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MISSISSIPPIAN CUNEATE CORALS

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ABSTRACT—Cuneate corals are compressed parallel with the cardinal-counter plane. Species are known among three families and six genera or subgenera. Arguments are advanced that larvae oriented themselves with regard to current direction and that later curvature of the corallite depended upon current action. Cuneate corals were streamlined and therefore were successfully adapted for life in marine currents. *Triplophyllites* is divided into subgenera on the basis of direction of curvature. Species-groups are erected on the nature of flattening. The following species are revised: *Cyathaxonia venusta, Zaphrentis ulrichi, Z. acuta, Z. elliptica, Z. carinata, Z. clinatus, Z. capuliformis, Z. reversa, Z. compressa*, and *Z. lanceolata*. A new variety is named.

INTRODUCTION

THE great majority of Mississippian corals were formerly referred to "*Zaphrentis*" (misapplication and misspelling of *Zaphrenthis*). Any conical coral with simple morphology was thrown into this catch-all so that eventually the generic reference became meaningless. Groups of zaphrenthids subsequently were segregated into other or new genera, but there still remain some species assigned to this primitive generic concept.

Among the most difficult of paleontologic problems is the assignment of creatures whose hard parts contain relatively few morphologic features. The simple "zaphrenthids" have been neglected because they do not have enough characters to enable them to be identified as readily as can be many other corals. Corals reviewed in this study have, for the most part, only a compressed cup containing septa, a cardinal fossula, and tabulae. Differentiation of systematic categories among these corals rests upon the closer study of a few features, rather than upon emphasis of some outstanding morphologic specialization such as colonial habit, dissepiments, carinae, tabellae, lamellae, etc. Nevertheless, the simple "zaphrenthids" discussed below are distinctive in their own way and can be used confidently in stratigraphic work.

When fossils with simple morphology are described cursorily and figured indifferently, the difficulties attendant upon their identification are increased disproportionately. Not only do these factors concern the present corals, but in addition there has been a bland disregard of prior studies on part of some systematists. Finally, the corals treated herein are variable and hence are conducive toward frustrating field applications of paleontology to stratigraphy.

METHODS OF STUDY

Having successfully avoided becoming involved with the simple "zaphrenthids" for some time, the writer was brought up against the problem again by seeing a simple compressed "zaphrenthid" from the collection of Dr. Alexander Stoyanow. A search of the literature revealed several species but their relationships were obscure and their distribution questionable. The writer therefore resolved to restudy the species concerned.

Through the financial assistance of the University of Southern California, the writer was enabled to visit several museums where pertinent material is available. All known types and comparative materials were located and studied in detail. In addition, considerable field work was done in Indiana and Kentucky to ascertain the exact occurrence of these fossils in place. Many of the type localities have been visited by the writer either as mentioned above or during previous years.

Inasmuch as these simple corals do not contain important morphologic features hidden within their inner recesses, it was not necessary to conduct extensive thin section studies. Early stages usually could be observed in immature specimens rather than by making sections.

STRATIGRAPHY

The pertinent areas of outcrop are along the Mississippi River in Iowa and Missouri and thence about 300 miles to the east across the Eastern Interior Basin in central and southern Indiana.

In Fig. 1(p. 382) the average thicknesses of the formations are given. Lithologies are those of each area of outcrop, not of any particular section. One is impressed with the increasing shaliness of the Warsaw southward in Indiana. Moreover, the Salem limestone thins into Kentucky and may be locally absent there. Subsurface studies demonstrate that Burlington-Keokuk limestones along the Mississippi River grade very abruptly into shales in western Illinois (Payne, 1940, p. 232, fig. 3); where these strata reappear as outcrops in Indiana, the calcareous facies of the Burlington-Keokuk is still missing and the silty shales are known as the Borden group.

ECOLOGY

Although the Burlington-Keokuk limestones are quite fossiliferous in the region of their type sections, the beds of the same age in Indiana and Kentucky are sparsely fossiliferous. The difference is related to the change from calcareous to shaly environment. Only where the Borden group becomes locally calcareous (as at the famous Button Mould locality near Louisville, Kentucky, or at the equally renowned crinoid bioherms at Crawfordsville and Lobo, Indiana) can one collect many fossils. For this reason, the parallel development of corals in the Indiana-Kentucky region and in the Iowa-Missouri region has not been substantiated for those species of pre-Meramecian age.

Similar ecologic conditions apply to the progressive increase in shaliness of the Warsaw and Salem limestones southward in Indiana. Corals are commonest in the calcareous facies and are rare or absent elsewhere. Some very notable examples of the preference of the rugose corals for a limy environment can be studied in alternating shale and limestone sequences in Indiana. At locality 7, for instance, the Borden-Harrodsburg contact consists of a transitional alternating series of shales and limestones. Corals are nearly confined to the limestones.

ACKNOWLEDGEMENTS

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MORPHOLOGICAL MODIFICATIONS

Compressed corals have long been known, but only one type of compression has been discussed in any detail. Grove (1935, pp. 355–358) recognized the flattening of the cardinal or of the counter side of several species of rugose corals and named these "calceolid" corals in allusion to their having the shape of a slipper. One of these calceolid corals, *Lophophyllum calceola* White and Whitfield, in 1862, occurs in Mississippian strata. It is the type of the subgenus *Hapsiphyllites* Easton, 1944, hereinafter emended.

