

DEFICIENT *MERLIA NORMANI* KIRKPATRICK, 1908, FROM THE CURAÇAO REEFS, WITH A DISCUSSION ON THE PHYLOGENETIC INTERPRETATION OF SCLEROSPONGES

by

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SUMMARY

A specimen of the sclerosponge *Merlia* lacking a basal skeleton of calcareous chambers (corresponding to the description of *Merlia deficiens* Vacelet, 1980) is reported from the underside of the coral *Agaricia* at a depth of 10 m on the reef of Curaçao, Netherlands Antilles. Its spiculation is identical to *Merlia normani* Kirkpatrick, 1908 specimens with the basal skeleton, from which it is concluded that *M. deficiens* and *M. normani* are probably conspecific.

The phylogenetic significance of a sclerosponge with an unstable calcareous skeleton is discussed and in accordance with Vacelet (in press) it is postulated that sclerosponges are polyphyletic. It is suggested that sclerosponge skeletons are an ancestral character for a large part of the Demospongiae. The relationships of Demospongiae and Calcarea are discussed in the same light.

RÉSUMÉ

Un exemplaire du Sclérospongiaire *Merlia* dépourvu du squelette basal de logettes calcaires, et correspondant à ce qu'avait été décrit comme *Merlia deficiens* Vacelet, 1980, a été découvert à la face inférieure du corail *Agaricia* à 10 m de profondeur sur le récif de Curaçao, Antilles Néerlandaises. La spiculation est identique à celle des exemplaires à squelette basal de *Merlia normani* Kirkpatrick, 1908, d'où il est possible de conclure à la conspécificité probable de *M. deficiens* et de *M. normani*.

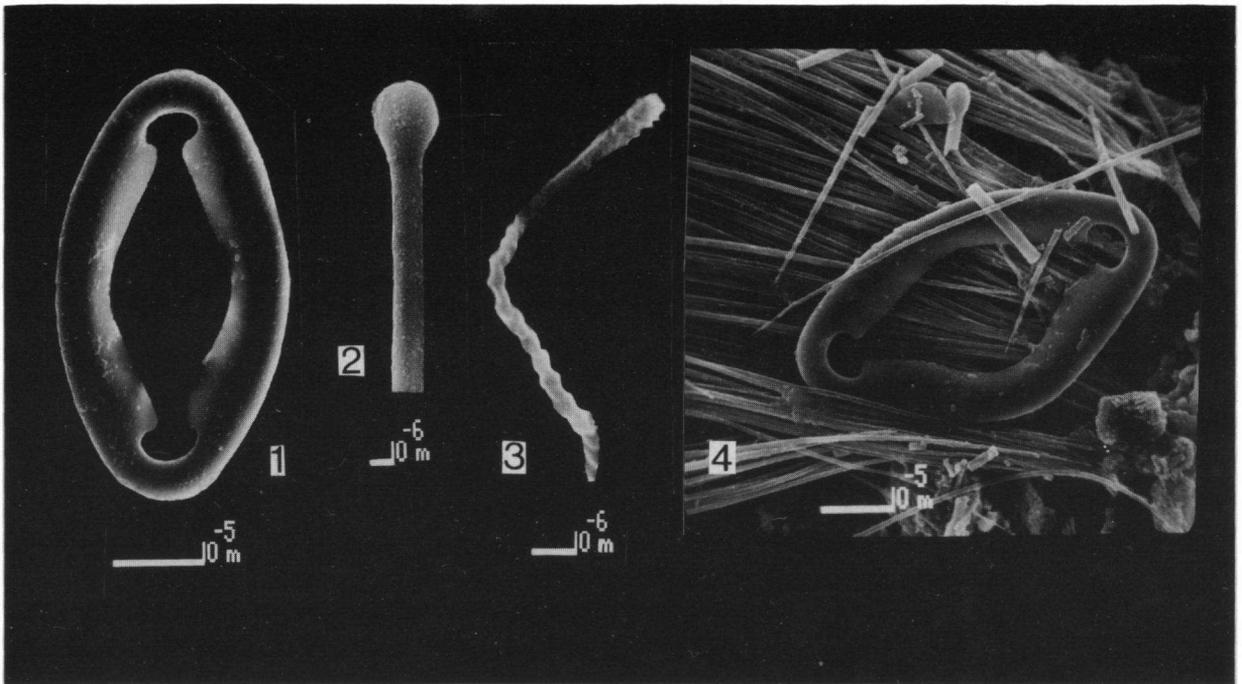
On discute de la signification phylogénétique d'un Sclérospongiaire à squelette calcaire instable et, d'accord avec Vacelet (sous presse) on conclut au caractère polyphylétique des Sclérospongiaires. On suggère que les squelettes des Sclérospongiaires représentent un caractère ancestral pour une grande partie des Demospongiae. Dans le même ordre d'idées, on discute des relations de parenté entre Demospongiae et Calcarea.

