PART F SUPPLEMENT 1

COELENTERATA: ANTHOZOA
SUBCLASSES RUGOSA, TABULATA

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INTRODUCTION TO PALEOZOIC CORALS

Paleozoic corals that can be referred with certainty to the Tabulata or the Rugosa, which are herein regarded as subclasses of Anthozoa, appeared late in the history of exploitation of the mineral skeleton, in the early Middle Ordovician. Though they flourished in the shallow-water environments in which carbonate reefs were formed, they were, with the possible exception of the Tabulata in parts of the Devonian, seldom the most important reef-builders.

Their origin is still uncertain; also uncertain are the relation of the two subclasses to one another and the relation of the Rugosa to the Scleractinia. Exciting possibilities exist for the elucidation of the evolutionary process in the Anthozoa, and rewards should be gained especially by careful study of Early and Middle Ordovician faunas, as well as by work on Late Permian and Early Triassic faunas.

The soft parts are universally considered to be polypal, as in the Scleractinia, with each polyp secreting an exoskeleton of calcium carbonate; but discussion still continues on whether the Paleozoic skeletons were originally of calcite or aragonite. The skeleton of a single polyp or of the protocorallite of a colony appears to be an inverted cone, thus differing from that of the Scleractinia, where an expanding cylinder seems to be the mode.

In the twenty years since publication of the first edition of the *Treatise,* Part F, there has been a remarkable increase in our knowledge of both Tabulata and Rugosa: the number of genera has doubled and the number of species has been multiplied many times. Much, perhaps most, of this growth has occurred in works published in the Russian language; and quite recently significant additions have been made in publications in Chinese. Indeed, this growth is such as to justify devoting a special part of the *Treatise* revision to the Paleozoic corals. The esthetic and intellectual appeal of the corals remains strong, and there is no lack of recruits to the ranks of specialists.

For this revision, only works published before the end of 1976 have been covered completely. Entries for new genera named between then and the end of September, 1978, have been made, but without illustration. The reviser has found it appropriate to be less audacious than in the first edition in placing generic names in subjective synonymy. Improvements in travel and communications make it possible and, indeed, essential to support judgments on subjective synonymy by study of the actual types and their supporting series, and we may look forward to work that is less peremptory but increasingly more definitive as future workers move by jet plane into such rigorous comparative studies. To facilitate such efforts, this revision indicates the name (see list of abbreviations, Editorial Preface, p. xxxi) and city of the institution conserving the type material, and the catalogue numbers of the holotypes or lectotypes of type species of genera wherever it has been possible to verify them.

Acknowledgments.—I am deeply indebted to my fellow workers on Paleozoic corals in all countries for sending me copies of their works and for correspondence quickening this revision of the *Treatise.* The soft-cover works have been bound in volumes of collected papers and, with the hardcover books, have been catalogued and placed in the Library of the University of Queensland in Brisbane.

I am beholden to officers of those museums where type specimens of type species of Paleozoic coral genera are held for correspondence concerning catalogue numbers, which have been incorporated in this revision for the convenience of traveling specialists—an innovation in *Treatise* convention. The correspondence has been filed with the Hill Papers in the archives section of the Fryer Memorial Library of the University of Queensland.

Many coral workers have kindly sent photographs of thin sections of type specimens of type species, and where these have been

published in the *Treatise* acknowledgment has been made in the text.

Since my retirement in 1972 I have been working full-time on this revision, the University of Queensland having made available to me an office and other facilities such as postage and photography. Dr. JOHN S. JELL, my colleague over many years, has continued to devote much time to discussion of coral matters and to details of photography.

Finally, I record my great appreciation of the devoted work of the editorial staff for *Treatise* revisions, Prof. CURT TEICHERT, Mrs. LAVON McCORMICK, Mr. ROGER B. WILLIAMS and, Mr. MICHAEL L. FREDERICK, and, since mid-1977, Prof. R. A. ROBISON and Mrs. VIRGINIA ASHLOCK.

MORPHOLOGY

TERMINOLOGY

There are a number of historical reviews, glossaries, and commentaries on rugosan terminology. HILL (1935) traced the evolution of MILNE-EDWARDS and HAIME's original terminology (1848a, bis 1850) through British and other English language publications and used updated results in the first edition of this *Treatise.* WEISSERMEL (1937, p. 87) commented on this terminology in the light of the German literature. In several studies on morphogenesis, culminating in SCHOUPPÉ and STACUL (1966), SCHOUPPÉ introduced some new terms and redefined old terms in the light of his morphogenetic assumptions. SOSHKINA (in SOSHKINA, DOBROLYUBOVA, & KABAKOVICH, 1962) set out the Russian terminology; IVANOVSKIY (1971a, p. 21, Engl. transl. 1971, p. 18) discussed several examples of lack of uniformity in usage and (1975a, p. 13) gave an updated glossary; and SOKOLOV, IVANOVSKIY, and KRASNOV (1971) presented a Russian terminological dictionary for the Coelenterata that included terms introduced in other languages. A glossary of equivalent morphological terms for Scleractinia in English, German, French, Italian, Spanish, Polish, Russian, and Bulgarian, edited by ZLATARSKY *et al.,* was circulated to coral specialists in "Fossil Cnidaria" (vol. 1973, no. 2). A handy modern French commentary is by SEMENOFF-TIAN-CHANSKY (1974, p. 32). Many authors sensibly clarify their own usage of terms, and several of them, such as MINATO and KATO (1965a, p. 1), have defined new and useful terms. The terms used herein are, as far as is humanly possible, objectively morphographic, and are intended to be used with descriptive adjectives or phrases appropriate to individual genera.

GENERAL FEATURES OF THE SKELETON

The Rugosa are an extinct Paleozoic subclass of corals forming calcareous exoskeletons in which the radial plates (**septa,** sing. **septum**) of each individual skeleton (**corallite**) are generally more noticeable than the transverse plates. The fundamental shape of the corallite is an inverted cone. Symmetry is bilateral, as indicated by the rugosan mode of septal insertion. The septa are typically of two orders, **major** and **minor,** the major (longer) septa alternating with the minor (shorter) septa. After insertion of the first four major septa, the remaining major septa are inserted serially at four points only. Minor septa are inserted serially and at an equal rate (but perhaps retroactively) with the major septa; in some forms they may be rudimentary and immersed in the corallite wall until late stages; they are confined to or extend but little beyond the **marginarium** (marginal zone), which in some forms is a peripheral stereozone of contiguous thick septa or septal bases without interseptal loculi. Septa are composed of cylindrical **trabeculae** directed distally and adaxially. In a very few Rugosa, there are no transverse plates; in many, the only transverse plates are the arched, flat, or sagging **tabulae** of the **tabularium** (wide axial space crossed by tabulae); in the others, the marginarium that surrounds the tabularium is a **dissepimentarium** with smaller, commonly arched plates inclined toward the tabularium and called **dissepiments. Axial structures,** which are **longitudinal skeletal elements** that in some forms are supported by transverse plates, may develop.

FINE STRUCTURE, MICROSTRUCTURE, AND ULTRASTRUCTURE

The calcareous tissue of the skeleton is **sclerenchyme.** With few exceptions, it is now of calcite. Diagenetic replacement of the original carbonate by silica, or more rarely by other substances, has occurred in some specimens.

Opinions differ on the original composition of the skeletal material. In many Rugosa, the apparent retention since the Ordovician of fibrous structure with extinction parallel to the long *(c)* axes of the fibers has been taken to support the view that the carbonate was originally calcite. *Lophophyllidium* skeletons found in impermeable Carboniferous shales and retaining their fibrous structure were of calcite, whereas orthocone cephalopod shells in the same shales were, as originally, of aragonite; further, the Sr/Ca ratios and $MgCo_3$ content of the rugosan skeletons were consistent with levels to be expected if the calcite were original (LOWENSTAM, 1963, p. 187). Skeletal inclusions found in authigenic quartz crystals formed in Devonian rugosan skeletons were of high-Mg calcite, whereas inclusions of other skeletons that were originally aragonite, but had transformed to calcite before their inclusion in the quartz, were of low-Mg calcite; consequently, RICHTER argued (1972, p. 211) that the rugosan skeletons were originally of calcite and not of aragonite.

On the other hand, OEKENTORP (1972, 1974a) has noted that some of the different types of microstructure in the rugosan skeleton appear to be the result of recrystallization, and are approximately the types that would be expected if the original skeleton had been aragonitic. OEKENTORP (1972, 1974a) has described many recrystallization patterns that are consistent with alteration from original aragonite to calcite, which he considered to be so similar to alteration patterns found in Scleractinia as to indicate an original aragonitic constitution in Rugosa also.

As seen under low magnifications, skeletal fine fabrics, where these have been retained, are fibrous and crystalline. The fibers extinguish with their long *(c)* axes perpendicular to the distal (growing) surface or edge of a skeletal element; they are commonly grouped in slender to very slender inverted cones, within which they spread apart slightly toward the depositional surface in the manner characteristic of conical segments of spherulites. In some very favorably preserved material, density (or light and dark) banding normal to the fibers and parallel to the growing surface is taken to indicate layered growth increments; apices of cones, where observed, are always directed toward the base of the layer.

Scanning electron microscope studies on the least altered material show that the fibrous structure is resolvable under higher and higher magnifications into a series of units decreasing in size, each of which is a narrowly to very narrowly conical aggregate of acicular crystals distally slightly spreading, again as in segments of spherulites (SORAUF, 1971, pl. 5-8). The smallest units are aggregated into larger ones of various dimensions; where the larger units are based one upon another, still with their long axes at right angles to the growing surface, the composite effect is the **fiber** seen through an optical microscope, which extinguishes parallel to its length. Altered material may show a secondarily lamellate structure (SORAUF, 1971, pl. 9-11).

In septa and other longitudinal skeletal elements, the fibers (and their constituent conical aggregates of distally slightly spreading needles) radiate from the axes of trabeculae, or less commonly from the axial plane of the septum. In tabulae and dissepiments, the fibers are directed at right angles to the growing surface of the plate. The patterns are those of spherulitic crystallization, plumose in the trabeculae and pilose in the tabulae. Where fibers are seen between septal bases in the outer wall (but not in its epitheca), they are perpendicular to the inner surface of the wall. The crystalline constitutions of the epitheca and of the basal 'dark line' (selvage appearing dark in transmitted light, but densely white in reflected light) to the tabulae and dissepiments have not been satisfactorily resolved.

Diagenesis commonly masks or destroys the original fabric of rugosan sclerenchyme (HILL & BUTLER, 1936, p. 523; KATO, 1963, p. 605; OEKENTORP, 1972, p. 49; 1974b, p. 15). The degree of alteration varies greatly

even in one corallum. Diagenesis of thick, contiguous trabeculae may produce holacanths immersed in pseudo–growth lamellae. **Holacanths** are clear calcite recrystallizations of the axial parts of trabeculae, particularly of rhabdacanths, and the **secondary lamellation** (possibly cleavage) is commonly somewhat oblique to the original growth lamellation. In some thick septa the 'median plane' (normally dark as seen by transmitted light, but densely white by reflected light) may be selectively recrystallized into clear calcite, commonly in patterns of some value taxonomically, as, indeed, other diagenetically induced patterns may be. The **zigzag** structure noted by Schindewolf (1942, pl. 12) is now seen to be a secondary (?cleavage) structure in originally normally structured, thick sclerenchyme. In many Rugosa, all or part of the original fibrous fabric is replaced by a secondary, fine or coarse calcite mosaic.

The microstructure (seen by means of the optical microscope) and the ultramicrostructure (shown by the scanning electron microscope) of the rugosan sclerenchyme are so similar to those of Scleractinia that the same processes are assumed to have formed them. The smallest unit (**microtuft**) yet found by ultramicroscopy in scleractinian sclerenchyme is probably composite. Etched material indicates that it tapers proximally but is terminated distally by pyramidal faces, and is 0.3 to 1.5 μm thick at the broadest part and 8 to 15 μm long; smaller crystals based on its distal end diverge somewhat from its long axis (Jell & Hill, 1974 ,p. 9, pl. 1, fig. 5). These units are arranged in layers parallel to the growing surface of the plate, and the axis of each unit is perpendicular to this surface. Aggregations of the units (Fig. 1) form a series of increasingly larger conical segments of spherulites (**tufts**); larger aggregates of tufts may project from the surface of the plate as **fascicles** (called **sclerodermites** by some). As in the Rugosa, a simple trabecula is composed of tufts or fascicles radiating orthogonally or clinogonally from its axis as in plumose spherulitic aggregates. In a tabula or dissepiment (except for the basal dark line), tufts and fascicles have their long axes perpendicular to the surface of the plate in a pilose spherulitic pattern
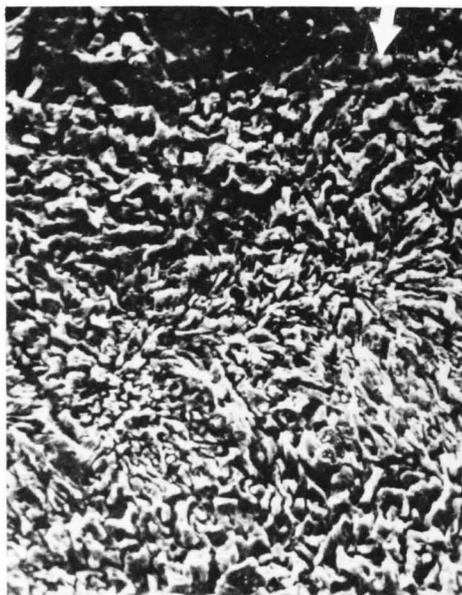
1a

1b   **Phacellophyllum**

Fig. 1. Rugose coral morphology; ultrastructure of septum of *Phacellophyllum caespitosum* (Goldfuss), M.Dev., Ger.——*1a*, transv. sec., arrow points to lateral margin of septum parallel to top of photo, $\times$435; *1b*, part of same, aggregates of microtufts radiate from trabecular centers, $\times$1,740 (Sorauf, 1971).

(Bryan & Hill, 1941, p. 89; Sorauf, 1972a; Jell & Hill, 1974).
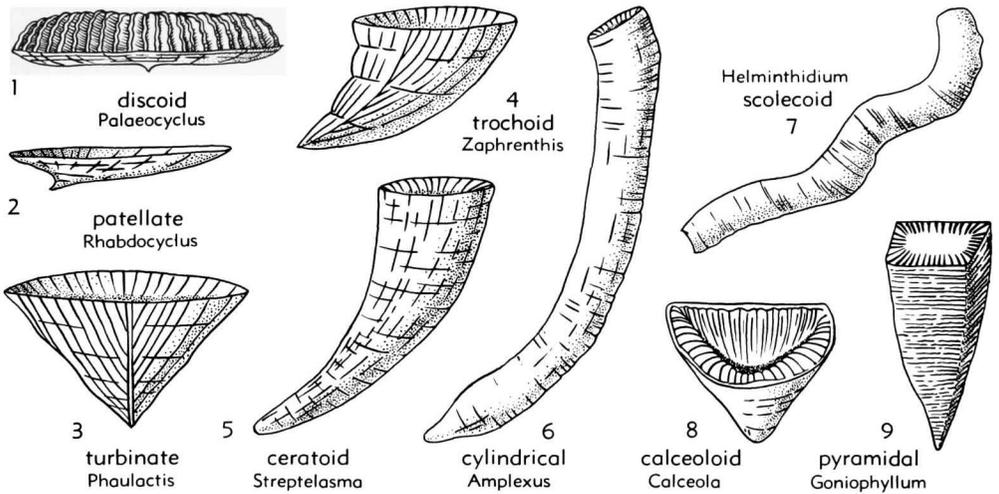
Fig. 2. Rugose coral morphology; types of simple coralla (after Hill, 1956b).——*1, Palaeocyclus porpita* (Linné), Sil., Eu.; ×2.——*2, Rhabdocyclus fletcheri* (Milne-Edwards & Haime), Sil., Eng.; ×1.5.—— *3, Phaulactis* sp., Sil., Eng.; ×1.——*4, Zaphrenthis* sp., M.Dev., N.Am.; ×1.——*5, Streptelasma* sp., Sil., Eng.; ×1.——*6, Amplexus* sp., L.Carb., Eng.; ×0.3.——*7, Helminthidium mirum* Lindström, Sil., Eu.; ×1.——*8, Calceola sandalina* (Linné), L.Dev.-M.Dev., Eu.; ×1.——*9, Goniophyllum fletcheri* (Milne-Edwards & Haime), Sil., Eng.; ×1.

FORM OF CORALLA

SOLITARY CORALS

Solitary corallites may be curved or erect, and the fundamental shape is an inverted cone. Depending on the angle of the **apex** and such characteristics as the growth form of the mature region and the occurrence of sharp angulations or flattened areas (assumed to be due to rejuvenescence), the shape (Fig. 2) may be designated as **ceratoid** (very slenderly conical, horn-shaped), **cylindrical** (nearly straight and of uniform diameter except in the apical region), **scolecoid** (like cylindrical but irregularly bent in the manner of a worm), **trochoid** (regularly expanding from an apical angle of about 40°), **turbinate** (like trochoid but with wider apical angle, 70°), **patellate** (with still wider apical angle, about 120°), **discoid** (nearly all in a single plane), **calceoloid** (like the tip of a slipper, as in *Calceola*), or **pyramidal** (with flattened sides meeting at angles).

COMPOUND CORALS

In compound corals the entire skeleton forms the **corallum.** This term is traditionally used for the skeleton of the whole organism whether a colony or a single polyp. A **compound corallum** (Fig. 3) is called **fasciculate** if the corallites are cylindrical and not in contact. Fasciculate corals may be classified as **dendroid** (irregularly branching) or **phaceloid** (with neighboring corallites more or less parallel but not in contact). In some phaceloid coralla the corallites may be connected here and there by connecting processes (outgrowths from the wall, commonly hollow); or they may be **catenoid** (contiguous in separate ranks as in *Palaeophyllum*); or they may be connected by periodic lateral expansions of the calicular platforms (**connecting platforms**) of the corallites that occur simultaneously throughout the corallum, which is thus alternately phaceloid and cerioid as in *Sanidophyllum*. In **verticillate** coralla, fasciculate offsets are given off laterally in verticils (whorls) as in *Crataniophyllum*.

Compound coralla are described as **massive** if neighboring corallites are in contact and polygonal in section. Massive coralla are clothed in a common epithecal sheath, the **holotheca,** which may show the epithecal furrows proper to outer walls of the peripheral corallites, and may also show growth rings. Massive coralla are distinguished as
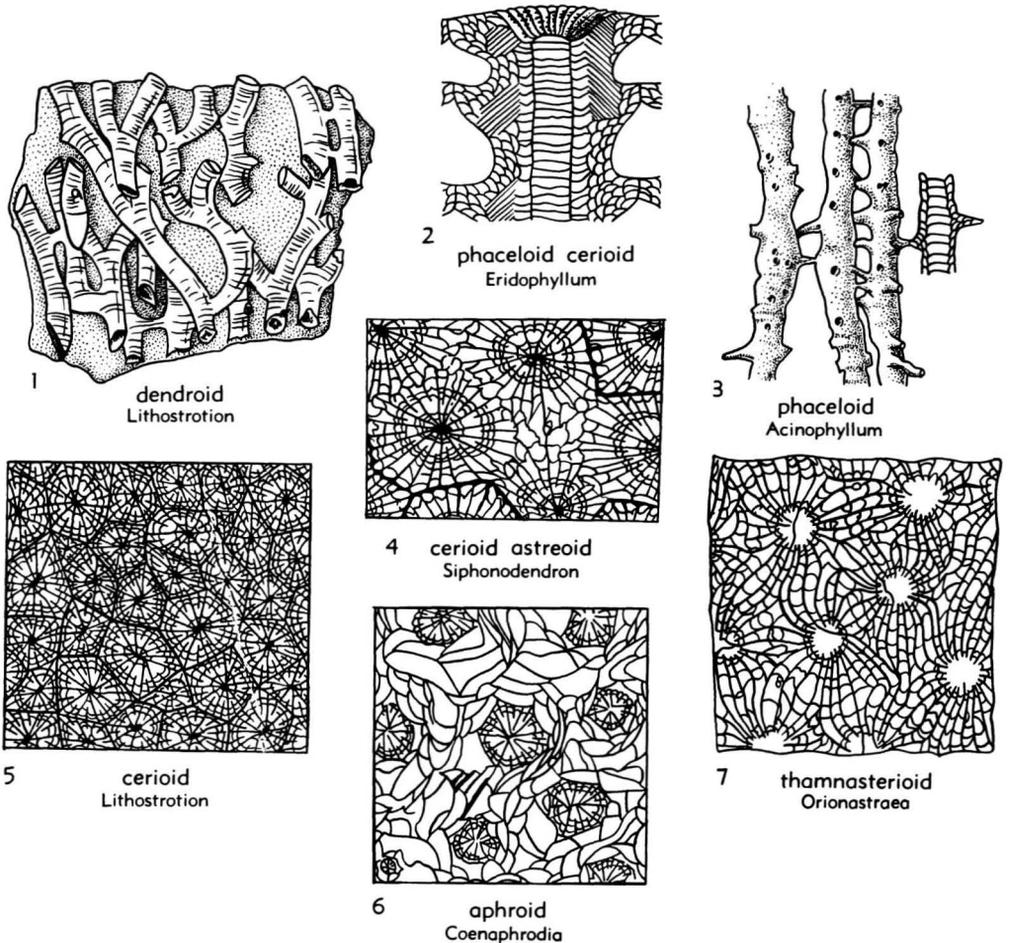
FIG. 3. Rugose coral morphology; types of compound coralla (after Hill, 1956b).——*1, Siphonodendron irregulare* (PHILLIPS), L.Carb., Eng.; ✕1.——*2, Eridophyllum colligatum* (BILLINGS), Dev., N.Am.; median long. sec., ✕1.3.——*3, Acinophyllum simcoense* (BILLINGS), Dev., N.Am.; corallite in median long. sec., ✕1.5.——*4, Lithostrotion columnare* ETHERIDGE, L.Carb., E.Australia; transv. sec., ✕1.5.—— *5, Lithostrotion arachnoideum* (M'COY), L.Carb., Eng.; transv. sec., ✕1.——*6, Coenaphrodia lonsdaleoides* (HILL), L.Carb., E.Australia (Queensl.); transv. sec., ✕1.5.——*7, Orionastraea garwoodi* HUDSON, L.Carb., Eng.; transv. sec., ✕2.

cerioid if each corallite is defined by a wall; some coralla are cerioid in some places, phaceloid in others. Coralla in which the corallites are not defined by walls are sometimes termed **plocoid,** though this term is used with a different meaning in Scleractinia; plocoid coralla are called 1) **astreoid** if the individual corallites lose their walls without reduction of the septa, which usually alternate in neighboring corallites; 2) **thamnasterioid (thamnastraeoid)** if the septa of neighboring corallites are confluent and arranged between the axes of corallites like the lines of force between poles in a magnetic field; or 3) **aphroid,** if the septa have become longitudinally discontinuous peripherally so that neighboring corallites are united by dissepiments only. Meandroid coralla are not known in Rugosa; some in which walls are locally discontinuous within neighboring series have been described as pseudomeandroid.

CALICE

The **calice** is the distal surface of a corallite, and is a mold of the base of the polyp

(Fig. 4,1). Many corallites have an evenly rounded, bowl-shaped calice, ranging in depth from very shallow (saucerlike) to deep (beakerlike). In some genera, particularly those with marginaria, the calice shows marked differentiation of inner and outer parts. The outer area, which may be nearly plane or even everted, constitutes the **calicular platform,** whereas the central part is abruptly depressed (**calicular pit**), or raised in a rounded or pointed prominence (**calicular boss**) (Fig. 4,3). In pyramidal or calceoloid coralla, the calice may be closed by an independent plate or plates, the **operculum** (Fig. 4,2), which is evidently drawn into a position of closure by the retraction of the polyp. Notable fossular depressions may occur at the edge of the tabularial floor, especially in solitary corals. The most marked of these is always the **cardinal fossula,** affecting the septal loculi on either side of the cardinal septum: it is most commonly located on the longest (**convex**) side of the corallite; in some it is on the shortest (**concave**) side; and in at least a small number of species it appears not to have taxonomic value in that it is variably placed in relation to the curvature of the corallite. It is much better developed in solitary corallites than in the corallites of compound coralla. In some solitary coralla, also, the calice is very deep, extending almost to the apex; in a few it is separated from the wall, not by tabulae and dissepiments but only by layers of sclerenchyme that thicken the wall and septa. Minor septa as well as major septa are ?always distinguishable at the calical edge. Epithecal growth rings mark the successive positions of the calical edge, which is commonly transverse to the erect or curving axis of growth of the corallite. WEYER (1972b, p. 722) has stressed the taxonomic importance of features of the calice.

WALLS

OUTER WALL

The **wall** (outer wall) is developed up to the edge of the calice in most solitary corallites and in the corallites of fasciculate coralla. Common double walls define the limits of neighboring corallites in cerioid coralla, but a common wall may be absent
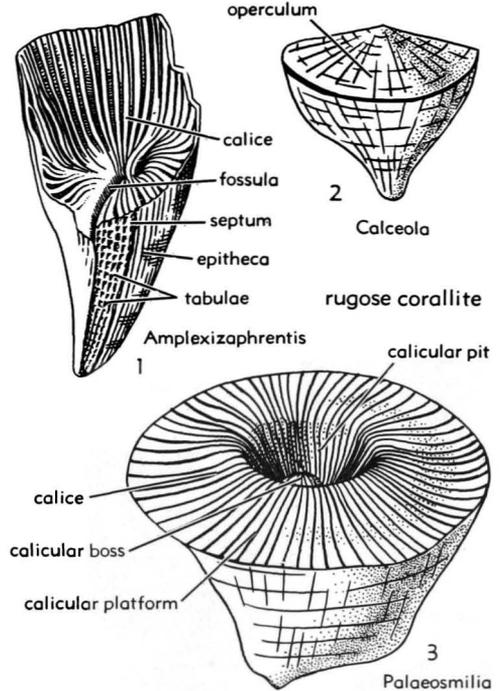
FIG. 4. Rugose coral morphology; calical characters (after Hill, 1956b).——*1, Amplexizaphrentis enniskilleni* (MILNE-EDWARDS & HAIME), L.Carb., Eu.; ×1.——*2, Calceola sandalina* (LINNÉ), M. Dev., Eu.; ×1.——*3, Palaeosmilia murchisoni* MILNE-EDWARDS & HAIME, L.Carb., Eu.; ×1.

or imperfectly developed in astraeoid, aphroid, and thamnasterioid coralla.

The wall may be extended as hollow or solid spines; or into **radiciform processes** (if tubular termed **rootlets** or flattened, **talons**) that fix the corallite to the substrate. In fasciculate coralla such processes fix a corallite to its neighbors and are termed **connecting tubules.**

The external surface of the wall is seldom smooth in the unworn state. It may show transverse **growth rings** or longitudinal furrows and ribs. The growth rings may show periodicity in spacing, and less commonly in strength of development (Fig. 5,2). The furrows coincide with the median planes of the septa and hence are called **septal furrows,** and the ridges lie opposite the interseptal loculi and are thus **interseptal ridges** or ribs. The furrows are commonly narrow and deep, and the intervening ridges broad and rounded, but in some species with thick

1 Coelostylis

2 Sutherlandinia

3 Stereolasma

4 Tryplasma

5a Ditoecholasma

5b
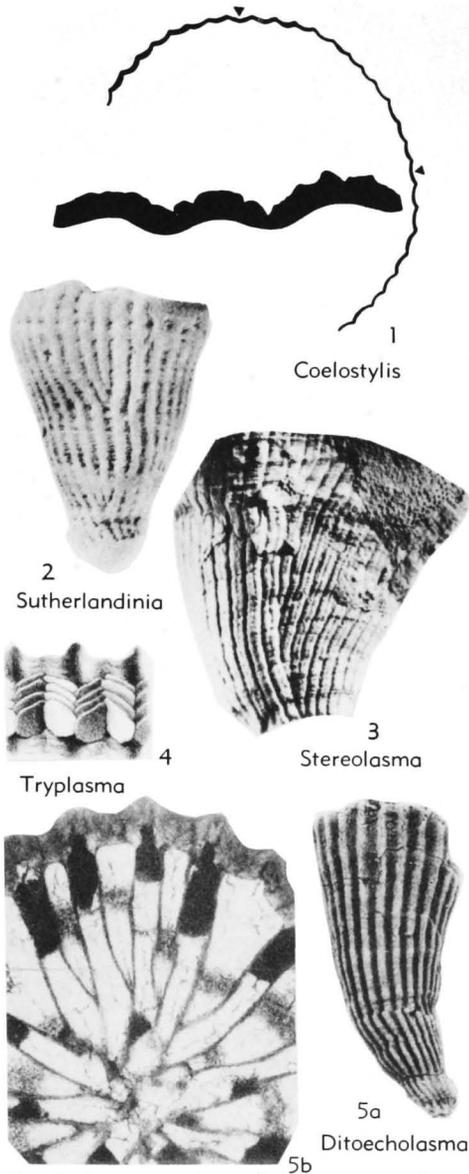
FIG. 5. Rugose coral morphology; outer wall.——
1, *Coelostylis* sp., M.Ord., erratic, Eu.(Ger. ?);
diagram showing broad shallow furrows and nodu-
lose upper surface of thick contiguous septa; enl.
(Weyer, 1972b).——2, *Sutherlandinia* sp., Sil.,
Gotl.; ×4.8 (Weyer, 1974b).——3, *Stereolasma
rectum* (HALL), M.Dev., N.Am.(N.Y.); showing
faint miniseptal (third order) furrows, ×2.4
(Weyer, 1974b).——4, *Tryplasma* sp., M.Sil., Eu.;
enl. (Lindström, 1883c).——5, *Ditoecholasma law-
rencense* SUTHERLAND, U.Sil., N.Am.; 5a, ext. view,
×2.4; 5b, transv. sec., showing lack of corres-
pondence between coarse furrows and median
septal planes, ×11.2 (Sutherland, 1965).

contiguous septal bases, the furrows may be
very broad and shallow, corresponding with
the entire septal base, and the ridges may
be narrow and sharp (Fig. 5,*1*). In a few
species with very coarse longitudinal ribbing
and grooving, there seems to be no corre-
spondence between furrow and median sep-
tal plane (Fig. 5,*5a,b*); these require study.

Small **scales** in overlapping series may be
attached to the furrows and ribs; they are
known not only in Rugosa (Tryplasmatidae
mainly), but also, rarely, in Tabulata (Fig.
5,*4*).

The plan of the septal furrows is diag-
nostic of the Rugosa. They are arranged in
four groups. In two of these, they lie pin-
nately to the cardinal septal furrow; in each
of the other two, they lie at an acute angle
to an alar septal furrow. Unworn apices
are very uncommon. In the few available
unretouched photographic illustrations (Fig.
5,*2,3*), a furrow that lies next to and parallel
with the cardinal or alar septal furrow ap-
pears additively composite due to the way
in which each successive furrow, whether
major or minor, joins (or nearly joins) it.
The length of furrow between successive
junctions may be approximately equal, or
unequal as in Figure 5,*2*. For discussion
of the initiation and lengthening of furrows,
see below in the section on septal insertion.
In a few genera, faint longitudinal furrows,
which may arise by intercalation, appear on
the ridges between neighboring major and
minor septal furrows (Fig. 5,*3*).

In thin section in well-preserved material,
the outermost part of the wall may be seen
to consist of a very thin layer of or with
growth rings, the **epitheca** *sensu stricto*.
Some authors use the term epitheca for the
whole of the outer wall, but herein only
the outer layer is termed epitheca, and the
total structure is called the outer wall, or
simply the wall. The epitheca has a texture
different from that of the rest of the wall,
which is much thicker and consists of fibers
like those of the septal trabeculae and tabu-
lae. In many Rugosa it appears that fibers
proper to neighboring septal bases may be
contiguous so that except for the epitheca
the wall is of septal origin; in many of these,
not only the base but much more of the
peripheral ends of the septa are so thickened
as to be contiguous and thus to widen the
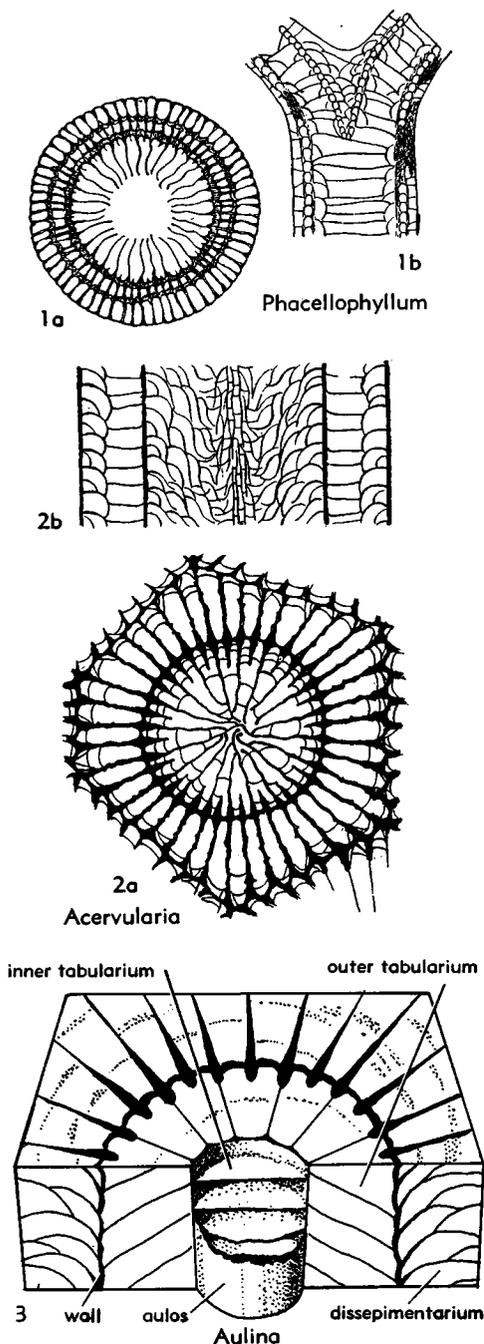
1b

Phacellophyllum

1a

2b

2a

Acervularia

inner tabularium   outer tabularium

3   wall   aulos   dissepimentarium

Aulina

wall into a peripheral **stereozone.** In other Rugosa the orientation of the fibers suggests that between the septal bases there may be distinct segments of wall connecting the septal bases.

A common outer layer with growth rings, the **holotheca** (HUDSON, 1929, p. 442), sheaths the outer walls of the peripheral corallites in massive Rugosa.

In corallites with exsert septal edges (i.e., with everted calical platforms), the wall does not keep pace with the distal growth of the septa.

INNER WALLS

Walls inside the lumen are quite varied in nature and are best described specifically (Fig. 6). One type, delimiting the tabularium from the dissepimentarium, develops when, as in most dissepimented genera, the proximal edge of each dissepiment of the innermost series rests on the distal surface of the dissepiment next below (Fig. 6,*3*). In some genera, however, the dissepiments interdigitate with the outermost tabellae and there is no continuous wall to the dissepimentarium (Fig. 6,*2*).

A wall separating inner and outer parts of a tabularium is an **aulos** when the axial space it encloses is crossed only by tabulae, and a **column wall** when it surrounds an axial column that contains both septal lamellae and tabellae (Fig. 192,*3*).

Walls within the dissepimentarium include a **pipe** of horseshoe dissepiments (in the Phillipsastreidae, Fig. 6,*1*) and a regular **inner septal stereozone** formed by a narrow zonal thickening to contiguity of neighboring septa (in Acervulariidae, Fig. 6,*2*). Both these types may have developed outside them a narrow zone of flat dissepiments and both types develop at the position of fanwise divergence of the septal trabeculae in the radial longitudinal planes of neighboring septa.

