during next winter by operating on water at about 39° F. In this case there should be no change of temperature unless the maximum density point is altered by pressure.

Monday, 6th June 1881.

PROFESSOR SIR WYVILLE THOMSON, Vice-President,
in the Chair.

The following Communications were read :—

1. On the Structure of the Skeleton of *Tubipora musica*, and on the Relation of the Genus *Tubipora* to *Syringopora*.
By H. Alleyne Nicholson, M.D., D.Sc.

The object of the present communication is to briefly consider the general and minute structure of the corallum of the recent *Tubipora musica*, with special reference to the association of the genus *Tubipora* with the extinct genus *Syringopora*, as advocated by many modern naturalists. The method of inquiry that I have pursued in carrying out this investigation has been principally that of preparing similar thin and transparent sections of both the recent and the extinct types ; and though there are special difficulties in the way of any examination of *Tubipora* by this method, I have been able to overcome these in a satisfactory manner, and to prepare a number of thin sections which answer all the requirements of the case. The results of my observations may be conveniently considered under the following heads :—

1. General structure of the corallum of *Tubipora*.
2. Minute structure of the corallum of *Tubipora*.
3. General structure of the corallum of *Syringopora*.
4. Minute structure of the corallum of *Syringopora*.
5. Supposed relationships between *Tubipora* and *Syringopora*.

1. *General structure of the corallum of Tubipora*.—The corallum of *Tubipora musica*, Linn., is one so familiar to naturalists that the peculiarities of its external form hardly need to be noticed. It consists of a number of fasciculate cylindrical tubes or thecæ, which are separated by small intervals from one another, and are upon the

whole parallel in their course, though they diverge to a greater or less extent as we pass from the fixed base to the surface of the colony. The entire corallum is of a bright red colour, the inner surfaces of the tubes being, however, usually lighter in colour than the outer surface. The cylindrical thecæ are bound together by horizontal calcareous floors (the so-called "external tabulæ") which are placed at varying distances apart in different specimens, but which are often disposed with considerable regularity, so as to form a series of concentric laminae parallel with the upper surface of the colony. These horizontal floors unite the *outer* surfaces of the corallites; and, as pointed out by Professor Perceval Wright ("Ann. Nat. Hist.," ser. 4, vol. iii. p. 381), they are really produced by the coalescence of periodically-produced horizontal offshoots or extensions from the upper extremity of the tubes. Each offshoot consists of "a fold of the ectoderm, into which some of the endodermic layer is tucked," and by the calcification of the ectodermal layer the connecting-floors are produced. From the upper surfaces of the connecting-floors new corallites are budded forth, the upward expansion of the colony being due to the interpolation in this way of new tubes, as can be readily observed in the dead corallum. Horizontal sections through the connecting-floors show them to be traversed by a system of comparatively large-sized, branching, horizontal canals, which open at their extremities directly into the cavities of the polypes (fig. 1, B). Hence, if we open one of the thecæ at what we may call one of its "nodes"—that is to say, at a point where it is embraced by one of the connecting-floors, we find a ring of rounded apertures corresponding with the openings of the canals just spoken of (fig. 1, A). If, also, we examine the broken or cut edge of one of the connecting-floors, we observe the round and comparatively large orifices of the same canals as they traverse the interior of the floor. By means of this system of canals, the visceral chambers of the polypes composing a colony are placed in direct communication.

Though the connecting-floors of the colony are often spoken of as "external tabulæ," they have in reality nothing in common with the transverse plates or true "tabulæ" which intersect the visceral chambers of the corallites in such forms as *Favosites*. The only structures in *Tubipora* which can be even remotely compared with

the proper tabulæ of *Favosites* or of *Syringopora* are to be found in a peculiar axial calcareous tube which may often be found in the centre of the visceral chambers of the corallites. When present, this tube (fig. 1, c) is never continuously developed throughout the entire length of the thecæ, but becomes dilated at every node (*i.e.*, at the levels corresponding with the external connecting-floors) into

