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XXXVII.—On the affinities of Palæozoic tabulate corals with existing species

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pressa; apertura latiuscula, brevior quam anfractus ultimus, basi sensim dilatata; columella brevis, incrassata, haud torta.
Long. $1\frac{1}{3}$ mill., diam. $\frac{3}{4}$.

Hab. Persian Gulf, 14 fathoms (*Col. Pelly*).

Its minuteness constitutes the principal distinctive character of this species. The tubercle which forms the apex is proportionally very large.

Planaxis puncto-striatus. B.M.

P. testa acuminato-ovata, nitida, alba, lineis spiralibus rufis, partim interruptis (in anfr. ult. circiter 9), cincta; spira elongata, apice obtuso; anfract. 6, parum convexi, primi 3 basimque versus transversim sulcati, cæteri crebre puncto-striati; apertura ovata, alba, spiram æquans; columella arcuata cum labro callositate juncta; labrum incrassatum, intus denticulatum; canalis basalis brevis.

Long. $7\frac{1}{2}$ mill., diam. $3\frac{3}{4}$.

Hab. Gulf of Suez (*M. Andrew*).

This pretty species may be recognized from any other by the nine transverse red lines and the punctured striæ, about twenty in the body-whorl.

XXXVII.—On the Affinities of Palæozoic Tabulate Corals with Existing Species. By A. E. VERRILL.*

THE works of Milne-Edwards and Haime upon corals are so extensive and important, and their classification is so well understood and generally adopted, especially by geologists, that it is of great importance that their errors of classification should be pointed out and fully understood.

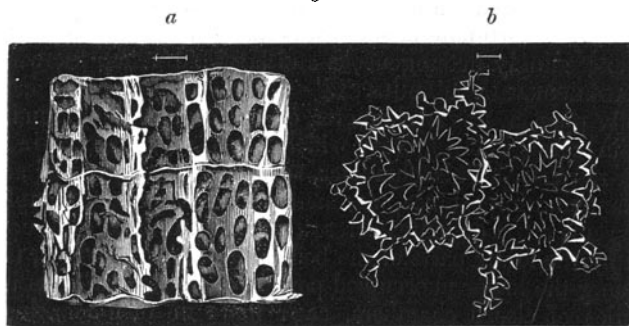
A very unfortunate mistake was made when they instituted the exceedingly heterogeneous and artificial group known as "MADREPORARIA TABULATA." This division was based wholly upon a single character of uncertain value, found in certain corals differing very widely among themselves in all other respects. This character, regarded by them as of such fundamental importance, was merely the existence of complete transverse septa or plates across the coral-tubes, or cells, occupied by the lower parts of the bodies of the coral-polyps, thus dividing the lower unoccupied portion of these coral-cells into a series of closed chambers, each plate in turn marking a former position of the base of the polyp which occupied the cell, as it grew upward. In most of the other corals, on the

* Communicated by the Author from the 'American Journal of Science' for March 1872.

contrary, there are either no transverse plates, or else they exist between the radiating lamellæ or septa, thus dividing each of the *radiating chambers* into a series of transverse cavities, which are *usually* not exactly on the same level in the different chambers. At the time when this classification was proposed, the polyps of but few of the "tabulate corals" had been examined, and no characters were drawn from the soft parts. The explanation of the transverse septa seems to be, judging from my own dissections and also from analogy with other animals, that they are formed after each discharge of ova; the vacuity thus produced, being useless, is cut off from the visceral cavity above it by the formation of a septum. Therefore, if the eggs be discharged from all the radiating chambers simultaneously, or if from any other cause the polyp abandons all the chambers simultaneously, it is obvious that a complete septum or transverse plate will be formed across the entire tube; but if the eggs be discharged at different times from the ovaries occupying the various radiating chambers, the septa formed below them in the different chambers will not be coincident or exactly at the same level in all. It would seem, therefore, that the existence or non-existence of complete transverse plates is simply a matter of periodicity in the discharge of ova.

