

AN APPROACH TO THE PHYLOGENETIC RECONSTRUCTION OF AMPHIDISCOPHORA (PORIFERA: HEXACTINELLIDA)

K.R. TABACHNICK AND L.L. MENSHENINA

Tabachnick, K.R. & Menshenina, L.L. 1999 06 30: An approach to the phylogenetic reconstruction of Amphidiscophora (Porifera: Hexactinellida). *Memoirs of the Queensland Museum* 44: 607-615. Brisbane. ISSN 0079-8835.

Two phylogenetic lines characterise Amphidiscophora (Porifera: Hexactinellida): the Pheronematidae-Monorhaphididae line and Hyalonematidae line. Both are derived from a lophophytous, cup-like sponge with an atrial cavity and osculum. Changing the body shape of the ancestral form gives rise to difficulties in water transport, hence the development of special types of compensation is required. The Pheronematidae-Monorhaphididae line leads to a columnar body with compensation developed in the form of expansion of dermal and atrial surfaces which penetrate into each other. The Hyalonematidae line leads to a conical body shape in which compensations developed in the form of cavities, atrial depressions and septa. Various body shapes which correspond to all Recent genera and subgenera of Amphidiscophora are discussed, emphasising their phylogenetic relations. □ *Porifera. Hexactinellida. Amphidiscophora, Pheronematidae, Monorhaphididae, Hyalonematidae, phylogenetic reconstruction, phenetics, systematics, external body shape.*

K.R. Tabachnick (email: bentos@bentos.ioras.msk.ru), Institute of Oceanology, Academy of Sciences of Russia, Krasikova str. 23, Moscow 117218, Russia; L.L. Menshenina, Moscow State University, Moscow, Russia; 22 January 1999.

Amongst the hexactinellids Amphidiscophora is a distinct and relatively stable taxon. Its stability and monophyletic status has not been challenged by either the discovery of hexadiscs in some taxa, or by more recent discovery of amphidiscs (spicules which were earlier considered to be specific for Amphidiscophora) as in some representatives of Hexasterophora (Tabachnick & Lévi, 1997). Recent Amphidiscophora consists of three families: Hyalonematidae, Pheronematidae and Monorhaphididae. All sponges belonging to Amphidiscophora can be easily assigned to a family, even if represented by only a small fragment, through the distinctness of their choanosomal megascleres (Ijima, 1927). By comparison, assigning species to genera is more complex, often depending on consideration of the external shape of the body; whereas spicule composition is less important. Species identifications require analysis of spicules, particularly microscleres, dermal and atrial spicules. Cases where spicules are unique or specific to a single taxon are very rare within Amphidiscophora, and moreover, some spicules previously considered to be monospecific have since been found in other taxa (e.g. four-toothed anchorate basalialia have since been found in a *Semperella*-like sponge (Pheronematidae) (Reiswig, pers. comm.); paradiscs and tylodiscs are reported in *Monorhaphis*

chuni, Hyalonema (Oonema) n. sp. and Pheronema conicum (series of publications by Tabachnick & Lévi, in press a, b & c).

The palaeontological history of Amphidiscophora, as well as of other Hexactinellida with loose skeletons, is poorly known. The occurrence of almost-complete specimens in the fossil record is restricted to several descriptions: *Uralonema* (Librovich, 1929), *Hyalonema* (Mehl & Hauschke, 1995) and problematic findings of Recent genera *Pheronema* and *Monorhaphis* (Mehl, 1992). The division of Amphidiscophora into Amphidiscosa and Hemidiscosa (Reid, 1958) (their earlier names Amphidiscaria and Hemidiscaria (Schramen, 1924), commonly used in the palaeontological literature), is now doubtful. This division was based on a single type of loose spicule, the latter taxon being characterised by presence of hemidiscs only. The discovery of hemidiscs among common amphidiscs in Recent *Pheronema conicum* and *Hyalonema (Oonema) n. sp.* (Tabachnick & Lévi, in press a & b) raises doubts about the validity of Hemidiscosa. Hence, palaeontological records provide no further clues for the reconstruction of phylogenetic process within Amphidiscophora.

The lack of any unique spicules and uniformity in spicule combinations among Recent amphidiscophorans do not allow these characters to be

