THE AXIAL SYMMETRY OF SPONGE SPICULES AND ITS PHYLOGENETIC SIGNIFICANCE

by

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Résumé

La symétrie axiale des spicules d'Eponges et sa signification phylogénétique

Les canaux axiaux et, par conséquent, les filaments axiaux présumés de toutes les Hexactinellides étudiées, sont carrés en section transversale. Les canaux et les filaments axiaux des Démosponges, lorsqu'ils sont observables au microscope optique, ont une section transversale triangulaire. Ce fait est vérifié pour la majorité des échantillons étudiés chez les Choristida, Spirophorida, Hadromerida, Axinellida et Poecilosclerida. Les canaux des Homosclerophorida, Haplosclerida et Halichondrida sont généralement trop petits pour être observables au microscope optique. Le rapport des axes secondaires avec la symétrie du filament axial primaire montre que la forme du filament primaire peut refléter les limites potentielles de la symétrie du spicule externe. La symétrie potentielle basique de l'axe peut exprimer ou non la morphologie du spicule externe. La présence de canaux axiaux triangulaires, dans toutes les sous-classes, Tetractinomorpha et Ceractinomorpha, comme l'a admis Lévi, indique une relation étroite entre les deux groupes. L'indépendance de l'évolution des spicules dans ces deux sous-classes de Démosponges, telle que l'ont suggérée Lévi et Reid, doit être rejetée d'après les résultats de cette étude. Des discontinuités dans la place taxonomique de plusieurs espèces et genres de Démosponges, indiquées dans les travaux des auteurs cités ci-dessus, sont confirmées par des différences dans la possibilité ou l'impossibilité de mettre en évidence, dans ces différents cas, un canal axial triangulaire par la microscopie optique.

External spicule form has been and still remains the primary source of information for taxonomic considerations in the Porifera. Dendy (1921) developed an evolutionary scheme of spicule development based only on external spicule form. He accepted the calthrops spicule of the homosclerophorids as the primitive spicule and from this derived all other spicule types, a scheme still held in favor by some (e.g., Brien, 1968). By employing a wider range of characters from embryology, cytology, and gametogenesis, Lévi (1957) suggested a new set of relationships between demosponge orders. He proposed an evolutionary scheme recognizing two subclasses, the Tetractinomorpha and Ceractinomorpha, each derived from primitive un-spiculated ancestral groups and each having independently developed the complex range of present spicule types of both megascleres and microscleres. A very long independent evolution was postulated to have occurred in the two major groups. In the Tetractinomorpha, Lévi accepted the tetraradiate spicule as primary, the monaxons of

allied hadromerids and axinellids derived from this by reduction of rays. In the ceractinomorphs, he considered the monaxon to be the primary and still the major spicule of the group, tetraradiality not now and never having been exhibited within this group. Reid (1970), in inspecting the available paleontological evidence dealing with external spicule form, substantiated Lévi's hypothesis, almost without modification.

The present report deals with the recent discovery of patterns of symmetry in the axial filament (protorhabd) of siliceous sponge spicules, previously reported from only one species, *Haliclona rosea* (Garrone, 1969). The symmetry of the axial filament is developed and expressed prior to the deposition of siliceous material on the outer surfaces of the filament. The distribution of axial symmetries within the Demospongiae casts doubt on the independent evolution of two spicule lines as developed by Lévi and reinforced by Reid.

Materials and methods

Spicules of a wide variety of sponges (Appendix 1) were observed in cross section to determine the shape of the organic axial filament or the canal left after extraction of the filament. In most cases, thin sections of preserved sponges, mounted in balsam and viewed under oil immersion, sufficed for determination of canal shape. To provide more critical information in difficult cases, cleaned spicule preparations were crushed on slides, mounted in balsam, and observed under oil immersion. Very thin sections of spicules (1-5 μ) were found scattered among the fragments.

The very thick, layered spicules of hexactinellids were embedded in epoxy and sectioned by razor blade. The shavings were soaked in sodium hypochlorite for extraction of the axial filament, rinsed, dried and observed under oil immersion.

