

ON THE GENERA HELIOLITES, TETRADIUM,  
AND CHAETETES.

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ABSTRACT.

The position of Zoantharia Tabulata Milne Edwards and Haime is discussed. It is decided that the subdivision contains a heterogeneous assembly of forms and has no real classificatory value. The criteria for recognition of Palaeozoic Alcyonaria and Rugosa are established and a critical study of several genera, formerly associated with the Tabulata, made. It is shown that some of these genera cannot be placed with the Alcyonaria, the Rugosa, or the Hexacoralla, but represent independent branches of the Anthozoa. Thus three families, the Heliolitidae, Tetradiidae, and Chaetetidae, represent a distinct sub-class of the Palaeozoic Anthozoa, to which the name Schizocoralla is given. The chief characteristics of the new sub-class are increase of the number of corallites by simple fission, and the absence of the true septa of the Zoantharian type.

My work on the Tetradiidae has led me to consider more closely the relationship and systematic position of several Palaeozoic corals, particularly the ones which seem to have some similarity to the Tetradiidae. The facts and conclusions here presented are a result of a detailed comparative study of the genera *Tetradium*, *Heliolites*, and *Chaetetes*, and of a shorter examination of *Stauria* and *Heliopora*. This work enables me to revise some of my earlier views on the relationship of *Tetradium* to other corals, but does not affect the results reached in the detailed study of this interesting group.

The main thesis of this paper is that some corals do not fit into the present scheme of classification, i.e. they are not Alcyonaria, Rugosa, or Hexacoralla. Such a situation is only natural, as there is no reason to expect that all corals should be members of the three main branches of the Anthozoa. Shorter branches must have existed as well. Three families,—the Tetradiidae, the Heliolitidae, and the Chaetetidae seem to be such branches. The three families possess some characteristics in common, and on basis of these, they are grouped as separate orders of the new sub-class Schizocoralla. The main characteristics of the new sub-class are increase of the number of corallites by simple fission, and the absence of true septa of the Zoantharian type.

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The Zoantharia Tabulata of Milne Edwards and Haime contains genera thus characterized: "Corallum essentially composed of well developed mural system, and having the visceral chambers divided into a series of stories by complete transverse tabulae or diaphragms. Septal apparatus rudimentary." Later workers found that the group so constituted contained a heterogeneous assemblage of forms. Closer research has demonstrated that most of the genera can be distributed among the Alcyonaria, Hexacoralla, Rugosa, and Bryozoa. However, some groups proved to be obstinate, and repeated efforts of the ablest investigators have failed to find a suitable place for them. Such forms belong to the families: Heliolitidae, Favositidae, Chaetetidae, Tetradiidae, Syringoporidae, Halysitidae, and Auloporidae. This is indicated by the fact that the last edition of Zittel's "Grundzüge der Paläontologie" by Broili (1924) lists these families (except the Heliolitidae) under the heading Tabulata. This notwithstanding the fact that Lindström in 1873, Nicholson in 1879, Zittel in 1879, and Bourne in 1900 abandoned the name Tabulata and have, supposedly definitely, established the relationship of these families with some one of the other groups.

Before reviewing the separate groups of the Tabulata it is well, to facilitate a critical attitude towards this discussion, to establish what criteria are available to distinguish between the fossil corals.

#### *Characteristics of Alcyonaria.*

Some of the most common living corals of today belong to the sub-class Alcyonaria. Their anatomy and physiology are fairly well known. Unfortunately for the palaeontologists the description and classification of modern forms is based chiefly on the soft parts of the animal. The general characteristics of any Alcyonarian, quoting Zittel are: "Composite colonies, rarely simple polyps, the individuals provided with eight mesenterial folds and eight broad, pinnately fringed, or plumose

tentacles, which form a single cycle about the mouth." Summarising the Alcyonarian characteristics as described by several authors, we get:

1) The skeleton of Alcyonarians is of subordinate value for taxonomic purposes (Bourne).

2) The calcareous skeleton usually consists of spicules, which may be fusiform, club-shaped, cross-shaped, or discoid; they are seldom smooth, but generally covered with spines or warty projections (Bourne).

3) In *Heliopora coerulea* the calcareous skeleton is not spicular but lamellar, like that of madreporarian corals. In many other respects this coral differs from the rest of Alcyonaria (Bourne).

4) It is characteristic of the Alcyonaria that buds are never formed directly from the mother zoöid, nor yet from the daughter zoöids; they are *always* formed on tubular outgrowths of the zoöids, which have variously been named stolons, nutritive canals, endodermic canals, etc. (Bourne).