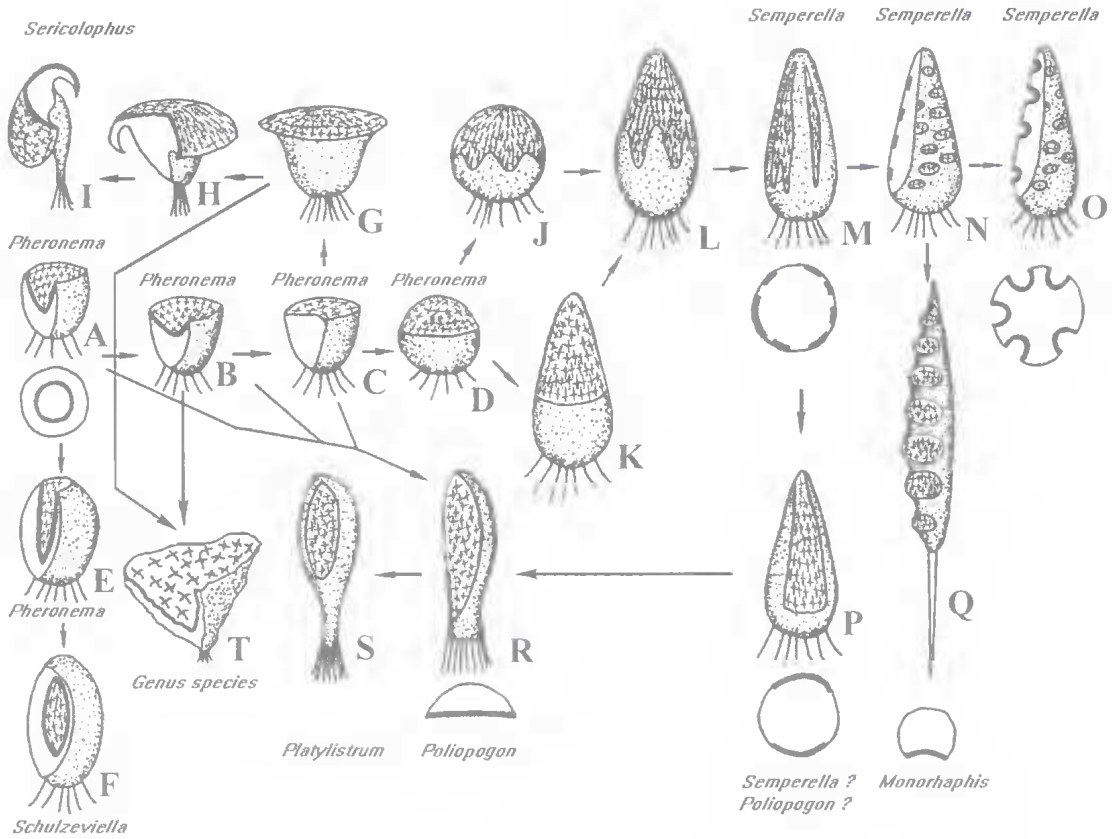


FIG. 1. Phylogenetic scheme for the Pheronematidae-Monorhaphididae line. A, cup-like, thin walled ancestral form and its transverse section; B-D, reduction of atrial cavity to a spherical form; E, barrel-like form with decreased osculum; F, oval form without osculum, atrial cavity inside the body; G, bell-like form with thickened marginalia; H, hypothetical form with thin marginalia twisted downwards and compact basal tuft; I, body form developed through bilateral deformation of the former form; J, hypothetical spherical form with deformed dermal-atrial border; K, hypothetical ovoid form with deformed dermal-atrial border; L, hypothetical ovoid form with atrialia divided into vertically distributed spaces; its transverse section; M, ovoid form with atrialia divided into numerous rounded spots; O, ovoid form with numerous atrial cavities and oscula; its transverse section; P, ovoid form with two vertical atrial spaces; its horizontal section; Q, columnar body with atrialia represented with oval spots organised in a linear vertical series; R, simple bilaterally, fan-like form; its transverse section; S, spoon-like form; T, thin-walled form (see Reiswig, 1999, this volume). Thin line in sections and dotted surface = dermalia; thick line in sections and surface covered with crosses = atrialia; arrows = suggested phylogenetic relationships.

used in any informative sense when considering their phylogeny. Conversely, variation in body shape among Recent species, which is very important in taxonomy, may be of greater value in reconstructing their evolution.

In this present work the systematics of Amphidiscophora is constructed using phenetic principles, developing the phylogenetic ideas of Reid (1964) who emphasised the significance of body form in the evolution of Hexactinellida. Cladistic analysis has only been applied to

Hexactinellida in ranking higher taxa (Van Soest, 1985), and for constructing some cladograms of Hexastrophora (Mehl, 1992), but these methods seem to be useless for Amphidiscophora given their lack of any obvious or easily defined apomorphies within constituent taxa. Thus, the phylogenetic scheme proposed here is based on the traditional school of evolutionary systematics, using functional morphological analyses and morphogenetic reconstructions. Under this scheme, evolution from the ancestral form rests on the assumption that increases in absolute body

size lead to disproportionate size changes of related parts (Huxley, 1932), with consequent demands on the development of special mechanisms to compensate for water-flow and other problems. The method of rectangular coordination in deformations (Thomson, 1917) mostly shows variations in related body forms, whereas some hydrodynamic requirements may explain peculiarities in internal body constructions.

PHYLOGENETICS

ANCESTORS. In analysing the variation in external body shape in Amphidiscophora it is necessary to emphasise the poriferan function. To develop the ideas of Oken (1809), who suggested characterising taxa with short aphorisms such as 'animal-eyes', 'animal-gut' and 'animal-lungs', it is possible to offer the term 'animal-settled-kidney' for most sponges. From this aphoristic definition further evolution of the external shape of amphidiscophorans may be explored.

