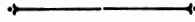


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## A REVIEW OF THE FAMILIES OF TETRACORALS\*

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**ABSTRACT.** A comprehensive review of the literature on Paleozoic corals reveals that 496 genera and 45 families and sub-families have been proposed. Of these 16 families are recognized as valid, the rest being synonyms or groups of inferior rank. The characters of these families are systematically reviewed and the genera belonging to each are listed.

### PART I

#### INTRODUCTION.

**T**HE literature on the Paleozoic corals is extensive, scattered, and in great need of comprehensive revision. This is especially true of the attempts at family grouping. To date over 45 families and nearly 500 genera have been proposed, yet no author has attempted to cover the whole field, and too often one author has paid little attention to the work of others. So great a compendium as the Zittel-Eastman "Textbook of Paleontology" recognizes but five families and these are undoubtedly artificial. In view of the existing confusion it has seemed desirable to make a thorough revision of all the families already proposed, to set forth succinctly the family characters in terms of a common denomination, and to record the genera that belong to each of these families.

The libraries of Yale University, Yale Peabody Museum, Harvard University, the American Museum, and the New York Public Library were used for this study.

#### ACKNOWLEDGMENTS.

I am indebted to Prof. Carl O. Dunbar who suggested the problem for study and has followed its development with encouragement and critical suggestions, and has read the manuscript.

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#### HISTORICAL REVIEW OF THE TAXONOMY OF TETRACORALS.

Prior to 1850 the few workers who studied corals confined their descriptions to genera and species. The early workers shortly after 1820 included Rafinesque and Clifford, Schweigger, Goldfuss, and Fleming.

In the 1840's other genera were described by Lonsdale, Michelin, M'Coy, Hall, Dana, and others. But it was not until 1850 and 1851 that any real coördination was given to the Paleozoic corals. In 1850 Milne Edwards and Haime published their "British Fossil Corals" which was the first systematic account and classification of the *Zoantharia Rugosa* (tetracorals). Their classification, while involving much speculation and uncertainty, has served as the basis for later classifications and, with some modification, it is still used in its essential features by general textbooks. Four principal families were established: the Stauridae, Cyathaxonidae, Cyathophyllidae, and Cystiphyllidae. The Cyathophyllidae were subdivided into the subfamilies Zaphrentinae, Cyathophyllinae, and Lithodendroninae. The first two subfamilies were raised to family rank later.

The study of corals subsequent to Edwards and Haime was considerably augmented by the use of thin and polished sections. This necessitated a reorganization and a redescription of the genera. The families, however, were little changed. During this period, therefore, there was a great tendency to concentrate upon the description of generic types. Nicholson and Thomson in the 1870's and 1880's were very active in this field in England. They were assisted by Duncan. Nicholson and Thomson early attempted but little reorganization of the families of Edwards and Haime. They concentrated, rather, upon accurately characterizing new and previously described genera and grouping them with their affinities about certain basic types. Thomson in 1882 proposed a new family, the *Diplocyathophyllidae*, which, however, has not been generally accepted.

At about the same time in Sweden, G. Lindström was working extensively upon the genera of corals. He described many new forms and also reorganized old ones. In 1883 he compiled a list

of all the genera of Paleozoic corals described up to that time. His chief contribution to the classification was a detailed study of operculate corals which, in 1883, he subdivided into two families, the Calceolidae and the Araeopomatidae.

In Russia in 1873, W. N. Dybowski published a monograph on tetracorals comprising four more or less distinct parts. The first reviewed the outstanding literature on the tetracorals prior to 1873. The second part dealt with a detailed anatomical investigation. As a result of this study, Dybowski established a very complete terminology of tetracoral structures. He used many of the previously established terms but suggested a multitude of new ones, making a set too bulky to be of practical use. Of principal interest here is the systematic account of coral taxonomy which Dybowski suggested in the third section of his monograph. He divided all of the tetracorals into two large groups, the *Inexpleta* and *Expleta*, based respectively upon the absence or presence of dissepiments and tabulae in the thecaium. These groups Dybowski divided in turn into subgroups, families and subfamilies. He proposed many new families in addition to those of Edwards and Haime. The accompanying table shows the classification as proposed by Dybowski.

*Zoantharia schlerodermata rugosa*

Group I. *Inexpleta*

Families *Cyathaxonidae*, *Palaeocyclusidae*

Group II. *Expleta*

Subgroup *Diaphragmatophora*

Families *Cyathophylloidea*, *Axophyllidae*, *Cyathopsidae*, *Ptychophyllidae*

Subgroup *Plenophora*

Families *Cyathophyllidae*, *Stauridae*, *Spongophyllidae*, *Aulophyllidae*, *Axaphyllidae*, *Craspedophyllidae*, *Arachnophyllidae*.

Subgroup *Cystiphora*

Families *Cystiphyllidae*, *Plasmophyllidae*, *Goniophyllidae*

The family *Palaeocyclusidae* is of principal importance since it has been adopted by other workers, but few of the other families suggested by him have been accepted. His grouping was based on the character and form of endothecal structures as interpreted by a study of thin sections. The main subdivisions and

the underlying principles of classification suggested by Dybowski were generally followed by other workers. The fourth section of his monograph was devoted to descriptions of corals. Many new genera and species were established. The validity of these new forms (1873, 1873a) was considerably questioned by other workers. Lindström (1883) pointed out that many of these so-called genera were synonyms of previously established forms and that others were founded on poor material and insufficient evidence.

A revision of the classification of corals was attempted by G. Dollfus in France (1875). Whereas Edwards and Haime subdivided the tetracorals into several families, Dollfus made a twofold subdivision based primarily upon the character of the septa. Corals of Group I possessed free, unfused septa with or without tabulae. Group II contained corals in which the septa were fused and were arranged in clusters about other well-developed septa. Not all tetracorals in this group were believed to possess tetrameral symmetry. The groups as established by Dollfus were higher in rank than the families. No families were recognized and the accepted genera were merely arranged directly under the groups. This classification was not followed by other workers.

A. Kunth (1869, 1870) made a study of the mode of septal insertion in tetracorals. His observations showed that tetrameral symmetry is achieved by the addition of septa in four regions in bilateral symmetry with respect to the plane of the cardinal and counter cardinal septa. His ideas proved to be fundamental and of great value. In the study of corals, Kunth did not greatly concern himself with classification. He accepted the classification of Edwards and Haime with the subfamilies suggested by them. Fromentel's classification was essentially the same. Kunth was much more concerned with basic structures common to all tetracorals and those which served to distinguish them from tabulate and hexacorals. In the light of his investigations upon the manner of septal insertion, Kunth made a study and gave descriptions of some of the unusual corals to determine whether they were, in reality, tetracorals. A number of the simpler and more common types was studied to give the fundamental characters of the tetracorals as a whole rather than to determine family relationships. Some corals, such as *Petraia*, Kunth recognized as not belonging to the fam-

ilies to which they were assigned but he made no attempt to constitute new families for these forms.

In Belgium, De Koninck (1872) published the results of a new research made on Carboniferous fossils. The old families of Milne Edwards and Haime and the Cyathophyllid subfamilies, Zaphrentinae, Cyathophyllinae, and Axophyllinae, were retained in his classification. Upon the basis of Kunth's investigation of *Petraia* he added the family *Petraia* Dybowski to his classification. The basis of his grouping was the simple or compound character of the coral, and the presence or absence of endothecal structures (tabulae, dissepiments, and columella). A description of the principal genera under each family was given by De Koninck.

In the same year (1872) Haeckel proposed the Order Tetracoralla—a term to be used instead of *Zoantharia Rugosa* which had been introduced by Edwards and Haime (1850). The term Tetracoralla was suggested to harmonize with *Hexacoralla* and *Octacoralla* then in use for the other types of corals. This usage has generally been accepted by later workers.

Karl von Zittel published his "Handbuch der Palaeontologie" in 1876. Although it contained little that was new on tetracorals, it did much to coördinate what had been done and to standardize the classification of this group. Zittel placed the corals and sponges under the phylum Coelenterata. The Order *Zoantharia* E. & H. was reduced to a class and the Tetracoralla, Haeckel, was given the rank of subclass. The classification suggested by him in 1876 is given in outline form.