The axial filament was directly observed in stained microtome sections of sponge tissue, with or without silica removal by hydrofluoric acid. The process of spiculogenesis was followed during development of larvae of *Mycale* sp. (the species described by de Laubenfels, 1936, p. 116, but erroneously referred to as *M. angulosa*).

In many cases the shape of the axial filament or its canal image is not resolvable by light microscopy due to extremely small diameters (less than 0.2 μ). In other cases, axial erosion of spicules (solution of the inner silica layers) is evidenced by large central canals in which the very thin axial filaments lie unsupported. Such erosion can be easily recognized in surveying a large number of spicules, and when obvious, the observed shapes of such canals—always circular—cannot be considered as primary.

Observations

Spicules of ten species of Hexactinellida, including representatives of both subclasses and four orders, all possess square canals in cross section (Plate I, 1 and Table 1). In both microscleres and megascleres,

lateral canals and thus axial filaments impinge upon the flat faces
of the primary canal, resulting in a cuboidal intersection (Fig. 1 A).
The primary square symmetry of the axial canal is present in all
hexactinellid spicules observed—in loose spicules as well as in the
fused elements of the rigid lyssacine and dictyonine skeletons of
Euplectella, Staurocalyptus and *Aphrocallistes.*

In the Demospongiae, members of all spicule-bearing orders
were surveyed, but in several cases limits of resolution or spicule
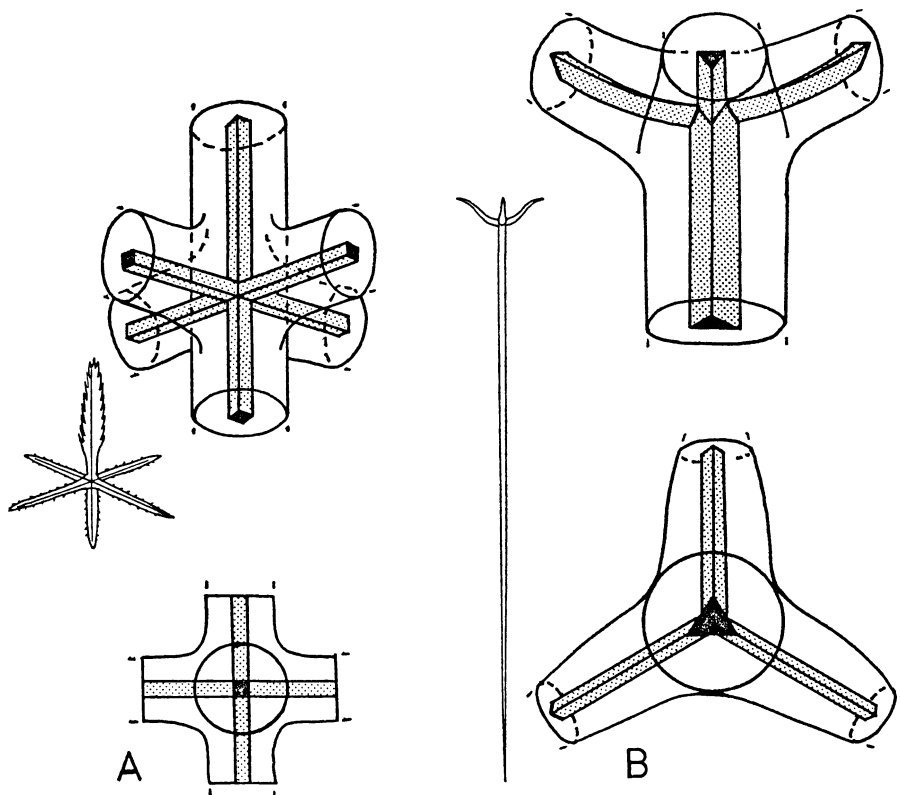erosion prevented determination of axial canal shape. In all resol-

FIG. 1.

