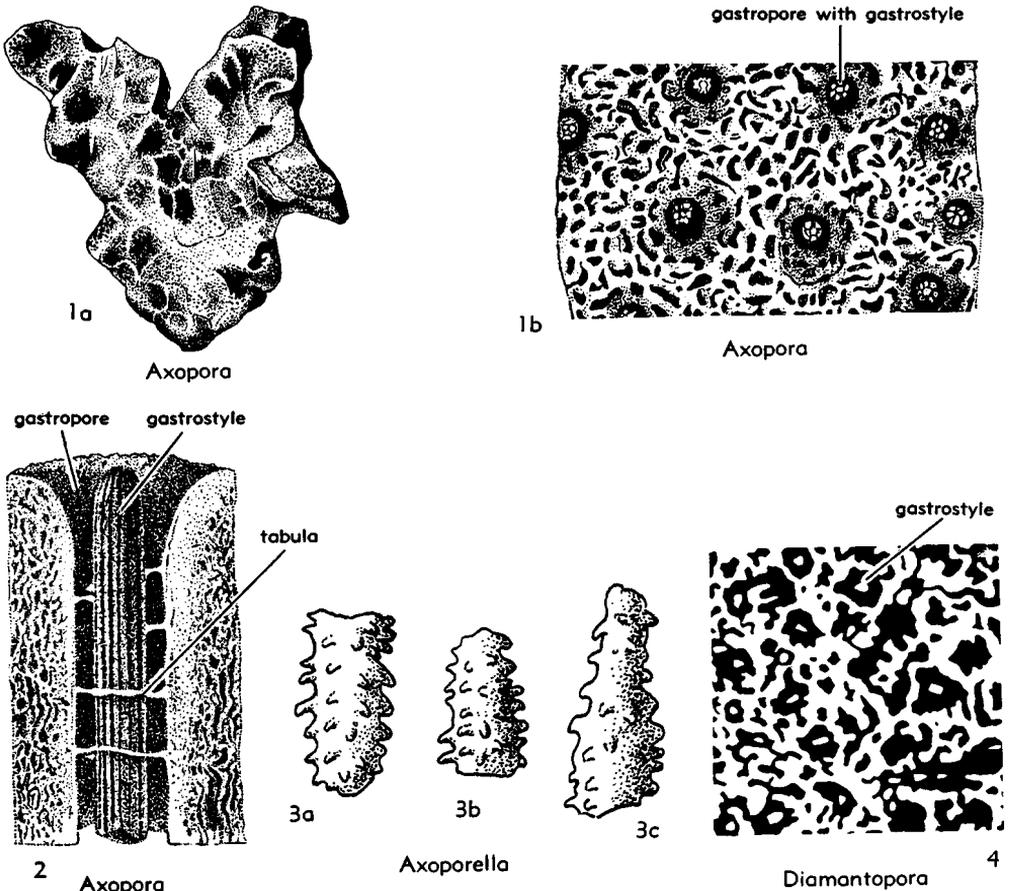
gastropore with gastrostyle

1a

Axopora

1b

Axopora

gastropore   gastrostyle

tabula

2   Axopora

3a   3b   3c

Axoporella

gastrostyle

4

Diamantopora

Fig. 78. Axoporidae. *1a,b, A. solanderi,* Eoc., ×1, ×20. *2, A. michelini,* Oligo., enlarged. *3a-c, A. kolosvaryi,* Eoc., gastrostyle fragments, ×100. *4, D. lotzi,* Eoc., ×20.
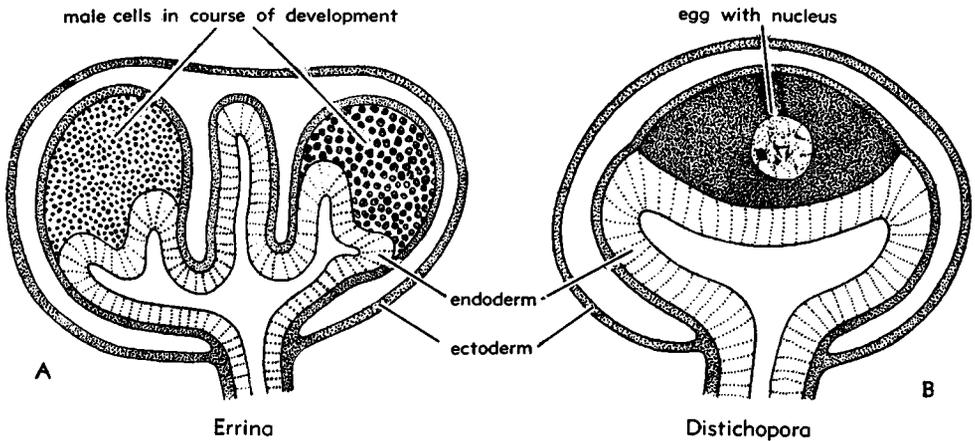
FIG. 79. Longitudinal sections of gonophores showing structure. *A*, Male gonophore of *Errina*, ×160. *B*, Female gonophore of *Distichopora*, ×160.

and an inner (endoderm) layer, which are joined to corresponding parts of the polyps and ampullae.

The gastrozooids are hydroid polyps of simple structure having a short cylindrical shape and a conical domelike hypostome that bears a round or four-cornered mouth at the top. A single whorl of filiform tentacles occurs at the base of the hypostome. The tentacles lack globular extremities differentiated from the stalklike lower part and thus are not capitate. Some stylasterine species possess long tapering tentacles (Fig. 84,*1b*) and others have short stubby ones (Fig. 81,*1b*), among which a few show slightly swollen extremities, although none are really capitate; in the gastrozooids of some genera tentacles are lacking.

The dactylozooids in all Stylasterina consist of polyps that have undergone strong reduction. They lack tentacles and indeed are themselves like simple tentacles; evidently they perform a tentacular function. The dactylozooids of *Pliobothrus* are simple elongate-conical mouthless bodies that are attached basally to the bottom of dactylopores. Those of *Sporadopora* differ only in being joined sideways to the lower part of dactylopores. In *Errina* and *Errinopsis* one side of the dactylozooids is attached to the median part of a grooved spine, leaving a free finger-shaped part that projects outward from the grooved spine (Fig. 84,*1b*). The dactylozooids of *Paraërrina* resemble those of *Errina* in shape, adhering

to one side of the dactylopore and attached also to the dactylostyle. The free extremity of dactylozooids, as well shown in genera of the Stylasterinae (Fig. 81,*1b*), projects inward toward the center of the cyclosystem.