We should naturally expect to find such variations in periodicity among the species and genera of many diverse groups; and this, I think, can easily be shown to be the case. Thus, for example, the genus *Cælastræa*, V., an undoubted Astræan coral, has the septa in all the chambers on the same level, thus forming true tabulæ; the genus *Alveopora* (fig. 1, *a*), and

Fig. 1.



a, a longitudinal section of *Alveopora spongiosa*, Dana; *b*, a vertical view of some of the cells: both much enlarged, copied from Dana's Atlas of the Zoophytes of the U. S. Expl. Exp. For the use of this cut I am indebted to Messrs. Dodd and Mead, the publishers of Professor Dana's new work on Corals and Coral Islands.

others allied to *Porites* and *Madrepora*, have true tabulæ; also the genus *Astræopsammia*, V., of the *Eupsammidæ*; the species of *Pocillopora*, a genus closely allied, in its animals and otherwise, to *Öculina* and *Stylophora*, have very numerous and perfect transverse septa; even among the Alcyonaria, the genus *Tubipora* occasionally has transverse internal septa; and the same is true of *Millepora*, belonging to the class of Acalephs.

Notwithstanding the very slight basis upon which the group of "Tabulata" was established, and disregarding the very great and important differences which exist among the corals thus unnaturally brought together, most writers upon corals, whether recent or fossil, during the past twenty years have adopted this classification without hesitation.

And yet this is but another instance forcibly illustrating the general rule that classifications based on single characters are very likely to be artificial and erroneous. It also illustrates the manner in which such an error often leads to others of still greater importance.

In 1857 Professor Agassiz made the very important discovery that the animals of *Millepora* are not true polyps, but genuine hydroids, belonging to the class of Acalephs or *Medusæ**. But, since *Millepora* is a genus belonging to the "Tabulata," he immediately concluded that all the "Tabulata" are, therefore, hydroid Acalephs! And, not content with this sufficiently bold generalization, he extended it likewise to the extinct "Rugosa" or Cyathophylloid corals†, at first apparently with some hesitation, but more recently without qualification‡.

From this conclusion, if admitted, it followed that in the Palæozoic ages there were few, if any, true polyp-corals, but, on the other hand, the class of Acalephs was abundantly represented by a great variety of coral-making forms, some of them of great size, and capable of building extensive coral-reefs, similar to those made by true polyp-corals in modern times! Thus the geological importance of these two classes of animals would be completely reversed, as well as our ideas of the nature of corals and coral-reefs.

These views have been held and advanced by Professor Agassiz for many years, and have been urged quite recently,

* Proceedings of the Boston Society of Natural History, vol. vi. p. 373, 1859. See also Pourtales, in Illustrated Catal. of the Mus. of Comp. Zoology, no. 4, p. 56, 1871.

† Contributions to the Natural History of the United States, vol. iii. pp. 61-63, and vol. iv. pp. 292-296 & 338.

‡ Bulletin of the Museum of Comparative Zoology, vol. i. no. 13, p. 384, 1870.

notwithstanding the great amount of evidence that has been published to show that the "Tabulata" include corals very diverse in structure and affinities. The proposition of Professor Agassiz to regard all "Tabulate" and "Rugose" corals as Acalephs has not been very generally adopted, but has been received with more or less hesitation and doubt by many zoologists and geologists. In fact it is not easy to see how Professor Agassiz could reconcile, in his own mind, the structure of many of the Tabulata and Rugosa with his own definitions of the two classes Polyps and Acalephs. The distinction upon which he and others have chiefly insisted is the existence in the former of radiating fleshy lamellæ, dividing the interior of the body into a number of radiating chambers, in the centre of which, in coral-making species, the radiating plates are formed; while in Acalephs no such radiating lamellæ and chambers exist. Therefore it would not be possible for an Acaleph to form a coral having distinct radiating plates or septa, unless we alter our definition of an Acaleph. In that case I do not know what distinction would remain. And yet we find many Tabulate corals, both recent and ancient, with twelve or even twenty-four well-developed radiating septa; and among the Rugosa there are very many genera in which numerous radiating septa are as highly developed as in the ordinary modern corals of undoubted polyp-origin, while in some there are not even traces of *transverse* septa. If we regard the relations of the soft parts to the corals, it will therefore be necessary to consider all corals in which *distinct radiating plates* are formed as true polyp-corals; but the absence of such plates is not of itself proof that the coral was not made by a polyp; for many corals now living, and formed by genuine polyps, have no radiating septa (e.g. *Tubipora*, some species of *Pocillopora*).