The corals restudied here are compressed, but the compression involves the alar sides of the corallite, that is, it is bilateral and parallel to the cardinal-counter plane. In comparison, it is arranged at right angles to that in the calceolid corals. Inasmuch as the resulting shape is that of a wedge, the English word "cuneate" is proposed (from

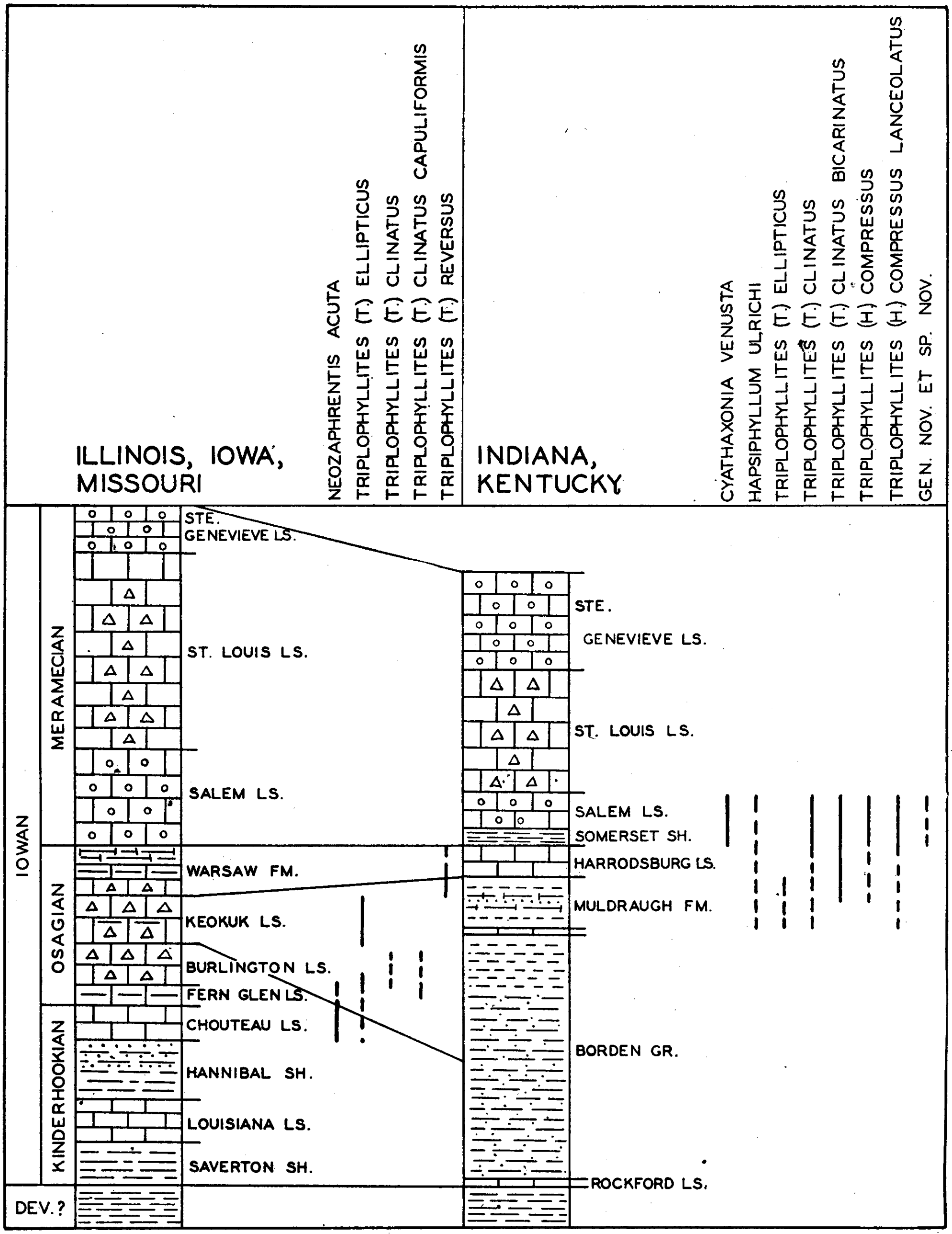


FIG. *1*—Composite columnar sections of strata within the Iowan series of Illinois-Iowa-Missouri and Indiana-Kentucky. The stratigraphic range of each species is shown by vertical lines to the right of the appropriate columnar sections. Correlation lines between sections are not intended to affect the vertical ranges of species.

the Latin cuneus, wedge) as a term descriptive of this morphological modification.

As among the calceolid corals, the cuneate corals belong to several different groups: in this case being *Cyathaxonia*, *Homalophyllites*, *Hapsiphyllum*, *Neozaphrentis*, *Triplophyllites*, and an unnamed new genus. The cyathaxonid corals and the zaphrenthid corals have somewhat different modes of septal insertion and therefore are quite distantly related. Among corals with a zaphrenthid type of septal insertion *Hapsiphyllum*, *Homalophyllites*, *Neozaphrentis*, and *Triplophyllites* still are not closely related, for the first genus has contratingent minor septa and the other three have straight minor septa. It follows then that the cuneate shape is present among three coralline groups of diverse initial relationship.