INTRODUCTION

Kirkpatrick (1908) described *Merlia normani* from Porto Santo, Madeira Archipelago. This species possesses a basal skeleton of calcareous chambers, in which and over which the soft parts of the animal are draped. These soft parts include a mineral skeleton of characteristic SiO₂ spicules: tylostyles, raphides, commata and clavidiscs. Subsequently, the species has been found in the Indian Ocean (Dendy, 1922), the Mediterranean (e.g. Vacelet, 1980; Pulitzer-Finali, 1972) and Jamaica (Hartman & Goreau, 1970).

Pouliquen (1972) was the first to record *Merlia* without its characteristic skeleton (from a cave near Marseille); Vacelet (1980) compared the two forms and concluded that they were closely related, but probably specifically distinct on account of consistently larger clavidiscs in the deficient form, which he named *Merlia deficiens*.

It will be shown below that these differences are slight and that Vacelet's new species is doubtful. Thus it appears that within one and the same species the calcareous base may be facultative or unstable. The phylogenetic significance of this fact is discussed below in the light of Vacelet's newest ideas put forward during a recent symposium (September, 1983) (Vacelet, in press). For this reason the soft parts of various other sclerosponges have been studied as well.



Figs. 1-4: 1, Clavidisc of deficient *Merlia normani* from the Curaçao reefs. 2, Head of tylostyle of deficient *Merlia normani*. 3, Acanthose comma of deficient *Merlia normani*. 4, Overall view of spicule complement of deficient *Merlia normani*, showing clavidisc, tylostyle and acanthose raphides.

SYSTEMATIC DESCRIPTION

Order POECILOSCLERIDA

Family Biemnidae

Merlia normani Kirkpatrick, 1908

Merlia normani Kirkpatrick, 1908: 510, pl. XV figs. 10-18.
Merlia deficiens Vacelet, 1980: 227, pl. I figs. 3-4; Vacelet, 1981: 321.

Material. — Zoölogisch Museum Amsterdam coll. no. ZMA POR. 4765, Curaçao, 4th buoy (500 m W. of Piscadera), depth 10 m, under surface of *Agaricia* colony, 2-I-1981, coll. L. Delvoye.

Description (figs. 1-5). — Extremely thin (≈ 0.5 mm), incrusting patch about 2 cm² in lateral expansion; in alcohol the specimen is invisible against the background of the coral substrate. In life the colour was red. The skeletal structure is difficult to study due to the

extreme thinness, but from scrapings it is clear that wispy bundles of tylostyles form the main support; microscleres are numerous.

Spicules: tylostyles with sinuous shaft and small but distinct heads: 137-160 by 1-2 μm ; clavidiscs (compound diancistras): 42-57 by 21-34 μm ; rugose (acanthose) raphides in thick dragmata: 44-84 by 0.5 μm ; sigmatose comata: 7-15 μm .

DISCUSSION

The decision to unite *normani* and *deficiens* is made on the basis of spicule comparisons of available *Merlia* material and literature data (cf. table I). Vacelet's suggestion that there is a difference in clavidisc size between normal and deficient specimens seems to be correct, but the

TABLE I
Spicule sizes (μm) of *Merlia* specimens.

