COELENTERATA

Article 2—SEPTAL ARRANGEMENT AND ONTOGENY IN THE PORPITID CORALS (pp. 1-16, pls. 1-3, figs. 1-4) ............... By Russell M. Jeffords

Article 3—MISSISSIPPIAN CORALS FROM NEW MEXICO AND A RELATED PENNSYLVANIAN SPECIES (pp. 1-12, pls. 1, 2, figs. 1-3)
By Russell M. Jeffords

MOLLUSCA

Article 5—ORIGIN AND ADAPTATION OF PLATYCERATID GASTROPODS (pp. 1-11, pls. 1, 2, fig. 1) ....................... By Arthur L. Bowscher

ECHINODERMATA

Article 1—NEW GENERA OF MISSISSIPPIAN CAMERATE CRINOIDS (pp. 1-23, pls. 1-6, figs. 1-4) ....................... By Arthur L. Bowscher

Article 2—PUBLICATIONS BY SHUMARD AND McCHESNEY CONCERNING CRINOIDS AND OTHER FOSSILS (pp. 1-4) By Edwin Kirk

VERTEBRATA

Article 5—SKELETON OF A MUSTELID, BRACHYPALIS, FROM THE MIocene OF NORTHEASTERN COLORADO (pp. 1-15, pls. 1, 2, figs. 1-11) ....................... By Edwin C. Galbreath

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ABSTRACT

Porpitid or paleocyclid corals comprise specialized and probably homeomorphic Rugosa that range in age from Silurian to Pennsylvanian. Classification of these corals depends importantly on nature of the theca, peculiarities in form of the corallite, and arrangement and character of the major septa, minor septa, and fossulae. This paper records data on the position of the protosepta and fossulae in many of the species previously referred to the family. The cumminsioid septal pattern, which is characteristic of Cumminsia, Dipterophyllum, and Gymnophyllum, includes a large cardinal fossula, distinct alar pseudofossulae, and a counter septum of normal length. Baryphyllum, which represents the baryphyllloid septal arrangement, has a strong cardinal septum and a distinct counter fossula. The hadrophylloid pattern comprises a cardinal fossula, alar pseudofossulae, and pinnately joined metasepta. The acanthocycloid and microcycloid septal arrangements are not understood adequately as yet, but they comprise long radially arranged septa that lack a fossula and pseudofossulae, and short peripherally disposed septa, respectively. Hadrophyllum ovale, H. pedunculatum, and H. tennesseense seem to have septal patterns most closely resembling that of Baryphyllum, and other species previously placed in Hadrophyllum, excepting the genotype, differ significantly from the hadrophylloid septal arrangement.

A series of individuals representing successive growth stages are described and illustrated for Gymnophyllum and Baryphyllum. These two genera are redescribed also on the basis of additional information on the position of the protosepta and on ontogenetic development.
INTRODUCTION

The genera and species of small button-shaped corals formerly called palaeocyclids (palaeocyclids of authors) have been characterized by Bassler (1937) and many of their features are relatively clear. These corals, which comprise one of the most distinctive groups of the Rugosa, have been placed rather consistently in the family Palaeocyclusidae (Dybowskii, 1873). Inasmuch as Palaeocyclus Edwards & Haime (1849, p. 71), the family type genus, has been shown by Cyclus to include peculiar and probably specialized differences in the species. The very short geologic range of these species would make them important genetic lines, it is not surprising to find important differences in the species. The very short geologic range of these species would make them important index fossils if the occurrence of most of them were not so localized.

SCOPE OF PRESENT PAPER

Although most features of porpitid corals have been discussed rather thoroughly, studies on similar corals from Pennsylvanian rocks of Oklahoma and Mississippian formations of New Mexico, indicate that identification of protosepta (cardinal, counter, and alar septa) in some of the species is not well established. Moreover, the marked effect of ontogenetic development on the appearance of the septa and the corallite in several genera seems to have received little attention. This paper, therefore, summarizes available information on the septal pattern and ontogeny among corals currently assigned to the Porpitidae. Other features of the porpitid corals are not considered specifically as they are available in the excellent discussion of the family by Bassler (1937). Available specimens and published illustrations are adequate, however, for study of only a part of the species. Also, several corals that have been placed in this family, such as Xenocyathellus thedfordensis (Stewart), Bojo-cyclus bohemicus Prantl (1939), and Hadrophyl-lum woodi Grabau, seem to differ importantly from the other porpitid corals.

Examination of the data has indicated need also for redefinition of the corals Barbyphyl-lum verneuili-anum Edwards & Haime (1850, p. lvii) and Gymnophyllum woldi Howell (1945, p. 2), and the genera based on these species.

PREVIOUS STUDIES

Porpitid corals have been described by several workers since the early descriptions by Edwards & Haime (1849, 1850). Bassler in 1937 redescribed and illustrated corals previously described and proposed one new genus and thirteen new species of porpitid corals. Following the appearance of Bassler's paper, Prantl (1939) described a small Middle Devonian coral from Czechoslovakia as Bojo-cyclus bohemicus, new genus and new species, and Northrop (1939, p. 139) described a Silurian coral from the Gaspé Peninsula as Palaeocyclus rotuloides magnus, new variety. Easton (1944) has redescribed Microcyclus blairi Miller (1892, p. 7), and Moore & Jeffords in 1945 redescribed Hadrophyl-lum aplatum Cummins (1891, p. 552) and designated it as the genotype of a new genus Cumminsia.

METHOD OF STUDY

Specimens available for study included about 65 corallites of Gymnophyllum wardi, 25 of Baryphyl-lum verneuili-anum, and numerous specimens of Dipteroptyllum glans (White, 1862), Hadrophyl-lum orbignyi Edwards & Haime (1850), and Cumminsia aplata. A few representatives of most other species assigned to this family were also available in the collections or have been examined during the past few years. Many of the data presented here, however, are obtained largely from photographs of particularly well-preserved specimens that have been published previously.

In order to simplify study of the arrangement of the septa and also to avoid the not insignificant cost of duplicating numerous photographs that are available readily elsewhere, representative septal patterns have been traced from photographs of the porpitid corals. These line diagrams given here at a uniform magnification permit rapid comparison of the arrangement and relative radial length of the septa. No attempt is made, however, to incorporate other significant details such as carinae, relative thickness of the septa, or form of the corallite.