FIG. 6. Rugose coral morphology; inner walls.——— *1, Phacellophyllum* sp., M.Dev., Eu.; *1a,b,* transv., long. secs., showing pipe of horseshoe dissepiments, ×3, ×1.5 (Lang & Smith, 1935).——*2, Acervularia ananas* (LINNÉ), Sil., Eu.; *2a,b,* transv., long. secs., showing inner wall near but not at inner edge of dissepimentarium, ×3 (Lang & Smith,

1927).——*3, Aulina rotiformis* SMITH, L.Carb., Eng.; diagramm., showing wall between dissepimentarium and tabularium, and also aulos between inner and outer tabularium, ×18 (Smith, 1917). See also Fig. 232, *3, Aulophyllum fungites* (FLEMING), showing wall between dissepimentarium and tabularium, and wall around axial column.
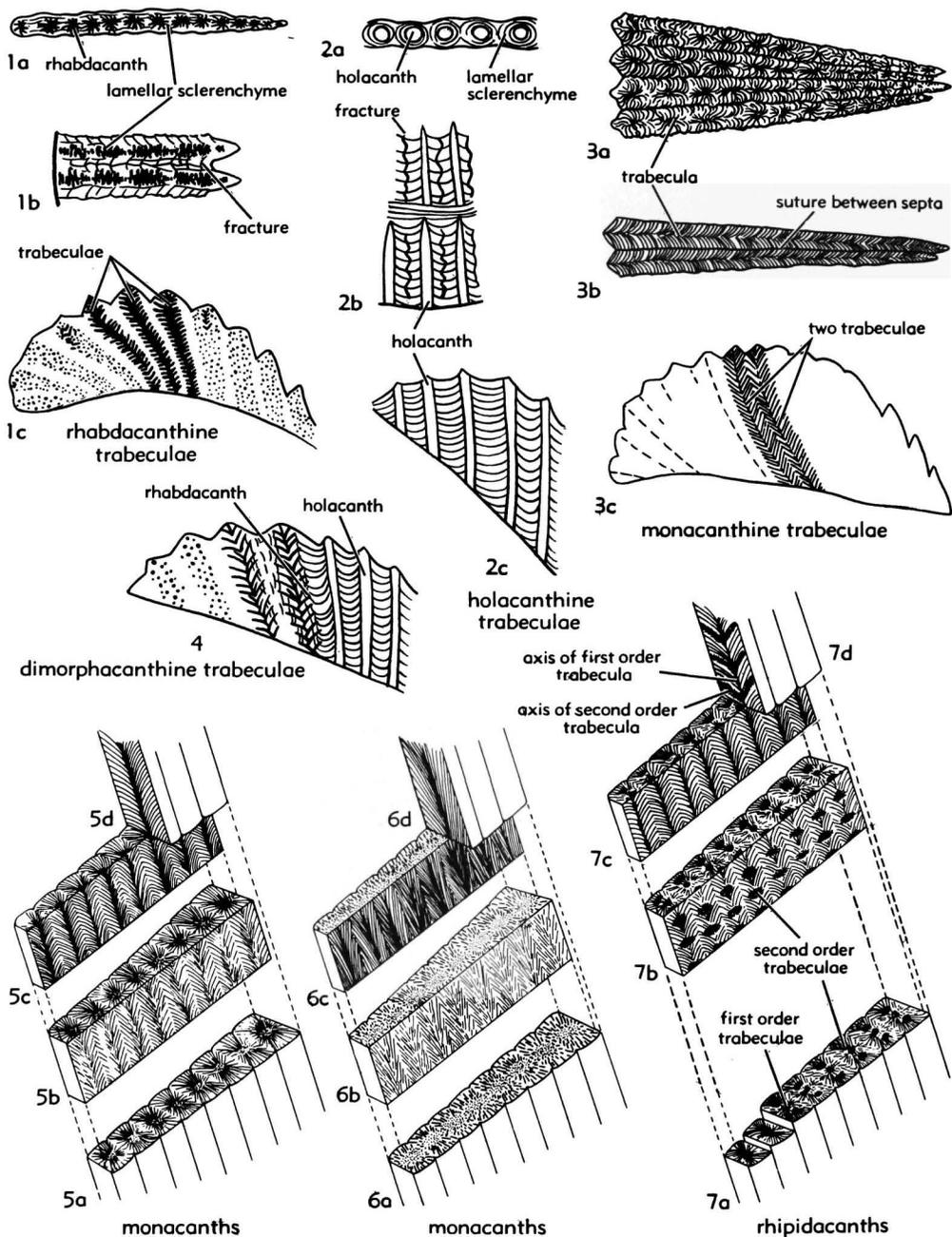
Fig. 7. Rugose coral morphology; types of trabeculae.——*1*, Rhabdacanths in *Rhabdocyclus porpitoides* (LANG & SMITH), Sil., Eng.; *1a*, transv. sec. cut at right angle to trabeculae; *1b*, transv. sec. cut obliquely to trabeculae; *1c*, long. sec. with three central trabeculae shown in median long. sec., others in tang. long. sec., all enl.——*2*, Holacanths (secondary structures formed during diagenesis) in *Tryplasma primum* HILL, M.Sil., Eng.; *2a*, transv. sec. cut at right angle to trabeculae; *2b*, transv. sec. cut obliquely to trabeculae; *2c*, long. sec., all enl.——*3*, Monacanths in *Palaeocyclus porpita* (LINNÉ), Sil., Eu.; *3a*, four septa in transv. sec. cut at right angle to trabeculae; *3b*, two septa in transv. sec. cut obliquely to trabeculae; *3c*, one septum in long. sec., structure of only two trabeculae being shown, all enl.——*4*, 'Dimorpha-

TRABECULAE

First order trabeculae have their axes entirely within the midplane of the septum, so that they end distally in the midline of its distal edge; **second order** trabeculae, which are shorter and finer, commonly originate either at the axis of a first order trabecula or in the midplane of the septum. Those originating in the midplane all diverge to end distally either on the lateral faces of the septa or on the lateral slopes of the round-arched distal edges of thick septa (Fig. 7).

First order trabeculae may be monacanths, rhabdacanths, or rhipidacanths. Second order trabeculae, as far as known, are always monacanthine in the arrangement of their constituent fibers. **Monacanths** have their fibers all related to one center only, radiating upward and outward from an axis formed by the upward shifting of the center *(Solipetra)*. A **rhabdacanth** has its fibers radiating from any number of separate, smaller transient centers so that it is composed of secondary trabeculae radiating upward and outward (Tryplasmatidae). In a **rhipidacanth**, those second order trabeculae directed laterally from the main axis are elongated relative to those in all other directions, and form closely spaced opposed carinae on the septal faces (Phillipsastreidae) (Fig. 8). First order trabeculae are commonly directed adaxially upward, but in some genera they may diverge inward and outward from a generally vertical or oblique **axis of divergence** in the septum. A septal carina (flange parallel to direction of distal growth of trabeculae) may be a single monacanthine trabecula, or a compound trabecula either of monacanthine elements branching prolifically, or of bundled trabeculae that branch infrequently or at a very low angle (SORAUF & OLIVER, 1976, p. 331).

axis of divergence of trabeculae

carinae of rhipidacanthine trabeculae
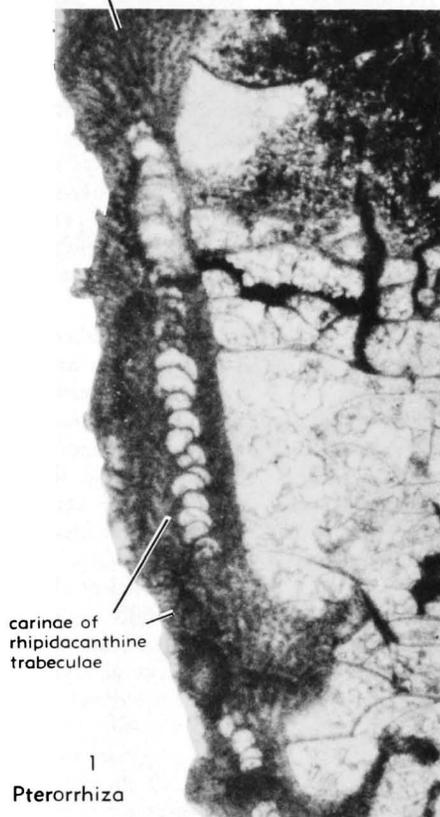
Pterorrhiza

FIG. 8. Rugose coral morphology; rhipidacanthine trabeculae. *Pterorrhiza gallica* (LANG & SMITH), Dev., Belg.; long. sec. showing carinae of rhipidacanth trabeculae and axis of divergence of trabeculae, ×8 (Hill, n).

SEPTA

Septa may be distinguished by the type of simple or compound trabeculae of which they are composed. Thus they may be **monacanthate, rhabdacanthate,** or **rhipidacanthate** when each consists of a single series of monacanths, rhabdacanths, or rhipida-

FIG. 7. (*Explanation continued from facing page.*)
canthine' septum in *Tryplasma primum* HILL, M.Sil., Eng.; long. sec., two rhabdacanth trabeculae cut medially, three trabeculae at right being holacanths, enl.——*5, Disphyllum* sp., U.Dev., W.Australia; monacanths in which fibers diverge from trabecular axes at a considerable angle; *5a,* transv. sec.; *5b,* tang. sec.; *5c,* median long. sec. in median plane of septum; *5d,* median long. sec. normal to median plane of septum, all enl.——*6, Gurievskiella* sp., L.Dev., Australia (N.Queensl.); monacanths in which fibers diverge from trabecular axes at low angle; *6a-d,* secs. as in 5, enl.——*7, Phillipsastrea* sp., M.Dev., Australia (New S.Wales); rhipidacanths showing first and second order trabeculae; *7a-d,* secs. as in 5, all enl. (Fig. 7,*1-4,* after Hill, 1956b; *7,5-7,* after Jell, 1969.)

canths; or they may be **holacanthine** when recrystallization has affected contiguous rhabdacanths (and possibly also monacanths) with the production of holacanths in secondarily lamellated sclerenchyme. Monacanthate and rhabdacanthate septa are **acanthine** when the trabeculae are not contiguous either wholly or distally; the latter type may be called **pectinate** (comblike); where the trabeculae are only periodically in contact (by elongation of their fibers), the septum is **perforate** (fenestrate), e.g., in *Calostylis*.

Septa may also be distinguished by the ways in which their trabeculae are related to their median planes. **Uniseriate** septa have a single series of trabeculae, either simple or compound, whose axes lie constantly in the median plane so that their distal ends are found at the axial septal edges, which may be more or less coarsely toothed as a result (Fig. 7,*3*). **Aseriate** septa (Fig. 9,*3*) are composed of short, fine trabeculae that curve laterally so as to end in the septal faces. An aseriate septum is best studied in sections cut at right angles to both the curvature of its distal edge and its midplane. In many, the fine or very fine short trabeculae clearly originate in the midline of the distal edge of the septum and then diverge; their divergence is commonly subopposite or alternate (FEDOROWSKI, 1974a, p. 471). In others, not all the fine trabeculae can be seen to have originated at the midplane, though they are always curved at right angles to the growth lamellae. This last type is common in the thick septa of peripheral stereozones where the broad distal edges of the septa are not angulate as in most uniseriate forms, but shallowly round-arched from side to side (*Schlotheimophyllum*; LANG, 1926, pl. 30, fig. 4-6). **Naotic** septa (Fig. 133,*1a-c*) are basically of this type also, but the thick peripheral parts are replaced by columns of arched, dissepimentlike plates that are connected within the columns by rods or granules representing the axes of fine short trabeculae *(Naos)*. Possibly also the apparently multiseriate septal crests seen in some parts of some *Cystiphyllum* are of this nature, the granules on the tops of the dissepiments representing the axes of the short fine trabeculae that may be found in septal crests

in other parts of the same coral (POČTA, 1902, pl. 36, fig. 9). Septa in which the fibers appear to be directed perpendicular to both median plane and the septal faces commonly show marked growth lamellae and have been called **lamellate** or lamellar; some may have their trabecular axes so closely together that the mode of spherulitic crystallization approximates the linear, and such have been described as atrabeculate. ILINA (1965, p. 15) and others (FEDOROWSKI, 1974a, p. 471) have shown at least in some of these that very fine close trabeculae are visible in sections cut in the median plane, from which they may diverge to the septal faces. In **arachnophylloid** septa (Fig. 133, *2a-c*), a rectilinear network replaces the thick, contiguous peripheral parts; it may be longitudinally discontinuous, developed on dissepimentarial floors. Its trabecular arrangement is not understood but may possibly be multiseriate.

Many other descriptive terms are in use for septa. Septa may be long or short, attenuate, thin, or commonly **dilated** (thickened) in whole or in part; in some families the septa may be thicker in the tabularium than in the dissepimentarium. **Rhopaloid** septa are expanded at their inner ends and appear clubshaped in transverse section. Thickening of the septa is effected by elongation of the fibers, growth (or accretion) lamellae showing that the process is periodic (possibly related to feeding times or to alternation of day and night). Where thickening affects the septa in a particular zone of a coral, a septal stereozone is formed.

The septum may not be continuous longitudinally and radially. Thus **amplexoid** septa (Fig. 79,*2c*) are fully developed only on upper surfaces of tabulae, but above this position they extend progressively a shorter distance from the wall, as in *Amplexus*. **Lonsdaleoid** septa are discontinuous toward the opposite peripheral edge; they do not extend continuously through the dissepimentarium, but may bound interseptal loculi for certain distances only, dying out toward the wall in a series of **septal crests,** each crest resting on dissepiments like the axial ends of amplexoid septa that rest on tabulae. **Perforate** and **retiform** septa are rare in Rugosa but occur in Calostylidae.

The distal edge of a septum seen in the
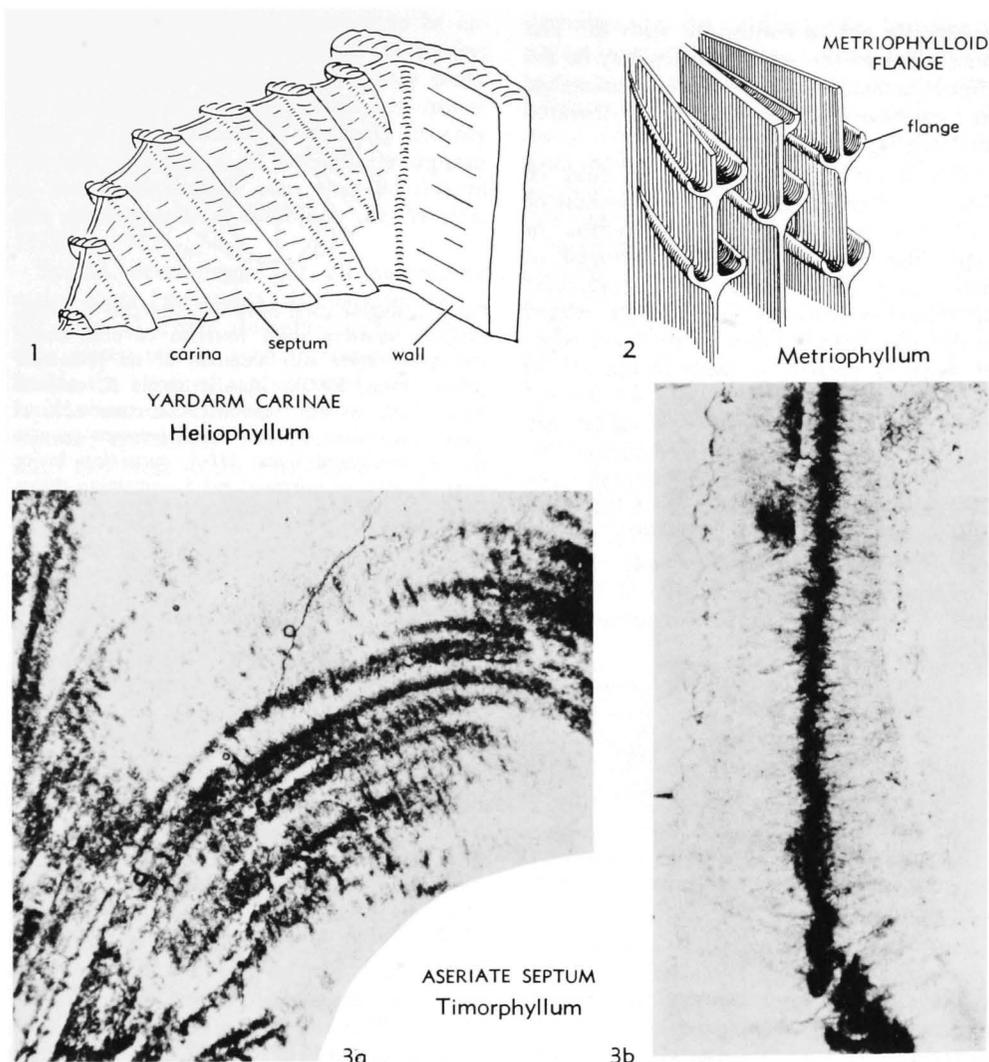
FIG. 9. Rugose coral morphology; types of septa.——*1*, Yardarm carinae, *Heliophyllum* sp., M.Dev., N.Am.; diagramm., enl. (Sorauf & Oliver, 1976).——*2*, Metriophylloid flange, *Metriophyllum* sp., Dev., Eu., diagramm., enl. (Holwill, 1964).——*3*, Aseriate septum, *Timorphyllum wanneri* GERTH, U.Perm., Timor; *3a*, median radial long. sec., *3b*, trans. sec., trabeculae very fine, short, originating in median plane but rapidly diverging to septal faces, both ×42 (Fedorowski, 1974a). See also Fig. 79,*2c*, for illustration of amplexoid septum, Fig. 133,*1a-c*, for illustrations of naotic septa, and Fig. 133,*2a-c*, for illustrations of arachnophylloid septa.

calice may be entire, toothed (denticulate), or pectinate; pectinate septa are sometimes described as septal combs. It may be declined at varying angles from the wall toward the axis, or be subhorizontal, or, as in an everted calice, it may be arched so that it rises above the distal edge of the epitheca and wall. Its profile is commonly nearly parallel with the surface of the dissepimen-tarial platform, and is normally at right angles to the direction of the trabeculae in uniseriate septa.

The axial edge of a septum may have springing from it a number of irregular, upwardly directed slender or cylindrical **axial lobes** as in Streptelasmatidae. A septum may be represented in axial structures by a **septal lamella,** which is a radial axial plate

commonly not in continuity with it. The distal edge of the septal lamella may be declined abaxially, and when it is uniseriate its component trabeculae are directed abaxially upward.

The sides (faces) of a septum may be smooth, or provided with denticulations or with tall ridges. The denticulations or **vepreculae** may be randomly arranged or may run in the direction of the trabeculae of uniseriate septa. Ridges may be related to the axes of trabeculae, to the distal edges of septa, or possibly in some to the axis of growth of the corallite. Those that are lateral expansions of trabeculae are called **carinae**, and these may be opposite, subopposite, or alternate on the opposing septal faces. Opposed carinae are sometimes called **yardarm** or cross-bar carinae (Fig. 9,*1*), though the adjective strictly applies only to their appearance in transverse section of the septum; alternate carinae are sometimes said to be **zigzag** or xyloid.

Ridges that are developed parallel to the distal edges of the septa are sometimes distinguished as **flanges** (Fig. 9,*2*), and this term is also applied to the scooplike metriophylloid ridges in *Metriophyllum* and others.

Synapticulae, rough, rodlike connections between neighboring septa, are found in Calostylidae.

SEPTAL INSERTION

The first septa appearing at the apex of the apical cone establish the bilateral symmetry of the plan of insertion (Fig. 10). In solitary Rugosa studied by serial grinding and thin sectioning (DUERDEN, 1902, 1906; CARRUTHERS, 1906, 1908; BROWN, 1909; FAUROT, 1909; SCHINDEWOLF, 1942) the first two septa, **cardinal *(C)*** and **counter *(K)*** major septa appear opposed in the one diameter, commonly connected at the axis as an **axial septum;** next to arise is a pair of major septa at the peripheral end of the cardinal septum. Though remaining attached to the wall and commonly to the axial septum also, this pair gradually spreads outward and becomes the two **alar septa** *(A)*; shortly afterward a second pair, the first **counter-lateral septa** *(KL),* develops similarly at the peripheral end of the counter septum but spreads outward only a short
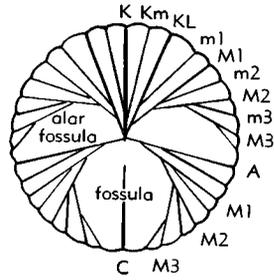
FIG. 10. Rugose coral morphology; septal insertion. Diagram showing serial insertion of both major and minor septa after insertion of six protosepta (after Faurot, 1909). *A,* alar septa; *C,* cardinal septum; *K,* counter septum; *KL,* counter-lateral septa; *Km,* minor septa in loculi between counter and counter-lateral septa; *M1-3,* remaining major septa in order of insertion; *m1-3,* remaining minor septa in order of insertion (Hill, 1935).

distance (Fig. 10). Thereupon, in CARRUTHERS' (1906, p. 358) view, a pause ensues; HUDSON (1936a, p. 70), however, recognized no such pause, though he noted that the first six septa, all major septa, were often formed simultaneously, especially in hysterocorallites. HUDSON considered as primary **(protosepta)** only the cardinal and counter septa; KUNTH (1869, p. 651), in showing that new septa were inserted at only four loci, nominated only the cardinal, counter, and two alar septa as primary. DUERDEN (1902, 1906) and CARRUTHERS (1906, 1908) considered the first six septa to be protosepta. WRIGHT (1969, p. 1232) has reviewed much of the literature on the septal plan.

SCHINDEWOLF (1942, p. 52) and FEDOROW-SKI (1973, p. 115) described as **pentaphylloid** a plan of development of the first six septa in which five short septa not joining one another are sequentially developed, first the cardinal, then the two alar septa, and then the (first) counter-lateral pair, but no trace of the counter septum is seen until a much later stage. Technically it is extremely difficult to maintain consistency of orientation of the ground or cut surfaces in an apical cone, especially in curved apices, in relation either to the calical edge or to the axis of growth of the corallum, and thus to establish the exact order of insertion of septa in the apex, and it is equally difficult to be consistent in the treatment of different specimens. Also, **septal stunting,** when the

septum is or becomes so short as to be entirely contained in the wall, or to project but very slightly from the wall, may mask the presence of septa, especially of minor septa, in thin transverse sections; possibly the late appearance of the counter septum in the pentaphylloid plan may be due to this phenomenon (*Reduktion* of WEYER, 1972b, p. 723).

Spatial development of all succeeding major septa (**metasepta**) is characteristic of the Rugosa. There are only four loci where they arise: one in each interseptal loculus beside the cardinal septum, and one in the loculus on the counter side of each alar septum; commonly they first appear very short and close to the peripheral end of the major septum that was formed immediately before them, and to which their adaxial ends may or may not be or become attached as they lengthen. Commonly more major septa are inserted in the counter quadrants than in the cardinal quadrants. This plan of septal insertion is associated with a differentiation in size and shape of at least the tabularial parts of the four interseptal loculi that are the loci of insertion; these loculi are commonly called fossulae; **cardinal fossula,** or just **fossula,** denotes the two combined cardinal loci and usually shows a notable depression of its tabular floor; **alar fossulae** are always so termed, and may not have depressed floors. The loculi between the counter septum and its neighboring counter-lateral septa may be enlarged in some and called a **counter fossula.** Nontechnical adjectives are used to describe different features and shapes of transverse sections of fossulae; thus, a **closed fossula** is one in which the axial ends of the neighboring septa curve around to form a fossular wall, whereas an **open fossula** is not so bounded axially.

The fundamental sequence of **minor septal** insertion appears also to be serial (counter-cardinal or dorsoventral). First, the pair of minor septa commonly symbolized as K_m appears, one on each side of K (Fig. 10); next, on the cardinal side of each alar septum and of each of the first counter-lateral septa, a new short septum arises and lengthens to become a major septum, whereupon two new short septa are inserted, one on each side of it. The one on the counter side remains short and is clearly a minor septum;

the other, on the cardinal side, becomes a major septum, and the process continues. In the septal plan of *Cyathaxonia* (FAUROT, 1909), of *Petraia* (SCHINDEWOLF, 1931), and many others, it is notable that the minor septa normally lie close to and adaxially touching the major septa on their counter side (**contratingent**).

Serial section studies suggested to CARRUTHERS (1908, p. 25) and to SMITH (1913, p. 62, and in discussion in SCHINDEWOLF, 1931, p. 648) and others that in many Rugosa, perhaps the majority, the appearance of the minor septa, though continuously potential, may be delayed until relatively late stages of development, when they may appear in rapid succession in all the loculi, after which new major and minor septa are inserted normally in each of the four loci of insertion. This process is best regarded as merely a modification of the normal plan, and not as a distinct plan with analogy to the cyclic insertion of Scleractinia (*fide* WEYER, 1972b, p. 72). Normal minor septal furrows are present throughout, and minor septa are always to be seen at the distal edge of the calice, provided that the edge is not damaged in any way during fossilization. Minor septal stunting seems a sufficient explanation for the modification.

In a few Rugosa, additional septa may appear in the loculi between major and minor septa. These are shorter and usually thinner than minor septa and are commonly described as septa of a third (and even of a fourth) order; perhaps the term **minisepta** may be found acceptable for them. Their mode of insertion has not been studied; a few solitary Rugosa show weak longitudinal furrows on their epithecate walls, inserted apparently by intercalation (WEYER, 1974b, p. 359, fig. 7.2) and possibly indicating minisepta.

SEPTAL FURROWS AND 'SEPTAL SPLITTING'

KUNTH (1869, p. 651, 663, fig. 1-3) deduced from the pattern of epithecal septal furrows and the arrangement of the septa in thin section that in each of four quadrants new major and minor septa were inserted alternately, in sequence, in a cardinal direction (dorsoventral). He did not use the verb *abspalten* (i.e., to split off); his litho-
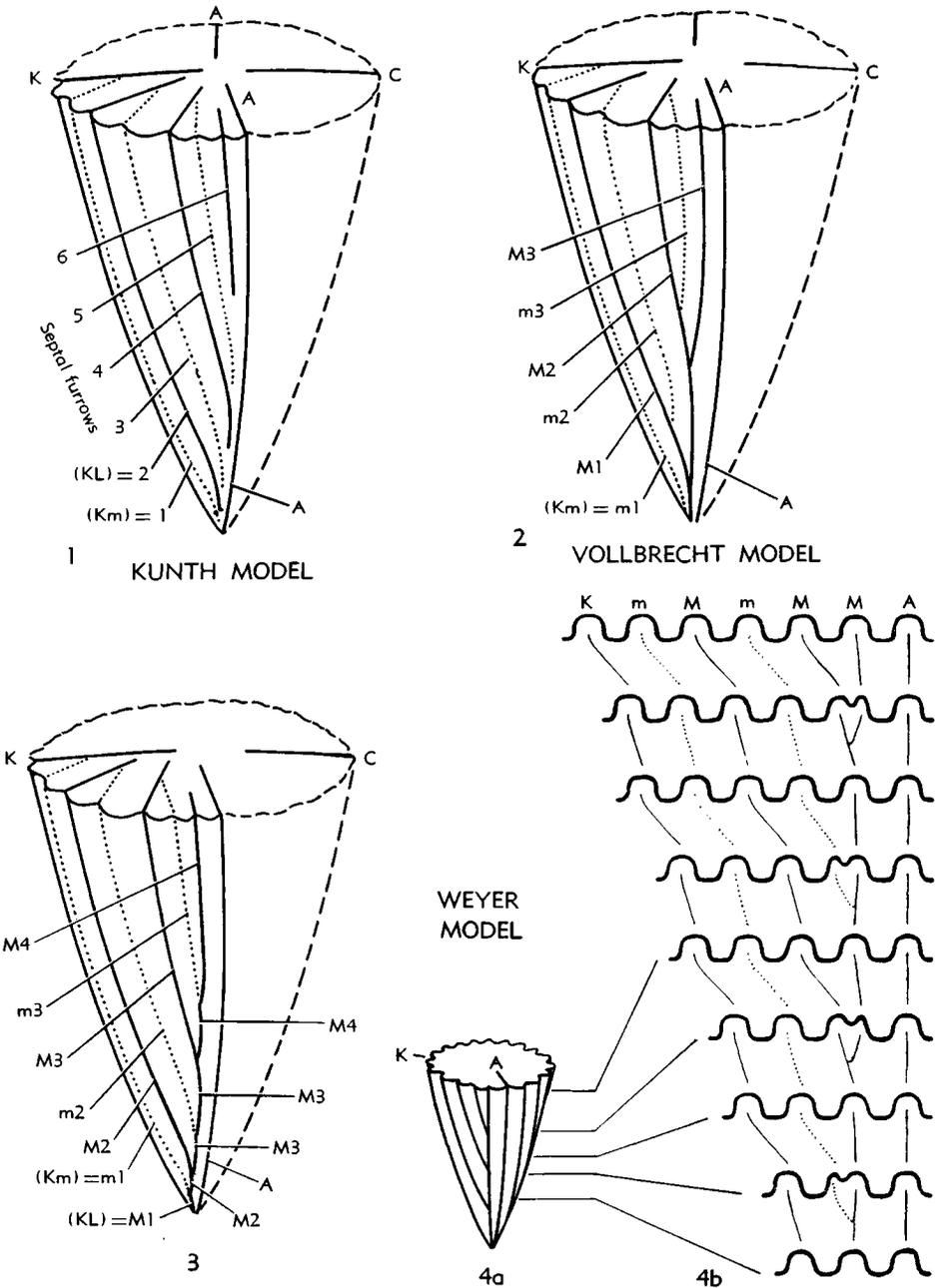
FIG. 11. Rugose coral morphology; septal furrows.——1, Order of appearance of longitudinal furrows (and corresponding septa) assumed by KUNTH, 1869.——2, Order of appearance of septa (and of furrows) assumed by VOLLBRECHT, 1928.——3, Order of appearance of furrows and septa to fit WEYER's (1974b) assumptions of 'septal splitting.'——4, WEYER's model of development of furrows (and corresponding major and minor septa); K, counter septum; A, alar septum; solid lines connect furrows for major septa at successively higher levels in corallum, while dotted lines connect furrows for each minor septum (Weyer, 1974b).

graph (pl. 18, fig. 1-2) of an external view showed the proximal end of each septal furrow being apparently confluent with its earlier formed neighbor on its counter side, but his description and his enlarged line-drawing (p. 651, fig. 3) showed them curving toward confluence but not confluent. In KUNTH's scheme, if the furrow next to the counter furrow were continuous, it would be composite, representing the sum of the curving portions of alternately developed minor and major septal furrows (Fig. 11).

On the other hand, WEYER (1974b) postulated that each rugosan metaseptum (major septum) will 'split' twice; first on its counter side to produce a new minor septum, and then on its cardinal side to produce a new major septum. With this postulate, presumably, in corals with contratingent septa, the minor septal 'split' detaches itself from its 'parent' and lengthens to attach itself contratingently to the penultimately formed major septum on its counter side (Fig. 11,3). Whether WEYER accepted this presumption or not is not apparent, since he did not give a lettered diagram showing the relation of the external septal furrows of *Sutherlandinia* sp. to its contratingent septa. Contratingency and closeness to one of the neighboring major septa is conceivably determined by differential growth rates by which the wall increases its circumference more rapidly on the cardinal side of a new minor septum than on the counter side. WEYER figures his 'septal splitting' only as the forking of a septal furrow (Fig. 11,4), by which a new septal rib arises within a septal furrow, so that two furrows are formed, from each of which the midplane of a septum would extend adaxially (1974b, fig. 4, p. 355).

VOLLBRECHT (1928, pl. 4, fig. 2c) conceived that the furrow of a contratingent minor septum would be confluent at its point of origin with the furrow of its neighboring major septum on its counter side; she based this on her view that each major septum (except the cardinal) 'split' off on its cardinal side first its new metaseptum, then, with distal growth of the corallum, its new minor septum. This would seem to be in conformity with the order of insertion deduced for *Cyathaxonia* by FAUROT (1909).

In both WEYER's and VOLLBRECHT's schemes, if the furrow next to the counter septum really is continuous, it would represent the sum of the curved proximal parts of successive major septal furrows. There are too few unretouched photographic illustrations of apices in which the epithecal septal furrows are sufficiently unworn to offer conclusive proof for any of the three views concerning the proximal ends of the furrows, but it can be said that, while rare apices are consistent either with KUNTH's view or with WEYER's, none is known that supports VOLLBRECHT's conception.

AXIAL STRUCTURES

Axial structures commonly project from the calicular floor and are formed from the axial parts of septa reinforced by transverse skeletal elements (Fig. 12); these axial parts tend to be continuous with the peripheral parts only in very early stages. The axial lobes of many of the Streptelasmatidae form a spongy axial structure. Many genera have a **columella** that is a dense axial structure, lenticular, barlike, or cylindrical in section, and which may be simply or complexly structured (Fig. 12,1). It commonly originates as an extended and thickened axial end of the counter (or in some cases the cardinal) septum, and may retain this connection or become free; in *Cyathaxonia* it apparently rises free right from the apical cone. In many it is augmented by septal lamellae that may be contiguous throughout or free laterally in places (*Amygdalophyllum*). Where little altered, the lamellae are seen to be composed of trabeculae like those of the septa; in some, the septal lamellae may be developed only on the upper surfaces of the tabellae. Other genera have an **axial coil** (formerly vortex) formed by the similar twisting of the axial ends of the long major septa (*Ptychophyllum*, Fig. 12,3). Coiling is commonly counterclockwise adaxially in calical view. Still others have an axial structure composed of septal lamellae that are usually discontinuous from the septa to which they belong and are united by transverse skeletal elements; such structures may be 1) **clisiophylloid**, like a spiderweb with a short medial plate derived from the conjoined cardinal and counter septa in the early stages (*Clisiophyllum*),
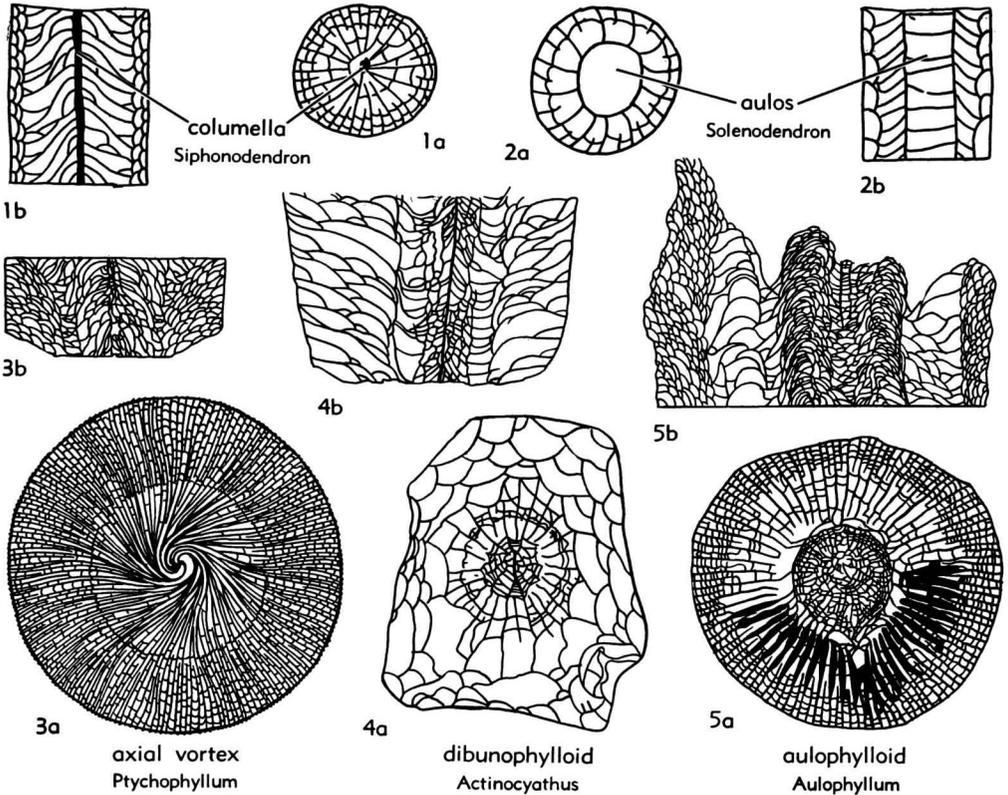
FIG. 12. Rugose coral morphology; axial structures (after Hill, 1956b).——*1, Siphonodendron* sp., L.Carb., Eu.; *1a,b,* transv., median long. secs., enl.——*2, Solenodendron furcatum* (SMITH), L.Carb., Eng.; *2a,b,* transv., median long. secs., ×2.——*3, Ptychophyllum stokesi* MILNE-EDWARDS and HAIME, Sil., Can.; *3a,b,* transv., median long. secs., ×1.——*4, Actinocyathus laticlavia* (SMITH), L.Carb., Eng.; *4a,b,* transv., median long. secs., ×1.7.——*5, Aulophyllum fungites* (FLEMING), L.Carb., Eu.; *5a,b,* transv., median long. secs., ×1.3.

2) **dibunophylloid** (Fig. 12,4), bisected by a medial plate *(Dibunophyllum)*, or 3) **aulophylloid** (Fig. 12,5), without a medial plate *(Aulophyllum)*. The aulophylloid structure, having a wall formed by tabellae, is sometimes called an **axial column**. An **aulos** (inner tube) may be formed from the similar turning aside of the axial edges of the septa to meet their neighbors, as well as by downturn of the tabulae and in other ways (Fig. 12,5).

TABULAE AND DISSEPIMENTS

Tabulae are present in all Rugosa except a few solitary coralla in which the calice extends right down to the apex of the corallite and is floored by sclerenchyme continuous with that of the wall and septa. They are the chief and in some families the only transverse skeletal elements to be developed, but in many others the central space in which they occur (**tabularium**) is surrounded by a marginarium with dissepiments (**dissepimentarium**) (Fig. 13). Successive tabular floors may each consist of a single tabula, then said to be **complete;** the floors may be domed, horizontal, or inversely conical, or have a median boss that may itself have an axial depression; commonly, the tabular floors are each composed of a series of smaller, subglobose plates, **tabellae,** so that the tabulae are **incomplete.** The inclination of the tabellae varies with the profile of the calicular floor, in which the order of their formation is from proximal to distal.