EVOLUTION

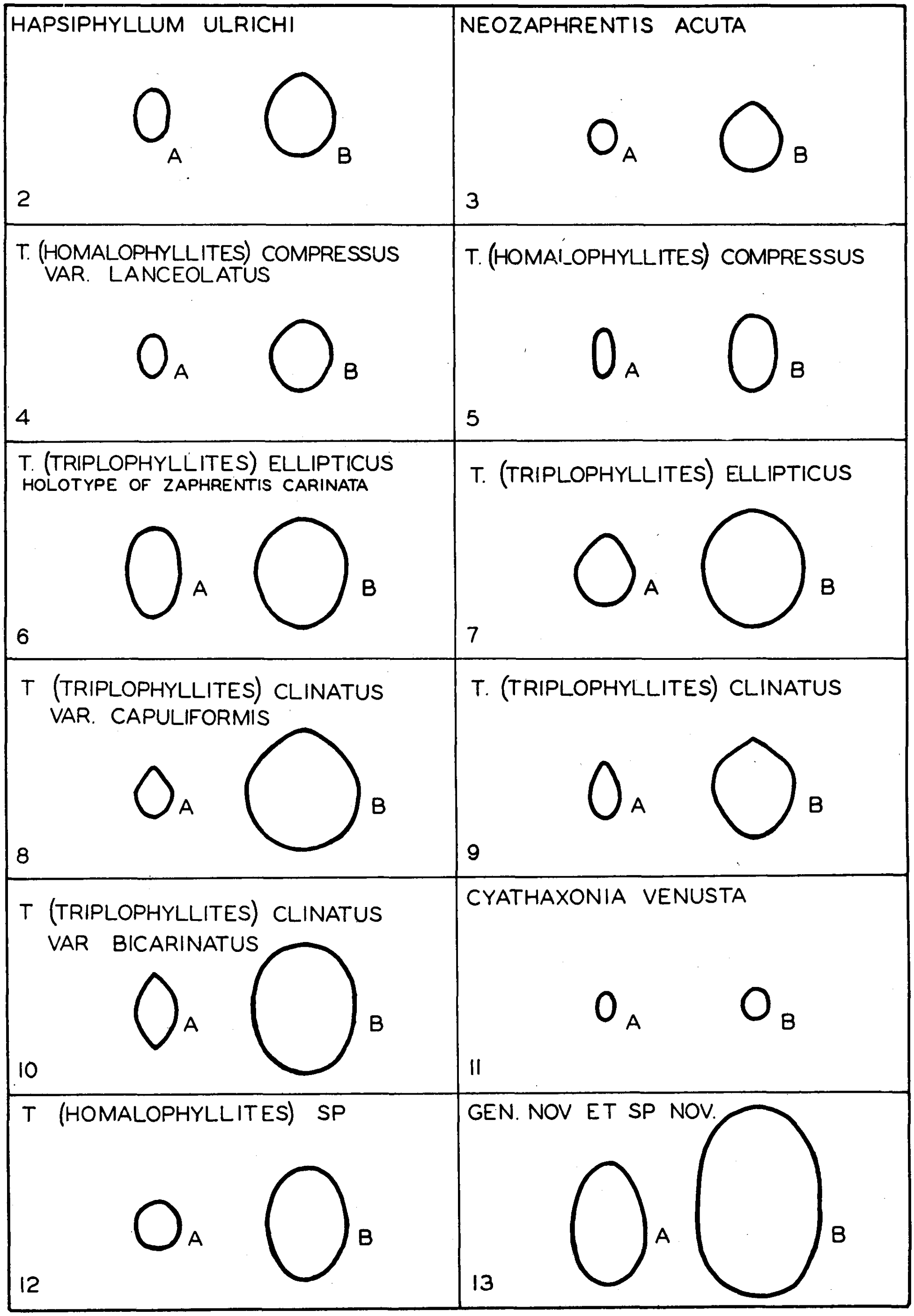
In the genera containing cuneate corals a similar developmental relationship exists. In earlier (or sometimes in contemporaneous) strata perfectly normal species belonging to a particular genus occur. That is, the zaphrenthid or cyathaxonid genera contain the features characteristic of the genotype. At some subsequent time (or as a result of apparent radiation) one or more morphologic features of less than generic rank are introduced. Some corals may become reoriented so that the cardinal fossula is on the convex side. Some corals become cuneate and either have the dominant or reoriented fossular position. Other corals become calceolid. From a stratigraphic point of view it is curious that the cuneate shape reaches its acme at about the same time in different genetic strains. From a biologic point of view it is curious that the particular strains which are cuneate or calceolid become so just before their disappearance from the geologic record.

It is quite apparent that there is only remote genetic relation between the various groups. The cuneate shape, therefore, must arise either because of orthogenetic tendency or by selective adaptation to environment. The corals discussed herein can be used to erect an argument for orthogenesis more far-reaching than that constructed on the basis of titanothere evolution, because the relationships are more diverse taxonomically among these particular anthozoans. By the same token, the arguments against such an interpretation are equally as forceful as those concerning titanothere evolution, and perhaps more so, for the corals are so simple that one can not be absolutely certain whether he is dealing with genetic strains or with parallel development. No entirely satisfactory method is known to the writer whereby a cuneate corallite will ensue from normal ancestors. No difficulty is encountered in explaining how a calceolid coral arises—as a matter of fact, two methods are known. In the first instance the calceolid coral may be equipped with an operculum which requires a straight side for hingement. In the second instance the corals may become flattened as an accommodation to bottom-dwelling habit, the corallite becoming flattened in recumbent species.

The cuneate corals are not known to have been operculate. Moreover, with two flattened sides it is hard to imagine one operculum having two hinge lines, but of course one can say that these forms had two opercula, each with its own hingement, but that they were not preserved or have never been found. In these cases nothing is gained in the way of intelligence.

Likewise, it is difficult to see how the flattening could be influenced by growth habit as in calceolids, for the corallites are flattened on two opposing sides. It hardly seems reasonable to conclude that they shifted their recumbent position from side to side.

About the only clue as to what function the keeled shape served lies in the sedimentary record of the region. During early Iowan time the seas covering the central states were moderately shallow and currents were not very strong. The limestones tend to be dense and crystalline and to occur in massive strata. By later Iowan time—specifically, at the beginning of the deposition of the Warsaw formation—the currents became stronger, presumably in accordance with a slight shallowing of the seas. Impure, thin-bedded, shaly limestones tend to be the dominant type of Warsaw sediment, but these grade laterally into granular limestones which may be oolitic. Above the



FIGS. *2–13*—Cross-sections of cuneate corals. In each pair, *a* is taken one-third of the distance from the calyx and *b* is at the calyx. All figures except *4*, *12*, *13* are of the holotypes, 1×.

Warsaw the succeeding limestones of the Iowan series are commonly oolitic and cross-bedded and are in large part shallow water deposits. It is in these sediments that the cuneate shape is best developed.

Two features concern explanation of the development of cuneate shape. These are the response to current-dwelling and the obtaining of food. Perhaps the elliptical shape was an adaptation to reduce resistance of the corals to the currents. At least the resistance would be less if the corals grew oriented with their long transverse dimensions in line with the currents. No instance is known in which a population of cuneate corals has been observed with the creatures erectly disposed, so there is not direct evidence as to how they might have been orientated on the sea floor.

The other feature is based upon observations made by Jones (1907, p. 529), who studied growth-forms of recent colonial corals in the Cocos-Keeling Islands. He reports that "vertical plates grow so that they offer their flat surfaces to the currents. The same thing is true of growths that are branching forms, for then the plane of greatest branching is that at right angles to the line of current." Jones assigned the cause of this orientation to the fact that the currents transported the food for the polyps and that the growth was directed so as to offer the most advantageous position for food-gathering.

