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## XLV.—On the Stromatoporoids and Eozoon.

By R. KIRKPATRICK.

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[Plates VIII. &amp; IX.]

IN a letter to 'Nature,' Aug. 15, 1912, p. 502, I wrote that the presence of siliceous spicules in the Stromatoporoids, similar to those found in *Merlia* and *Monticulipora*, had led me to the conclusion that Stromatoporoids were Sponges. I must now state that I was misled to that conclusion, for it has become evident to me that the supposed spicules are the calcified chitinous rings and half-rings belonging to the canals and chambers of Foraminifera. It is now clearly obvious also that the calcareous skeleton of Stromatoporoids has a structure similar to that of the higher forms of Perforate Foraminifera.

It is not surprising that palæontologists have failed to arrive at a correct solution of the problem of the Monticuliporas, for these organisms, when alive, exhibit extraordinary phenomena without parallel elsewhere in biology, and wholly impossible to understand without observing living specimens. Most fortunately the discovery of the living *Monticulipora* (*Merlia*) *normani* off Porto Santo Island will enable me to explain the real nature of the Palæozoic examples.

The Stromatoporoids, on the other hand, carry in themselves the clue to the problem they present, and it is at first sight a little surprising that this clue has eluded the patient search of so many investigators. This result was, I believe, due to the use of insufficiently high magnifying-powers.

Stromatoporoids are commonly in the form of hemispherical or cake-like masses, but they may be incrusting or digitate.

The surface has a roughly granular aspect and presents scattered stellate patterns (astrophizæ). A vertical section (or weathering of the edges) shows that the mass is built up of concentric laminæ or crusts.

Slight magnification of a vertical section shows apparently a meshwork of regular or irregular radial and concentric calcareous strands, these being really the edges of walls of Foraminiferal chambers.

The so-called "tabulæ" are present in the usually darker calcified soft tissues filling the meshes or spaces not only in *Stromatopora*, but also in *Actinostroma*. Stromatoporoids are found in the Ordovician, Silurian, and Devonian strata.

From Nicholson's great monograph on the British Stromatoporoids I extract a few historical data.

The history of the group practically begins with Goldfuss (1826), who described a fossil (probably from the Devonian of Gerolstein), which he named *Stromatopora concentrica* and placed near *Millepora*.

In the following list I give the name of the author, the date, and his views as to the nature of Stromatoporoids :—

- GOLDFUSS, 1826. Hydrocorallinæ.  
 STEININGER, 1834. Sponges.  
 F. RÖMER, 1843-4. Corals.  
 HALL, 1847. Alcyonarians near *Tubipora*.  
 D'ORBIGNY, 1850-51. Sponges.  
 The two SANDBERGERS, 1850-56. Polyzoa.  
 F. RÖMER, 1851-56. Polyzoa, but later tabulate corals like *Favosites* and *Chaetetes*.  
 BILLINGS, 1857. *Beatricea* (a Stromatoporoid), a vegetable.  
 RICHWALD, 1860. Horny sponges.  
 HYATT, 1865. Some Stromatoporoids regarded as Cephalopoda.  
 BARON VON ROSEN, 1867. Horny sponges.  
 DR. G. LINDSTRÖM, 1870. Foraminifera, and, in 1873, *Labechia* allied to Hydractinia.  
 SALTER, 1873. Calcareous sponges.  
 NICHOLSON, 1873-4. Calcisponges.  
 DAWSON, 1875. Between Foraminifera and Sponges.  
 SOLLAS, 1877. Hexactinellid sponges, and, later, partly siliceous sponges, partly Hydrozoa.  
 CARTER, 1877. Hydrozoa.  
 NICHOLSON, 1886 (the Monograph). Partly Hydroida, partly Hydrocorallinæ.  
 ZITTEL, 1903. Hydrozoa.  
 GEIKIE, 1903. Polyzoa.  
 STEINMANN, 1907. Hydrozoa.  
 KIRKPATRICK, August 1912: Sponges. September 1912: Foraminifera.