Clinotabulae, found mainly in Waagenophyllidae, are elongate periaxial tabellae that
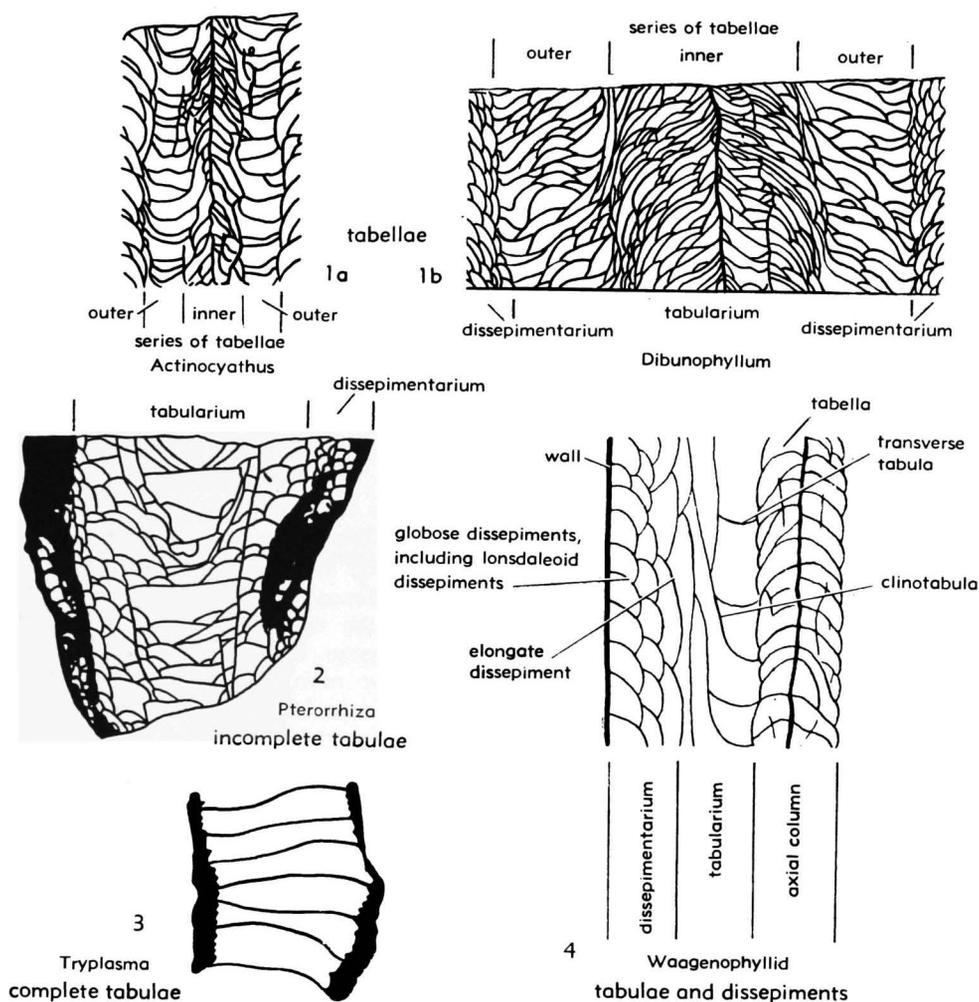
Fig. 13. Rugose coral morphology; types of tabulae.——*1*, Tabellae; *1a*, *Actinocyathus laticlavia* (SMITH), L. Carb., Eng.; enl.; *1b*, *Dibunophyllum bipartitum* (M'COY), L.Carb., Eng., ×2.——*2*, Incomplete tabulae; *Pterorrhiza* sp., U.Dev., Eu.; median long. sec., ×1.5.——*3*, Complete tabulae; *Tryplasma* sp., Sil., Eu.; median long. sec., ×1.5.——*4*, Waagenophyllid tabulae and dissepiments; waagenophyllid specimen, Perm., Asia; part of median long. sec., enl. (Figs. 13,*1-3*, after Hill, 1935; 13,*4*, after Minato & Kato, 1965a.)

are steeply declined from the dissepimentarial wall and then either cross transversely to meet the axial column or abut onto the upper surface of an earlier clinotabula (MINATO & KATO, 1965a, p. 1); the term **"clinotabellae"** was used (MINATO & KATO, 1965b, p. 22) to distinguish shorter, more globose inclined tabellae of the Durhaminidae.

Very thin, horizontal skeletal elements that appear to have no direct parallelism with the calicular floor are found in genera in which the interseptal loculi are much restricted by synapticulae (Calostylidae) or by long vepreculae *(Multicarinophyllum)*; some may extend from wall to wall, with some change of curvature at or near the inner boundary of the marginarium.

Dissepiments are small, curved or globose plates inclined parallel to the calical slope of the dissepimentarium, each overlapped slightly by its outer, younger neighbor (Fig. 14). They normally extend across the loculi between major and minor septa,
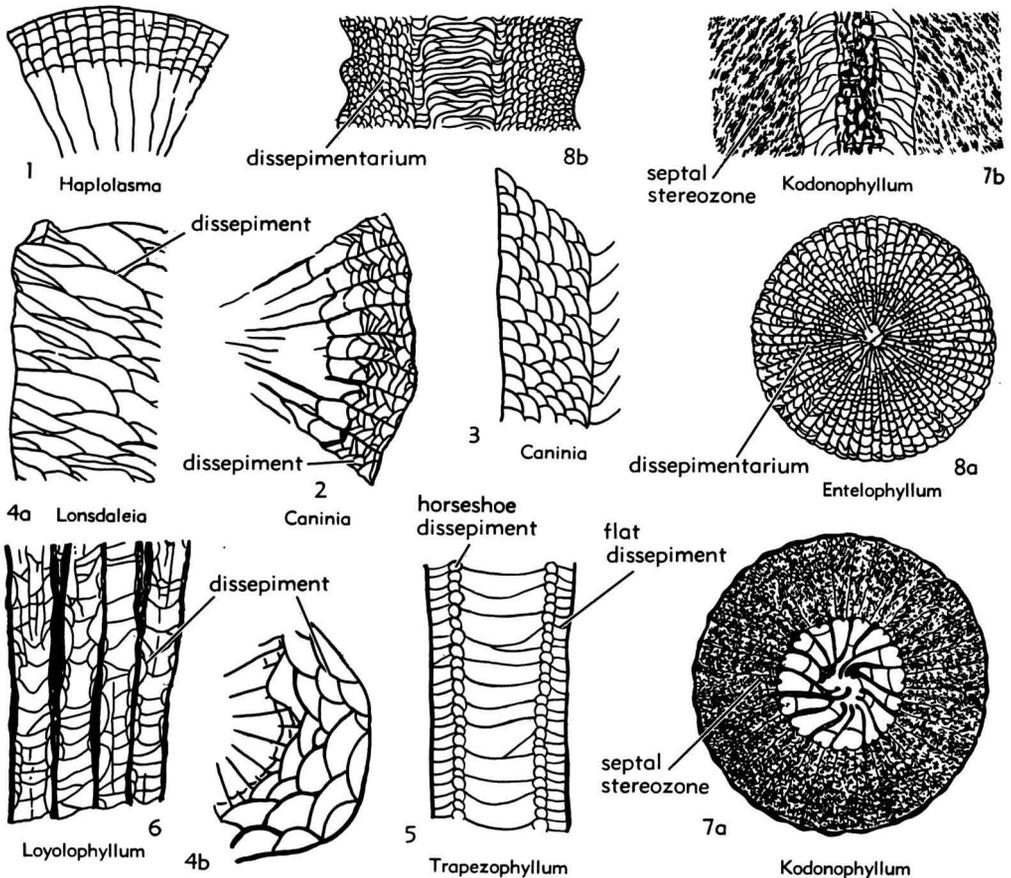
FIG. 14. Rugose coral morphology; dissepiments and marginaria (after Hill, 1956b).——*1, Haplolasma subibicinum* (M'COY), L.Carb., Eu.; part of transv. sec. showing dissepiments arranged in regular concentric pattern, enl.——*2, Caninia juddi* (THOMSON), L.Carb., Eu.; part of transv. sec. showing dissepiments arranged in herringbone (inosculating) pattern, enl.——*3, Caninia* sp.; part of median long. sec. showing many vertical series of dissepiments, corresponding to structure of *1, 2,* enl.——*4a,b, Lonsdaleia duplicata* (MARTIN), L.Carb., Eu.; parts of long. and transv. secs. showing lonsdaleoid (transeptal) dissepiments, enl.——*5, Trapezophyllum elegantulum* ETHERIDGE, L.Dev., Australia (Vict.); median long. sec. showing inner series of horseshoe dissepiments and outer series of flat dissepiments, ×3.——*6, Loyolophyllum cresswelli* CHAPMAN, L.Dev., Australia (Vict.); median long. sec. showing isolated dissepiments, ×3.——*7a,b, Kodonophyllum truncatum* (LINNÉ), Sil., Eu.; transv. and median long. secs. showing marginarium composed of septal stereozone, ×2.——*8a,b, Entelophyllum articulatum* (WAHLENBERG), Sil., Eu.; transv. and median long. secs. showing marginarium composed of dissepimentarium, ×2.

their lateral edges rising toward the confining septa; such a dissepimentarium, where the dissepiments appear in transverse section as concentric series of which each plate is concave toward the axis, is called regular or **concentric**; in some corals this upward concavity may become **angular**. A **herringbone** dissepimentarium forms when the minor septa become longitudinally discontinuous while the major septa remain continuous, so that the dissepiments between major septa inosculate (Fig. 14,*2,3*). Where major septa also are longitudinally discontinuous, all the dissepiments, including those passing through discontinuous septa, may be distally arched and thus present transverse sections that are convex toward the axis; these are **transeptal** (SEMENOFF-TIAN-CHANSKY, 1974, p. 35) (i.e., **lonsdaleoid**) when the septa are represented by septal

crests on their upper surfaces (Fig. 14,4), or **cystiphylloid** where the septal crests are of separate or only in part contiguous trabeculae. In the Cystiphyllidae, periodic thickening of the combined dissepimental and tabularial floor occurs, possibly due to rejuvenescence, forming a stereozone in the shape of an inverse cone (**septal cone**) in which the constituent separate or contiguous trabeculae of the septal crests are visible.

In some genera with thick septa, these septa are replaced in their peripheral parts each by a column of **naotic** dissepiments, distally arched plates connected to one another by their bases and also by granules or short rods. In others, radially disposed, **lateral** dissepiments may line the septal faces, narrowing the interseptal loculi.

The successive dissepimentarial floors, like the tabularial floors, are conformable with the floor of the calice; commonly they are declined adaxially from the wall; in some they are horizontal except at the boundary with the tabularium, where they are usually steeply declined adaxially; in a few they are everted, those in a narrow-to-wide peripheral zone being declined abaxially from an axis of divergence of the trabeculae in each of the septa. In a calicular floor in any interseptal loculus, dissepiments are formed in centrifugal sequence, their proximal edges overlapping the distal and upper surface of the preceding dissepiment.

In a considerable number of genera, however, the interseptal loculi on either side of a moderately long minor septum are notably different. In some Laccophyllidae, for instance, where the minor septa are **contratingent** (each with its axial edges contingent on the major septum next on its counter side), horizontal skeletal elements developed within the triangular loculus so bounded are adaxially declined or horizontal, recalling periaxial tabellae rather than dissepiments. In the longer loculi, open adaxially, complete tabulae are declined abaxially right to the wall. WEYER (1972c, p. 439) advocated describing such genera as having a **biform tabularium.** In some genera, where dissepiments are lacking, the wall may be thicker in the loculus to the counter side of each short minor septum, and each such loculus may be narrower than that on its
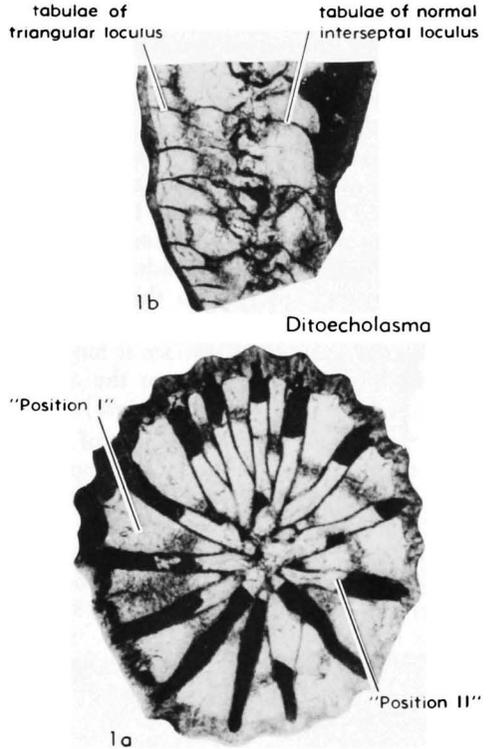
FIG. 15. Rugose coral morphology; biform tabularium.——*1a,b, Ditoecholasma lawrencense* SUTHERLAND; transv. and median long. secs., ×8, ×6. The differing profile of the tabularial floor is shown on the two sides of *1b*; on the right, an interseptal loculus that goes right to the axis when seen in transv. sec. has a floor descending from axis to periphery, very steeply near periphery (Position II of SUTHERLAND, 1965);˙ on the left is the second form, in a loculus which, in transv. sec.(*1a*), is seen to be terminated adaxially by the axial end of a minor septum resting on the major septum to its counter side; such a loculus is labelled Position I on the transv. sec. and the profile of that part of the tabularial floor enclosed within it is subhorizontal or declined slightly toward the axis. (Sutherland, 1965.)

cardinal side. In some aulophyllids and palaeosmiliids, the width of the dissepimented interseptal loculi on either side of a minor septum may differ, those on the counter side being narrower, and the minor septa may be **contraclined** or even contratingent, but the dissepiments in both types of loculus are normal and declined adaxially. Such a dissepimentarium may perhaps be described as biform. It would seem prob-

able that all these differences between neighboring interseptal loculi are inherent in the septal insertion specific to the Rugosa.

In a few Columnariidae and Stauriidae, isolated dissepiments may develop in single series, both their upper and lower edges being adherent to the inner surface of the wall.

In some Entelophyllidae and Disphyllidae, the outermost series of dissepiments may be **peneckielloid,** that is, subquadrate in longitudinal section, swollen so that the distal surface is horizontal or rising slightly adaxially, and the adaxial surface is longitudinal, its lower edge resting on the dissepiment next below (e.g., *Peneckiella*).

In the Phillipsastreidae, a pipe of **horseshoe** dissepiments commonly develops in a zone that encloses the axes of trabecular divergence of all the septa; in radial longitudinal section of the corallum cut through the interseptal loculi, the section of each superposed dissepiment in the pipe appears like a horseshoe, its ends based on the one below. Also in the Phillipsastreidae, and again in the Acervulariidae, a longitudinal series of **flat** dissepiments may develop in the zone immediately peripheral to the pipe of horseshoe dissepiments or to the zone of the axes of divergence of the septal trabeculae.

SKELETAL GROWTH RATES

There is considerable agreement that limits between species may be clarified by comparison of the ratios of the number of their septa to their diameter at successive growth stages (OLIVER, 1960a, p. 65; PEDDER, JACKSON, & PHILIP, 1970, p. 227), though errors may arise because of difficulty in maintaining strict control over the orientation of thin sections, and because of the phenomenon of septal stunting. Some species appear to show identifiable points of change in the ratios as growth proceeds, points which may perhaps be identifiable with particular growth stages (KULLMAN, 1972).

Much of the increase in the circumference of the rugosan wall is effected at the four loci of septal insertion, as evidenced by the pattern of the epithecal septal furrows. There is also, clearly, some increase in circumference in the wall segments bounding the interseptal loculi during development; and in corals with contratingent septa this amount is greater in the segment on the cardinal side of the minor septum than in that on the counter side.

PERIODICITIES IN SKELETAL GROWTH

Of the periodicities noted in the skeletal growth of Rugosa, Tabulata, and Scleractinia, the fine epithecal rings known as growth ridges (average width 0.05 mm) are the best known (WELLS, 1963, p. 949; 1970, p. 4). Few specimens show these delicate ridges very clearly (Fig. 16). In Scleractinia they may be found not only in reef corals but also in deepwater corals without zooxanthellae, which indicates that daily variation in light intensity is not the primary or only control. They are, however, widely regarded as daily in their periodicity, and BARNES (1972, p. 344) found that in the scleractinian reef coral *Manicina areolata* (LINNÉ) they could be related to a daily cycle of expansion and contraction of the polyp; but he thought that, in the ahermatypic *Gardineria* sp., which he studied and which grew in shaded positions below 50 m, it was very improbable that the rings represented daily increments. He pointed out that they could be related to almost any stimulus that shifted the position of the free body wall of the polyp, such as feeding or any other (perhaps long-term) rhythmical event.

WELLS (1970, p. 7) had already commented that daily fluctuations in the nutrient supply (e.g., diurnal movements of plankton), daily tidal flux, and diurnal variations in terrestrial magnetism are conceivable mechanisms for the rhythm; he ruled out daily temperature variations because at-depth temperatures are constant. He suggested that to account for the growth rings in both reef corals and such deep-sea corals with zooxanthellae as *Flabellum curvatum* MOSELEY obtained by the Challenger Expedition at a depth of 1,200 m off the Rio de la Plata and figured by STUBBS (1966, p. 828) (Fig. 16,*3*), a biologic clock control, i.e., daily changes effected by internal biochemical action, perhaps inherited from the distant past, might be needed.

SCRUTTON (1965, p. 552; 1970, p. 11) examined 10 specimens referable to several genera of Rugosa from the Middle De-
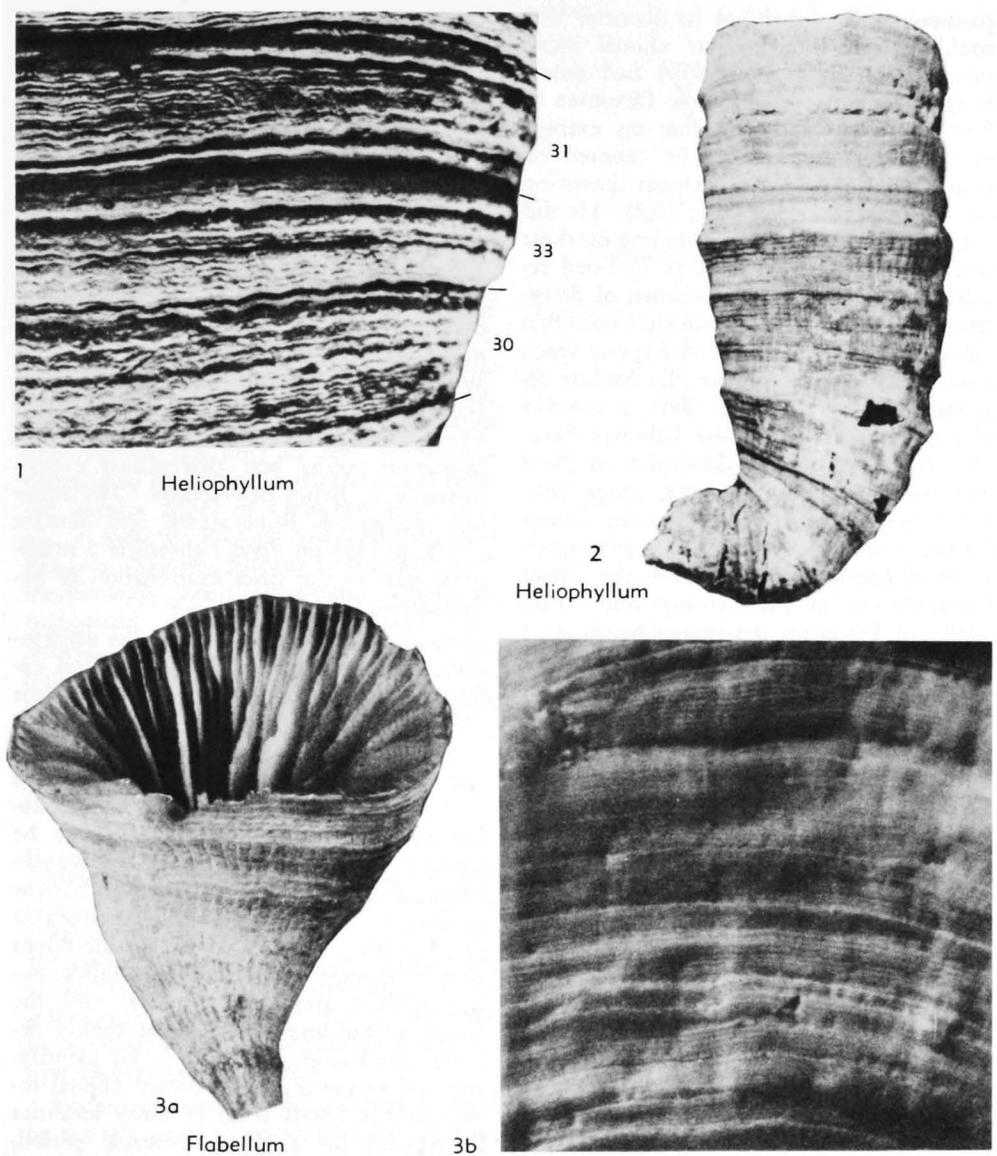
FIG. 16. Rugose coral morphology; periodicities in growth.——*1,* ?Lunar monthly bands and ?daily growth ridges, *?Heliophyllum* sp., M.Dev., N.Am.(N.Y.); three well-developed bands, with figures indicating ridge counts between successive constrictions in diameter, ×10 (Scrutton, 1965).——*2,* ?Annual increments, *Heliophyllum* sp., M.Dev., N.Am.(N.Y.); with 13 annulations indicating annual increments, ×1 (Wells, 1966).——*3a,b,* Growth rings (ridges) in the scleractinian *Flabellum curvatum* MOSELEY, Holo., Atlantic Ocean; ×2, enl. (Stubbs, 1966).

vonian of Michigan and Belgium. He assumed the growth rings to be daily, and judged that they were developed in groups (bands) limited above and below by constrictions, usually deep grooves around the circumference of the epitheca, but occasionally emphasized by a change in thickness of the corallite. He counted an average of 30 growth rings to a band (min. 27, max. 35) and regarded each band as formed during a single lunar month. His specimens were not characterized by alternating ex-

pansions and contractions in diameter that could be taken to indicate annual increments. WELLS (1963, p. 950) had noted, in specimens from the Middle Devonian of New York and Ontario, that an average of about 400 rings could be counted on each presumed annual increment shown on the specimens he used (Fig. 16,2). He did not observe lunar monthly banding on these specimens. He later (1970, p. 7) listed results obtained from one specimen of *Streptelasma* from the Upper Ordovician of Ohio (about 412 daily rings per year); one specimen of *Ketophyllum* from the Middle Silurian of Gotland (about 400); a number of specimens, including the Tabulata *Favosites* from the Middle Devonian of New York and Ontario (avg. 398, range 385–405); one *Lithostrotion* from the Lower Carboniferous of Wales (398); two specimens of *Lophophyllidium* from the Upper Carboniferous of Pennsylvania and Texas (380 and 390 layers per year). Assuming a constant rate of decrease in the number of days per year from the Cambrian to the Holocene, he plotted his values of days per year against the radioactive age data for the periods as accepted in 1961, and noted that his very limited readings were consistent with the view of certain astronomers that there has been a deceleration of the earth's rotation on its polar axis. He suggested that the potentiality of corals as geological chronometers would be worth investigation.

Subsequently there has been very little rugosan work published that either supports or negates these preliminary speculations, possibly because individual specimens on which epithecal growth rings, bands, and annual groupings are all sufficiently distinct for counting are very rare, and because recognition of lunar monthly and annual groupings can be very subjective.

SCRUTTON and HIPKIN (1973, p. 266) pointed out that the only data in which both days per month and days per year are implied to have been counted on the same specimens are those of MAZZULLO (1971, p. 1085), but that even here the number of days per month appears to be simply the days per year divided by 13 in each case. Recently JOHNSON and NUDDS (1975, p. 31) estimated lunar months of 30.5 days for

Lithostrotion from the Visean of Great Britain, based on the number of epithecal growth rings between narrow constrictions which they interpreted as lunar monthly; they thought the absence of "annual" constrictions on their specimens consistent with tropical latitudes deduced for the region from paleomagnetic data.

JOHNSON and NUDDS also suggested (1975, p. 40) that there was a linkage between lunar monthly constrictions and the spacing of the tabulae such that 6.5 to 7.5 tabulae may have been formed each lunar month. Whether successive horizontal skeletal plates (tabulae, dissepiments) have a daily, weekly, or other temporal rhythm in their formation seems best determined experimentally in living Scleractinia. The staining studies of BUDDEMEIER and KINZIE (1975, p. 135) on *Porites* chronicle a promising start to the strict examination of periodicity in Scleractinia.

MA, in a series of papers on his observations of longitudinal thin sections and externals of Paleozoic and Holocene corals (MA, 1933, 1937, 1956), has interpreted as annual, seasonal, and therefore temperature-controlled, certain rhythmic alternations of zones of narrowly and widely spaced tabulae and dissepiments. In many cases he noted an associated thickening and lengthening of the septa in the zones of narrow spacing as well as a reduction in diameter of corallite. These rhythmic alterations should be most marked in the corals growing farthest from the equator, and the length of the annual increment should decrease away from the equator. By identifying and measuring the assumed annual increments in corals from as many localities as possible for a given Paleozoic period, and plotting them on maps, he deduced the position of the equator and the tropics of Capricorn and Cancer for each continent in each Paleozoic period. These equators did not coincide with the Holocene equator but approximated those calculated from paleomagnetic data, assuming continental drift.

In some instances, the intervals MA regarded as annual coincided with a rhythmic rejuvenescence in a corallum; rejuvenescence (Fig. 18,1) is commonly considered to represent recovery of a corallite after a period

of reduction caused by adverse circumstances, of which seasonal temperature lowering would be only one. In Heliolitina, alternation of closely spaced tabulae with dark-colored, vertical skeletal elements, and widely spaced tabulae with light-colored, longitudinal skeletal elements has been attributed to alternation of sexual and asexual reproduction (BONDARENKO, 1971a, p. 23). This recalls SCRUTTON's (1965) suggestion that "lunar monthly banding" of epithecal growth rings may be due to control of reproduction by phases of the moon.

Periodicity of skeletal structure on fine and ultrafine scales is seen in the lamellation apparent in the sclerenchyme of both septa and tabulae, not only in reef Scleractinia but also in ahermatypic scleractinians from the aphotic zones of Holocene seas. It is also notable in Rugosa and Tabulata, and has been discussed already in the section on morphology. Daily increments cannot be recognized with any confidence; each lamella on successive examination under higher and higher magnifications by optical and electron microscopes is seen to be composed of successively smaller and smaller increments (JELL & HILL, 1974, p. 10; JELL, 1974, p. 308).

INCREASE OF THE CORALLUM

Rugosan colonies are assumed to have arisen from single polyps, as in scleractinian colonies, by asexual reproduction. The parent polyp of the colony is the protopolyp, which lays down the **protocorallite**, and the subsequent or daughter polyps are the hysteropolyps or buds, which lay down the **hysterocorallites** or **offsets.**

Documentation of the **patterns** formed by the sequential three-dimensional development of offsets in a compound corallum is not plentiful. OLIVER (1968) has reviewed what is known. In most such coralla, the general pattern is consistent, at least after the first few generations of offsets. Diagrams of common patterns given by lateral (marginarial) increase in both fasciculate and massive coralla as well as by axial (tabularial) increase are shown in Figure 17,*1-3* (OLIVER, 1968, p. 21).

In **tabularial** modes of increase, the offsets arise in part in the axial (tabularial) region; the tabularium of the parent ceases to grow;
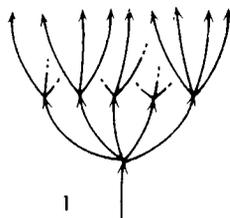
1

tabularial increase
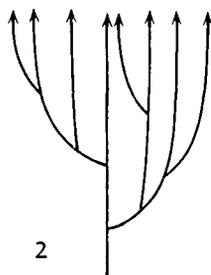
2

marginarial increase
(fasciculate coralla)
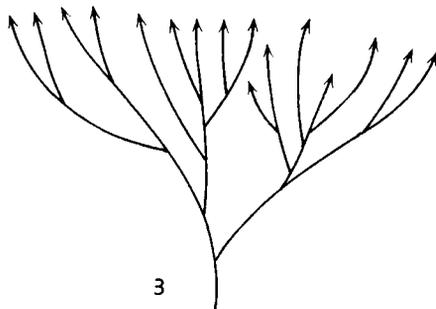
3

marginarial increase
(massive coralla)

FIG. 17. Rugose coral morphology; patterns in Paleozoic coral colonies. Each line represents one corallite; arrowheads indicate position of calice and direction of growth (Oliver, 1968).

the increase is thus **parricidal.** In these, two or more offsets are formed and may occupy the whole of the calice of the parent, either initially or by more or less rapid expansion toward the axis *(adaxial increase).* Over the marginarium of the parent they are built up by the extension of the septa and wall of the parent; the tissue carried forward from parent to offset and common to both is the **atavo-tissue. Neotissue** in the form
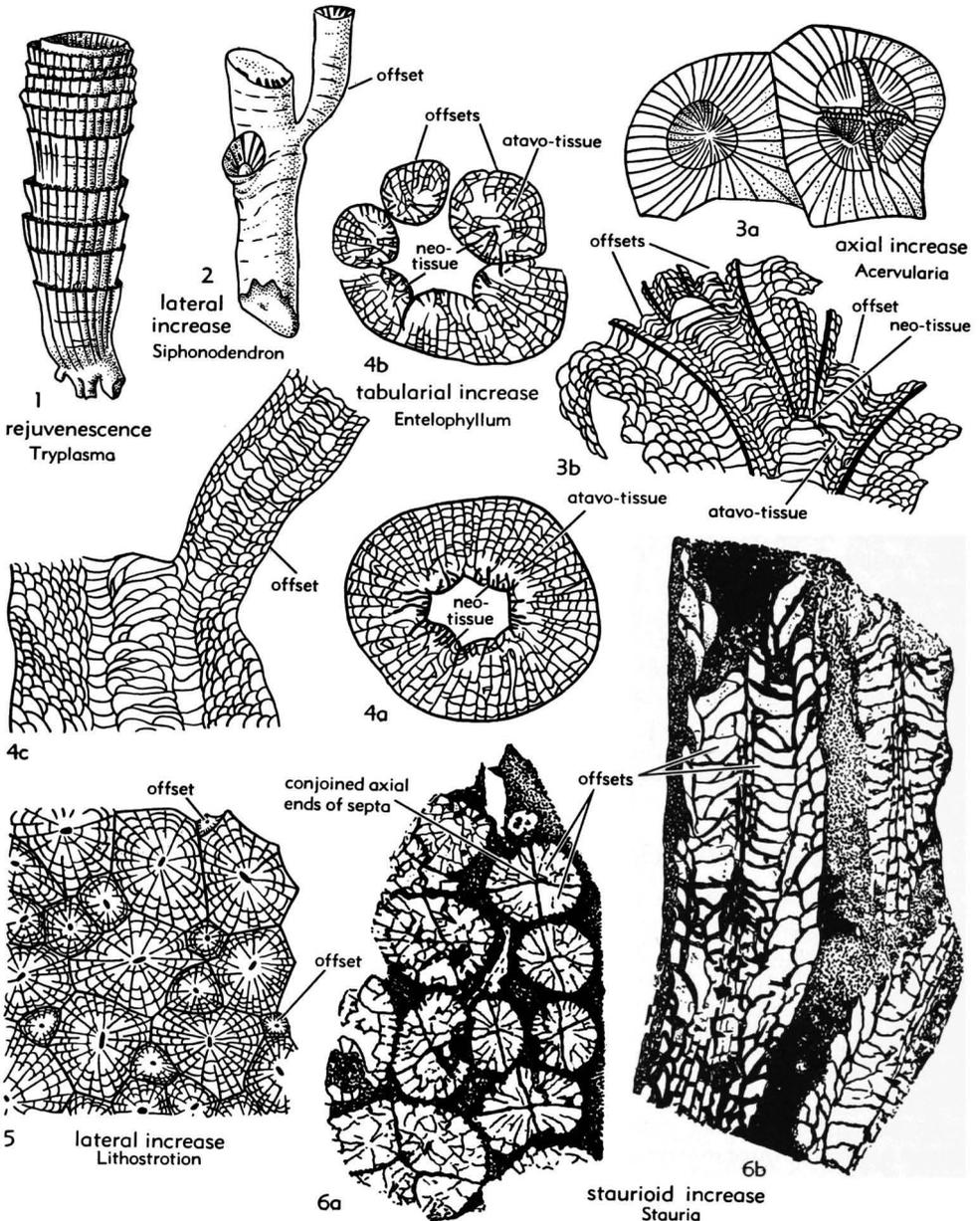
Fig. 18. Rugose coral morphology; increase and rejuvenescence. *1*, rejuvenescence; *2,5*, lateral (marginarial) increase; *3,4,6*, axial (tabularial) increase.——*1, Tryplasma loveni* (MILNE-EDWARDS & HAIME), Sil., Eu.; ×1.0.——*2, Siphonodendron* sp., L.Carb., Eng.; ×1.0.——*3a,b, Acervularia ananas* (LINNÉ), M.Sil., Eu.; calical view and median long. sec., enl.——*4a-c, Entelophyllum articulatum* (WAHLENBERG), Sil., Eu.; *4a,b*, successive transv. secs., *4c*, median long. sec., all enl.——*5, Lithostrotion* sp., L.Carb., Scot.; transv. sec., enl.——*6a,b, Stauria favosa* (LINNÉ), Sil., Gotl.; transv., long. secs., ×2.6; conjoined axial ends of commonly four major septa become new walls defining offsets. (Fig. 18,*1-5*, after Hill, 1956b, 18,*6*, after Ting, 1940.)

of new wall and septa arises upon the tabularial floor of the parent calice. Two types

of **tabularial increase** have been distinguished. In the staurioid type, commonly

four, in some three or five, offsets arise simultaneously, their new dividing walls arranged in a cross at the axis of the parent. In *Stauria* itself (Fig. 18,*6*), two opposite walls may grow upon the old cardinal and counter septa; but in *Acervularia* and others, there appears to be no general relationship to the protosepta of the parent. In the entelophylloid type (Fig. 18,*4a-c*), neowalls arise within the tabularium but toward its outer edge, and the offsets may then expand toward or to meet at the axis. In some examples studied the *C/K* plane of the offset in general lies at a tangent to the tabularium of the parent. In some species, there may be transitions between staurioid and entelophylloid types.

Other modes of increase involve only the marginarium and have commonly been termed **lateral**. Herein the term **marginarial** is preferred in most cases. With few exceptions these modes are nonparricidal; that is, the tabularium of the parent continues to grow and the parent competes with its offsets for living space. The offsets are commonly smaller than those produced in tabularial increase and in general make little use of atavo-tissue. In some, the original diameter of the offset is so small that there is only room for the protosepta and a few meta- and minor septa; in such cases, septal insertion, as interpreted from serial transverse acetate peels or thin sections, follows, with slight irregularities, the normal rugosan mode more or less from the beginning. In others, the original diameter within the neowalls is larger, and more metasepta and minor septa may be found; but here again, in the later stages of hystero-ontogeny, insertion of new septa has, with perhaps few exceptions (JULL, 1973), been found to follow the rugosan mode, though in some with irregularity. Even in the large offsets of tabularial increase, the rugosan mode can be traced at least in the later stages. The preferred orientation of the *C/K* plane in the offsets in marginarial increase is radial to the axis of the parent, though less common examples of tangential orientation also occur. JULL (1965, 1967, 1969a, 1974) has given valuable detail on the relations between atavo- and neotissue, the adaptation of old or the insertion of new septa, and the orientation of the offsets, and has referred

to the recent work of others. (See also SPASSKIY & KRAVTSOV, 1974, p. 165; FEDOROWSKI & JULL, 1976, p. 37.)

The ontogeny of a protocorallite has been studied in only one species, *Hexagonaria anna* (WHITFIELD), and by only two authors (see JULL, 1973). The species is exceptional in having a relatively large and long-lasting protocorallite, but it is a difficult one in which to ensure correct interpretation of septal insertion from peels and sections, due to the exceeding shortness of the septa and a tendency for them to be obscured by thickening in the very narrow dissepimentarium. JULL could not identify a rugosan mode in either protocorallite or offsets. No description of the arrangement of the septal epithecal furrows in a protocorallite is known.

Solitary corals may show offsets; in many species such offsets may remain small relative to the parent corallite and do not themselves increase; the resultant corallum can then scarcely be called compound. In other species there are grounds for assuming that either phaceloid or massive coralla may develop from normally solitary coralla.

Rejuvenescence is often observed. A corallite, instead of continuing its growth with increasing or constant diameter, suddenly becomes much constricted, usually leaving a ledge of older calice around the constricted part. It then increases in diameter again, and the process may be repeated (Fig. 18,*1*). During rejuvenescence, the internal structure of the corallite may revert to the morphology of an earlier growth stage. It is possible that some of the short-lived offsets found in the calices of normally solitary species are rejuvenescence phenomena (see SPASSKIY & KRAVTSOV, 1974, p. 168).

"Total rejuvenescence" is suggested by BIRENHEIDE and SOTO, 1977, p. 12, as responsible for the production of small, solitary Rugosa with a wall-free apex. Perhaps transverse fission like that in the Holocene scleractinian *Fungia* sp. may be involved.