The great majority of simple rugose corals are curved. Usually the curvature is consistently in one direction among the individuals of any one species. Moreover, most species are curved in the direction of the cardinal fossula (or it is said that the cardinal fossula is on the concave side). Very few corals are consistently erect in the form of right cones, although this may have been the archetypal habit. It would seem then, that there is a dominant tendency of ancient origin for corals to curve. The fact that the curvature is relatively constant within a species would indicate that when each larva established itself upon the substratum, it orientated itself in some characteristic position with regard to prevailing currents. Failure to do so would cause aberrant curvature of the corallite subsequently. Haphazard orientation, which seems to have existed in some species, would result in all manner of curvature with respect to location of the cardinal position. From these considerations the writer concludes that the orientation of the larva with respect to currents is probably governed by a genetic factor, whereas the curvature itself is probably due to an environmental factor. In this way it is possible to explain biologically how members of a coral species that consistently curve in one direction occasionally show aberrant curvature. This defection could arise if the larva failed to become properly oriented with respect to prevailing currents and then developed a curvature toward the food-transporting currents after the protothecae were secreted. If the tendency toward curvature in some particular direction were a genetic feature, then the aberrant curvature is harder to explain. One is reminded of the vexatious problems concerning the nature and importance of spiralling in dextral and sinistral gastropods. Sometimes it is of a genetic nature and is of apparent taxonomic value and other times it is probably due to embryologic accident.

In review, it is interesting to note that the curving of a coral so as to present the polyp's greatest surface to the currents would be in the same plane that the flattening of the cuneate corals occurs. Probably the cuneate shape is a late modification causing improvement in streamlining of the corallites whose orientation and tendency toward curvature are of early standing. Cuneate shape seems to be of a genetic nature within any species, for this feature is always developed in the same way, regardless of aberrations in curvature.

Currents were not peculiar to post-Iowan seas. Low velocity currents are known even in abyssal waters, so light currents obviously ran in the epeiric seas of Lower Mississippian time in the Midwest. In post-Iowan time, however, the currents seem to have increased in velocity. The culmination of the cuneate shape coincides with the presence of strong currents.

SYSTEMATIC PROBLEMS

Several species of corals which resemble each other in general appearance possess dissimilar internal morphology. Genetic

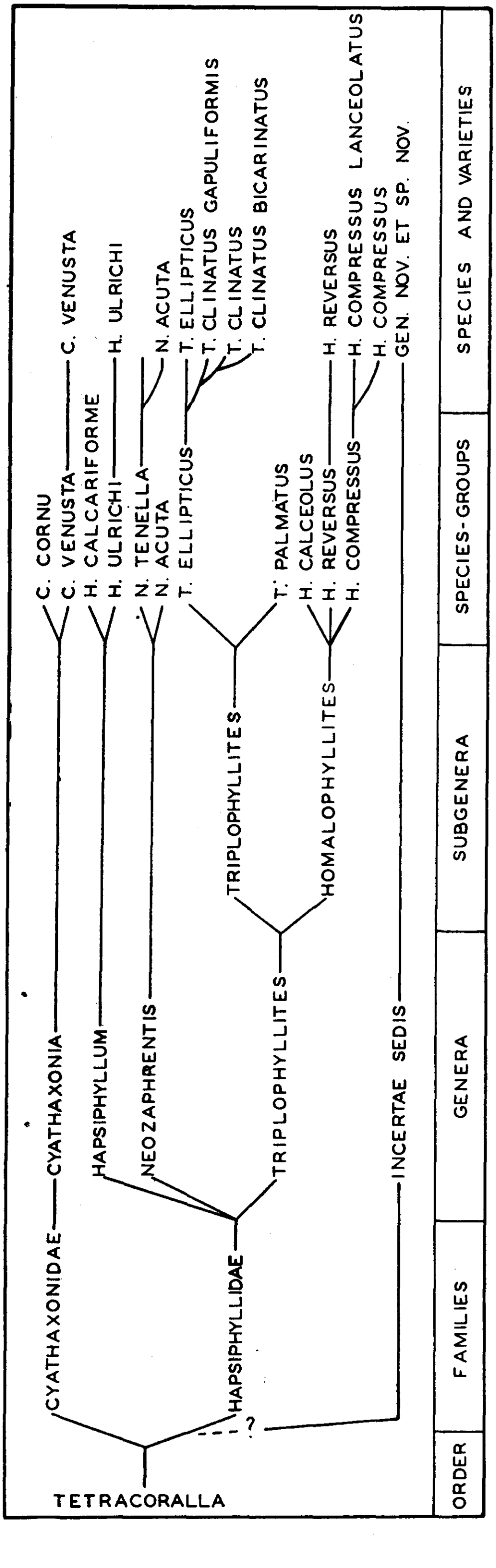


FIG. 14—Taxonomic categories and phylogeny used in this paper.

relationship is presumed to be manifest when coral species contain the same morphologic features but in different degrees of development. Accordingly, the corals considered below can be divided into four genetic groups, all of which contain thecae, septa, tabulae, and some indication of a cardinal fossula, but which individually may be characterized as follows:

Cyathaxonia.—Has "cyathaxonid" order of septal insertion and a columella.

Triplophyllites.—Has "zaphrenthid" order of septal insertion and usually has dissepiments at some stage in development. Usually is conical, rather than being cylindrical or flaring.

Neozaphrentis.—Has "zaphrenthid" order of septal insertion and cardinal fossula bounded by unfused inner edges of septa.

Hapsiphyllum.—Has "zaphrenthid" order of septal insertion, contratingent minor septa and lacks dissepiments.

The only reason that it becomes necessary to consider these genera together is that the shapes of the individuals of some species are unique and the same in each group. The species of different or even similar genera would possibly be considered to be conspecific if only external features were observed. Likewise, different species within a genus may resemble each other in their curious shape, yet be otherwise specifically separable. The first of these conditions (similar but unrelated species) is commonly termed isomorphism. The latter condition (similar related species) is commonly called homoeomorphism. Inasmuch as both conditions are found among cuneate and calceolid corals, the first problem to be settled involves distinguishing between isomorphs and homoeomorphs. Otherwise, any proposed classification would be deficient.