In the present state of science, the only stony corals which are *known* to be formed by hydroids are the several species of *Millepora*. We can reasonably infer that a few other genera having essentially the same structure, or belonging properly to the same family, are also the corals of Hydroids. But as to the great majority of the "Tabulata" and "Rugosa," there can no longer be any reasonable doubt that they were made by true polyps, essentially similar to those of the existing corals*.

* The following quotation from the 'Bulletin of the Mus. of Comp. Zoology,' vol. i. no. 13, p. 384, Nov. 1869, will serve to illustrate the views of Professor Agassiz:—

"If we now remember that the Acalephian affinities of the Tabulata are unquestionable, and that, with them, the Rugosa must be removed from the class of Polyps and referred to that of the Acalephs, and if we further take into consideration the fact that *Palæodiscus* belongs to the

But among the Tabulate corals, after excluding the *Milleporidæ*, great diversities of structure still remain ; and no doubt representatives of several families that ought to be widely separated in a natural system are thus combined together on account of a single unimportant character. Many of these genera are extinct and apparently have no very closely allied representatives among living corals. The affinities of such genera may long remain doubtful. But in other cases there are living corals having very close relations with certain Palæozoic genera, and these we are even now able to classify with as much certainty as we can the ordinary forms of existing corals.

Among the best-known of the tabulate corals are the numerous species of *Pocillopora* and allied genera, which evidently constitute a distinct family (*Pocilloporidæ*), largely represented in the tropical waters of the Pacific and Indian oceans. These corals are characterized by rather small tubular cells, usually with 6, 12, or 24 radiating septa, which, even in the same specimen, may be obsolete in some of the cells, by *im-perforate* compact walls, and by a more or less abundant compact cœnenchyma between the lateral cells, which may, however, be absent where the cells are crowded, as at the ends of the branches. The writer has shown in several previous papers* that the *Pocilloporidæ* are the corals of *true polyps*.

type of Rugosa, and not to the family of Fungians, it becomes evident that in their order of succession from the Mesozoic era, in which they first make their appearance, the great types of the class of Polyps have succeeded one another in the following order :—first Turbinolians, next Fungians, next Astræans, and last Madreporæ—in exactly the sequence in which these types stand to one another, as far as their structural gradation is concerned, and in exactly the same order in which, during their growth, these corals pass from one stage to another."

But on the other hand, since we now find that the Acalephian affinities of the Rugosa and most of the Tabulata are wholly imaginary and without the slightest foundation in nature, all this beautiful theory of geological sequence falls to the ground, and we find the Madreporæ represented even in the Lower Silurian rocks by *Favosites* and other *Alveopora*-like forms, which are certainly neither *low* nor *embryonic* types! And even in Mesozoic times the Astræans appear in force quite as early as the Fungians or the Turbinolians. If there has ever been such a definite geological sequence of the groups of corals as Agassiz imagines, it must have taken place in the ante-Silurian ages, concerning the life of which we know nothing. In the Lower Silurian seas the order was already well developed and highly diversified.

* "On the Affinities of the Tabulate Corals," in Proceedings of the American Association for Advancement of Science, 1867, p. 148. Proceedings of the Essex Institute, vol. vi. p. 90, 1869. Transactions of the Connecticut Academy, vol. i. p. 518, 1870. American Journal, vol. i. p. 389, May 1871.