To sum up, within the last eighty-six years Stromatoporoids have been regarded as Foraminifera; calcareous, horny, Monaxonellid, and Hexactinellid Sponges; Hydroida, Hydrocorallinæ, *Alcyonaria*, corals (Anthozoa), Polyzoa, Cephalopoda, vegetables.

Kepler wrote a treatise, which is said to be highly instructive, entitled 'A Book of Mistakes.' A few observations on some of the errors recorded in the above list will not be without interest.

The "Cœlenterate" view was mainly held on account of the presence of "tabulæ," the Sponge theory owing to the oscule-like astrorhizæ, to the incrusting and enveloping character of some species, and to the resemblance of the skeletal

framework to that of a Dictyonine sponge. *Beatricea* was compared to an *Orthoceras*-like mollusc.

I myself at first mistook altered chitinous rings and coils for siliceous spicules, the astrorhizæ for oscules, and the tabulæ for diaphragms and dissepiments like those of *Cliona*, and regarded the general skeletal framework as an originally spicular structure altered by mineralization, for I could often see rings and apparent sigmas imbedded in it. I found later, however, that the supposed "spicules" were altered chitinous hoops and spirals. The astrorhizæ appear to be due to the fusion of several outer openings of tubuli, thereby leading to the converging of finer pseudopods into main trunks. Pl. IX. figs. 13, 14, representing a longitudinal vertical section of *Polytrema cylindricum*, shows, for instance, tubuli with a relatively large single external opening and one, two, or three smaller inner openings, a compound system being funnel-shaped with a cribriform mouth directed inwards. A growth and extension of this simple system would result in the formation of an astrorhiza. Further, a more careful examination revealed the typical Foraminiferal structure of the skeleton itself.

What chiefly led me to regard the Stromatoporoids as siliceous sponges was the discovery, in the sections of those fossils, of little "pockets" of coiled sigma-like bodies and also tubular canals lined with these bodies in scalariform fashion. I had seen a somewhat similar arrangement of ring-like real siliceous spicules in the sponge part of "*Merlia normani*," which at one stage of my devious gropings after the clue to this mystery I had named *Noronha scalariformis*. But presently I found similarly shaped rings in the soft tissues of decalcified recent Foraminifera\*. Here the chitin has resisted the acid used for decalcifying, and the rings seemed to be chitinous, but in the fossils they looked like siliceous spicules. I now examined the skeletal framework, and saw that it was penetrated by tubuli and channels of communication between chambers.

The so-called tabulæ, which were supposed by Nicholson to be similar to those of *Millepora*, are diaphragms formed in the chambers and in the course of the canals.

These "tabulæ" are present in the spaces filled by the soft tissues, both in the *Stromatopora* type and in the *Actinostroma*

\* Evidently the function of the chitinous hoops and coils is to give support to the soft monilated branching sarcode. The swellings on many of them are due apparently to lateral compression arising from the pull of the extensile sarcode along an axis at right angles to the plane of the hoops.

type of Stromatoporoids. Apparently Nicholson failed to see them in the latter, supposing the holes in the regular "tangential laminæ" to represent the "zooidal tubes."

Nicholson's classification, based on the erroneous idea that one group of Stromatoporoids (the Actinostromidæ) was related to *Hydractinia*, and the other (Stromatoporidæ) to *Millepora*, needs revision. As Nicholson himself pointed out, there are transitions between Actinostromids and Stromatoporids. In both there are concentric layers, astrorhizæ, "tabulæ," and a capacity for incrusting and enveloping other objects, such as corals. In the Actinostromid or rectilinear type the calcareous skeleton has a more regular and definite arrangement of chambers than has the Stromatoporid type.

My intention in the present paper, however, is not to enter into the question of the classification of Stromatoporoids, but mainly to announce that these fossils have a calcareous skeleton showing the Foraminiferal structure.