A. - The pattern of junction of primary and secondary axial canals in a pinnulated
hexactine of *Sympagella nux* (Hexactinellida).
B. - The pattern of junction of the axial canals of the clads and rhabdome of
triaenes of *Geodia gibberosa* (Demospongiae).

vable instances, axial canals were found to be triangular in cross
section (Plate I, 2 and 3). The distribution of determined symmetries
and unresolvable filaments among species of the orders of the Demos-
pongiae are summarized in Table 1 following the taxonomic system
of Bergquist and Hartman (1969). In all cases where the organic
axial filament was directly observed, e.g., before silica deposition in
Mycale sp., or after silica removal in *Mycale* sp., *Tethya crypta,* and
Geodia sp., it was also found to be triangular in section. Shape of
the axial canal was not resolvable by light microscopy in either of

the surveyed species of Homosclerophorida, nor in most Halichondrida and Haplosclerida. The triangular sections were easily resolvable in all Spirophorida, Choristida, and Axinellida, and in most Hadromerida and Poecilosclerida.

TABLE 1

Major Taxa	Number of species of sponges with axial symmetry as indicated.	
	square/unresolved	p. 100 with square
C. Hexactinellida	10/0	100
SC. Amphidiscophora	2/0	100
O. Amphidiscosa	2/0	100
SC. Hexasterophora	8/0	100
O. Hexactinosa	1/0	100
O. Lychniscosa	1/0	100
O. Lyssacinosa	6/0	100
	triangular/unresolved	p. 100 with triangular
C. Demospongiae	55/26	69
« (SC. Tetractinomorpha) »	36/6	86
O. Homosclerophorida	0/2	0
O. Spirophorida	3/0	100
O. Choristida	8/0	100
O. Hadromerida	18/4	82
O. Axinellida	7/0	100
« (SC. Ceractinomorpha) »	19/20	49
O. Poecilosclerida	16/8	67
O. Halichondrida	1/2	33
O. Haplosclerida	2/10	20

Total species investigated : 91

The relationship of the symmetry of the principle rhabd axis to the axis of the cladi was studied in the triaenes of *Geodia* sp., *Goedia gibberosa, Geodia papyracea,* and *Stelletta clarella*. In all cases the canals of the cladi are also triangular in section and meet the principle rhabd axial canal on its edges (Fig. 1 B), not its faces as found in the hexactinellids. The axes of all cladi are oriented in the same

PLATE I.

1. Cross section of a large spicule of *Crateromorpha sp.* (Hexactinellida) with square axial canal. × 3,250.
2. Cross section of a large strongyle of *Tethya crypta* (Hadromerida) with triangular axial canal. The spicule has been heated at 500 °C, resulting in solution of outer layers, evolution of water of hydration, and formation of a vacuolar layer. × 2,100.
3. Cross section of a bundle of tylostyles of *Mycale* sp. in microtome section. The dark triangular centers are the stained axial filaments, surrounded by a very thin layer of opaline silica. × 2,460.
4. Longitudinal section of a nearly mature larva of *Mycale* sp. (Poecilosclerida) with dark centers of development of bilobed connective tissue structures (arrows). × 80.
5. A magnified center of development of bilobed connective tissue straps in a larvae of *Mycale* sp., several such elements in the field of focus in side and section views (arrows). × 1,000.