The specimens of Gymnophyllum wardi illustrated in this paper are in the paleontological collections of the University of Kansas, and the original illustrations of Baryphyl-lum verneuili-anum are from specimens in the collections of the Tennessee Geological Survey.

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SEPTAL CHARACTERS AMONG PORPITID CORALS

IDENTIFICATION OF PROTOSEPTA AND FOSSULAE

Protosepta in rugose corals are identified commonly by recognition of the four points where major septa are inserted. One of these points lies on each side of the cardinal septum and the other two places are on the counter sides of the alar septa. The pattern of septal grooves and interseptal ridges on the exterior of the theca or traces of the septa where the theca has been removed and serial sections are useful for most of the Rugosa, as noted by KUNTH (1870), JEFFORDS (1942), and many others. These techniques are not applicable to the porpitid corals, and accordingly the tetraleral pattern of the septa as exposed in the calyx comprises the most useful method for identification of the septa in these corals. As observed in several genera belonging to other families, the most recently inserted septa tend to be shorter than the earlier ones and also to be inclined away from the point of development (Fig. 1). The spaces left by the poorly developed last septa and this tendency to lean away from the adjacent protoseptum are termed pseudofossulae. A fossula, on the other hand, is considered to be a space formed by the partial or complete abortion of a septum.


Figure 2. (Continued from facing page.)

1.—Porpites porpita (LINNAEUS), genotype of Porpites (=Palaeocyclus) from Lower Gotlandian, Silurian, on the Island of Gotland. Protosepta are not identified (after BASSLER, 1937).
2.—Combophyllum osismorum EDWARDS & HAIME, genotype of Combophyllum, from the Lower Devonian of Brest, France; protosepta are not identified (after EDWARDS & HAIME, 1851).
3.—Acanthocyclus porpitoides LANG & SMITH, from the Wenlockian, Silurian, of Dudley, England; protosepta are not identified (after EDWARDS & HAIME, 1854).
4.—Porpites rotuloides (HALL) from the Clinton group, lower Niagaran Series, Middle Silurian, near Clinton, New York; protosepta are not identified (after HALL, 1852).
5.—Dipterophyllum glans (WHITE), genotype of Dipterophyllum, from the Burlington limestone, Osagian Series, Mississippian, in Iowa. The septal formula, as determined from the location of the pseudofossulae, is K 7 A 5 C 2 5 A 7 K; the cardinal septum seems to be almost completely aborted (after BASSLER, 1937).
6-14.—Gymnophyllum wardi HOWELL, genotype of Gymnophyllum, from near the base of the upper Wewoka formation, Desmoinesian Series, Pennsylvanian, on the north shore of Lake Okmulgee, west of Okmulgee, Oklahoma.
6, Small immature specimen (Univ. Kansas No. 7998-21e); the septal formula is K 5 A 4 C 3 A 4 K.
7, Small immature specimen (Univ. Kansas No. 7998-21i); the septal formula is K 4 A 3 C 3 A 4 K.
8, Specimen of average size (Univ. Kansas No. 7998-21a); the septal formula is K 5 A 3 C 3 A 5 K.
9, Small mature specimen (Univ. Kansas No. 7998-21d); the septal formula is K 5 A 3 C 3 A 5 K.
10, Large gerontic specimen (Univ. Kansas No. 7998-21f); the septal formula is K 5 A 3 C 3 A 5 K.
11, Small specimen (Univ. Kansas No. 7998-21k); the septal formula is K 3 A 2 C 2 A 3 K.
12, Specimen of average size (Univ. Kansas No. 7998-21l); the septal formula is K 4 A 3 C 3 A 4 K.
13, Immature specimen (Univ. Kansas No. 7998-21e); the septal formula is K 4 A 3 C 3 A 4 K.
14, Larger immature specimen (Univ. Kansas No. 7998-21a); the septal formula is K 5 A 3 C 3 A 5 K.
15-21.—Baryphyllum verneuilianum EDWARDS & HAIME, the genotype of Baryphyllum, from the New Providence formation, Osagian Series, Mississippian, in Tennessee.
15, Small immature specimen from Popes Chapel. The septal formula is K 5 A 4 C 3 A 4 K.
16, Mature specimen from Roper Knob. The septal formula is K 6 A 4 C 3 A 4 K.
17, Mature specimen from Popes Chapel (after BASSLER, 1937). The septal formula is K 6 A 5 C 5 A 5 K.
18, The type specimen (after EDWARDS & HAIME, 1851). The septal formula is K 7 A 6 C 6 A 7 K.
19, Large specimen from Popes Chapel (after BASSLER, 1937). The septal formula is K 5 A 4 C 5 A 5 K.
20, Large gerontic specimen from Popes Chapel. The septal formula is K 7 A 6 C 6 A 7 K.
21, Mature specimen from Popes Chapel. The septal formula is K 6 A 5 C 3 A 6 K.
FIGURE 2.—Septal diagrams of *Porpites*, *Combophyllum*, *Acanthocyclus*, *Dipterophyllum*, *Gymnophyllum*, and *Baryophyllum*. All figures are two times natural size. The septal diagrams are oriented with the cardinal septum at the bottom except where this septum is not identified. Protosepta are indicated by small arrows. (Continued on facing page.)
Commonly, the cardinal septum is shortened so as to produce a conspicuous cardinal fossula that includes also the cardinal pseudofossulae. A fossula, however, is not confined to the vicinity of the cardinal septum.

Although largely concealed by surficial bilateral symmetry in mature individuals of some old genetic lines, metasepa may decrease in radial length from the alar to the cardinal septum in the cardinal quadrants and from the counter to the alar septa in the counter quadrants. The abrupt change from the long alar septa and metasepa of the cardinal quadrants to the short septa most recently added to the counter quadrants is a feature of many porpitid genera. This character, plus the occurrence of the counter and cardinal septa along a more or less well-marked plane of bilateral symmetry, may permit positive identification of the protosepta. Determination of the fossula and pseudofossulae is dependent upon correct interpretation of the septal arrangement and the position of the protosepta.