5) The cavities of the Alcyonarian zoöids never communicate directly with one another, but always by means of solenia; these may be long, much branched, anastomosing passages, or they may be so much reduced that the zoöids seem at first sight to be in direct communication (Bourne).

6) Pseudo-septa or septal spines may be present or absent, when present the number may vary from 8 to 20 (Gregory).

7) Septa of Helioporidae are not homologous with the septa of Madreporaria; for they are remnants of walls and not special outgrowths from the margin of corallites (Gregory).

8) A tendency to dimorphism exists in the Alcyonaria; it is absent in the Tetracoralla (Hickson).

#### *Characteristics of the Rugosa.*

Since Rugosa are found only as fossils their classification is based exclusively on their skeletons. It is therefore easy to state the criteria by which we recognize and distinguish Tetracorals from the other Anthozoa. Such definitions can be found in any standard book of palaeontology. The order is essentially characterised by the typical arrangement of its septa, its compact and solid sclerenchyma, imperforate septa and epitheca, and the development of endothelial tissue. The coralla are never dimorphic. The order is confined to the Palaeozoic.

In the following review of some genera of the tabulate corals I will attempt to compare their characteristics with the definitions of the Alcyonaria and Rugosa as stated above. It is my contention that unless these genera fit naturally into the above mentioned groups it is better to leave them in a group or groups by themselves, rather than to stretch the definitions, and force them into unnatural companionship.

#### TETRADIDAE.

The relationship of *Tetradium* to other corals has received much attention; Nicholson (1879) and Ruedemann (1898) gave good summaries of previous work and opinions. In my paper on the Tetradiidae (1935) I also considered this question and although I pointed out the similarity existing between the Tetradiidae and *Stauria* on one hand and *Heliolites* on the other, came to no definite conclusion. Additional work in this field permits me now to reconsider the subject.

Tetradiidae, like other corals (see Lang, 1917), have a line of evolution from simple, through dendroid and fasciculate, to massive stages (*T. syringoporoides*, *T. laxum*, *T. clarki*, *T. fibratum*). These stages offer superficial resemblance to other corals, and this explains why *Tetradium* has been compared to such numerous and different genera, as *Chaetetes*, *Halysites*, *Syringopora*, *Favosites*, and *Heliolites*. A most careful study is required not to fall into the trap, and see relationship in what is only a case of homeomorphy.

I have shown (1935) that *Tetradium* is not a member of the Chaetetidae. Septal budding or fission of *Tetradium* offers, however, some similarity to fission of *Chaetetes* and possibly points to a very distant relationship. Other points of similarity are the long imperforate corallites and numerous complete tabulae. I have also mentioned that there are points of similarity between *Heliolites* and *Tetradium*. The similarities mentioned are as follows:—a columella may be present in both the Tetradiidae and Heliolitidae, the walls are imperforate in both; the corallites are long, slender, and either prismatic or cylindrical; in *T. fibratum*, occasional corallites are larger and remind one of the "autopores" of *Heliolites*; the smaller corallites increase by fission; tabulae are very much alike, and both have septa which are not comparable to those of the Zoantharia.

An extensive study of the literature concerning Heliolitidae and a study of thin sections of European and American specimens of *Heliolites* has convinced me that there is no close relationship between the two families. There are some important differences between the two. *Tetradium* has only four septa, or if secondary septa are present they are conspicuously shorter than the four primary septa. *Heliolites* constantly has twelve equal septa; the septa of Tetradiidae are either outgrowths or plications of the wall, the septa of the "autopores" of Heliolitidae are, as was shown conclusively by Bourne (1895), remnants of walls of adjacent coenenchymal tubes projecting as twelve pseudo-septa into the cavity of the "autopore"; *Tetradium* has no coenenchymal tubes; the larger corallites, occasionally seen in *T. fibratum*, do not differ essentially from the smaller ones, the latter being true corallites in every respect, i.e. provided with definite septa and tabulae, and evidently originally inhabited by independent zoöids; that is, *Tetradium* is definitely not dimorphic. The holotheca which is well developed in many specimens of *Heliolites* has not been observed in any of the massive species of *Tetradium*, i.e. in species most resembling *Heliolites*.