ONTOGENY

It has sometimes been thought useful to distinguish different morphological stages in the ontogeny (development) of a corallite, and to apply to the successive stages

such terms as embryonic, neanic (adolescent), brephic (adult), and gerontic (senile). Arbitrary limits to the stages have been put at convenient places, such as the insertion of the protosepta, insertion of the first few meta- and minor septa, appearance of dissepiments, and abaxial withdrawal of septa. In this volume, stage terminology is left more fluid, early and late being used in comparison with the average. Morphological variation during ontogeny has been discussed by NEUMAN (1974, p. 151).

The sequence of morphological changes to be observed by serial sectioning, e.g., in the length of septa and the septal arrangement, is commonly found to distinguish families, and indeed, FEDOROWSKI (1973, p. 89) has considered pentaphylloid ontogeny to be so distinctive as to warrant the separation of a new suborder Tachylasmatina. The shortage of specimens with complete apical cones restricts the practical use that can be made of serial section studies; nevertheless, an expansion of such work is much to be desired.

Apparent differences between the ontogenies of offsets in the one corallum as well as the ontogeny of protocorallites have been discussed above in the section on Increase.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO PALEOZOIC CORALS

Terms commonly used in this revision are printed in boldface capitals; less generally used terms are printed in boldface lower case letters. The capital letters in parentheses after each definition indicate whether the term applies to R, Rugosa, H, order Heterocorallia of subclass Rugosa, or T, Tabulata. Terms applying only to the Tabulata are to be found in the section on morphology of the Tabulata.

abaxial declination of dissepimentarial or tabularial floors. Floors slope down away from axis (H, R).

acanthine septum. Type composed of a single series of trabeculae with free distal ends forming spinose projections (R, T).

adaxial declination of dissepimentarial or tabularial floors. Floors slope down toward axis (R).

adaxial (axial) increase. Offsets arise from parent corallite by growth of new dividing walls from wall toward axis (R, T).

ALAR FOSSULA. Relatively prominent interseptal space at locus of insertion of new septa on counter

side of alar septum (see fossula, cardinal fossula, counter fossula) (R).

ALAR SEPTUM (symbol A). One of two protosepta located about midway between cardinal and counter septa, distinguished by insertion of newly formed metasepta on side facing counter septum (see other types: cardinal, counter, counter-lateral) (R).

amplexoid septum. Type characterized by shortness except where septum is extended adaxially on distal side of a tabula, as in *Amplexus* (R).

APEX. Conical tip at proximal end of solitary corallite (R) or protocorallite (R, T).

aphroid. Massive corallum like astreoid type but septa shortened peripherally, adjacent corallites being united by a dissepimental zone (R).

arachnophylloid. Type of septum consisting of a rectilinear network of short trabeculae based on dissepiments and connected by transverse rods, as in *Arachnophyllum* (R).

aseriate septum. Type of septum composed of short, fine trabeculae that curve laterally so as to end in septal faces, not on the distal or axial septal edges (R).

astreoid. Massive corallum in which septa of each corallite are fully developed but walls between corallites are lacking; septa of adjacent corallites are generally in alternating position (R).

atavo-tissue. Skeletal elements of parent corallite that proceed distally without change and are incorporated in architecture of offset (R, T).

aulophylloid. Type of axial structure like that termed clisiophylloid but lacking a medial plate and outlined by a tabellar wall, as in *Aulophyllum* (R).

AULOS. Tubular axial structure that divides inner, commonly horizontal parts of tabularial floors from outer, abaxially declined parts (R).

axial coil. Longitudinal structure in axial region of corallite formed by twisting of inner edges of major septa commonly associated with transverse skeletal elements; coiling is commonly counter-clockwise adaxially in calical view (R).

axial column. Axial structure with wall formed by tabellae each with its outer edge based on the one next below (R).

axial lobe. Digitate or veriform adaxial septal projection (R).

axial septum. Longitudinal plate composed of cardinal and counter septa conjoined at axis (R).

axial structure. Collective term for various longitudinal structures in axial region of corallite, whether solid or nonsolid, a rodlike columella or an axial coil (R, T).

axis of divergence. Generally vertical or oblique line in septum from which trabeculae diverge inward and outward (R).

biform tabularium. Type commonly found in corallites with contratingent minor septa; the slope of the outer part of the tabularial floor is reversed or reduced in loculi between the minor septa and

the major septa against which they impinge (R).

calceoloid. Solitary corallite shaped like tip of pointed slipper as in *Calceola,* with angulated edges between flattened and rounded sides (R).

CALICE. Distal surface of corallite, generally bowl-shaped (R, T).

calicular boss. Protuberance in central part of calice in some corallites; may rise from calicular pit (R).

calicular pit. Abruptly depressed central part of calice in some corallites, surrounded by a calicular platform (R).

calicular platform. Part of floor of calice, having a subhorizontal orientation or outwardly sloping (everted) form; generally surrounds a calicular pit (R).

CARDINAL FOSSULA. Relatively prominent interseptal space developed in position of cardinal septum and generally with deepening of tabular floor; comprises the two cardinal loci of metaseptal insertion (R).

CARDINAL SEPTUM (symbol C). Protoseptum in plane of bilateral symmetry of a corallite, distinguished from other protosepta by insertion of newly formed metasepta adjacent to it on either side (R).

CARINA. Keel-like elevation on face (side) of septum, parallel with axis of septal trabecula (R).

catenoid. Corallum with corallites united laterally as palisades which appear chainlike in cross section (R).

ceratoid. Very slenderly conical, horn-shaped solitary corallite (R).

cerioid. Massive corallum in which walls of adjacent polygonal corallites are closely united (R, T).

clinotabella. Somewhat globose short tabella declined adaxially from dissepimentarial wall and abutting on earlier tabella (R).

clinotabula. Elongate tabella steeply declined adaxially from dissepimentarial wall and either crossing transversely to meet axial column or abutting on upper surface of earlier clinotabula (R).

clisiophylloid. Type of axial structure with short medial plate in cardinal-counter plane, in transverse section resembling a spider web, as in *Clisiophyllum* (R).

closed fossula. Prominent interseptal space enclosed toward axis of corallite by united edges of septa (R).

COLUMELLA. Solid or nonsolid axial structure formed by various modifications of inner edges of septa; commonly projects into calice in form of a calicular boss (R).

COMPLETE TABULA. Type consisting of a single platform, not composed of several small plates joined together (H, R, T).

COMPOUND CORALLUM. Type consisting of protocorallite and offsets (R, T).

concave side. The side of lesser curvature in a curved solitary corallite (R).

concentric dissepimentarium. Type with septa longitudinally continuous and dissepiments with their edges drawn up toward septa so that their cross sections are concave toward axis of corallite (R).

connecting platform. Found in phaceloid coralla where simultaneous extensions of calicular platforms of all corallites develop periodically (R, T).

connecting tubule. Subhorizontal tubular connection between neighboring corallites in fasciculate corallum (R, T).

contraclined. Minor septum that inclines toward but does not connect with major septum adjacent on side toward counter septum (R).

contratingent. Minor septum that leans against major septum adjacent on side toward counter septum (R).

convex side. The side of longest curvature in a curved solitary corallum (R).

CORALLITE. Exoskeleton of a solitary polyp or of a bud in a colony (H, R, T).

CORALLUM. Exoskeleton of a coral colony or a solitary coral (H, R, T).

counter fossula. Relatively prominent interseptal space developed in position of counter septum (R).

COUNTER-LATERAL SEPTUM (symbol KL). One of two presumed protosepta that adjoin counter septum on either side (R).

COUNTER SEPTUM (symbol K). Protoseptum opposite cardinal septum in position (R).

cylindrical. Type of corallite of nearly uniform diameter except in the apical region of solitary forms (H, R, T).

cystiphylloid dissepiment. Type found in corals in which septa are longitudinally discontinuous and are represented by septal crests of separate or only in part contiguous trabeculae (R).

dendroid. Irregularly branching types of fasciculate corallum (R, T).

dibunophylloid. Type of axial structure like that termed clisiophylloid but with longer medial plate and fewer septal lamellae, as in *Dibunophyllum* (R).

dilated septum. Type partly or wholly thickened (R).

discoid. Solitary corallite with buttonlike form (R).

DISSEPIMENT. Small domed plate forming cystlike enclosure in marginarium of a corallite (R, T).

DISSEPIMENTARIUM. Peripheral zone of corallite interior occupied by dissepiments (R).

distal. Direction away from point of origin of a corallite (see proximal) (H, R, T).

EPITHECA. Thin external sheath covering inner fibrous part of outer wall of corallite (R, T).

exsert. Type of septum with axis of trabecular divergence such that distal ends of abaxially inclined trabeculae rise free above upper edge of epitheca (R).

fascicle. Microstructural unit, a conical aggregate of fibers of $CaCO_3$, expanding distally (H, R, T).

fiber. Fine structural unit, composed of tufts of needles of $CaCO_3$ grouped into fascicles (H, R, T).

fine structure. The fine skeletal structure as it appears in study by hand lens (H, R, T).

first order trabecula. Type that extends from wall to distal or axial edge of septum; commonly large (H, R, T).

flange. Keel on face of septum and directed parallel to distal edge of septum or horizontal (R).

foliose. Type of corallum with laminar branches (R, T).

FOSSULA. Interseptal space distinguished by unusual shape and size; when used alone refers to cardinal fossula (R).

groove. See septal furrow.

growth ridges (rings). Fine accretion rings of epitheca (R, T).

herringbone dissepimentarium. Type in which dissepiments between major septa inosculate, minor septa being longitudinally discontinuous (R).

holacanth. Seeming trabecula consisting of clear calcite, an effect of diagenesis on axial part commonly of rhabdacanth or monacanth (R, T).

holotheca. Epithecal sheath common to peripheral corallites of a compound corallum (R, T).

horseshoe dissepiment. Type with horizontal base and strongly arched top part, arranged in a pipe in single vertical series (R).

hysterocorallite. New corallite formed in compound corallum (see offset) (R, T).

incomplete tabula. Type consisting of several small plates (tabellae) joined together (R, T).

INCREASE. Addition of corallites to compound corallum (see offset, hysterocorallite) (R, T).

inner septal stereozone. Wall within dissepimentarium and formed by localized thickening of septa (R).

interseptal ridge. Longitudinal elevation on outer side of corallite wall, corresponding in position to space between a pair of adjacent septa inside of wall (R).

keyhole fossula. Prominent interseptal space at position of cardinal septum, expanding more or less suddenly toward its closed adaxial end (R).

laminar septum. Longitudinal radial partitioning wall in corallite formed of trabeculae that are contiguous throughout their length (H, R, T).

lateral dissepiment. Type having blisterlike form developed in isolated manner on sides of septa (R).

lateral increase. Formation of new corallite in fasciculate corallum by sideward growth (R, T).

longitudinal skeletal element. Element of coral skeleton oriented in direction of growth of corallite (H, R, T).

lonsdaleoid dissepiment. Transeptal dissepiment developed across longitudinal discontinuities in septa, as in *Lonsdaleia* (R).

lonsdaleoid septum. Type characterized by longitudinal discontinuity toward peripheral edge, as in *Lonsdaleia* (R).

lumen. Interior of corallite bounded by outer wall (H, R, T).

MAJOR SEPTUM. One of the protosepta or metasepta (H, R).

MARGINARIAL INCREASE. Type in which offsets arise wholly within marginarium (R, T).

MARGINARIUM. Peripheral part of interior of corallite distinguishable from tabularium by difference in constituent structures, generally abundant dissepiments, or dense deposit of skeletal tissue producing a stereozone (R, T).

MASSIVE. Corallum composed of corallites closely in contact with one another (R, T).

METASEPTUM. One of the main septa of a corallite other than protosepta, generally distinguished by their extension adaxially much beyond minor septa (R).

microstructure. Skeletal structure as it appears in study by optical microscope (H, R, T).

microtuft. Smallest conical aggregate of crystallites resolvable under electron microscope (R, T).

miniseptum. Short septum found in some corals in interseptal loculi between adjacent major and minor septa (R).

MINOR SEPTUM. One of the relatively short septa that are inserted between adjacent major septa (H, R).

monacanth. Simple trabecula in which fibers are related to a single center of calcification (R, T).

naotic septum. Type characterized by development peripherally in a series of closely spaced dissepimentlike plates, as in *Naos* (R).

neotissue. New skeletal tissue formed during increase and belonging to the offset alone (R, T).

OFFSET. New corallite formed during increase in a compound corallum (R, T).

open fossula. Prominent interseptal space not enclosed toward axis of corallite by united edges of septa (R).

operculum. Lidlike covering of calice in some corallites, formed of one or more independent plates (R).

parricidal. Term applied to increase in which tabularium of parent corallite ceases to grow distally (R, T).

patellate. Low solitary corallite with sides expanding from apex at angle of about $120°$ (R).

pattern. Arrangement of offsets in compound corallum (R, T).

pectinate septum. Type in which distal ends of first order trabeculae are separate and project like teeth of comb (R, T).

peneckielloid dissepiment. Type formed in a peripheral vertical series, such that in longitudinal section the upper part is flat or declined slightly outward, and the inner part is globose adaxially, as in *Peneckiella* (R).

phaceloid. Fasciculate corallum having subparallel corallites (R, T).

pipe. Single vertical series of dissepiments, of either horseshoe or flat longitudinal section (R).

plocoid. Massive corallum in which corallites are not defined by walls (R).

protocorallite. The first-formed corallite of a compound corallum (R, T).

PROTOSEPTUM. One of six first-formed septa of a corallite (H, R).

proximal. Direction toward point of origin of a corallite (H, R, T).

pyramidal. Solitary corallite with flattened sides that meet at angles, as in *Goniophyllum* (R).

quadrant. Space in interior of a corallite bounded by cardinal septum and an alar septum or by counter septum and an alar septum (R).

radiciform process. Rootlike epithecate outgrowth of a corallite wall, serving for fixation (see also rootlet, talon) (R, T).

ramose. Branching form of cerioid or plocoid corallum (R, T).

rejuvenescence. Type of growth in which diameter is periodically suddenly reduced before again increasing; the reduction may be accompanied by revision of internal structure to that of earlier stage of development (R, T).

retiform septum. Type of perforate septum composed of an irregular network of skeletal tissue (R, T).

rhabdacanth. Compound trabecula with second order trabeculae grouped around its primary axis of growth (R, T).

rhipidacanth. Compound trabecula with second order trabeculae projecting perpendicular to median septal plane (R).

rhopaloid septum. Type characterized by distinctly thickened axial edge appearing club-shaped in cross section (R).

rootlet. See radiciform process (R, T).

scale. Small platelike structure attached to septal grooves or ridges or to smooth epitheca (R, T).

SCLERENCHYME. Calcareous tissue of corallite (H, R, T).

sclerocone (septal cone). Zone of skeletal thickening on selected old calicular floors, more or less widely spaced in the corallite, and affecting septal trabeculae, dissepiments, and tabulae; of inverted conical form (R).

scolecoid. Solitary subcylindrical corallite bent irregularly in wormlike manner (R).

second order trabeculae. Small trabeculae commonly originating either at axis of first order trabecula or in median plane of septum (R, T).

secondary lamellar structure. Fine structure of parallel lamellae commonly oblique to growth lamellae, or zigzag, produced during diagenesis (H, R, T).

septal comb. Septum that is laminar near outer wall of corallite but spinose on distal and axial edges (see pectinate septum) (R, T).

septal cone. Alternative term for sclerocone, which see.

septal crest. Short laminar part of longitudinally discontinuous septum based on upper surface of dissepiment or tabula (R).

septal face. Side of laminar septum (R, T).

septal furrow (groove). Longitudinal furrow on outer side of corallite wall, corresponding in position with a septum on inner side of wall (R).

septal lamella. Radially disposed longitudinal plate in axis of corallite, aligned with a septum but discontinuous with it (R).

septal (axial) lobe. Fingerlike or scolecoid process extending adaxially from axial edge of septum (R).

SEPTUM. Radially disposed longitudinal partition of corallite (H, R, T).

SOLITARY. Corallite of polyp not forming part of a colony (H, R).

spongy columella. Type consisting of axial lobes and septal lamellae associated with tabulae or tabellae (R).

STEREOZONE. Area of dense skeletal deposits in a corallite, generally peripheral or intradissepimentarial in position (R, T).

stunted septum. Type that projects briefly or not at all into lumen, though represented on outside of wall by septal furrow (R).

synapticula. Small rod or bar connecting opposed faces of adjacent septa (R).

TABELLA. Small subglobose plate in axial part of corallite forming part of an incomplete tabula (R, T).

TABULA. Transverse partition of corallite, nearly plane, or upwardly convex or concave, extending to outer wall or to inner marginarial wall (H, R, T).

tabularial floor. Calical surface or vacated calical surface in tabularium (H, R, T).

TABULARIAL INCREASE. Type in which neowalls of offsets arise first in part in axial (tabularial) region, and the tabularium of the parent then ceases to grow (R, T).

TABULARIUM. Axial part of the interior of a corallite in which tabulae or tabellae are developed (H, R, T).

talon. Buttress produced by outgrowth of corallite wall, serving as aid in fixation (see radiciform process) (R).

thamnasterioid. Massive corallum characterized by absence of corallite walls and by confluent septa that join neighboring corallites together, with pattern of septa resembling lines of force in a magnetic field (R).

TRABECULA. Pillar of radiating calcareous fibers comprising skeletal element in structure of septum and related components (H, R, T).

trabecular fan. Fan of septal trabeculae radiating in plane of septum from an axis of divergence (R).

transeptal dissepiment. Type developed across longitudinal discontinuity in septum (R).

TRANSVERSE SKELETAL ELEMENTS. Plates developed transverse to the direction of growth of corallite (H, R, T).

trochoid. Solitary corallite with sides regularly expanding from apex at angles of about 40° (R).

tuft. Fine or ultrafine structural unit, a cone of crystallites as seen with aid of high power optical or electron microscope (H, R, T).

turbinate. Solitary corallite with sides expanding from apex at angle of about 70° (R).

ultrastructure. Skeletal structure as seen by electron microscope (H, R, T).

umbelliferous. Corallum having corallites arranged like ribs of an umbrella, growing outward in whorls (R, T).

uniseriate septum. Type in which trabeculae are arranged in single series with their axes in median plane of septum (R, T).

vepreculae. Fine denticules ornamenting face of septum (R).

verticillate. Arranged in whorls; see umbelliferous (R, T).

WALL. Outer wall of a corallite, normally consisting of an outer sheath (epitheca) and an inner deposit of fibrous sclerenchyme (narrow peripheral stereozone) (R, T).

yardarm carinae. Oppositely placed carinae that give appearance of yardarms along a mast to cross sections of septum (see zigzag carinae) (R).

zigzag carinae. Not quite oppositely placed carinae on the two sides of a septum (see yardarm carinae) (R).

zigzag structure. Diagenetically induced zigzag lamellation in sclerenchyme (R, T).

ASSUMPTIONS ON THE SOFT PARTS

POLYP

The rugosan polyp is assumed to have been like other cnidarian polyps, a cylindrical body terminated above and below by transverse oral and aboral body walls, with a ring or rings of tentacles either near or at the edge of the oral body wall, the tentacles having sensory, tactile, and food-capturing functions (Fig. 19).

As in other Anthozoa with retractile or contractile polyps, the scleractinian mouth, and presumably the rugosan mouth, is connected with the gastrovascular cavity (coelenteron or enteron) by the esophaguslike stomodaeum, and the enteron is radially and longitudinally divided by soft plates or mesenteries that extend from the oral to the aboral body wall and inward from the cylindrical (column) wall, and which may or may not be connected to the stomodaeum (i.e., complete or incomplete). In its aboral end the scleractinian enteron is further divided by radial upfolds in the aboral body wall (septal invaginations) in which the calcareous septa are formed, and which alternate with the mesenteries.

The body wall consists of three tissue layers, two epithelial and one, the mesogloea, supportive. The inner epithelium is the endoderm. The outer epithelium, the ectoderm, is modified on the aboral body wall in Scleractinia and presumably in Rugosa also, by the development of calicoblast cells involved in the production of the calcareous exoskeleton. Muscle fibrils forming sheet-like muscle fields are developed mainly in the admesogloeal parts of the endoderm, which has the important metabolic and reproductive functions as well.

Scleractinians are carnivores, using tentacles, nematocysts, cilia, mucus, and mesenterial filaments to remove zooplankton and other animal fragments from suspension in sea water, selecting by chemical cues. Although ahermatypic corals and some hermatypic corals feed primarily with tentacles, most hermatypic corals rely on ciliary mucoid feeding mechanisms. The majority of corals expand and feed at night, whereas others do so during the day. The stimuli governing such behavior are not yet known (MUSCATINE, 1973, p. 78). Possibly the rugosan polyps had similar devices.

ZOOXANTHELLAE

Also to be found in the endoderm of hermatypic Scleractinia (i.e., those that are reef-builders, or are found only in waters of temperature, depth, and salinity conducive to the formation of reefs), are resting phases of dinoflagellate algae known as zooxanthellae. These do not occur in ahermatypic Scleractinia, which are found in waters too deep or too cold for hermatypic corals. It has been suggested that those Paleozoic corals that are reef-builders also had zooxanthellae.

Zooxanthellae enhance metabolic efficiency by absorbing waste products, and by increasing the rate of calcareous skeletal formation. They may also assist qualita-
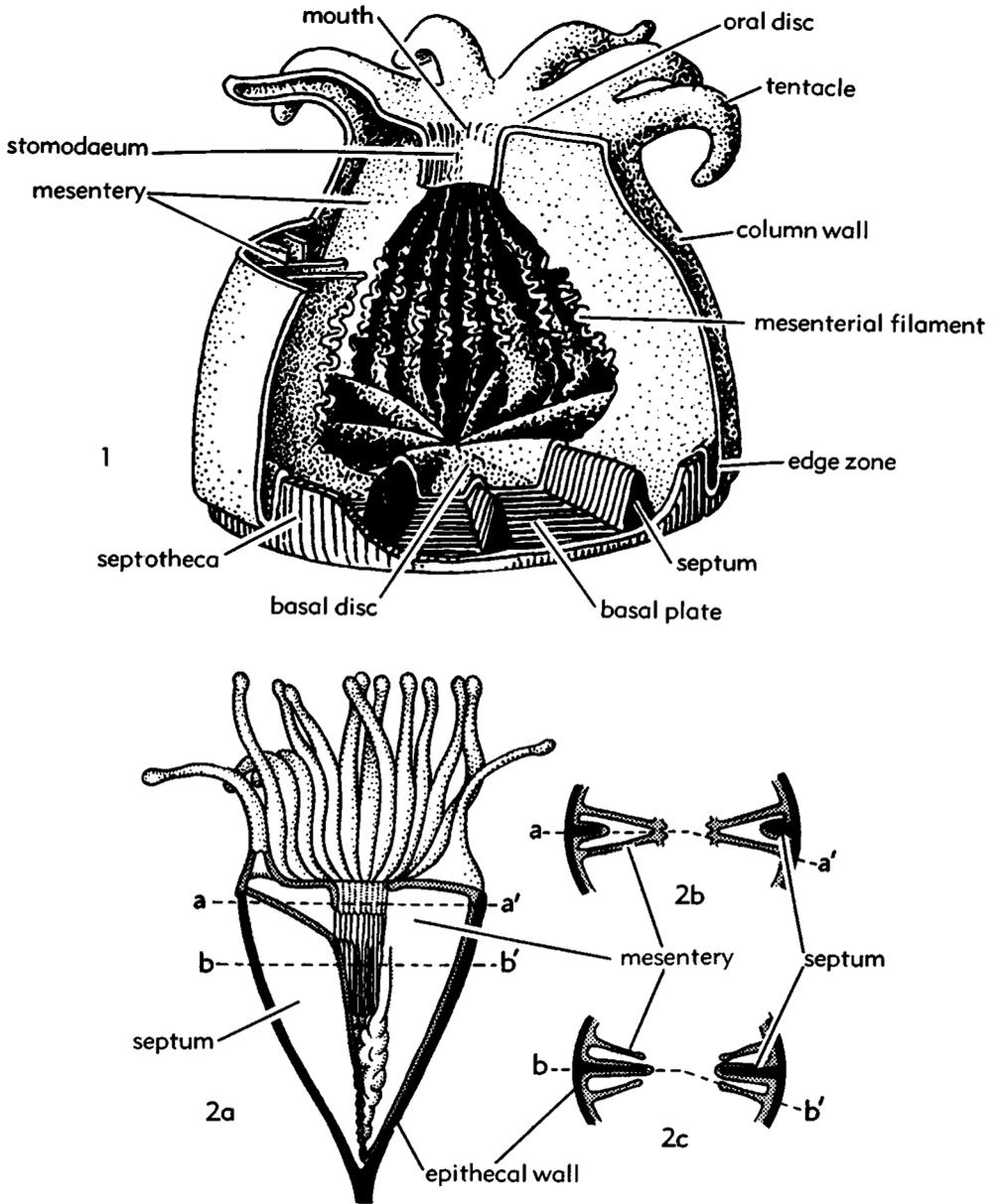
FIG. 19. Assumptions on rugose coral soft parts; the scleractinian polyp.——*1*, Relation of polyp and skeleton; young caryophyllid with edge zone (mesenteries not shown between septa in foreground).—— *2, Flabellum; 2a*, lacking edge zone; *2b,c*, transv. secs. of *2a* along lines a-a′ and b-b′ (after Wells, 1956).

tively, if not quantitatively, in nutrition. Whereas there is no conclusive evidence that zooxanthellae are digested by corals, there are experimental data showing that soluble products of photosynthesis may be released by zooxanthellae into the host cells and thus may be available in metabolism; zooxanthellae may be essential as a source of such nutrients as phosphorous, even though they may be inadequate in some cases as a source of reduced organic carbon (MUSCATINE, 1973, p. 111).

MESENTERIES

The mesenteries are the most vital parts of recent Anthozoa. With their filaments extending from their axial edges below the aboral end of the stomodaeum, they are the organs of digestion, absorption, and excretion; they are also the site of development of the gonads. The muscle fibers in the mesenteries are always more strongly developed on one side, where folds or pleats of mesogloea develop as a result. By the contraction of their endodermal muscle fibrils (longitudinal, radial, and parietobasilar), the mesenteries retract the scleractinian polyp down into the protection of its calice and assist in controlling hydrostatic pressure within the polyp. (For a review of recent work, see FLÜGEL, 1975b, p. 421.)

Scleractinian mesenteries are inserted and arranged in couples, each one of a couple being placed opposite the other, which forms its mirror image on the other side of the plane of bilateral symmetry of the polyp that runs diametrically and longitudinally through mouth and stomodaeum. Mesenteries are also arranged in pairs of neighbors in which the mesogloeal pleats are symmetrically placed, facing either toward or away from one another (Fig. 20; FLÜGEL, 1975b, p. 417, fig. 7b,c). The outward-facing condition is found in the so-called dorsal and ventral (directive) pairs, but the inward-facing condition characterizes the other four primary pairs; thus is established the primary bilateral symmetry of the Scleractinia. The site on the column wall of the planula where the first bulge appears as a precursor of the first couple of mesenteries is arbitrarily termed dorsal.

In the free-swimming scleractinian planula, the mesenteries appear in successive couples in a complex dorsoventral sequence that includes some translation around the perimeter (Fig. 21). It is not until six primary pairs of mesenteries have been established that the symmetry is seen to be hexameral and biradial; this is effected before the planula settles. Upon fixation the scleractinian polyp lays down a tenuous flat circular disc of $CaCO_3$ and the first six calcareous septa are initiated within the six primary mesenterial pairs. A secondary entocoelic pair of mesenteries (i.e., with in-
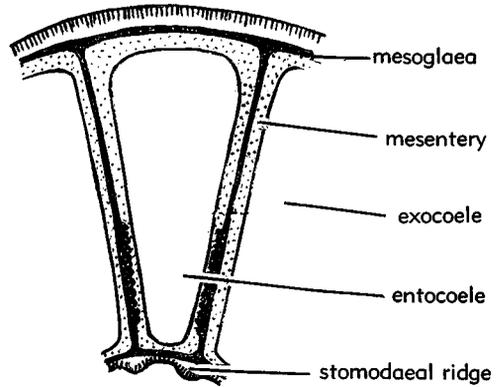
Fig. 20. Assumptions on rugose coral soft parts; generalized transv. sec. of part of scleractinian polyp, showing relations of normal mesenterial couple (Wells, 1956).

ward-facing pleats) and enclosed calcareous septum is then established in each of the six exocoelic spaces alternating with the primary pairs, commonly in dorsoventral sequence. The tertiary entocoelic pair (and enclosed septum) is inserted in each of the 12 spaces (exocoeles), alternating with the secondary and primary pairs, again commonly in dorsoventral sequence. In the Dendrophyllidae, however, the attainment of 12 tertiary entocoeles and 24 quaternary entocoeles is complicated by a substitution process involving 'splitting' of the peripheral ends of six calcareous exosepta (septa formed in exocoeles) of the second cycle and later of the peripheral ends of the 12 calcareous septa of the third cycle.

The development of the first part of the rugosan skeleton indicates that, on settling of the planula, no flat basal calcareous disc was formed, but instead, a cuplike epithecate wall was deposited; the first septa were probably initiated immediately. First, on opposite radii, the cardinal and counter (C and K), commonly conjoined as an axial septum; the next two pairs of septa appeared in cardinal-dorsal sequence, the first pair becoming the alar septa, the second the first counter-lateral septa.

Whether the metasepta and minor septa that pseudoradially ridge the floor of the rugosan calice were, like those of the scleractinian calice, located within entocoeles, either from the beginning or after a substitution process (as for instance in dendro-

phyllids), is still a matter of opinion.

WELLS and HILL (1956) explored the possibility that the metasepta of Rugosa were formed within entocoeles of incomplete mesenteries, inserted, like the calcareous septa within them, in dorsoventral sequence in four sectors, which might correspond to the lateral and ventrolateral exocoeles of Scleractinia (see Fig. 38). This figure shows only major septa; minor septa could be accommodated by showing them (within entocoelic pairs of incomplete mesenteries) formed in seriation with the metasepta. On this assumption the Rugosa are reasonably considered Zoantharia. If KUNTH's mode of septal insertion were involved, minor septal entocoeles of incomplete mesenteries might arise between the newest metaseptum and the cardinal or alar septum; if WEYER's mode were involved, they might arise on the other (counter) side of the newest metaseptum. Differential rates of growth in the circumference of the wall between minor septa and their neighboring major septa might also be involved.

BIRENHEIDE (1965a, p. 31; 1969c, p. 65) did not accept WELLS and HILL's reconstruction. In his view, new major septa were formed by peripheral 'splitting' from the cardinal side of the last-formed major septum. He noted that 'splitting' was described in dendrophyllid Scleractinia in which septa of second and later cycle formed temporarily in exocoeles, and were later 'substituted' by septa formed in permanent entocoeles (WELLS, 1956, fig. 238, 239). Only 'exosepta' were ever noted as being 'split' (branched) in Scleractinia. There is no evidence, such as pali, that substitution occurred in the Rugosa. He concluded that the rugosan metasepta (and perhaps also minor septa) were exosepta, and as such were not enclosed in mesenterial pairs; and thus that mesenteries were probably absent from rugosan polyps. He further considered that the Rugosa, with the Heterocorallia, should therefore be regarded as a separate, new subclass, the Eoanthozoa. His conclusions were not accepted by SCHINDEWOLF (1968) nor by SCHOUPPÉ and STACUL (1968).

'Splitting' as a process in rugosan septal formation requires critical examination. It may possibly involve only the septal fur-
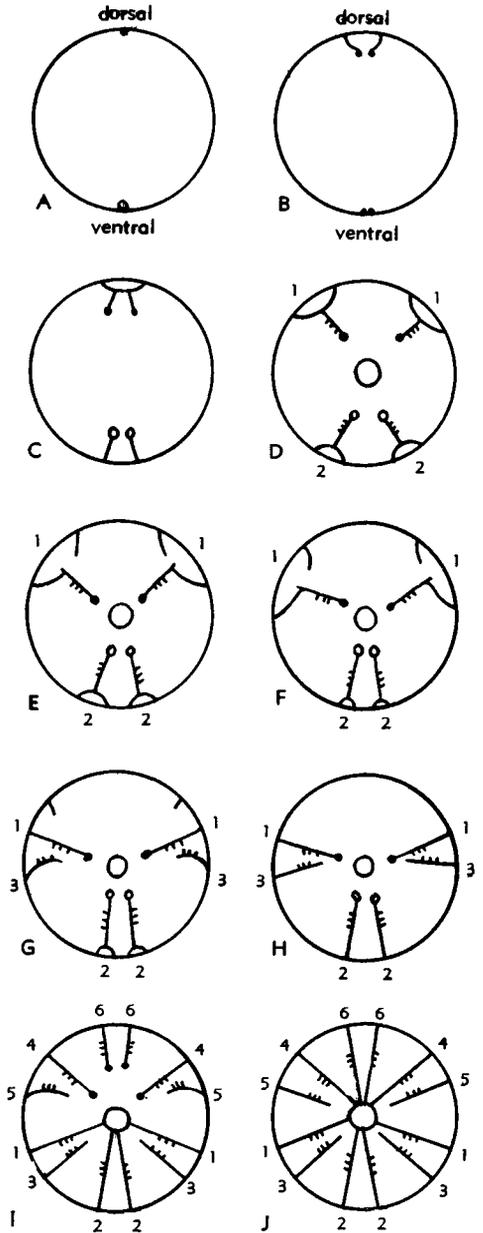
FIG. 21. Assumptions on rugose coral soft parts; development of first cycle of mesenteries (protocnemes) in the scleractinians *Pocillopora* and *Seriatopora; 1,2,4,6,* orthocnemes; *3,5,* sterigmatocnemes. Position of muscular pleats indicated by short lines perpendicular to mesenteries (after Wells, 1956).

rows. WEYER's figured external view of *Sutherlandinia* sp. suggests that the center
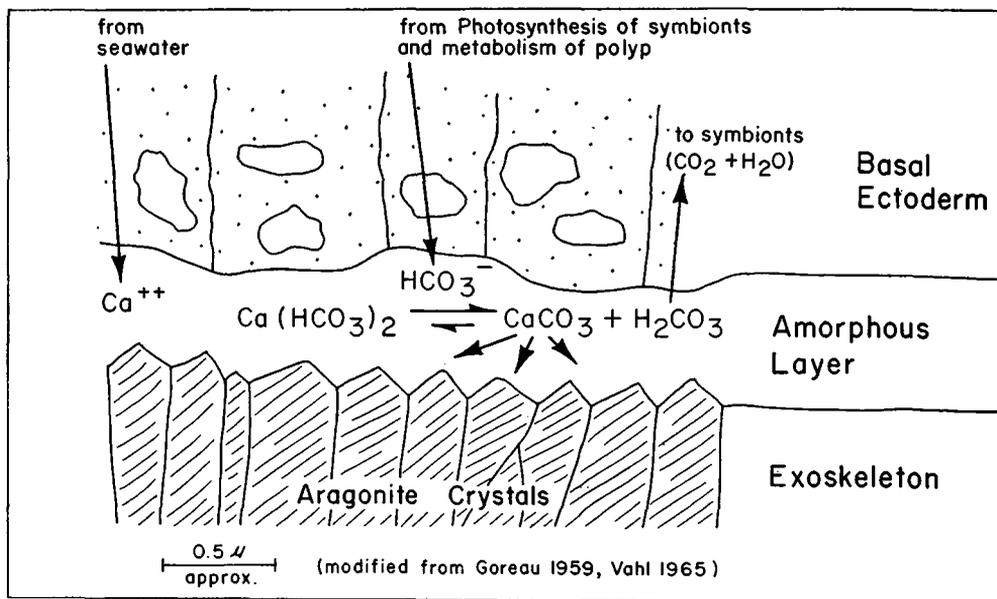
FIG. 22. Assumptions on rugose coral soft parts; biocrystallization. Diagram to illustrate sources of calcium and bicarbonate ions, and their precipitation to form skeletal aragonite needles growing into a 'mucopolysaccharidelike' amorphous layer lying between the basal ectoderm of the scleractinian polyp and the exoskeleton (Sorauf, 1972a).

of calcification for the first trabecula of a new septum may originate at the epithecal septal furrow of a previously formed septum, then shift away as the septal invagination lengthens with the development of subsequent trabeculae. There seems no evidence to suggest that several neighboring peripheral trabeculae of a septum laterally give off secondary trabeculae that collectively diverge as a 'split' septum; 'splitting,' if it occurs at all, presumably occurs only at a point right at the periphery, and not ad-axially along the septum.

BIOCRYSTALLIZATION

In a working hypothesis of biocrystallization of the scleractinian sclerenchyme, clusters of aragonite needles are assumed to form extracellularly in the patterns and modes of spherulitic crystallization in a gel matrix secreted by the basal ectoderm of the polyp. The needles are directed at right angles to the surface of the calicoblast layer. The most active centers of calcification are located at indentations into the calicoblastic layer, and their arrangement and spacing are characteristic of species and even genera

(BRYAN & HILL, 1941; SORAUF, 1972a, p. 89). The processes governing arrangement and spacing have not as yet been investigated. Carbohydrates (?chitin), proteins, and lipids have been found in the gel, which forms the organic matrix for the calcareous skeleton. The source of the Ca^{++} and CO_3^{--} ions used in the crystallization process and the biochemically and physiologically suggested paths taken by them to the sites of calcification are indicated in Figure 22 and further discussed by CHAPMAN (1974, p. 116). The hypothesis may be applied to the rugosan sclerenchyme, though there is a probability that calcite, not aragonite, may have been involved.