In some species of Rugosa, the tetrameral pattern caused by the insertion of major septa at only four points is marked throughout growth. Thus, it is to be expected that major septa of many corals will be progressively shorter in each quadrant going towards the point of insertion of the septa. As a genetic line progresses, however, the arrangement of the septa commonly becomes more and more nearly radially symmetrical. A similar change can be observed by means of serial sections of a single corallite. A tetrameral pattern of the septa, therefore, does not necessarily indicate close phylogenetic relationship, and is not confined to the porpitid corals.

**PROTOSEPTA IN PORPITID CORALS**

*Porpites* SCHLOTHEIM, 1820

Illustrations of *Porpites porpita* (Linnaeus, 1767), which is the genotype, indicate a radially symmetrical arrangement of the septa without recognizable fossulae or pseudofossulae (Pl. 3, figs. 2a-c; Fig. 2, 1). *P. rotuloides* (Hall, 1852) from Middle Silurian rocks of New York is similar in septal arrangement (Fig. 2, 4). Identification of the protosepta in this genus, however, may be possible by examination of immature specimens.

*Acanthocyclus* DYBOWSKI, 1873

This genus, which is separated from *Porpites* largely by the elongate peduncle on the base, seems to resemble *Porpites* closely in septal arrangement, and protosepta are not identified from published illustrations (Fig. 2, 3). *Acanthocyclus* fetlcheri (Edwards & Haeime), from Middle Silurian rocks of England, is shown in Pl. 3, figs. 4a-c.

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**Figure 3.** (Continued from facing page.)

1-2.—*Hadrophyllum* pedunculatum Bassler, from the Fort Payne chert, Osagian Series, Mississippian, from 2 miles north of Nobob, Barren County, Kentucky (after Bassler, 1937).

1. Syntype in which the septal formula is K7A5C4A9K.

2. Syntype in which the septal formula is K6A4C4A5K.

3-4.—*Hadrophyllum* romingeri Bassler, from the New Providence shale, Osagian Series, Mississippian, at Button Mold Knob, Kentucky (after Bassler, 1937).

3. Syntype in which the septal formula is K5A3C3A6K.

4. Syntype in which the septal formula is K5A4C4A5K.

5.—*Hadrophyllum* pauciradiatum Edwards & Haeime, from the Devonian of Eifel, Germany (after Bassler, 1937). The septal formula seems to be K5A5C5A7K.

6.—*Hadrophyllum* bifidum Bassler, from the lower part of the Hamilton shale, Devonian, 3 miles west of Green Spring, Virginia (after Bassler, 1937). The septal formula shows as can be determined is K5A4C3A9K.

7.—*Hadrophyllum* tennesseense Miller & Gurley, from the Fort Payne chert, Osagian Series, Mississippian, near Florence, Alabama (after Bassler, 1937). The septal formula seems to be K10A4C5A9K.

8.—*Hadrophyllum* neumayeri Bassler, from the Kookuk formation, Osagian Series, Mississippian, near Nauvoo, Illinois (after Bassler, 1937). The septal formula in this holotype is K5A3C4A5K.

9.—*Hadrophyllum* delicatum Bassler, from the St. Louis limestone, Meramecian Series, Mississippian, at Roundhouse Hill, Elizabethown, Kentucky (after Bassler, 1937). The septal formula as undoubtedly determined in the holotype is K9A6C6A9K.

10.—*Hadrophyllum* ooele Bassler from the Fort Payne chert, Osagian Series, Mississippian, near Florence, Alabama (after Bassler, 1937). The septal formula is K7A4C6A7K.

11-14.—*Hadrophyllum* orbignyi Edwards & Haeime, genotype of *Hadrophyllum*, from the Middle Devonian.

11. Specimen from the Falls of the Ohio, Louisville, Kentucky (after Bassler, 1937); the septal formula is K5A5C6A8K.

12. Specimen from the same locality (after Bassler, 1937); the septal formula is K7A6C6A7K.

13. Specimen from the same locality (after Bassler, 1937); the septal formula is K6A6C6A5K.

14. Specimen from Kentucky (after Davis, 1885); the septal formula is K8A7C6A8K.

15-20.—*Cumminsia* aplata (Cummins), genotype of *Cumminsia*, from the Smithwick shale, Bendian (=Derryan or Lampasan) Series, Lower Pennsylvanian, in San Saba County, Texas.

15. Immature specimen in which the septal formula is K4A3C3A5K (after Moore & Jeffords, 1945).

16. Immature specimen in which the septal formula is K5A3C3A4K (after Moore & Jeffords, 1945).

17. Immature specimen in which the septal formula is K4A3C3A4K (after Moore & Jeffords, 1945).

18. Large specimen in which the septal formula is K7A5C5A7K (after Moore & Jeffords, 1945).

19. Mature specimen in which the septal formula is K7A4C3A7K.

20. Mature specimen in which the septal formula is K6A3C3A6K (after Cummins, 1891).
FIGURE 3.—Septal diagrams of Hadrophyllum and Cumminsia. All figures are two times natural size. The septal diagrams are oriented with the cardinal septum at the bottom except where this septum is not identified. Protosepta are indicated by small arrows. (Continued on facing page.)
Hadrophyllum Edwards & Hämë, 1850

The genotype, which is *Hadrophyllum orbignyi* Edwards & Hämë (1851, p. 387), has a long slender cardinal septum that lies in a prominent cardinal fossula (Fig. 3,11-14). The counter septum does not seem to be shortened, and the alar pseudofossulae are moderately well developed. Metasepta, however, are joined in characteristic pinnate groups about the counter septum or other metasepta. Alar pseudofossulae are represented by conspicuous open spaces located normal to the counter-cardinal plane. The large cardinal fossula permits ready identification of the cardinal septum, and commonly the alar pseudofossulae and adjacent short septa on the counter side of the alar identify the alar septa. Typically, the counter septum is joined by the axial ends of one or two pairs of metasepta. The corals from Mississippian rocks, *Hadrophyllum ovale* Bassler (1937), *H. pedunculatum* Bassler (1937), and *H. tennesseense* Miller & Gurney (1885, p. 87), differ importantly in having a markedly short counter septum, and long cardinal septum (Fig. 3,1,2,7,10). Moreover, the fossula occurs about the axial edge of the counter rather than the cardinal septum. Whereas *H. ovale* and *H. pedunculatum* seem definitely to be characterized by this septal pattern, available specimens of *H. tennesseense*, as well as the descriptions and illustrations given by Bassler, are not adequate in preservation to confirm the septal pattern.

