2. A Speculation on the Phylogeny of the Hexactinellid Sponges.

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(With 2 figs.)

eingeg. 1. Dezember 1904.

By the classical memoirs of Schulze, supplemented by the more recent investigations of Ijima, the body-structure of the Hexactinellids has become thoroughly well known in spite of their deep-sea habitat. The body-wall of a typical sponge belonging to this class consists of five layers, namely, proceeding from without inwards, [1] a dermal membrane, [2] a subdermal trabecular layer, [3] a layer of flagellated chambers, [4] a subgastral trabecular layer, and [5] a gastral membrane. To these facts, first made known by Schulze [10], Ijima [3] has added the discovery, of most fundamental importance in the theoretical interpretation of the sponge-body, that all these layers, with the exception of the chamber-layer, consist of a uniform type of trabecular tissue representing the dermal layer of the sponge, while the gastral layer builds up the chambers. Thus as in all other sponges, the body is made up of the dermal and gastral layers, together with a certain number of undifferentiated cells or archaeocytes, from which are furnished the wandering cells (amoebocytes) and the reproductive cells.

It is not necessary to make further reference to the gastral layer, the cells of which form, as in other sponges, an epithelium of collar-cells, remarkable in many points of structure, but not calling for special notice here. The dermal layer, on the other hand, presents features which are unique in the whole group of sponges, and probably of a primitive type in the phylum. In the first place, according to the Ijima's observations, the dermal layer shows no differentiation into epithelial and skeletogenous layers, as in other groups of sponges, but the cells anastomose with one another to form a continuous and uniform system of trabeculae, between which the currents flow, and in which the spicules arise. In short, the inhalant and exhalant canal-system is not formed in Hexactinellids by definite canals lined by a flat epithelium, as in the Calcarea and the Demospongiae, but consists simply of the meshes of the trabecular system. Secondly, the cells of the dermal layer do not secrete in Hexactinellids any gelatinous ground-substance or mesogloea as in every other known sponge. Thirdly, the trabeculae of the dermal layer are developed not only on the exterior of the gastral layer, but also to an equal extent towards the inner side of the gastral layer. We thus find a condition which, to anyone brought up on the ordinary or text-book notions concerning the structure of the sponge body, may seem at first sight very paradoxical; namely that the gastral layer, the endoderm of orthodox schematic morphology, does not form the innermost layer of the body-wall, but is suspended in the middle of the dermal layer, which thus forms both the inner and outer layers of the sponge-body. Nevertheless, I may point out, this fact is by no means without a parallel in sponges belonging to other groups. In the embryonic development of Ascons I have shown [7 p. 71] that the gastral cavity at its first appearance is entirely surrounded by cells of the dermal layer, which form at this early stage a continuous epithelium shutting out the cells of the gastral layer, the future collar-cells, from contact with the gastral cavity. At a later stage these internally situated dermal cells migrate outwards to form the pore-cells of the Ascon, a class of cells apparently not represented in the Hexactinellids; but even in the adult Ascon, the pore-cells return to their primitive position on the interior of the collar-cell layer whenever the sponge passes into the condition of complete contraction, and pass out again as the sponge becomes once more expanded. Further, in my account of *Clathrina coriacea* [6], I showed that in one form of the sponge a network of trabeculae, formed of cells of the dermal layer similar to the pore-cells, is always found extending through the entire gastral cavity. Similar endogastral networks have been described by Dendy [1, p. 13. pl. 8. fig. 1, 2] in other Calcarea, and appear to have been seen also by Haeckel [2, III, pl. 22, fig. 3*c*; pl. 58, fig. 4 etc.]. Such networks are comparable in every way to the trabecular system of Hexactinellid sponges, but though the facts were known to me their significance was not clear to my mind until Ijima published his investigations upon Hexactinellids. The interpretation which I place upon them is that the gastral layer, the collared epithelium, is not the primitively innermost layer of the sponge-body, but was originally suspended in the midst of the dermal layer, as we still find in Hexactinellids. In Calcarea, with the development of the supporting spicular skeleton, the whole of the dermal layer has come to place itself to the exterior of the gastral layer, but the primitive state of things is still found not only in the embryo, but even in the adult when the conditions of the environment make the additional support of an endogastral network advantageous to the sponge. In the Demospongiae there is less evidence, so far as I am aware, for the former existence of an internally placed portion of the dermal layer, but it has seemed to me possible that the much-discussed central cell of the flagellated chamber, first observed by Delage in some Monaxonida, might represent a last remnant of dermal cells situated internally to the collar-cell layer. I may finally point out that the gastral layer being primitively not the most internal layer of the body-wall, is a hypothesis which makes the reversal of the layers at the metamorphosis much more intelligible, and bridges over to some extent the change from the larval to the adult condition, so far as the relative position of the layers composing the body is concerned.