The **gonophores** of the Stylasterina are sexual individuals that remain attached to the colonies. Most species are dioecious, some colonies bearing only male gonophores and others having only female ones, but both types have been observed in a single colony of *Distichopora* and *Stylaster*. The gonophores develop in separate cavities (ampullae) and their highly simplified structure suggests that they belong to the styloid type of hydrozoan polyps with the endoderm enlarged into a spadix. The spadix may bifurcate or be divided into several parts, the top portion bearing the genital cells that in the male develop into sperm cells (Fig. 79*A*) and in the female into egg cells (Fig. 79*B*). The spadix and genital cells are covered by a layer of ectoderm, around which is another ectoderm layer that envelops the whole gonophore and covers the ampulla in a position next beneath the calcareous wall of the ampulla. Eggs are fertilized within the ampullae, developing there into planulae, which are larvae consisting of a solid inner mass of endoderm covered by a layer of ectoderm. After an ampulla has fulfilled its function, the cavity becomes filled by coenosteum traversed by the canal system as in adjacent parts of the skeleton.

HARD PARTS

The skeleton secreted by stylasterine colonies is distinctly harder than that of members of the Milleporina and it has narrower pores between the calcareous elements. The somewhat brittle coenosteum of the milleporines is composed of trabeculae that are not closely joined, and the surface of colonies appears opaque. The surface of most colonies of the Stylasterina is more or less glossy.

The gastropores normally are tubes of cylindrical shape, which (as in *Stylaster*) may widen in funnel-shaped manner near the orifice. Fairly commonly they are divided by a girdle of inwardly projecting spines or a calcareous ridge into a proximal "ventral chamber" (or **gastrostyle chamber**) and a distal more or less flaring open chamber (Fig. 80,2) with margins not pronouncedly elevated above the general surface of the colonial skeleton or, less commonly, with a raised lip on one side directed
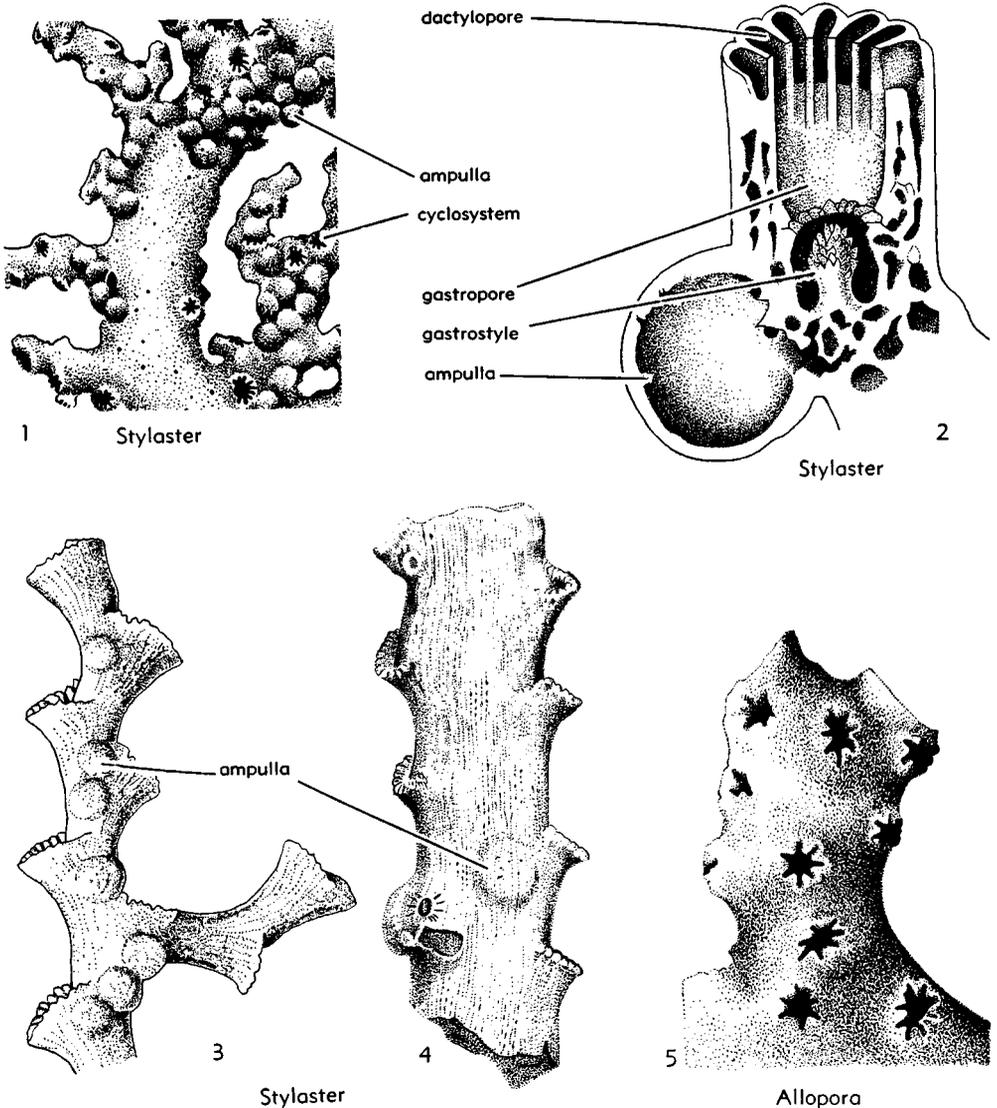

FIG. 80. Stylasteridae. *1, S. rossus,* Rec., ×5. *2, S. densicaulis,* Rec., ×9. *3, S. microstriatus,* Rec., ×10. *4, S. mooraboolensis,* Mio., ×8. *5, A. norvegica,* Rec., ×6 (p. F99-F100).

toward the apex of the colony (Figs. 84,*1a;* 85,*2a,b*). Some gastropores (as in *Pliobothrus* and *Sporadopora*) show the presence of **tabulae.**

The dactylopores are tubular openings in the skeleton narrower than the gastropores, and like the gastropores, they tend to widen toward the orifice. In some genera (as *Astya*), the dactylopores form a very regular circular row of openings around a gastropore, but in others arrangement is less definite. The margins of dactylopores may be even with the surface of the colony or they may be raised as small papillae (Fig. 85,*1b*), and some are characterized by projection of a grooved spine that represents upward continuation of the dactylopore (Fig. 83,*1b;* 84,*1c*).