Fig. 1.—A, Part of a tube of *Tubipora musica*, Linn., divided longitudinally, showing the openings of the canal-system of the connecting-floors into the visceral chamber of the polype. B, Part of a horizontal section taken at the level of one of the connecting-floors, showing the canal-system of the connecting-floor. C, Part of a corallite of *Tubipora* divided longitudinally, showing the axial tube; in the lower portion of the figure the axial tube is laid open. All the figures are enlarged five times.

a funnel-shaped expansion, which fuses with the wall of the visceral chamber. The axial tube itself, so far as I have seen, is always open along its entire length, and is not crossed by any internal partitions; nor have I ever observed it to be in any way connected with the inner wall of the visceral chamber, except in the manner above indicated at the nodal points of the theca.

The above-mentioned axial tube seems in some specimens not to be developed in any of the corallites; at other times it is developed in many of the corallites of a colony, but not in others. Its existence was first pointed out by Mr Charles Stewart, F.L.S., in a paper which I unfortunately have not seen, by whom it was compared with the infundibuliform tabulæ and axial tube of *Syringopora*, a view which has been since adopted by Mr Moseley (*“Voyage of H.M.S. Challenger,”* vol. ii. p. 125). I shall, however, subsequently give

the reasons which lead me to believe that there is in reality insufficient ground for this comparison, and that the structures in question are morphologically different.

Finally, no traces of *septa*, either in the form of radiating lamellæ, or of vertically disposed spinules, or even as those plications of the wall which constitute the "pseudosepta" of *Heliopora*, have been detected in *Tubipora*.

2. *Minute structure of the skeleton of Tubipora*.—The microscopic structure of the corallum of *Tubipora* was first investigated by Kölliker ("Die Bindesubstanz der Cœlenteraten," p. 169, 1866), and very correctly described and figured. Professor Perceval Wright subsequently showed ("Ann. Nat. Hist.," ser. 4, vol. iii. p. 377), that the corallum is really formed of fusiform calcareous spicula, secreted by the ectoderm. Over the greater part of the theca these spicules become completely amalgamated with one another, so as to form a rigid case; but they remain loosely united or separate at the growing summits of the tubes, which are thus capable of withdrawal, during the retraction of the polypes, into the dense portion of the thecæ.

As the result of my own recent observations, carried on principally by means of thin transparent sections, I find that the entire calcareous skeleton of *Tubipora*, as pointed out by Kölliker, is permeated throughout by a system of minute, parallel, closely approximated tubules or canaliculi, which sometimes bifurcate, and occasionally anastomose. In the walls of the corallites themselves these tubuli (fig. 2 A), run at right angles to the inner and outer surfaces of the thecæ, opening both externally and internally by well-defined, rounded, and slightly dilated apertures (fig. 2, B), which can be readily observed by the examination of any fragment of the skeleton by means of a hand-lens or with a low power of the microscope. In the connecting-floors of the corallum, these tubuli are just as numerous and as well-developed as in the walls of the corallites, but here they run at right angles to the floor, either passing right through from the upper to the lower surface, or, more usually, opening internally into the large ramified canals which run in substance of the connecting-floors, and connect the visceral chambers of adjoining polypes. It follows from the above that the skeleton of *Tubipora* is in reality completely porous, the canaliculi by which it

is penetrated, though minute, being quite large enough to be at once recognised by the use of a lens. The precise appearances presented by these canaliculi in thin slices, vary according to the direction in which the section has been taken. Thus, in sections taken transversely to the corallites (fig. 2, A), the tubuli are cut in

Fig. 2.—A, Transverse section of a corallite of *Tubipora musica*, Linn., taken at the level of one of the connecting-floors, enlarged twenty times, showing the tubuli of the wall. B, Portion of the surface of one of the connecting-floors, enlarged twenty times, showing the external openings of the tubuli of the skeleton. C, Fragment of the corallum of *Tubipora*, enlarged sixty times, showing the composition of the skeleton out of spicules. The figure is taken from a thin section which divides the tubuli of the skeleton at right angles.

the direction of their length; and the same is true of sections which are taken parallel to the corallites, but which lay open the visceral chambers of the latter. On the other hand, sections through the walls of the corallites taken parallel to the visceral chamber, and sections of the connecting-floors taken parallel to their upper or lower surfaces, cut the canaliculi at right angles, so that these appear as minute rounded or oval pores in the skeleton.

