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XXXI.—On *Hexactinellid* Sponge Spicules and their Names.
By R. KIRKPATRICK.

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[Plate VIII.]

HEXACTINELLID spicules are often divided into two classes, megascleres and microscleres. The former uphold, fix, and protect the body as a whole, and the latter support the strands of the trabecular network.

The spicules may be classified in another way and on a purely morphological basis. Let it be supposed that examples of all known recent Hexactinellida have been put into a huge cauldron and boiled up with nitric acid, and the residual spicules arranged into groups according to their morphological characters, the sorter being biased by no phylogenetic fancies or speculations whatsoever. It would be found that the immense multitude of spicules would fall into two great main groups: let us call them for the moment A and B. In group A all the rays would be hollow (*i. e.* with axial canal) throughout, but in group B only the central end would be hollow and the rest of the ray or ray-system solid.

Definition.—The part of the ray with the axial canal is here termed the “actine,” the solid part or parts of the so-called ray or ray-system being termed end-spines or “distal appendages.”

In describing specimens I shall continue to use the terms main or primary and end or secondary “ray”; but here it is necessary to emphasize the fundamental difference between the hollow and solid parts found in the rays of spicules belonging to group B. The use of the term end ray, as contrasted with main ray, is not, however, quite logical, because the difference is not merely one of position, like, say, the stem and branch of a tree, but there is a fundamental difference of character, the main ray being hollow and the so-called end ray solid.

What names should be given to groups A and B? Hom-axial or homactinal and heteraxial or heteractinal at first suggested themselves; but I soon found that these terms were wholly illogical. For both groups of spicules, *i. e.* all the spicules, are homaxial and homactinal, but group B has distal appendages or end-spines at the ends of its actines.

The names hexactin, hexaster, aster, are already in use, and the two former could not well be made to include pentactins,

Morphological grouping of:—

Hexactinellid spicules.

* For convenience the terms “centripetal” &c. are used instead of “centripetally directed” &c., and the centre referred to is the centre of the spicule, where the axial canals now cross or where they once crossed. Again, centripetal and centrifugal may be taken to mean shaftward or away from the shaft.

diasters, &c. Accordingly I suggest the terms Holactine* and Astral.

Holactine spicules have only actines. Astral spicules have end spines or distal appendages at the ends of the actines.

Notes on some of the above terms.

(1) Since there are no known hemipentasters &c., and, of course, no holopentasters &c., the prefix "mono-" is not required before "stauraster," "diaster," &c.

(2) Stauractin is used for spicules with four actines in one plane, and tetractin for spicules with rays forming a pyramid as in *Aulorossella longstaffi*, Kirkp.

(3) The correct designation for the spicule for which I suggested the name monoxyhexaster in the "Report on the 'Discovery' Hexactinellida," p. 3, footnote, has been the subject of controversy. The term was proposed for hexasters with only one end-spine to each actine. Ijima (Contrib. ii. p. 10, and iii. p. 118) called these spicules hexactinose hexasters, and "monoxyhexaster" was suggested by me as a convenient single word. Schulze (Abhand. Akad. Wiss. Berlin, 1903, p. 8) prefers the "actin" to the "aster" suffix, and in Prelim. Rep. 'Gauss' Hexactinellida (Zool. Anzeig. Jan. 4, 1910, p. 296) he uses the terms heterohexactin &c. In my opinion the use of such a term gives an undue importance to the question of the number of the end-spines.

The spicule which I term monohexaster is one with a centrifugal end-spine or distal appendage at the end of each actine, and therefore it must be grouped with the Astral group of hexasters with centrifugal end-spines, and not with the hexactins, in which the actines are wholly without end-spines or distal appendages. The relative unimportance of the mere number of spines is seen in the endless variation of these structures not merely in different spicules, but even in one and the same spicule (as in hemihexasters, hemicalycomomes, &c.). In my opinion the presence or absence of end-spines is the all-important point. If end-spines are absent the spicule is an "actin" spicule, if present an "aster" spicule.

The solid appendages at the ends of the (cored) actines of spicules of the Astral group are probably merely spines like the Seitenstacheln, as Schulze has already pointed out (Phys. Abhand. Akad. Wiss. Berlin, 1886, p. 15).

The variation in number &c. of end-spines is indicated by the prefixes holo-, hemi-, mono-. Strictly I should have

* ὅλος, sole or solely.

used the prefixes "holomono-" (all actines with one end-spine) and "holopoly-" (all actines with more than one end-spine), in contrast with "hemi-" (some actines with more than one, some with only one end-spine), but the sight of the word holopolydiscohexaster made me forbear! Even that apparently terrible word, however, is in reality a convenient shorthand term.

Monoxyhexasters often bear a deceptive resemblance to hexactins, but the presence of the coreless end-spine betrays the real nature. "Das also war des Pudels Kern"!

Ijima was the first to suggest what seems to me the logical terminology for spicules with one end-spine to each actine.

It is my conviction that the spicules of *Corbitella speciosa* (Q. & G.) and *Heterotella corbicula*, Bowbk., which Ijima terms spiny microhexactins will certainly be found to be monoxyhexasters (see Contrib. ii. pl. figs. 3, 9, 20-23) *.

Monoxyhexasters are found only in the suborder Hexasterophora, and microhexactins are never found in that suborder.