While I was examining sections of the aberrant genus *Beatricea* I was reminded of the peculiar structure of *Eozoon*, and was thereby led to examine specimens of the latter, despite the fact that current opinion is almost wholly opposed to a belief in their organic nature. Zittel\*, following Prof. Karl Möbius†, refers to *Eozoon* as a product of purely mineral origin. Steinmann‡ does not even mention this, perhaps the most interesting of all fossils, but writes, "Aus der eozooischen Periode kennen wir kaum sichere Spuren organischer Wesen." Likewise in Lister's§ memoir on the Foraminifera there is no reference to *Eozoon*. Hartog|| writes in a footnote: "The alleged Archæan genus *Eozoon*, founded by Carpenter and Dawson on structures found in the Lower Laurentian serpentines and referred to the close proximity of Nummulites, has been claimed as of purely mineral structure by the petrologists; and recently biologists have admitted the claim." Geikie||, while stating the pros

\* Zittel, K., 'Grundzüge der Paläontologie,' Abth. i. 2nd edition, 1903, p. 35.

† Möbius, K., 'Palæontographica,' xxv. 1878, p. 175. Also Carpenter, on Möbius's results, 'Nature,' vol. xx. 1880, p. 272.

‡ Steinmann, G., 'Einführung in der Paläontologie,' ed. 2, 1907, p. 7.

§ Lister, J. J., 'Treatise of Zoology' (ed. by E. R. Lankester), Memoir "Foraminifera."

|| Hartog, M., 'Cambridge Natural History' (Harmer and Shipley), Memoir "Protozoa," 1906, p. 70.

|| Geikie, A., 'Text-book of Geology,' 1903, p. 878. See also Sherborn, 'Bibliography of the Foraminifera,' under Dawson, Möbius, Carpenter, &c.

and cons of the opposing views, apparently inclines to a belief in the mineral theory, and demands, in view of the antiquity of the rocks and the changes to which they have been subjected, the clearest possible evidence of organic structure before accepting the theory of the organic nature of *Eozoon*.

I consider that the sections made by the late Dr. Carpenter yield abundant evidence of organic structure.

*Eozoon canadense* is a Foraminiferan. Its calcareous skeleton shows clearly the Foraminiferal structure of pores and tubuli, and, further, chitinous rings and coils are present.

Dr. Carpenter's specimens must have died peacefully on the Lower Laurentian sea-bottom, and have been buried and slowly metamorphosed by infiltration, but in such a way as to preserve a good deal of their structure. Possibly igneous eruptions may have occurred later within varying distances of the dead specimens, leading to varying degrees of mineralization. I suppose the theory of the mineral origin of *Eozoon* is due to the existence of much metamorphosed specimens.

Fortunately Dr. Carpenter had several very fine examples of *Eozoon* in his magnificent collection (now in the British Museum, Nat. Hist.). About the time of his death he was engaged in writing a monograph which would have finally settled the whole question. A friend of mine who knew him tells me that Dr. Carpenter could scarcely listen with patience to the arguments of the mineralists, and I can appreciate this attitude when I look at his beautiful sections. Sir William Dawson, too, had occasion to resent the charge of "subjectivism" brought against him by an upholder of the mineral theory.

Sir W. Logan\* was the first to notice the resemblance of *Eozoon* to the Stromatoporoids.

The recent Foraminiferan *Polytrema cylindricum*, Carter, recalls in certain respects both *Beatricea* and *Eozoon*. This pretty little branching Foraminiferan, of a brilliant yellow or red colour, has a surface-layer of large chambers, but at the same time the central axis of the branches is occupied with a smaller vesicular tissue. A transverse section of *Beatricea* has somewhat the appearance of that of a megalospheric Foraminiferan.