I pass to the consideration of another structural feature, in which all existing Hexactinellid sponges are less archaic than the Ascons among the Calcarea. In the latter we find the only instance known to occur among sponges of the gastral being a continuous, uninterrupted layer, not folded to form distinct flagellated chambers. In the Hexactinellids, on the other hand, even in the youngest specimens that have been examined, the gastral layer occurs invariably in the form of thimble-shaped chambers, forming the middle or chamber-layer of the body-wall, and an Ascon-like condition is nowhere found in recent members of this group. Nevertheless, all the facts and analogies of sponge-morphology lead irresistibly to the conclusion that the homocoele condition is the more primitive, and must have preceded the heterocoele condition with distinct flagellated chambers. We may therefore assume for the Hexactinellids also an ancestral type of structure in which the collar-cells were arranged as a continuous layer, as in the present-day Ascons, but here suspended in the midst of the body-wall, with the trabeculae of the dermal layer situated both internal and external to it. (A, fig. 1). I think it extremely probable that such a type of structure was the ancestral condition both in the Hexactinellids and the Calcarea,

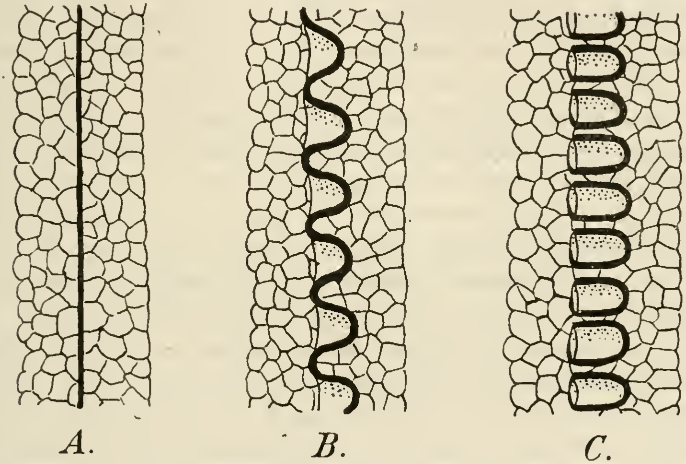

Fig. 1. Diagrams to represent the hypothetical evolution of the structure of Hexactinellida, as shown by vertical sections of the body-wall. The thick black line represents the gastral layer, the finer lines the trabecular system of the dermal layer. The outer surface is towards the right hand, the inner surface towards the left, in each illustration. For further explanations, see the text.

confining my speculations for the present to these two groups. From such a hypothetical ancestral form the *Olynthus*, and consequently all existing Calcarea, would be derived by the more or less complete restriction of the dermal layer to the outer or dermal side of the gastral layer, as above pointed out and the acquisition of the calcareous skeleton, while the Hexactinellids as known to us at the present day, on the other hand, would be derived from it by folding of the gastral layer to form the chambers, and by the acquisition of the characteristic skeleton of siliceous triaxon spicules.

In the evolution of the chamber-system of Hexactinellids we may assume, therefore, three phylogenetic stages, which may be termed conveniently *A*, *B*, and *C* (fig. 1). In stage *A* we should have the collar-cells as a continuous sheet of epithelium, not folded in any way, as in most Ascons. In stage *B* this epithelium would be commencing to increase in superficial extent by becoming thrown into folds, leading to a condition similar to that found in some Ascons, as for example *Ascandra falcata*. In stage *C*, represented by present-day Hexactinellids, the folds of stage *B* have become distinct flagellated chambers. Stages *A* and *B* are both hypothetical, but the condition found in Hyalonematidae approaches closely to stage *B*, since the chambers grouped round each excurrent canal are continuous with one another at their excurrent apertures, the gastral epithelium passing without interruption from chamber to chamber.