In the Scleractinia, the septa and their constituent trabeculae are formed from the calicoblast layer in radial septal invaginations in the aboral body wall; other longitudinal skeletal elements are similarly formed; centers of calcification for the trabeculae are located in minor indentations along the crest of the invaginations. Presumably the longitudinal skeletal elements of Rugosa are similarly related to the soft parts. The dissepiments and tabulae, ex-

cept for their basal dark line, are formed by the calicoblast layer of those uninvaginated portions of the aboral body wall between the septal invaginations (SORAUF, 1972a). The outer wall and its epitheca are formed, as BARNES (1972, p. 341) showed, at the region where the cylindrical polyp wall joins the aboral body wall and a ring-like lappet is developed. The epitheca *sensu stricto* is initiated at the top of the crease between the lappet and the aboral body wall, with a periodicity due to the expansion and contraction of the polyp; the inner, thicker part of the wall is deposited on the inner face of the epitheca by those parts of the calicoblast layer between the peripheral ends of the septal invaginations. Whether the basal dark lines seen in dissepiments and tabulae of both Scleractinia and Rugosa are formed by adaxial horizontal infolds from this part of the aboral body wall, as SORAUF (1972a) and others suggest, requires confirmation, as also does his view that the dark line has an axis or median plane (his "septotheca") from which very fine conical spherulitic segments radiate as shown diagrammatically in his 1972a figure 3.

Distal growth of septa (and septal lamellae) and their constituent trabeculae is apparently continuous apart from the possibly diurnal periodicity evinced by growth lamellae. These growth lamellae may be seen to be continuous with, though differing in thickness from, the growth lamellae of the tabulae and dissepiments that adjoin the septa. Successive growth lamellae of a septum may appear to be continuous, the one with one dissepiment or tabula, the next with the subsequent dissepiment or tabula; yet there may be a considerable space between the two successive dissepiments or tabulae (Fig. 23).

The continuation of lamellae from septum to dissepiment or tabula may perhaps indicate either a relatively rapid change in the position of the calicoblastic layer, or the formation of a new calicoblastic layer. Speculation runs on three main lines. Two assume uplift of the aboral body wall to a new position. One of these suggests that tensile stresses are set up in the aboral body wall due to differential rates of growth between septa and dissepiments or tabulae, and that the stress is relieved by periodic uplift of
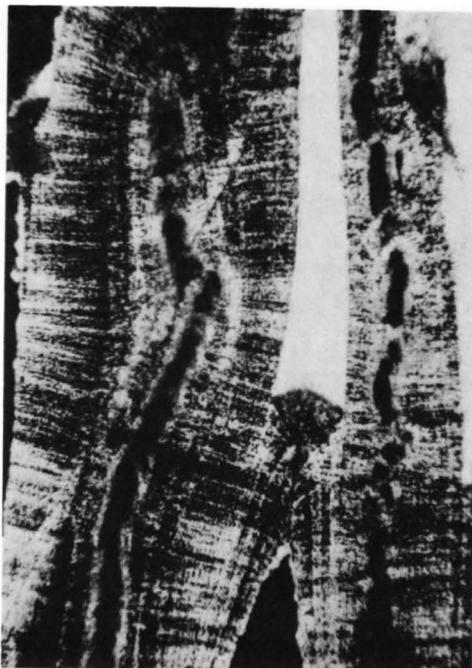
Calophyllum

FIG. 23. Assumptions on rugose coral soft parts; biocrystallization. *Calophyllum rossicum* (SCHINDE-WOLF), M.Perm., Russia; transv. sec. showing growth lamellae of two thick septa continuous with those of thick tabula between them, ×48 (Schindewolf, 1942).

the soft aboral wall between the septal invaginations. The difficulty of releasing intact soft tissue passing through fenestrate or cribriform septa of common walls is considered by some to negate this view. The second assumes uplift due to pressure generated by the secretion of gas or liquid between skeleton and calicoblast layer, i.e., by 'blistering.' The third line deduces that by an infolding of the soft wall, a proximal part of the polyp is cut off by strangulation so that the cut-off part dies; the infold provides the new calicoblast layer for the formation of a new dissepiment or tabula. (For reviews see WELLS, 1969; SORAUF, 1970; WEYER, 1972b, p. 715; FLÜGEL, 1975b.)

FUNCTIONAL MORPHOLOGY OF THE SKELETON

A useful review of speculations on the functional morphology of the rugosan skele-
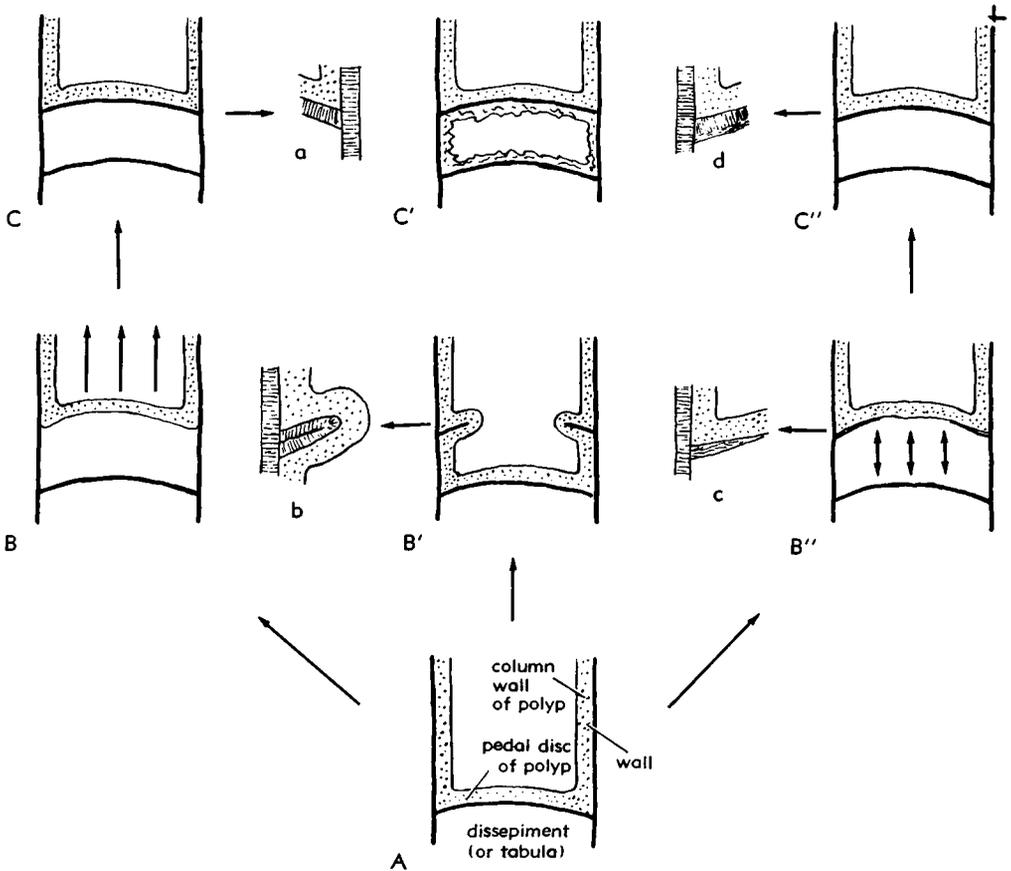
FIG. 24. Assumptions on rugose coral soft parts; theories of dissepimental and tabular development (highly schematic).——*A*, Simplified polyp-corallum relations.——*B, C*, Tractive updrawal of polyp away from dissepiment (or tabula), followed by deposition of fibers *(a)* normal to secreting surface of pedal disc.——*B′, C′*, Horizontal infolding of column wall (MATTHAI; WEYER) with ingrowth of dissepiment (or tabula) with inner 'dark line' *(b)* eventually cutting off lower part of polyp *(C′)* that becomes necrotic.——*B″, C″*, Hydraulic up-pushing of pedal disc and column wall (WEDEKIND), accompanied by centripetal ingrowth of thin dissepimental (or tabular) rings of more or less horizontally oriented fibers *(B″, c)*, followed by secretion of fibers normal to pedal disc *(C″, d)* (Wells, 1969).

ton has been given by FLÜGEL (1975b, p. 421).

The calice, into which the polyp must, as in Scleractinia, have been retractable, had important protective functions. The ridging of its floor by septa imparted greater resistance against dislodgement, and the spaces between major septa in the tabularial region are considered to have supplied greater accommodation for the retracted soft parts, particularly the mesenteries and their mesenterial filaments. Retraction, like distension, was presumably controlled by contraction of the sheets of muscle fibrils, which varied the hydrostatic pressure in the enteron; this complexly coordinated mechanism also controlled the manner of feeding and the ways in which the polyp shed sediment.

Observations on recent Scleractinia suggested to HUBBARD and POCOCK (1972, p. 617) that a positive correlation exists between the strength of retractional and distensional muscular activity of polyps, and the following features of the skeleton: larger number of septa, complexity of septal ornament, fenestrate septa, higher calical relief, V-shaped calical floor, and lighter skeleton. Such features in Rugosa may thus have had similar functional significance.

Whether or not the septa supply fulcra

for sheets of muscle fibrils appears not yet to have been established by direct observation of Scleractinia, in which the mesenteries are attached to the cylindrical, oral, and aboral body walls; in the floor of the calice the lines of their attachment to the aboral body wall alternate with the septal invaginations. BOURNE (1899, p. 499) noted that desmoid processes in the soft wall are concentrated exactly opposite the junctions with the mesenteries, and WISE (1970, p. 978) noted on the inner face of the calcareous wall (theca) between septa, and infrequently on the upper surfaces of tabulae, certain minute depressions that he interpreted as attachment pits for the desmoid processes opposite the mesenteries. So far, no such pits have been described from the lateral faces or distal edges of scleractinian septa, nor have any been recorded on rugosan skeletons.

Another feature of the rugosan calice to which functional significance has been ascribed is the fossula. It has variously been suspected to house a receptacle for enlarged gonad-bearing directive mesenteries or for collections of excrement, and as part of a diametral channel for gastrovascular currents, ciliary and otherwise (see FLÜGEL, 1975b, p. 423). It is much better developed in solitary corallites than in corallites of compound coralla, which presumably had asexual as well as sexual increase.

The position of the fossula in the calice, i.e., in the plane of symmetry, and very commonly on the convex (curved or longer) side of a curved solitary corallum, may possibly be related to a preference of the planula to settle on its cardinal side, though the reason for this preference is unclear (?possibly phototaxy) (FLÜGEL, 1975b, p. 424). A positive phototaxy conceivably leads the polyp by muscular activity to keep its calice perpendicular to the direction of light, i.e., commonly parallel with the surface of the sea, so that the under (commonly cardinal) side may grow distinctly faster than the opposite side (SCRUTTON, 1965, pl. 87, fig. 3). A second explanation, explored for example by WEISSERMEL (1897, text-fig. 2), is that the unequal growth is determined by positive rheotaxy in reaction to unilateral food-bearing currents. Against this it is argued that corals are not filter feeders, which commonly show positive rheotropism, but suspension feeders (MUSCATINE, 1973, p. 78), which are more likely to show positive phototaxy.

Withdrawal of septa in an amplexoid manner from the axis of a solitary rugose corallum, together with development of both a pseudoradial arrangement of the septa and a cylindrical form, were considered by CARRUTHERS (1910, p. 525) to be modifications that ensured the most economical way to use $CaCO_3$ to lift the polyp above rapidly accumulating sediment.

An axial structure might provide selective advantage to the coral in two ways, chemical and physical. Firstly, by protruding into the calice and indenting the aboral body wall of the polyp, the axial structure may have displaced fluid from the enteron, increasing concentration of nutrients therein and the efficiency of absorption. Secondly, attachment of the aboral body wall to the axial structure may have increased muscular efficiency and hence feeding activity (EASTON, 1973, p. 127).

Clearly, however, investigations on functional morphology of the various skeletal elements of the scleractinian skeleton are required to give credence to or invalidate assumptions made for the Rugosa.

EVOLUTION

ORIGINS OF THE RUGOSA

It has been suggested that the Rugosa and Tabulata shared common roots in the early Paleozoic (SOKOLOV, 1962c, p. 211, and fig. 8 on p. 212), and that the common ancestor of the early Rugosa (Streptelasmatidae and Stauriidae) shared some features with the early Tabulata *Aulopora* and *Lichenaria*. IVANOVSKIY (1966, p. 455) concluded that all Rugosa descended from the Auloporida, whereas FLOWER (1961, p. 33; FLOWER & DUNCAN, 1975, p. 177, and figure) saw in *Lichenaria* the common ancestor for the Rugosa and Tabulata. There is as yet no solid evidence to substantiate any of these opinions on origin.

Also, it does not seem likely that the new

Family Cothoniidae JELL and JELL (1976, p. 181), of compound calcareous skeletons composed of conical operculate corallites with radially corrugated and septate calices and fibrous and possibly trabeculate microstructure, from the lower Middle Cambrian of New South Wales, could have been the ancestor of the Rugosa. It has not been possible to establish that members of that family have rugosan septal insertion; it seems that, although increase in circumference of wall takes place at four positions, these positions lie one on each side of each end of a plane of bilateral symmetry, not one on each side of one end and the other two lateral as in the Rugosa.

TRENDS OF DEVELOPMENT

Whether the appearances of particular features in the rugosan skeleton are to be seen as manifestations of evolutionary trends may be debatable. Authors have presumed that some features are primitive and that others, more advanced, have evolved from them. Such presumptions are difficult to assess, because the accumulation and study of sufficiently extensive biostratigraphical evidence is so time-consuming.

Among features of taxonomic value that appeared (or disappeared) at different times (or even approximately simultaneously) in different genera and families are: axial structures of various types; elongation or shortening or stunting of septa; lateral contiguity (or discontiguity) of trabeculae within septa; peripheral or axial longitudinal discontinuity within septa; other complexities of septal structure; marginaria of different types; contours of tabular floors; and compound (or solitary) nature of the corallum. SPASSKIY (1971a, p. 56) has codified the features he considered diagnostic in Devonian superorders, orders, suborders, families, and genera, has devised formulae for genera, and supplied a key to his classification. SPASSKIY and KRAVTSOV (1971, p. 5) and SPASSKIY (1974, p. 127) discussed the appearance and disappearance of such features in terms of heterochronous or isochronous parallelism or homeomorphy, and considered that new features were produced by adaptive variation primarily within marine basins isolated by regression of the seas after epochs of folding; they listed five

peaks of concentration in the appearance of new features of higher taxonomic value, one each at the beginnings of the Middle Ordovician, Late Ordovician, Silurian, Devonian, and Carboniferous.

Other recent discussions of such apparent trends of evolution and of some of the taxonomic implications may be found in IVANOVSKIY (1971b, p. 9; 1975a, p. 26) and WEYER (1973-1977).

ORIGINS OF AND PHYLOGENY IN THE SUBORDERS

It is perhaps not as yet very profitable to speculate on the origin of the 16 suborders of the Rugosa, and only a few tentative suggestions are put forward herein. Two of the three suborders of nondissepimented small solitary Rugosa, the Stereolasmatina and the Plerophyllina, may have evolved from the Metriophyllina, and these three might therefore be regarded as forming an order. However, the idea that either or both arose from the Streptelasmatina is not untenable.

Another possibility is that the Columnariina arose from the Stauriina; if so, the Acervulariidae should perhaps be divorced from the former. The Ketophyllina and Ptenophyllina also may well have developed from the Stauriina. The Streptelasmatina possibly gave rise to the Arachnophyllina and Lycophyllina as well as to the Cyathophyllina, from which perhaps the Aulophyllina derived. The Caniniina are a problem; an origin from the Lycophyllina is possible. Both the Lithostrotionina and Lonsdaleiina may conceivably have derived from the Aulophyllina.

Different sets of speculations have been offered in diagrams by SPASSKIY (1974, p. 133) and IVANOVSKIY (1965a, p. 53; 1967, fig. 7 on p. 18; 1975a, p. 39). IVANOVSKIY (1971b, p. 9) has also discussed stages in the evolution of the Rugosa. Many authors, notably WEYER, have included in their discussions of families, subfamilies, genera, and species, opinions on the relationships between them.

Phylogenetic relations between families of Ordovician and Silurian Rugosa have been suggested by IVANOVSKIY (1965a, fig. 7 on p. 51; 1968, fig. on p. 86) and between genera within families by IVANOVSKIY

(1965a, p. 46; 1969, fig. 21 on p. 55; and fig. 28 on p. 97) and by LAVRUSEVICH (1971a, fig. 22 on p. 96).

For Devonian families, SOSHKINA (1952, fig. 21, on p. 28; 1954, table 3 on p. 20) has suggested schemes. SPASSKIY (1960a, fig. 4 on p. 93; 1964, fig. 1,2; 1965a, fig. 1-4) has provided diagrams of possible phylogenetic relationships between genera in his families and suborders of Devonian Rugosa, and IVANIYA (1965, p. 226) has also speculated on Devonian phylogenies. ROZKOWSKA (1953, fig. 40 on p. 73) has suggested relationships within the Polish species and genera with pipes of horseshoe dissepiments, and (1969, fig. 5 on p. 27) for the Upper Devonian Polish families and genera of small, mainly nondissepimented, solitary Rugosa.

Possible relations between Carboniferous families have been suggested by IVANOVSKIY

(1967, fig. 8 on p. 19) and for Carboniferous genera and species of the Urals by DEGTYAREV (1973a, figure on p. 81). For the Pennsylvanian Pseudopavonidae, KATO and MINATO (1975, fig. 4 on p. 112) have suggested a scheme of relationship between genera. MINATO and KATO (1970, fig. 2 on p. 6) deduced phylogenetic lines between and within the Carboniferous and Permian families Durhaminidae, Waagenophyllidae, and Lithostrotionidae.

For the Devonian to Permian plerophyllinan families and genera, ILINA (1974, fig. 1 on p. 212) and SOKOLOV (1960, fig. 2 on p. 51) have given phylogenetic schemes, and both of these authors subscribe to the view that genera of Scleractinia arose from this suborder.

This *Treatise* does not accept the theory that the Scleractinia evolved from the Rugosa.

DIVERSITY GRADIENTS

Both horizontal (geographical) and to a lesser degree vertical (bathymetric) gradients in generic diversity have been analyzed for the Holocene scleractinian reef corals, based on taxonomic distribution data provided mainly by WELLS (1954) and analyzed using statistical methods by STEHLI and WELLS (1971) and ROSEN (1971). ROSEN's horizontal diversity contour map (Fig. 25) shows three foci of maximum diversity, each roughly centered on the equatorial region: one in the western Pacific about New Guinea, a second of slightly lesser diversity in the western Indian Ocean which, with further data, may prove to be continuous with the first, and a third, much less diversified, in the western Atlantic (West Indies). Whereas the contours are more or less latitudinal, there is a distinctly greater extension northward than southward, in the western part of the oceans particularly. The western regions are no doubt favored by the Holocene circulation patterns of the surface equatorial currents; the western faunas are enriched and the eastern faunas winnowed by the net direction of transport of planulae. The warm northerly or northeasterly currents of the western regions (Gulf Stream and Kuroshio Current) penetrate farther toward the pole

than do the southern currents. These regional diversity contour patterns closely resemble the equal temperature contour patterns. ROSEN's (1971, p. 275) diversity-temperature curve for the Indian Ocean becomes less steep at about 25°C and suggests a peak at about 28 or 30°C, thus according well with the acknowledged optimum for reef-coral growth (25-29°C, WELLS, 1957a, p. 1088). As temperatures rise to 40°C, diversity theoretically will be reduced to nil.

As one moves out from a focus of maximum diversity, the same genera drop out, generally in the same sequence, and the remaining peripheral faunas are of the same generic composition and include only genera also found more centrally (WELLS, 1954, p. 389). The genera with extensive distribution are usually the oldest (STEHLI & WELLS, 1971, p. 125) and also the most important reef contributors (ROSEN, 1971, p. 279). In reef Scleractinia, maximum diversity apparently occurs within limits that are optimal for maximum skeletal production: at temperatures from 25 to 29°C, normal salinities between 34 and 36‰, depths up to 18 m, in agitated water with nutrient-bearing currents, minimum supply of terrigenous detritus, and bulk supply of calcareous skeletal
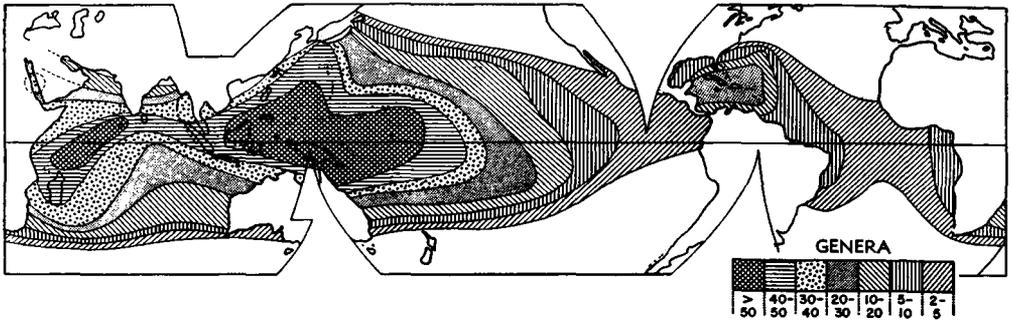
FIG. 25. Diversity gradients; world variation in reef coral diversity (Rosen, 1971).

and algal detritus.

Temperature is considered to be the most important single controlling factor for horizontal (geographical) diversity, and the influence of minimum temperature on reproduction of chief importance (YONGE, 1940, p. 380).

The principal controls for vertical (bathymetric) diversity gradients in Holocene reef Scleractinia appear to be, first, the amount of radiant energy available to the symbiont zooxanthellae for photosynthesis, which decreases with increase of depth, latitude, and amount of suspended matter; second, possibly, the decrease of water movement with depth. Temperature appears not to apply in depth diversity, because diversity at depth is invariably lower than the prevailing temperature would permit (WELLS, 1954, p. 386, 406). Present depth records indicate that diversity is greatest between 0 and 18 m, decreasing rapidly downward to a limit between 45 and 110 m (see also WELLS, 1967, p. 350).

Rugosan diversity gradient studies are complicated by the difficulty we have in precisely identifying the fauna proper to even a single age over the whole world; a third gradient, the chronological gradient, almost inevitably obscures the geographic and bathymetric gradients. Analogy with scleractinian reef corals is generally assumed.

OLIVER (1976a, p. 40), from his studies on the Lower and Middle Devonian colonial Rugosa of New York, concluded that environmental factors permitting high species diversity also permit greater variation within the species. Thus in the Edgecliff bioherm facies, there is high species diversity and high intercolony variation. At the other extreme is the Moorehouse *Acinophyllum-Eridophyllum* bed with only two species of corals; although coralla are abundant, intercolony variation is minimal.

Of the few precise geographical diversity studies attempted, that published by ANSTEY and CHASE (1974, p. 1142) confines itself to the Upper Ordovician corals (presumably both Rugosa and Tabulata) of North America. It suffers, perhaps, from the small number of Upper Ordovician genera and species. The results, considered in relation to a paleoequator based on paleomagnetic data, were interpreted as indicating that the lithofacies control of coral diversity overrode that of latitude; they found a marked correlation between carbonate lithofacies and diversity.

Many initial surveys of geographical distribution have been used herein in the preparation of the chapter on distribution. Based on analogy with scleractinian reef corals, it may be assumed that rugosan rates of evolution increased in regions of maximum diversity, that new species and genera spread outward therefrom, and that cosmopolitan genera, in addition to being those successful over the widest range of environments, may well have had the longest ranges in time.

Little is known of bathymetric diversity gradients in rugosan faunas, though several authors have indicated that assemblages change with changing depth and with related changes in degree of water turbulence (LOWENSTAM, 1957, p. 231; BIRENHEIDE, 1962c, p. 21; KLOVAN, 1964; LECOMPTE,

1968, p. 26; EMBRY & KLOVAN, 1971, p. 738; JAMIESON, 1971, p. 1311; STEVENSON & GAUNT, 1971, p. 128; TSIEN, 1971, p. 121; BROADHURST & SIMPSON, 1973, p. 370).

PALEOECOLOGY

The Rugosa were epifaunal benthos, predominantly neritic, most profuse and diverse in carbonate perireefal and reefal environments, though they were seldom significant reef-builders. It is assumed that in the Paleozoic, as in the Holocene, carbonate provinces with reefs characterized warm (tropical to warm-temperate), shallow (epicontinental and shelf), well-oxygenated seas with high radiant energy, normal salinity, and rich nutrient sources. These generalizations are supported by much observed sedimentological data, though there are many uncertainties in detail.

Three gradational facies faunas are recognized. The first is a fauna of very small to small, solitary nondissepimented genera, not of great diversity, but accompanied by two or three genera of Tabulata developing colonies of small size, and by small brachiopods. This fauna is commonly found in dark or olive calcareous shale with or without thin-bedded argillaceous limestone or thin-bedded crinoidal limestone. In rare occurrences of a limited number of species in bioherms (e.g., *Amplexus* in the Lower Carboniferous knoll reefs), members of the fauna may attain considerable size while retaining simple internal structure. It is regarded as adapted to the muddier, darker, quieter, and therefore deeper parts of epicontinental or shelf sea floors. Also, in the middle and late Paleozoic beds of the Variscan geosyncline, very small laccophyllids occur as sparse benthos in cephalopodan limestone originally deposited as abyssal oozes composed largely of the skeletons of pelagic organisms; depth of deposition was assumed to be between 200 and 4,000 m below sea level (BANDEL, 1974, p. 112). This fauna may thus be ecologically analogous to the Holocene ahermatypic scleractinian fauna; its members are largely Metriophyllina and Plerophyllina and it has been variously called a zaphrentid, *Cyathaxonia,* syringaxonid, or polycoeliid fauna (or facies or phase) (VAUGHAN, 1910, p. 190; HILL, 1938, p. 5; HUDSON & COTTON, 1945, p. 281; BANDEL, 1974, p. 112; KULLMAN, 1975, p. 161).

The second gradational facies fauna, predominantly of larger, dissepimented solitary corals, appears in all periods from Ordovician to Permian, and is to be found in the somewhat more calcareous rocks, mainly in argillaceous limestones. The greater size of coralla and, in many cases, the greater diversity of species and genera in these limestones seem to indicate conditions more favorable than those tolerated by the first fauna. Where paleoslopes or transgressions or regressions have been deduced, this fauna occupied shallower zones than the smaller, nondissepimented coralla (BIRENHEIDE, 1962c, p. 22). In some coral beds, coralla are found upright, indicating growth on quiet bottoms; in others, they lie on their sides and may be curved, irregularly or regularly, with the growth rings on their epitheca reflecting attempts to keep their calical floors perpendicular to the surface of water or source of light, or to the rain of zooplankton. In some beds they lie on their sides with the upper parts eroded, and this is taken to indicate that water movement, possibly due to storm action, has winnowed away the supporting muds (HUBBARD, 1970, p. 193). Attachment to substrate was commonly abandoned soon after settling of the planula. The fauna of these 'turnip reefs' or 'cabbage stalk patches' may include some representatives of the first fauna, but these are commonly larger than in the more tolerant fauna. In the Middle Devonian of the Eifel, this fauna represents a slightly deeper-water subfauna than the common, quiet-water coral meadows or turf-reefs in which the solitary Rugosa, like those of forereef aprons, commonly possess rootlets or talons to keep them upright (BIRENHEIDE, 1962c, p. 23); in the turf-reefs the solitary coralla are somewhat eclipsed by the vigorous development of fasciculate coralla and the rather sparse massive coralla. The fasciculate habit so characteristic of this turf-reef subfauna is that found in lagoonal or backreef

or other quiet but shallow environments of modern reefs. In the Devonian the solitary corals of these subfaunas are predominantly Ptenophyllidae and cystimorphs; in the Carboniferous, Caniniina or Aulophyllina have replaced the Devonian taxa, and there are suggestions that the Aulophyllidae, with their complex axial structures, represent more propitious conditions than the Caniniina limestones. This fauna grades into the third as the compound coralla came to dominate the solitary corals.

In limestone with little or no argillaceous matter, or deposited in more agitated waters, compound coralla may outnumber solitary coralla, and thus the second fauna grades into the third or perireefal fauna. In exposed parts of Silurian or Devonian reefs, its hemispherical coralla may compete with blocky stromatoporoids. In still more exposed waters, subject presumably to surf action, its massive coralla may be extensiform, increasing their ability to withstand translocation by waves. This third fauna compares best with the scleractinian fauna with symbiotic zooxanthellae that is characteristic of Holocene reefs. Whether its members also possessed zooxanthellae is uncertain. Manten (1971, p. 466) considers this fauna to have been so profuse in the Silurian as to suggest that they did, but Coates and Oliver (1973, p. 24) assumed that the Rugosa were without zooxanthellae.

The most clearly defined geological factor controlling the distribution of these three faunal types is the sedimentary environment; an increase in size and in complexity of structure of corallum accompanies decreasing terrigenous content, an increase that is accompanied (as the work of Oliver, 1976a, p. 40, shows) by increasing taxonomic diversity and intercolonial variability. Conditions for corals clearly improved at the same rate as conditions favoring reef growth.

There are also suggestions that these faunas replace one another vertically, either in topographic zones up paleoslopes (Birenheide, 1962c, p. 22) or with fall in sea level or with the growth upward into shallower waters of reefal bodies or sedimentary piles (Lecompte, 1958, p. 390).

Scleractinian hermatypes flourish and breed best in water temperatures between 25 and 29°C. Although, in general, organic diversity is dependent mainly on temperature, in Scleractinia with zooxanthellae the number of species is controlled by light intensity and radiant energy rather than by temperature or by oxygen supply (i.e., by aeration) (Wells, 1957c, p. 611; 1967, p. 352). Thus, the symbiotic algae appear to increase evolution rates as well as skeletal carbonate production. That ambient light has an important effect on reef coral growth form has been supported by a computer simulation program by Graus and MacIntyre (1976, p. 895). The scleractinian *Monastrea annularis* in the Caribbean area is approximately hemispherical in shallow water (1-5 m), peaked or columnar at depths between 5 and 25 m, and platelike at the greatest depths for the species (25 m); over the same depth intervals, maximum annual skeletal growth decreases from 1.1 to 0.3 cm. The salinity range favored is the normal 34 to 36‰, and the optimum depth lies above 25 m and probably within the top 15 m. Planulae settle only on a firm, smooth substrate. Corals cannot survive where large amounts of sediment are shifted over the bottom by waves or currents. Sediment in suspension is not inhibiting, but corals are suffocated if the accumulation of sediment is too great to be removed by normal water movement assisted by the very considerable sediment-removing or rejecting activities of the polyps. These mechanisms include hydrodistension, tentacular movement, and mucus and ciliary currents (Yonge, 1930, p. 16; Marshall & Orr, 1931, p. 130; Hubbard & Pocock, 1972, p. 617).

Ahermatypic scleractinians are insignificant as reef constructors and have a very wide range of habitat. They live at depths from 0 to 6,000 m in both lighted and aphotic zones, though the greatest variety is at moderate depths, from 50 to 300 m, where they flourish in almost complete darkness. They tolerate temperatures from 0.5 to 28°C, and are found in all seas where salinities are not below 34‰ (Wells, 1957a, p. 1089; 1967, p. 353).

Our assumption that the two rugosan faunas found in or near Paleozoic reefal environments flourished within the same general ranges of temperature, salinity, radi-

ant energy, and depth as did the scleractinian reef fauna with zooxanthellae should be tested as far as possible in future research. Whether or not the Rugosa of the Paleozoic reef possessed zooxanthellae seems at present to be incapable of proof. On the basis of conditions as deduced from the form of the corallum and enclosing sediments, or by analogy with modern corals, WELLS (1957b, p. 774) considered that most Paleozoic corals lived in ecological niches similar to those occupied by the nonsurface, essentially lagoon reef corals of the present day: 1) to a maximum depth of about 50 m; 2) well within the lighted zone; 3) in temperatures with annual minima between 16 and 21°C; 4) in well-oxygenated, gently circulating water; and 5) on bottoms free, or relatively free, from rapid accumulation of sediment, but not necessarily in clear, nonturbid water. These generalizations are still in accord with the collected data. WELLS also considered the Paleozoic corals relatively unimportant as reef-builders and suggested that the reason might be their failure to develop adequate capacity to adhere strongly to substrate.

Variation within species with change in environmental niche has been suggested. Thus, BIRENHEIDE (1963b, p. 405) indicated that *Peripaedium planum* developed flat colonies with strongly everted calices in the uppermost zone of greatest water agitation dominated by blocky stromatoporoids in the Middle Devonian of the Eifel, whereas in slightly less turbulent conditions this species developed hemispherical colonies with only shallowly everted or flat calicular platforms. TSIEN (1970, p. 161) remarked that in the quiet-water *(sous-turbulente)* zone of the Frasnian basin facies of Belgium, colonies of *Disphyllum goldfussi* are small and erect, while on the shelf, where they preferred subturbulent or turbulent zones, colonies are larger and more bushy; and also that, in general, *Disphyllum* possessed more or less rounded calicular platforms in a reefal or turbulent milieu, but in lagoonal or restricted environments its calicular platforms were steeply declined adaxially. HUBBARD and POCOCK (1972, p. 617) associated deep, V-shaped calices with stronger activity in the polyp's rejection of sediment, and indicated other features that might also be correlated with efficiency in sediment rejection.

Commensalism. Intergrowths of fasciculate or more rarely of solitary Rugosa with stromatoporoids are not uncommon; there seems little evidence on which to base a discussion on possible mutual benefit from such intergrowths. The Silurian ?stauriid *Prisciturben* KUNTH, 1870, p. 28, may be one example.

Tubes situated commonly in or between the common walls and seldom at the angles between walls of corallites of species of the Devonian ptenophyllid *Xystriphyllum* HILL, 1939b, p. 62, have been considered by KRAVTSOV (1965, p. 126) to be the tubes of a commensal worm, a spiral annelid, of a type previously known in Tabulata.

PALEOZOOGEOGRAPHIC PROVINCES AND SEQUENCE OF FAUNAS

Paleozoogeographical regions and provinces suggested in the literature on Rugosa up to the present can only be regarded as tentative and preliminary; substantial modifications must be expected as rugosan taxonomy and chronostratigraphy become more precise. The broad outline of the sequence of faunas that follows includes references to relevant reviews.

ORDOVICIAN

The Middle Ordovician Blackriveran Stage of North America provides the oldest proven rugosan fauna, but its few small solitary corals and cerioid stauriid *Favistina* are still inadequately described. In a probably slightly younger fauna from New South Wales (Fauna 1; McLEAN & WEBBY, 1976, p. 232), a small rugosan with discrete monacanthine septa *(Hillophyllum)* is at present regarded as the first tryplasmatid, though its relationship to the probable calostylid *Lambeophyllum* of North America needs further evaluation. Faunas of probably Trenton age are known not only from North America, but also from Europe, the
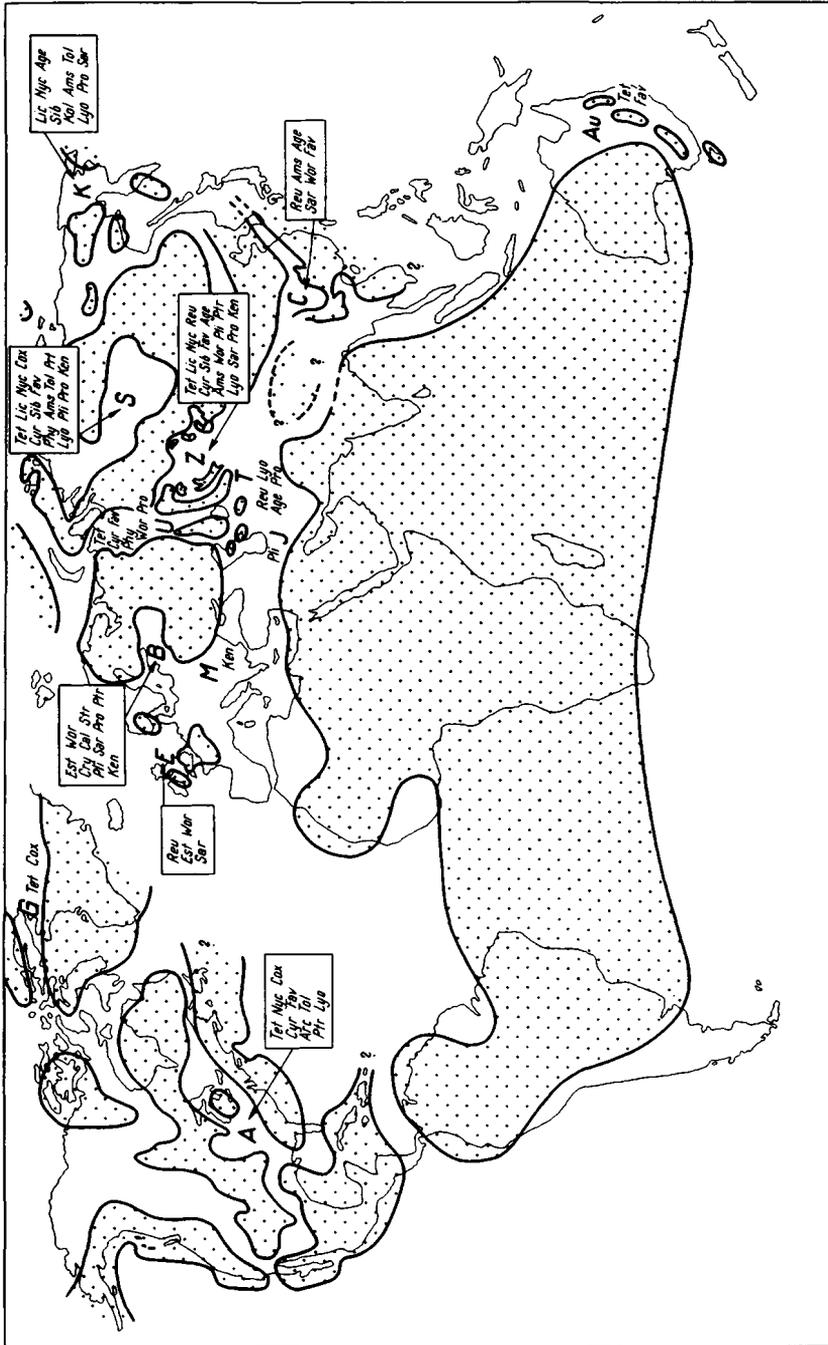
Fig. 26. Paleozoogeographic provinces; distribution of Late Ordovician corals (after Kaljo & Klaamann, 1973). Legend: *A*, North America; *Au*, Australia; *B*, Baltic and Scandinavia; *C*, China; *E*, Great Britain; *G*, Greenland; *I*, Iran; *K*, northeastern USSR; *M*, Bohemia and Podolia; *S*, Siberia; *T*, Tadzhikistan; *U*, the Urals; *Z*, Kazakhstan, the Sayans, and the Altai; spotted areas, land; white areas, sea. Abbreviations of generic names: *Age*, *Agetolites*; *Ams*, *Amsassia*; *Arc*, *Arcturia*; *Cal*, *Calostylis*; *Cox*, *Coxia*; *Cry*, *Cryptolichenaria*; *Cyr*, *Cyrtophyllum*; *Est*, *Esthonia*; *Fav*, *Favistella*; *Ken*, *Kenophyllum*; *Kol*, *Kolymopora*; *Lic*, *Lichenaria*; *Lyo*, *Lyopora*; *Nyc*, *Nyctopora*; *Phy*, *Phytopsis*; *Pli*, *Paliphyllum*; *Pro*, *Propora*; *Prt*, *Protaraea*; *Ptr*, *Proterophyllum*; *Reu*, *Reuschia*; *Sar*, *Sarcinula*; *Sib*, *Sibiriolites*; *Str*, *Strombodes*; *Tet*, *Tetradium*; *Tol*, *Tollina*; *Wor*, *Wormsipora*.