2

3

4

5
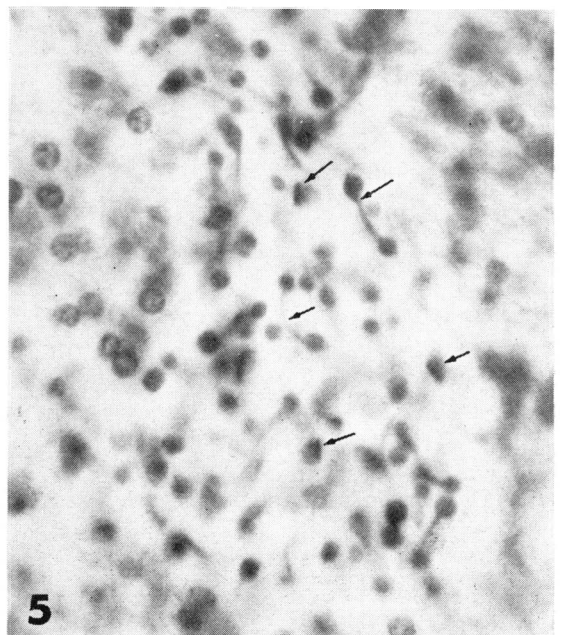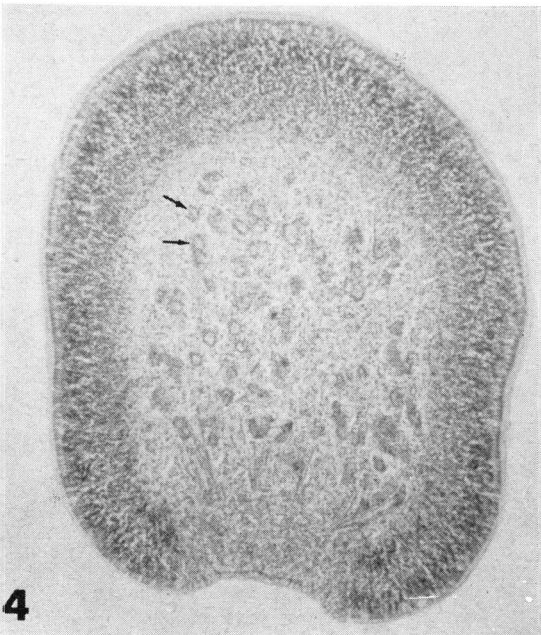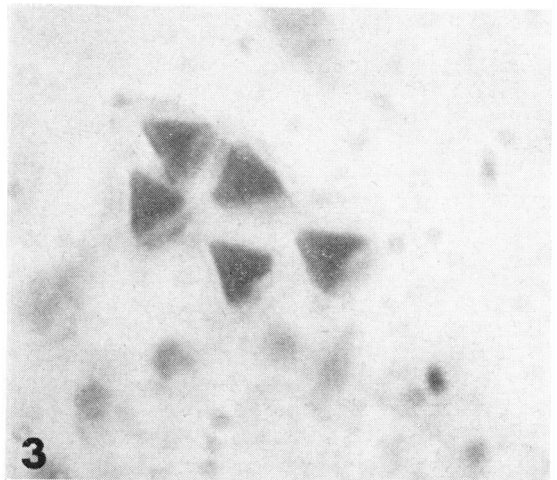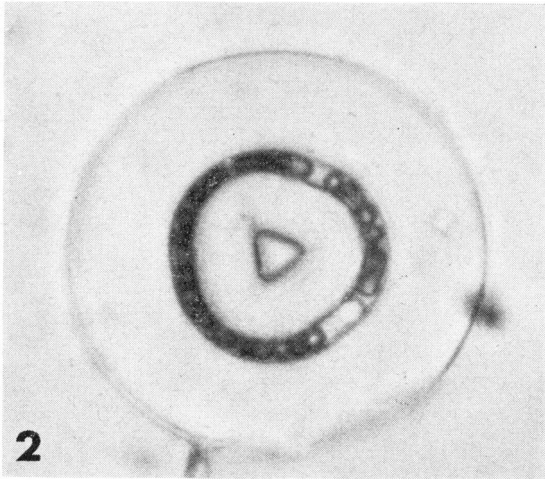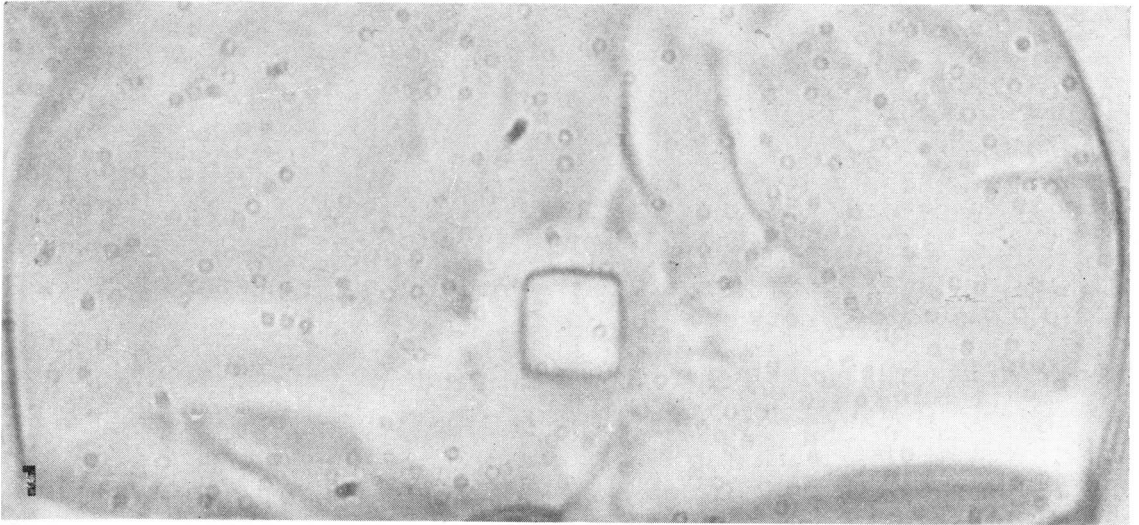
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Plate I