I think therefore that *Tetradium* cannot be a member of the Heliolitidae. There is no similarity between the corallites of *Tetradium* and the "autopores" of *Heliolites*. However, considerable similarity exists if we compare the corallites of *Tetradium* with "syphonopores" of *Heliolites*. This we can do if we consider that "syphonopores" were inhabited by the normal heliolitidian zoöid, and that the "autozooids" served only as specialized, temporary, sexual zoöids of the colony. Should such a view be accepted the terms "autopore" and "syphonopore" could be dropped and replaced by "asexual" and "sexual" corallites.

The similarity of the asexual corallites of *Heliolites* to the normal corallites of *Tetradium* is considerable. Both are slender prismatic tubes, with imperforate and thin walls, provided with complete tabulae, and increasing by fission. It is not uncommon to find a corallite of *Heliolites* splitting into four (see Lindström, 1899, pl. I, Fig. 9, pl. XI, Figs. 31 and 35). The fissional partitions or septa of the genera have much in common. The resemblance is increased by appearance in *Tetradium* of occasional corallites with greater number of septa, and thus comparable to the sexual corallites of *Heliolites*.

Next the question arises whether *Tetradium* could not be

related to the other groups of Alcyonarians. To decide this question we will have to turn back to the Alcyonarian characteristics which were assembled in the first part of this paper. Considering them we see that:—the skeleton of *Tetradium* is solid and never has been shown to be made of spicules; the increase is by fission and not by means of stolonal gemmation of any kind; solenia are absent and the zoöids are not in communication with each other; there is no well marked tendency to the dimorphism which exists in the Alcyonaria; in most Alcyonarians the number of septa is irregular and varies from complete absence or an occasional projecting spine to 20 in *Heliopora* and *Polytremacis*, in *Tetradium* it is mostly four, or if secondary septa appear before fission takes place the number may be increased to twelve, but the two orders of septa are always definite and regularly arranged.

It is my carefully considered conclusion that Tetradiidae have no affinities with the Alcyonaria, and the resemblances pointed out by some authors are only superficial.

We have next to consider the possible relationship of Tetradiidae with the Tetracoralla. As has been pointed out by Lindström and others there are several points of similarity. The tetracoral resembling *Tetradium* most is the Silurian genus *Stauria*.

G. Von Koch (1883) has studied and described the method of increase in *Stauria*. He has shown that the increase is effected by fission into four, when the four main or "division" septa forming the characteristic cross in *Stauria*, split each in halves or "leaves" and thus four new corallites are produced, each new corallite being made of the wall of the parent calice and the two "leaves" of two main septa. The superficial resemblance to the quadripartite fission of *Tetradium* is quite striking. However, Koch was not quite right in his interpretation of the thin sections he prepared. Stanley Smith and T. A. Ryder (1927) have shown that the daughter or hystero-corallites of *Stauria favosa* are not produced by simple fission of the parent corallite. They say: "Gemmation is parricidal, and the gemmae, which are large and only few in number, entirely cover the surface of the parent calice. Typically four buds are developed, one on each of the four quadrants . . . . Over the central part of the calice the daughter corallites lay down new epitheca and septa, which bear little or no relationship to the structures upon which they are super-

posed, but at the margin of the older corallite they carry forward its epitheca and septa."

The new septa thus do not arise directly from four divisional septa but from new epithecal tissue. This process is so different from the simple quadripartite fission of *Tetradium* that there can be no doubt that these two genera are not related to each other.

I further believe that they are not related to any known Tetracoralla. It is true that there are some superficial resemblances such as presence of four main septa, fission somewhat similar to *Stauria*, presence or absence of a columella, imperforate nature of the walls, and a solid skeleton. However, most of these are simply general anthozoan characters not necessarily confined to the Tetracoralla. The differences are much more important. It can be shown without much difficulty that *Tetradium* is not a Tetracoral.

The four septa of *Tetradium* are not arranged in the same manner as the four main septa of the Tetracorals. There are no cardinal, counter, and alar septa in the Tetracoral sense. Secondary septa of *Tetradium* come in between main septa, but are not inclined to any of the main septa. The order of septation in *Tetradium* is very different from the order of septation of tetracorals; it does not follow any of the schemes described by Kunth, Duerden, Brown, or Caruthers. The main difference, however, is the special function of the septa of the Tetradidae. They appear to be nothing more than fissional partitions, incipient cell-walls, rather than septa, and as such are not comparable to the septa of the Zoantharia. *Tetradium* has no fossula; the theca is not formed by bifurcation and coalescence of the septa; the dissepiments commonly found in the Tetracoralla are lacking.