Siberian Platform, and eastern Australia. In the latter, *Hillophyllum* is joined by the fasciculate stauriid *Palaeophyllum*; in eastern North America the small, solitary *Lambeophyllum* and *Lambelasma,* at present considered to be early calostylids, and *Palaeophyllum* together with *Streptelasma,* join *Favistina*. In Europe *Favistina* and *Palaeophyllum* are absent, or rare locally, but new small, solitary, calostylid genera and *Streptelasma* appear together with the early palaeocyclids or tryplasmatids *Primitophyllum* and *Neotryplasma*. In Kazakhstan, only *Kenophyllum* (a streptelasmatid) and the stauriid *Proterophyllum* are known so far. Mongolia has the earliest metriophyllinan *(Protozaphrentis),* and China has possibly the earliest *Calostylis* and some fasciculate ?calostylids.

These data are too few for meaningful discussion of Middle Ordovician provincialism of Rugosa.

The Upper Ordovician faunas are somewhat richer and better known, but grounds for distinguishing zoogeographical provinces are still slight.

Favistina, Crenulites, Palaeophyllum, Streptelasma, Helicelasma, and *Grewingkia* are cosmopolitan, being found in North America, Europe, Asia, and eastern Australia. There are, however, various genera, mainly of solitary corals, that up to now have been described and recognized from one continent only. Thus, North America, including the Arctic regions and Greenland, is characterized by the angulate or longitudinally grooved streptelasmatids *Lobocorallium* and *Deiracorallium* (NELSON, 1963, p. 34). Northern Europe (Balto-Scandia) has several streptelasmatid genera not so far recognized elsewhere (NEUMAN, 1969, p. 70; 1975, p. 346).

Solitary corals with acanthine septa referable to Palaeocyclidae or Tryplasmatidae have been described from Balto-Scandia and the Urals (SHURYGINA, 1973, p. 147) and others from eastern Australia (McLEAN & WEBBY, 1976, p. 239); others have been listed from South China (YI, 1974, p. 22). Fasciculate and columellate stauriids known only from Tadzhikistan (LAVRUSEVICH, 1975a, p. 25) or the Altay (CHEREPNINA, 1960, p. 389) distinguish those parts of central Asia, supplemented by *Calostylis* and

a doubtful lambelasmatin *(Sogdianophyllum)* (LAVRUSEVICH, 1971c, p. 3).

Several genera of rather large, solitary, dissepimented Rugosa, referred to the Paliphyllidae, have been described from the Siberian Platform (IVANOVSKIY, 1963, p. 71), the Altay (CHEREPNINA, 1960, p. 390), Tadzhikistan (LAVRUSEVICH, 1971c, p. 5), and the Balto-Scandian regions (NEUMAN, 1968, p. 230). This family, and possibly the Lykophyllidae, may also be represented in North America (NELSON, 1963, p. 43). Some specimens referred to the Lykophyllidae have been reported but not illustrated by LAVRUSEVICH (1975b, p. 124) from Tadzhikistan.

How much these apparent differences are due to our limited knowledge of Upper Ordovician Rugosa, which are always overshadowed by the associated Tabulata, and how much they reflect provincialism is at present doubtful. KALJO and KLAAMANN (1973, p. 39) (Fig. 26) considered that, based on the Tabulata and Rugosa, only two faunal provinces existed in both Middle and Late Ordovician times, the Americo-Siberian and the Eurasiatic. YI (1974, p. 22) considered that in North China, Middle and Late Ordovician faunas were most closely related to the fauna of the North American-Siberian province, but that those of South China showed an admixture of Baltic Tabulata with North American elements, and that South China should occupy an independent province.

SILURIAN

Silurian rugosan faunas are much richer than those of the Ordovician, from which they differ, as do those of later periods, in being dominated by corals with dissepimentaria (pleonophoric corals). Of the non-dissepimented (diaphragmatophoric) corals, solitary streptelasmatids are the most important. Laccophyllidae are rare until the Late Silurian. HILL (1959, p. 151) noted that Rugosa are rare to absent in southern Europe, Africa, South America, Antarctica, and New Zealand, and thought that on the whole the Silurian fauna was cosmopolitan, though there were suggestions of Australasian and North American subprovincialism. IVANOVSKIY (1965a, p. 109) commented on

FIG. 27. Paleozoogeographic provinces; distribution of selected Ludlovian corals (after Kaljo & Klaamann, 1973). Legend as in Fig. 26. Abbreviations of generic names: Ace, *Acervularia*; Axu, *Axulites*; Bar, *Barrandeolites*; Coe, *Coenites*; Dal, *Daljanolites*; Ent, *Entelophyllum*; Fos, *Fossopora*; Gya, *Gyalophyllum*; Kod, *Kodonophyllum*; Lac, *Laceripora*; Mes, *Mesosolenia*; Muc, *Mucophyllum*; Nip, *Nipponophyllum*; Pli, *Plicatomurus*; Pro, *Propora*; Rip, *Riphaeolites*; Sax, *Syringaxon*; Sch, *Schedohalysites*; Squ, *Squameofavosites*; Ste, *Stelliporella*; Str, *Strombodes*; Sub, *Subalveolites*; The, *Thecostegies*; Tra, *Trachypora*; Yas, *Yassia*; Zel, *Zelophyllum*.

FIG. 28. Paleozoogeographic provinces; distribution of Silurian corals (after Pickett, 1975). Legend: triangles = coral faunal localities; gray areas = probable land areas.

the roles of regression and transgression in promoting, respectively, provincialism and cosmopolitanism. KALJO and KLAAMANN (1973, p. 40) (Fig. 27) reviewed known stratigraphic and geographic distribution on maps with continents in their present positions, but PICKETT (1975, p. 147) attempted a contribution to the testing of some current theories of plate tectonics by plotting distributions on the speculative continental reconstructions assumed for the Lower Devonian continents by SMITH, BRIDEN, and DREWRY (1973), for Silurian–very Early Devonian continents by CREER (1973) and for Pangea by RICKARD and BELBIN (in PICKETT, 1975) (Fig. 28).

The small lower and middle Llandoverian rugosan faunas known so far from Europe, Asia, Australia, and the Americas are very similar to the Upper Ordovician faunas. Dissepimented paliphyllids are still outnumbered by nondissepimented fasciculate and cerioid stauriids and solitary streptelasmatids, including now the columellate *Dalmanophyllum*. Rare *Calostylis* and, in Siberia, *Palaearaea* are found; the earliest *Cystiphyllum* may be those of the middle Llandovery of Tadzhikistan, the western Siberian Platform, and New South Wales. Some new genera are reported from one continent or state only, but, as in the Upper

Ordovician, our knowledge is too fragmentary for reliable zoogeographical deductions to be drawn.

By the end of the late Llandoverian, the distinctive, rich Silurian rugosan fauna had entered in a great burst of vigor; it is richest in reefal carbonate regions. Pycnostylidae, Dinophyllinae, Kodonophyllidae, Mucophyllidae, Entelophyllidae, Arachnophyllidae, Ketophyllidae, Endophyllidae, Lykophyllidae, Ptychophyllidae, Palaeocyclidae, Holmophyllidae, and Goniophyllidae had all appeared. Not all of these families have as yet been recognized in all the known regions of marine Lower Silurian, and as knowledge increases it may become possible to establish points of origin for families. The European fauna is the best known, containing a great number of species and genera common to Great Britain, Gotland, and Estonia. An association of *Arachnophyllum* with *Palaeocylcus, Goniophyllum, Dinophyllum,* and *Schlotheimophyllum* characterizes the top of the Llandoverian in all three countries; and, as elements of the assemblage are found as far west as the southwestern United States and as far east as the Siberian platform, it would appear that migration was possible throughout this vast region. None of these five genera are yet known from eastern Australia. Some Australian

taxa appear to be endemic, or to have Siberian affinities; others are relicts of the Ordovician fauna.

After the beginning of the Middle Silurian (Wenlockian), evolutionary vigor decreased into the Early Devonian, with gradual extinction of the characteristically Silurian families and genera. Some Llandoverian taxa died out before or early in the Wenlockian. Nondissepimented streptelasmatids declined. Some new genera and families entered, such as the Acervulariidae, Expressophyllidae, Spongophyllidae, Actinocystinae, and rare Laccophyllidae; the cystiphyllids proliferated, as did in some areas holmophyllids and tryplasmatids. Some Wenlockian genera were apparently restricted in both geographical and chronological range. IVANOVSKIY (1965b, p. 85) thought that Scandinavian-Baltic and North American biogeographical regions became discernible with the retreat of the Early Silurian transgression; he cited the basins of the Urals and the Siberian Platform as being intermediate between the two, while the basins south of the Siberian Platform together with eastern Kazakhstan and southern China were apparently semi-isolated separate provinces, as possibly were Britain and Czechoslovakia within the Scandinavian-Baltic province.

In Upper Silurian (Ludlovian and Pridolian) strata some few new families are found. Included are the eastern North American transients Amsdenoididae and Anisophyllidae; the Polycoeliidae, represented by *Amandaraia* in Tadzhikistan, which did not reach its acme until the late Paleozoic; the subfamily Ptenophyllinae that became so characteristic of the Lower and Middle Devonian; and a possible early representative of the eastern North American family Eridophyllidae. Only doubtful records of Silurian disphyllids exist, however. Regression of the seas from Asia probably began early in the Ludlovian, reaching a maximum in the earliest Devonian (NIKIFOROVA & OBUT, 1965). Several short-lived new genera may indicate isolation of possible subprovinces, such as in eastern North America in Henryhouse time.

Rich faunules (as yet only partially illustrated) from the Ludlovian and Pridolian of southwestern United States, Alaska, the Yukon, and the Canadian Arctic Archipelago include not only several new genera but also new records of genera previously known either from the near-Arctic Soviet Union, Tadzhikistan, Siberia, China, or Australia, with implications for Late Silurian zoogeography that have not yet been analyzed (for references see PEDDER, 1976a, p. 285, 1976b, p. 287; PEDDER & McLEAN, 1976, p. 131).

DEVONIAN

Broadly, one may conclude that two zoogeographical regions (realms) characterized the Devonian seas until the Givetian: the eastern North American (including northeast South America), and the Euraustralasian plus western North American (HILL, 1957b, p. P49; OLIVER, 1976b, p. 365). The eastern North American region, characterized mainly by two endemic families Eridophyllidae and Zaphrentidae, was isolated on the west by a midcontinental land barrier, and on the east, at least in part, by a second land barrier. Rugosa are rare to absent in Devonian seas transgressing South America, southern Africa, and Antarctica.

In the earliest Devonian in Asia (Tiverian), late Silurian regression appears to have left several basins more or less isolated (NIKIFOROVA & OBUT, 1965, unnumbered color plate) (Fig. 29), each with some degree of endemism (SPASSKIY, 1974, p. 131). But, as Devonian transgression proceeded, and the basins merged, characteristically Devonian families developed in a great and sustained burst of vigor, so that by Couvinian times the diversity and profusion of rugosan faunas reached its maximum in the history of the subclass. Notable were the Ptenophyllidae, Disphyllidae, Phillipsastreidae, Stringophyllidae, and Digonophyllidae (SPASSKIY, 1967, p. 51; 1968, p. 3; DUBATOLOV & SPASSKIY, 1970, p. 15; SPASSKIY et al., 1975, p. 68). KRAVTSOV (1970, p. 36) has suggested Lower Devonian Asiatic migration routes to and from the Taymyr. Suggestions of barriers to migration decreased during the Middle Devonian, at the same time that the rates of diversification and profusion passed their acmes and decreased, and by the Givetian the evidence suggests only subprovinciality (Fig. 30). In North America also, barriers around the eastern North American region were breeched in
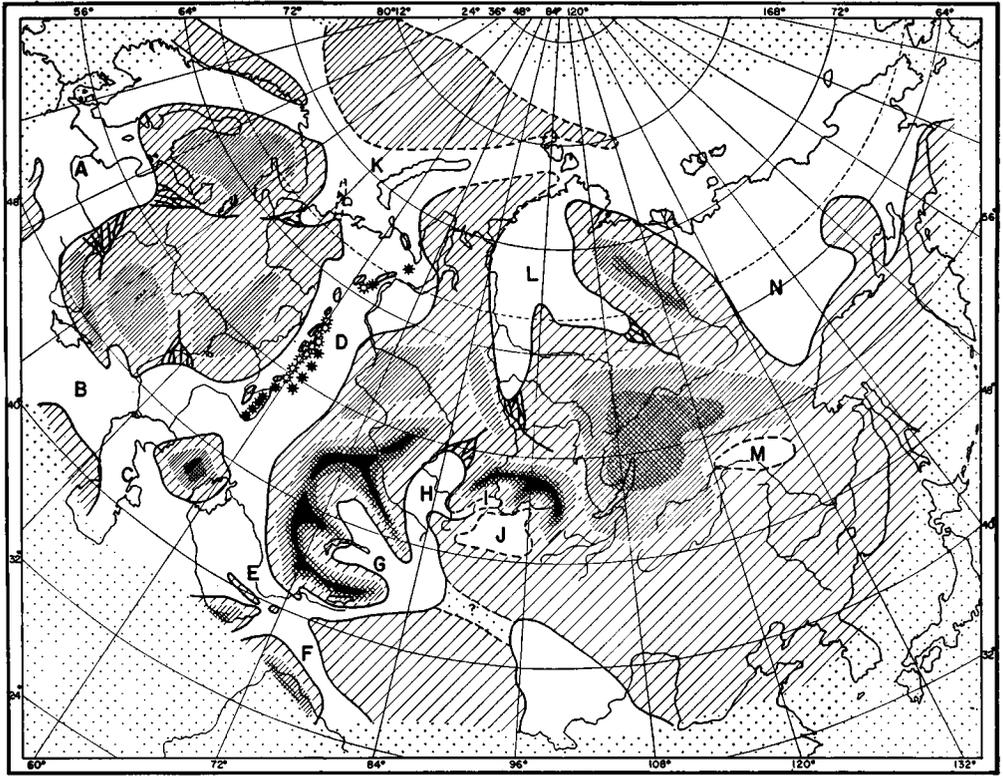
Fig. 29. Paleozoogeographic provinces; Tiverian geography of Eurasia (Hill, 1967). Legend: Open stars, volcanoes of Pacific Ocean type; closed stars, volcanoes of Mediterranean Sea type; dotted pattern, unknown or not analysed areas; white area, sea; contouring of land indicated by closeness of lining; mouths of rivers are shown. Letter symbols: *A*, Paleo-Baltic Sea; *B*, South European Sea; *D*, Ural Sea with volcanoes; *E*, Tien Shan Sea; *F*, Tadzhik Sea; *G*, Balkhash-Karaganda Sea; *H*, Altai Sea; *I*, Sayan Gulf; *J*, Tuva-Mongolian remnant basin; *K*, Novozemel Sea; *L*, Tungus Sea; *M*, Amur remnant basin; *N*, Verkhoyan Sea.

the Givetian, and by Frasnian time a greatly impoverished fauna may be considered almost universal.

On Spasskiy's maps coral localities were plotted on the continents shown in their present relative positions, though Dubatolov (1972c, p. 88, 109), in discussion of tabulatan distribution, showed a Devonian equator running from southeast Australia through Indo-China, Taymyr, southeast Greenland, and off the eastern North American coast to Guatemala. Ivanovskiy (1974a, p. 21) plotted Paleozoic coral localities onto a map with the continents arranged in predrift positions as assumed reasonable in 1969 for Lower Triassic time. Oliver (1976b, fig. 5) (Fig. 31) plotted Middle Devonian coral localities onto a map with

the continents translocated to accord with current (1975) assumptions on paleomagnetic latitude and with Oliver's views on paleolongitude. His equator runs from California through southern Greenland, Denmark, and New Guinea. The barrier separating eastern North America, Spain, and northwest Africa he showed (1976a, p. 28) as largely of Old Red Sandstone facies. Also, dispersal between eastern Australia and western North America does not seem to be improved on this model.

By Frasnian time the Ptenophyllidae and Digonophyllidae and probably also the Stringophyllidae had become extinct, and by Famennian time the rich Devonian rugosan fauna had dwindled away to mere remnants, even in the biohermal facies of

Coelenterata—Anthozoa
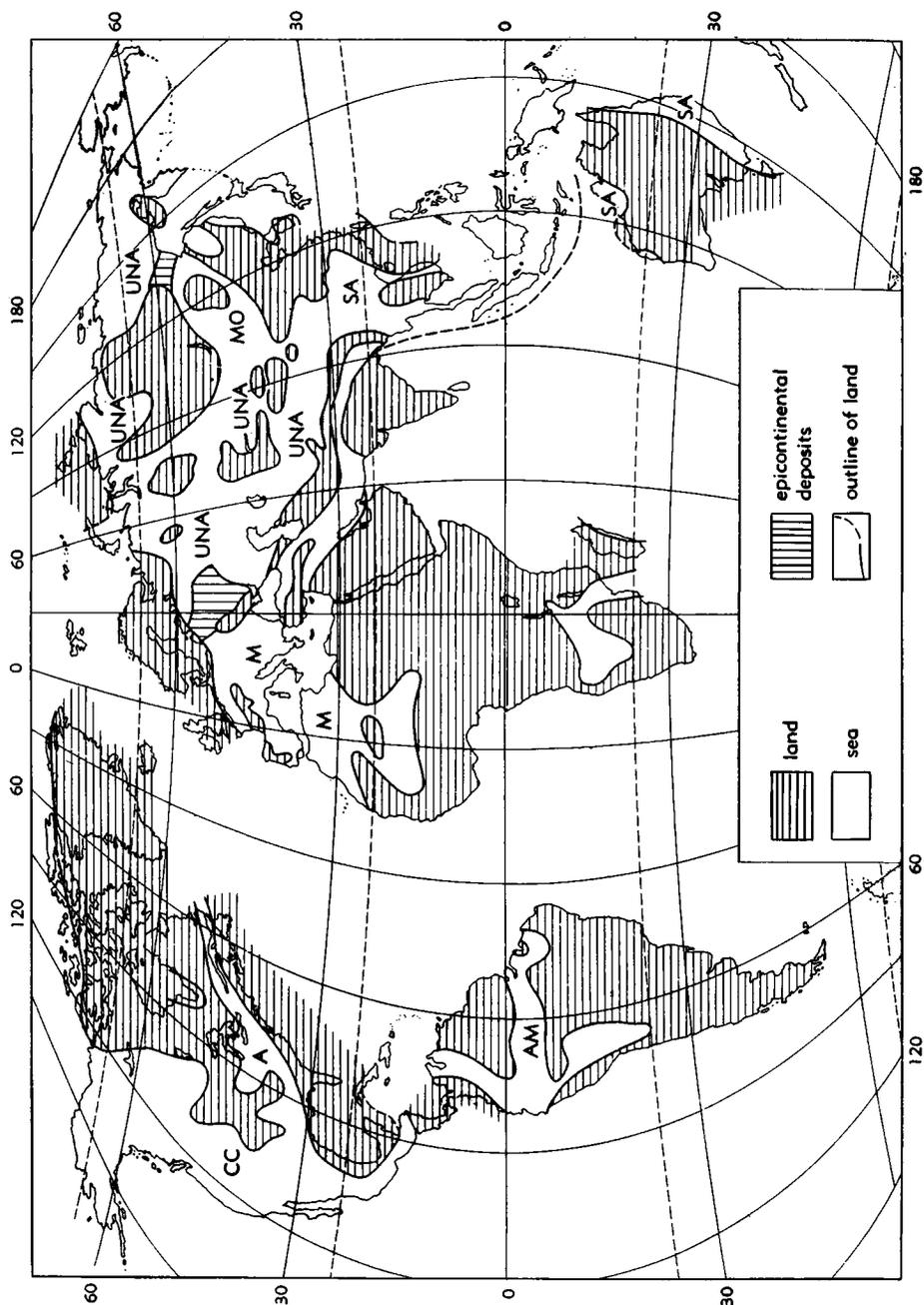
FIG. 30. Paleozoogeographic provinces; Middle Devonian (Givetian) (after Dubatolov & Spasskiy, 1970). Province letter symbols: *A*, Appalachian, *AM*, Amazonian; *CC*, Californian-Canadian; *M*, Mediterranean; *MO*, Mongolian-Okhotsk; *SA*, Sino-Australian; *UNA*, Ural-Northern Asiatic.
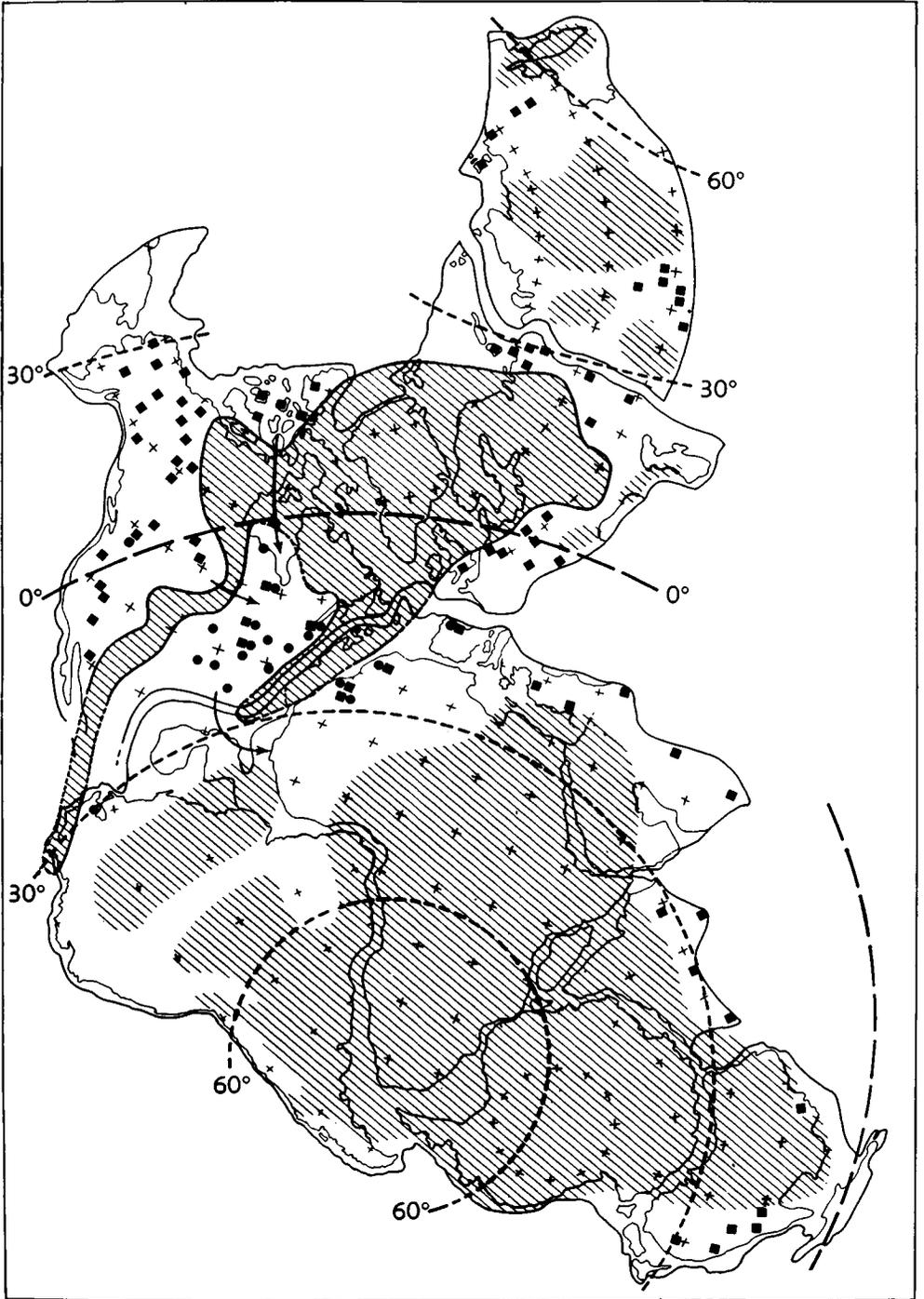
Fig. 31. Paleozoogeographic provinces; Middle Devonian world (generalized, China omitted) (after Oliver, 1976b). Known coral assemblages are shown as follows: Eastern Americas Realm, circles; Old World Realm, squares. Land areas lined. Arrows indicate probable seaway connections and directions of coral migrations.

Fig. 32. Paleozoogeographic provinces; Early Carboniferous coral faunal regions and provinces (after Hill, 1973).
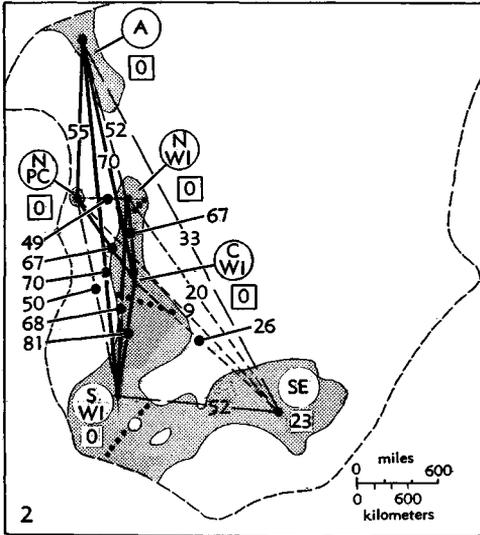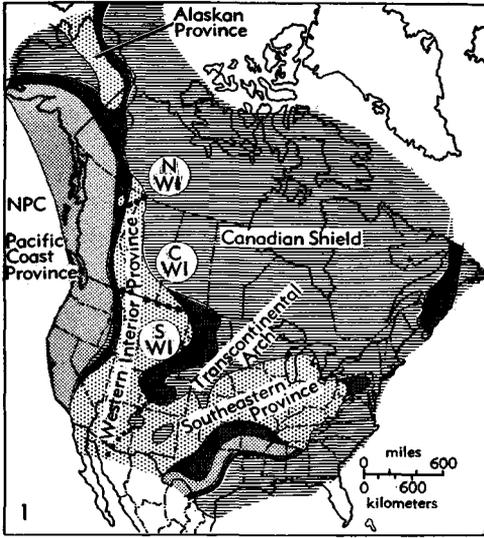
FIG. 33. Paleozoogeographic provinces; North America during Meramecian time.——*1*, Paleogeographic map of coral subprovinces; horizontal line pattern, land; dark dot pattern, shallow-water noncoralliferous facies; medium dot pattern, deep-water noncoralliferous facies; light dot pattern, shallow-water coralliferous facies.——*2*, Outline map of coral facies (shaded), showing similarity indices (uncircled numbers) and endemism indices (in boxes); solid lines between zoogeographic regions indicate high similarity; long-dash lines, moderate similarity; short-dash lines, low similarity (after Sando, Bamber, & Armstrong, 1975). Letter symbols: *A*, Alaskan province; *CWI*, Central Western Interior subprovince; *NPC*, North Pacific Coast subprovince; *NWI*, Northern Western Interior sub-

Western Australia; practically all the Famennian Rugosa are small, solitary corals mostly lacking dissepiments, like the small Polish fauna made known by Rozkowska (1969, p. 32).

CARBONIFEROUS

The Carboniferous rugosan fauna is characterized by new suborders of dissepimented forms: Caniniina, Aulophyllina, Lithostrotionina, and Lonsdaleiina, and by the continuation of long-ranging families of the small, nondissepimented forms, which now became dominated by the Hapsiphyllidae and Zaphrentoididae. After the rugosan poverty of the Famennian, some slight enrichment occurred in the Tournaisian, but it was not until the Visean transgressions that the characteristically Carboniferous fauna really diversified and proliferated. Many genera are wide-ranging and some are cosmopolitan.

Three distinctive zoogeographical regions are apparent for the Dinantian and Namurian, those of North America, Eurasia, and Eastern Australia (Hill, 1957b, p. P55; 1973, p. 133) (Fig. 32). The North American region has recently been assessed by Sando, Bamber, and Armstrong (1975, p. 661) (Fig. 33) on degrees of endemism and generic similarities as being divisible into five provinces and five subprovinces. Those provinces on the periphery of the continents had favorable connections for migration to the Eurasian region, but those in the interior were relatively isolated and were characterized by low to high endemism; however, dispersal was possible between the subprovinces and was aided in areas of carbonate facies and impeded in areas of terrigenous facies of sedimentation. An exception was that the Visean Nova Scotian province had relatively free migration to the Eurasian region and is, indeed, to be classed as part of that region. Similarly, the great Eurasian region shows considerable provincialism within itself, although barriers to dispersal within it were by no means absolute. Patterns of degrees of endemism and generic

province; *SE*, Southeastern province; *SWI*, Southern Western Interior subprovince.
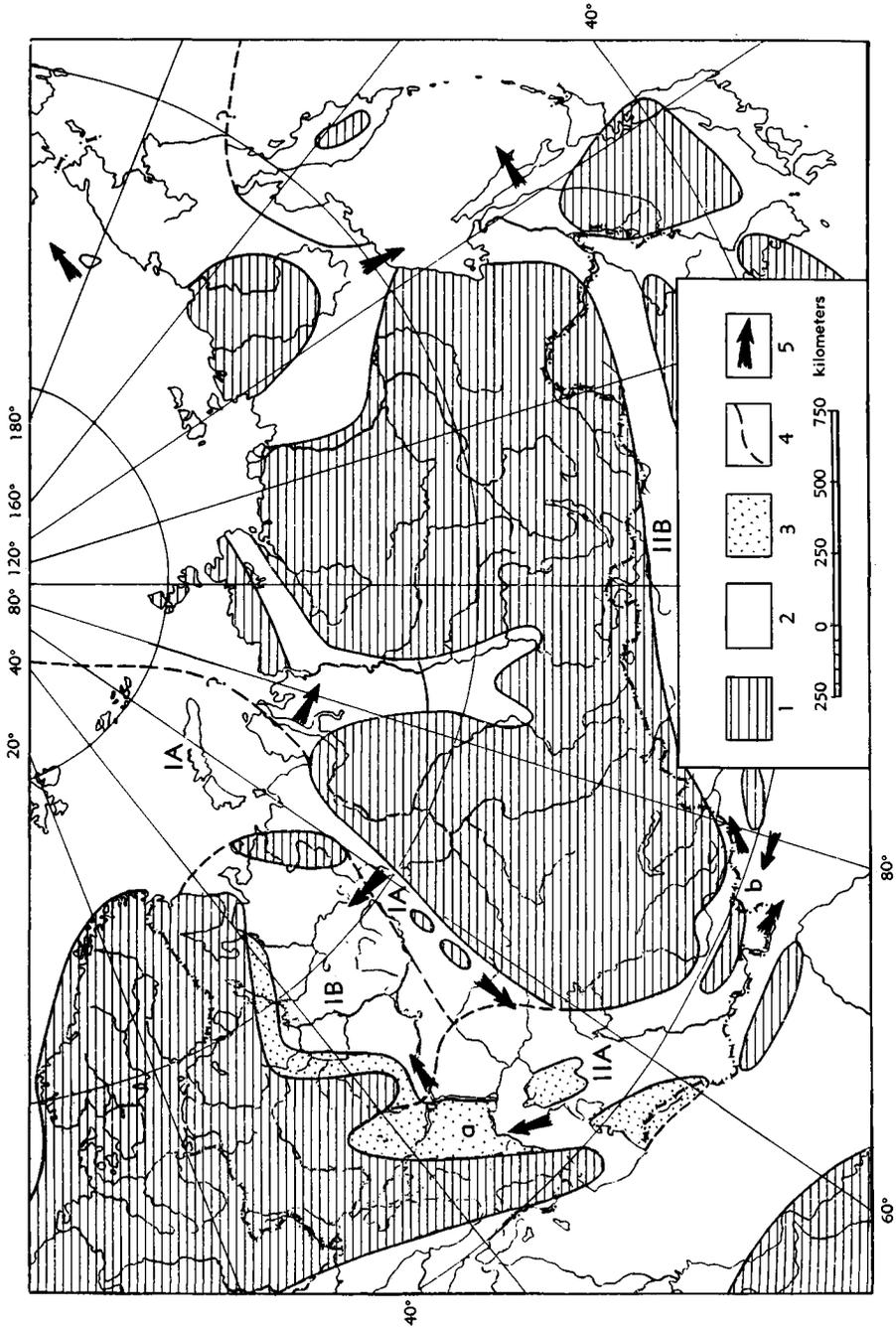
FIG. 34. Paleozoogeographic provinces; paleobiogeographic subdivision based on coelenterate faunas in the Moscovian of the USSR (after Vasilyuk, Kachanov, & Pyzhyanov, 1970). Legend: *1*, land; *2*, sea; *3*, paralic; *4*, province boundaries; *5*, probable direction of migration. Provinces: *I*, East European; *II*, Mediterranean. Subprovinces: *IA*, Ural; *IB*, Moscow; *IIA*, Central Mediterranean (regions *a*, Donbas, and *b*, Pamir); *IIB*, Chinese.
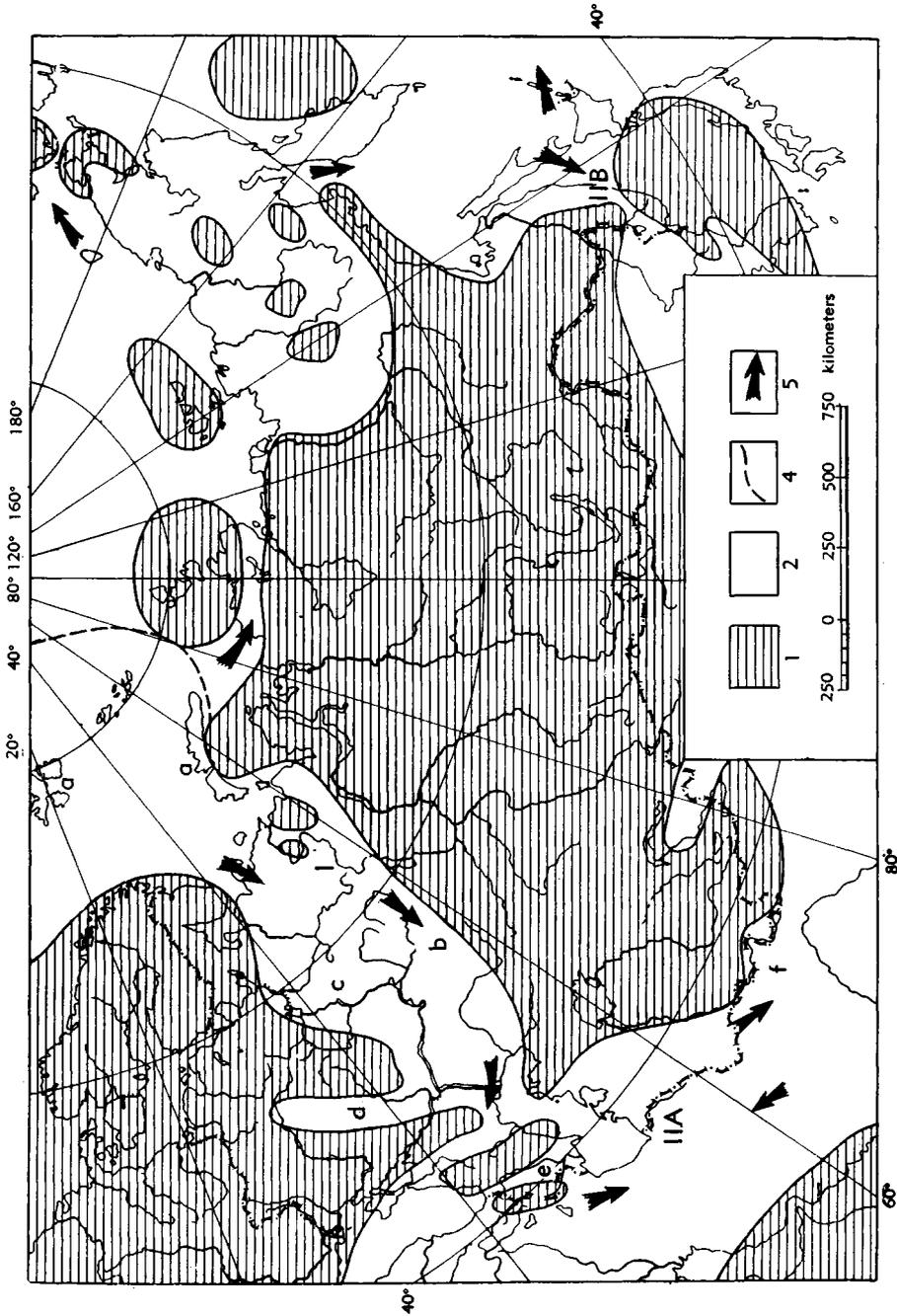
Fig. 35. Paleozoogeographic provinces; paleobiogeographic subdivision based on coelenterate faunas in the Early Permian of the USSR (after Vasilyuk, Kachanov, & Pyzhyanov, 1970). Legend as for Fig. 34. Provinces: *I*, Uralo-Arctic, with regions *a*, European-Arctic, *b*, western slopes of Urals, and *c*, Moscow basin; *II*, Mediterranean, with *IIA*, Central Mediterranean subprovince (including regions *d*, Donbas, *e*, trans-Caucasia, and *f*, Pamir), and *IIB*, Eastern Mediterranean subprovince.
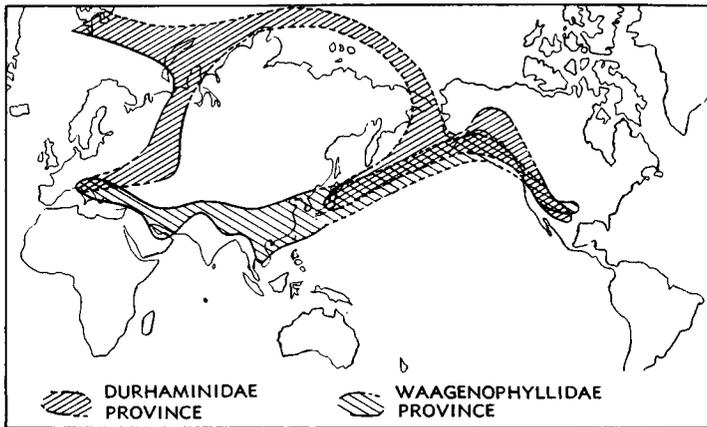
FIG. 36. Paleozoogeographic provinces; Durhaminidae and Waagenophyllidae biogeographical provinces in the Early Permian (*Pseudschwagerina* and *Pseudofusulina* zones) (after Minato & Kato, 1970).

similarity are like those of North America; some genera dispersed throughout the region, others were limited to one or more provinces or even subprovinces (VASILYUK, KACHANOV, & PYZHYANOV, 1970, p. 45; HILL, 1973, p. 136). VASILYUK (1974, p. 10) considered that a great faunal change occurred between Namurian A and Namurian B, i.e., approximately at the end of the Mississippian. The eastern Asiatic or *Kueichouphyllum* province has an outlier in the Kimberly district of northwestern Australia. The eastern Australian region is characterized by the endemic family Aphrophyllidae, but is also rich in the cosmopolitan genus *Lithostrotion*.