sense, with an apex of the triangular section directed along the main axis of the spicule towards the tip of the rhabd, and a face of the triangle directed towards the distal cladome end of the spicule.   At the intersection, the axes of the three cladi intersect the rhabd axis perpendicularly, not in the tetrahedral symmetry of the calthrops form.

Detailed studies of spiculogenesis of the larvae of *Mycale* sp. showed that megascleres are formed in the outer layer of larval cells prior to cellular differentiation.   All megascleres of a single larvae are formed synchronously, the axial filaments being formed in full length and breadth before silica deposition takes place.   From its earliest stages of development, the axial filament is triangular in section and this symmetry is retained in the shape of the fully completed spicule (Plate I, 3).

Bilobed structures identical to those described by Lévi (1963, 1964) as early stages of spicule formation in the larvae of *Mycale contarenii* arise in the larvae of the species of *Mycale* studied here after cellular differentiation and long after megasclere development (Plate I, 4).   Intensive studies of development and distribution of these structures (Plate I, 5) prove that they are not stages of spicule formation, but stages in the development of flat strap-like strands of connective tissue—probably spongin A.   Detailed descriptions of their development and ultimate products will be published elsewhere.

Discussion

All siliceous sponge spicules, from the variety of very small asters, sigmas, and toxas to megascleres, contain a definite organic axial filament system, and presumably all siliceous spicules are formed in a similar manner.   In both hexactinellids and demosponges, a relationship has been found to exist between the cross sectional shape of the axial filament and the pattern of junction of the secondary axes.   It appears that a square canal limits the branching pattern from 0 to 4 rays, each meeting the principle axis and the other secondary axes at right angles.   Just such a range of external spicule form is found among the megascleres and microscleres of the hexactinellids.   In the demosponges, the triangular axial fiber appears to limit secondary branching from 0 to 3 axes, the latter meeting the principle axis normally and with 120° between adjacent secondary rays.   Again this coincides with the major range of both megascleres and microscleres found among the demosponges—including the entire spectrum of triaenes, several forms of cheloids, sigmadiscorhabds, development stages of sphaerancorae and crepids of many lithistid desmas (see Dendy, 1921, and de Laubenfels, 1955, for reviews of spicule form).   It seems highly probable that the symmetry of the axial filament, secreted and formed before silicification takes place, provides a template with definite potentiality and also constraint on the symmetry of the subsequently completed spicule.

The discovery of a triangular axial filament in both subclasses of the Demospongiae implies that this structure has either been independently evolved in two separate lines, following the suggestion of

Lévi and Reid, or it has been evolved once and the two subclasses are related in this character. If it has been independently evolved in the Ceractinomorpha, this entire group has retained a basic tetraradial potential since its inception, but has never expressed it, at least in megasclere form. A triangular axis does not appear to be necessary for the process of silica deposition, since monaxons are successfully formed in the hexactinellids with square axes. The alternative explanation seems the more likely of the two—that the triangular axis and the potential tetraradial symmetry was evolved once and is shared in both of the subclasses erected by Lévi. The arguments for an independant evolution of the spicules of both subclasses as proposed by Lévi and Reid is not consistent with the results of this study.