Gastrostyles, which are axial structures projecting upward from the floor of gastropore tubes, occur in many genera of the Stylasterina but are lacking in others. On their entire surface they bear small spines.

An axial structure in dactylopores of many genera, consisting of a longitudinal row of spicules, is designated as a dactylostyle.

Arrangement of gastropores and dactylopores in cyclosystems, with a varying number of dactylopores grouped around a gastropore, is an important structural character of stylasterine colonies. Radially arranged ridges between the dactylopores (pseudosepta) give the cyclosystems of some Stylasterina the appearance of the calice of a scleractinian coral. Cyclosystems may be scattered indiscriminately over the whole surface of the colony (as in *Allopora, Stylantheca, Conopora*) or may tend to be more abundant on the anterior surface than the posterior surface. In *Stylaster,* cyclosystems are chiefly or entirely restricted to lateral surfaces of the branches; in *Congregopora* they tend to show a linear arrangement on the branches; in *Stenohelia, Crypthelia* (except *C. trophostega* Fisher), and *Astya,* they are almost confined to the anterior surface of the colony. Although the cyclosystems generally are circular in outline, they may be distinctly oval with longer axis disposed longitudinally (as in *Stylaster bellus*) or transversely *(S. gemmascens)* with respect to the branches or horseshoe-shaped (Figs. 80,*3,4*). The pores of *Disticho*

pora are disposed in lines, rather than cyclosystems, a median row of gastropores being flanked on each side by a row of dactylopores (Fig. 83,*2b*).

The characters of ampullae are various. In *Stylaster* they occur normally on the posterior surface as well as on the anterior surface of the colony, although in some species they are concentrated on a single surface. The ampullae are more or less spherical cavities in the skeleton, generally with a roof that forms a well-marked bulge on the surface of the colony (Figs. 80,*1-4*), but expression of their occurrence in this manner may be very weak or even lacking entirely if the ampullae are buried completely in the coenosteum. The covering roof may have a smooth outer surface or it may be marked by ridges, tubercles, or spines. A small opening in the basal part or on the top can be observed in some ampullae. Those enclosing female gonophores are generally much larger than ampullae that serve for lodgment of male gonophores. Each sort occurs singly or in clusters and ampullae may be closely packed in the coenosteum between cyclosystems (as in *Stylantheca*).

OCCURRENCE

Recent species of Stylasterina are known to live in shallow waters, especially in the tropics, but they occur also in deeper seas (for example, *Crypthelia* to a depth of 2,745 m.). They are known from nearly all parts of the world, including the northern Atlantic and Pacific and waters adjacent to Antarctica.

The oldest fossils that are referred definitely to the Stylasterina occur in Upper Cretaceous (Danian) rocks of northwestern Europe. These include 7 genera and subgenera *(Conopora, Astya, Errina, Inferiolabiata, Pliobothrus, Sporadopora, Congregopora),* of which all but the last-named range to Recent. Species of 3 genera make first known appearance in Tertiary strata, *Stylaster* and *Distichopora* occurring in the Eocene and *Allopora* being recorded from the Oligocene. Eight genera seem to be confined to the Recent.

SYSTEMATIC DESCRIPTIONS
Family STYLASTERIDAE Gray, 1847
Characters of the order. *U.Cret.-Rec.*

Subfamily STYLASTERINAE Gray, 1847

[*nom. transl.* STECHOW, 1921 (*ex* Stylasteridae GRAY, 1847)]

Pores arranged in distinct cyclosystems. *U.Cret.(Dan.)-Rec.*

Stylaster GRAY, 1831 [**Madrepora rosea* PALLAS, 1866; SD M.EDW.-H., 1850] [=*Cyclopora* VERRILL, 1866 (*non* RAF., 1815); *Deontopora* HALL, 1893; *Eustylaster* BROCH, 1914]. Colony arborescent, generally flabelliform, branches slender, rarely coalescent. Cyclosystems on young branches alternating on left and right sides but a few on flat surfaces in older parts of colonies. Gastropores more or less cylindrical, commonly with gastro-style chamber and bearing a gastrostyle; each surrounded by 6 to 18 dactylopores, which bear dactylostyles. Ampullae scattered singly or grouped in clusters on the flat surfaces, where they form subhemispherical bulges or rarely are not elevated above the surface. *Eoc.-Rec.*——FIG. 80,*1.* **S. roseus* (PALLAS), Rec., W.Indies; colony with female ampullae, ×5 (35*).——FIG. 80,*3. S. microstriatus* BROCH, Rec., Japan; part of branch, ×10 (35*).——FIG. 80,*4. S. mooraboolensis* (HALL), Mio., Vict., Austral.; part of branch, ×8 (35*).