It must be admitted that if there is a relationship between Tetradidae and the Tetracoralla it cannot be direct or close. The main line of Tetracoral evolution was already well established in the middle Ordovician, as is shown by such genera as *Streptelasma* and *Columnaria*. The Tetradidae may best be regarded as an independent line of Anthozoan evolution with no near relatives and no descendants. There are some similarities, but there are even greater differences between the two lines, and I think that it will be impossible to prove that any of the later corals evolved from *Tetradium*. Probably the *Tetradium* line separated from the general line of anthozoan evolution considerably before the more standard types of tetra-

corals appeared, i.e. in the lower Ordovician or Cambrian. This must have happened when the anthozoan ancestor had only four mesenteries.

I have shown that important differences exist between *Tetradium* and the Alcyonaria and the Tetracoralla. *Tetradium* is obviously not a Hexacoral. This leaves us with a question whether it is a coral at all? I believe it is. The septa of the Tetradiidae resemble closely the true septa of corals. They are slender and lamellar, always definitely located in the corallite; their development follows a definite plan and they are not haphazardly placed. In species with a columella the septa may or may not be influenced by it. *Tetradium* goes through the typical anthozoan stages of evolution outlined by Lang (1917), as mentioned above. Tetradiidae resemble closely several coral families. The long grooves on the outside of the tubes exactly opposite the septa are a common anthozoan characteristic.

Tetradiidae very definitely do not resemble the Bryozoa. Nothing even remotely resembling an ancestrula or protoecium has ever been observed. The corallites do not differ in their young and mature stages. In massive forms there is no curving out to come to the surface at right angles. The walls are of uniform thickness throughout the length of the corallite. All other specifically bryozoan characters are also missing. It seems, therefore, that Tetradiidae are an independent, short lived branch of the Anthozoa. I therefore propose that Tetradiidae be regarded as members of a third sub-class of the Anthozoa—the Schizocoralla.

#### HELIOLITIDAE.

The structure and relationship of Heliolitidae has been discussed and described so often that merely to mention the views of every author would take too much space. To avoid this I shall confine myself to the discussion of the systematic position of the family, basing my views on my own observations of *Heliolites* and *Heliopora* and the work of the more recent authors.

The description of *Heliopora coerulea* by Moseley (1876) has provided a strong incentive to compare *Heliolites* and its allied forms with the Alcyonaria. Nicholson (1879) says: "From the researches of Mr. Moseley we know that *Heliolites* and its allies are essentially similar as regards the structure of

the corallum to the living *Heliopora*, and we have therefore the right to conclude that this resemblance extended to the soft parts as well. We have therefore every right to conclude that *Heliolites* and its relations were Alcyonarian Zoöphytes, with polyyps of two different kinds . . . ." However, not all palaeontologists agreed with Nicholson. Although Bourne (1895) and Gregory (1899) expressed themselves in favour of classifying *Heliolites* with Helioporidae as members of the order Coenothecalia of Bourne, others, including such prominent men as Hinde (1883), Lindström (1899), Wentzel (1895), Neumayr, and lately Lang (1917), have been doubtful of such close relationship. Summarising the views for and against, we can tabulate the results as follows:

*Similarities of Heliolites and Heliopora.*

- 1) Coralla of both genera are made of small and large tubes.
- 2) The septa are not comparable to true septa of the Zoantharian corals, but appear in both to be remnants of walls of coenenchymal tubes, which coalesced to form the "autopore" (see Gregory and Bourne).
- 3) Small and large tubes are provided with complete tabulae.
- 4) The walls of each tube of *Heliopora* and *Heliolites* are not even originally distinct, but are common to it and adjacent tubes.
- 5) *Polytremacis* may indicate the transition from Palaeozoic Heliolitidae to the living *Heliopora* (see Gregory).

*Differences between Heliolites and Heliopora.*

- 1) There is an essential difference between the calicular walls of *Heliolites* and *Heliopora*. In *Heliopora* the wall of the calice is made by fusion of the vertical rods or echinulations, which also form its blunt pseudo-septa extending as ridges down the inner sides of the calice; in *Heliolites* the walls are complete and appear to be made of lamellar elements representing the walls of adjacent coenenchymal tubules. Although the structures are to some extent homologous the appearance of the walls of *Heliopora* and *Heliolites* is strikingly different.
- 2) The walls of coenenchymal tubes of *Heliolites* are much thinner than in *Heliopora*.

3) The coenenchymal tubes of *Heliolites* are regularly polygonal in section, and closely contiguous, those of *Heliopora* are very irregular in cross-section and are spaced at irregular intervals.