The septal pattern in *Hadrophyllum romingeri* Bassler (1937, p. 198) from Mississippian rocks of Kentucky is not entirely clear but alar pseudofossulae seem to be well developed and both the counter and cardinal septa are relatively strong (Fig. 3,3,4). A somewhat similar condition exists in immature stages of specimens of *Cumminsia apilata* (Cummins, 1891, p. 552). *H. nauvoense* Bassler (1937, p. 199) has a septal arrangement essentially similar to that of *H. romingeri*, but the specimen illustrated by Bassler (1937, Pl. 31, fig. 43) seems to represent a more primitive or immature stage than is known in *H. romingeri*. *Hadrophyllum pauciradiatum* Edwards & Hämë (1851, p. 358), also, has a septal arrangement similar to that described for these species, but minor septa are developed more strongly (Fig. 3,5). Available specimens and published illustrations of *Hadrophyllum bifidum* Bassler (1937, p. 198) and *H. delicatum* Bassler (1937, p. 199) do not permit reliable judgment as to the septal pattern (Fig. 3,6,9). These corals, however, seem generally similar to *H. pauciradiatum* and *H. romingeri*.

These data indicate a considerable variation in the septal patterns of corals that have been referred to *Hadrophyllum*. The genotype, *H. orbignyi*, differs materially from other described species. *Hadrophyllum ovale*, *H. pedunculatum*, and *H. tennesseense* have a septal pattern like that in *Baryphyllum* whereas *H. nauvoense*, *H. pauciradiatum*, *H. romingeri*, and probably *H. bifidum* and *H. delicatum* also resemble the genotypes of *Cumminsia*, *Dipterophyllum*, and *Gymnophyllum* in septal arrangement.

Cumminsia Moore & Jeffords, 1945

The genotype of *Cumminsia*, which is *Hadrophyllum apilatum* Cummins (1891, p. 552), from Lower Pennsylvanian rocks of Texas, has easily identified protosepta (Fig. 3,15-20). In mature
Figure 4. Septal diagrams of Bojocycclus and Microcycclus and schematic representation of various types of septal patterns. All figures are two times natural size, except figures 13 to 17. The septal diagrams are oriented with the cardinal septum at the bottom except where this septum is not identified. Protosepta are indicated by small arrows. (Continued on facing page.)
stages the cardinal septum is very short and lies in a conspicuous fossula, the counter septum is relatively long, and the alar pseudofossulae are clearly marked by the strong angle between the long alar septa and the short septa in the adjacent part of the counter quadrants. *Hadrophyllum romingeri*, which was referred to *Cumminnia* by Moore & Jeffords (1945, p. 165), is described under *Hadrophyllum* above.

**Dipterophyllum Roemer, 1883**

The Lower Mississippian coral, *Zaphrentis glans White* (1862, p. 32), which is the genotype of *Dipterophyllum* (Pl. 3, figs. 10a,b), has a septal arrangement essentially like that of *Cumminnia aplata*. The cardinal septum is very short and the alar pseudofossulae are relatively large. The counter septum seems slightly shortened in some specimens so that the large fossula lies along the countercardinal plane (Fig. 2,5).

**Gymnophyllum Howell, 1945**

The single species, *Gymnophyllum wardii* Howell (1945, p. 2), that has been referred to this genus (Pl. 2, figs. 1-14; Pl. 3, fig. 7), has a septal pattern in early maturity very similar to that seen in *Cumminnia* (Fig. 2, 6-14). This basic pattern is seen also in *Dipterophyllum* and several species referred to *Hadrophyllum*. Mature specimens, however, do not permit identification of the protosepta except where the cardinal fossula persists as a slight depression on the smooth axial portion.

**Baryphyllum Edwards & Haime, 1850**

The genotype, which is *Baryphyllum verneuili-anum Edwards & Haime* (1850, p. lxvi) from Middle Mississippian rocks of Tennessee, has long thickened cardinal and alar septa and a short counter septum that lies in a small fossula (Pl. 3, fig. 8; Fig. 2,15-21). In some mature forms the reduction in alar pseudofossulae and the crooked character of the septa may make identification of the protosepta difficult. The septal pattern seen in *B. verneuili-anum* is developed also in *Hadrophyllum ovale, H. pedunculatum*, and *H. tennesseense*, as has been described above.

**Microcyclus Meeck & Worthen, 1868**

This genus includes very thin disc-like corals that commonly have septa restricted to the periphery only. *Microcyclus discus Meeck & Worthen* (1868, p. 420) has short septa that are arranged essentially radially about the periphery (Pl. 3, figs. 5a-c; Fig. 4,9-11). Possibly protosepta are identifiable on immature specimens but they are recognized only doubtfully on illustrated material and the few available specimens. *Microcyclus thedfordensis Basser* (1937, p. 194), from Devonian rocks of Ontario, has recognizable alar pseudofossulae and a long cardinal septum (Fig. 4,6,7) in young specimens, but a more regular arrangement of the septa in maturity (Fig. 4,8). Seemingly, the septal pattern resembles that of *Cumminnia* except that the cardinal septum is more prominent in youthful stages. *Microcyclus lyroratus Bassler* (1937, p. 195) resembles *M. thedfordensis* in the development of alar pseudofossulae but the cardinal septum in the former species is short and lies in a fossula (Fig. 4,12). Alar pseudofossulae are well developed in *M. intermedius* Bassler (1937, p. 195), also, and the counter septum seems slightly shortened (Fig. 4,2,3). *Microcyclus leonensis* (Verneuil & Haime, 1850, p. 161) seems to show inconspicuous alar pseudofossulae and a long cardinal septum, but the protosepta are not identified reliably (Fig. 4,5). *Microcyclus blairi Miller* (1899, p. 261) has a septal pattern like that of *Cumminnia aplata* in the youthful stage and a more radial arrangement of the septa in maturity (Fig. 4,4).