In the Stromatoporoids and *Eozoon* there is a many-chambered (Polythalamous) calcareous skeleton with the walls of the chambers penetrated by fine tubuli. Altered chitinous hoops and coils are found in the communication-

\* Logan, W., 'Geology of Canada,' 1863, p. 49.

channels between chambers and in the chambers themselves, *i. e.* in the spaces formerly filled with sarcode. Similar structure to the above is found in the recent Perforate Foraminifera. Weathered edges of specimens of *Eozoon* are finely laminate.

With regard to *Eozoon*, two objections are urged against the organic theory, viz. the immense antiquity of the Lower Laurentian limestones and the unlikelihood that any organic structure could survive the effect of metamorphosing agencies. Concerning the first objection, it may be said that when once an organism is entombed and infiltrated the time factor *per se* is not an important one. Many Devonian Stromatoporoids are less well preserved than those of Silurian age, and a Foraminiferan might retain its structure as well in a Laurentian as in a Wenlock limestone. The effect of igneous action on the fossils of any particular formation is apparently more or less a matter of chance, and examples of late origin may fare worse than those of earlier date.

Leaving hypotheses and coming to facts—to wit, the specimens themselves,—I find that the Foraminiferal theory is wholly adequate, and I am certain it is unnecessary to go further afield in search of some highly complicated and problematical theory of mineral origin. As a matter of course, the evidence for the mineral theory, based mainly on the existence in *Eozoon* of minerals of igneous origin, falls to the ground in presence of the least trace of indubitable organic structure.

*Summary.*—The Stromatoporoids are Foraminifera.

*Eozoon canadense* likewise belongs to the Foraminifera, and is nearly related to *Labechia* and *Beatricea*.

#### *Note on Caunopora.*

Many of the *Caunopora* tubes so frequently found in Stromatoporoids are not corals, but Chaetopod worms, apparently belonging to the group Spioniformia.

It is sometimes possible to see anatomical features, such as the introvert, pharynx, intestine, peristomial cirri, and acicula. The supposed “tabulæ,” which have misled some investigators, are simply the expression of Annelidan segmentation or, rather, annulation.

I have found what appears to be a similar kind of worm in the living *Monticulipora* (*Merlia*) *normani*, and at Porto Santo Island have often watched it extending and drawing in its peristomial cirri or “tentacles.” The Palæozoic Monticuliporas are frequently infested with a worm possibly related to this modern one. If this is so, we have a curious instance of the conservatism of Nature.



EXPLANATION OF THE PLATES.

PLATE VIII.

- Fig.* 1. *Stromatopora concentrica*, Goldfuss, from Devonian of Gerolstein. Wall of a chamber, showing tubuli.  $\times 325$ .  
*Fig.* 2. Larger tubuli from an older wall.  $\times 550$ .  
*Fig.* 3. Hoops and coils in chambers and canals of *S. concentrica*. 3 a. Ditto from *Actinostroma clathratum*, Nich. Both  $\times 1300$ .  
*Fig.* 4. Ditto from sarcode of *Polytrema cylindricum*, Carter.  $\times 1300$ .  
*Fig.* 5. Part of wall of chamber of *Eozoon canadense*, Dawson, from Lower Laurentian limestones, Burgess, Canada, showing mural pores and tubuli.  $\times 140$ .  
*Fig.* 6. The same.  $\times 550$ .  
*Fig.* 7. Old branching canals in *Eozoon*.  $\times 1300$ .  
*Fig.* 8. Branching system of canals in *Eozoon*.  $\times 35$ . 8 a. The same showing hoops.  $\times 325$ .  
*Fig.* 9. Hoops and coils in chambers and canals of *Eozoon*.  $\times 1300$ .  
*Fig.* 10. The same from another specimen.  $\times 1300$ .

PLATE IX.