Subclass Tetracoralla Haeckel

Family Inexpleta Dybowski

Tribes Cyathaxoninae Edwards and Haime, Palaeocyclinae Dybowski, Petrainae Dybowski

Family Expleta

Subfamily Diaphragmatophora Dybowski

Subfamily Plenophora Dybowski

Subfamily Cystophora Dybowski

Tribes Cystiphyllinae Edwards and Haime, Plasmophyllinae Dybowski, Fletcherinae Zittel, Goniophyllinae Dybowski

In the Zittel-Eastman "Textbook of Paleontology" (1900) this classification was simplified to but five families: the Cyath-

axonidae, Paleocyclidae, Cyathophyllidae, Zaphrentidae, and Cystiphyllidae.

Recognizing the value of the classification of Milne Edwards and Haime but noting Dybowski's modification of this system, Ferd. Roemer (1883) presented a new grouping of the genera in the light of new work. Seeing the need of a more detailed taxonomy he established five new families: the Phillipsastraeidae, Calostylidae, Polycoelidae, Coelophyllidae, and Palaeoastraeidae. The other families recognized by him were: the Cyathophyllidae, Zaphrentidae, Cystiphyllidae, Axophyllidae, and Cyathaxonidae of Edwards and Haime; the Calceolidae of Lindström; and the Petraiadae of De Koninck. The principal genera were listed and described under each of these families. Considering the previous work that had been done, this paper represents a remarkable step in the organization of corals. A practical key was provided for the identification of corals together with a discussion of the general features of the structures. Roemer recognized the importance of tetrameral symmetry and was quick to apply Kunth's ideas concerning septal insertion. Further subdivision of the coral groups was made upon the basis of the character of the septa, the endothecal structures, the presence of a columella, and the nature of the corallite wall. Although this work has not been extensively followed except by Germans, it deserves more recognition than it has received.

Another German worker nearly contemporaneous with Roemer was Fritz Frech. He likewise recognized the importance of tetrameral symmetry and septal arrangement in addition to the presence of endothecal structures. Frech used essentially the same classification as Roemer (1885, 1885a). However, he could not accept the Phillipsastraeidae as a separate family but included them with the Cyathophyllids. The family Coelophyllidae was incorporated with *Amplexus* in the Zaphrentids. The paleocyclid-like corals he recognized as a common group but did not make a separate family of them. Frech's principal contributions were systematic descriptions of genera and species with little emphasis on the families. In a slight revision of the Cyathaxonidae (1890) he subdivided the group into two subfamilies, proposing a new subfamily, the Gigantostylinae, for one genus. The validity of this subfamily has not been established.

Work on the tetracorals in America was decidedly less advanced than that in Europe in the nineteenth century. C. Rominger (1876) made a study of corals in Michigan. He patterned his work after Edwards and Haime but, realizing the intergradations between the families as described, he placed all his genera under the one family Cyathophyllidae. Such forms as *Cystiphyllum* and *Zaphrentis*, as well as *Cyathophyllum*, were included. He found no representatives of the family Stauridae. Rominger's work is of value chiefly for the genera and species described.

Another descriptive work on fossil corals was published by W. J. Davis (1885) of Kentucky. This work may have been patterned after Rominger for he also includes all his genera under the one family Cyathophyllidae of Edwards and Haime.

Other workers on the tetracorals in America include Meek and Worthen and James Hall. The work of Hall in New York, like that of contemporaneous American workers, was largely one of the mere descriptions of genera and species based primarily upon external features. After Hall, these analyses were continued by G. B. Simpson (1900). The generic and specific descriptions were excellent but no systematic relationships were indicated.

The first American attempt to organize the tetracorals in a systematic relationship was made by W. H. Sherzer (1891). After examining the available literature on tetracorals, he compiled a table showing all the genera described and the families to which they were assigned. He presented the work with the purpose of making a comparative study in chart form which would be of practical value in the identification of corals. Upon close examination it may be seen that he has followed Zittel (1876) almost exclusively and has made little in the line of an original contribution himself. His list of genera may not be considered complete up to 1891. The main value of his work is that it represents the first attempt at a systematic study in this country and a broader recognition of the work being carried on in Europe.

An organization of the corals in Europe in 1889 by H. A. Nicholson and R. Lydekker segregated them into three main groups. The families under these groups were not, in all cases,

considered distinct so they were arranged in the groups as follows:

Section Madreporaria Rugosa

I. Cyathophylloidea

Family Cyathophyllidae

Family Heliophyllidae

Family Clisiophyllidae

II. Zaphrentoidea

Family Zaphrentidae

Family ? Hadrophyllidae ("provisionally")

Family ? Palaeocyclidae ("the second group")

Family ? Streptelasmaidae ("may be . . . another group")

Lindströmia type

III. Cystiphylloidea

Family Cystiphyllidae

Family Calceolidae

The allocation of many genera in this scheme is contrary to the opinion of other workers. *Cyathaxonia*, *Duncanella*, *Petraia*, *Calostylis* and others were not classed as tetracorals.

P. Pocta (1902) found eight families of tetracorals represented in Bohemia. To the seven groups proposed by other workers Pocta added a new family, the Lindströmiidae, based upon endothecal structures and the columella. Pocta arranged these families into three large groups—the Expleta and Inexpleta of Dybowski and a third group, the Semiplena, proposed by Pocta. The latter group contained simple forms having endothecal structures which were poorly developed and confined to the lower part of the thecaium. The following is the classification of Pocta:

Order Zoantharia rugosa

Group Expleta Dybowski

Family Zaphrentidae—Edwards and Haime

Family Cyathophyllidae—Edwards and Haime

Family Cystiphyllidae—Edwards and Haime

Family Calceolidae—Lindström

Family Palaeostreidae—Roemer

Group Semiplena Pocta

Family Lindströmiidae—Pocta

Family Polycoelidae—Roemer

(*Cyathaxonidae* not represented but belonging here)

Group Inexpleta Dybowski

Family Petraiidae

Excellent family and generic descriptions were given and thirty genera were classified. A detailed history of the taxonomy of corals was also included.

The work on taxonomy since 1900 is incorporated in the body of this paper but some of the more outstanding taxonomists will be mentioned. In England, Hudson, Lang, S. Smith, Hill, and others have contributed to the classification. Heritsch and Wedekind have done considerable work in Germany. Tolmatchoff, Yakowlew, and Soshkina are among the Russian students. A number of papers upon corals have been published by Salée in Belgium and Scheffen in Norway. Grabau has contributed much to the study of corals in America and China. American workers include Bassler and Grove.

The preceding history has dealt almost entirely with the evolution of the classification. Although closely related to taxonomy, the history of ideas of morphology of the coral is a distinct study in itself. The development of these ideas has been traced by B. H. Grove (1934), D. Hill (1935), and earlier writers and will not be treated in this paper.

#### TERMINOLOGY OF THE TETRACORALS.

A concise account of the families of corals requires a special terminology free of ambiguity. Since no scheme of terminology has gained general acceptance, it will be desirable to describe at the outset the structural elements of the coral skeleton and fix the meanings of the terms to be used later.

Although many of these structures were described and named by Milne Edwards and Haime as early as 1848, our present knowledge represents the accretion of many researches, and our terminology the contribution of many minds. Three recent reviews of coral studies involving addition to and revision of the terminology are those of Grabau (1922), Hill (1935), and Wedekind (1937).

In the following paragraphs the various features of the coral are considered in the order in which they will be noted in the family diagnoses that follow.

#### GENERAL FEATURES.

**HABIT.**—The living animal is termed a *polyp* and its skeleton a *coral*. Tetracorals that live singly are said to be *solitary*

or *simple*, and the colonial forms are *compound*. The skeleton secreted by an individual is a *corallite*, and the aggregate of corallites in colonial forms is a *corallum*. The latter term is also used commonly for the corallite of solitary corals.