Allopora EHR., 1834 [**A. oculina* (=*Millepora norvegica* GUNNERUS, 1768)] [=*Cryptaxis* REUSS, 1865 (*non* LOWE, 1855); *Cryptaxiella* KÜHN,
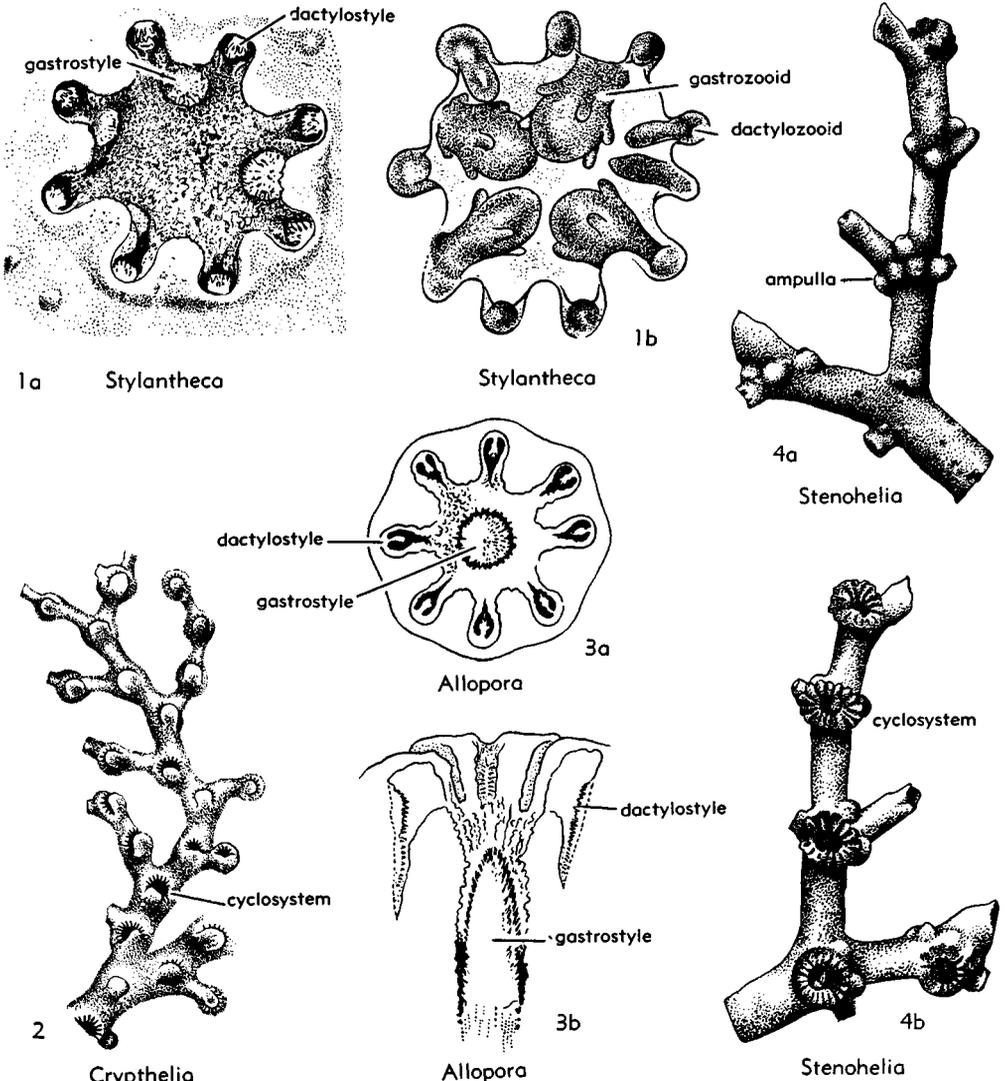

FIG. 81. Stylasteridae. *1a,b, S. porphyra*, Rec., ×30. *2, C. affinis*, Rec., ×2. *3a,b, A. verrilli*, Rec., ×30. *4a,b, S. profunda*, Rec., ×6 (p. F100).

1939]. Colony with rather thick branches, arborescent, flabelliform, lobed, or forming lumpy incrustations. Cyclosystems scattered on all surfaces. Structure as in *Stylaster*. Ampullae buried in coenosteum, with little or no swelling at surface, rarely hemispherical. *Oligo.-Rec.*——FIG. 80,*5*. *A. norvegica* (GUNNERUS), Rec., Norway; part of branch, ×6 (35*).——FIG. 81,*3a,b*. *A. verrilli* DALL, Rec., N.Pac.; *3a*, surface view of cyclosystem, ×30 (40); *3b*, long. sec., ×30 (40).

Stenohelia KENT, 1870 [*Allopora maderensis* JOHNSON, 1862]. Colony arborescent, flabelliform, branches slender, not coalescent. Cyclosystems as in *Stylaster* but all directed toward anterior surface. Gastropores surrounded by 8 to 12 dactylopores. Ampullae hemispherical, prominent, on posterior surface, commonly in groups behind cyclosystems. *Rec.*——FIG. 81,*4a,b*. *S. profunda* MOSELEY, Rec., Kermadec I.; *4a,b*, posterior and anterior surfaces, ×6 (35*).

Stylantheca FISHER, 1931 [*S. porphyra*]. Colony encrusting. Like *Allopora* in structure but cyclosystems generally with 3 to 7 gastrostyles; 8 to 12 dactylopores around gastropores. Ampullae in coenosteum, not bulging surface. *Rec.*——FIG. 81, *1a,b*. *S. porphyra*, Rec., N.Pac.(Calif.); *1a,b*, cyclosystems with 8 dactylostyles around 4 gastrostyles and 10 dactylozooids around 4 gastrozooids, ×30 (40).

Crypthelia M.EDW.-H., 1849 [*C. pudica*] [=*Endhelia* M.EDW.-H., 1849; *Endohelia* (*nom. van.*), *Cryptohelia* M.EDW.-H., 1857]. Colony flabelliform, branches slender, rarely coalescent. Cyclosystems only on anterior surface (except in *C. trophostega* FISHER) partly covered by marginally adherent lid; gastropores without gastrostyles, surrounded by 10 to 25 dactylopores without dactylostyles; ventral chamber of gastropore separated by diaphragm with circular opening. Ampullae in coenosteum near cyclosystems or in lid, commonly marked by distinct swellings. *Rec.*——FIG. 81,*2*. *C. affinis* MOSELEY, Rec., W.Indies; part of branch, ×2 (31).——FIG. 82,*1a*. *C. stenopoma* HICKSON & ENGLAND, Rec., E. Indies; upper view of cyclosystem, ×21 (42).——FIG. 82,*1b*. *C. pachypoma* HICKSON & ENGLAND, Rec., E.Indies; oblique view of cyclosystem, ×21 (42).