The only other points connected with the minute structure of the skeleton, as revealed by thin sections are,—*firstly*, that it is easy to observe that the corallum is made up, as pointed out by Professor Perceval Wright, of a network of irregular fusiform spicules fused together (fig. 2, c), and *secondly*, that the marked red coloration of the skeleton resides chiefly in outer layer of the thecæ, the inner layer being nearly or quite white.

3. *General structure of the corallum of Syringopora.*—The genus *Syringopora*, Goldfuss, is one well known to naturalists, and its leading structural characters have been fully described by myself, (“Palæozoic Tabulate Corals,” p. 207). As my object on the present occasion is simply to compare it with *Tubipora*, it will be unnecessary for me to do more than merely to draw attention to some of its more striking characters. The corallum in this genus is composed of fasciculate cylindrical calcareous tubes, which are placed at variable but slight intervals, and diverge slightly as the surface of the colony is approached, owing to the interpolation of new tubes. The visceral chambers of adjoining corallites are placed in direct connection by means of hollow, usually cylindrical, horizontal connecting-processes or tubes. These connecting-tubes are generally quite distinct from one another, and placed at tolerably regular and moderately distant intervals; but they are sometimes developed in successive whorls (as in *S. verticillata*, Goldf.), or the verticils may coalesce so as to give rise to almost uninterrupted horizontal connecting-floors (as in *S. tabulata*, Van Cleve). In this latter case, the mere external similarity of the corallum to that of *Tubipora* is very striking.

As regards the internal structure of the corallites of *Syringopora*, the visceral chamber of each tube is always subdivided by a remarkable and well developed system of tabulæ. These tabulæ are, typically, more or less infundibuliform, and they generally become invaginated in such a manner as to give rise to a central cylindrical tube, which occupies the axis of the visceral chamber (fig. 3, A). This axial tube, however, is in no respect a distinct or separate structure; but it is simply a central space left by the union of funnel-shaped tabulæ, and often broken up by the inward prolongation of these across its central cavity. In all the species of *Syringopora*, also, the corallites are provided with a well-developed system of *septa*. The *septa* (fig. 3, A and B), are entirely of the “Favositoid” type, or of the type of the *septa Porites*, being never lamellar, but having in all cases the form of slender spines arranged in vertical rows. They never extend more than a limited distance into the visceral chamber, but they vary in length, the larger species seeming to have about twenty rows of septal spines to each corallite.

4. *Minute structure of the corallum of Syringopora.*—The minute structure of the corallum of *Syringopora* is best studied in thin transverse sections of the corallites. When examined in such sections, the wall of the tubes is seen to be composed of dense indistinctly fibrous or granular sclerenchyma (fig. 3, A), and to be

Fig. 3.—A, Transverse section of a corallite of *Syringopora reticulata*, Goldf., enlarged twelve times, showing the thick compact wall, the cut edges of the infundibuliform tabulæ, and the septal spines. B, Part of the wall of the same section enlarged still further, showing the composition of the wall out of an outer light layer and an inner dark layer, and the origin of the septal spines from the outer layer. C, Longitudinal section of a corallite of the same, enlarged twelve times. The section passes obliquely through the corallite, and consequently shows different appearances in different parts of its course. At *a* it cuts through the inner layer of the wall, and exhibits the divided bases of the septal spines as rows of light-coloured spots (these are unfortunately left quite white, as if they were actually foramina, whereas they should properly have been faintly shaded); at *b* it cuts through the visceral chamber near its periphery, and shows the cut ends of the septal spines as rows of dark spots; and below this point it becomes more nearly central, and shows the infundibuliform tabulæ. From the Carboniferous Limestone, Westmoreland.