(4) Microhexactins are only found in the Amphidiscophora. Often these spicules have a granular surface excepting at the smooth centre, where alone the axial canals can be seen, being invisible in the rest of the length, for the same reason that it is impossible to see below the ruffled surface of a lake. It is nearly always possible to trace the canals, however, in other smoother examples from the same specimen.

(5) Hexadisk is not an entirely satisfactory term, because most calyccomes are also, in a sense, hexadisks. In the Amphidiscophoran hexadisks the end-spines are centripetal, but in the calyccomes they are directed centrifugally away from the disk or capitulum. The *essential* morphological difference is solely the direction of the end-spines, and the term that expressed that essential feature would have been the most suitable. For, according to my definition, a hexadisk as usually understood is undoubtedly a hexaster with centripetal end-spines (see Pl. VIII. fig. 9, showing the actine of an amphidisk with the end-spines).

I have put forward the theory that the difference between amphidisks and hexasters is due to differences in centripetal pressure at an early stage in the history of the Hexactinellida (Ann. & Mag. Nat. Hist. (8) iv. 1909, p. 479). The form of the amphidisk and hexaster is the index of the resultant

* Since the above was written I have managed to remove the window-pane cover slip from a valuable slide of *H. corbicula* in the Bowerbank Collection and to view the spicules under oil-immersion. I find, as I anticipated, that the so-called spiny microhexactins are spiny monoxyhexasters.

of centrifugal and centripetal pressure. No transitional forms are known. There is no fixed intermediate stage in an umbrella when it is held up in a high wind, and disaster (or the pointing of ribs in an opposite direction) is imminent. We get amphidisks in Monaxonellid sponges, especially in Spongillidæ, where these spicules may be definitely orientated in the gemmule coats, or scattered, and the spines of the disks may be at right angles to the shaft or bent down. Here the history is entirely different, and the resemblance with Hexactinellid amphidisks furnishes an instance of convergence. The effects of pressure on Hexactinellid spicules are abundantly in evidence. The subfamily Acanthascinae is apparently an example of the effects of centripetal pressure leading to the formation of discostasters, and suppressing more or less completely the actines of all the hexasters. In *Anoxycalyx ijimai*, K., one sees many hexasters with a bayonet kink at the base of the end-spines.

(6) Discostasters are, as Schulze has shown, simply hexasters with the actines suppressed and the end-spines fused with neighbouring end-spines to form a new combination of eight groups of end-spines. The six axial canals of the atrophied actines are still visible in the centre of the spicule, as Ijima has pointed out. There is no difficulty about the position of these spicules in the morphological scheme sketched out above. The central node with its cross of six axial canals represents the six actines, and the eight secondary so-called rays which are without axial canals are the fused end-spines.

Turning aside from the morphological classification, it is very interesting to note how the morphological groups of spicules are distributed among Hexactinellida. Megascleres (A), *i. e.* macrohexactins and, I may now say, their derivatives, are found in both suborders; microhexactins (B) only in Amphidiscophora; centripetal hexasters and their derivatives (C) only in Amphidiscophora; and centrifugal hexasters (D) only in Hexasterophora. Amphidiscophora has groups A, B, C; Hexasterophora has groups A, D.

The association of B with C and the non-association of B with D are deeply significant facts, and are probably due to a common cause. I have suggested (Ann. & Mag. Nat. Hist. (8) iv. 1909, p. 481) that the existence of the amphidisks (diasters or reduced hexasters with centripetal end-spines) is due to the gathering of the trabecular tissue into strong concentric laminæ at the dermal, gastral, and canalar surfaces, and that the effect of the pressure on the end-spines was to give them a shaftward bend. Possibly the pressure of contractile surface laminæ may have prevented the development

of end-spines in the parenchymal microhexactins; or possibly, again, the parenchymal trabecular tissue was prevented from developing a complicated system of meshes requiring to be supported by centrifugal end-spines, as in the Hexasterophora. The end-spines of amphidisks appear to function as balancers for maintaining the orientation of vertical props, and the office of the end-spines* of hexasters is probably to support strands of a complicated network of secondary formation, the development of such meshes apparently being unhampered in the Hexasterophora.

The correct appreciation of the relation—in regard to absence or presence and direction—of the end-spine to the actine is not, as it might at first seem, a trivial matter, but important from the point of view not only of morphological classification of spicules, but also of phylogenetic interpretation.

EXPLANATION OF PLATE VIII.

Group A. Holactine Spicules (without end-spines).

- Fig.* 1. Hexactin.
- Fig.* 2. Stauractin.
- Fig.* 3. Triactin.
- Fig.* 4. Diactin.
- Fig.* 5. Microhexactin.
- Fig.* 6. Actine of same (in glycerine), $\times 1400$.

Several of these figures are slightly diagrammatic, the outline of the axial canals being exaggerated.

Group B. Astral Spicules (with end-spines).

- Fig.* 7. Hexadisk.
- Fig.* 8. Amphidisk.
- Fig.* 9. One end of amphidisk in optical section, showing axial canal terminating at upper end of actine and not prolonged into the centripetally directed teeth or end-spines (in glycerine), $\times 1000$.
- Fig.* 10. Part of hexaster (calyccome).
- Fig.* 11. Monoxyhexaster.
- Fig.* 12. Stauraster.
- Fig.* 13. Triaster.
- Fig.* 14. Diaster.

* In the *Ann. & Mag. Nat. Hist.*, Dec. 1909, p. 507, I spoke of end-spines acting as spandrils. This was an error, because spandrils (or spandrels) are spaces of a certain kind. I should have said "supporting rods."