FORM.—In form, the solitary corals vary from *discoid* to broadly or narrowly *conical*. Hill (1935) proposed four terms based upon the rate of expansion of conical forms: *patellate*, for those with an apical angle of  $120^\circ$  or more; *turbinate*, for those with an apical angle of about  $70^\circ$ ; *trochoid*, with an apical angle of about  $40^\circ$ ; *ceratoid*, with an apical angle of about  $20^\circ$ . The mature part of some corals is *cylindrical*. Forms of this type having an irregular direction of growth are termed *scolecoïd* (Smith, 1930). The solitary corals are curved or straight. *Calceoloid* forms, flattened on one side, and *pyramidal* forms represent aberrant types of solitary corals.

If the corallites of a compound coral are not in actual contact the form is *fasciculate*, but if they are closely touching, the colony is *massive*. Fasciculate types may further be subdivided into *dendroid* (when the corallites assume a branching habit) and *phaceloid* (when the corallites are more or less closely parallel). In massive corals the corallites may remain *cylindrical* or may be so crowded as to be *prismatic*. Massive corals retaining the individual corallite wall are *cerioid*; those lacking corallite walls are *plocoid*.

#### EXTERIOR.

SURFACE.—The initial point of growth is the *apex* and is considered the *proximal* end of the corallite. The upper end, to which the polyp was attached, is considered *distal*.

Irregularities in growth are termed *growth-lines*, if fine, or *varices*, if coarser than lines. The latter may take the form of alternate *expansions* (also called *bourrelets*) and *constrictions*. The outer surface of the coral may be *smooth* or may show longitudinal grooves, *septal sulci*, which correspond in position to the septa of the interior. The exterior of some corals also bears *root-like processes* or, in some cases, well-developed *spines*.

CALYX.—The distal end of most corallites possesses a cup or depression in which the polyp resided. This cup is the *calyx*. It may be of various shapes, from *deep* to *shallow*, *steep-sided* to very gently *concave*. In certain types the calyx has a flat

bottom, *platform*, and steep sides, *calyx walls*; in others, the center of the calyx contains a depression—*calicular pit*, or an elevation—*calicular boss*, which is the projecting distal end of the axial structure. An *operculum*, a special lid-like structure covering the calyx, was developed in some corals. Opercula consist of one or four plates.

OUTER WALL.—It has been common among workers describing corals to speak of the outer wall of the corallite as an *epitheca*. This term implies that the structure is a layer deposited upon, and later than the regular coral wall or *theca*. Such usage appears, as Grabau (1922) has suggested, to be without justification. Thin sections of the wall give no support to the idea that this outer layer is secondary, and well-preserved corals, where the wrinkled surface layer extends to the highest brim of the calyx, show that it is the first formed and, therefore, the basic element of the wall. In sections of the extreme proximal end of some corals the outer wall is present even before the septa or other structures are added, likewise showing it to be of basic character. Since the wall, therefore, is a true primary structure, the term outer wall or *theca* is used in this discussion instead of *epitheca*.

Compound corals which have a suppression of the theca of the corallite may have the outer wall of the corallum considerably thickened to form a common covering for the colony, termed *peritheca* (*holotheca* of Hudson).

#### INTERIOR.

The entire inner area of the corallite enclosed by the theca is the *thecarium* (Grabau, 1922). Many definite skeletal elements are developed in this area. In addition, there may be a secondary deposition of calcareous material, *stereoplasm*, upon these primary structures.

SEPTA.—A number of longitudinal plate-like elements called *septa* are built in the thecarium. In the normal corallite they extend from the proximal end to the calyx and from the theca inward toward the center. In some cases that part of the septa next to the theca is lacking and the septum is said to be *interrupted*.

The manner of addition of the septa to the corallite of the tetracoral is very distinctive. It is illustrated diagrammatically

in Fig. 1. The earliest stage of a coral skeleton consists of a simple theca. Two septa soon appear on opposite sides of the inner surface of the theca. They occur as ridges and later may elongate to meet in the center. These two septa—the *cardinal* and *counter cardinal* septa—indicate the plane of bilateral symmetry about which all later septal insertion takes place. A pair of lateral septa—the *alar* septa—may develop at the same

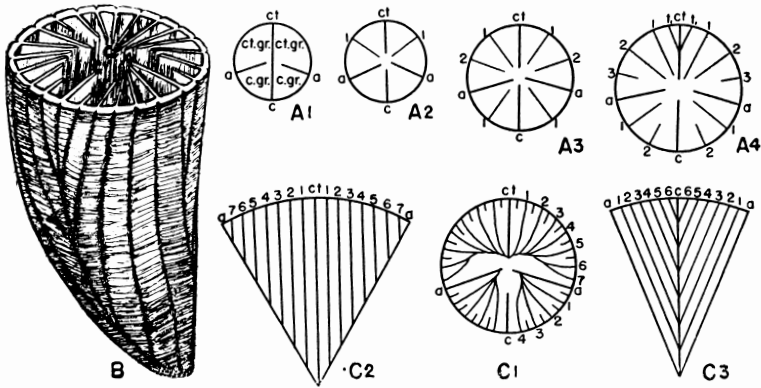


Fig. 1. Symmetry of the Tetracoral.

A<sub>1</sub>—A<sub>4</sub>. Successive transverse sections of a corallite showing the order of insertion of the septa, a, alar; c, cardinal septum; ct, counter septum; c. qr., cardinal quadrant; ct. qr., counter quadrant; 1, 2, etc., secondary septa numbered in order of appearance; t, tertiary septum. (after Grabau).

B. Diagram of entire corallite showing tetrameral symmetry.

C<sub>1</sub>—C<sub>3</sub>. Diagrams of transverse section, exterior on side of counter septum, and exterior on side of cardinal septum, respectively, to show arrangement of the septa. (after Grabau).

time as the cardinal and counter septa or, more commonly, appear soon afterwards. Their addition divides the corallite into quadrants—two *cardinal quadrants* (adjacent to the cardinal septum) and two *counter quadrants* (next to the counter septum). The cardinal, counter, and alar septa are called the *primary septa* since they are the basic elements about which the later-added septa are grouped.

The *secondary septa* are added in pairs in the cardinal and counter quadrants alternately, and grow to be equal or nearly equal to the primary septa. The first pair of these, inserted in the counter quadrant, arise almost as soon as the alars and give the appearance of hexamerall symmetry. This special

pair is known as the *counter laterals* and they have been considered by some students to belong to the primary group.

Additional secondaries are inserted in a definite order, those in the counter quadrant appearing directly adjacent to the alars, and those in the cardinal quadrants next to the cardinal septum. The primary and secondary septa together are called the *principal septa*.

Later in the development of some corals other smaller septa, *tertiary septa*, appear in a cycle alternating with the principal septa. In *Cyathaxonia* and *Stereolasma* they are first introduced in the counter quadrants next to the counter septum (Faurot, 1909 and Brown, 1907, respectively), but in *Zaphrentis* and *Lophophyllidium* their appearance throughout the coral is almost simultaneous (Duerden, 1906).

The apices of the tetracorals, and the mature stage in certain forms, show on the exterior a characteristic *tetrameral* symmetry of the principal septa, the secondary septa converging apically in the counter quadrants toward the counter septum, and in the cardinal quadrants toward the alars, as shown in Fig. 1 B and 1 C. On the exterior, the secondary septa in the cardinal quadrants converge toward the cardinal septum but lie approximately parallel to the alars; the septa of the counter quadrants, introduced next to the alars, lie parallel to the counter septum. (See Fig. 1 B, 1 C<sub>2</sub>, and 1 C<sub>3</sub>.)

In the mature part of most corals the corallum elongates without expansion and here the septa assume a radial position.

Although in most tetracorals the secondary septa are introduced equally in all four quadrants, there are some genera in which the counter quadrants develop more than the cardinals and others in which this discrepancy is reversed. The first of these irregularities is known as *acceleration of the counter quadrants*, the second as *acceleration of the cardinal quadrants*.

Microscopic examination of the septa reveals that they are made up of a number of vertical spicular elements termed *trabeculae*, composed of calcareous fibers. In a typical coral such as *Zaphrentis*, the trabeculae are completely fused together to form a solid, unbroken plate—a *continuous* septum (Blattseptum of Wedekind). (See Figs. 2 A and 2 C.)