Conopora MOSELEY, 1879 [*C. tenuis*]. Colony branching irregularly, rarely flabelliform, not coalescent. Cyclosystems generally on all sides but in flabelliform types on anterior surface; 3 to 16 dactylopores around gastropore, interconnecting with lower part of gastropore; no gastrostyles or dactylostyles. Ampullae subhemispherical swellings, mostly on surface turned away from cyclosystems. *U.Cret.(Dan.)-Rec.*——FIG. 82,*2c*. *C. major* HICKSON & ENGLAND, Rec., Mauritius; part of branch with cyclosystems and ampullae, ×9 (36).——FIG. 82,*2a*. *C. tenuis*, Rec., Mauritius; long.

sec. of cyclosystem showing openings to dactylopore in lower part of gastropore, ×19 (36).——FIG. 82,*2b*. *C. pauciseptata* BROCH, Rec., Antarct.; 3 cyclosystems on anterior surface of stem, ×15 (35*).

Astya STECHOW, 1921 [*pro Astylus* MOSELEY, 1879 (*non* LAPORTE, 1836)] [*Astylus subviridis* MOSELEY, 1879]. Colony flabelliform, branches slender, not coalescent. Cyclosystems all directed toward anterior surface; about 20 dactylopores around gastropore, which has ventral chamber separated by diaphragm with crescentic opening. No gastrostyles or dactylostyles. Ampullae in circular rows around cyclosystems on anterior surface, surface slightly bulged. *U.Cret.(Dan.)-Rec.*——FIG. 82,*3*. *A. subviridis* (MOSELEY), Rec., SW.Pac.; part of branch, ×3 (44).

Congregopora NIELSEN, 1919 [*C. nasiformis*]. Colony arborescent to flabelliform. Cyclosystems on all sides of branches, tending to linear arrangement; 2 or 3 dactylopores united with a gastropore, forming 3-cornered opening surrounded by slightly raised wall, other isolated dactylopores scattered over surface. No gastrostyles or dactylostyles. Ampullae seemingly hemispherical. *U.Cret. (Dan.).*——FIG. 82,*4a-c*. *C. nasiformis*, Dan., Denm.; *4a*, colony, ×1 (45); *4b,c*, parts of branches, ×6, ×8 (35*).

Subfamily DISTICHOPORINAE Stechow, 1921

Pores in linear rows, with median row of gastropores flanked on each side by a row of dactylopores. *Eoc.-Rec.*

Distichopora LAMARCK, 1816 [*Millepora violacea* PALLAS, 1766]. Colony flabelliform, with branches generally flattened antero-posteriorly. No cyclosystems, pores being arranged in rows at lateral margins of branches or rarely (*D. irregularis* MOSELEY) on flat surface of branches also; pores deep; gastropores with long gastrostyle, dactylostyles absent. Ampullae forming slight to hemispherical bulges on anterior and posterior surfaces, generally in clusters or united in solid mass. *Eoc.-Rec.*——FIG. 83,*2a*. *D. violacea* (PALLAS), Rec., "South Sea"; colony with many ampullae, ×1 (39).——FIG. 83,*2b*. *D. serpens* BROCH, Rec., SW. Pac.; side view of branch, ×20 (36).

Subfamily ERRININAE Hickson, 1912

[*nom. correct.* STECHOW, 1921 (*ex* Errinina HICKSON, 1912)] [=Sporadoporidae GREGORY, 1930]

Pores not in distinct cyclosystems; if in linear rows, gastropores are somewhat widely separated from dactylopores. *U.Cret. (Dan.)-Rec.*