The origin of the triaxon skeleton must now be considered. In his masterly monograph of the Hexactinellida collected by the Challenger expedition [10], Schulze has pointed out how exactly the type of spicule regarded as most primitive in this group, namely the regular hexactine, is adapted to form the support of a simple Hexactinellid sponge. While in such a form one of the six rays is directed radially between the chambers, the four rays at right angles to this lie tangentially in the body-wall between the chambers. This theory gives a perfectly feasible and natural explanation of the origin of the triaxon spicules, on the supposition that the skeleton was acquired after the gastral layer had become folded to form the flagellated chambers. It is obvious, however, that the hypothesis requires modification, at least, if we suppose the skeleton to have been already present during the earlier stages of evolution when the gastral layer was still in the condition of a continuous sheet of collar-cells. It was certainly during a stage corresponding to my stage *A*, that the skeleton first appeared in the Calcarea, as proved by the existence of the Homocoela, and it is my belief that the same is true for the Hexactinellida also. If this were the case, it is at once evident that the primitive form of spicule in the latter group is not the hexactine, as Schulze's theory assumes, since the radially directed ray would then have pierced the gastral layer, which no spicules ever do in the Hexactinellida; but rather the form of spicule known as the stauractine, a tetractine in which the four rays meet each other at right angles and lie in the same plane; in other words a spicule belonging to the triaxon series, but in which the two radially directed rays are lacking. Spicules of this type are of common occurrence in the Hexactinellids, but are generally regarded as derived by reduction of the rays of a regular hexactine. While I am by no means prepared to deny that the stauractines ordinarily met with in adult Hexactinellids at the present day, may in many, perhaps in all cases, have originated in this way from hexactines, I am nevertheless of opinion that there is strong evidence, apart from such speculations as I have set forth above, for regarding the stauractine as an older type, phylogenetically, than the hexactine, and for deriving the hexactine primitively from the stauractine by the addition to the latter of the radially directed rays; this addition having taken place at the time when the gastral layer became folded to form the flagellated chambers.

In support of the hypothesis that the stauractine represents the most archaic type of spicule in the Triaxonia, two classes of facts may be adduced.

In the first place, Ijima has succeeded in finding larvae in various stages of development in the tissues of some of his specimens. In these larvae spicules are formed before they are set free from the maternal sponge, and the first formed spicules are stauractines in all cases. In the second place, in all palaeozoic Hexactinellids of which the spicular structure can be made out, it is found in all cases to consist entirely or at least principally of stauractines, for which reason Schrammen [8] has founded an order Stauractinophora to include the palaeozoic families Protospongidae, Dictyospongidae, and Plectospongidae, all characterized by the possession of a skeleton composed of stauractines. Schrammen has, it is true withdrawn his name Stauractinophora in his later publication [9], and merely groups the three above-mentioned families together under the heading Incertae Sedis, but in my opinion this is a retrograde step. The stauractinal skeleton is especially well seen in the oldest known fossil sponge Protospongia, from the Cambrian, in which it was described by Sollas [12]. The description given by Sollas also brings out another point of great importance in the present connection, namely the the extreme thinness of the body wall in Protospongia, which inclined Sollas to the belief that the layer of stauractines seen by him represented only the dermal spicular layer of the sponge. On the hypothesis, however, that Protospongia was in a stage of evolution in which the gastral or collar-cell layer was still in a continuous sheet, and not folded to form chambers, the thinness of the body-wall is just what might have been expected.