The animals of *Pocillopora* are exsert in expansion, with a regular circle of 12, nearly equal, stout, tapering tentacles surrounding the circular disk*; and 12 internal, radiating, fleshy lamellæ show through the disk. Thus they closely resemble the polyps of *Stylophora*, *Porites*, and *Madrepora*, which are among the most typical of true polyps. The existence of stellate cells, with 6 or even 12 well-developed radiating septa, in several species of *Pocillopora* (e. g. *P. elongata*, Dana, *P. plicata*, D., *P. stellata*, V.) should be sufficient evidence that such corals have no Acalephian affinities whatever, even without the conclusive evidence derived from a study of the living polyps.

The Silurian genus *Columnaria* appears to belong to a different family; and if not actually a member of the *Astræidæ*, it should at least be referred to a family very near that group. It has from 24 to 36 well-developed, imperforate, radiating septa, those of the first cycles wider and, in *C. stellata* (Hall, sp.), reaching the centre, while those of the last cycle are quite narrow. The larger septa have the upper edge finely serrate. The walls of the adjacent cells are united together as in *Cælastræa* and *Goniastrea*; they are solid and apparently imperforate. The genus closely resembles *Cælastræa*; but the budding is marginal or interstitial, while in the latter the cells divide across the middle.

Another well-known and important group of tabulate corals was abundantly represented in the Palæozoic seas by the genus *Favosites*, with its numerous species, and by several other allied genera, constituting the subfamily *Favositinæ* of Edwards and Haime. In these corals the walls are thin and perforated by more or less numerous pores or foramina, which are small in *Favosites*, but large and numerous in *Koninckia*. The cells are usually crowded and polygonal; and there is no coenenchyma. The radiating septa are sometimes obsolete, but usually 12 or 24, which may be continuous or represented only by vertical rows of spine-like points, as in *Favosites* and the existing genus *Alveopora* (fig. 1, *b*). The transverse septa are variously developed, being often nearly flat but with the intervening spaces variable (as in *Favosites*), sometimes partly vesicular and incomplete (as in *Emmonsia*), not unfrequently convex and vesicular (as in *Michelinia*), rarely infundibuliform (as in *Ræmeria*). It is obvious that this group has no relationship with the *Milleporidæ*, and at best only a distant

* Trans. Conn. Academy, vol. i. p. 523 (*Pocillopora lacera*, V.). The polyps of *P. damicornis*, as figured by Quoy and Gaimard in the 'Voyage of the Astrolabe,' are quite similar.

one with the *Pocilloporidæ*, although Edwards and Haime placed it in the same family with the latter.

In the 'Report on the Zoophytes of the U.-S. Exploring Expedition,' 1846, p. 509, Professor Dana instituted the family *Favositidæ*, in which he included three subfamilies:—1st, *Alveoporinæ*, including the genus *Alveopora*; 2nd, *Favositinæ*, embracing *Stylophora*, *Pocillopora*, *Seriatipora*, with *Favosites* and other extinct genera; 3rd, *Helioporinæ*, for *Heliopora*, *Millepora*, *Heliolites*: this family was placed next to the *Poritidæ*. Although more recent discoveries have shown that this arrangement is incorrect in several points, it is nevertheless much nearer correct than the classifications of Edwards and Haime and Agassiz. In thus bringing *Alveopora* and *Favosites* near together, Prof. Dana made a very important step in advance, and one that has unfortunately been lost sight of, or overlooked, by recent writers, and most unfortunately by Edwards and Haime, by whom these genera are very widely separated. In describing the genus *Alveopora*, Professor Dana gives, as one of its characters, "transverse septa remote;" and on plate 48. fig. 3, *d*, of his 'Atlas,' from which the accompanying cut has been copied, he figured a vertical section of *Alveopora spongiosa*, in which the transverse septa are well shown (fig. 1, *a*). In this species the walls of the cells are exceedingly thin and pierced by numerous large openings, often leaving a mere skeleton of a wall. The transverse septa, although thin, are perfectly developed and imperforate, completely closing the cells at intervals of about .05 to .20 of an inch, varying even more than this in some parts of the coral, but not more than do many species of *Favosites*. Moreover the septa in many adjacent cells are situated at the same level, giving the coral the appearance of being divided into successive layers by broad, thin transverse plates. This appearance is due merely to the thinness and porosity of the walls and coincidence of the plates. The same arrangement of plates is found in the Silurian genus *Dania*, which, however, is said to have imperforate walls.