Errina GRAY, 1835 [*Millepora aspera* LINNÉ, 1767] [=*Labiopora* MOSELEY, 1879]. Colony arborescent, flabelliform to irregular bushy, branches generally not coalescent. Pores not arranged in distinct cyclo-
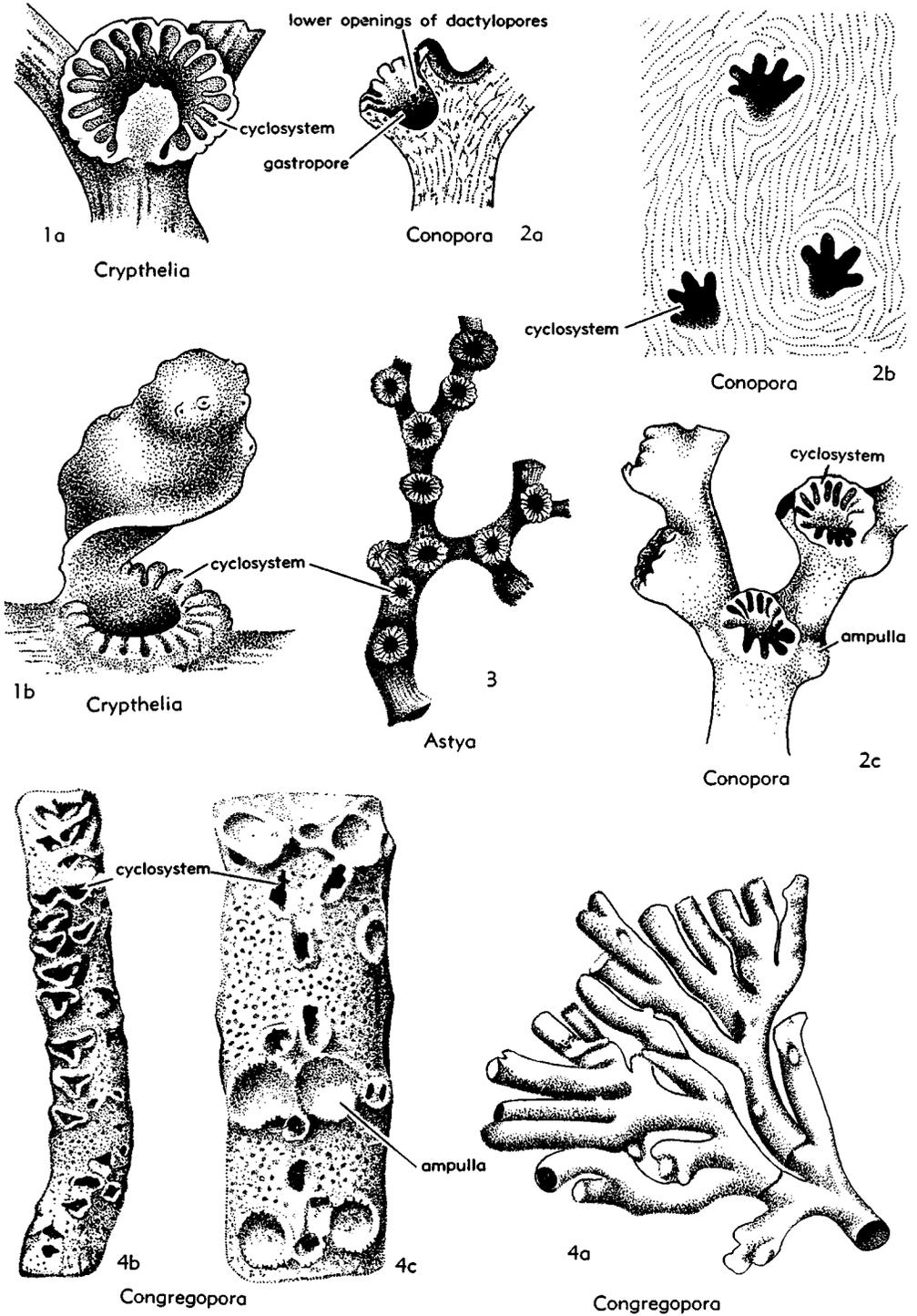
FIG. 82. Stylasteridae. *1a, C. stenopoma*, Rec., ×21. *1b, C. pachypoma*, Rec., ×21. *2a, C. tenuis*, Rec., ×19. *2b, C. pauciseptata*, Rec., ×15. *2c, C. major*, Rec., ×9. *3, A. subviridis*, Rec., ×3. *4a-c, C. nasiformis*, Dan., ×1, ×6, ×8 (p. F100).
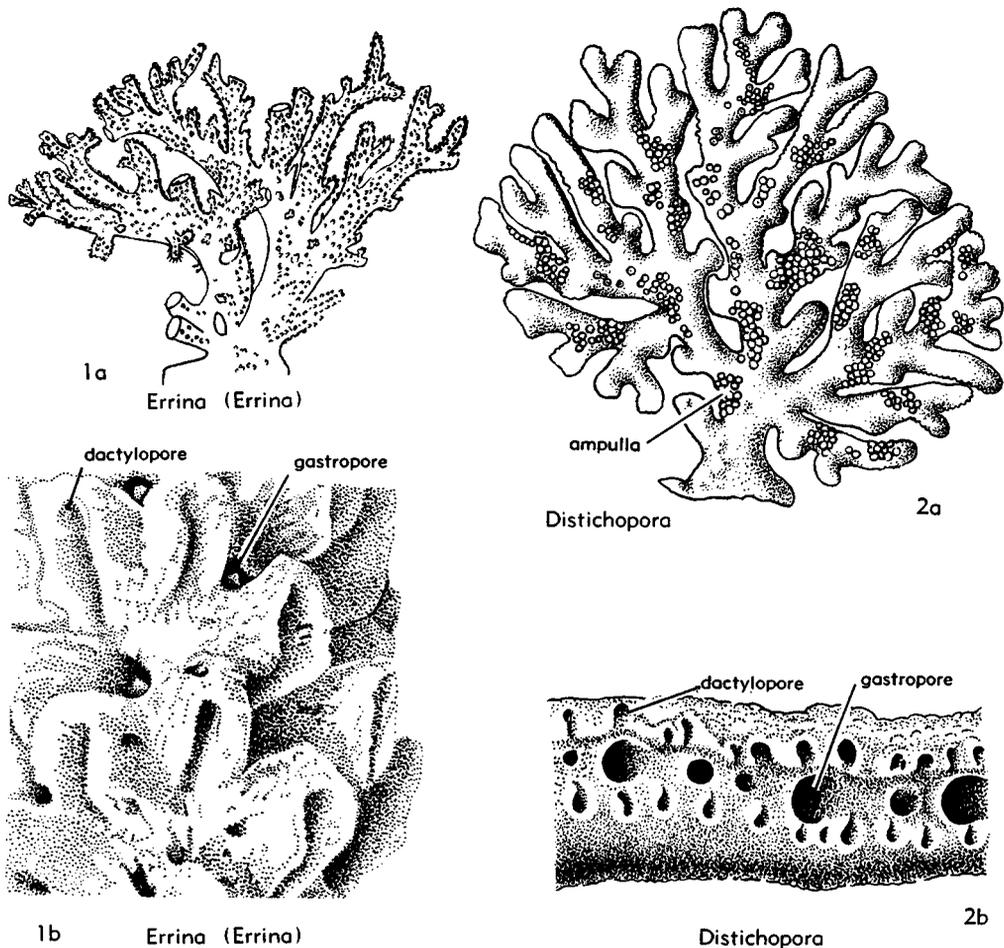
FIG. 83. Stylasteridae. *1a, E. (E.) novaezelandiae*, Rec., *ca.* ×1.2. *1b, E. (E.) antarctica*, Rec., ×16. *2a, D. violacea*, Rec., ×1. *2b, D. serpens*, Rec., ×20 (p. F100-F102).

systems; gastropores with well-developed gastrostyle, not surrounded by a wall. Dactylopores without dactylostyles. Ampullae embedded in coenosteum or making slight to hemispherical bulge at surface. *U.Cret.(Dan.)-Rec.*

E. (Errina) [=*Euerrina* BROCH, 1942]. Dactylopores at base and in groove of a grooved spine with opening directed toward base of colony, some dactylopores without spines scattered over surface. *U.Cret.(Dan.)-Rec.*——FIG. 83,*1a. E. (E.) novaezelandiae* HICKSON, Rec., N.Z.; colony, slightly enlarged (41).——FIG. 83,*1b. E. (E.) antarctica* (GRAY), Rec., Antarct.; side of part of branch, ×16 (30).

E. (Inferiolabiata) BROCH, 1951 [*Errina labiata* MOSELEY, 1879] [=?*Lepidopora* POURTALÈS, 1871; *Acanthopora* MOSELEY, 1876 (*non* ORB., 1849); *Spinipora* MOSELEY, 1879 (*non* AGASSIZ, 1846); *Labiata* BROCH, 1942 (*non* FABRICIUS,

1823)]. Grooves of grooved spines turned toward top of branches. Some species (*"Lepidopora"*) have gastropores with lip at lower margin present both on anterior and posterior surfaces of colony; dactylopores in a continuous line on lateral margins of branches and scattered among gastropores. *U.Cret.(Dan.)-Rec.*——FIG. 84,*1a. E. (I.) glabra* (POURTALÈS), Rec., W.Indies; anterior surface of branchlet, ×6 (46).——FIG. 84,*1b,c. E. (I.) echinata* MOSELEY, Rec., S.Atl.; *1b*, gastrozooid and 4 dactylozooids with connecting canals, ×15; *1c*, side of part of branch, ×7 (both 44).