There is thus concrete evidence from two distinct sources in support of the theory of Hexactinellid phylogeny here advanced. It is of course possible to discount the facts in both cases, and to explain them in other ways. With regard to the larval spicules, Ijima [3, III. p. 43] is of opinion that "the stauractinic form of the spicules — in ontogeny is due to the suppression of one of the three primitively present axes, in adaptation to a certain secondary condition of the larva — assumably to circumstances of the space in which the spicules develop themselves". On fossil sponges there is no one whose opinion bears greater weight than Dr. G. J. Hinde, and in regard to the question under consideration he writes to me as follows: — "I do not think Schrammen's sub-order Stauractinophora is very firmly based, for it is very probable that in sponges of the families he includes in this group there are six-rayed spicules as well as the cruciform ones. This has been pointed out in descriptions of these sponges, in some instances small knobs or prominences can be seen giving indications that the spicules were at least five-rayed. But as most of these sponges are merely flattened impressions in shale it is impracticable to ascertain whether the cruciform spicules did or did not, in some instances at least, possess another axis at right angles to the plane of compression. Some of the sponges described by Dawson from the Ordovician of Metis, Quebec, (Trans. Roy. Soc. Canada Vol. VII. 1889) give strong indications of having 5-rayed spicules — whether a sixth ray was originally present is less evident. Also in Hall & Clarke's Dictyospongidae it is stated that 'regular hexactins' are in the parenchyma, and the figures on p. 30 show 'primary hexactins or pentactins in place' apparently forming part of the »Stützskelett« of the sponge.

"At the same time there seems good evidence that cruciform spicules did take a very prominent part in the skeleton of these palaeozoic sponges [the italics are mine], though not more so than the elongate rod-shaped spicules which Clarke says 'mostly compose the vertical and horizontal bundles of the Dictyospongidae'".

The statement just quoted concerning the stauractines is of the greatest importance, for, as I may point out, it is by no means necessary, on the theory here put forward regarding the origin of the spicules in these sponges, that all the palaeozoic forms should possess a skeleton composed exclusively of stauractines; on the contrary we should rather expect to find other forms of spicules occurring with them. Similarly, there was probably a stage in the evolution of the Calcarea in which the skeleton consisted entirely of monaxons, but such a condition is very rare in this group, and appears to have been seen only by Haeckel. A skeleton made up entirely of stauractines might, however, be expected to occur in the most ancient members of the group Hexactinellida, such as Protospongia, and this expectation appears to be perfectly realized.

While therefore neither the embryological nor the palaeontological facts, if considered separately, furnish a complete proof of my theory, yet if taken both together the accumulated weight of evidence becomes much greater, especially when it is seen that on theoretical grounds the facts are just what might have been expected and foretold. The palaeozoic group of Stauractinophora is, in fact, one which it would be necessary to invent, if it did not exist, on the theory of Hexactinellid phylogeny here put forward. In theories of spicule-origin in sponges, there is generally a tendency to assume that the forms with many rays are more primitive than those with fewer. This assumption works very well for Demospongiae, though even in this group Maas [4, 5] has described the asters of *Tethya* as arising from fusion of tetraxon spicules. On the other hand the reduction-theory, as it may be called, certainly does not apply in the case of the Calcarea, where it is above dispute that the triradiate spicules are more primitive than the quadriradiates, as was recognized on general grounds by Haeckel and Schulze, and as I may claim to have proved definitely by my observations upon the mode of formation of these spicules. There is, therefore, no a priori reason against the hexactine being derived from the stauractine by the addition of rays to it, but, on the contrary, from the known facts in other sponges, there is if anything rather a presumption in favour of such an origin.

There is, however, one point in the evolution of the spicules which requires further discussion, and which is, indeed, as great a difficulty on Schulze's theory of the origin of the hexactines, as on my view that the stauractines were the more primitive form. On either hypothesis the question at once arises, why should the four rays that lie tangentially in the body-wall between the chambers meet so definitely at right angles? If they first appeared as stauractines during my stage *A*, there does not seem at first sight any reason why the rays should meet symmetrically at all. There would be nothing to prevent the rays enclosing any sort of angle at their junction. Schulze's theory ascribes the rectangular junctions of the rays to the arrangement of the chambers, which would mean that the spicules first acquired their regular form in stages *B* or *C*, and would also necessarily imply that the diverticula of stage *B*, or the chambers of stage *C*, had a regular arrangement in rows crossing each other in a rectangular pattern, as shown in *a*, fig. 2. But if we enquire further why the chambers should have been arranged at any time in this manner, it seems impossible to suggest any reason whatever. If, on the contrary, the folding of the collar-cell layer was brought about in order to increase its superficial extent, as seems very likely, it might rather be supposed that the diverticula would tend to take on an arrangement like the cells of a honeycomb (fig. 2*b*), since such an arrangement gives, as is well known, a much greater economy of space, and would allow of the diverticula being much more closely packed. If, however, the diverticula had the honeycomb arrangement, and the spicules were adapted to this pattern, the result would not be a stauractine or other form of spicule with rays meeting at right angles, but a triradiate spicule, as in Calcarea, with the rays meeting at angles of 120°.