The reality of a natural division between the two subclasses of Demospongiae was recognized as possibly doubtful by Lévi when these taxa were proposed (Lévi, 1957). The data from studies of amino acid analysis by Bergquist and Hartman (1969) has led these authors to suggest rejection of subclass Tetractinomorpha and retention of ordinal groupings as the highest recognizable entities for these sponges. The results of the present study indicate a close affinity between most of the orders Spirophorida, Choristida, Hadromerida, Axinellida and some of the Poecilosclerida. The Homosclerophorida stand apart form the other tetractinomorph orders in possessing extremely small axial filaments of unresolvable shape in cross section. The sponges grouped as Ceractinomorpha by Lévi and found to have a generally consistent pattern of amino acid content by Bergquist and Hartman are found to be extremely diverse in the size (resolution ability) of the axial filament. The continuing uncertainty of placements of species, genera, and families in the various recognized orders, and the lack of definite separations between the orders of demosponges, has been largely ignored by Reid (1970) in his attempt to project the unlikely natural separation of Lévi's subclasses into a phylogeny of the Demospongiae.

In interpretation of the fossil record, it must be considered that simple spicule form (monaxons) may provide little information as to taxonomic position. Monaxon spicules may be produced by groups of sponges with triangular axes (including the choristids proper), square axes (hexactinellids), and no organic axes (Calcarea, Jones, 1967). Since internal symmetry potential may or may not be expressed in external spicule form, the possibility exists for alternate expression and non-expression to have occurred repeatedly in the evolution of any of the demosponge groups. The recognition of such alternatives of expression in the fossil record is extremely unlikely. Such alternations of expression may also be responsible for the difficulties faced by systematists working with extant species.

In several cases, the ability or inability to resolve the shape of the axial canal of closely placed taxa coincides with discontinuities discovered in biochemical assays by other workers. In the Poecilosclerida, where triangular axes are present in most genera, that of *Agelas* was unresolvable. *Agelas* has also been found to possess a pattern of amino acids distinctive among the Poecilosclerida (Bergquist and Hartman, 1969). Among the Halichondrida, the canals of which are generally unresolvable, *Hymeniacidon* has obvious trian-

gular axes. The same discontinuity has been recognized in both amino acid patterns (Bergquist and Hartman, 1969) and sterols (Bergmann, 1949). Among the Hadromerida, with a typically triangular canal, those of *Anthosigmella varians, Spheciospongia vesparia, Spirastrella cuspidifera* and *Cliona celata* were unresolvable, this division also reflected in sterol types (Bergmann, 1949). Finally, among the Haplosclerida, with typical unresolvable canal shape, *Foliolina peltata* is found to have clear triangular axes, a discontinuity also seen in amino acid patterns (Bergquist and Hartman, 1969.). The symmetry relationships of axial canals of sponge spicules appear to hold promise as an easily available taxonomic character, useful primarily at higher taxonomic levels. The usefulness of the ability or inability to resolve canal shape with light microscopy has been successfully tested in several cases of unknown sponges.

Since the axis is probably basic to spicule form, the determination of symmetry patterns of axial filaments in other demosponges and in the new class of Sclerosponges (Hartman, 1969; Hartman and Goreau, 1970) may provide new information of relationships between these groups of siliceous sponges. Electron microscope studies of the spicules of *Haliclona rosea* (Haplosclerida) clearly indicate that the axial filament is hexagonal in section and is composed of a protein crystallized in three primary rays, 120° between planes of the array (Garrone, 1969). Garrone noted the differences between his results and those of Lévi (1964), but he did not suspect that the structures investigated by the latter were not stages of spiculogenesis at all. The structures described and figured by Lévi were stages of connective tissue formation, thus the differences in their results are now under standable. The nature of the intermediate layer, between the crystalline axial protein and silica, was not studied closely by Garrone, although it was determined to be a non-protein organic material. It is very likely that this material is the polysaccharide postulated and determined by staining reactions in spicules of fresh-water sponges (Drum, 1968). Garrone (1969) has also convincingly shown that the opaline " crystallites " of siliceous spicules described by Fjerdingstad (1970) are certainly nothing more than artifacts produced by the chatter of a diamond blade on the opaline silica. The bilateral symmetry of spicules proposed by Fjerdingstad is thus erroneous.