The structure of the walls in the tabulated genus *Koninckia*, from the Cretaceous, is very similar to that of *Alveopora*. Moreover the latter, like *Alveopora* (fig. 1, *b*), has vertical rows of spine-like points, representing the twelve radiating septa. In some, if not all, species of *Favosites* the septa were likewise represented by just such rows of slender points. And the same is true of other extinct genera belonging to the same group. Whether all the species of *Alveopora* have complete transverse septa is uncertain; for they appear to have been generally overlooked by the describers. Edwards and Haime

make no allusion whatever to such septa in their descriptions of the genus and its species. In all the species which I have examined, however, these septa are to be found; but they are usually more remote and less evident than in *A. spongiosa*, while the walls in most of the other species are thicker and perforated by fewer and smaller openings, thus producing firmer corals. In *A. dædalea*, Dana*, the walls are much thicker and perforated by smaller rounded orifices, of which there are two or three vertical series on each side of a cell. The cells are very deep; and the transverse septa are complete though distant, and coincident in adjacent cells. The radiating septa are represented by twelve vertical rows of stouter spines, which often meet at the centre. Mr. W. S. Kent† has described and figured a recent coral, under the name of *Favositipora Deshayesii*, which has well-developed transverse septa, and agrees in all other respects, according to Mr. Kent, with *Alveopora*. But as the presence of such septa appears to be characteristic of *Alveopora*, the *Deshayesii* should be regarded as a species of *Alveopora* in which the transverse septa are, perhaps, unusually numerous. Mr. Kent also mentions a palæozoic fossil coral, supposed to be from North America, which he refers to the same genus (*F. palæozoica*). This may prove to be an ancient species of the genus *Alveopora*, and in any case cannot be more than generically separated, either from *Alveopora* or *Favosites*, as remarked by Mr. Kent. The genus *Koninckia* of the Cretaceous is, perhaps, not generically distinct from *Alveopora*, approaching *A. dædalea* very closely, and differing from *A. Verrilliana*, D., chiefly in having but six vertical rows of septal spines, instead of twelve. The genus *Goniopora* is closely related to *Alveopora*, differing chiefly in having about 24 radiating septa, which are more fully developed, but perforated by large irregular openings, and a distinct columella. The walls are usually rather firm and rough, as if composed of coarse irregular granules so united together as to leave many openings through the wall. The lateral and younger cells are often very shallow, with a large rough columella, and with six small paliform lobes arising from the inner part of the septa; while in some cases the walls are much thickened and roughly granulous at the surface, in these characters closely resembling *Porites*, to which it is also allied in the internal structure of the coral. In fact *Goniopora* combines many of the characters of *Alveopora* and

* This species, which proves to be distinct from the *dædalea* of Forskål &c., has been named *A. Verrilliana* by Prof. Dana in his recent work on Corals and Coral Islands.

† Ann. & Mag. Nat. Hist. vol. vi. p. 384, Nov. 1870.

Porites, and has some additional special characters. The transverse septa are usually quite numerous and thin, usually irregular, but with an evident tendency to coincide in height in all the chambers of the same polyp-cell, though much broken up and forced out of the transverse plane by the presence of the large irregular columella. In one species of *Goniopora* I have occasionally seen cells with a deeply infundibuliform septum completely closing the cavity below, thus recalling the septa of *Ræmeria*.