In the Middle and Upper Carboniferous (Bashkirian to Orenburgian; = Pennsylvanian), there was a decrease in the area of epicontinental seas and a gradual decline toward extinction of the Aulophyllidae, Lithostrotionidae, and Axophyllidae, although some new genera developed locally; the entrance of the Pseudopavonidae, Geyerophyllidae, Durhaminidae, and Waagenophyllidae greatly changed the faunal constitution; of these Pseudopavonidae are known in Japan (and possibly in Sinkiang) but the others are common to America and Eurasia. Neither Middle nor Upper Carboniferous Rugosa have been identified from Australia. Eurasian and American zoogeographical provinces are recognizable (HILL, 1957b, p. P55; VASILYUK, KACHANOV, & PYZHYANOV,

1970, p. 53) (Fig. 34). The Eurasian region is considered divisible into two provinces, a Uralo-Arctic province and a Mediterranean (Tethyan) province; the former, the durhaminid province, comprising Spitsbergen, the Moscow basin, the Urals, and Novaya Zemlya, and the latter including Spain, Carnic Alps, Czechoslovakia, Donetz Basin, Tien Shan, Pamirs, China, and Japan. The distribution of several families in these paleozoogeographical regions and provinces from the Middle Carboniferous to the Late Permian has been discussed in a series of papers by MINATO and KATO (1965a,b; 1970; 1975a,b), KATO and MINATO (1975), and ROWETT (1975b). MINATO (1975, p. 111, 116) considered that coral reefs have not been proved to have existed in Japan, though OTA (1968, p. 1) interpreted the Akiyoshi Limestone Group as a geosynclinal atoll or organic reef complex developed upon submarine volcanics.

PERMIAN

Permian faunas were dominated by the Waagenophyllidae among the dissepimented Rugosa, and by the Plerophyllidae, Polycoeliidae, and Lophophyllidae among the nondissepimented solitary small forms, though stragglers from and some new genera of characteristically Carboniferous families may still be found.

Two major zoogeographical regions appear to be distinguishable, the American
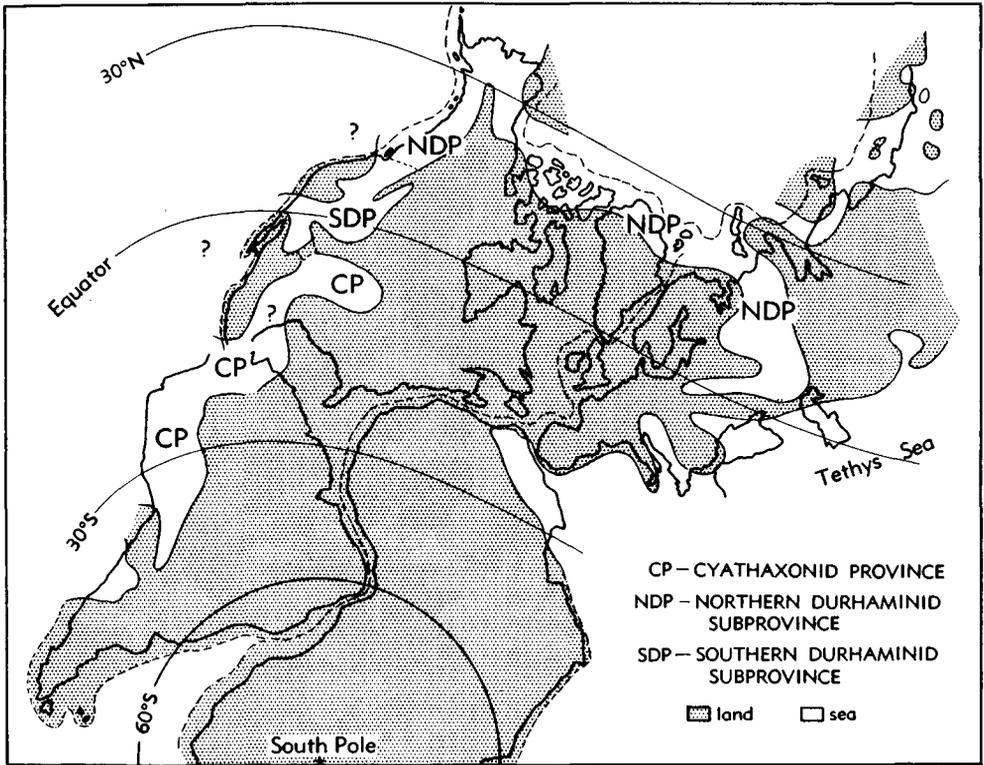
Fig. 37. Paleozoogeographic provinces; Early Permian coral provinces (after Rowett, 1975b).

and the Eurasian, in the latter of which Australia and New Zealand may be included. In the Eurasian region two provinces are fairly clearly defined in the Early Permian (Fig. 35): a Uralo-Arctic province with Durhaminidae dominant, including the European Arctic, the west slope of the Urals, and the Moscow basin, and 2) a Tethyan province with Waagenophyllidae dominant, extending from Tunisia, Sicily, and the Carnic Alps eastward across southern Asia and possibly continuing around the Pacific into Japan and western North America (Fig. 36) (MINATO & KATO, 1970, fig. 6; VASILYUK, KACHANOV, & PYZHYANOV, 1970, p. 57; HILL, 1957b, p. 56). In Japan and western America, elements of both durhaminid and waagenophyllid faunas are found. In North America, a transcontinental arch may have separated a western from a midcontinent subprovince (ROWETT, 1975a, p. 205; 1975b, p. 79). In discussing

Permian distribution patterns of both dissepimented and nondissepimented Rugosa, ROWETT (1975b, fig. 1 on p. 82) (Fig. 36) considered that translocation of continents would eliminate some anomalies in distribution.

Rugosa appear to have become extinct nearly everywhere at the end of the *Yabeina* zonal time; a few plerophyllids lingered on into strata in Soviet Armenia regarded as Lower Triassic by some (ILINA, 1965, p. 8) but by WATERHOUSE (1976, p. 157) as Late Permian; similar strata with corals in neighboring Iran were adjudged Late Permian by TEICHERT, KUMMEL, and SWEET (1973). TEICHERT & KUMMEL (1976, p. 43) concluded also that some fragmentary solitary Rugosa in the Kap Stosch area in East Greenland were Late Permian fossils redeposited in Early Triassic beds with *Glyptophiceras (Hypophiceras)*.

TECHNIQUES OF STUDY

Techniques used in the preparation of Rugosa or Tabulata for study are those aimed at the interpretation of internal structure, microstructure, and ultrastructure, and those used in clearing matrix from the exterior so that calical and epithecal characters become visible. The preparation of thin transparent sections for use with a microscope or hand lens is by far the most commonly used.

Internal structure can be mentally reconstructed in three-dimensional architecture by coordinating observations made from sections cut in controlled directions through the corallum. The routine sections are a pair for each corallum, one transverse to and the other one parallel with the direction of growth. Thin sections for use with the microscope are essential for good quality work. The best thickness is greater than that for petrological thin sections, because, as one approaches rock-slice thinness, recrystallization fabrics begin to mask traces of the original microstructure of the skeletal plates. Additional thin sections are made for special purposes; for cylindrical or branching coralla, a tangential section just below the surface is always taken, because the walls may be modified there by thickening. For study of the microstructure of the tabulatan wall and septal elements and the characters of mural pores, a longitudinal section parallel with and within the wall, or very oblique to the wall, and another radially through the septal elements are necessary.

For the study of 1) the pattern in which offsets are inserted, 2) the nature of the increase, and 3) the ontogeny of the protocorallite and offsets, serial sectioning at controlled intervals is necessary, the intervals being smallest when septal insertion is being studied. Thin sectioning and thin serial sectioning procedures have been described in KUMMEL and RAUP's *Handbook of Paleontological Techniques* (1965). A recent refinement is the use of the Capco saw, applications of which were described by JOYSEY and BREIMER (1963, p. 473).

For the photography of thin sections, transmitted light is used; negatives prepared ×2 are recommended, for enlargement to ×4, or, for microstructural illustrations, up to ×10.

An inferior but quick method of preparation for study is to make cellulose acetate peels, also described in the *Handbook*; a cut and polished surface is prepared like the surface of a thin section before mounting; it is then weakly etched, and cellulose acetate is applied, dried, and a film drawn off. Much microstructural detail is lost by this method and photographs prepared from peels cannot be recommended. Controlled serial grinding rather than thin sectioning is commonly used for ontogenetic studies, and camera lucida or lantern-projected drawings are made from the successive acetate peels. This use of peels is acceptable because of the reduction in loss of coral material, inevitable in sectioning; but there is some loss in accuracy due to the subjectiveness of the drawings.

A new field of study is presently being developed by application of the scanning electron microscope; preparational technique was outlined by SORAUF (1972a, p. 89) for Scleractinia, but the assistance of highly skilled technicians is required for effective use. This study is aimed at elucidating the original ultrastructure of the skeleton, and is rendered difficult by all the postmortem changes whose effects must necessarily be identified.

In the cleaning of marly or clayey sheaths from coralla released by natural weathering from sedimentary rocks, industrial vibrotools, adaptations of dental probes, and steel needles may be used. Matrix softer or more cleaved than coral is flaked away by mechanical force; action at the point of the instrument is observed by means of a binocular microscope of low power. Sandblasting from industrial mini-airbrasive units may be used when the matrix is softer than the fossil; experiment is necessary to find the most suitable size and kind of abrasive grain for the specimens from each formation and locality.

Chemical cleaning may be found useful. Alternate wetting and drying, with water or kerosene, sometimes works. Oxalic acid, or sometimes potassium hydroxide, may be found effective. If the coral has been re-

placed by silica, calcareous matrix may be dissolved away in HCl or other acids of appropriate dilution. As well as the sectioning and grinding techniques, cleaning techniques have been described in KUMMEL and RAUP's *Handbook*.

As a technique in classification, KRAVTSOV and SPASSKIY (1967, p. 89) have outlined a method for the codification of the principal characters of Rugosa on punched cards, and constructed by this means a key to a classification of orders, suborders, and families of Devonian Rugosa. SPASSKIY (1971a) expanded the key to give formulae for genera, and noted that it could be extended to species and subspecies.

CLASSIFICATION

HISTORY OF CLASSIFICATION

From the early eighteenth century, when LEOPOLD in 1720 and BROMELL in 1728 illustrated species from Gotland (REGNÉLL, 1949, p. 15), the similarity of those fossil corals later called Rugosa to those later termed Scleractinia was recognized. The two orders suffered together during the gropings after a natural system of classification in the eighteenth and early nineteenth centuries. Corals had long been regarded as members of the vegetable kingdom because of their sessile habit and their flowerlike polyps. In 1749, LINNÉ's *Corallia Baltica* appeared, the first work devoted entirely to fossil corals. By that time, observations already published had indicated that these organisms belonged, with their relatives, to the animal kingdom. LINNÉ in the tenth edition (1758) of his *Systema naturae* exemplified the prevailing perplexity: although he grouped the stony corals in his genus *Madrepora* in the animal kingdom, and removed its constituents from the Zoophyta (this name reflecting the then commonly held view of the dual nature of these betentacled, sessile, radiated, and flowerlike organisms), he yet employed instead the name Lithophyta (JOHNSTON, 1847, p. 407 *et seq.*). Eighteenth century and earlier workers noted their tentacles, whence is derived the term polyp, and called these organisms Polypi (from their analogy with cuttlefish) or Radiata (from their seeming radial symmetry). Early in the nineteenth century, their characteristic gastrovascular cavity (coelenteron) was seen to distinguish them from such other radiate animals as echinoderms, and hence the name Coelenterata was introduced, as well as the name Cnidaria from their capacity to sting (HILL & WELLS, 1956, p. F5).

By the time MILNE-EDWARDS and HAIME introduced their classification in 1850 and MILNE-EDWARDS (1857) improved it, Protozoa, Porifera, and Polyzoa had been recognized as distinct. Coelenterate classification then remained reasonably stable for many decades. Indeed, the classification adopted in this *Treatise* was and is in most essentials an updated version of the MILNE-EDWARDS and HAIME classification. There has been considerable discussion on the possible relationships between the Rugosa and the recent orders of Zoantharia and on the appropriateness of ranking the Rugosa as an order of the subclass Zoantharia of the Class Anthozoa as is the prevailing practice. Suggestions (e.g., CHAPMAN, 1893, p. 93) that the Rugosa (with the Tabulata) are closer to Hydrozoa than to Anthozoa, or that they might be classified with the Scyphomedusae because of their alleged tetraradial symmetry (VAN BENEDEN, 1898, p. 179) have received little support.

The Anthozoa are exclusively polypoid, mostly sedentary coelenterates with one or more rings of tentacles around an oral disc. A stomodaeum leads from the mouth into the coelenteron, which is radially partitioned by mesenteries, some of which have endodermal gonads. They are exclusively marine. They are divided into three subclasses, Ceriantipatharia, Octocorallia (or Alcyonaria), and Zoantharia, on the nature of their mesenteries and tentacles; the first two have unpaired mesenteries whereas the Zoantharia have paired mesenteries (WELLS & HILL, 1956, p. F164).

The Zoantharia include solitary and colonial polyps, with calcareous trabecular skeletons in some orders. The polyps have simple or divided tentacles, never pinnate or cyclically arranged, and are essentially dis-

tinguished by paired mesenteries. Basically, there are eight complete mesenteries and almost invariably two additional lateral couples making a total of six pairs (Fig. 38,*e*); generally, additional cyclically arranged pairs are present. New mesenterial pairs are inserted according to several different plans (Fig. 38,*f-h*). The subclass includes four orders separated largely on the presence or absence of a skeleton and by the arrangement and development of the mesenteries. These orders are Zoanthiniaria, Corallimorpharia, Scleractinia, and Actiniaria; the first edition of this *Treatise* also included as orders the extinct Rugosa, Heterophyllia, and more tentatively, the Tabulata. Montanaro-Gallitelli (1975, p. 21) has recently named a new order of Triassic Zoantharia, the Hexanthiniaria.

PRESENT CLASSIFICATION

The Zoanthiniaria (zoanthids) are weakly colonial, anemonelike forms lacking a skeleton. The mesenteries are in a single cycle with two directive pairs, of which only the ventral one is complete, and new pairs of mesenteries beyond the first six are inserted only in the ventrolateral exocoeles on either side of the ventral directive pair (Fig. 38,*f*). They are unknown as fossils but are believed by some to be representative of the most primitive zoantharians.

The orders Corallimorpharia, Scleractinia, and Actiniaria are together sometimes called the Hexactiniaria; they include the living sea anemones and corals, all lacking a skeleton except the Scleractinia, which are distinguished from the corallimorphs largely by this criterion. The mesenterial plan is practically identical in all and differs from that of the Zoanthiniaria and perhaps of the extinct Rugosa in that the mesenterial pairs beyond the first cycle of six are inserted in dorsoventral order in all six primary exocoeles (hexactinarian) rather than in two or four (Fig. 38,*h*); in some groups septa may also develop in the endocoeles of the lateral pairs. The Scleractinia alone have a fossil record, from the Middle Triassic to recent.

The Rugosa are extinct, known only from the Paleozoic, and their relationships to recent Zoantharia are still speculative. Their

mesenterial arrangement and development can only be inferred from the mode of septal insertion, and this is capable of several interpretations. Many investigators are inclined to see closest affinities of the Rugosa in the Zoanthiniaria, from which they would differ only by having a calcareous exoskeleton and by insertion of new septa (and mesenterial pairs) not only in exocoeles on either side of the cardinal septum (ventral mesenterial pair), as in the zoanthiniarians, but also in spaces between the alar and counterlateral septa (between lateral mesenterial pairs), that is, in four instead of two primary exocoeles (Fig. 38,*g*). Relationships to the endocoelactarian actiniarian anemones (Carlgren, 1918) and to the scleractinian corals has also been claimed (Schindewolf, 1942, p. 267).

Schindewolf considered that there was evidence, both from stratigraphical sequence and skeletal morphology, that the Scleractinia, which have septa inserted in cycles of six but in dorsoventral sequence both in cycles and in primary interseptal loculi, evolved from the Rugosa, which have septa inserted in countercardinal sequence in only four of six primary interseptal loculi. However, when subsequently reexamined, his evidence has not produced strong support. Weyer (1974b, p. 358) reaffirmed that only four of the rugosan septa are primary, but he based his affirmation in part on the grounds that each metaseptum 'splits' twice, first on its counter side to produce a minor septum, and second on its cardinal side to produce a new major septum (metaseptum). He thus considered the major septa next to the counter septum, one on each side, to be metasepta, and not primary septa like *C, K,* and the two alar septa, none of which, in his view, 'split off' a minor septum.

In direct contrast to the view that Scleractinia evolved from Rugosa, Birenheide (1965a, p. 33) proposed a new Class Eoanthozoa composed of two orders, Rugosa Milne-Edwards and Haime, 1850, and Heterocorallia Schindewolf, 1941, on the basis of his views: 1) that new septa are formed in these by 'splitting' from previously formed septa; 2) that in Scleractinia the only septa that 'split' are exosepta formed
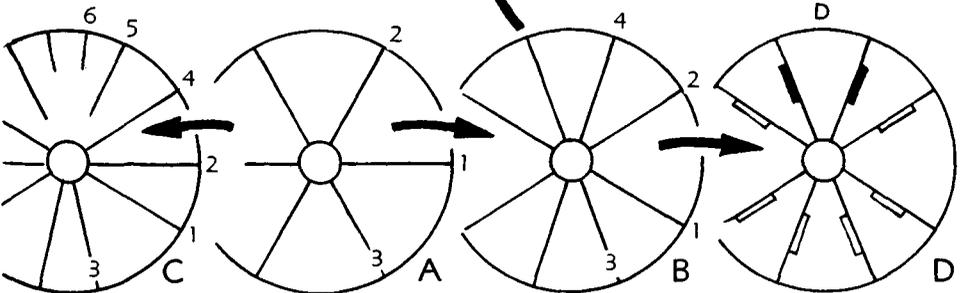
FIG. 38. Anthozoan classification; suggested relations and mesenterial arrangements of principal anthozoan groups (Wells & Hill, 1956).

in exocoeles; and 3) that (although no sub-
stitution such as occurs in dendrophylliid
Scleractinia is known in Rugosa), the septa
of Rugosa are exosepta and *ipso facto* were
not separated by mesenteries (i.e., that
mesenteries were not present in the Rugosa,
which thus could not have been Anthozoa).
IVANOVSKIY (1966, p. 455) named an antho-
zoan subclass Sclerocorallia to comprise or-
ders Rugosa, Heterocorallia, Scleractinia,
Actiniaria, and Corallimorpharia. Neither
the class Eoanthozoa nor the subclass Sclero-
corallia are adopted in this revision of the
Treatise.

Clearly, the position of the Rugosa is still
far from settled. It does not seem likely to
me that the Rugosa gave rise to the Sclerac-
tinia. They are herein considered to be
Anthozoa, since it seems so highly probable
that their septate calices indicate that they
had mesenteries to retract their polyps. The
assumption made by WELLS and HILL
(1956, p. *F*163) that they had paired mesen-
teries like those of recent Zoantharia still
seems quite reasonable; nevertheless, this
revision does not continue the assumption.
An agnostic position is taken by which the
Rugosa are classified as a subclass of Antho-
zoa, as are the Tabulata and Heterocorallia.

SUBDIVISION OF THE RUGOSA

Several reviews with commentaries are
available on the many successive classifica-
tions that have been attempted within the
Rugosa as new generic taxa have been intro-
duced at an ever-increasing rate; perhaps
the most comprehensive are those of POČTA
(1902), WANG (1950), SOSHKINA, DOBROLY-
UBOVA, and KABAKOVICH (1962), and IVA-
NOVSKIY (1965a, 1973a,b).

MILNE-EDWARDS and HAIME (1850, 1851),
founders of the Rugosa, relied mainly on
the longitudinal continuity or discontinuity
of the septa and the presence or absence of
dissepiments or tabulae to group the genera
then known into four families: Stauri-
idae,[1] Cyathaxoniidae, Cyathophyllidae
(with subfamilies Zaphrentinae, Cyatho-
phyllinae, and Axophyllinae), and Cysti-
phyllidae.

DE FROMENTEL (1861) grouped these and

several new families according to the ex-
ternal form of the corallum, whether solitary
(Monastrées), compound with calices of
corallites separated (Disastrées), or massive
(Polyastrées). Within the families, genera
were distinguished mainly by septal char-
acters, presence or absence of a fossula or
columella, and the nature of the wall and
tabulae. Later examples of the use of
growth form as an initial discriminant are
those of SPASSKIY (1965a) and COTTON
(1973). SPASSKIY divided the "Sub-class
Tetracorallia" into two superorders, Asso-
ciata (compound coralla) and Solitaria
(solitary coralla) on the basis of asexual
reproduction (which he regarded as primi-
tive) in the former, and sexual reproduction
in the latter. These superorders he divided
into orders mainly on the form of 'budding'
and the type of septa (e.g., laminar, acan-
thine, wedge shaped). He distinguished
suborders by the types of horizontal skeletal
elements (complete or incomplete tabulae,
presence or absence of dissepiments), and
families by the characters of construction
of their offsets and of their horizontal skele-
tal elements. COTTON's version was pro-
fessedly an identification key, not a classifi-
cation, and he named no suprageneric taxa.

DYBOWSKI (1873-74), on the other hand,
used the horizontal skeletal elements as the
prime differentiator. He recognized two
groups, the first being the Inexpleta, in
which neither tabulae nor dissepiments
were developed, and in which he included
Cyathaxoniidae and Palaeocyclidae. The
second, the Expleta, possessed horizontal
skeletal elements and comprised the Dia-
phragmatica, with tabulae, and the Adia-
phragmatica (or Cystiphora), without com-
plete tabulae but with cystose horizontal
skeletal elements. The Diaphragmatica
comprised the Diaphragmatophora, with
complete tabulae and without dissepiments,
and the Pleonophora, those with incomplete
tabulae but with dissepiments present. The
Cystiphora had two subdivisions, Anopercu-
lata (Cystiphyllidae and Plasmophyllidae)
and Operculata (Goniophyllidae). The
families within these divisions and subdi-
visions were distinguished mainly by the
characters of their septa, external walls, and
axial structures if present. DYBOWSKI's
scheme was expanded by POČTA (1902),

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[1] In this section original spellings of taxa are amended in
accordance with the current rules of the International Com-
mission on Zoological Nomenclature.

who introduced an intermediate group, Semiplena, for solitary forms (Lindstroemiidae, Polycoeliidae) in which tabulae were weakly developed, occupying scarcely more than the proximal quarter of the corallite. DYBOWSKI's and POČTA's suprafamilial taxa have been little used, but their work certainly led to greater taxonomic value being given to horizontal skeletal elements than formerly.

WANG (1950) attempted a revision of the classification on the basis of such microstructural features of the septa as trabeculae; however, this is a particularly difficult character to use because of insufficient understanding of the effect of diagenesis on the microstructure. KATO (1963) and OEKENTORP (1972; 1974a) subsequently described many diagenetic effects.

Experience seems to show that a simplistic approach to overall classification within the Rugosa is inappropriate and leads to too many apparently absurd unions and separations. Most classifications now attempt to apply evolutionary theory and to express the most likely phylogenetic relationships as well as degrees of morphological similarity and dissimilarity. Some regard a feature that is stable over a considerable time as of family or suprafamily taxonomic value, and use the more variable characters for subdividing such a grouping. Others may regard a particular feature or aspect of a feature as primitive, perhaps because it is noted in the oldest known forms. Environmental changes and natural selection operate to produce species with features fitted to particular environments; ontogeny may be considered a reasonable guide to phylogeny, particularly when changes are followed through successive stages.

As knowledge expands, the process of classification becomes difficult. To be entirely objective in the evaluation of lineages is almost impossible. A weakly based hypothesis may be treated as acceptable theory and we tend to argue in a circle. A classification stands or falls on its subsequent usefulness, and, indeed, on its capacity to be improved by more or less minor amendments.

In this revision of the *Treatise,* as in the first edition, an attempt has been made to present a classification that expresses degrees of relationship as well as degrees of morphological similarity. Published evidence of variation within species and genera and families both in space and in time has been evaluated; however, the reasoning leading to the choices made is omitted because of its volume. A practical classification that accords with the actual evidence and reflects understanding of the need for stability has been the aim throughout.

SUBDIVISION ADOPTED IN THE TREATISE

The subclass Rugosa is divisible into two orders, both of which first appear in the Middle Ordovician, the Cystiphyllida and the Stauriida.

The Cystiphyllida are a relatively small order that became extinct in the late Middle or Late Devonian. Members are distinguished by the possession of septa formed each of a single longitudinal series of coarse monacanths or rhabdacanths that are commonly thickened to contiguity within each septum and between neighboring septa so as to form a more or less narrow peripheral stereozone, adaxial to which their distal ends are free. Diagenesis may convert the thick trabeculae into holacanths and the sclerenchyme of the peripheral stereozone into a secondarily lamellate structure. The Palaeocyclidae lack tabulae and dissepiments, and the Tryplasmatidae have complete and horizontal tabulae but lack a dissepimentarium; but the other families have dissepimentaria in which the trabeculae may be discontinuous between successive dissepimentarial floors, and they have tabular floors that are commonly inversely conical and replaced by tabellae.

The Stauriida, on the other hand, are divided herein into 16 suborders, four of which, the Stauriina, Streptelasmatina, Calostylina, and Metriophyllina, entered during the Middle Ordovician. Stauriida, except for the Calostylina, have laminar septa in each of which the constituent trabeculae are contiguous. They have marginaria that in some orders are peripheral stereozones, and in others are either normal dissepimentaria in which the septa are longitudinally continuous plates, or lonsdaleoid dissepimentaria in which the septa are longitudinally discontinuous, being developed in whole or

in part as crests upon the surfaces of the dissepiments. Except for a few genera without tabulae but with thickened walls, they have complete or incomplete tabulae that are fundamentally conical or domed, commonly with upturned margins, or horizontal to mesashaped, and may develop axial depressions or become inversely conical axially.

In the first edition of this *Treatise,* the Rugosa were divided into three suborders, the Streptelasmatina, the Columnariina, and the Cystiphyllina. In merging the first two into the Stauriida in this revision, I have taken account of the lack of a clear separation between families with lonsdaleoid dissepimentaria (i.e., former Columnariina) and families with normal dissepimentaria (i.e., former Streptelasmatina), and have preferred a somewhat more agnostic arrangement with the sum of the old Columnariina and Streptelasmatina divided into 16 suborders on combinations of septal characters (including longitudinal continuity or discontinuity), marginarial characters, and tabularial characters.

Of the four suborders that are known from the Middle Ordovician, the Calostylina resemble the Cystiphyllida in having coarse uniserial septal trabeculae, but those of each septum are here discontiguous more or less regularly periodically and further may be connected to those of neighboring septa by rough synapticulae. The marginaria of Calostylina may have rather irregular filmy dissepiments and the tabulae similarly may be filmy and without the rigid curvature characteristic of the tabulae and tabellae of the other Stauriida; an axial complex may be present. The Calostylina became extinct at or near the boundary between Silurian and Devonian.

The Stauriina are commonly compound, cerioid, or fasciculate; they mostly lack dissepimentaria but may have elongate and sporadic dissepiments in single series. Their tabulae are complete and subhorizontal or mesashaped or with axial depression, and the axial edges of their laminar septa are not lobed but may become amplexoid, i.e., developed only as crests on upper surfaces of tabulae.

The Streptelasmatina are dominantly solitary and are characterized by a more or less wide peripheral stereozone; in most families dissepiments are absent; the septa are laminar, commonly with coarse contiguous trabeculae, and their axial edges are lobed and may or may not form an axial structure; their tabular floors are domed and tabulae are commonly complete. As did the Stauriina, they became extinct in the Middle Devonian.

The Metriophyllina are the first of the suborders of small, solitary, nondissepimented Rugosa. They have a narrow peripheral stereozone and all but a few lack dissepiments; their septa are laminar, commonly with fine trabeculae, and are longitudinally continuous; minor septa may be long and contratingent; a columella may be present in some, an aulos in others; and tabulae are abaxially declined and commonly complete. The Metriophyllina reached their acme in the Devonian and became extinct during the Permian.

Five suborders entered early in the Silurian; they are the Arachnophyllina, Ketophyllina, Lycophyllina, Ptenophyllina, and Columnariina. The first three reached maximum diversification in and are characteristic of the Silurian; the last two reached maximum diversification in and are characteristic of the Devonian; all became extinct by the end of the Devonian.

The Arachnophyllina are dominantly colonial, with wide dissepimentaria in which interseptal dissepiments are small and subglobose; tabular floors are domes with upturned edges and axial depressions, and the tabulae are incomplete; in one family complex septal structure is developed. They became extinct early in the Devonian.

The Ketophyllina include solitary and compound forms, and corallites are large; septa are commonly thickened and disrupted by lonsdaleoid dissepiments but they thin adaxially; tabular floors are flat or mesashaped or low domes with axial depressions, and tabulae are commonly complete. They became extinct during the Upper Devonian.

The Lycophyllina are mostly solitary, a few are fasciculate; septal thickening is common and is retained longest in cardinal quadrants of the tabularium; a dissepimentarium is commonly wide with normal concentric and angulo-concentric dissepiments, and tabular floors are variable.

The Ptenophyllina are dominantly colonial with a wide dissepimentarium that is commonly normal but may be lonsdaleoid at least in part; tabular floors are concave with a median notch or groove. The suborder died out in the Late Devonian.

The Columnariina are commonly compound; septal trabeculae may be rhipidacanthine; the dissepimentarium of small subglobose dissepiments may include a pipe of horseshoe dissepiments in some, surrounded by a pipe of flat dissepiments; the tabular floor is flat or slightly arched with a broad inversely conical depression.

It is somewhat doubtful whether the Cyathophyllina developed before the Devonian, in which it was one of the characteristic suborders; the Silurian Ptychophyllidae are tentatively included in it herein. They are characterized by solitary or colonial forms with large corallites, numerous long septa that may be complexly structured in some, wide normal dissepimentaria, and domed tabular floors that may be depressed axially.

The Stereolasmatina and the Plerophyllina are two suborders of small, solitary Rugosa without dissepiments. The Stereolasmatina have long septa with smooth axial edges that may be rhopaloid (expanded axially) in some, or may form a solid axial structure that does not project as a calical boss; septa may have subhorizontal flanges in some; minor septa are short, except Km in some; and tabulae are declined abaxially; the cardinal septum is commonly shortened and K may be long. In the Plerophyllina, one or more of the six first major septa are longer than the others and the metasepta (which may be of unequal length), and are commonly more rhopaloid; cardinal or counter septa or both may be shortened, minor septa, including $Km,$ seldom extend inward from the peripheral stereozone; an axial structure, commonly formed from the axial end of $K,$ may extend as a boss from the calical floor. The oldest Stereolasmatina appear to be early Middle Devonian, but the oldest genus assigned to the Plerophyllina is from the Kunzhak horizon of Tadzhikistan, which is variously regarded as Late Silurian or Early Devonian. Both ranged into the Late Permian.

Of the characteristically Carboniferous and Permian suborders of dissepimented Rugosa, the Caniniina are dominantly large and solitary, with wide dissepimentaria commonly with lonsdaleoid dissepiments dominant at least in late stages; septa are thick in early stages, thinning from the axis and toward the cardinal fossula, and are amplexoid in the tabularium; tabular floors are mainly flat with downturned edges, and tabulae complete.

The Aulophyllina also are predominantly large and solitary, with wide dissepimentaria that are commonly normal or angulate; an axial structure is commonly present —a platelike columella, or a complex of septa or septal lamellae and tabellae that may include a median plate, or a sharply bounded axial column; tabular floors are declined abaxially.

The Lithostrotionina and Lonsdaleiina are the two dominantly colonial orders of Carboniferous and Permian dissepimented Rugosa. Each is characterized by axial structures; the former has commonly a simple platelike columella, but the latter has a complex axial structure commonly with a median lamella and septal lamellae. The dissepimentarium of the Lithostrotionina is commonly normal, that of the Lonsdaleiina commonly lonsdaleioid; in the Lonsdaleiina clinotabulae may develop in the outer part of the tabularium.

For other recent proposals for subdivision of the Rugosa, see IVANOVSKIY (1971b, p. 9; 1975a, p. 36), and, for the Devonian, SPASSKIY (1971b, p. 56; 1977, p. 23).

OUTLINE OF CLASSIFICATION OF THE SUBCLASS RUGOSA

The following outline of the subclass Rugosa summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each supra-generic group from order to subfamily. A single number refers to genera; where two numbers are given, the second indicates subgenera additional to nominotypical ones.