Simple corals are most commonly in the shape of a curved cone with a circular cross-section throughout. Cuneate or calceolid corals usually tend toward a "normal" cross-section at some stage in their ontogeny and hence are considered to be modifications of the original round stock. Among the simply organized creatures considered herein, the cuneate or calceolid modification is the principal feature by means of which isomorphism or homoeomorphism is manifested. Therefore, these modifications of existing structure are given a subordinate position in the systematic arrangement of the species. Major modifications are considered to be of specific value, whereas minor modifications of these in turn are considered to be of varietal magnitude.

The second problem concerns the systematic importance to be attached to curvature of the coral. Four orientations are known: (*a*) the cardinal fossula is on the concave side when the corallite is viewed from either alar side; (*b*) the cardinal fossula is on the convex side with similar orientation; (*c*) the cardinal fossula is variably located; (*d*) the corallite is a right cone, that is, it is not curved, and hence, the cardinal fossula is not demonstrably on one side or another.

Case *d* is rarely encountered. Case *c* is known but is not common. It is, however, common among groups of specimens of *Zaphrentis calcariformis* Hall, 1882. In a large number of specimens one finds that more than half of them have the cardinal fossula on the concave side. Among the other specimens, some will be contorted so that the position of the fossula varies in one specimen. Some will be contorted or straight and the fossula will be in some position of greatest concavity. Others will, more rarely, have the fossula somewhere on the convex half of the coral. Lastly, some specimens may have elongate scars of attachment in the apical portions of the corallites and then may be curved or contorted distally; in both these latter instances, the trace of the cardinal septum usually lies along the greatest diameter of the scar of attachment. In the majority of all foregoing conditions, the cardinal fossula is somewhere on the concave side, even though it may not be at the place of greatest concavity.

Even though some variation in the location of the cardinal fossula with respect to curvature is established, the writer still considers the character to be of taxonomic value. After all, its variable location is merely a manifestation of the natural tendency of organisms to vary. It would seem, then, that *Z. calcariformis* Hall is merely a species from which one could expect a new strain of corals to evolve, with the cardinal fossula located on other than the concave side. Viewed in this fashion, the species becomes additionally significant from an evolutionary standpoint.

It is a well-known fact that the counter quadrants of rugose corals usually contain more major septa than do the cardinal quadrants. Inasmuch as the rugose corals are commonly curved toward the cardinal septum, it naturally follows that the counter quadrants are potentially expanded (as if they were stretched around the calyx rim) by the greater curvature on that side. Additional septa occur in the counter quadrants in the expanded regions, but it is not known whether the expansion necessitates their insertion or vice versa. On the other hand, it can be observed among the corals studied herein that the counter quadrants are consistently accelerated no matter on which side the cardinal fossula lies. This runs counter to the principle observed among rugose corals in general (which mostly have their cardinal fossulae on the concave side). If the coral is convex on the cardinal side, one would assume before observing the septa that they would not be accelerated on the counter side, or even that they might be accelerated on the cardinal side. It is concluded, then, that as a general rule, the distribution of septa within the quadrants of a calyx results from a strong genetic requirement. Moreover, deviations from the normal situation are usually minor in effect. If these conclusions are valid, then one may further conclude that the distribution of septa within a calyx has been determined by long established genetic lines. In other words, the distribution of septa will tend to remain constant for a time even though the shape of the coral may begin to change. From these matters, the writer has concluded that the orientation of the cardinal fossula with regard to curvature is less important taxonomically than is the nature and degree of acceleration of the septa. Accordingly, the location of the cardinal fossula is assigned subgeneric status.

The third problem is to arrange the various corals into such taxonomic groups that their inter-relationship is apparent, yet assuring that the cuneate (or round, or calceolid) corals of one genus or subgenus may be distinguished by a collective term from the cuneate (or round, or calceolid) corals of another higher category. The term "circulus" has been proposed (Gregory, 1896, p. 22) as a systematic group, the members of which bear the same relation to some standard species as did the rings of listeners to each of several speakers in a Roman forum. This original usage implies lack of genetic relationship and also a rather haphazard but necessary collection. It is essentially a term to include isomorphic species. It could be used to designate all cuneate, all calceolid, or all conical corals. Circulus has been used in other senses, however, and would possibly be suitable under one of these latter, but not under its original meaning.

Vaughan (1905, p. 183) proposed "gens" for "the aggregate of all the species which possess, in common, a large number of essential properties, and are continuously related either in space or time."

It is not possible to say that the corals under discussion contain a large number of properties in common for their structure is quite simple. Yet their structure is ample enough for careful differentiation. Possibly distinctive groups of these corals could be alluded to as gentes.

On the other hand, the straight-forward appellation "species group" conveys just what is desired. Groups of species which differ collectively from other similar groups, yet whose similarities are not of generic or subgeneric rank, may conveniently be encompassed in species-groups.

SYSTEMATICS

Investigation of the following corals has revealed morphologic features not hitherto known. Philosophical consideration of relationships results in rearrangement of some genera and species previously studied by the writer. Whenever systematic reorganization is required, the writer puts forth the background and reasons for these changes.

In the following section, AMNH refers to the American Museum of Natural History. IGS refers to Illinois State Geological Survey. UA, to the University of Arizona. USC, to the University of Southern California. UI, to the University of Illinois. UM, to the University of Michigan. USNM, to the U. S. National Museum.

Phylum COELENTERATA
Class ANTHOZOA
Order TETRACORALLA
Family CYATHAXONIDAE Milne-Edwards & Haime, 1850
Genus CYATHAXONIA Michelin, 1847

Cyathaxonia cornu species-group

Diagnosis.—*Cyathaxonia* with the cardinal fossula on the concave side of the corallite and with a conical shape.

Remarks.—Most species of *Cyathaxonia* belong here.

Cyathaxonia venusta species-group

Diagnosis.—*Cyathaxonia* with the cardinal fossula on the convex side of the corallite and with a cuneate shape.