entirely devoid of any system of minute tubuli or canaliculi. The wall, in fact, is quite compact, and the visceral chambers of the polypes communicate with one another at no points except where the connecting-tubes of the colony may be developed. Very generally, the wall is distinctly composed of two layers, viz., the outer dense layer just spoken of and an internal layer of laminated

or markedly fibrous sclerenchyma (fig. 3, A and B). When this is the case, the outer layer is usually of a conspicuously lighter colour than the internal layer, and this gives rise to certain phenomena which deserve a moment's notice. When, namely, these two layers exist, the septal spines (fig. 3, B) always take their origin from the outer light-coloured layer, and penetrate through the inner laminated and dark layer on their way to the visceral chamber. Hence, in longitudinal sections which divide the *wall* of the corallites (fig. 3, c), we observe vertical rows of small rounded spaces, which have a lighter colour than the surrounding tissues. These light circular spaces might easily be mistaken for pores in the wall, or for transverse sections of canals running in the wall; but they are really the cut ends of the spiniform septa divided near their bases.

5. *Supposed relationships between Tubipora and Syringopora.*—Owing to the marked external resemblance which subsists between the corallum of *Tubipora* and that of *Syringopora*, it has been commonly held by naturalists that the two genera are nearly related, and that the latter genus is, therefore, referable to the *Alcyonaria*. Amongst the later authorities who have adopted this view may be mentioned Zittel ("Handbuch der Palæontologie," vol. i. p. 211) and Moseley ("Voyage of H.M.S. Challenger," vol. ii. p. 125). My own view, on the other hand, has been that there is no real affinity between *Tubipora* and *Syringopora*, and that the latter is really referable to the *Zoantharia perforata*, and allied to the Favositidæ ("Palæozoic Tabulate Corals," p. 213). In considering this question with a view to arriving at some decided conclusion, it may be as well to summarise the chief points of likeness and unlikeness between *Tubipora* and *Syringopora*. The points of resemblance between the two genera are as follows:—

(a.) It must be admitted, in the first place, that there exists a very remarkable general likeness of the corallum of *Tubipora* to that of *Syringopora*. In both, namely, the corallum consists of slightly separate cylindrical corallites, of comparatively great length, bound together by horizontal processes or floors.

(b.) A still more striking point of likeness, as of a really much more fundamental character, is to be found in the fact that in both genera the visceral chambers of the polypes are placed in direct

communication by horizontal canals, which run in the interior of the connecting-processes or connecting-floors, to which I have alluded above.

(c.) A third point in which it has been alleged that the corallum of *Tubipora* resembles that of *Syringopora*, is the presence in both genera of an axial tube occupying the centre of the visceral chambers of the corallites. Here, however, we have, in my opinion, to deal with a merely apparent similarity and not with a case of true homology. It is true that the axial tube of *Tubipora*, when it is present, is not unlike in appearance to the axial tube of *Syringopora*, but there are important differences between these structures to be noted. Thus, the axial tube of *Tubipora* is an apparently independent calcareous structure, which has no connection with the wall of the visceral chamber save only at the nodal points of the corallite (*i.e.*, at the points opposite to the origin of the horizontal connecting-floors), where it becomes connected with the inner surface of the theca by a funnel-shaped expansion of both its upper and lower extremities. In my view, therefore, there exist *no* “*tabulæ*” in *Tubipora*. Moreover, the axial tube entirely resembles the wall of the theca in being composed of fused spicules, and it is penetrated by the same close-set canaliculi. What its precise nature may be it is difficult to say, but it is possibly due to a progressive calcification of the wall of the gastric sac from below upwards as the polype grows upwards in the progressively lengthening theca. At any rate, it is interesting to notice that the only points at which it has any connection with the wall of the theca are just those points which, as shown by Professor Perceval Wright, mark the periodic growth from the summit of the polype of the horizontal outgrowths which give rise to the connecting-floors of the colony. On the other hand, the so-called axial tube of *Syringopora* is not in any way an independent and definite structure, with an independent and definite wall. It is, rather, simply the axial space formed by the fitting into one another of a number of irregular funnel-shaped *tabulæ*; and this difference is well shown by a comparison of a transverse section of a corallite of *Tubipora* with a similar section of a corallite of *Syringopora*. In the former case, we see simply two concentric rings, one representing the wall of the theca, while the much smaller inner ring represents the axial tube, the two having absolutely no

connection with one another. In the latter case, on the contrary, the section of the corallite shows a number of irregularly concentric lines, marking the cut edges of the ensheathing tabulæ, the outer of these lines being in connection (as a rule) with the wall of the theca, while the innermost encloses the cavity of the axial tube.