The clear illustration of three axes of crystallization in the axial protein of *Haliclona rosea* indicates that all of the unresolvable axial filaments found in this study may be triangular when viewed with higher resolution. The success of this preliminary study has led to the initiation of an extensive survey of the phylum with the scanning microscope to test this hypothesis. The data, when obtained and assessed in relation to present embryological, biochemical and morphological data, may provide new evidence of basic relationships between all groups of sponges and a possible revision of the higher taxonomy of the Porifera.

Summary

Axial canals and thus presumably axial filaments of all Hexactinellida surveyed are square in cross section. Axial canals and filaments of Demospongiae, where resolvable by light microscopy, are triangular in cross section. This

includes the majority of samples studied in the orders Choristida. Spirophorida, Hadromerida, Axinellida, and Poecilosclerida. The canals of the Homosclerophorida, Haplosclerida, and Halichondrida are generally too small to resolve by light microscopy. The relationship of secondary axes to the symmetry of the primary axial filament indicates that the shape of the primary filament may reflect the potential limits of external spicule symmetry. The basic potential symmetry of the axis may or may not be expressed in external spicule morphology. The presence of triangular axial canals in both subclasses, Tetractinomorpha and Ceractinomorpha, as proposed by Lévi, indicates a close relationship between the two goups. The independent evolution of spicules in these two subclasses of demosponges as suggested by Lévi and Reid is rejected by the results of this study. Discontinuities in the taxonomic placements of several species and genera of demosponges, indicated in the work of previous authors, are re-emphasized by differences in the ability or inability to resolve a triangular axial canal with light microscopy in these cases.

Zusammenfassung

Sämtliche untersuchte Hexactinellida haben Axial-Kanäle und somit wohl auch Axial-Filamente, deren Querschnitt quadratisch ist. Die Axial-Kanäle und Filamente der Demospongiae sind, wo Auflösung des Lichtmikroskops zugänglich, dreieckig. Dieses betrifft die Mehrzahl der studierten Proben der Choristida, Spirophorida, Hadromerida, Axinellida und Poecilosclerida. Die Kanäle der Homosclerophorida, Haplosclerida und Halichondrida sind, in der Regel, zu klein für die Auflösung des Lichtmikroskops. Die Beziehungen der sekundären Axen zur Symmetrie der primären Axial-Filamente zeigen, dass die Form der primären Filamente die möglichen Grenzen der Symmetrie der Externen Spikeln abspiegeln mag. Entweder findet die fondamentale mögliche Symmetrie der Axis ihren Ausdruck in der äusseren Morphologie der Spikeln, oder sie findet ihn nicht. Das Vorhandensein triangulärer Axial-Kanäle in den beiden Unterklassen Tetractinomorpha und Ceractinomorpha, von Levi vorgeschlagen, zeigt eine enge Verwandtschaft zwischen beiden Gruppen. Die unabhängige Evolution von Spikeln in dieser beiden Unterklassen der Demospongien, von Lévi und Reid vorgeschlagen, wird durch die Ergebnisse dieser Untersuchung zurückgewiesen. Diskontinuitäten in der taxinomischen Einstufung verschiedener Arten und Gattungen von Demospongien, die von der Arbeiten verschiedener früherer Autoren indiziert wurden, werden in solchen Fällen wiederum verstärkt durch Unterschiede in der Fähigkeit oder Unfähigkeit, den Axial-Kanal mittels Licht-Mikroskopie aufzulösen.

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Appendix I.

Species surveyed, their taxonomic position after Bergquist and Hartman (1969), and the cross-sectional shape of the axial filament as determined by light microscopy as square, triangular, or unresolvable.

Class Hexactinellida

Subclass **Amphidiscophora**
> Order Amphidiscosa
> > square: *Pheronema annae* Leidy; *Hyalonema seiboldi* Gray.

