UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

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SEPTAL ARRANGEMENT AND ONTOGENY IN SOME PORPITID CORALS

By RUSSELL M. JEFFORDS

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ABSTRACT

Porpitid or palaecyclid 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 cumminsoid 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 baryphylloid septal arrangement, has a strong cardinal septum and a distinct counter fossula. The hadrophyllid 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 oseae, 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 hadrophyllid 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 (1837) 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 Palaeocyclidae (Dybowski, 1873). Inasmuch as Palaeocyclus Edwards & Haimé (1849, p. 71), the family type genus, has been shown by Lang, Smith, & Thomas (1940, p. 94) to be an objective junior synonym of Porpites Schlotheim (1820, p. 349), Moore & Jeffords (1945, p. 164) proposed the new name Porpitidae. This family, as now understood, includes peculiar and probably specialized rugose corals that occur only sparingly in Paleozoic strata. Inasmuch as this family seems to be an assemblage of homeomorphs derived from several different 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 as 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 Barayphyllum verneuilianum Edwards & Haimé (1850, p. lvii) and Gymnophyllum wardi 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 & Haimé (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 bairi Miller (1892, p. 7), and Moore & Jeffords in 1945 redescribed Hadrophyl-lum apulatum 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 Baryphyllum verneuilianum, and numerous specimens of Dipterophyllum glans (White, 1862), Hadrophyl-lum orbignyi Edwards & Haimé (1850), and Cumminsia apulata. A few representatives of most other species assigned to this family were available also 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 Baryphyllum verneuilianum are from specimens in the collections of the Tennessee Geological Survey.

ACKNOWLEDGMENTS

I am indebted to R. C. Moore of the University of Kansas for his helpful suggestions made during the progress of this investigation and for use of the card file on corals prepared with financial support of the State Geological Survey of Kansas and the Graduate Research Committee of the University of Kansas. Acknowledgment is made also to C. W. Wilson, Jr., formerly at Vanderbilt University, for the loan of specimens of Baryphyllum from the collection of the Tennessee Geological Survey, and to C. L. Foster for making the specimens of Gymnophyllum available for study.
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 tetrameral 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 protoseptum.


**Figure 2.** (Continued from facing page.)


2. (Continued from facing page.)

3. Small immature specimen (Univ. Kansas No. 7998-21d); the septal formula is K 5 A 3 C 3- A 5 K.

4. Larger immature specimen (Univ. Kansas No. 7998-21a); the septal formula is K 5 A 3 C 3 A 5 K.

5. Small immature specimen from Roper Knob. The septal formula is K 5 A 4 C 3 A 4 K.

6. Large gerontic specimen (Univ. Kansas No. 7998-21e); the septal formula is K 4 A 3 C 3 A 4 K.

7. Small immature specimen (Univ. Kansas No. 7998-21b); the septal formula is K 5 A 3 C 3 A 5 K.

8. Specimen of average size (Univ. Kansas No. 7998-21f); the septal formula is K 4 A 3 C 3 A 5 K.

9. Small mature specimen (Univ. Kansas No. 7998-21i); the septal formula is K 4 A 3 C 3 A 4 K.

10. Large gerontic specimen (Univ. Kansas No. 7998-21h); the septal formula is K 5 A 4 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. Immature specimen from Plants 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 6 K.

17. Mature specimen from Plants Chapel (after Bassler, 1937). The septal formula is K 6 A 5 C 5 A 5 K.

18. The type specimen (after Edwards & Haimé, 1851). The septal formula is K 7 A 6 C 6 A 7 K.

19. Large specimen from Roper Knob (after Bassler, 1937). The septal formula is K 5 A 4 C 5 A 5 K.

20. Large gerontic specimen from Plants Chapel. The septal formula is K 7 A 6 C 6 A 7 K.

21. Mature specimen from Plants Chapel. The septal formula is K 6 A 3 C 3 A 6 K.
FIGURE 2.—Septal diagrams of *Porpites*, *Combophyllum*, *Acanthocyclus*, *Dipterophyllum*, *Gymnophyllum*, and *Baryphyllum*. 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 superficial bilateral symmetry in mature individuals of some old genetic lines, metasepta 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 metasepta 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 tetramerall 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 tetramerall 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 Dybowskii, 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 fitcheri* (Edwards & Haime), from Middle Silurian rocks of England, is shown in Pl. 3, figs. 4a-c.
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 & Haimé, 1850

The genotype, which is Hadrophyllum orbignyi Edwards & Haimé (1851, p. 357), 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 & Gurley (1935, 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 Cumminsi a aplata (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. 45) seems to represent a more primitive or immature stage than is known in H. romingeri. Hadrophyllum pauciradiatum Edwards & Haimé (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 Bayrophyllum whereas H. nauvoense, H. pauciradiatum, H. romingeri, and probably H. bifidum and H. delicatum also, resemble the genotypes of Cumminsi a, Dipterophyllum, and Gymnophyllum in septal arrangement.