- Fig.* 11. Canals in *Eozoon*.  $\times 140$ .  
*Fig.* 12. *Eozoon*. Young chambers forming just below surface of specimen. a, mural tubuli; b, diaphragm across opening in chamber.  $\times 140$ .  
*Fig.* 12 A. Series of young chambers.  $\times 50$ .  
*Fig.* 12 B \*. Minute Foraminiferan found in one of the chambers of *Eozoon*.  $\times 190$ .  
*Fig.* 13. Vertical longitudinal section of *Polytrema cylindricum*, Carter.  $\times 12$ .  
*Fig.* 14. Wall of chamber of same, showing branching tubuli.  $\times 100$ .  
*Fig.* 15. *Caunopora* tube in *Stromatopora bucheliensis*, Bargatzky, Devonian, showing Spioniform worm inside. a, acicula.  $\times 35$ .  
*Fig.* 16. Another *Caunopora* tube from same section, showing surface annulations of annelid inside.  $\times 17$ .

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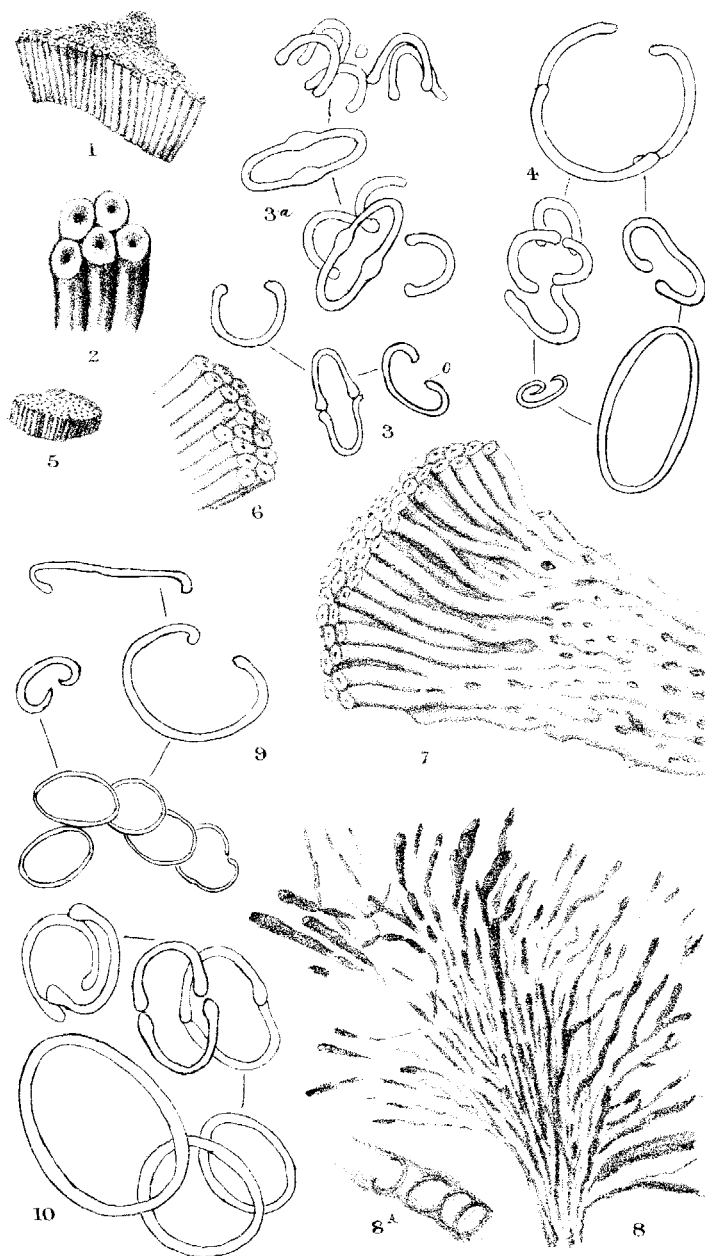
XLVI.—*The Anatomy and Classification of the Teleostean Fishes of the Order Lyomeri.* By C. TATE REGAN, M.A.

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Order LYOMERI.