Subclass **Hexasterophora**
> Order Hexactinosa
> > square : *Aphrocallistes* sp.
>
> Order Lychniscosa
> > square: *Dactylocalyx pumiceus* Stutchbury.
>
> Order Lyssacinosa
> > square: *Euplectella* sp.; *Staurocalyptus dowlingi* (Lambe); *Sympagella nux* Schmidt; *Crateromorpha* sp.; *Walteria leukhardti* Ijima; *Calycosoma* sp.

Class Demospongiae

Subclass **Tetractinomorpha**
> Order Homosclerophorida
> > unresolvable: *Plakortis* sp.; *Plakina monolopha* Schulze.
>
> Order Spirophorida
> > triangular: *Cinachyra* sp.; *Craniella arb* (de Laubenfels); *Tetilla* sp.
>
> Order Choristida
> > triangular: *Stelletta clarella* de Laubenfels; *Stelletta* sp.; *Geodia gibberosa* Lamarck; *Geodia papyracea* Hechtel; *Geodia* sp. 1; *Geodia* sp. 2; *Jaspis* sp.; *Erylus* sp.
>
> Order Hadromerida
> > triangular: *Suberites ficus* (Johnston); *Polymastia infrapilosa* Topsent; *Polymastia andrica* de Laubenfels; *Polymastia pachymastia* de Laubenfels; *Timea* sp.; *Tethya aurantia* (Pallas); *Tethya crypta* (de Laubenfels); *Terpios zetecki* de Laubenfels; *Didiscus* sp.; *Anthosigmella* sp.; *Cliona lampa* de Laubenfels; *Cliona vermifera* Hancock; *Cliona* sp.; *Ulosa* sp.; *Spirastrella* sp.; *Tentorium* sp.; *Weberella* sp.; *Placospongia carinata* (Bowerbank).
> > unresolvable: *Cliona celata* Grant; *Anthosigmella varians* (Duchassaing and Michelotti); *Spheciospongia vesperia* (Lamarck); *Spirastrella cuspidifera* (Lamarck).
>
> Order Axinellida
> > triangular: *Axinella polycapella* de Laubenfels; *Axinella nanaspiculata* Hartman; *Axinella* sp.; *Homaxinella rudis* (Verrill); *Pseudoaxinella rosacea* (Verrill); *Higginsia stigilata* (Lamarck); *Phakellia ventilabra* (Linnaeus).

Subclass **Ceractinomorpha**
> Order Poecilosclerida
> > triangular: *Neofibularia nolitangere* (Duchassaing and Michelotti); *Thalysias* sp.; *Petrosia* sp.; *Stylinos* sp.; *Iotrochota birotulata* (Higgin); *Microciona microjoana* de Laubenfels; *Microciona* sp. 1; *Microciona* sp. 2; *Mycale laevis* (Carter); *Mycale* sp. 1; *Mycale* sp. 2; *Hemectyon hyle* de Laubenfels; *Ophlitaspongia pennata* (Lambe); *Tedania* sp.; *Acarnus erithacus* de Laubenfels; *Lissodendoryx* sp.
> > unresolvable: *Desmacella vagabunda* Schmidt; *Axocielita hartmani* Simpson; *Agelas* sp. 1; *Agelas* sp. 2; *Neopetrosia subtriangularis* (Duchassaing and Michelotti); *Esperiopsis* sp.; *Neopetrosia longleyi* (de Laubenfels); *Microciona* sp. 3.
>
> Order Halichondrida
> > triangular: *Hymeniacidon* sp.
> > unresolvable: *Halichondria verrilli* Burton; *Halichondria panicea* (Pallas).
>
> Order Haplosclerida
> > triangular: *Foliolina peltata* Schmidt; *Xestospongia muta* (Schmidt).
> > unresolvable: *Haliclona erina* de Laubenfels; *Haliclona rubens* (Pallas); *Gelliodes ramosa* (Carter); *Gelliodes* sp.; *Desmapsamma anchorata* (Carter); *Xestospongia diprosopia* (de Laubenfels); *Xestospongia* sp.; *Stylocordyla borealis* (Loven); *Spongilla lacustris* (Linnaeus); *Heteromyenia ryderi* Potts.