Cumminsi a Moore & Jeffords, 1945

The genotype of Cumminsi a, which is Hadrophyllum aplata 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 *Bojocyclus* and *Microcyclus* 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 pseudofoossilae 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 *Cumminisia* 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 *Cumminisia aplata*. The cardinal septum is very short and the alar pseudofoossilae are relatively large. The counter septum seems slightly shortened in some specimens so that the large fossula lies along the counter-cardinal plane (Fig. 2,5).

**Gymnophyllum Howell, 1945**

The single species, *Gymnophyllum wardi* 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 *Cumminisia* (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 & Haimé, 1850**

The genotype, which is *Baryphyllum verneuilii-anum Edwards & Haimé* (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 pseudofoossilae and the crooked character of the septa may make identification of the protosepta difficult. The septal pattern seen in *B. verneuilii-anum* is developed also in *Hadrophyllum ovale, H. pedunculatum*, and *H. tennesseenae*, as has been described above.

**Microcyclus Meek & Worthen, 1868**

This genus includes very thin disclike corals that commonly have septa restricted to the periphery only. *Microcyclus discus Meek & 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 Bassler* (1937, p. 194), from Devonian rocks of Ontario, has recognizable alar pseudofoossilae 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 *Cumminisia* except that the cardinal septum is more prominent in youthful stages. *Microcyclus lysulatus Bassler* (1937, p. 195) resembles *M. thedfordensis* in the development of alar pseudofoossilae but the cardinal septum in the former species is short and lies in a fossula (Fig. 4,12).

Alar pseudofoossilae 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 & Haimé, 1850, p. 161) seems to show inconspicuous alar pseudofoossilae and a long cardinal septum, but the protosepta are not identified reliably (Fig. 4,5). *Microcyclus blairi* Miller (1892, p. 261) has a septal pattern like that of *Cumminisia aplata* in the youthful stage and a more radial arrangement of the septa in maturity (Fig. 4,4).

**Combophyllum Edwards & Haimé, 1850**

The characters of this monotypic genus are only partially known. The protosepta of *Combophyllum osismorum Edwards & Haimé* (1851, p. 359), 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 pseudofoossilae are not identified.

**Bojocyclus Prantl, 1939**

This genus, which has *Bojocyclus 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 porpitid corals for which data are available seem to fall into several distinct patterns. The cumminsioid pattern, which characterizes *Cumminisia aplata, Dipterophyllum glans, Gymnophyllum wardi, Hadrophyllum romingeri, H. nassoense, H. pauciradiatum, Microcyclus lysulatus, M. thedfordensis, and M. blairi*, comprises a shortened cardinal septum, long counter septum, and well-developed alar pseudofoossilae (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 *Cumminisia* and *Gymnophyllum*, corresponds to early stages in other rugose corals. As shown recently for *Triplophysa palmaris* Easton (1944, Pl. 8, figs. 3a-4c) and *Stereostylus lenis* 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 cumminsioid pattern is essentially that present in immature stages of many other rugose corals, and therefore, it does not necessarily indicate close affinity. The baryphyllloid pattern, as seen in
Baryphyllum verneuilianum, 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 hadrophylloid 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 microcycloid and acanthocycloid patterns (Fig. 4,13,16) that are characteristic of Microcyclus and of Porpites and Acanthocyclos, 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 (acanthocycloid) and restricted to the periphery of the corallite (microcycloid).

The porpitid 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 verneuilianum. 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 verneuilianum; 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 nauvooense, 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.

ONTGENETIC 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 porpitid 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 porpitid corals for preparation of the previous part of this paper makes possible mention of some features of ontogenetic development in the Porpitidae. 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 verneuilianum 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 aplatata 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 disclike 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. Tabulae, dissepi- ments, 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 verneuilianum* 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* (1850, p. lxvii), 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 to 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. *Microcyclus Meek & Worthen* (1869, p. 420) 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. tenesseeense* Miller & Gurley are characterized by a baryphyllid 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>Description</th>
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| 1-9. *Baryphyllum verneuilianum* Edwards & Haime, from the New Providence formation, Osagian Series, Mississippian, Tennessee | 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)  
2. Small immature specimen from Popes Chapel showing the crooked septa reaching mostly to the axis. The cardinal septum is directed downward  
3. Large specimen from Popes Chapel that shows the septa clearly. The cardinal septum is directed upward (after Bassler, 1937)  
4. Basal view of well preserved specimen from Popes Chapel (after Bassler, 1937)  
5. Mature specimen from Roper Knob showing the well developed cardinal septum (directed downward) and the tetrameral pattern of the septa  
6. Mature specimen from Popes Chapel in which the cardinal septum is directed downward  
7. Lateral view of thick specimen from Popes Chapel (after Bassler, 1937)  
8. Large gerontic specimen from Popes Chapel. The protosepta are indistinct in the axial region. The cardinal septum is directed upward  
9. The type specimen (after Edwards & Haime, 1851) showing the counter fossula and the strong cardinal septum which is directed downward |
EFFORDS — Porpitid Corals
JEFFORDS — Porpitid Corals
Baryphyllum verneuilianum Edwards & Haime

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


---Roemer, 1882, Lethaea geognostica, pt. 1, Leth. Pal., p. 373, fig. 81. ---Basilewsky, 1932, Tennessee Geol. Survey, Bull. 38, pl. 28, fig. 16.