It is my belief, therefore, that the disposition of the folds or chambers was not the cause of the rectangular junctions of the tangentially placed spicule-rays, but that, on the contrary, the possession of regular stauractines was an antecedent condition, and that the folds or diverticula of the gastral layer owed their peculiar arrangement to the fact that they grew out into the rectangular meshes of a skeleton composed of stauractines; just such a skeleton, in fact, as is shown in Sollas's figure of Protospongia. It is not improbable that the folds of the gastral epithelium in stage *B* arose pari passu with the development of radially directed rays upon the stauractines, just as in *Ascandra falcata* the folding of the gastral layer is correlated apparently with the great development of the gastral rays of the quadriradiates. We are then forced to seek some other cause for the symmetry of the stauractine, and there are only two possible explanations which suggest themselves to me. One is that the form of the stauractine was due to a rectangular arrangement of the meshes of the trabecular framework in which it arose. There is however, not a particle of evidence to show that the trabecular framework has, or ever had, such a regular arrangement of its constituent trabeculae as

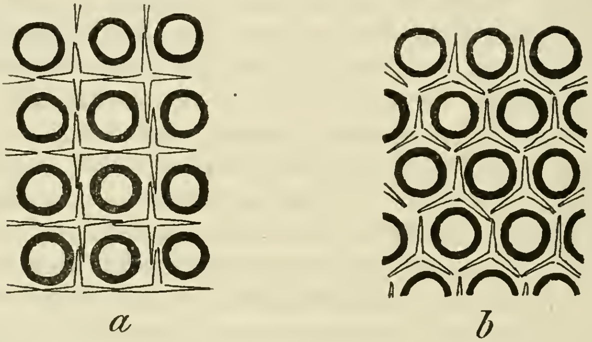

Fig. 2. Diagrams to show two possible arrangements of the chambers or diverticula, as seen in tangential sections of the body-wall, and the forms of spicule that would result from adaptation to the arrangement in each case.

this hypothesis would require. In all recent Hexactinellids the trabeculae are disposed quite irregularly, without any definite pattern. The second explanation which seems to me not only possible, but highly probable, is that the symmetry of the stauractine and other forms of triaxon spicules was due in the first instance to the inherent properties of the material of which they were formed. In a brief but highly suggestive memoir Schulze [11] has pointed put how exactly the symmetry of the axes of the triaxon spicule, in all its diverse forms, corresponds with the axes of crystals of the cubic system. As I have said elsewhere [7, p. 120], the many startling coincidences adduced by Schulze invite a renewed investigation of the physical nature of the material of which the spicules are formed. Such an investigation might give a clue to the origin of the symmetry of the triaxon spicule, and explain from what cause the primitive stauractine derived the constant right-angles at the junction of its rays, in spite of the fact that it took origin, apparently, under circumstances in which no adequate biological reasons can be adduced to explain the constant and characteristic symmetry.

I may now sum up briefly, in conclusion, my views upon the phylogeny of the Hexactinellida in the following propositions: —

1) In the ancestral form of the Hexactinellids, and perhaps of all sponges, the gastral layer was in the form of a continuous sheet of collar-cells suspended evenly in the midst of the dermal layer, which formed a trabecular system developed as much towards the interior as towards the exterior of the gastral layer.

2) The spicular skeleton arose first in the trabecular system situated externally to the gastral layer, and the earliest regular form of spicule was the stauractine. This stage of evolution is represented by the palaeozoic Stauractinophora of Schrammen, especially by the Protospongidae.

3) The next step in phylogeny was the folding of the gastral layer to form distinct flagellated chambers, and with this change the stauractines developed additional rays directed radially, thus producing the hexactines found in all Hexactinellida after the palaeozoic epoch, and probably also in many even at that early time.

List of Works Quoted.