Errinopora FISHER, 1931 [*Errina pourtalesii* DALL, 1884] [=*Protoërrina* BROCH, 1935]. Colony dendritic or flabelliform. Cyclosystems rarely distinct, with 5 to 7 dactylopores around a gastropore, dactylopores commonly scattered irregularly among gastropores, which are not surrounded by wall; dactylopores with grooved spines, groove oriented
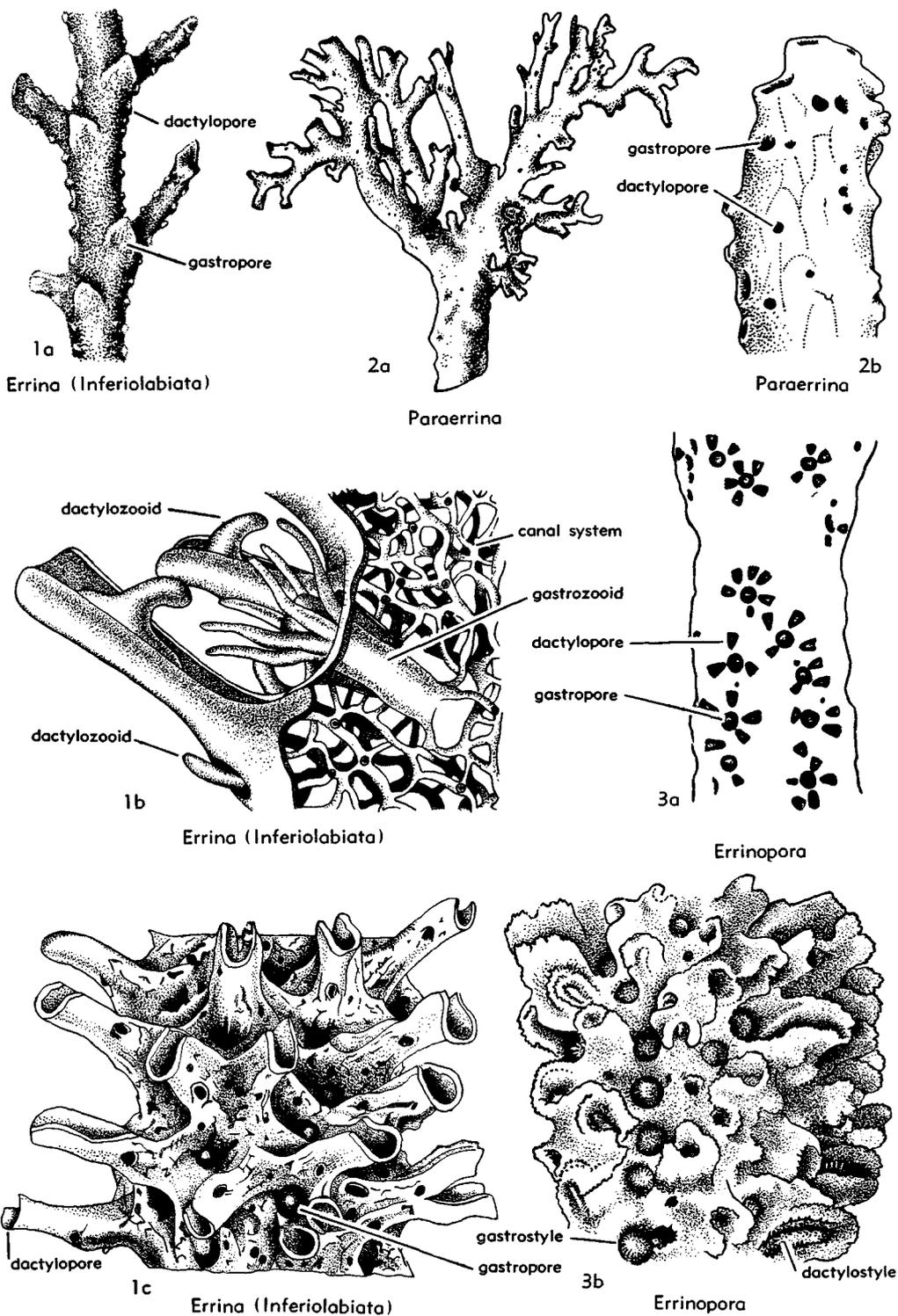
FIG. 84. Stylasteridae. *1a, E. (I.) glabra*, Rec., ×6. *1b,c, E. (I.) echinata*, Rec., ×15, ×7. *2a,b, P. decipiens*, Rec., ×1, ×20. *3a, E. stylifera*, Rec., ×5.5; *3b, E. pourtalesii*, Rec., ×15 (p. F102-F104).

variously. Gastrostyles and dactylostyles present, latter prolonged in grooves of spines. Ampullae form slight swellings or hemispherical bulges at surface. *Rec.*——Fig. 84,*3a*. *E. stylifera* (Broch), Rec., Okhotsk Sea; side of part of branch showing cyclosystems, ×5.5 (36).——Fig. 84,*3b*. **E. pourtalesii* (Dall), Rec., NE.Pac.(Calif.); side of part of branch, ×15 (40).

Paraërrina Broch, 1942 [**P. decipiens*]. Like *Errinopora* but gastropores and dactylopores surrounded by low wall only in young branches, opening flush with surface in older parts of colony; no grooved spines. Ampullae form slight swellings to hemispherical bulges. *Rec.*——Fig. 84,*2a,b*. **P. decipiens*, Rec., Mauritius; *2a*, colony, ×1 (36); *2b*, end of branchlet, ×20 (36).

Errinopsis Broch, 1950 [**E. reticulum*]. Like *Errina* but flabelliform, branches strongly coalescent, forming a network. Ampullae in coenosteum, not forming bulges at surface. *Rec.*——Fig. 85,*4*. **E. reticulum*, Rec., Antarct.; part of colony, ×1 (36).