Some corals possess *discontinuous* septa in which all of the septal elements are not completely fused. Wedekind (1927,

1937) has suggested a terminology for discontinuous septa. *Acanthine* septa (Hill, 1935) [Septalstacheln of Wedekind] are made up of unfused trabeculae. (See Figs. 2 B and 2 D.) Septa may be discontinuous vertically, being present only on the upper surface of the transverse partitions. When the trabeculae are fused this gives rise to band-like septa, *septal*

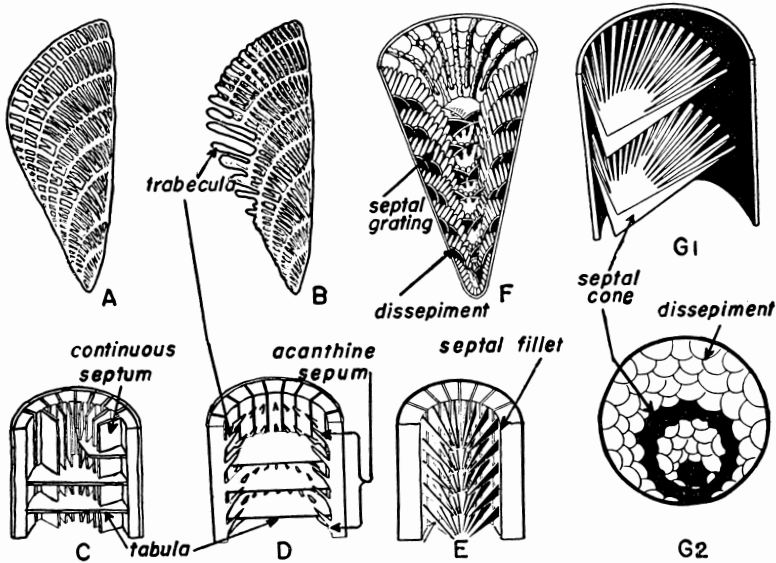


Fig. 2. Septal Characters. (after Wedekind).

- A. Diagram of a single continuous septum segregated from the coral.
- B. Diagram of a single discontinuous septum segregated from the coral.
- C. Diagram of a longitudinal section through the center of a coral with continuous septa.
- D. Diagram of a longitudinal section through a coral with acanthine septa.
- E. Section similar to C through a coral with septal fillets.
- F. Section similar to C through a coral with septal grating.
- G. Diagrams of a coral with septal cones.
  - G<sub>1</sub>— Longitudinal section through the center.
  - G<sub>2</sub>— Transverse section.

*fillets* (Septalleisten of Wedekind). (See Fig. 2 E.) Unfused trabeculae form septa of a superimposed comb-like structure. Septa of this type are termed *septal grating* (Rostsepten of Wedekind). (See Fig. 2 F.)

A limited number of corals, the family Calostylidae, possess *perforate* septa—formed of an irregular open meshwork of trabeculae.

Some corals have *carinae*, more or less vertical flanges on the septa seen in transverse section. They usually occur in pairs on either side of the septum and adjacent pairs coalesce in special cases. In the peripheral area of some corals where the septa are interrupted, the *carinae* occur as separate crossbar elements septal in position. These are *crossbar carinae* (Riegelsepten of Wedekind) and are possessed by genera such as *Cosmophyllum* and *Mochlophyllum*.

In some corals with abundant dissepiments a series of special structures called *septal cones* (Kegelsepten of Wedekind) are developed one above the other in the theca. (See Fig. 2, G<sub>1</sub> and G<sub>2</sub>.) The septal cones are hollow conical in form with the apex pointing downward. The apex may be axial in position in the coral or may be off center, causing the septal cone to impinge on one side. Upward and outward from the apex where the cone is very thick, there is a progressive thinning toward the brim of the cone and a splitting of the structure near the brim into outward tapering bands.

**FOSSULAE.**—The calyxes of some corals have a marked depression, *fossula*, about one or more of the septa. It is formed by the weak development, *abortion*, of a septum and a sagging of the floor of the calyx at that point. In transverse section the fossula appears as a large unoccupied interseptal area. The *cardinal fossula*, formed about the cardinal septum, is most commonly developed, but *alar fossulae* and a *counter fossula* may occur.

**TABULAE.**—*Tabulae* are transverse partitions one above the other, separating off the portions of the theca abandoned by the polyp. *Complete* tabulae extend from the theca across the central area; *incomplete* tabulae fail to reach the theca since the peripheral area is occupied by other elements. Tabulae are not necessarily perfectly horizontal. In some cases they are concave upward; in others, convex.

**DISSEPIENTS.**—In addition to, or in place of, the tabulae, much less continuous transverse structures, *dissepiments*, may occur. Commonly they are small interseptal partitions peripheral in position and arched convex upward. They are subordinate to the septa and do not interrupt them. (See Figs. 3 A<sub>1</sub> and 3 A<sub>2</sub>.) In some corals dissepiments nearly fill the theca.

Convex transverse partitions, much like dissepiments but originating as elevations of the polyp independent of the septa, are called *cystosepiments*. They derive their name from their cyst-like appearance. (See Figs. 3 B<sub>1</sub> and 3 B<sub>2</sub>.) They may attain considerable size and irregularity, peripherally interrupting as many as 10 septa. All gradations between the true dissepiment and cystosepiment are known.

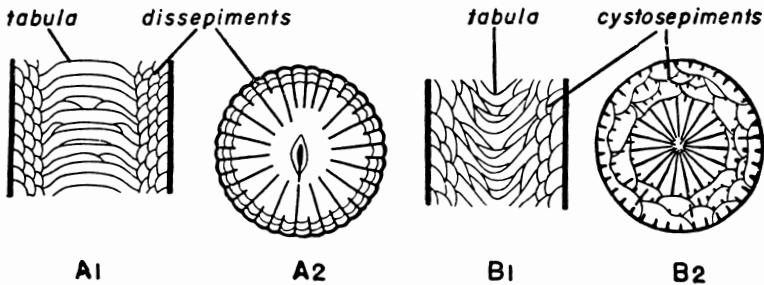


Fig. 3. Dissepiments and Cystosepiments. (after Wedekind).

- A. Diagrams showing dissepiments.  
 A<sub>1</sub>— Longitudinal section.  
 A<sub>2</sub>— Transverse section.  
 B. Diagrams showing cystosepiments.  
 B<sub>1</sub>— Longitudinal section.  
 B<sub>2</sub>— Transverse section.

**AXIAL STRUCTURES.**—The axial region of some tetracorals is occupied by an *axial structure*, which projects upward as a boss or spike into the calyx. Except in rare cases, it is continuous from near the apex to the calyx. In some, the axial structure appears as a solid, round or compressed rod or column running upward through the axis of the theca and this has suggested the name *columnella* (L. *column* + *ella*, a small column). *Cyathaxonia* and *Lophophyllum* are examples of this type. (See Fig. 4 A.) However, not all axial structures are entirely solid and compact, like columns, but some show considerable diversity in origin and structure. (See Figs. 4 B<sub>1</sub>, 4 B<sub>2</sub>, 4 C<sub>1</sub>, 4 C<sub>2</sub>, 4 D, 4 E, and 4 F.) These structures are called *pseudocolumellae*.

True columellae may be formed as a thickening or fusion of the septa with later independent growth. In *Lophophyllum* the counter septum is prolonged and thickened; in *Cyathaxonia* the counter and cardinal are the main septa represented; in

other forms a number of the principal septa are joined and thickened.