While the above are the real or supposed points of resemblance between *Tubipora* and *Syringopora*, there are the following very important differences between the two genera to be observed.

(a.) In the first place, there is the very important and remarkable difference in the minute structure of the calcareous skeleton in the two types in question. In *Tubipora* the corallum is made up of fused calcareous spicules, which are so disposed as to give rise to a universally distributed system of minute canaliculi or tubuli, which open on both the outer and inner surfaces of the skeleton by well-marked apertures. The size of these tubuli is comparatively so great that it is quite impossible that their presence could be overlooked in thin sections of *Syringopora*, if they really existed in this genus. On the other hand, the skeleton of *Syringopora*, as regards its minute structure, is quite compact, and shows no signs whatever either of being penetrated by a system of tubuli, or of being formed by the fusion of ectodermal spicules.

(b.) True tabulæ are always present in *Syringopora*, and, in all the typical forms of the genus, have the character of a series of invaginated cones, which give rise centrally to an axial tube. In no specimens that I have ever seen, can there be recognised any similar series of funnel-shaped tabulæ in *Tubipora*. I cannot, in fact, recognise that any true tabulæ are present in *Tubipora*, so far as my own observations enable me to come to a conclusion on this point, and, as already stated, I do not regard the axial tube of *Syringopora* as being formed in the same way as the somewhat similar-looking structure in *Tubipora*, or as really being homologous with it.

(c.) The corallites of *Syringopora* are provided with a well-developed septal system, of which absolutely no traces can be recognised in *Tubipora*. Moreover, the septa of *Syringopora* are not mere marginal plicæ, such as form the "pseudosepta" of *Heliopora*, but they are in the shape of vertically-arranged rows of spines which may be well compared with the septal spines of such

undoubted Zoantharians as *Porites*. A still closer comparison might be made with the septal spines of many species of *Favosites*, but it is unnecessary to do this, as the reference of *Favosites* to the *Zoantharia* would not be universally admitted. Owing to their spiniform character (instead of being lamellar), transverse sections of the corallites can rarely or never show a complete cycle of the septa; and it is, therefore, difficult to determine how many rows of septal spines are present in each coralite. There is, however, no sufficient reason to doubt that the septal spines of *Syringopora* are like those of *Porites* in being really partial calcifications of the mesenteries, so that they are properly of a septal nature.

Taking the whole of the preceding evidence together, I cannot avoid coming to the conclusion that the points of difference between *Tubipora* and *Syringopora* are decidedly more important and fundamental than the points of resemblance. I am not, therefore, at present disposed to alter my previously-expressed opinion that there exists in reality no actual relationship between these two genera, nor am I prepared to admit that *Syringopora* should be rightly referred to the *Alcyonaria*. On the contrary, I think the evidence which is at present available to be decidedly in favour of the view that *Syringopora* belongs to the *Zoantharia perforata*, and that its nearest allies are to be sought for in the Favositidæ, the singular genus *Syringolites* (Hinde), forming a transition between *Favosites* and *Syringopora*. I am aware that Mr Moseley, whose opinion in such a matter deservedly carries exceptional weight, is inclined rather to believe that *Favosites* and its allies should be referred to the *Alcyonaria*. Into this question I cannot enter at this moment; but I hope to be able on a future occasion to show, by means of thin sections of both types, that the affinities of *Favosites* are distinctly with *Porites*, and that the former genus properly belongs, as maintained by Verrill, Zittel, and myself, to the *Zoantharia perforata*.