All representatives of Amphidiscophora are lophophytous sponges attached by anchorate spicules which often raise the body high above the substratum. This feature provides taxa with the ability to dwell on most types of oceanic substrata, from rocks to mud (Tabachnick, 1991). In body shape, the tube-like form is hypothesised to be the ancestral hexactinellidan form (Mehl, 1991; Tabachnick, 1991). The tube-like body allows filtered and unfiltered water to remain separate, also providing a means for passive filtration (Vogel, 1974). Thus, the amphidiscophoran ancestor would be a lophophytous sponge with numerous basalia, a cup-like body with atrial cavity and a single terminal osculum (Figs 1A; 4A). Two principal amphidiscophoran lines, Pheronematidae-Monorhaphididae and Hyalonematidae, are easily derived from this ancestral form. Tube-like or cup-like body forms are observed in most species of *Pheronema* (Pheronematidae) (Fig. 1A, E). Representatives of Hyalonematidae are more divergent except for a single monotypic genus, *Platella*, known from 3 specimens which preserve some of the ancestral features. One specimen is cup-like with compact untwisted basalia (Fig. 4B); 2 other specimens have probably the same form but the basalia are twisted (Fig. 4C) (Tabachnick, unpub. data).

PHERONEMATIDAE-MONORHAPHIDIDAE LINES OF EVOLUTION. The main tendency for most genera of Pheronematidae is to

reduce the atrial cavity through several stages, probably through adaptation to high sedimentation conditions (Tabachnick, 1991). Some of these stages are present in several species of *Pheronema* (Fig. 1B-D): *P. circumpalatum*, *P. globosum* and *P. nascaniensis* have low atrial depression (Fig. 1B) or hemispherical body form (Fig. 1C). The spherical form is realised in some specimens of *P. nascaniensis* (Fig. 1D). This process, as well as wall thickening, is accomplished with intensive development of subdermal and subatrial cavities or canals, hence water must pass through larger distances inside the sponge between dermal and atrial surfaces. The extension of the evolutionary tendency for Pheronematidae to invert the atrial cavity and to elongate the spherical body form in the vertical direction should lead to an ovoid sponge where the dermal surface is represented on the lower part, and the atrial surface on the upper part of the ovoid body. Similar results were obtained using mathematical techniques applied to growth modelling, where the ovoid body form is a result of simulation of the radial accretive growth derived from an initially spherical object (Kaandorp, 1994). In visualising water flow through a sponge with an ovoid body, two distinct zones (the lower and upper) may not be sufficiently associated in pumping-filtering activity (Fig. 2). Even large cavity and canal development would not facilitate water transport because the total surface area is limited by sponge diameter. Conversely, the proportions of a spherical form seems to be theoretically more probable. Moreover, spherical body form is practically realised in some specimens of *Pheronema nascaniensis* whereas the closest theoretical descendant growth form — the ovoid one — has not been practically realised, and is probably 'unstable', hypertrophied or non-functional.

To avoid the problems connected with an ovoid body form (long distance to transport water), compensation takes place by development of deformation of the border between dermal and atrial surfaces (Fig. 1J-L). In such sponges each sector of the dermal surface in the middle part of the body is connected by two close atrial sectors, and vice versa. Thus, the distance required for water transport is more restricted (Fig. 3). This process enables an increase in body length in the vertical direction and leads to a number of theoretical body forms which in reality are seen united in *Semperella* (Fig. 1M-P). The most primitive of these forms seem to be hydrodynamically

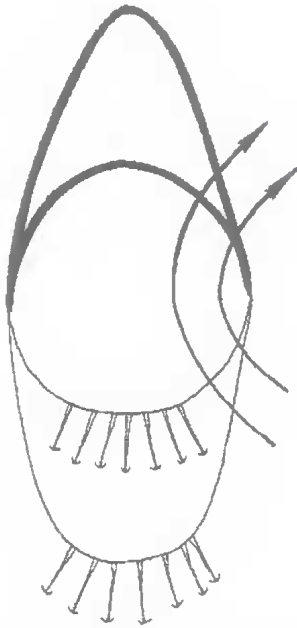


FIG. 2. Superposition of vertical sections of spherical and ovoid forms of Pheronematidae with the same maximal diameter. Thin line = dermalia; thick line = atralia; arrows = water flow. The scheme shows the difficulties of water transport through distinct parts of the ovoid form compared to the spherical one.

plausible but it is not so far known among any Recent species (Fig. 1L). The more developed stages, with fragmentation of the atrial area, are quite common. The least specialised form with columnar body has several longitudinally directed atrial areas: *Semperella schulzei* and *S. n. sp.* (Fig. 1M) (Tabachnick & Lévi, in press a) and *S. alba* (Fig. 1P). A more advanced sponge body form has the same type of columnar body but where atrial surface consists of numerous rounded atrial spots separated by the dermal area: *Semperella cucumis* and *S. n. sp.* (Fig. 1N) (Tabachnick & Lévi, in press a), or forms with the rounded atrial spots bent inwards inside the body forming numerous atrial cavities with corresponding oscula: *Semperella stomata* and probably *S. spirifera* (Fig. 1O).

The growth form which apparently can be easily transformed from a columnar body with numerous rounded atrial spots is known for *Monorhaphis*, the atrial surface of which is represented by a linear vertical series of rounded spots (Fig. 1Q).