CYATHAXONIA VENUSTA Greene, 1904
Plate 61, figures 10–14; text-figure 11

1879. not *Cyathaxonia compressa* THOMPSON, Proc. Phil. Soc. Glasgow, vol. 11, no. 18, p. 197, pl. 1, fig. 6.
1899. *Cyathaxonia compressa* GREENE, Contributions to Indiana Palaeontology, pt. 2, p. 9, pl. 4, figs. 14–17.
1904. *Cyathaxonia venusta* GREENE, Contributions to Indiana Paleontology, pt. 19, p. 187, pl. 56, figs. 10–14.
1906. *Cyathaxonia venusta*. BEEDE in Beede and Cumings, Indiana Dept. Geol. Nat. Res., 30th Ann. Rept., p. 1202, pl. 11, figs. 2, 2a.
1906. *Cyathaxonia venustum*. BEEDE in Beede and Cumings, Indiana Dept. Geol. Nat. Res., 30th Ann. Rept., p. 1373.
1922. *Cyathaxonia venustum*. CUMINGS, Handbook of Indiana Geology: Indiana Dept. Cons., Pub. 21, pt. 4, p. 505.

Description of Holotype.—Corallite an elliptical cone slightly curved away from the cardinal fossula. Cross-section lanceolate near the apex and ovate near the calyx. Surface smooth except for faint traces of septa due to weathering. Theca rather thick.

Calyx shallow, 2.5 mm. deep. Septa in two orders, totaling 32. Cardinal fossula nearly parallel-sided, deep, slightly wider than other loculi. Cardinal septum extends one-third length of fossula in calyx. Counter septum similar to the other major septa but joined near its axial end by the minor septum on either side. On each side of the calyx are seven major septa which join the columella. They are a little thicker near the theca than along most of their length.

Alternating with these is an equal number of minor septa which do not extend as far distally as the majors and which lean in the counter direction to fuse with the majors just before reaching the columella. The minors are very thin most of their length but are as thick as majors near the theca. At the calyx rim major and minor septa are the same length. Columella smooth, slightly oval near the calyx floor, about 2.0 mm. high.

Dimensions.—Height 15 mm. Greatest diameter of calyx 5 mm. Least diameter of calyx 4 mm.

Description of Paratypes and Hypotypes.—The paratypes all have 32 septa also and are arranged as in the holotype. In one of the paratypes the cardinal septum is perfectly preserved and its upper edge can be seen to slope steeply into the fossula and then swing over to the columella. There is some small variation in the length of the counter septum. In some calices it is slightly longer and in others, slightly shorter than are the neighboring majors.

Greene's hypotypes are like the holotype except that they are a little more narrowly elliptical and two of them have 34 septa.

Material.—Specimens studied: nine. Holotype: AMNH Nos. 23413–23415. Greene's hypotypes: AMNH Nos. 24045–24049.

Type locality.—Greene gave the type locality as "Warsaw division of the St. Louis group" at Georgetown and Lanesville, Indiana. In terms of recent geological usage, this probably means that the fossils came from the Salem limestone (Meramecian series of the Mississippian). One particular locality in the Salem limestone at Lanesville was and is a favorite collecting locality of many paleontologists. Inasmuch as Greene had all the syntypes together (and they are similarly preserved) one might assume that they came from one locality. The only places where this species has been collected by others than Greene is from the Salem limestone at Lanesville, Paynter's Hill, and Spergen Hill, so there is some reason to believe that Lanesville is the type locality.

Localities.—12, 13 (type locality).

Remarks.—The types are all reddish silicified replacements. The writer removed red clay from the loculi between septa when studying them. At Lanesville the Salem fauna is obtained by washing red residual clay to obtain the silicified fossils.

Family HAPSIPHYLLIDAE Grabau, 1928, emend. Easton, 1944

Genus HAPSIPHYLLUM Simpson, 1900

Diagnosis.—Simple tetracorals with long contratingent minor septa. Cardinal fossula long and slender. Alar pseudofossulae more or less distinct. Counter septum joined by adjacent minors to form a tripartite structure. Tabulae present. Dissepiments absent. Cardinal fossula usually on concave side of corallite.

Genotype.—*Zaphrentis calcariformis* Hall, 1882.

Remarks.—The writer (1944, p. 42) emended the genus *Hapsiphyllum* so as to include the subgenus *Homalophyllites* Easton, 1944. This procedure brought together corals with normal short minor septa and corals with longer contratingent minor septa. Since 1944 the writer has had occasion to study in new species many more specimens of corals with contratingent minor septa. It has been concluded that this feature is stable enough to warrant separation of the subgenera *Hapsiphyllum* and *Homalophyllites*. Therefore, the emendation proposed in 1944 is considered inapplicable. The effect of this action is to suppress *Hapsiphyllum* as a subgenus and to reassign the subgenus *Homalophyllites* to another genus. (For further remarks, see under *Triplophyllites*).

Hapsiphyllum contains two parallel series of corals, one with a normal conical shape, the other with a cuneate shape. These are the basis for recognizing two species-groups in the genus.

Hapsiphyllum calcariforme species-group

Diagnosis.—*Hapsiphyllum* with a conical shape.

Remarks.—Included here are *Hapsiphyllum calcariforme* (Hall), 1882 and *Hapsiphyllum cassedayi* (Milne-Edwards), 1860.

Hapsiphyllum ulrichi species-group

Diagnosis.—*Hapsiphyllum* with a cuneate shape.

HAPSIPHYLLUM ULRICHI (Worthen), 1890
Plate 60, figures 11a–c; text-figure 2

1889. *Zaphrentis ulrichi* MILLER, N. Amer. Geol. and Paleontology, p. 210 (nomen nudum).
1890. *Zaphrentis ulrichi* WORTHEN, Geol. Survey Illinois, vol. 8, p. 76, pl. 10, figs. 10, 10a.
1898. *Zaphrentis ulrichi* WELLER, U. S. Geol. Survey Bull. 153, p. 649.