Phalangopora Kirkpatrick, 1887 [**P. regularis*]. Colony flabelliform, branches not coalescent. Gastropores generally in single row on anterior and posterior surfaces of branches, with feebly developed lip at lower margin; dactylopores in linear row on lateral margins of branches and scattered among gastropores. Gastrostyles and dactylostyles absent. Ampullae form hemispherical bulges on flat sides of colony. *Rec.*——Fig. 85,*2a,c*. **P. regularis*, Rec., Mauritius; *2a,b*, anterior surface and lateral view of part of branch, ×12; *2c*, part of colony, ×1.5 (both 43).

Pliobothrus Pourtalès, 1868 [**P. symmetricus;* SD Kühn, 1928]. Colony ramose, more or less regularly flabelliform, with flattened cylindrical branches. Gastropores without wall or gastrostyle; dactylopores opening at top of round tubercles, without dactylostyles. Ampullae in coenosteum, not visible externally. *U.Cret.(Dan.)-Rec.*——Fig. 85, *1a,b*. **P. symmetricus*, Rec.,N.Atl., W.Indies; *1a*, colony, ×1 (36); *1b*, part of branch, ×6 (46).

Sporadopora Moseley, 1879 [*pro Polypora* Moseley, 1876 (*non* M'Coy, 1844)] [**Polypora dichotoma* Moseley, 1876]. Colony consisting of stout vertical stems with some irregular branches, more or less flabelliform, flattened in anterior-posterior direction. Gastropores and dactylopores opening nearly flush with surface; gastrostyles present, dactylostyles absent. Ampullae in coenosteum, not bulging at surface. *U.Cret.(Dan.).-Rec.*——Fig. 85,*3a*. **S. dichotoma* (Moseley), Rec., S.Atl.; part of colony, ×0.5 (44).——Fig. 85,*3b*. *S. mortenseni* Broch, Rec., SW.Pac.(N.Z.); part of branch, ×20 (36).

?Steganopora Hickson & England, 1905 [*non Steginopora* Orb., 1853] [**S. spinosa* (?=*Pliobothrus spinosus, fide* Broch, 1942)]. Branch circular, tapering toward end. Gastropores opening flush with surface, dactylopores with orifice at top of long narrow tube; gastrostyles and dactylostyles absent. Ampullae hemispherical. *Rec.*

GENERA ERRONEOUSLY ASSIGNED TO STYLASTERINA

Aphyllacis Reuss, 1872.
Cylindropora Woods, 1880.
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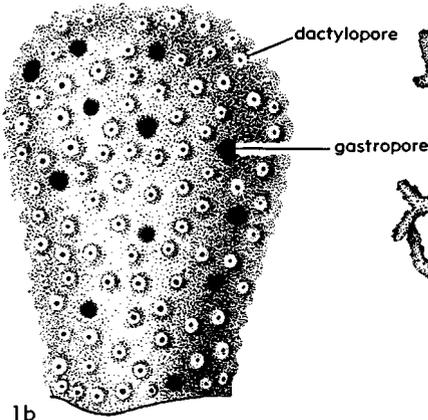(10) 1942, *Investigations on Stylasteridae (hydrocorals):* Same, 1942, no. 3, 113 p., 6 pl., 38 fig.
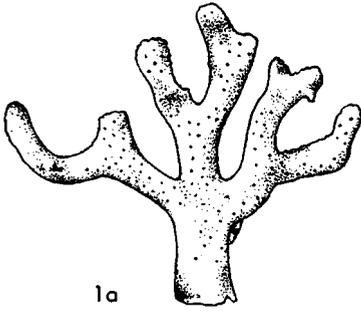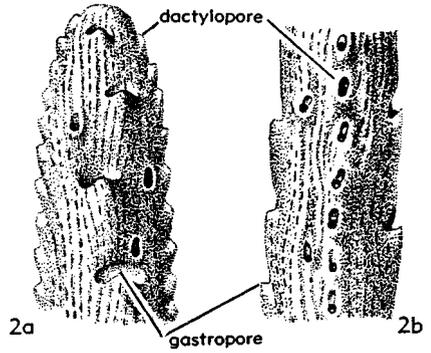
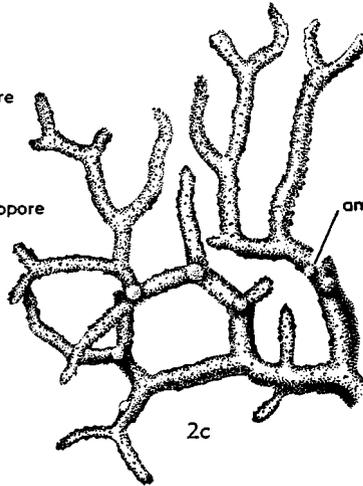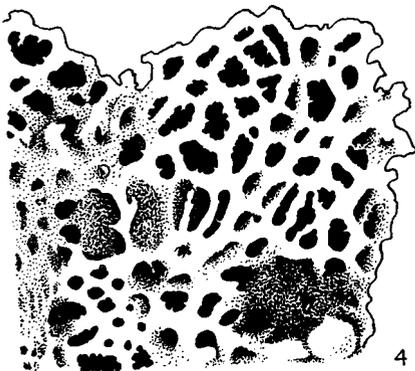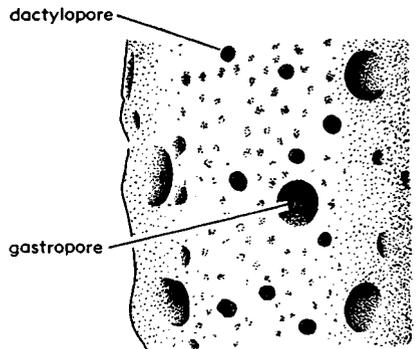FIG. 85. Stylasteridae. *1a,b, P. symmetricus*, Rec., ×1, ×6. *2a-c, P. regularis*, Rec.; *2a,b*, ×12; *2c*, ×1.5. *3a, S. dichotoma*, Rec., ×0.5. *3b, S. mortenseni*, Rec., ×20. *4, E. reticulum*, Rec., ×1.

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SOURCES OF ILLUSTRATIONS

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

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