1) Dendy, A., The Organisation and Classification of the Calcarea Homocoela etc. Trans. R. Soc. Victoria. III. p. 1—81. pls. 1—11.
2) Haeckel, E., Die Kalkschwämme. Berlin, 1872. 3 Vols.
3) Ijima, I., Studies on the Hexactinellida. I. Journ. Coll. Sc. Tokyo. XV. 1901. 299 pp., 14 pls. III. ibid. XVIII. 1903. 124 pp., 8 pls. IV. ibid. 1904. 307 pp., 23 pls.

4) Maas, O., Über Entstehung und Wachstum der Kieselgebilde bei Spongien. SB. Akad. München. XXX. p. 553—569. pl. V.
5) —— Die Knospenentwicklung der Tethya usw. Zeitschr. wiss. Zool. LXX. p. 263—288. pls. XII, XIV.
6) Minchin, E. A., Éponges calcaires. *Clathrina coriacea* (Montagu). Zoologie Descriptive des Invertébrés. Paris, 1900 (1899). I. Chapter v. p. 107—147. figg. 35—52.
7) —— Sponges, in: Lankester, A Treatise on Zoology. II. Chap. III. 178 p. 97 figg.
8) Schrammen, A., Neue Hexactinelliden aus der oberen Kreide. Mitt. Mus. Hildesheim. XV. 1902. 26 p. 4 pls.
9) —— Zur Systematik der Kieselschwämme. Ibid. XIX. 21. p.
10) Schulze, F. E., Hexactinellida. Challenger Rep. Zool. XX. Vol. 3. text and plates. 1887.
11) —— Symmetrieverhältnisse bei Hexactinelliden-Nadeln. Verh. Deutsch. Zool. Ges. 1897. p. 35—37.
12) Sollas, W. J., On the Structure and Affinities of the Genus Protospongia (Salter). Quart. Journ. Geol. Soc. Aug. 1880. p. 362—367, 2 figg.

3. Rudimentäre obere Eckzähne bei einem Elch (Alces alces [L.]).

Von Prof. Dr. Einar Lönnberg, Stockholm.

(Mit 2 Figuren.)

eingeg. 3. Dezember 1904.

Es ist bekannt, daß einige Cerviden immer mit oberen Eckzähnen versehen sind, andre aber solcher stets entbehren. Außerdem gibt es noch andre, bei welchen das Vorkommen von oberen Eckzähnen nicht konstant ist, bei welchen aber solche bisweilen auftreten. Der Elch gehört zu der Gruppe, bei welcher obere Eckzähne immer fehlen sollen. In der Literatur habe ich keine Ausnahme von dieser Regel finden können, da mir eine solche aber neulich bekannt geworden ist, glaube ich, daß sie der Erwähnung wert ist. Etwa vor einem Monat wurde während eines Besuches in Upsala meine Aufmerksamkeit von einem der Präparatoren im Dienste des Herrn Konservator G. Kolthoffs darauf gelenkt, daß »einige eigentümliche Hartgebilde« im Gaumen eines großen Elchkopfes sich vorfanden. Diese schienen ihm um so mehr bemerkenswert, weil er nie etwas Ähnliches gesehen hatte, obwohl er während vieler Jahre jährlich etwa 50 Elchköpfe präpariert hatte. Als mir der betreffende Elchkopf vorgezeigt wurde, sah ich sogleich, daß es sich um rudimentäre obere Eckzähne handelte. Dieselben saßen nicht in Alveolen, sondern nur im festen Bindegewebe des weichen Gaumens eingebettet, so daß sie nur wenig hervorragten. Das Aussehen und die Form dieser Rudimente werden durch die beigegebenen Figuren in natürlicher Größe vom rechten Eckzahnrudiment deutlich gemacht. Sie sind also ganz kurz, und zwar ohne ausgezogene Wurzelenden (nach oben in den Figuren), was mit der Abwesenheit von Alveolen zusammenhängt. Übrigens stimmt die Gestalt ziemlich mit den

Zeitschrift/Journal: Zoologischer Anzeiger

Jahr/Year: 1904

Band/Volume: 28

Autor(en)/Author(s): Minchin E.A.

Artikel/Article: A Speculation on the Phylogeny of the Hexactinellid Sponges. 439-448