Description of holotype.—Corallite an elliptical cone, curved in the direction of the cardinal position. Cross-section somewhat more narrowly elliptical near the apex than near the calyx. Depth of calyx not known. Cardinal fossula very deep, extending slightly past the center of the calyx, and broadest in its inner portion. Cardinal septum very short near the calyx but crossing the fossula farther down. Other septa of two types: the majors fuse at their inner ends to form the fossular wall; the minors lean toward the counter position and each fuses with the next adjacent major septum about one-third of the distance to the axis. The counter septum is fused with the next adjacent minor septum on either side about half of the distance to the axis. The right cardinal quadrant contains six pairs of septa; the right counter quadrant contains seven pairs; the left counter quadrant contains eight pairs; and the left cardinal quadrant contains five pairs. Thus, the calyx contains 28 major septa (counting the cardinal septum). Alar pseudofossulae are distinct because they extend farther axially than do the neighboring loculi.

Dimensions.—Holotype, height 20 mm. Greatest diameter of calyx 11.5 mm. Least diameter of calyx 10 mm.

Material.—Specimens studied: six. Holotype and paratype, IGS (Worthen Collection) No. 2573. Topotypes, USNM No. 42743.

Type locality.—Warsaw formation (Meramecian group, Mississippian system), Colesburg, Kentucky. (Coalsburg [sic] on label).

Remarks.—The Worthen collection contains four specimens bearing the number 2573. One of these specimens, which is of different preservation than the other three, is a species of *Triplophyllites.* It is so different from the other three that it is doubtful that Worthen included it among the original types. Possibly this specimen became associated with the type labels accidentally and was so numbered.

Of the other three specimens, one, which is the basis of Worthen's figures of the species (Worthen, 1890, pl. 10, figs. 10, 10a) is hereby designated the holotype. The dimensions of the figure agree with those of the "medium size individual" mentioned in Worthen's description. The actual measurements of the specimen differ slightly from the stated measurements. One concludes that Worthen's measurements were taken from the drawings, with which they agree.

The two remaining specimens are not at all well preserved. The smallest is not identifiable. The largest specimen probably belongs to *Hapsiphyllum ulrichi*, but it is not possible to decide even how many major septa it had. Even so, it becomes a paratype. Its calical diameters are 13 mm. by 14 mm.

The largest specimen seen (USNM lot 42743) measured 34 mm. in length, with calical diameters of 15 mm. by 13.5 mm. The usual number of septa is 26, but specimens with 28 and 29 have been studied.

Occurrence.—Localities 1 (type locality), 2.

Genus NEOZAPHRENTIS Grove, 1936

Remarks.—Since Grove erected *Neozaphrentis* upon *Zaphrentis tenella*, the species *Z. acuta*, *Z. palmeri*, and *Z. parasitica* have also been referred to the genus. Of these, *Z. acuta* shows a cuneate tendency, and so it is necessary to make two species groups in the interests of consistency.

Neozaphrentis tenella species-group

Diagnosis.—*Neozaphrentis* with a circular cross section.

Neozaphrentis acuta species-group

Diagnosis.—*Neozaphrentis* with a cuneate shape.

Remarks.—*Neozaphrentis acuta* is not consistently cuneate, but it still is reasonable to establish this species group. It is probable that *N. acuta* is very close to the point of separation of the two species-groups and that the cuneate tendency is not well established in the species because only a small evolutionary period elapsed since the tendency originated.

NEOZAPHRENTIS ACUTA (White & Whitfield) 1862

Plate 61, figures 6, 7; text-figure 3

1862. *Zaphrentis acutus* WHITE & WHITFIELD, Proc. Boston Soc. Nat. Hist., vol. 8, p. 306.
1865. not *Zaphrentis acutus*? WINCHELL, Acad. Nat. Sci. Philadelphia Proc., p. 111.
1883. *Z.* [*aphrentis*] *acuta*. WHITE, U. S. Geol. Geog. Survey Terr., 12th Ann. Rept. (1878), p. 159. (Advance printing, 1880).
1889. *Zaphrentis acuta*. MILLER, N. Amer. Geol. and Paleontology, p. 208.
1894. not *Zaphrentis acuta*. KEYES, Missouri Geol. Survey, vol. 4, p. 109, pl. 13, fig. 4.
1897. not *Zaphrentis acuta*. KEYES & ROWLEY, Iowa Acad. Sci., vol. 4, p. 30.
1898. *Zaphrentis acuta*. WELLER, U. S. Geol. Survey Bull. 153, p. 644.
1908. not *Zaphrentis acuta?* ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, pp. 31, 62, 63; pl. 16, figs. 19, 20.
1908. not *Zaphrentis acute* [sic]? ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, p. 33.
1908. not *Zaphrentic* [sic] *acuta*. ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, p. 62.
1943. *Neozaphrentis*? *acuta*. WILLIAMS, U. S. Geol. Survey Prof. Paper 203, p. 56 (not pl. 6, figs. 31–33).

Description.—Simple corallites in the form of curved cones, rarely cuneate. Epitheca smooth, with encircling swellings. Calyx oblique, sloping down toward the concave side. Cardinal fossula very deep, axially widened, and bordered by axial ends of major septa which are only slightly fused. Holotype with 24 major septa, of which five are in each cardinal quadrant and six in each counter quadrant; cardinal septum very short; counter septum slightly longer than neighboring majors. Minor septa short. Alar pseudofossulae slightly wider than other loculi. The figured paratype has 32 major septa, with six in each cardinal quadrant and nine in each counter quadrant; cardinal septum extends across axially swollen cardinal fossula and bends to the right; counter septum longer, higher, and thicker than neighboring majors. Alar pseudofossulae distinct. Minor septa almost absent and very short. Unfigured paratype with 31 major septa, of which each cardinal quadrant contains six, the right counter quadrant contains nine, and the left counter quadrant contains eight; cardinal septum short but extends straight across the nearly vertically-walled cardinal fossula near the bottom. Counter septum longer than neighboring majors and of the same thickness. Alar pseudofussulae quite distinct. Minor septa rather short at calyx margin. Calyx very deep, about 9 mm.