Another body form typical of Pheronematidae is bilaterally-symmetrical, fan-like, with dermal and atrial surfaces located on the opposite sides,

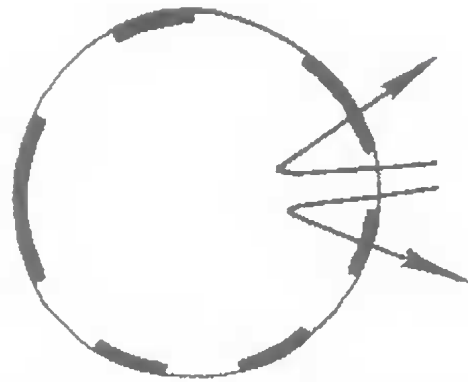


FIG. 3. Transverse section of a *Semperella*-like sponge (like Fig. 1M, N, P). Thin line = dermalia; thick line = atralia; arrows = water flow. The scheme shows facilitation of water transport in forms with deformed dermal-atrial borders due to reduction of the distance of water transport which becomes possible in the horizontal direction.

as in the genus *Poliopogon* (Fig. 1R). Similar to it is the spoon-like body form which characterises *Platylistrum* (Fig. 1S), a slightly divergent variant of the fan-like form. The fan-like body may be interpreted as a result of irregular growth of a hemispherical body, or by asymmetrical growth of a wall sector in a tube-like body (both from a *Pheronema*-like ancestor), or from the columnar body with longitudinally directed atrial areas through to reduction of these atrial areas to a single one (from a *Semperella*-like ancestor). A body form with two atrial and two dermal surfaces on opposite sides is known in *Semperella alba* (Fig. 1P) (Tabachnick, 1988), which could be considered to be transitional between *Semperella* and *Poliopogon*.

A very peculiar bilateral body form known in *Sericolophus* (Fig. 1I) may also be derived from the hemispherical growth form, but with several transitional stages: a bell-like form with thin marginalia (Fig. 1G) — eversion of thin marginalia downwards (Fig. 1H) — irregular body growth. The transitional forms (Fig. 1G-H), which seem to be hydrodynamically plausible, are, however, so far unknown among Pheronematidae although common among the related Hyalonematidae.

The other theoretical possibility in the development of the Pheronematidae line is a body form with an entirely closed atrial cavity, as seen in the problematic genus *Schulzeviella* (Fig. 1F) (Tabachnick, 1990). This genus contains a single species with two subspecies: *S. gigas gigas* (pro