**Combophyllum Edwards & Haime, 1850**

The characters of this monotypic genus are only partially known. The protosepta of *Combophyl-lum osismorum Edwards & Haime* (1851, p. 389), as illustrated by these authors, are not identified reliably, although a shortened septum may represent the cardinal septum (Pl. 3, figs. 6a-c; Fig. 2,2). Alar pseudofossulae are not identified.

**Bojocycus Prantl, 1939**

This genus, which has *Bojocycus bohemicus* Prantl (1939, p. 3), from Middle Devonian rocks of Czechoslovakia, as genotype, is not known sufficiently to permit identification of the protosepta (Pl. 3, figs. 1a,b; Fig. 4,1).

**SUMMARY OF SEPTAL ARRANGEMENTS**

Septal arrangement in poritoid corals for which data are available seem to fall into several distinct patterns. The cumminsidoid pattern, which characterizes *Cumminnia aplata, Dipterophyllum glans, Gymnophyllum wardii, Hadrophyllum romingeri, H. nauvoense, H. pauciradiatum, Microcyclus lyroratus, M. thedfordensis, and M. blairi*, comprises a shortened cardinal septum, long counter septum, and well-developed alar pseudofossulae (Fig. 4,15). Typically, the metasepta shorten progressively toward the cardinal septum in the cardinal quadrants and toward the alar septa in the counter quadrants. An unshortened cardinal septum, which occurs in immature specimens of *Cumminnia* and *Gymnophyllum*, corresponds to early stages in other rugose corals. As shown recently for *Triplophyllites pal-matus Easton* (1944, Pl. 8, figs. 3a-4c) and *Stereostylus lenus Jeffords* (1947, Fig. 8), the cardinal and counter septa meet at the axis near the apex of the corallite (a very early stage) and the cardinal septum is conspicuously shortened only in later stages. This cumminsidoid pattern is essentially that present in immature stages of many other rugose corals, and therefore, it does not necessarily indicate close affinity. The baryphyllidoid pattern, as seen in
Baryphyllum tenerneense, Hadrophyllum ovale, H. pedunculatum, and H. tennesseense, is superficially like the arrangement of the septa in Cumminsia, but the counter, rather than the cardinal septum, is shortened (Fig. 4,17). The hadrophyllid pattern seems to be represented only by Hadrophyllum orbignyi. It consists of a long cardinal septum within a prominent cardinal fossula, well-developed alar pseudofossulae, counter septum, and a pinnate grouping of the metasepta (Fig. 4,14).

The microcylind and acanthocylid arrangements (Fig. 4,13,16) that are characteristic of Microcyclus and of Torpites and Acanthocyclus, respectively, are tentatively considered as separate types. These septal arrangements, however, may represent a specialized condition that is superimposed on one of the other patterns. As shown subsequently for Gymnophyllum and Baryphyllum, both of these genera have early gerontic stages in which the septa are essentially radial in arrangement (acanthocylid) and restricted to the periphery of the corallite (microcylind).

The porpilid corals have relatively simple structures and lack an axial column, tabulae, and dissepiments. The form of the corallite in nearly all specimens is somewhat similar; typically discoidal or short and broadly conical. Classification, therefore, must be based on the nature of the theca, peculiarities of corallite form, and arrangement and nature of the major septa, minor septa, and fossulae. Consistent combinations of several characters are deemed the most satisfactory criteria for generic separation of these fossils, recognizing that one or more of the characters may be homeomorphic. Inasmuch as the position of the major fossula and shortened protosepta seem less subject of duplication than the shape of the corallites, it seems desirable to point out possible generic reassignments for some species.

Among species placed in Hadrophyllum, none resembles the genotype in general septal arrangement. Hadrophyllum ovale, H. pedunculatum, and H. tennesseense have the baryphylloid arrangement of septa, although these are not well exposed over the base of the corallite, as in Baryphyllum tenerneense. It seems probable, therefore, that the three mentioned species that have been assigned to Hadrophyllum should be referred to Baryphyllum in spite of the somewhat different growth form. It is noted, also, that the baryphylloid arrangement of the septa is observed only in these three species and in Baryphyllum tenerneense; all of which are known only from the Osagian Series of the Mississippian.

Hadrophyllum romingeri has a septal pattern very similar, if not identical, to that of Cumminsia, so that on the basis of growth form and septal character it is referred to Cumminsia. Hadrophyllum naucoraeense, H. pauciradiatum, H. bifidum, and H. delicatum do not seem closely related to the genotype of Hadrophyllum and are tentatively referred to Cumminsia on the basis of general similarity in septal patterns. There is possibility, however, that they may be more closely related to some species now placed in Microcyclus.

**ONTOGENETIC DEVELOPMENT**

Inasmuch as ontogenetic development has major importance in the separation of Paleozoic rugose corals and in recognition of phylogenetic relationships, serial sections have become requisite in the study of most Rugosa. Among the porpilid corals where sectioning commonly does not yield satisfactory information, similar valuable data may be obtained by study of a series of individuals that represent different degrees of maturity.

Examination of relatively large numbers of specimens of some species of porpilid corals for preparation of the previous part of this paper makes possible mention of some features of ontogenetic development in the Porpilidae. Gymnophyllum wardi is represented by specimens showing gradation from small immature corallites in which the septa are relatively long to large gerontic forms that lack a conspicuous fossula and septa on the central axial region (Pl. 2). The cardinal septum is relatively long and the cardinal fossula is inconspicuous in the earliest stages, but this septum progressively shortens and the fossula increases in size until maturity. Gerontic specimens differ so markedly from the others that estimation of the correct relationships would be doubtful without such a series of specimens.

The development of Baryphyllum tenerneense is not known adequately for the immature stages, but seems to change about as in Gymnophyllum (Pl. 1). Septa in mature corallites are somewhat crooked and less distinct on the axial portions. The septa are restricted to the periphery in the gerontic stage. The material studied, however, indicates that the typical button-like or discoidal form persists through all growth stages for this species.

Growth changes in Cumminsia aplata have been described in an earlier paper (Moore & Jeffords, 1945, p. 166). The septa in the calyx change progressively, as in Gymnophyllum, by a shortening of the cardinal septum and a slight reduction in the septa on the central portion of the corallite (Moore & Jeffords, 1945, Pl. 14, figs. 16-18, 22b, 23). Gerontic individuals, which differ greatly in appearance from mature specimens, result from deposition of successive layers of stereoplasm over the calyx so as to produce an elongate cylindrical or barrel-shaped corallite. This growth form, however, may possibly be due to attempts to raise the polyp rapidly above the mud of the surrounding sea bottom.