Scaleless soft-rayed fishes with a long slender tail, dorsal and anal fins long, no caudal, pectorals (when present) small and pelvics absent. Gill-openings small, separate. Mouth

\* The discovery of the beautiful little coiled shell (*fig.* 12 B) in one of the chambers of *Eozoon canadense* settles the "*Eozoon controversy*" beyond the possibility of further dispute. I do not think that the shell is a young stage of *Eozoon*, but rather that it has been ingested as food from without.

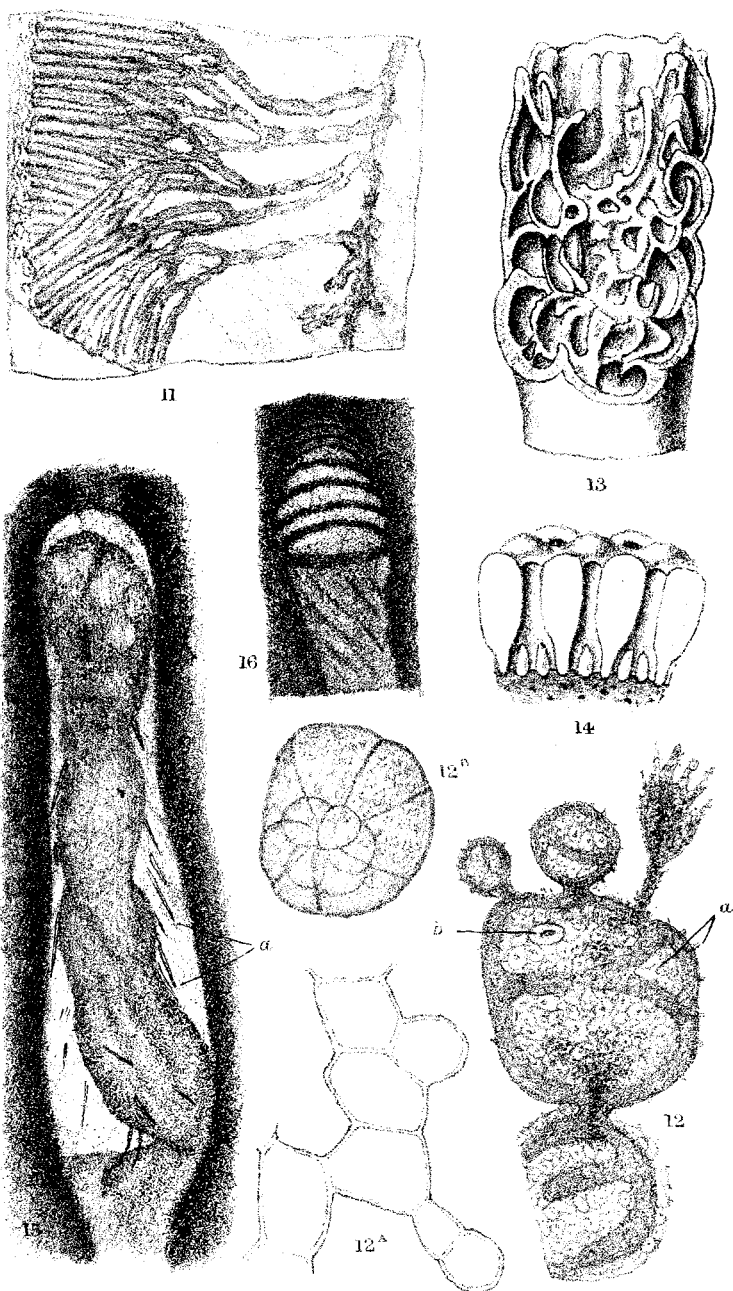


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1-3<sup>a</sup> STOMATOPORA. 4. POLYTREMA.

5-10 EOOZON



Percy Highley, del et lith.

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11-12 B. EOOZON. 13-14 POLYTREMA.

15-16. CAUNOPORA.