There is a wide diversity of structures making up pseudocolumellae: 1) The inner ends of the principal septa may fuse and thicken in the center, with or without twisting, as in the *Streptelasma*idae. (See Figs. 4 B<sub>1</sub> and 4 B<sub>2</sub>.) 2) Tabulae form pseudocolumellae by being strongly arched upward in the

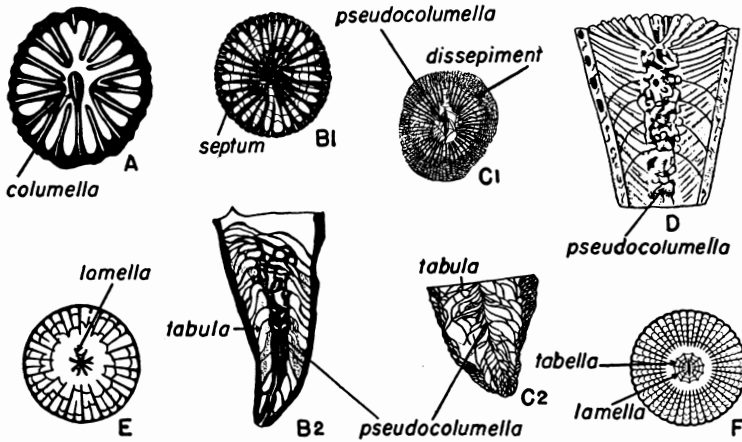


Fig. 4. Axial Structures.

A. Transverse section of *Lophophyllum* showing the columella. (after Duerden).

B. *Lopholasma*. Showing the pseudocolumella formed by the thickened ends of the septa. (after Simpson).

B<sub>1</sub>— Transverse section.

B<sub>2</sub>— Longitudinal section.

C. *Acrophyllum*. Showing the pseudocolumella formed by the uparching of the tabulae. (after Thomson).

C<sub>1</sub>— Transverse section.

C<sub>2</sub>— Longitudinal section.

D. Longitudinal section of *Enterolasma* showing the pseudocolumella formed of irregular rods. (after Simpson).

E. Transverse section showing pseudocolumella formed of lamellae.

F. Transverse section of *Dibunophyllum* showing the pseudocolumella formed of tabellae and lamellae. (after Wedekind).

center, with or without twisting, as in *Acrophyllum*. (See Figs. 4 C<sub>1</sub> and 4 C<sub>2</sub>.) 3) Cystosepiments, although rarely in the center, may form axial cyst-like structures—as in some forms of *Heliophyllum*. 4) Irregular discontinuous convoluted rods commonly connected to the inner ends of the septa may form a discontinuous pseudocolumella, as in *Enterolasma*. (See

Fig. 4 D.) 5) Stereoplasm alone may be deposited in the axial region as in *Lopholasma*. 6) A more complex pseudocolumella may be formed of a number of short longitudinal plates ("columnellar septa"), termed *lamellae*, which are independent of the true septa though usually corresponding with them in radial position. In some corals the lamellae impinge against a long *medial lamella* which extends across the pseudocolumella usually

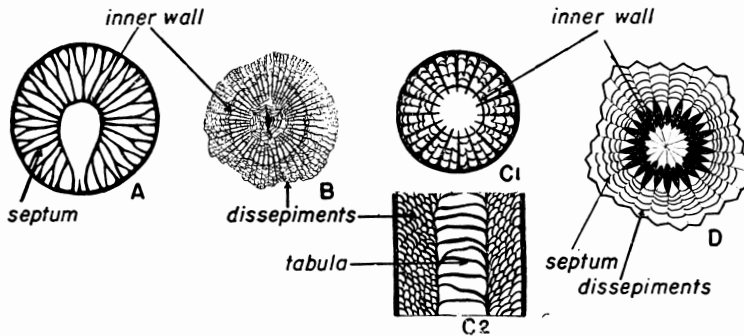


Fig. 5. Inner Walls.

- A. Transverse section showing a phyllotheca. (after Simpson).  
 B. Transverse section showing a sclerotheca. (after Grabau).  
 C. Diagrams showing a cyathotheca.  
 C<sub>1</sub>—Transverse section.  
 C<sub>2</sub>—Longitudinal section.  
 D. Transverse section showing a stereotheca. (after Grabau).

in the plane of the cardinal-counter septa; in others, the lamellae are nearly radially arranged. (See Fig. 4 E.) 7) Small, transverse arched elements within the pseudocolumella, similar to, and commonly connected with, the tabulae and dissepiments, are termed *tabellae*. In complex pseudocolumellae they occur between the lamellae and give the structure the pattern of a spiderweb as seen in cross section. *Dibunophyllum* is an example. (See Fig. 4 F.)

INNER WALL.—The thecarium may be longitudinally subdivided by an *inner wall* concentric within the corallite, separating an inner *axial* and an outer *peripheral* area. (See Fig. 5.) According to Grabau (1922), the inner wall may originate in four different manners. (1) The axial ends of the septa may be bent at right angles and fused to form a *phyllotheca*; (2) A dense growth of dissepiments may form a *sclerotheca*; (3) The tabulae may be arched downward at their outer margins to con-

tact the preceding ones, forming a *cyathotheca*; (4) In a few forms stereoplasm is deposited about the internal elements to form a *stereothecca*. More than one inner wall may be present in the theca. (See Figs. 5 A to 5 D.)

**INNER ZONATION.**—When stereoplasm is deposited in a wide area so that the skeletal elements are dilated and fused, a definite solid zone, termed the *stereozone*, is formed. The stereo-

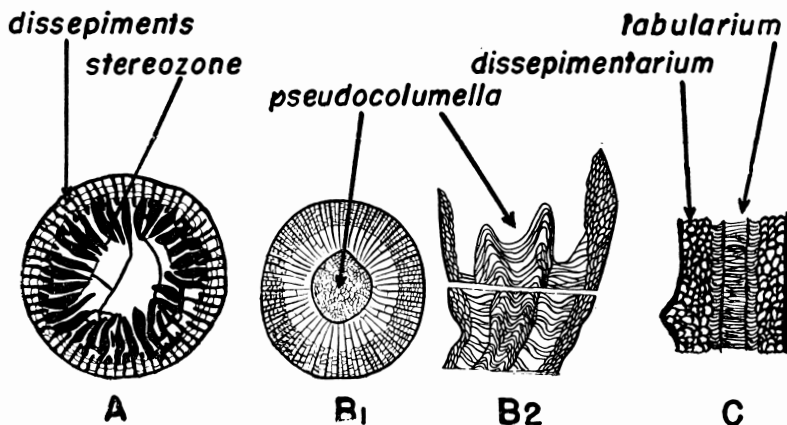


Fig. 6. Inner Zonation.

- A. Transverse section showing a stereozone. (after Wedekind).  
 B. A coral showing three distinct zones. (after Roemer).  
 B<sub>1</sub>— Transverse section.  
 B<sub>2</sub>— Longitudinal section.  
 C. Longitudinal section showing two zones. (after Simpson).

zone may be peripheral in position or may be an enlarged stereothecca. (See Fig. 6 A.) A marked peripheral zone of dissepiments is called a *dissepimentarium*; a zone of tabulae, usually axial, is a *tabularium*. (See Fig. 6 C.) The pseudocolumella constitutes a central zone. Other zones may be a combination of structures—tabulae and septa adjacent to a zone of tabulae alone, dissepiments and septa next to a zone of dissepiments alone, and many other combinations. As many as four definite zones may be conspicuous in a coral. They are best seen in transverse sections. (See Figs. 6 B<sub>1</sub> and 6 B<sub>2</sub>.)

#### GENERAL DISCUSSION.

A study of all of the available literature on tetracorals shows that, although a great many systems of taxonomy have been proposed, no one of them is serviceable alone. The five simple

families suggested in the later volumes of Zittel's "Textbook of Paleontology" (1900) are broad and overlapping and yet fail to include some special genera. At the other extreme, in creating a great many families, Dybowski (1873) assigns generic characters to families or bases them on unreliable criteria.

The purpose of the following outline is to present a concise and serviceable account of the valid families of tetracorals, giving a list of the genera included under each.

Concerning the complex problem as to what constitutes family characters, there has been little agreement among workers in the past. Each family character was examined separately and no single character proved sufficiently diagnostic in itself to serve as the sole basis of separation of the families. It is concluded that a subdivision of tetracorals must be made on a combination of characters.

One of the major tasks of this paper has been the compilation of a catalogue of all the genera of tetracorals described. In 1883, Lindström compiled a list of genera up to that time, and in 1891 Sherzer presented the principal genera in chart form. The present list not only brings both of these works up to date but supplements them.

In all, very nearly 500 genera have been described, many of which are invalid. Some generic names are synonyms; others have been discarded because of poor descriptions or because they were based on poor and inadequate material; still others should be ranked as subgenera or species.