4) Septa may be present or absent in *Heliolites*. When present they are long and lamellar, often nearly reaching the centre of the corallite. Such long septa could not be independent of the mesenteries of the zoöid. The septa of *Heliopora* are blunt wedge-like ridges, formed by the vertical rods, which by fusion produced the walls of the calice.

5) The tubules of *Heliopora* are not capable of increase either by fission or otherwise, they are not independent entities; their number is increased by special *down-growths* of the tubular off-sets of the polyp cavity. The tubules of *Heliolites* continuously and independently increase by fission, into two or four, therefore each tube is continuous and branches many times as it grows *upward*.

6) The fission of coenenchymal tubes of *Heliolites* is effected by a growth of fissional partitions, resembling septa of such corals as *Tetradium* and *Chaetetes*; nothing of this sort is present in the coenenchymal tubes of *Heliopora*.

7) *Heliopora* has a well marked axial region made of thin-walled parallel tubes. The tubes bend outward and reach the surface of the corallum at right angles, at the same time thickening their walls. No difference of any nature is observable between the deeper and superficial portions of *Heliolites*. There is no axial region, and the corallites grow as straight radiating tubes from the basal holothea.

8) A long time interval separates the Silurian and Devonian *Heliolitidae* from the recent *Heliopora* and even from the Cretaceous *Polytremacis*.

Professor J. W. Gregory (1899) reviewed the relationship of *Heliopora* and *Heliolites*, and criticized the views of Lindström and Hinde that the septa of the two corals are different and that *Heliopora* lacks the calicular theca of the *Heliolitidae*. I agree with Professor Gregory that the septa of neither of these genera are true septa in the Zoantharian sense. Nevertheless the fact remains that the septa of *Heliolites* are long, slender, lamellar structures entirely different from the ridges running down the inner sides of the calice of *Heliopora*. The septa of *Heliolites* may be walls of the coenenchymal tubes that entered the formation of the calice, but in some instances appear to be independent growths. The septa of *Heliopora*

are never anything but fluted ridges caused by thickening and fusion of the vertical echinulations.

As regards the calicular theca, it is a much more definite structure in Heliolitidae than in Helioporidae. But even granting that these two differences are not as important as they appeared to Hinde and Lindström, additional important differences remain.

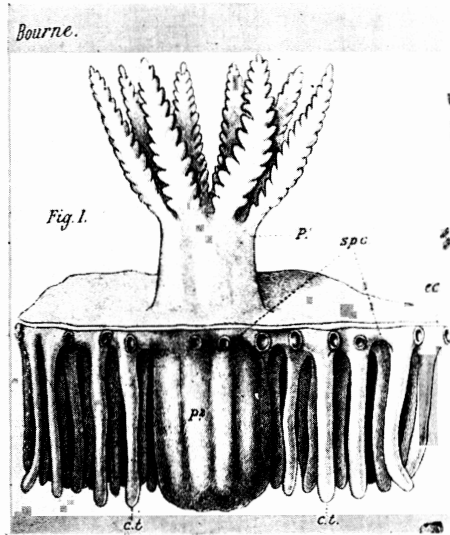


Fig. 1. A single polyp with the adjacent soft tissues of *Heliopora*, as seen after removal of the skeleton by decalcification. Partly diagrammatic. P<sup>1</sup>, the exsert moiety of an expanded polyp, bearing eight pinnate tentacles. P<sup>2</sup>, the proximal insert moiety of same. ec., the continuous sheet of ectoderm which clothes the whole surface of the colony. spc., superficial canal system lying directly beneath the ectoderm. ct., coenenchymal caeca or tubules (after Bourne).

Bourne (1895) in describing *Heliopora coerulea* stated that "the coenenchymal tubes of *Heliopora* appear to me to be nothing more than specialized portions of a system of tubular off-sets of the polyp cavity." Very excellent illustrations of the animal of *Heliopora* illustrate this idea (see Fig. 1).

The tubules are therefore necessarily closed at the bottom and cannot increase in number in any other way, than by insertion of new tubular *down-growths*. This is precisely what happens. Thus Bourne in describing *Heliopora* says that

coenenchymal tubes of *Heliopora* are intercalations between and not (with few exceptions) branches of pre-existing tubes. They start growing as small triangular cavities, usually in the spaces where the walls common to three contiguous chambers unite, and end blindly below.