Order Cystiphyllida, 47;15. *M.Ord.-?U.Dev.*
  Palaeocyclidae, 4. *M.Ord.-M.Dev.*
  Tryplasmatidae, 11. *M.Ord.-?M.Dev.*
    Tryplasmatinae, 10. *M.Ord.-?M.Dev.*
    Wenlockiinae, 1. *M.Sil.*
  ?Fletcheriidae, 2. *L.-M.Sil.*
  Holmophyllidae, 8. *Sil.-M.Dev.*
  Goniophyllidae, 6. *L.Sil.-M.Dev.*
  Cystiphyllidae, 11;10. *U.Ord.-?U.Dev.*
  Digonophyllidae, 5;5. *M.Dev.*
Order Stauriida, 697;16. *M.Ord.-U.Perm.*
Suborder Stauriina, 37. *M.Ord.-U.Miss.*
  Stauriidae, 18. *M.Ord.-M.Dev.*
  Pycnostylidae, 9. *Sil.-Dev.*
  Neocolumnariidae, 1. *M.Dev.*
  Centristelidae, 1. *M.Dev.*
  Amplexidae, 6. *L.-M.Sil., L.-M.Dev., Miss.*
  Kiziliidae, 2. *L.Carb.*
Suborder Streptelasmatina, 83. *M.Ord.-M.Dev.*
  Streptelasmatidae, 50. *M.Ord.-M.Dev.*
    Streptelasmatinae, 32. *M.Ord.-M.Dev.*
    Nevadaphyllinae, 1. *L.Dev.*
    Dinophyllinae, 5. *L.-?M.-U.Sil.-?base Dev.*
    Dalmanophyllinae, 2. *U.Ord.-M.Sil.*
    Homalophyllinae, 4. *L.-M.Dev.*
    Enterolasmatinae, 4. *U.Sil.-L.Dev.*
    Breviphyllinae, 2. *L.Dev.*
  Ditoecholasmatidae, 1. *U.Sil.*
  Paliphyllidae, 8. *U.Ord.-M.Sil.*
  Kodonophyllidae, 12. *?U.Ord., Sil.-M.Dev.*
  Mucophyllidae, 8. *L.Sil.-L.Dev.*
  Acrophyllidae, 2. *Up.L.Dev.*
  Amsdenoididae, 2. *U.Sil., ?M.Dev.*
Suborder Calostylina, 13. *M.Ord.-U.Sil.* or *L.Dev.*
Superfamily Calostylicae, 13. *M.Ord.-U.Sil.* or *L.Dev.*
  Calostylidae, 5. *M.Ord.-U.Sil.* or *L.Dev.*
  Lambelasmatidae, 8. *M.-L.Sil.*
    Lambelasmatinae, 4. *M.-U.Ord.*
    Coelostylinae, 4. *Mid.M.Ord.-L.Sil.*
Suborder Metriophyllina, 53. *M.Ord., L.Sil.-U.Perm.*
  Cyathaxonidae, 5. *U.Sil., U.Dev.-L.Penn., L.-U.Perm.*
  Petraiidae, 4. *M.Ord., U.Sil., L.Dev., U.Dev.*
  Metriophyllidae, 5. *L.Sil.-?Miss., ?L.-U.Perm.*
  Laccophyllidae, 27. *Sil.-Perm.*
    Laccophyllinae, 12. *L.Sil.-U.Dev., ?L.-U.Perm.*
    Guerichiphyllinae, 1. *M.-U.Dev.*
    ?Friedbergiinae, 1. *U.Dev.*

    Neaxoninae, 6. *L.Dev.-L.Carb.*
    Taralasmatinae, 1. *L.Dev.*
    Amplexocariniinae, 5. *U.Dev.-Perm.*
    Subfamily uncertain, 1.
  Kielcephyllidae, 3. *U.Dev.*
  ?Lindstroemiidae, 1. *Dev.*
  Hadrophyllidae, 2. *?L.-M.Dev.*
  Combophyllidae, 1. *L.-M.Dev.*
  Family uncertain, 3.
Suborder doubtful, 2. *M.Dev., M.Penn.*
Suborder Arachnophyllina, 29. *L.Sil.-M.Dev.*
  Entelophyllidae, 15. *Sil.-L.Dev.*
  Expressophyllidae, 4. *M.-U.Sil., ?L.Dev.*
  Arachnophyllidae, 10. *L.Sil.-M.Dev.*
Suborder Ketophyllina, 25. *U.Ord.-?Carb.*
  Ketophyllidae, 7. *Sil.-L.Dev.*
  Kyphophyllidae, 7. *U.Ord.-L.Dev.*
  Endophyllidae, 11. *L.Sil.-?Carb.*
Suborder Ptenophyllina, 43;1. *L.Sil.-U.Dev.*
  Spongophyllidae, 5. *L.Sil.-?M.Sil.-M.Dev.*
  Ptenophyllidae, 29. *Sil.-Dev.*
    Ptenophyllinae, 25. *U.Sil.-U.Dev.*
    Actinocystinae, 4. *Sil.-L.Dev.*
  Fasciphyllidae, 3. *L.-M.Dev.*
  ?Stringophyllidae, 6;1. *L.-M.Dev.*
Suborder Lycophyllina, 24. *Sil.-M.Dev.*
  Lykophyllidae, 17. *Sil.-L.Dev.*
  Halliidae, 7. *L.-M.Dev.*
    Hallinae, 3. *M.Dev.*
    Papiliophyllinae, 3. *L.Dev., ?M.Dev.*
    Aspasmophyllinae, 1. *M.Dev.*
Suborder Columnariina, 58. *M.Sil.-Dev.*
  Acervulariidae, 3. *M.-U.Sil.*
  Columnariidae, 4. *Dev.*
  Disphyllidae, 35. *U.Sil.-U.Dev.*
    Disphyllinae, 17. *Dev.*
    Paradisphyllinae, 8. *U.Sil.-M.Dev.*
    Hexagonariinae, 3. *M.-U.Dev.*
    Spongonariinae, 7. *Dev.*
  Phillipsastreidae, 16. *Dev.*
    Group 1, 3. *L.-M.Dev.*
    Group 2, 5. *Dev.*
    Group 3, 6. *Dev.*
    Group 4, 2. *?L.-U.Dev.*
Suborder Cyathophyllina, 35. *Sil.-Dev., L.Carb.*
  Eridophyllidae, 8. *U.Sil.-M.Dev.*
    Eridophyllinae, 4. *U.Sil.-M.Dev.*
    Cylindrophyllinae, 4. *L.-M.Dev.*
  Zaphrentidae, 5. *L.-M.Dev.*
  Cyathophyllidae, 16. *Dev.*
  ?Bethanyphyllidae, 2. *M.Dev.*
  Campophyllidae, 1. *M.Dev.* or *L.Carb.*
  Ptychophyllidae, 3. *L.Sil.-L.Dev.*
Suborder Stereolasmatina, 38. *L.Dev.-U.Perm.*
  Stereolasmatidae, 5. *M.Dev., L.-M.Carb.*
  Antiphyllidae, 9. *L.Carb.-L.Perm.*
    Antiphyllinae, 8. *L.Carb.-L.Perm.*
    Pseudoclaviphyllinae, 1. *L.Carb.*

Hapsiphyllidae, 16. *Dev.-Perm.*
  Hapsiphyllinae, 15. *M.Dev.-Perm.*
  Adradosiinae, 1. *L.Dev.*
Zaphrentoididae, 8. *L.Miss.-L.Penn., U.Perm.*
  Zaphrentoidinae, 6. *L.Miss.-L.Penn., U.Perm.*
  Cumminsiinae, 2. *Miss.-L.Penn.*
Suborder Plerophyllina, 49. *U.Sil.-U.Perm.*
  Polycoeliidae, 17. *U.Sil.-L.Dev., L.Carb.-Perm.*
    Polycoeliinae, 16. *U.Sil.-L.Dev., L.Carb.-Perm.*
    Prosmiliinae, 1. *U.Perm.*
  Anisophyllidae, 1. *U.Sil.*
  Plerophyllidae, 6. *Dev.-U.Perm.*
    Plerophyllinae, 4. *Dev.-U.Perm.*
    Baryphyllinae, 2. *L.Carb.*
  Endotheciidae, 1. *U.Perm.*
  Adamanophyllidae, 3. *L.-U.Carb.*
    Adamanophyllinae, 2. *L.-U.Carb.*
    Tachyphyllinae, 1. *L.Carb.*
  Pentaphyllidae, 9. *Dev.-L.Carb., Perm.*
    Pentaphyllinae, 7. *Dev.-L.Carb., Perm.*
    Commutiinae, 1. *U.Dev.*
    Dalniinae, 1. *U.Dev.* or *L.Carb.*
  Lophophyllidae, 6. *L.Carb.-U.Perm.*
  Timorphyllidae, 1. *U.Perm.*
  Verbeekiellidae, 5. *L.Miss.-L.Penn., U.Penn.-Perm.*
Suborder Caniniina, 32. *Carb.-low.U.Perm.*
  Cyathopsidae, 13. *Carb.-L.Perm.*
  Bothrophyllidae, 10. *Carb.-L.Perm.*
  Uraliniidae, 7. *L.Carb.*
  Endamplexidae, 2. *U.Perm.*
Suborder Aulophyllina, 61. *?U.Dev.-L.Perm.*
  Aulophyllidae, 47. *L.Carb.-L.Perm.*
    Aulophyllinae, 6. *L.Miss.-U.Penn.*

    Amygdalophyllinae, 8. *L.-U.Carb.*
    Clisiophyllinae, 4. *L.-U.Carb.*
    Dibunophyllinae, 27. *L.Carb.-L.Perm.*
    Heterocaniniinae, 2. *L.Carb.*
  Ekvasophyllidae, 4. *L.Carb.*
  Palaeosmiliidae, 3. *?U.Dev.-U.Carb.*
  ?Aphrophyllidae, 7. *L.Carb.*
Suborder Lithostrotionina, 42;2. *Carb.-Perm.*
  Lithostrotionidae, 31. *L.Carb.-L.Perm.*
    Lithostrotioninae, 6. *L.Carb.-?L.Perm.*
    Diphyphyllinae, 5. *L.Carb.-L.Perm.*
    Aulininae, 6. *Carb.*
    Acrocyathinae, 4. *L.Carb.-L.Perm.*
    Thysanophyllinae, 6. *L.Carb., ?U.Carb., L.Perm.*
    Yatsengiinae, 4. *U.Carb.-L.Perm.*
  Durhaminidae, 11;2. *L.Carb.-Perm.*
Suborder Lonsdaleiina, 55;13. *L.Carb.-U.Perm.*
  Axophyllidae, 6. *Carb.*
  Petalaxidae, 9. *L.Carb.-L.Perm.*
  Geyerophyllidae, 10. *U.Carb.-L.Perm.*
  Koninckocariniidae, 1. *U.Carb.*
  Waagenophyllidae, 22;13. *U.Carb.-U.Perm.*
    Waagenophyllinae, 13;8. *U.Carb.-U.Perm.*
    Wentzelellinae, 9;5. *Perm.*
  Pseudopavonidae, 7. *U.Carb.-?L.Perm.*
    Pseudopavoninae, 5. *U.Carb.-?L.Perm.*
    Taisyakuphyllinae, 2. *U.Carb.*
?Order Heterocorallia, 4;1. *Low.M.Dev., up.U.Dev., Carb.*
  Heterophylliidae, 4;1. *Low.M.Dev., up.U.Dev., Carb.*
Order and family uncertain, 20.
Order uncertain, 2.

RANGES OF TAXA

Only records accompanied by illustrations from which I have been able to make myself reasonably sure that the generic identifications are correct have been incorporated in the range data that follow the diagnosis of each genus. Nevertheless, these data are still defective. Preparation of the diagnoses from the literature has made it clear to me that the greatest impediments to precise taxonomy are the incompleteness of descriptions and the imperfection of illustrations of type species, and the lack of analyses of variation in topotypes. A very great improvement in our knowledge would result from critical redescriptions and new figures by specialist officers of museums housing such types. Without precise taxonomy little of real value can be contributed to current debates on plate tectonics and continental drift. Uncritical use of "faunal lists" is merely stultifying.

The stratigraphic distribution of orders, suborders, superfamilies, families, and subfamilies of Rugosa recognized in the *Treatise* is indicated graphically in the table that follows (compiled by JACK D. KEIM).

TABLE 1. *Stratigraphic Distribution of the Rugosa.*

	Cambrian	Ordovician	Silurian	Devonian	Mississippian	Pennsylvanian	Permian
	L M U	L M U	L M U	L M U	L M U	L U	L M U	L U

RUGOSA
  CYSTIPHYLLIDA
    Palaeocyclidae
      Primitophyllum
      Palaeocyclus
      Rhabdocyclus
      Bojocyclus
    Tryplasmatidae
      Tryplasmatinae
        Hillophyllum
        ?Bowanophyllum
        ?Neotryplasma
        Rhabdelasma
        Aphyllum
        Tryplasma
        Cantrillia
        Polyorophe
        Maikottia
        Stortophyllum
      Wenlockiinae
        ?Wenlockia
    Cystiphyllidae
      Cystiphyllum
      Cysticonophyllum
      Hedstroemophyllum
      Asperophyllum
      Microplasma
      Cruciphyllum
      Gyalophyllum
      Ceriocysta
      Gyaloplasma
      Comanaphyllum
      Cystiphylloides
      Pseudodigonophyllum
      Zonophyllum
      ?Bucanophyllum
      ?Cladionophyllum
      Coleophyllum
      ?Diplochone
      Edaphophyllum
      Lythophyllum
      Mackenziephyllum
      Skoliophyllum
    ?Fletcheriidae
      ?Parafletcheria
      Fletcheria

EXPLANATION

SUBORDER and above	(stippled band)
SUPERFAMILY	(double line)
Family	(fine dotted band)
Subfamily	(hatched band)
Genus	(solid black bar)
Occurrence questionable	? ? ?
Occurrence inferred	– – – –

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Holmophyllidae
  Xiphelasma
  Holmophyllum
  Cystiphorolites
  Dendroholmia
  Nipponophyllum
  Mesouralinia
  Mazaphyllum
  ?Nodophyllum
Goniophyllidae
  Araeopoma
  Goniophyllum
  Rhizophyllum
  Rhizophylloides
  Rhytidophyllum
  Calceola
Digonophyllidae
  Dialytophyllum
  Digonophyllum
  Hemicosmophyllum
  Lekanophyllum
  Mesophyllum
  Mochlophyllum
  ?Paracystiphylloides
  Stereophyllum
  Zonodigonophyllum
  Parazonophyllum
STAURIIDA
  CALOSTYLINA
    CALOSTYLICAE
  Lambelasmatidae
    Lambelasmatinae
      ?Lambeophyllum
      Lambelasma
      Dybowskinia
      ?Sogdianophyllum
    Coelostylinae
      Coelostylis
      Coelolasma
      Estonielasma
      ?Prototryplasma
  Calostylidae
    ?Ningnanophyllum
    ?Yohophyllum
    Calostylis
    Palaearaea
    Helminthidium

TABLE 1. (Continued)

	Cambrian	Ordovician	Silurian	Devonian	Mississippian	Pennsylvanian	Permian
	L M U	L M U	L M U	L M U	L U	L M U	L U

STREPTELASMATINA
  Streptelasmatidae
    Streptelasmatinae
      Streptelasma
      Leolasma
      Helicelasma
      Axiphoria
      Bighornia
      Borelasma
      Deiracorallium
      Densigrewingkia
      Grewingkia
      Kaljolasma
      Kenophyllum
      Lobocorallium
      ?Parabrachyelasma
      Rectigrewingkia
      Ullernelasma
      ?Paramplexoides
      ?Pycnactoides
      Siphonolasma
      ?Archaeozaphrentis
      Axolasma
      ?Densiphrentis
      ?Densiphyllum
      ?Pterophrentis
      Rhegmaphyllum
      Briantelasma
      Asthenophyllum
      ?Aknisophyllum
      ?Ogilvilasma
      Kionelasma
      Altaiophyllum
      Bowenelasma
      Triplophyllum
    Dalmanophyllinae
      Bodophyllum
      Dalmanophyllum
    Dinophyllinae
      ?Crassilasma
      ?Porfirieviella
      Tenuilasma
      Dinophyllum
      Neobrachyelasma
    Enterolasmatinae
      ?Soshkinolites
      Enterolasma

Table 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian			Permian		
	L	M	U	L	M	U	L	M	U	L	M	U	L	U		L	M	U	L	U		

Streptelasmatidae (cont'd)
   Palaeocyathus
   ?Paterophyllum
  Breviphyllinae
   Breviphrentis
   Breviphyllum
  Nevadaphyllinae
   Nevadaphyllum
  Homalophyllinae
   Compressiphyllum
   Homalophyllum
   Angustiphyllum
   Xenocyathellus
Paliphyllidae
   Paliphyllum
   Protocyathactis
   Sumsarophyllum
   Sclerophyllum
   ?Cystipaliphyllum
   Gissarophyllum
   ?Protoramulophyllum
   Neopaliphyllum
Kodonophyllidae
   Kodonophyllum
   Pilophyllia
   Schlotheimophyllum
   Circophyllum
   ?Cronyphyllum
   Niajuphyllum
   Bulvankeriphyllum
   Chlamydophyllum
   Pseudoblothrophyllum
   Symphyphyllum
   Zelophyllia
   Sinochlamydophyllum
Mucophyllidae
   Kungejophyllum
   Pseudamplexus
   "?Ningqiangophyllum"
   Mucophyllum
   Stylopleura
   Pseudamplexophyllum
   Briantia
   Pseudotryplasma
Ditoecholasmatidae
   Ditoecholasma

Tᴀʙʟᴇ 1. *(Continued)*

Stratigraphic range chart with period columns: Cambrian, Ordovician, Silurian, Devonian, Mississippian, Pennsylvanian, Permian (each subdivided L M U, with Pennsylvanian and Permian as L U).

Taxa listed (top to bottom):

Amsdenoididae
  Amsdenoides
  ?Multicarinophyllum
Acrophyllidae
  Acrophyllum
  Scenophyllum
STAURIINA
  Stauriidae
    Favistina
    Proterophyllum
    Palaeophyllum
    Crenulites
    Modesta
    Palaeoentelophyllum
    Palaeolithostrotion
    Cyathophylloides
    Parastauria
    Ceriaster
    Stauria
    ?Columnolasma
    ?Neotabularia
    Loyolophyllum
    Dendrostella
    Astrictophyllum
    ?Nadotia
  Doubtfully Stauriidae
    ?Prisciturben
  Pycnostylidae
    Protopilophyllum
    Pycnostylus
    ?Synamplexus
    Zelophyllum
    ?Thecacristatus
    ?Fletcherina
    Cyathopaedium
    Depasophyllum
    Synaptophyllum
  Amplexidae
    Amplexoides
    ?Lindstroemophyllum
    ?Siphonophrentis
    ?Heterophrentis
    Bordenia
    Amplexus
  Centristelidae
    Centristela

TABLE 1. *(Continued)*

Stratigraphic distribution chart. Column headers (with L, M, U subdivisions): Cambrian, Ordovician, Silurian, Devonian, Mississippian, Pennsylvanian, Permian.

Row labels:

- Neocolumnariidae
  - ?Neocolumnaria
- Kiziliidae
  - Kizilia
  - Melanophyllidium
- METRIOPHYLLINA
- Petraiidae
  - Protozaphrentis
  - Petraia
  - Haptophyllum
  - Petraiella
- Metriophyllidae
  - ?Duncanella
  - Metriophyllum
  - ?Metrioplexus
  - Petronella
  - ?Asserculinia
- Laccophyllidae
  - Laccophyllinae
    - Syringaxon
    - Laccophyllum
    - Schindewolfia
    - Sutherlandinia
    - Boolelasma
    - Saucrophyllum
    - Barrandeophyllum
    - ?Metrionaxon
    - Alleynia
    - Pedderelasma
    - Bitraria
    - ?Kabakovitchiella
  - Taralasmatinae
    - Taralasma
  - Neaxoninae
    - Neaxonella
    - Neaxon
    - Catactotoechus
    - ?Czarnockia
    - ?Hillaxon
    - Trochophyllum
  - Guerichiphyllinae
    - Guerichiphyllum
  - ?Friedbergiinae
    - Friedbergia
  - Amplexocariniinae
    - Nicholsoniella
    - Amplexocarinia

TABLE 1. *(Continued)*

Column headers (geologic periods): Cambrian | Ordovician | Silurian | Devonian | Mississippian | Pennsylvanian | Permian

Subdivisions: L M U | L M U | L M U | L M U | L M U | L U | L M U | L U

- Laccophyllidae (cont'd)
  - Gorizdronia
  - Nalivkinella
  - Paralleynia
- Uncertain
  - Retiophyllum
- Cyathaxoniidae
  - ?Columnaxon
  - Cyathaxonia
  - ?Cyathaxonella
  - Lophotichium
  - Epiphanophyllum
- Hadrophyllidae
  - Hadrophyllum
  - Microcyclus
- Combophyllidae
  - Combophyllum
- ?Lindstroemiidae
  - Lindstroemia
- Kielcephyllidae
  - Kielcephyllum
  - Kozlowskinia
  - ?Thecaxon
- Uncertain
  - Rhipidophyllum
  - Ridderia
  - Famaxonia
- DOUBTFULLY METRIOPHYLLINA
  - Lyliophyllum
  - Gymnophyllinae
  - Gymnophyllum
- KETOPHYLLINA
  - Kyphophyllidae
    - Donacophyllum
    - Strombodes
    - ?Pilophylloides
    - ?Maikottaphyllum
    - Pilophyllum
    - Wintunastraea
    - Neokyphophyllum
  - Ketophyllidae
    - ?Dentilasma
    - ?Ketophylloides
    - Heterolasma
    - ?Tabularia
    - Dokophyllum
    - ?Nataliella

TABLE 1. (Continued)

Column headers (periods with L/M/U subdivisions): Cambrian, Ordovician, Silurian, Devonian, Mississippian, Pennsylvanian, Permian

L M U | L M U | L M U | L M U | L M U | L U | L U | L M U | L U

Taxa (left column):

Ketophyllidae (cont'd)
?Chavsakia
Endophyllidae
?Mictocystis
?Yassia
Grabauphyllum
?Klamathastraea
Endophyllum
Iowaphyllum
Tabulophyllum
?Smithiphyllum
Sanidophyllum
Blysmatophyllum
?Neospongophylloides
ARACHNOPHYLLINA
Entelophyllidae
Petrozium
Altaja
Entelophyllum
Nanshanophyllum
Evenkiella
Shensiphyllum
Tenuiphyllum
Prohexagonaria
?Trachyphyllum
Medinophyllum
Migmatophyllum
Ornatophyllum
Ramulophyllum
Scyphophyllum
Kysylagathophyllum
Arachnophyllidae
?Angullophyllum
Arachnophyllum
?Chonophyllum
?Ningqiangophyllum
Idiophyllum
?Naos
?Pseudomucophyllum
?Zenophila
?Craterophyllum
Werneckelasma
Expressophyllidae
Pseudopilophyllum
Miculiella
Micula
Contortophyllum

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian		
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

LYCOPHYLLINA
   Lykophyllidae
     ?Onychophyllum
     Pseudophaulactis
     Rukhinia
     ?Zeravschania
     Holophragma
     Phaulactis
     Pycnactis
     Ryderophyllum
     Sverigophyllum
     Neocystiphyllum
     ?Pseudocystiphyllum
     ?Strephophyllum
     Plasmophyllum
     Hercophyllum
     Svetlania
     ?Camurophyllum
     ?Reimanophyllum
   Hallidae
    Papiliophyllinae
     Kobeha
     Papiliophyllum
     ?Blothrophyllum
    Aspasmophyllinae
     Aspasmophyllum
    Hallinae
     Aulacophyllum
     Hallia
     Odontophyllum
PTENOPHYLLINA
   Spongophyllidae
     ?Heterospongophyllum
     Spongophyllum
     Denayphyllum
     Carlinastraea
     Nevovepresiphyllum
   Ptenophyllidae
    Actinocystinae
     Cymatelasma
     Spongophylloides
     Cymatella
     Dubrovia
    Ptenophyllinae
     Imennovia
     Weissermelia
     Toquimaphyllum

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	U

Ptenophyllidae (cont'd)
  Salairophyllum
  Shastaphyllum
  Neomphyma
  Xystriphyllum
  Embolophyllum
  Lyrielasma
  Acmophyllum
  ?Pseudogrypophyllum
  ?Tonkinaria
  Hezhangophyllum
  Windelasma
  Paleogrypophyllum
  Pseudochonophyllum
  Aphroidophyllum
  Australophyllum
  Dohmophyllum
  Taimyrophyllum
  Acanthophyllum
  ?Redestonea
  Psydracophyllum
  Grypophyllum
  Hankaxis
Fasciphyllidae
  Vepresiphyllum
  Fasciphyllum
  ?Crista
?Stringophyllidae
  Stringophyllum
  Neospongophyllum
  Melrosia
  Sociophyllum
  ?Solipetra
  ?Sunophyllum
  Parasociophyllum
CYATHOPHYLLINA
  Ptychophyllidae
    Ptychophyllum
    ?Cyathactis
    Implicophyllum
  Eridophyllidae
    Eridophyllinae
      Capnophyllum
      Tipheophyllum
      Grewgiphyllum
      Eridophyllum

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian			Permian		
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Eridophyllidae (cont'd)
  Cylindrophyllinae
    Acinophyllum
    Asterobillingsia
    Cylindrophyllum
    Prismatophyllum
  Zaphrentidae
    Aemulophyllum
    Cyathocylindrium
    Heliophyllum
    Zaphrenthis
    ?Phymatophyllum
  Cyathophyllidae
    Heterophaulactis
    Sterictophyllum
    Cyathophyllum
    Loomberaphyllum
    Radiophyllum
    Glossophyllum
    Mansuyphyllum
    Moravophyllum
    Orthocyathus
    Peripaedium
    ?Acanthophyllia
    ?Houershanophyllum
    ?Qiannanophyllum
    ?Commutatophyllum
    ?Mictophyllum
    Sinodisphyllum
  ?Bethanyphyllidae
    Bethanyphyllum
    ?Tortophyllum
  Campophyllidae
    Campophyllum
COLUMNARIINA
  Acervulariidae
    Diplophyllum
    Acervularia
    Oliveria
  Disphyllidae
    Paradisphyllinae
      Radiastraea
      Paradisphyllum
      Xystrigona
      Gurievskiella
      Martinophyllum
      Exilifrons

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Disphyllidae (cont'd)
  Ivdelephyllum
  Xystriphylloides
Disphyllinae
  ?Eoglossophyllum
  ?Hemiaulacophyllum
  ?Chalcidophyllum
  Disphyllum
  ?Dushanophrentis
  ?Kunthia
  Minussiella
  ?Ceratophyllum
  Crateriformis
  Spinophyllum
  Alaiophyllum
  Amaraphyllum
  Pseudocampophyllum
  Argutastrea
  Temnophyllum
  Aristophyllum
  Charactophyllum
  ?Aphraxonia
  Hunanophrentis
Spongonariinae
  Spongonaria
  Tropidophyllum
  Zelolasma
  Breviseptophyllum
  ?Variseptophyllum
  Disphyllia
  Utaratuia
Hexagonariinae
  Hexagonaria
  Haplothecia
  Marisastrum
Columnariidae
  ?Circumtextiphyllum
  Planetophyllum
  Spasskyella
  Columnaria
Phillipsastreidae
  Farabophyllum
  Sulcorphyllum
  Thamnophyllum
  Trapezophyllum
  Vestigiphyllum
  Peneckiella

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian			
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Phillipsastreidae (cont'd)
   Phillipsastrea
   Stellatophyllum
   Phacellophyllum
   Bensonastraea
   Keriophylloides
   Protomacgeea
   Pterorrhiza
   Frechastraea
   Scruttonia
   Sudetia
PLEROPHYLLINA
  Anisophyllidae
   Anisophyllum
  Polycoeliidae
   Polycoeliinae
    Amandaraia
    Pseudocryptophyllum
    Calophyllum
    Tetralasma
    Pleophyllum
    Kinkaidia
    Stereocorypha
    Empodesma
    Sochkineophyllum
    Calophylloides
    ?Sassendalia
    ?Svalbardphyllum
    Gerthia
    Hexalasma
    ?Huangophyllum
    Groenlandophyllum
   Prosmiliinae
    Prosmilia
  Pentaphyllidae
   Pentaphyllinae
    Oligophyllum
    Antikinkaidia
    Pentaphyllum
    Cystelasma
    Carinotachylasma
    Tachylasma
    Pentamplexus
   Commutiinae
    Commutia
   Dalniinae
    Dalnia

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Plerophyllidae
  Plerophyllinae
    Ufimia
    Plerophyllum
    Barbarella
    Pleramplexus
  Baryphyllinae
    Barylasma
    Baryphyllum
Adamanophyllidae
  Tachyphyllinae
    Tachyphyllum
  Adamanophyllinae
    Flagellophyllum
    Adamonophyllum
Verbeekiellidae
  ?Cravenia
  ?Pseudowannerophyllum
  Leonardophyllum
  ?Zeliaphyllum
  Verbeekiella
Lophophyllidae
  Lophophyllum
  ?Sugiyamaella
  Stereostylus
  Lophamplexus
  Lophocarinophyllum
  Lophophyllidium
Endotheciidae
  Endothecium
Timorphyllidae
  Timorphyllum
STEREOLASMATINA
Hapsiphyllidae
  Adradosiinae
    Adradosia
  Hapsiphyllinae
    Hapsiphyllum
    Zaphrentites
    Famennelasma
    Amplexizaphrentis
    Clinophyllum
    Meniscophyllum
    ?Neozaphrentis
    ?Zaphrentula
    Canadiphyllum
    Allotropiophyllum

TABLE 1. *(Continued)*

	Cambrian L M U	Ordovician L M U	Silurian L M U	Devonian L M U	Mississippian L U	Pennsylvanian L M U	Permian L U
Hapsiphyllidae (cont'd)						▓▓▓▓	▓▓▓▓
Longiclava						▬	
Barytichisma							▬
Allophyllum							▬
Euryphyllum							▬
?Duplophyllum							▬
Stereolasmatidae					▬ ▬▬	▬▬	
?Amplexiphyllum					▬		
Stereolasma					▬		
?Stewartophyllum					▬		
Lopholasma					▬ ? ?		
Saleelasma							
Antiphyllidae						▓▓▓▓	▓▓▓
Pseudoclaviphyllinae						▨	
Pseudoclaviphyllum						▨	
Antiphyllinae						▨	▨
Fasciculophyllum						▬	
Claviphyllum						▬	
Clavilasma						▬	
Rotiphyllum						▬▬	
Bradyphyllum							▬
Actinophrentis							▬
Pseudobradyphyllum							▬
?Lytvolasma							▬
Zaphrentoididae						▓▓▓	▬ ▬ ▓
Cumminsiinae						▨	
?Dipterophyllum						▬	
Cumminsia						▬	
Zaphrentoidinae						▨	▬ ▬ ▨
Homalophyllites						▬	
Sychnoelasma						▬	
Zaphrentoides						▬	
Ankhelasma						▬	
Fasciculiamplexus						▬	
?Basleophyllum							▬
AULOPHYLLINA						?▓▓▓	
Palaeosmiliidae						?▓▓▓▓	▓▓▓▓
Palaeosmilia						? ▬▬ ?	▬▬
Qinghaiphyllum						▬	
Palastraea						▬	
?Aphrophyllidae						▓▓▓▓	
Naoides						▬	
Aphrophylloides						▬	
Aphrophyllum						▬	
Coenaphrodia						▬	
Merlewoodia						▬	
Nothaphrophyllum						▬	

TABLE 1. (Continued)

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian			
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

?Aphrophyllidae (cont'd)
   Symplectophyllum
Ekvasophyllidae
   Ekvasophyllum
   Faberophyllum
   ?Zaphriphyllum
   Turbophyllum
Aulophyllidae
  Heterocaniniinae
   Heterocaninia
   Kueichouphyllum
  Clisiophyllinae
   Clisiophyllum
   Cyathoclisia
   Axoclisia
   Neoclisiophyllum
  Amygdalophyllinae
   Rozkowskia
   ?Rylstonia
   Carruthersella
   ?Echigophyllum
   Arachnolasmella
   Kazachiphyllum
   Amygdalophyllum
   ?Kumpanophyllum
  Aulophyllinae
   ?Zakowia
   Auloclisia
   Aulophyllum
   Berkhia
   Staurophyllum
   Nervophyllum
  Dibunophyllinae
   Eostrotion
   Arachnolasma
   Arachniophyllum
   ?Haplolasma
   Katranophyllum
   Turbinatocaninia
   Yuanophyllum
   Biphyllum
   Slimoniphyllum
   Corwenia
   Spirophyllum
   Copia
   Koninckophyllum
   ?Nagatophyllum

TABLE 1. (Continued)

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U		

Aulophyllidae (cont'd)
  Dibunophyllum
  Neokoninckophyllum
  Heintzella
  Caninostrotion
  ?Diaschophyllum
  Faberolasma
  ?Lophophrentis
  Orygmophyllum
  Sestrophyllum
  ?Cystilophophyllum
  Yakovleviella
  Koninckophylloides
  Yuanophylloides
CANINIINA
  Uraliniidae
    Cystophrentis
    Uralinia
    Bifossularia
    Enygmophyllum
    Keyserlingophyllum
    Liardiphyllum
    Vesiculophyllum
  Bothrophyllidae
    Calmiussiphyllum
    Bothrophyllum
    ?Caninella
    Caninophyllum
    Gshelia
    Pseudotimania
    Siedleckia
    Timania
    Bothroclisia
    Hornsundia
  Cyathopsidae
    ?Menophyllum
    Siphonophyllia
    Lublinophyllum
    ?Dagmaraephyllum
    Kusbassophyllum
    ?Melanophyllum
    Caninia
    Pseudozaphrentoides
    Arctophyllum
    Fomichevella
    Crataniophyllum
    Skolekophyllum

TABLE 1. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	U

Cyathopsidae (cont'd)
  Paracaninia
Endamplexidae
  Endamplexus
  Spineria
LITHOSTROTIONINA
Lithostrotionidae
  Aulininae
    ?Paraaulina
    Vesiculotubus
    Aulostylus
    Solenodendron
    Aulina
    Aulokoninckophyllum
  Acrocyathinae
    Chonaxis
    Stelechophyllum
    Acrocyathus
    Eastonoides
  Lithostrotioninae
    Schoenophyllum
    Akiyosiphyllum
    Cionodendron
    Orionastraea
    Lithostrotion
    Siphonodendron
  Thysanophyllinae
    Dorlodotia
    Sciophyllum
    Thysanophyllum
    ?Corphalia
    Pseudodorlodotia
    Stylastraea
  Diphyphyllinae
    Kwangsiphyllum
    Nemistium
    Diphyphyllum
    Tschussovskenia
    Opiphyllum
  Yatsengiinae
    Arachnastraea
    Donophyllum
    ?Pseudoyatsengia
    Yatsengia
Durhaminidae
  Protodurhamina
  Protolonsdaleiastraea

Coelenterata—Anthozoa

TABLE 1. (Continued)

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian			
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Durhaminidae (cont'd)
Yabeiphyllum
Durhamina
Minatoa
Amandophyllum
Heritschioides
Porfirievella
?Pamirophyllum
?Protowentzelella
Kleopatrina
Eoheritschioides
Tanbaella
LONSDALEIINA
Axophyllidae
Actinocyathus
Axophyllum
Gangamophyllum
Tatjanophyllum
Pareynia
Lonsdaleia
Petalaxidae
Paralithostrotion
Petalaxis
Cystolonsdaleia
Nephelophyllum
Antheria
Lytvophyllum
?Huanglongophyllum
Ivanovia
Lithostrotionella
Koninckocariniidae
Koninckocarinia
Pseudopavonidae
Taisyakuphyllinae
Taisyakuphyllum
Ibukiphyllum
Pseudopavoninae
Ozakiphyllum
Amygdalophyllidium
Hiroshimaphyllum
Omiphyllum
Pseudopavona
Geyerophyllidae
Axolithophyllum
Darwasophyllum
Kionophyllum
Carniaphyllum

TABLE 1. (Continued)

	Cambrian			Ordovician			Silurian			Devonian			Mississippian			Pennsylvanian		Permian				
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U

Geyerophyllidae (cont'd)
 Geyerophyllum
 ?Jintingophyllum
 ?Paracarruthersella
 Lonsdaleoides
 Amygdalophylloides
 Carinthiaphyllum
Waagenophyllidae
 Waagenophyllinae
 Huangia
 Parawentzellophyllum
 Chielasma
 Heritschiella
 Akagophyllum
 Chihsiaphyllum
 Pseudocarniaphyllum
 Sakamotosawanella
 Chaoiphyllum
 Thomasiphyllum
 Pavastehphyllum
 Ipciphyllum
 Yokoyamaella
 Pseudohuangia
 Waagenophyllum
 Parawentzelella
 Miyagiella
 Paraipciphyllum
 Huayunophyllum
 Maoriphyllum
 Liangshanophyllum
 Wentzelellinae
 Pseudopolythecalis
 Chusenophyllum
 Wentzelophyllum
 Szechuanophyllum
 Iranophyllum
 Laophyllum
 Lonsdaleiastraea
 Polythecalis
 Praewentzelella
 Wentzelellites
 Wentzelella
 Multimurinus
 Battambangia
 Wentzelloides

TABLE 1. *(Concluded)*