Of this great number of corals there are many which the writer has not had the time and opportunity to study. These corals are tentatively placed on the authority of previous students, whose names are cited in parentheses following the several names in the generic lists.

The following sixteen families are recognized in this paper under the Subclass Tetracoralla:

- |                     |                       |
|---------------------|-----------------------|
| 1. Petraiidae       | 9. Lophophyllidae     |
| 2. Polycoelidae     | 10. Clisiophyllidae   |
| 3. Lindströmiidae   | 11. Lithostotientidae |
| 4. Cyathaxonidae    | 12. Zaphrentidae      |
| 5. Paleocyclidae    | 13. Cyathophyllidae   |
| 6. Streptelasmaidae | 14. Calostylidae      |
| 7. Hapsiphyllidae   | 15. Calceolidae       |
| 8. Laccophyllidae   | 16. Cystiphyllidae    |

## SYSTEMATIC ARRANGEMENT OF TETRACORALS.

## Phylum COELENTERATA

## Class ANTHOZOA (Actinozoa)

Subclass (or Order) TETRACORALLA Haeckel, 1872 (Zoantharia Rugosa Milne Edwards, 1850; Pterocorallia Frech, 1890; Tetraseptata Grabau, 1922)

1. Family PETRAIAIDAE<sup>1</sup> L. De Koninck, 1872.

Family Petraiaidae L. De Koninck, 1872; W. Dybowski, 1873; F. Roemer, 1883; (emend.) A. W. Grabau, 1928.

FAMILY DESCRIPTION.—*Habit* solitary; *form* conical, curved to straight; *calyx* deep, reaching to the bottom of the theca; *theca* distinct.

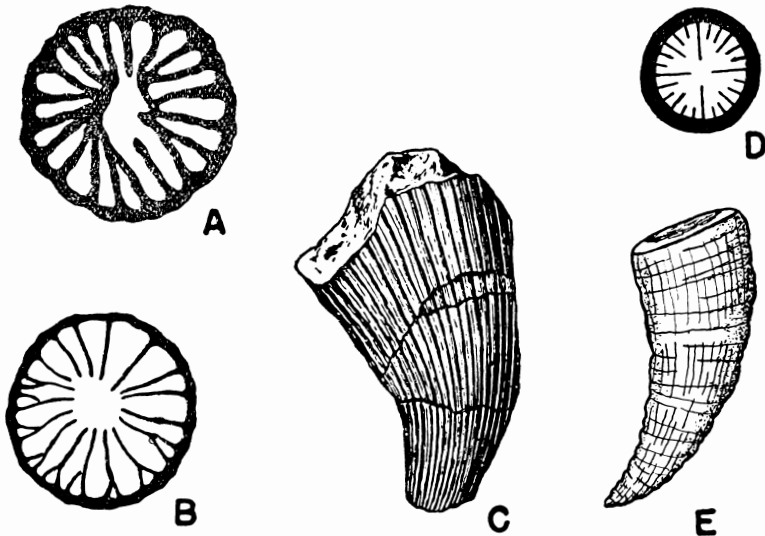


Fig. 7. FAMILY PETRAIAIDAE (after Pocta).

- A. Diagram of a transverse section of *Petraia discreta*. X 1½.  
 B. Diagram of a transverse section of *Orthophyllum praecox*. X 1½.  
 C. Diagram of *Orthophyllum bifidum*. Side view. Natural size.

## FAMILY POLYCOELIDAE (after Pocta).

- D. Diagram of a transverse section of *Polycoelia profunda*. X ½.  
 E. Diagram of *Polycoelia profunda*. Side view. X ½.

*Septa* continuous; *symmetry* nearly radial; *acceleration* lacking, or inconsistent; *primary septa* present; *secondary septa*

<sup>1</sup>This is the correct spelling of the family name formerly written as Petraiaidae.

present; principal septa, in primitive types, being mere ridges on the calyx wall (near the base may be lacking altogether); in advanced types septa well developed, uniting in groups, and reaching nearly to the center but not joining; *tertiary septa* rarely present; *fossulae* lacking; *tabulae* lacking; *dissepiments* lacking; *axial structure* lacking (central stereoplasm may be present); *inner wall* lacking.

**GEOLOGIC RANGE.**—Ordovician to Upper Devonian.

**INCLUDED GENERA.**—*Petraia* Münster, 1839; *Orthophyllum* Pocta, 1902 (fide Grabau, 1928); *Paterophyllum* Pocta, 1902 (fide Grabau, 1928); ? *Ditoecholasma* Simpson, 1900 (fide Grabau, 1928). *Duncanella* Nicholson, 1874 appears to belong to this family. The septa are better developed than those of the other genera. In all other features it conforms to the description of the family.

**COMMENTS.**—The simplicity of this group of corals and its range from the Ordovician to the Devonian suggests that this family is one of the most primitive ones. It will be noticed that the *Petraiaidae* correspond in nearly every characteristic with the family *Polycoelidae*. However, the latter are confined exclusively to the Permian, whereas the former are much earlier forms, as Grabau (1928) pointed out. For this reason they must be considered as separate families, at present.

## 2. Family POLYCOELIDAE F. Roemer, 1883.

Family *Polycoelidae* F. Roemer, 1883; A. W. Grabau, 1928; Y. S. Chi, 1931.

**FAMILY DESCRIPTION.**—*Habit* simple; *form* conical, curved to straight; *calyx* deep; *theca* distinct.

*Septa* continuous; *symmetry* nearly radial; *acceleration* none, or perhaps in counter quadrants; *primary septa* present, may be thickened; *secondary septa* present; principal septa reaching nearly to the center but not uniting; *tertiary septa* may be present, usually short; *fossulae* lacking; *tabulae* lacking (in some specialized forms sparse, incomplete, horizontal tabulae present in the lower portion of the thecarium); *dissepiments* lacking (sparse peripheral dissepiments may occur in association with the tabulae when they are present); *axial structure* lacking; *inner wall* lacking.

**GEOLOGIC RANGE.**—Permian.

**INCLUDED GENERA.**—*Polycoelia* King, 1849; *Gerthia* Grabau, 1928.

**COMMENTS.**—This family, as now constituted, is confined to the Permian system. The simplicity of structure present in

these corals suggests two possible explanations—a long-lived primitive group or a simplification by the degeneration of some higher type. As far as can be determined, no related types have been found to support either of these possibilities. The finding of associated types will serve to coördinate these corals with other families but at present they must be considered a separate family. Reference should be made to the Petraiidae for possible relationship with that family.

### 3. Family LINDSTRÖMIIDAE P. Pocta, 1902.

Family Lindströmiidae P. Pocta, 1902; A. W. Grabau, 1928; W. Scheffen, 1933.

FAMILY DESCRIPTION.—*Habit* solitary, may be compound; *form* conical, curved to cylindrical (fasciculate to massive); *calyx* deep with a prominent calicular boss; *theca* distinct.

*Septa* continuous; *symmetry* nearly radial; *acceleration*

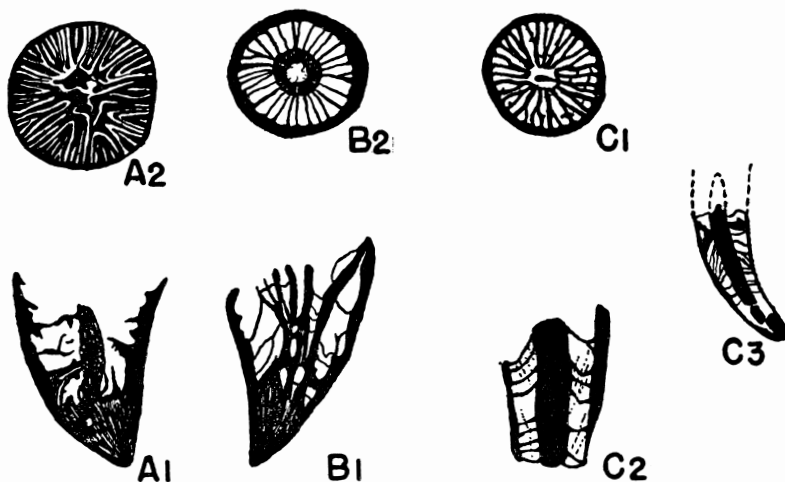


Fig. 8. FAMILY LINDSTRÖMIIDAE (after Nicholson and Etheridge).