Some specimens of Microcyclus, as M. blairi Miller (Easton, 1944, Pl. 16, figs. 9, 10) and M. thedfordensis Bassler (1937, Pl. 31, figs. 5, 8, 9), seem to change during growth by a progressive
shortening of the septa so that the septa of mature corallites are indicated only on the periphery. Immature specimens of most species of this genus are inadequately known, however.

This examination of the ontogenetic characters of a few porpitid corals indicates that, where available, large suites of specimens should be described and illustrated in order to permit adequate recognition of a species. Moreover, such data probably will serve to unravel some of the complexities of genetic affinity that now are little understood for this group.

**DESCRIPTIONS OF GENERA AND SPECIES**

**Family Porpitidae** Moore & Jeffords, 1945

**Genus Baryphyllum** Edwards & Haime, 1850

This genus consists of small disklike solitary corals having septa exposed over the upper and lower surfaces. The septa of the flattened base are indicated by raised ridges except in the small central area, which contains a slightly depressed peduncle of attachment. The upper surface has strong major septa over the entire calyx. The long stout cardinal septum and the alar septa reach to the axis, but the counter septum is weakly developed. Minor septa seem to be lacking. Metasepta of the cardinal quadrants are directed conspicuously towards the cardinal septum and those of the counter quadrants toward the alar septa. Tabulæ, dissepiments, and axial structures are absent. The counter septum seems to lie in a weak fossula, and prominent pseudofossulae are developed on the counter sides of the alar septa and either side of the cardinal septum.

*Genotype.*—Baryphyllum venuerianum Edwards & Haime (1850, p. lxvi). Osagian Series, Mississippian (Lower Carboniferous), Tennessee.

*Discussion.*—The septal arrangement of *Baryphyllum* has been described as essentially the same as in *Hadrophyllum* Edwards & Haime. It differs, however, in the flattened under side of the coralite, which has septa exposed over nearly all its surface. *Hadrophyllum orbignyi* Edwards & Haime (1850, p. lxvi), the genotype of *Hadrophyllum*, has a large closed cardinal fossula and small alar pseudofossulae. The alar septa and the counter septum, which are not thickened, reach the axis. *Baryphyllum*, on the other hand, shows the presence of a long, thick cardinal septum, thickened alar septa, and a short counter septum, that lies in a small fossula. The strong cardinal septum and weakly developed counter septum are especially diagnostic features of *Baryphyllum*.

*Baryphyllum* resembles *Combophyllum* Edwards & Haime (1850, p. lxvii), from the Lower Devonian of France, in the persistence of the septa on to the lower surface, but the former genus lacks carinae on the septa of the base and the septa of the upper surface are notably shorter. *Microcylus* Meek & Worthen (1869, p. 430) differs from *Baryphyllum* in that the theca covers the base, and the corallites have a characteristic flat discoidal shape. Comparison with *Gymnophyllum* Howell (1945, p. 1) is given under discussion of that genus.

The Mississippian corals described as *Hadrophyllum ovale* Bassler, *H. pedunculatum* Bassler, and *H. tennesseense* Miller & Gurley are characterized by a baryphylloid arrangement of the major septa, and so seem to belong with *Baryphyllum* in spite of the probable difference in the form of the corallites.

*Occurrence.*—*Osagian* Series, Mississippian (Lower Carboniferous), Tennessee, Alabama, and Kentucky.

**Explanation of Plate 1**

All figures are three times natural size.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
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<tbody>
<tr>
<td>1-9. <em>Baryphyllum venuerianum</em> Edwards &amp; Haime, from the New Providence formation, Osagian Series, Mississippian, Tennessee</td>
<td></td>
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<tr>
<td>1. Large mature specimen from Popes Chapel that shows the septa indistinctly near the axis but projecting strongly from the periphery. The cardinal septum is directed upward (after Bassler, 1937)</td>
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<tr>
<td>2. Small immature specimen from Popes Chapel showing the crooked septa reaching mostly to the axis. The cardinal septum is directed downward</td>
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<tr>
<td>3. Large specimen from Popes Chapel that shows the septa clearly. The cardinal septum is directed upward (after Bassler, 1937)</td>
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<tr>
<td>4. Basal view of well preserved specimen from Popes Chapel (after Bassler, 1937)</td>
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<tr>
<td>5. Mature specimen from Roper Knob showing the well developed cardinal septum (directed downward) and the tetrameral pattern of the septa</td>
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<tr>
<td>6. Mature specimen from Popes Chapel in which the cardinal septum is directed downward</td>
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<tr>
<td>7. Lateral view of thick specimen from Popes Chapel (after Bassler, 1937)</td>
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<tr>
<td>8. Large gerontic specimen from Popes Chapel. The prozoneata are indistinct in the axial region. The cardinal septum is directed upward</td>
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<tr>
<td>9. The type specimen (after Edwards &amp; Haime, 1851) showing the counter fossula and the strong cardinal septum which is directed downward</td>
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Jeffords — Porpitid Corals
JEFFORDS — Porpitid Corals
**Baryphyllum verneuiianum Edwards & Haime**

Plate 1, figures 1-9; Plate 3, figure 8; Figure 2,15-21

*Baryphyllum verneuiianum* Edwards & Haime, 1851, Arch. Mus. Hist. Nat., vol. 5, p. 352, pl. 6, figs. 7,1a—


Disc-shaped corallites having septa indicated on both upper and lower surfaces characterize this species. The cardinal septum and alar septa are long, whereas the counter septum is short and lies in a small fossula. Other septa are directed toward the cardinal septum in the cardinal quadrants and toward the alar septa in the counter quadrants. Minor septa are lacking. In mature forms the septa become crooked or irregularly twisted. A few gerontic individuals show septa that are prominent at the periphery but so greatly thickened in the broad central area as to be only weakly marked there. The septal formula of the type specimen illustrated by Edwards & Haime (1851, pl. 6, fig. 7a) is K7 A6 C6 A7 K. The specimens that were examined and those illustrated by Bassler (1937) also show a smaller number of septa in the cardinal quadrants than in the counter quadrants. The corallites having well-developed septa average 18 mm in diameter and 8 mm in height. The available gerontic individuals are larger but not as high; the largest being 25.7 mm in diameter.