This is very different from *Heliolites*, the coenenchymal tubes of which increase by fission as they grow upward. This different mode of increase indicates a very differently constructed animal inhabiting the skeleton. The smaller tubes of *Heliolites* could not be filled by "tubular off-sets of the polyp cavity" but must have been inhabited by independent zoöids, capable of individual increase by fission. *Heliolites* then must have been truly dimorphic, the two sets of tubes occupied by different types of zoöids. The larger tubes are formed by coalescence of several smaller ones, as was shown by Lindström and others. After a certain length of existence they are closed over again by encroachment of coenenchymal tissue. This shows that the larger zoöids had a temporary function, most likely being the sexual zoöids of the colony. If this be the case the smaller zoöids must have been the normal type, increasing asexually by fission.

Another important difference is in the structure of the corallum as a whole. *Heliopora* is characterized by the presence of a definite axial region, composed of thin-walled tubes; these tubes are from time to time deflected and reach the surface of the corallum at right angles. The larger tubes, "autopores," never penetrate the axial region. Nothing comparable to this can be seen in *Heliolites*. Both large and small tubes grow in essentially straight lines, diverging radially, because of increase in number: there is no difference between the older and the younger parts of the corallum. In some cases the corallites start growing from the holotheca, or new corallites may be produced by calicinal gemmation. All these facts cast serious doubt upon the theory that *Heliolites* and *Heliopora* are closely related.

I have to add here that I cannot agree with Lindström in regard to his hypothesis, that the coenenchymal tubes of *Heliolites* and its allies, are endothecal structures, and that the larger calices can be compared to the inner cavity of such corals as *Acervularia*, the apparent theca being a homologue of the inner wall of *Acervularia*, and the coenenchyma to the septate zone. The work of Gregory (1899), Bourne (1895), and

Hinde (1883), and my own observations cannot be reconciled with such a view.

As regards the "coenenchyma" of the Heliolitidae, several explanations of its function can be advanced. It is certainly not analogous to the syphonozooids of some Alcyonarians, serving to increase the circulation of water. Of such function it is incapable, for the separate tubes apparently are not in communication with each other, since there are no mural pores or stolons connecting them. Neither are the coenenchymal tubes tubular off-sets of the cavity of the larger zooids (as in *Heliopora*), as has been shown already. It is possible that the so-called coenenchymal tubes are occupied by regular zooids; this is suggested by their ability to increase independently by fission. The larger calices might have been inhabited by specialized zooids capable of sexual reproduction. This idea is indirectly supported by the fact that larger calices appear temporarily by coalescence of several smaller tubes, and then, as was pointed out by Lindström, and observed personally, disappear again, being closed off by development of several smaller tubes. This would indicate that after the large zooid was functional sexually for a certain period, its usefulness or vitality has decreased and the normal type of zooid would take its place.

On the other hand, the smaller tubes may be just an ordinary type of true coenenchyma common in several types of corals. This opinion is supported by the presence of vesicular, instead of tubular, coenenchyma in such genera as *Plasmopora*, etc.

If we admit that the evidence adduced is sufficient to remove *Heliolites* from affinity with *Heliopora*, the question arises, can there be an affinity with the other Alcyonaria? In favour of this are the tendency to dimorphism and the pseudosepta of the Heliolitidae. Strongly against such an affinity are:—the solidly calcareous and not spicular skeleton, the long, well developed septa, the absence of solenia or stolons, and even mural pores, the increase of the smaller corallites by fission, the lack of resemblance to other Alcyonarian corals. With the *Tetracoralla* or the *Hexacoralla* there is evidently no relationship.

I am therefore forced to agree with Lindström, though for somewhat different reasons, that the Heliolitidae are corals not closely related to any of the groups above mentioned, and must stand in a group by themselves.

The only other group with which they may have a distant

relationship are the Tetradiidae. But this relationship can be understood only in case we agree that the normal zooids of *Heliolites* are those inhabiting the smaller tubes, and not the larger "autozooids." Should this be the case, there are points of similarity between the two families, and both can be included as separate orders of the new sub-class—Schizocoralla.

#### CHAETETIDAE E. & H.

The Chaetetidae, as here discussed, are limited to forms of which *Chaetetes radians* Fisher from the Moscovian of Russia is the type.

The Chaetetidae have had a very unfortunate history. Many bryozoan genera have been included in the family, and even referred to the genus *Chaetetes*. Afterwards, when the bryozoan nature of these intruders was established, *Chaetetes* proper was suspected by many palaeontologists of being a bryozoan. Recently (1930) Smith and Lang revised the genus *Chaetetes*. They take *Chaetetes radians* Fisher as the type, and give the following diagnosis of the genus. "Ceriod or meandroid Tabulate corals, which form tumular or stratiform masses, and have small corallites with thin, complete, horizontal tabulae, but no septa, and probably no mural pores. The walls separating the individual corallites are often incompletely formed, and may appear like solitary septa; or they may be locally absent, and then give rise to meandroid colonies."