#### A. *Lindströmia dalmani*.

A<sub>1</sub>—Diagram of longitudinal section through the center. X  $\frac{5}{8}$ .

A<sub>2</sub>—Diagram of a transverse section. Natural size.

#### B. *Lindströmia columnaris*.

B<sub>1</sub>—Diagram of longitudinal section through the center. Natural size.

B<sub>2</sub>—Diagram of a transverse section. Natural size.

#### FAMILY CYATHAXONIDAE (after Carruthers).

#### C. *Cyathaxonia cornu*.

C<sub>1</sub>—Diagram of a transverse section. X  $2\frac{1}{2}$ .

C<sub>2</sub>—Diagram of longitudinal section through the center. X  $2\frac{1}{2}$ .

C<sub>3</sub>—Diagram of longitudinal section through the center. Natural size.

lacking; *primary septa* present; *secondary septa* present; principal septa are well developed and extend to the center (in some mature forms septa failing to reach the center); *tertiary septa* may be present; *fossulae* lacking (obscure cardinal fossula present in some forms); *tabulae* sparse, horizontal or uparching in the center in the lower part of the theca; *dissepiments* lacking or sparse (see Comments); *axial structure*, a columella formed by the joining and thickening of some or all of the principal septa; septal ends may or may not be twisted; columella may secondarily be absent; *inner walls* lacking.

GEOLOGIC RANGE.—Silurian to Devonian.

INCLUDED GENERA.—*Lindströmia* Nicholson and Thomson, 1875; *Kionelasma* Simpson, 1900; ? *Strobilasma* Scheffen, 1933; ?? *Stegophyllum* Scheffen, 1933; ?? *Tyria* Scheffen, 1933.

COMMENTS.—What are commonly designated as dissepiments in the Lindströmiidae appear, upon examination of the plates and figures, more continuous and extensive than dissepiments, and agree more with the definition of tabulae as presented in this paper.

This family agrees rather closely with the Cyathaxonidae. This is discussed under the comments on that family.

#### 4. Family CYATHAXONIDAE M. Edwards and J. Haime, 1850.

Family Cyathaxonidae Edwards and Haime, 1850, 1851; W. Dybowski, 1873; F. Roemer, 1883; L. De Koninck, 1872; F. Frech, 1890; M. Neumayr, 1889; L. M. Lambe, 1901; E. Soshkina, 1928; A. W. Grabau, 1928; B. Grove, 1935.

FAMILY DESCRIPTION.—*Habit* solitary; *form* conical, curved; *calyx* moderately deep with prominently projecting, styliform columella; *theca* distinct.

*Septa* continuous; *symmetry* nearly radial; *acceleration* moderate in the counter quadrants; *primary septa* well developed, reaching to the center; *secondary septa* well developed, as long as the primary septa; *tertiary septa* well developed; *fossulae*, cardinal fossula present or obscure; *tabulae*, numerous fine tabulae, uparching in the center, present (Carruthers, 1913); *dissepiments* lacking; *axial structure*, columella originating by a joining in the center of the ends of the principal septa, largely the cardinal and counter septa, in mature corals appearing as a compact independent structure not connected with the septa; *inner wall* lacking.

GEOLOGIC RANGE.—Silurian to Carboniferous.

INCLUDED GENERA.—*Cyathaxonia* Michelin, 1846; *Cyathaxonella* Stuckenberg, 1896; *Cyathocarina* Soshkina, 1928; *Crassiphyllum* Miller, 1892 (fide Grove, 1935).

COMMENTS.—In 1846, Michelin established the genus *Cyathaxonia* containing three species, none of which was designated as the genotype. In 1850 Edwards and Haime, in describing the coral, established *C. cornu* Michelin, 1846, as the genotype, and stated that tabulae and dissepiment were lacking. Caruthers (1913) made careful, thin sections of *C. cornu* from the same locality and found numerous fine tabulae uparching about the columella making this family only slightly different from the Lindströmiidae (Grabau, 1928). The columella of the Cyathaxonidae is styliform, smaller, and projects more prominently in the calyx than that of the Lindströmiidae. All the characteristics of the two groups appear to represent a relationship of the two families and it is possible that the former developed directly from the latter.

#### 5. Family PALEOCYCLIDAE W. Dybowski, 1873.

Family Paleocyclusidae W. Dybowski, 1873; K. von Zittel, 1876; W. H. Sherzer, 1891; L. M. Lambe, 1901; R. S. Bassler, 1937.

FAMILY DESCRIPTION.—*Habit* solitary; *form* discoidal to depressed conical; *calyx* moderately concave; *theca* well developed.

*Septa* continuous to acanthine; *symmetry* radial to tetrameral; *primary septa* well developed, reaching to the center and joining; *secondary septa* similar to the primary septa; *tertiary septa* present; *fossulae*, cardinal fossula present, counter and alar fossulae may be present, absent in some early genera; *tabulae* lacking; *dissepiments* lacking; *axial structure* lacking; *inner wall* lacking.

GEOLOGIC RANGE.—Silurian to Pennsylvanian.

INCLUDED GENERA.—*Paleocyclus* Edwards and Haime, 1849; *Acanthocyclus* (*Acanthodes*) Dybowski, 1873; *Microcyclus* Meek and Worthen, 1868; *Combophyllum* Edwards and Haime, 1850; *Xenocyathellus* Bassler, 1937; *Hadrophyllum* Edwards and Haime, 1850; *Dipterophyllum* Roemer, 1883; *Baryphyllum* Edwards and Haime, 1850 (fide Bassler, 1937); ? *Porpites* Schlotheim, 1820 (fide Lindström, 1883).

COMMENTS.—The genera of this family possess definite characters distinctive to this group, but it is possible that this

family is a collection of homeomorphs produced by a certain environment or by parallel trends in evolution. A more detailed study of thin sections should be made to prove a family relationship.

#### 6. Family STREPTELASMAIDAE A. W. Grabau, 1922

Family Streptelasmaidae A. W. Grabau, 1922; E. Sochkine, 1925; P. R. Wedekind, 1927; E. Soshkina, 1928; S. S. Yoh and T. K. Huang, 1932; T. K. Huang, 1932; W. Scheffen, 1933.

FAMILY DESCRIPTION.—*Habit* solitary; *form* conical to sub-cylindrical; *calyx* of moderate depth; *theca* distinct.

*Septa* continuous; *symmetry* tetrameral to radial; *acceleration*, counter quadrants showing marked acceleration except in primitive forms; *primary septa* well developed, noticeably

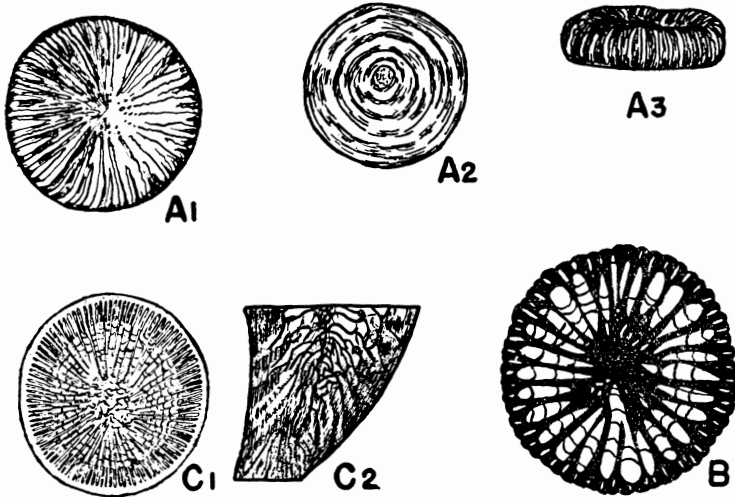


Fig. 9. FAMILY PALEOCYCLIDAE (after Bassler).