Discussion.-The 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 geronic 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 Basilewsky (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 geronic individuals are larger but not as high; the largest being 25.7 mm in diameter.

Discussion.—The position of the proteosepta 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 Basilewsky (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, Basilewsky (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 discike 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

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 Wewoka 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 proteosepta, 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) 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
generic 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
generic 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
domed in mature forms but distinctly flattened in
at the border, the axial area being broad and
were not observed.

Strongly differentiated. Minor septa are rudimen-
tum is short and the cardinal septum is strongly
corallites.

FIGURE 2a-c.—Porpites porpita
3a,b.—Hadrophyllum orbi
gnyi
5a-c.—Microcyclus discus
Meek & Worthen, Devonian, Grand Tower, Illinois (after Bassler), × 2
6a-c.—Combophyllum osismorum Edwards & Haime, Lower Devonian, Brest, France (after Edwards & Haime), × 3

Gymnophyllum wardi Howell
Plate 2, figures 1-14; Plate 3, figure 7; Figure 2, 6-14
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

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<tr>
<td>1a,b.—Bojocyclus bohemicus Prantl (1939), from Middle Devonian beds at Holyňe, Czechoslovakia (after Prantl), × 6</td>
<td>10</td>
<td>7.—Gymnophyllum wardi Howell, Wewoka formation, Desmoinesian Series, Pennsylvanian (after Howell), × 2</td>
<td>14</td>
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<tr>
<td>2a-c.—Porpites porpita (Linnaeus), from the Lower Gotlandian, Silurian, Island of Gotland (after Bassler), × 1.5</td>
<td>6</td>
<td>8.—Baryphyllum venuelliium Edwards &amp; Haime, from the New Providence formation, Osagian Series, Mississippian, Tennessee (after Bassler), × 1.5</td>
<td>13</td>
</tr>
<tr>
<td>3a,b.—Hadrophyllum orbignyi Edward &amp; Haime, from Middle Devonian beds at Falls of the Ohio, near Louisville, Kentucky (after Bassler), × 2</td>
<td>8</td>
<td>9a,b.—Xenocyathellus thedfordensis (Stewart), from the Arkona beds, Devonian, Arkona, Ontario (after Bassler), × 2</td>
<td>15</td>
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<tr>
<td>4a-c.—Acanthocyclus fletcheri (Edwards &amp; Haime), Wenvlockian, Silurian, Dudley, England (after Bassler), × 1.5</td>
<td>6</td>
<td>10a,b.—Dipterophyllum glans (White), from the Burlington limestone, Lower Mississippian, at Burlington, Iowa (after Bassler), × 2</td>
<td>10</td>
</tr>
<tr>
<td>5a-c.—Microcyclus discus Meek &amp; Worthen, Devonian, Grand Tower, Illinois (after Bassler), × 2</td>
<td>10</td>
<td>11a-c.—Cumminsta oplata (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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JEFFORDS — Porpitid Corals
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 gerontic 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 $K_5 A_3 C_3 A_5 K$.

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 gerontic 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 gerontic 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 *Microcyclus discus* Meek & Worthen, but that species has a base covered by concentrically wrinkled theca. *Gymnothyllium wardi* is similar to *Combophyllum osismorum* 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. Kansas loc. 7998), and by N. D. Newell just west of spillway along highway east of Lake Okmulgee, about 6 miles west of Okmulgee (Univ. Kansas 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 gerontic) individuals of the genotype species. Accordingly, immature or gerontic specimens may have characters differing importantly from those given for the genera.

**Key for Identification of Porpitud 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 ............. *Gymnothyllium*
6. Counter fossula present, cardinal septum strong ............ *Baryphyllum*
7. Carinae present ........................................ 9
8. Carinae lacking ........................................ 11
9. Corallite flat, disclike .................................. *Porites* (syn. *Paleocyclops*)
10. Elongate peduncle ....................................... *Acanthocyclus*
11. Corallite slipper-shaped ................................ *Xenocyathellus*
12. Corallite having elongate peduncle; approaching conical form ..................................... 14
13. Corallite disclike ........................................ 16
14. Peripheral border of calyx septate ........................ *Dipterophyllum*
15. Peripheral border of calyx free of septa .................. *Boycyclops*
16. Septa low, reaching axis, pinnately joined ................ *Hadrophyllum*
17. Septa high, long unj oined; strong alar pseudo-fossulae ..... *Cumminsia*
18. Septa indicated near periphery only, not reaching axis in maturity .......................... *Microcyclus*
REFERENCES