The three genera *Goniopora*, *Alveopora*, and *Porites* agree closely in the characters of their polyps; the first, however, has 24 tentacles, while the others usually have but 12, although there are often a few larger polyps with 24 tentacles, scattered among the smaller ones, in both the latter genera. It seems necessary, therefore, to place these genera and the others that are evidently closely allied to each of them in one family, *Poritidæ*. It will also be understood, from what has already been said, that it is impossible to assign any characters sufficient for separating the *Favositinæ*, even as a family, from the *Poritidæ*. It is very doubtful whether the group can be maintained even as a subfamily; for *Alveopora* and *Goniopora* combine the characters of both groups. The family PORITIDÆ*, thus extended, might, perhaps, be provisionally divided into three subfamilies:—PORITINÆ, for *Porites* and the closely allied genera; ALVEOPORINÆ, to include *Alveopora*, *Goniopora*, *Litharæa*, and, if considered distinct, *Koninckia* and *Favositipora*; FAVOSITINÆ, to embrace *Favosites*, *Emmonsia*, *Michelinia*, and the other closely allied genera. It is probable, however, that even such a slight separation of *Alveopora* and *Favosites* is greater than the differences actually observed will warrant.

Admitting these necessary changes in the classification†, it follows that the *Madreporaria perforata* or *Madreporacea*, which is generally regarded as the highest division, or sub-order, of the true corals, was abundantly represented even in

* The genus *Montipora*, for which Edwards and Haime constituted their second subfamily of *Poritidæ* (*Montiporinæ*), belongs properly to the *Madreporidæ*, as explained elsewhere by the writer (Trans. Conn. Acad. vol. i. p. 501), and where it was also placed by Prof. Dana.

† The opinion that the *Favositinæ* belong to the *Madreporacea* was advanced by the writer in 1870 (Trans. Conn. Acad. i. p. 518). Mr. Kent, in the article referred to, published simultaneously with mine, expressed the same opinion and used independently nearly the same arguments. He also uses the argument with reference to the impossibility that a coral with radiating septa could be formed by hydroid polyps, as I had also done both in the paper referred to and in that of 1867. This coincidence of opinion, arrived at through studies pursued in different ways and approached from different directions, could not fail to be gratifying both to the writer and to Mr. Kent.

the Silurian seas. Moreover the family *Poritidæ*, which now includes many of the most important of reef-building corals, was also, even in palæozoic ages, a family rich in reef-forming species; for some of the species of *Favosites* grew into hemispherical masses eight or ten feet in diameter. It also seems probable that the genus *Alveopora* has existed through all periods from the palæozoic to the present time, which would seem the more remarkable considering the extreme delicacy and fragility of these corals, and also the fact that, so far as known, they are all shallow-water and reef species.

XXXVIII.—*On the Morphology and Affinities of Graptolites.*

By Prof. ALLMAN, F.R.S., F.L.S., &c.*

AMONG the extinct forms of life few possess more interest than these remarkable fossils, absolutely confined, as they are, to one great section of the palæozoic rocks, where their vast abundance, wide geographical distribution, and easy recognition render them of special value to the practical geologist.

The Graptolites are now by most palæontologists referred to the Hydroida: and their living representatives are sought for among the calyptoblastic genera of this order. While, however, I am unable to recognize their hydroid relations from the point of view from which palæontologists have generally agreed to regard them, I believe that their affinities with the Hydroida are too decided to justify their omission from any complete exposition of the palæontological history of this group of the animal kingdom.

The typical form of a graptolite is that of a narrow tube, straight or more or less curved, emitting from one side a series of hollow denticles, which are the free extremities of little cups or calicles, through which the cavity of the tube opens

* The following paper is mainly a portion of a chapter on the Distribution of the Hydroida in Time contained in the second part of the author's 'Monograph of the Gymnoblasic Hydroids' now nearly ready for delivery; and as it contains some new views of a question much agitated at this moment, it was thought that its regular publication might be here anticipated. The section of the work to which it properly belongs was printed off some time ago, and consequently before the appearance of Dr. Nicholson's 'Monograph of the British Graptolitidæ,' the first part of which, just published, will be welcomed by the palæontologist as a very valuable introduction to the systematic study of the graptolites. This difference of date will explain the absence of reference to Dr. Nicholson's work in the Monograph of the Gymnoblaster. Dr. Nicholson, however, does not seem to have essentially modified the views contained in his earlier publications and discussed in that Monograph.