Dimensions—Holotype: length about 20 mm.; calical diameters 9 mm. by 10 mm. Dimensions of figured paratype: length about 16 mm.; calical diameters 10 mm. by 11.5 mm. Dimensions of unfigured paratype: length, about 22 mm. (incomplete); calical diameters 11 mm. by 12.5 mm.

Material.—Specimens studied: three. Holotype and paratypes, AMNH No. 6366/1.

Locality.—22 (type locality).

Occurrence.—Kinderhook beds, Burlington, Iowa.

Remarks.—The holotype has a carinate counter edge, giving it a cuneate shape, but the paratypes have circular cross-sections.

This species has been imperfectly understood for many years, indeed, the accompanying figures are the first to be published of the types.

The epitheca is smooth and apparently always was, contrary to the doubtful statement in the original description that the smoothness may be due to weathering. The "transverse septa" mentioned by White and Whitfield were questionably considered to be dissepiments by Williams (1943, p. 56). It is the confident belief of this writer that the "transverse septa" are really the tabulae as understood in recent usage. Inasmuch as early American students modeled their descriptions on European works, it is reasonable to assume that the concepts of vertical and horizontal septa reflect merely the translated French equivalents from such works as Haime's. Perforations in the peripheral portions of the "transverse septa" mentioned by White and Whitfield (and visible in the types) are nothing but occasional holes mechanically broken through the tabulae.

The specimens usually called *Z. acuta* will be considered by the writer in a forthcoming paper.

Genus TRIPLOPHYLLITES Easton, 1944

Diagnosis.—Simple, medium to large, curved corals. Cardinal fossula prominent. Alar pseudofossulae usually prominent. Major septa long, minor septa short. Tabulae usually well developed. Dissepiments usually sparse, commonly restricted to lower portions of the corallite.

Remarks.—When originally proposed it was stated (Easton, 1944, p. 39) that the genus might sometime be divided into two subgenera on the basis of the position of the cardinal fossula. At that time only *Zaphrentis reversa* Worthen, 1890 was thought possibly to possess the cardinal fossula on the convex side. Since that time several corals have been studied which require the division of *Triplophyllites* into two subgenera.

Subgenus TRIPLOPHYLLITES Easton, new usage

Diagnosis.—*Triplophyllites* with the cardinal fossula on the concave side of the corallite.

Type.—*Triplophyllites palmatus* Easton, 1944.

Remarks.—Most species of *Triplophyllites* belong here. It has been pointed out (Easton, 1944, p. 37) that *Zaphrentoides* may be a senior synonym of *Triplophyllites* but that the status of *Zaphrentoides* is so confused as to be (in the opinion of the writer) inapplicable at present. If the genus *Zaphrentoides* should be proved (by some future study of the genotype) to be the same as the genus *Triplophyllites*, then the subgenus *Triplophyllites* would be reassigned to the genus *Zaphrentoides*. (See under *Homalophyllites*).

The genus *Zaphrentoides* has been formally introduced into the literature of the North American Carboniferous by Moore and Jeffords for a Lower Pennsylvanian coral. These authors (Moore and Jeffords, 1945, pp. 129–130) reviewed the status of the genus and its position relative to several other genera and reached different working assumptions than the writer did in 1944. Subsequently, *Zaphrentoides* was used for certain Mississippian corals by Laudon et al. (1949, pp. 1502–1552), but without explanation. Dr. Laudon, (correspondence, 10 October 1949) informs me that the usage corresponds to what has been formerly known as *Triplophyllum.*

As interpreted herein, the subgenus contains both cuneate and normally conical corals. Two species-groups are set up to accommodate these different forms.

Triplophyllites palmatus species-group

Diagnosis.—*Triplophyllites* (*Triplophyllites*) with a circular cross-section.

Remarks.—Most species of *Triplophyllites* belong here.

Triplophyllites ellipticus species-group

Diagnosis.—*Triplophyllites* (*Triplophyllites*) with a cuneate cross-section.

Remarks.—*Zaphrentis ellipticus*, *Z. carinatus*, *Z. capuliformis*, *Z. clinatus*, and a new variety of the last species are referred to this species-group.

EXPLANATION OF PLATE 59

Calyces 2× except as otherwise indicated; lateral views 1×.

FIGS. *1–4*, *6*, *8–18*—*Triplophyllites* (*Homalophyllites*) *compressus* var. *lanceolatus* (Worthen), 1890. *1*, Calyx; approaches *T. clinatus;* USNM 115209a. *2*, Calyx in late maturity; AMNH 24006. *3*, Calyx; USNM 115208; approaches *T. clinatus*. *4*, Calyx; USNM 115208; approaches *T. clinatus*. *6a*, Calyx; *6b*, cardinal side; *6c*, left alar side; USNM 115212. *8a*, Cardinal side; *8b*, calyx; *8c*, left alar side; holotype of *Z. lanceolatus;* IGS (Worthen Coll.) 2572. *9a*, Cardinal side; *9b*, calyx; *9c*, left alar side; specimen less compressed than usual and more curved; USNM 37286. *10*, Calyx; USNM 115212. *11*, Calyx; AMNH 24003. *12*, Calyx in early maturity; AMNH 24004. *13*, Calyx in late youth; USNM 42878. *14*, Calyx in late youth; USNM 42878. *15*, Calyx in early maturity; USNM 42878. *16*, Calyx, AMNH 24005. *17*, Calyx; USNM 42878. *18a*, Cardinal edge; *18b*, right alar side; *18c*, calyx; USNM 115212. (p. 401)

5, *7*, *19*—*Triplophyllites* (*Homalophyllites*) *compressus* (Milne Edwards), 1857. *5a*, Calyx; "magnified"; from Milne Edwards; *5b*, lateral view of a specimen, probably not the same as *5a;* may actually be var. *lanceolatus;* "natural size"; from Milne Edwards; specimen lost. *7a*, Cardinal side; *7b*, calyx to match *5a;* *7c*, right alar side; USNM 115202a. *19a*, Left alar side; *19b*, cardinal side; *19c*, calyx; USNM 37286. (p. 399)

20—Genus and species unknown. *20a*, Left alar side; *20b*, calyx, 1×; *20c*, cardinal side; USNM unnumbered specimen. (p. 402)