The specimens I studied were mostly *C. radians* from the Carboniferous of Russia and some less perfect specimens from the Carboniferous of the United States. A few additional notes on the specimens at hand will be made.

The corallum of *Chaetetes radians* is composed of closely contiguous irregularly prismatic or irregularly cylindrical corallites, on the average 0.35 mm. by 0.54 mm. in cross-section. The walls are from 0.05 mm. to 0.10 mm. in thickness. Many of the larger coralla appear to be made up of several small bunches of corallites, each bunch having a more or less definite central area from which the corallites radiate. The corallites are provided with complete horizontal tabulae, spaced, in well preserved specimens, at intervals equal to one or two diameters of the corallite. The tabulae are arranged at different heights in adjacent corallites, and stratiform masses such as those mentioned by Smith and Lang were not seen in any of the specimens studied. The tabulae are thinner than

the walls, and are not preserved in some specimens. The walls of the corallites are fairly uniform in thickness and are imperforate. Walls of adjacent corallites, in the great majority of cases, are fully amalgamated; only in one or two instances was a line separating the walls observed.

One specimen of *C. radians* had a portion of the holotheca preserved. It is a thin, strongly wrinkled film, resembling somewhat the similar structure of *Heliolites*. The corallites grow at right angles to it, and appear as fully developed tubes from the very beginning. There is no indication of stolonial canals in the holotheca.

The corallites increase in number by fission. A tooth or partition begins to grow on one side of the corallite and on reaching the opposite side splits the corallite in two. In some cases a similar "septum" starts at the same time from the opposite wall, the two meeting in the middle. Rarely one corallite may have three or four such fissional partitions at once, when the resemblance to *Tetradium*, or the asexual corallites of *Heliolites*, is considerable. The fission is very rapid, and in all observed cases, was completed in the space enclosed between the two tabulae. Not all Chaetetidae increase only by fission, for Peterhans (1927, 1929) has described *Bauneia*, a coral very similar to *Chaetetes*, as increasing both by fission and by gemmation.

Parasitic worm tubes were observed attached to the holotheca and also embedded within the corallum. The ones inside the corallum probably belong to the spiral worm *Streptindytes*.

According to observations of Heritsch (1935) and Smith and Lang (1930), which I can fully support, *C. radians* Fisher, *C. septosus* (Fleming), and *C. millemoraceous* E. & H. are conspecific. Lack of material prevents further comparisons of genera and species included in the family Chaetetidae at present.

#### *Affinities of Chaetetidae.*

*Chaetetes* differs so much from the more familiar Anthozoa that it is necessary to consider the possibility of it being a bryozoan. The absence of definite septa, the small size of the corallites, and completely amalgamated walls are the most important similarities.

However, the importance of these similarities is more apparent than real. The absence of real septa is also true of both small and large corallites of *Heliolites*, and of *Prismostylus* and

*Tetradium* of the Tetradiidae; the size of the corallites is not less than that of *Tetradium minus* or *Prismostylus aseptatus*; the complete amalgamation of walls is not a characteristic by which Anthozoa and Bryozoa can be distinguished.

On the other hand the differences are very great, even if we compare *Chaetetes* with Trepostomata Amalgamata, the order of Bryozoa which most resembles Chaetetidae. The increase by fission is not characteristic of the bryozoa, cysts and cysti-phragms are wanting, communication pores are absent, nothing comparable to acanthopores or mesopores exists, protoecium and ancestrula are absent, no mature or immature regions are distinguishable, and the corallites grow in straight radiating lines, essentially as do those of *Favosites* or *Tetradium*. The walls are of uniform thickness throughout, the tubes do not bend outward, and the tabulae are not more abundant in the peripheral region.

It is evident that there is nothing in common between the Chaetetidae and the Rugosa. The absence of septa in the Chaetetidae is a sufficiently important characteristic to definitely remove all possibility of a relationship.

I do not believe either that there is a relationship with the Alcyonaria. The method of increase does not resemble that of any of the undoubted Alcyonarians. Solenia or stolons are absent, there is absolutely no tendency to dimorphism, there is no coenenchyma, the skeleton is not made of spicules, and the walls appear to be fully amalgamated.