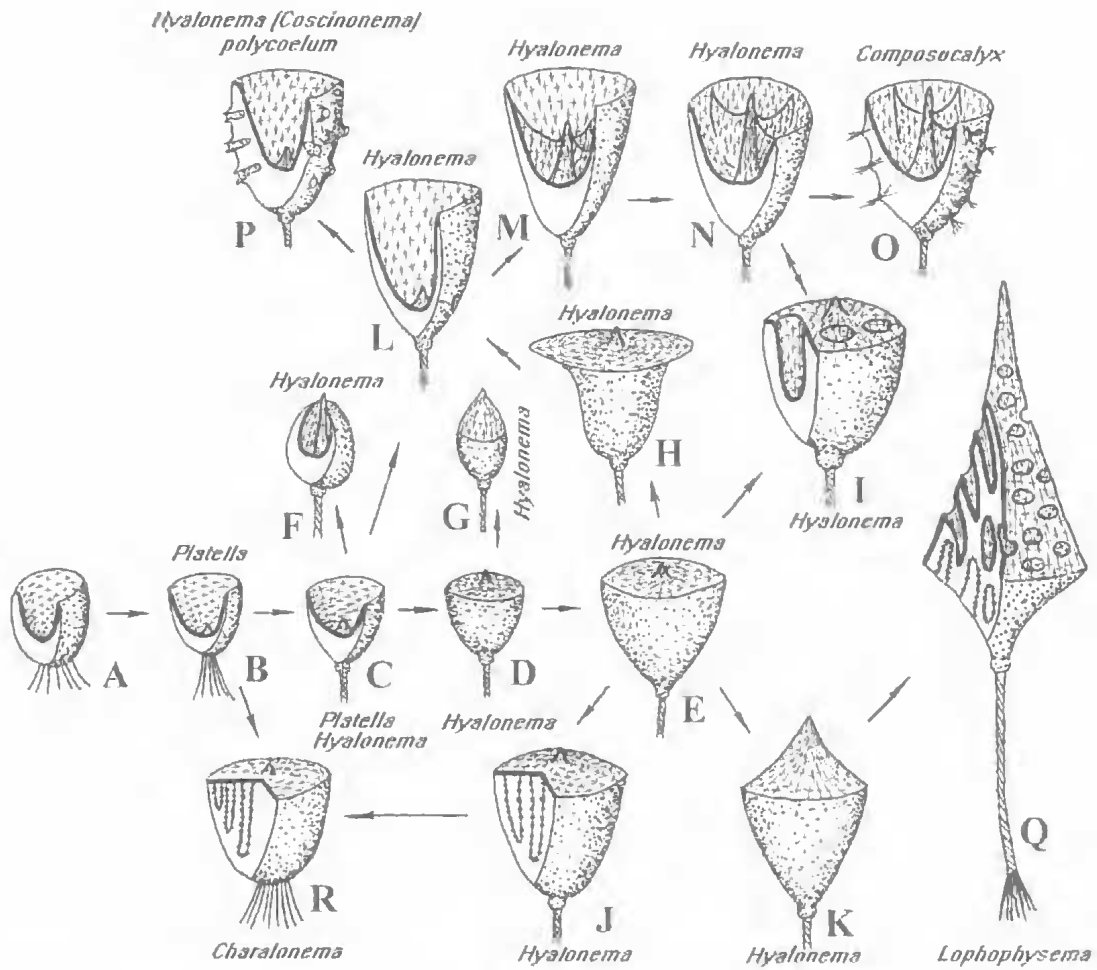


FIG. 4. Phylogentic scheme for the Hyalonematidae line. A, hypothetical cup-like, thin walled ancestral form; B, the same with compact tuft of basalialia and apical cone; C, the same with twisted basalialia; D, conical form with reduced atrial cavity; E, enlarged previous form; F, ovoid form with vast atrial cavity, narrow osculum and apical cone penetrating it; G, ovoid form in which atrial surface is present as the upper hemisphere and dermal surface as the lower one; H, bell-like form with thin marginalialia; I, conical form with developed atrial depressions; J, conical form with developed subatrial cavities; K, body form of two cones fused to each other by their widest bases; L, body form which originated from the 'C' by its enlargement or from the 'H' by twisting marginalialia upwards; M-N, septate cup-like forms; O, same with tufts of prostalia lateralia; P, cup-like form with dermal depressions; Q, body form of two cones fused to each other by their widest parts with subdermal cavities and atrial depressions; R, conical form with subatrial cavities and broad untwisted basalialia. Thin line in sections and dotted surface = dermalia; thick line in sections and surface covered with crosses = atrisialia; dotted line in sections = subatrial cavities; arrows = suggested phylogenetic relationships.

Poliapogon gigas Schulze, 1887) and *S. gigas spinosum* (Tabachneik, 1990). The latter subspecies is represented by a slightly damaged specimen. The reconstruction of its body shape shows that it must be an oval sponge in which the atrial cavity is entirely enclosed inside the body (no osculum was observed). This body shape may be derived from the most primitive ancestral form by the overgrowth of the osculum with

marginal walls. The intermediate body forms with large atrial cavity and small osculum (Fig. 1E) are known among species of *Pheronema*. If this interpretation of the body of *Schulzeviella* is correct it may be worthy of recognition as a separate genus, given that all genera of Pheronematidae are characterised by specific body forms. If not, however, these sponges should be returned

to *Pheronema* as suggested by Reiswig (1992) and Dawson (1993).

To understand the functionality of the body form seen in *Schulzeviella* it is necessary to study other sponges with analogous construction among the Hexasterophora (e.g. *Aphrocallistes* and *Euplectella*), given that this type of body form is otherwise absent among the other Amphidiscophora. *Euplectella* has thin walls with numerous lateral oscules and orifices in the sieve-plate which covers the main osculum. The sieve-plate of *Euplectella* is considered to appear from the lateral walls (Ijima, 1901) as in *Schulzeviella*. The out-flow of water must pass through the sieve-plate and lateral oscules. The walls in *Schulzeviella* are thin (in relation to its huge size) and they become thinner toward the upper end of the sponge. Inside these walls there are numerous canals. In *Schulzeviella* the out-flow of water may penetrate through the sieve-plate as it does in *Euplectella*-like sponges, although water movement from atrial to dermal surfaces is an uncommon mode among Hexactinellida. Similarly, comparison with *Hyalonema* body forms provide a clearer understanding of body functionality in *Schulzeviella*, whereby they develop large subatrial cavities beneath the atrial surface, which is represented by the sieve-plate (Fig. 4J).

A new type of pheronematid body-form is described by Reiswig (1999, this volume), consisting of a widely open funnel with thin walls and a short, thin tuft of basalia (Fig. 1T). This form might be interpreted as a descendant of cup-like *Pheronema*, or of a hypothetical ancestor of *Sericolophus* (Fig. 1G). The affinities of this sponge to *Poliopogon* may be ancestral, or vice versa, but based on evidence presented here I consider that this sponge is more probably allied to *Pheronema* than to *Poliopogon*.

HYALONEMATIDAE LINE OF EVOLUTION.

Evolution of most Hyalonematidae is connected with the gathering of basalia into a compact tuft. This process is correlated with the appearance of an apical cone — a conical protrusion from the middle of the atrial cavity where the proximal parts of anchorate basalia are gathered beneath the atrial surface. In most hyalonematid representatives the basal tuft is compact and twisted, presumably a functionality to increase its strength and flexibility. A minute widening in the lower part of the body containing special spicules (acanthophores) also correlates with the appearance of a compact tuft of basalia. This body form

is common for some species of most subgenera of *Hyalonema* (i.e. *H. (Pteronema)*, *H. (Thamnonema)*, *H. (Prionema)*, *H. (Paradisconema)*, *H. (Oonema)*, *H. (Leptonema)*, *H. (Cyliconema)*, *H. (Coscionema)*, *H. (Corynonema)*; (Fig. 4C). A similar body form with numerous dermal depressions also appears to be present in *H. (Coscionema) polycoelum* (Fig. 4P) (Lévi & Lévi, 1989). Two principal lines of evolution may be derived from this body form.

The first line leads to the appearance of an oval body with a small osculum, a deep atrial cavity and an apical cone which protrudes above the osculum penetrating it (e.g. *H. (Phialonema)*, some species of *H. (Oonema)*, *H. (Onconema)* and *H. (Leptonema)*; (Fig. 4F). The further development of several vertical septa between the lateral wall and the apical cone could also be anticipated (see below) (Fig. 4M-N).