Discussion.—The position of the protosepta in most specimens belonging to this species can be determined from the arrangement of the metasepta. In the cardinal quadrants they are shortest next to the cardinal septum and become progressively longer toward the alar septa. These metasepta are directed very strongly toward the cardinal septum. The septa of the counter quadrants are directed similarly toward the alar septa and are shortest next to the alar septa.

**Occurrence.**—The specimens examined in preparation of this description are from the New Providence formation, Osagian Series, Mississippian (Lower Carboniferous). They were collected in Williamson County, Franklin quadrangle, Tennessee, at Popes Chapel by E. R. Pohl and at Roper Knob by L. C. Glenn. The specimens described by Bassler (1937) were from these localities also. Edwards & Haime report this species from the Devonian of Perry County, Tennessee, but no corals of this age or locality are known that resemble the illustration of the species. Inasmuch as the species does occur at several places in Williamson County, Tennessee, however, Bassler (1937, p. 201) considers this the correct type locality.

**Material studied.**—The specimens available for study included five well-preserved corallites from Popes Chapel and 20 slightly weathered specimens from Roper Knob. All the material is silicified.

**Genus Gymnophyllum Howell, 1945**

Corals assigned to this genus are solitary individuals of low disclike shape. The septa are exposed over the upper and lower surfaces and project strongly from the circular periphery. On the base they reach nearly to the central depressed point of attachment. Both surfaces of the corals and the septa are smooth and lack striae or other markings. The major septa are long and somewhat crooked in the very immature specimens. They withdraw from...

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**EXPLANATION OF PLATE 2**

All figures are three times natural size. The dorsal views of the corallites are oriented with the cardinal septum directed downward.

**Figure 1-14.** *Gymnophyllum wardi* Howell, from the Westwok formation, Desmoinesian Series, Pennsylvanian, on the shore of Lake Okmulgee, about 6 miles west of Okmulgee, Oklahoma. 14

1. Small immature specimen (Univ. Kansas No. 7998-21e) having unequal development of the septa
2. Small immature specimen (Univ. Kansas No. 7998-21k)
3a, b. Small specimen (Univ. Kansas No. 7998-21m) showing rejuvenation. a. View of the calyx. b. Side view; the calyx is to the left
4. Immature specimen (Univ. Kansas No. 7998-21b)
5a-c. Well preserved specimen (Univ. Kansas No. 7998-21a). a. View of the calyx showing the protosepta, cardinal fossula, and alar pseudofossulae. b. View of the base showing the septa and the small peduncle. c. Side view; the calyx is to the left
6. Incomplete specimen (Univ. Kansas No. 7998-21h)

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**Figure 7998-21l) showing the cardinal fossulae and alar pseudofossulae**

7. Small specimen (Univ. Kansas No. 7998-21j) lacking septa in the central portion
8. Similar specimen (Univ. Kansas No. 7998-21d) showing much shortened septa that protrude from the periphery
9. Specimen of average size having shortened septa (Univ. Kansas No. 7998-21g)
10. Specimen (Univ. Kansas No. 7998-21n) showing the septa only near the periphery and poorly developed cardinal fossula
11a, b. Large mature specimen (Univ. Kansas No. 7998-21l). a. View of the calyx. b. View of the base
12. Specimen (Univ. Kansas No. 7998-21c) showing the septa only near the periphery
13. A typical specimen (Univ. Kansas No. 7998-21f) showing protruding septa
14. Large gerontic specimen (Univ. Kansas No. 7998-21h) having a smooth central region
the axis progressively throughout growth until in
gerontic specimens the septa in the calyx occur only
at the border, the axial area being broad and
smooth. The nonseptate axial portion is gently
domed in mature forms but distinctly flattened in
gerontic corallites. The cardinal septum is short in
both young and mature specimens, whereas the
counter septum is long and thickened. The counter
quadrants are strongly accelerated. A conspicuous
counter septum is long and thickened. The counter
genera, such as Lophophyllidium Grabau (1928), Stereostylus Jeffords
(1947), Lophampelus Moore & Jeffords (1941),
and Lophotichium Moore & Jeffords (1945), for
example, have been shown to have nearly identical
characters. Despite the seeming similarity of these
corals, the position of the fossula and the differences
in the counter and cardinal septa are deemed ade-
quate to justify their separation.

Combophyllum also has septa exposed on the
base and seems to have protosepta similar to those
of Gymnophyllum. The carinae on the septa of the
base, long major septa, and distinct independent
minor septa are characters that serve to distinguish
Combophyllum. Other genera of porpitis do not
have the septa exposed on the base.

Occurrence.—Desmoinesian Series, Pennsyl-
vanian (Upper Carboniferous), Oklahoma.

Gymnophyllum wardi Howell.

Plate 2, figures 1-14; Plate 3, figure 7; Figure 2, 6-14
Gymnophyllum wardi Howell, 1945, Wagner Free Inst.

Flat disclike solitary corallites comprise this
species. The base has septa exposed over its sur-
face except at the central depressed peduncle. The
upper surface shows short septa and a large smooth
axial area. In young forms, the septa are long
and slightly crooked. The short thick cardinal septum
lies in a deep fossula occupying the axial portion of
the corallite. The counter septum and alar septa
are strong and slightly longer than the metasepta.
In somewhat older individuals, the septa are short
but project from the edge to give an appearance
resembling a toothed wheel. The axial area is