We are therefore forced to the conclusion that Chaetetidae are an aberrant branch of the Anthozoa. Their method of increase resembles to some extent the fission of Tetradiidae and the fission of the small corallites of *Heliolites*. The corallites are slender, prismatic, imperforate, with complete horizontal tabulae; true septa are lacking, the partitions apparently serving only the purpose of increase. These characteristics are probably sufficient to justify the inclusion of the Chaetetidae as the third order—the Chaetetina—in the Schizocoralla.

#### SYRINGOPORIDAE, HALYSITIDAE, AND FAVOSITIDAE.

Time did not permit me to enter into consideration of these families. I have therefore no right to speak of their relationship either with the Schizocoralla, or with the other groups of corals. The work of S. J. Hickson, Bourne, and others strongly suggests, however, that these families are Palaeozoic

Alcyonaria. This conclusion is best reached by elimination of other possibilities.

The Hexacoralla are immediately taken out of the question because of the development of their septa and their chronological position. The Tetracoralla differ materially from all the genera under question by the arrangement of their septa, and the generally imperforate nature of both the septa and walls (*Calostylis* is the exception to the general rule). The Schizocoralla differ by their method of increase and absence of any indication of solenia or stolons.

Therefore Halysitidae, Syringoporidae, and Favositidae are either Alcyonaria, or belong to a distinct sub-class of the Anthozoa. The latter seems hardly possible, since the above mentioned families possess some strongly Alcyonarian characteristics. Of special importance in this respect are a tendency to dimorphism in some genera, stolonal gemmation, and presence of solenia. Until further work is done in this field it is possibly best to regard them as Palaeozoic Alcyonaria.

#### CONCLUSIONS.

From the preceding review of some of the genera of Tabulate corals it is seen that Tetradiidae, Heliolitidae, and Chaetetiidae stand apart from other Anthozoan groups, whereas the Syringoporidae, Halysitidae, and possibly the Favositidae may best be regarded as Palaeozoic Alcyonaria.

Increase by fission, and absence of true septa characterises the first mentioned families. In each, all or some of the corallites increase in number by building of partitions across the corallite and thus splitting it into two or four. In other respects the families are widely different from each other.

It is with some hesitation that I propose a new sub-class of the Anthozoa to include these aberrant families. Such a classification is to some extent artificial; however, it is no more so than the present one. In my support I may quote the distinguished British zoölogist, Professor S. J. Hickson, whose accurate and thoroughly reliable work is a model of scientific precision. He says: "The classification [of the Alcyonaria] is at present frankly an artificial one, and it seems to me that if we have to choose between two artificial systems, one consideration should influence our choice, and that is the convenience of the systematist . . . ."

The new sub-class Schizocoralla will include the orders Tetradina, Heliolitina, and Chaetetina; its characteristics are as follows:—

Class Anthozoa.

Sub-class Schizocoralla nov.

*Diagnosis*:—Mostly Palaeozoic Anthozoa forming simple, branching or massive coralla. Corallites long, slender, with imperforate walls, and numerous, complete, horizontal or slightly arching tabulae. The walls of most of the corallites are completely amalgamated. Corallites provided with lamellar, vertical plates, arranged around the circumference of the corallite and so resembling the septa of the Zoantharia. The main function of these plates or septa is to provide asexual reproduction through simple fission of each corallite in two, three, or four. A columella is present in some genera.

*Order 1, Tetradina nov.*

Schizocoralla characterized by four long septa, square, rectangular, or polygonal corallites, which reproduce by quadripartite fission. Confined to the Ordovician of North America and Beeren Island.

Family Tetradidae Nicholson.  
Genus Tetradium Dana.  
Genus Prismostylus Okulitch.

*Order 2, Heliolitina nov.*

Schizocoralla characterized by dimorphic corallites, the normal, smaller corallites increasing by fission into two or four, the larger corallites probably serving sexual reproduction. In some members of the order the normal corallites are reduced to irregularly vesicular tissue. Walls of corallites fully amalgamated. Silurian and Devonian.

Family Heliolitidae Lindström.  
Genus Heliolites Dana.  
Genus Plasmopora E. & H.  
Genus Propora E. & H.  
etc.

*Order 3, Chaetetina nov.*

Schizocoralla forming cerioid or meandroid coralla, composed of simple prismatic corallites with fully amalgamated walls. Reproduced by fission in two, or rarely, four. Carboniferous and Mesozoic.

Family Chaetetidae E. & H.

Genus Chaetetes Fisher.

Genus Baunea Peterhans.

etc.

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