The second line leads to a reduction of an atrial cavity and formation of a so-called sieve-plate from the atrial surface (Fig. 4D-E). These conical forms are known in some species of *H. (Thamnonema)*, *H. (Pteronema)*, *H. (Prionema)*, *H. (Paradisconema)*, *H. (Oonema)*, *H. (Leptonema)*, *H. (Cyliconema)* and *H. (Coscionema)*. The extension of this process leads to oval forms, similar to the pheronematid tendency where the dermal surface corresponds to the lower hemisphere and the atrial surface to the upper one (Fig. 4G). This body form is rarely found among Hyalonematidae, represented only by small sponges in several species of *H. (Coscionema)* and *H. (Corynonema)*. Forms with a reduced atrial cavity are common in most subgenera of *Hyalonema* and are typical for all its known juveniles. The proportional enlargement of these forms does not seem to be successful because of the concomitant water transport problems associated with increased body volume (Fig. 5). Hence such large forms require special types of compensation.

One form of compensation is the development a large body composed of two cones fused together at their widest part (Fig. 4K). Intensive development of subdermal cavities beneath thin, net-like dermalia and numerous atrial depressions with oscular openings on the upper cone are presented in the form seen in *Lophophysema* (Fig. 4Q). The development of large subdermal cavities is a rare event, hence the inhalant orifices near the dermal surface should be smaller than exhalant ones near the atrial surface to facilitate the water transport. That is why large subatrial cavities and atrial depressions are common while

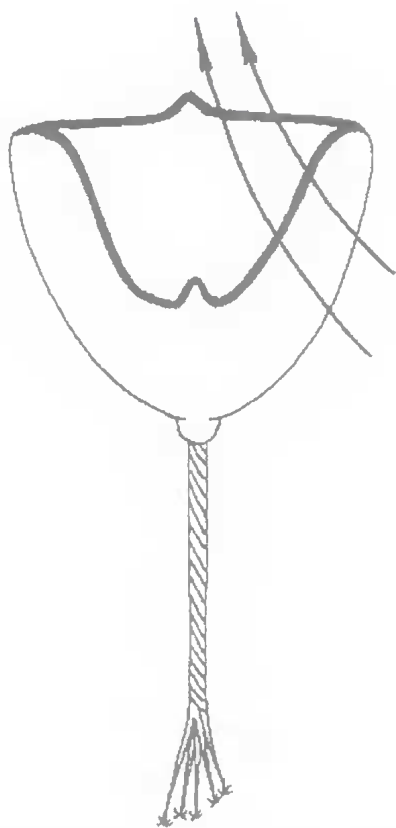


FIG. 5. Superposition of the sections of cup-like and conical forms of Hyalonematidae with coexisting external borders. Thin line = dermalia; thick line = atrialia; arrows = water flow. The scheme shows prolongation of water transport through central part of conical form in comparison to cup-like one.

such cavities and depressions in the vicinity of dermal area are rare.

A second possible form of compensation is the development of large subatrial cavities in large conical forms, seen in some *H. (Thamnonema)*, *H. (Pteronema)*, *H. (Hyalonema)* (pro *Hyalonema (Euhyalonema)*); (Hooper & Wiedenmayer, 1994) and *H. (Coscinonema)* (Fig. 4J). *Charalonema* may be considered to be a descendent of this form in which the tuft of basalia became less compact and untwisted (Fig. 4R). Conversely, the other possibility for the origin of *Charalonema* is from a *Platella*-like ancestor with a tendency, parallel to that of *Hyalonema*, to reduce the atrial cavity and to develop subatrial canals.

A third possible method of compensation for a large bell-like form without an atrial cavity is seen in the development of several (often four) atrial depressions directed downwards (Fig. 4I)

(e.g. some species of *H. (Coscinonema)* and *H. (Corynonema)*). This body form may be considered to be a further step in the evolution towards septate forms.

The appearance of septate forms must take place mainly in thin-walled sponges with an elongate apical cone. Septa may have developed to increase the rigidity of the enlarged thin-walled body. Nevertheless other possibilities of septate-form appearance can be considered: from conical forms with atrial depressions (see above), or from bell-like forms with thin and well developed edges (Fig. 4H) (this form is known for *H. (Prionema)*). The septate sponges are known among *H. (Hyalonema)*, *H. (Onconema)*, *H. (Leptonema)*, *H. (Cyliconema)* and *H. (Coscinonema)* (Fig. 4M-N). *Composocalyx* also corresponds to the septate body type but it has specific tufts of prostalia lateralia composed of diactines situated on the conical prominences of dermal surface (Fig. 4O).

DISCUSSION

PROBLEMS IN TERMINOLOGY. There are several problems remaining in the terminology pertaining to sponge body form. 1) The sieve-plate described in some representatives of Hyalonematidae is not homologous to the sieve-plate of other Hexactinellida since it is constructed from the atrial surface and not from the wall, as suggested for *Euplectella* and *Regadrella* (Ijima, 1901), and even for *Schulzeviella*. 2) The origin of secondary oscula in Amphidiscophora also requires some clarification. In all known representatives of Pheronematidae, including *Semperella stomata* (Fig. 1O) there appear to be orifices and borders between dermally- and atrially-lined surfaces. The secondary oscules of Hyalonematidae, where known (Fig. 4I), are also orifices but they are surrounded with an atrially-lined surface while the border between dermalia and atrialia marks the ancestral position of the primary osculum.