EXPLANATION OF PLATE 3

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
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</thead>
<tbody>
<tr>
<td>1a,b.—Bojoecyclus bohemicus Prantl (1939), from Middle Devonian beds at Holyně, Czechoslovakia (after Prantl), × 6</td>
<td>10</td>
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<tr>
<td>2a-c.—Porpitida porpita (Linnaeus), from the Lower Gotlandian, Silurian, Island of Gotland (after Bassler), × 1.5</td>
<td>6</td>
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<tr>
<td>3a,b.—Bathyphyllum orbignyi Edwards &amp; Haime, from Middle Devonian beds at Falls of the Ohio, near Louisville, Kentucky (after Bassler), × 2</td>
<td>8</td>
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<tr>
<td>4a-c.—Acanthocyclus fletcheri (Edwards &amp; Haime), Wenlockian, Silurian, Dudley, England (after Bassler), × 1.5</td>
<td>6</td>
</tr>
<tr>
<td>5a-c.—Microcystus dioicus Meek &amp; Worthen, Devonian, Grand Tower, Illinois (after Bassler), × 2</td>
<td>10</td>
</tr>
<tr>
<td>6a-c.—Combophyllum osismorum Edwards &amp; Haime, Lower Devonian, Brest, France (after Edwards &amp; Haime), × 3</td>
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<th>Page</th>
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</thead>
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<tr>
<td>7.—Gymnophyllum wardi Howell, Wewoka formation, Desmoinesian Series, Pennsylvanian (after Howell), × 2</td>
<td>14</td>
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<tr>
<td>8.—Baryphyllum verneuilianum Edwards &amp; Haime, from the New Providence formation, Osagian Series, Mississippian, Tennessee (after Bassler), × 1.5</td>
<td>13</td>
</tr>
<tr>
<td>9a,b.—Xenocyathellus thedfordensis (Stewart), from the Arkona beds, Devonian, Arkona, Ontario (after Bassler), × 2</td>
<td>15</td>
</tr>
<tr>
<td>10a,b.—Dipterophyllum glans (White), from the Burlington limestone, Lower Mississippian, at Burlington, Iowa (after Bassler), × 2</td>
<td>10</td>
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<tr>
<td>11a-c.—Cumminsia apicala (Cummins), from the Smithwick shale, Bendian Series, Lower Pennsylvanian, at San Saba County, Texas (after Moore &amp; Jeffords), × 2</td>
<td>8</td>
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large, and is indented by the cardinal fossula. Other septa are nearly equal in size and length, and pseudofossulae are not recognized. In yet more advanced forms, short minor septa are introduced and become attached to the cardinal side of the major septa. Mature forms have a wide smooth axial area showing little evidence of a fossula. The septa project from the periphery of this central area on the top only, but they extend almost to the small peduncle on the base. Very old geronic forms are flat and have a theca between the septa of the base. Septa are short and somewhat deformed, and a fossula is not indicated. The septal formula of an average slightly immature specimen is K5 A3 C3 A5 K.

Several specimens in the collection available for study show one corallite directly over a slightly smaller one, to which it is joined (Pl. 2, fig. 3). The structural connection of the two indicates rejuvenescence. Other features of these peculiar corallites are similar to the typical discoidal corallites.

Discussion.—The abundant well-preserved material available for study shows specimens in nearly all stages of growth from small immature forms to large flat geronic specimens. The species resembles Baryphyllum verneuilianum in the presence of septa on both the upper and lower surfaces, the small area of attachment, occurrence of crooked septa during growth, projection of the septa at the periphery, and similarity of geronic individuals. It differs in the broad open axial area of mature forms, the presence of numerous minor septa, and especially in the well-developed counter septum and short cardinal septum. The smooth central area suggests comparison with Microcyclycus discus Meek & Worthen, but that species has a base covered by concentrically wrinkled theca. Gymnophyllum wardi is similar to Combophyllum osimorum Edwards & Haime in having septa that show on the base and in the presence of a cardinal fossula. G. wardi lacks the carinae on the septa of the base, however, and has a definite peduncle, shorter septa, minor septa that are closely joined to the major, and a definite radiation of the septa from the cardinal septum or the alar septa in the cardinal and counter quadrants, respectively. This species can be distinguished from Cumminsia aplata (Cummins, 1891), another Lower Pennsylvanian species from the Smithwick shale of Texas, by the persistence of the septa on the base.

Occurrence.—Near base of upper division of the Wewoka formation, Desmoinesian Series, Pennsylvanian (Upper Carboniferous). The specimens here described were collected on the north shore of the lake at Okmulgee, Oklahoma, by C. L. Foster (Univ. Kans. loc. 7998), and by N. D. Newell just west of spillway along highway east of Lake Okmulgee, about 6 miles west of Okmulgee (Univ. Kans. loc. 3228).

Material studied.—About 60 specimens of this species collected by Foster and 3 specimens from the collection of the University of Kansas were examined. These specimens may be from the type locality "a few miles west of Okmulgee, Oklahoma" (Howell, 1945, p. 2), although doubtless these fossils occur at several exposures in this vicinity.

DIFFERENTIATION OF PORPITID GENERA

A key for identification of described genera of porpitid corals, prepared in the course of this study, may be useful to other students of this group of fossils. Characters used in this key are those of mature (not geronic) individuals of the genotype species. Accordingly, immature or geronic specimens may have characters differing importantly from those given for the genera.

Key for Identification of Porpitid Genera

1. Septa exposed on base ........................................... 3
2. Septa not exposed on base ........................................... 7
3. Carinae present ..................................................... Combophyllum
4. Carinae lacking ........................................... 5
5. Cardinal fossula present, counter septum strong .................. Gymnonphyllum
6. Counter fossula present, cardinal septum strong .................. Baryphyllum

7. Carinae present ..................................................... 9
8. Carinae lacking ..................................................... 11
9. Corallite flat, disclike ........................................... Porphites (syn. Palaeocyclycus)
10. Elongate peduncle ........................................... Acanthocyclus
11. Corallite slipper-shaped ........................................... Xenocyclathus
12. Corallite having elongate peduncle, approaching conical form ........................................... 14
13. Corallite disclike ..................................................... 16
14. Peripheral border of calyx septate ........................................... Diptherophyllum
15. Peripheral border of calyx free of septa ........................................... Bofocyclus
16. Septa low, reaching axis, pinnately joined ........................................... Hadrophyllum
17. Septa high, long unjoined; strong alar pseudofossulæ ........................................... Cumminsia
18. Septa indicated near periphery only, not reaching axis in maturity ........................................... Microcyclycus
REFERENCES


Phantl, Ferdinand (1939) Bojocyclus nov. gen., a new rugose coral from the Hublopecy = limestone (γ': Phiroda Brno, vol. 32, pt. 3, p. 104-107, text figs. 1a-1b.