#### A. *Paleocyclus porpita*.

A<sub>1</sub>—Diagram of the entire coral. Top view. Looking into the calyx. X  $\frac{3}{4}$ .

A<sub>2</sub>—Diagram of coral. Base view. Looking at point of attachment. X  $\frac{3}{4}$ .

A<sub>3</sub>—Diagram of coral. Side view. X  $\frac{3}{4}$ .

#### FAMILY STREPTELASMAIDAE.

B. *Lopholasma carinatum*. Diagram of transverse section. Natural size. (after Simpson).

#### C. *Streptelasma corniculum* (after Nicholson).

C<sub>1</sub>—Diagram of a transverse section. Natural size.

C<sub>2</sub>—Diagram of longitudinal section through the center. Natural size.

thickened in some genera; *secondary septa* well developed; principal septa usually reaching to or nearly to the center; rare primitive septa having short septa; *tertiary septa* usually present; *fossulae* generally lacking. Specialized late paleozoic types, such as *Stereolasma*, showing a cardinal fossula; *tabulae* generally lacking; sparse horizontal tabulae in specialized types; *dissepiments* present but not abundant, occurring in the peripheral region; *axial structure* usually lacking, a central structure may occur by a joining of the septa in the center with a thickening of stereoplasm or a twisting of the septa or both, separate convoluted rods may occur on the inner ends of the septa to form an irregular central structure as in *Enterolasma* Simpson; *inner wall* may be present; *inner zonation* generally triareal: outer zone of septa and dissepiments, zone of septa, central area.

**GEOLOGIC RANGE.**—Ordovician to Permian.

**INCLUDED GENERA.**—*Streptelasma* Hall, 1847; *Stereolasma* Simpson, 1900; *Lopholasma* Simpson, 1900; *Enterolasma* Simpson, 1900 (fide Grabau, 1922); *Helenterophyllum* Grabau, 1909; *Bradyphyllum* Grabau, 1928; *Heterelasma* De Koninck, 1872; *Kunthia* Schlüter (fide Grabau, 1922); *Kenophyllum* = *Kanophyllum* Dybowski, 1873 (? fide Grabau, 1922).

Subfamily Plerophyllinae Grabau, 1928; *Plerophyllum* Hinde, 1890 (*Pentaphyllum* De Koninck, 1872, preoccupied); *Oligophyllum* Pocta, 1902; and *Cryptophyllum* Carruthers, 1919 (fide Grabau, 1928); *Endothecum* Koker, 1924; *Duplophyllum* Koker, 1924.

Subfamily Tachylasmatinae Grabau, 1928; *Tachylasma* Grabau, 1922; *Ufimia* Stuckenberg, 1896 (fide Grabau, 1928); ? *Lytvolasma* Sochkine, 1925; *Hexalasma* Soshkina, 1929 (doubtful).

Subfamily Sochkineophyllinae Grabau, 1928; *Sochkineophyllum* Grabau, 1928.

Doubtful Genera (belonging to the family Streptelasmatae Wedekind, 1927): *Dybowskia* Wedekind, 1927; *Grewingkia* Dybowski, 1873; *Kiaerophyllum* Wedekind, 1927; ? *Dinophyllum* Lindström, 1882.

**COMMENTS.**—The family Streptelasmatae, as diagnosed by Grabau (1922), contained many diverse genera which have, since then, been placed in separate families. Some other genera, while somewhat related, must likewise be placed in other families before this group can be crystallized.

In 1927, P. Wedekind proposed a new family, the Streptelasmatae, which corresponds largely with that of Grabau. The group is more inclusive, containing forms with well developed horizontal tabulae and those with short septa. Forms with a complication of the axial ends of the septa in the center are

excluded. The classification of Grabau seems preferable to that of Wedekind.

7. Family HAPSIPHYLLIDAE A. W. Grabau, 1928.

Family Hapsiphyllidae A. W. Grabau, 1928; C. C. Yü, 1933, B. H. Grove, 1935.

FAMILY DESCRIPTION. — *Habit* solitary; *form* conical, straight to curved; *calyx* circular, comparatively deep, with a prominent calicular pit; *theca* distinct, well developed.

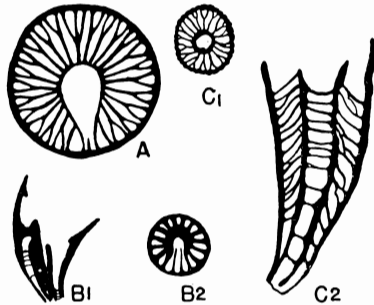


Fig. 10. FAMILY HAPSIPHYLLIDAE (after Simpson).

A. *Hapsiphyllum calcariforme*. Diagram of a transverse section. Natural size.

B. *Meniscophyllum minutum*.

B<sub>1</sub>—Diagram of longitudinal section through the center. X 5%.

B<sub>2</sub>—Diagram of a transverse section. X 5%.

FAMILY LACCOPHYLLIDAE (after Simpson).

C. *Laccophyllum acuminatum*.

C<sub>1</sub>—Diagram of a transverse section. Natural size.

C<sub>2</sub>—Diagram of longitudinal section through the center. Natural size.

*Septa* continuous; *symmetry* tetrameral to radial; *acceleration*, marked counter quadrant acceleration; *primary septa* not reaching to the center. The cardinal septum may be short and poorly developed; *secondary septa* abundant; principal septa being of about equal length (see inner wall); *tertiary septa* may be present, short; *fossulae*, marked cardinal fossula; *tabulae* may be present, restricted to the inner area; *dissepiments* usually present, not abundant, may bridge the cardinal fossula; *axial structure* lacking, a median, more or less crescentic mass of stereoplasm in rare cases present; *inner wall*, the counter quadrant septa united by their inner ends and sometimes fused to form a horseshoe-shaped inner wall facing the cardinal fossula; the alars and counter quadrant septa may, likewise, be

included in inner wall; *inner zonation*, common zonation: outer zone of septa and dissepiments, inner wall, inner zone open or with tabulae.

**GEOLOGIC RANGE.**—Devonian to Permian.

**INCLUDED GENERA.**—*Hapsiphyllum* Simpson, 1900; *Meniscophyllum* Simpson, 1900 (fide Grabau, 1928); *Allotrophiophyllum* Grabau, 1928; *Cystophrentis* Yü, 1931; *Uralinia* Stuckenberg, 1896 (fide Yü, 1933) *Pseudouralinia* Yü, 1931; *Clinophyllum* Miller, 1891 (fide Grove, 1935); ? *Agonophyllum* (see Simpson, 1900).

**COMMENTS.**—Several other genera not included here have been assigned to this family almost entirely on the basis of the horseshoe-shaped inner wall. The presence of a cardinal fossula together with an inner wall can produce this distinctive structure in any coral. For this reason this criterion must not serve as the sole basis of the family.

O. H. Schindewolf (1938), after an examination of some corals commonly grouped together in the Zaphrentidae—principally *Zaphrentoides*, *Triplophyllum*, and *Hapsiphyllum*, segregated them from that family and placed them in a new family, the Zaphrentoididae. A study of the genus *Hapsiphyllum* was, for a large part, the basis of this work. This genus he considered to be a subgenus of *Zaphrentoides*. *Hapsiphyllum*, however, differs from the latter in a number of respects. The inner wall of the former is formed by the joining of the principal septa which is not always the case in the latter. There is but one well-developed fossula instead of three and, as Schindewolf points out, this fossula is on the concave side of the polyp instead of on the convex. Dissepiments are much more prevalent in *Zaphrentoides*. The fossula may be open towards the center and a complete inner wall may be lacking. Schindewolf believed that the true Zaphrentids differ from the Zaphrentoididae in possessing carinae, toothed septa, a well-developed peripheral zone of dissepiments, and a fossula open toward the center. The latter character is not diagnostic of *Zaphrentoides* and *Triplophyllum* and the former characters can hardly be considered sufficient in themselves for family distinction. For these reasons *Zaphrentoides* and *Triplophyllum* are retained in the family Zaphrentidae. The characters mentioned in the family description above, as well as those here mentioned, serve to establish *Hapsiphyllum* in a family distinct from the Zaphrentidae.

[To be continued]