PHYLOGENETICS. The common trend for both Hyalonematidae and Pheronematidae-Monorhaphididae lines of the Amphidiscophora is to reduce the atrial cavity. The former line mostly develops the conical body with corresponding compensation in large specimens through the appearance of depressions, septa and subatrial cavities. The latter line shows tendency to invert the atrial cavity, which leads to a columnar body and corresponding compensation through the changing position of dermal and

atrial areas which penetrate into each other; hence the ancestral form is represented by a large number of species of one genus (*Pheronema*). Nevertheless, *Sericolophus* (Pheronematidae) evolves into a form reminiscent of Hyalonematidae, while *Lophophysema* (Hyalonematidae) displays some pheronematid features of evolution. The presence of bilaterally symmetrical forms also emphasises the differences between these lines. In the Pheronematidae-Monorhaphididae line, forms with bilateral symmetry are known in many genera, while in the Hyalonematidae line they are entirely absent. This state of bilateral symmetry is achieved by curvation of the stalk in any direction, under the influence of water flow (Tabachnick, 1991).

PHYLOGENETICS AND SYSTEMATICS. Phylogenetic reconstruction of the Pheronematidae-Monorhaphididae line shows the distinct relationship between *Pheronema*, *Semperella* and *Sericolophus*. These genera can be connected only through hypothetical, functionally unstable forms (as in the two former genera), or through forms which have not so far been encountered in Recent representatives of this family (as in the latter genus). The numerous variants of these hypothetical forms (Fig. 1J-L) do not challenge the monophyly of *Semperella* since they all seem to originate from a common ancestor. The possibility of a polyphyletic origin of *Poliopogon* may be related to the difficulties connected with its identification (Tabachnick & Lévi, in press). Nevertheless, the phylogenetic reconstruction does not provide arguments to improve the situation with *Poliopogon*. The close relationship between *Monorhaphis* and *Semperella* was also recognised in the classical systematics literature, where *Monorhaphis* was placed in Semperellidae (Schulze, 1887) with a single genus *Semperella*, prior to the subsequent inclusion of *Monorhaphis* (Schulze, 1904). Later this family was rejected by Ijima (1927), and *Monorhaphis* was placed in a separate family. The distinct taxonomic position of *Monorhaphis* is a result of clear spicule divergence, due probably to its extremely elongate body. The choanosomal skeleton composed of taactines and the single giant anchorate spicule are specific features which apparently justified its recognition as a separate family. The Monorhaphididae probably originated from Pheronematidae, as indicated by this present phylogenetic reconstruction. Another support for this suggestion is that only representatives of Pheronematidae (*Semperella* and *Poliopogon*) possess basalial of

different kinds: a mixture of anchorate spicules and monaxons-diactins. The single basal spicule of *Monorhaphis* is likely to be the same monaxon-diactin, and the loss or reduction of all the other basalial in a *Semperella*-like ancestor is very probable. To solve the problem of the validity of *Schulzeiella* requires new data. Confirmation of its specific body shape is necessary to maintain the validity of the genus.

Most of the specific body-forms, or their close series, correspond to a single taxon of Amphidiscophora within the generic range. This emphasises the generic status of *Hyalonema* with its numerous subgenera, differing from each other by combinations of several features; the corresponding body forms are not specific for each subgenus. The subgenera of *Hyalonema* were raised to generic level by Lévi (1964), but this action was reversed in his subsequent papers. The generic status of *Composocalyx* and *Charalonema* is not obvious since these genera have close relations with the diverse complex of *Hyalonema*. The genus *Charalonema* was considered to be close to *H. (Pteronema) topsenti* (Ijima, 1927) and in the scheme suggested here it may be the ancestor of that subgenus. Nearly all extrapolated body forms of the hyalonematid line of evolution are present in nature. The absence of gaps explains the problems with their close relationships and difficulties in identification.

Amphidiscophoran representatives seem to realise all the possible body forms which can be derived from their suggested ancestors, excepting several forms which are unfavourable for pumping-filtering activity.

ACKNOWLEDGEMENTS

The authors are grateful to the two anonymous reviewers and to J.N.A. Hooper for their critical notes on the manuscript and assistance with language. This work was supported by the grant of the International Science Foundation no. MOR000, MOR300.

LITERATURE CITED

- DAWSON, E.W. 1993. The Marine Fauna of New Zealand: Index to the Fauna. 2. Porifera. New Zealand Oceanographic Institute Memoir 100: 1-98.
- HOOPER, J.N.A. & WIEDENMAYER, F. 1994. Porifera. Zoological catalogue of Australia, Vol. 12 13: 1-625.
- HUXLEY, J.S. 1932. Problems of relative growth. (Methuen & Son: London).

- IJIMA, I. 1901. Studies on the Hexactinellida. Contribution 1. (Euplectellidae). Journal of the College of Science, Imperial University of Tokyo, Japan 15: 1-299.
1927. The Hexactinellida of the Siboga Expedition. Pp. 1-383. In Siboga Expedition Reports. Vol. 40(6) (E.J. Brill: Leiden).
- KAANDORP, J.A. 1994. Growth models of sponges using geometric modelling techniques. Pp. 235-240. In Soest, R.W.M. Van, Kempen, T.M.G. van & Braekerman, J.C. (eds) Sponges in time and space. (Baalkema: Rotterdam).
- LÉVI, C. 1964. Spongiaires des zones bathyale, abyssale et hadale. Galathea Reports 7: 83-112.
- LÉVI, C. & LÉVI, P. 1989. Spongiaires (Musorstom I & 2). In Resultats des Campagnes Musorstom Vol. 4. Memoires de Muséum National d'Histoire Naturelle (A) 143: 25-103.
- LIBROVICH, L.S. 1929. *Uralonema karpinskii* nov. sp. and other silicispongia from Carboniferous of the eastern slope of the Urals. Memoirs of the Committee of Geologie, Leningrad 179: 1-57.
- MEHL, D. 1991. Are Protospongiidae the stem group of Modern Hexactinellida?. Pp. 43-53. In Reitner, J. & Keupp, H. (eds) Fossil and recent sponges. (Springer-Verlag: Berlin, Heidelberg).
1992. Die Entwicklung der Hexactinellida seit dem Mesozoicum - Palaeobiologie, Phylogenie und Evolutionsoekologie. Berliner Geowissenschaftliche Abhandlungen E (2): 1-164.
- MEHL, D. & HAUSCHKE, N. 1995. *Hyalonema cretacea* n.sp., ertekoeperlich erhaltne Amphidiscophora (Porifera, Hexactinellida) aus dem Mesozoicum. Geologie und Palaeontologie (Westfalia) 38: 89-97.
- OKEN, L. 1809. Lehrbuch der Naturphilosophie. Vol. 1: 1-228; Vol. 2: 1-188; Vol. 3: 1-374 (Jena).
- REID, R.E.H. 1958. A monograph on the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part I. Paleontographical Society Monographs (1957): 1-46.
1964. A monograph on the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part II. Paleontographical Society Monographs (1963): 49-94.
- REISWIG, H.M. 1992. First Hexactinellida (Porifera) (Glass sponges) from the Great Australian bight. Records of the South Australian Museum 26(1): 25-36.
1999. New Hexactinellid sponges from the Mendocino Ridge, northern California, USA. Memoirs of the Queensland Museum (this volume).
- SCHRAMMEN, A. 1924. Die Kiesel-spongien der oberen Kreide von Nordwestdeutschland. III und Letzter Teil. Mit Beiträgen zur Stammgeschichte. Monographes der Geologie und Palaentologie. Berlin (I, H) 2: 1-159.
- SCHULZE, F.E. 1887. Report on the Hexactinellida collected by HMS 'Challenger' during the years 1873-1876. In Report of the Scientific Results of HMS 'Challenger' 21: 1-513. (Her Majesty's Stationery Office: London, Edinburgh, Dublin).
1904. Hexactinellida. Wissenschaftliche Ergebnisse der Deutschen Tiefsee. Expedition auf dem Dampfer 'Valdivia' 1898-1899 4: 1-266.
- SOEST, R.W.M. VAN 1985. Toward a phylogenetic classification of sponges. Pp. 49-64. In Ruetzler, K. (ed.) New perspectives in sponge biology. (Smithsonian Institution Press: Washington, DC).
- TABACHNICK, K.R. 1988. Hexactinellid sponges from the mountains of West Pacific. Pp. ????. In Kuznetsov, A.P. & Sokolova, M.N. (eds) Structural and functional researches of the marine benthos. (Academy of Sciences of the USSR P.P. Shirshov Institute of Oceanology: Moscow).
1990. Hexactinellid sponges from the Nasca and Sala-y-Gomez. Trudi of the Institute of Oceanology, Academy of Sciences of the USSR 124: 161-173.
1991. Adaptation of the Hexactinellid sponges to deep-sea life. Pp. 378-386. In Reitner, J. & Keupp, H. (eds) Fossil and recent sponges. (Springer-Verlag: Berlin, Heidelberg).
- TABACHNICK, K.R. & LÉVI, C. 1997. Amphidiscophoran Hexasterophora. Part 1. Berliner Geowissenschaftliche Abhandlungen (E) 20: 147-157.
- In press a. Pheronematidae (Porifera, Hexactinellida, Amphidiscophora) off the New Caledonia. Revision of *Sericolophus* (including materials off Hawaii and Australia) and *Pheronema giganteum*. In Resultats des Campagnes Musorstom. Memoires du Muséum National d'Histoire Naturelle, Paris.
- In press b. Hyalonematidae (Porifera, Hexactinellida, Amphidiscophora) off the New Caledonia. The origin of uncinates and paradises in the Hexactinellida. In Resultats des Campagnes Musorstom. Memoires du Muséum National d'Histoire Naturelle, Paris.
- In press c. Revision of the genus *Monorhaphis* (Porifera, Hexactinellida, Amphidiscophora). Zoosystema.
- THOMPSON D'ARCY, W. 1917. Growth and form. (Cambridge University Press: Cambridge).
- VOGEL, S. 1974. Current-induced flow through the sponge *Halichondria*. Biological Bulletin 147: 443-456.