Locality	Habit	Authority	Tylostyles	Clavidiscs	Rhaphides	Commata
Porto Santo, Madeira Archipelago	sclerosponge	present paper	144-152/2-3	30-44.0-53/29-36	48-74	14-15
Mediterranean	sclerosponge	Vacelet, 1980	—	38.6	—	—
Mediterranean	sclerosponge	Pulitzer-Finali, 1972	136-153/1.5	41-47	54-80	15-17
Jamaica	sclerosponge	Hartman & Goreau, 1970	142-171	28-33/24-28	—	—
Jamaica	sclerosponge	Vacelet, 1980	—	34.3	—	—
Mediterranean	deficient	Vacelet, 1980	—	56.7	—	—
Curaçao	deficient	present paper	137-160/1-2	42-49.3-57/21-34	44-84	7.5-15
Mediterranean	unknown	Pulitzer-Finali, 1983	122-173/1.5-2	29-78	44-90	—
Chagos Archipelago, Indian Ocean	unknown	Dendy, 1922	—	57-66/41	—	—

matching of the other spicule sizes is so great that a separate specific status seems doubtful. A further reason for uniting the two is found in the geographic distribution of both forms, which overlaps completely in the tropics and subtropics.

The acceptance of this has the heavy implication that the calcareous basal skeleton is unstable within the species, a suggestion already put forward by Vacelet (1980).

The polyphyly of the "class" Sclerospongiae will be discussed below. Vacelet (1979) erected a separate order Merliida for *Merlia* within the Demospongiae, which was followed by Pulitzer-Finali (1983). For various reasons this is not accepted here, the most important being the great correspondence in spiculation of *Merlia* with members of the poecilosclerid family Biemnidae. In a previous paper (Van Soest, 1984) I outlined this family as comprising among others the genera *Biemna* Gray (1867), *Desmacella* Schmidt (1870), *Hamacantha* Schmidt (1870), and *Neofibularia* Hechtel (1965). *Merlia normani* shares the tylostylote megascleres with *Desmacella*, the roughened microxea (rhaphides) with *Neofibularia*, the commata with *Biemna* and *Neofibularia*, and finally there is an undeniable

structural correspondence between the diacistras of *Hamacantha* and the clavidiscs of *Merlia*. These shared characters can only be explained in one way: shared ancestry at the family level.

PHYLOGENETIC IMPLICATIONS OF THE SCLEROSPONGE SKELETON

Apart from *Merlia normani* I was able to study specimens of several other sclerosponges (listed in the Acknowledgements below), which allows me to draw firsthand conclusions. I did not look at fossil specimens, but discussions with Mr. Theo van Kempen (Geological Institute, University of Amsterdam) and Mr. Theo van Koolwijk, who did a literature survey of fossil hypercalcified sponges, contributed in shaping my opinion.

The polyphyletic nature of the class Sclerospongiae

The existence of this class is widely accepted among neontologists (e.g. Hartman & Goreau, 1970, 1975; Hartman, 1972, 1979; Lévi, 1973; Bergquist, 1978, and in press). The only confessed critic among recent spongologists is Vacelet (1979, 1980, 1981, and in press), and

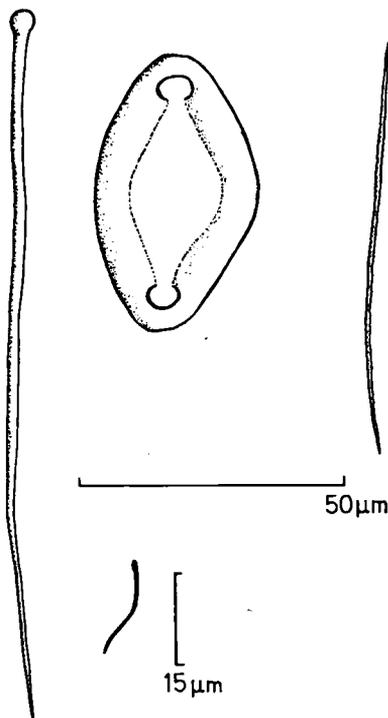


Fig. 5. Line drawings of spicules of deficient *Merlia normani*.

his reasoning is here supported. A brief survey of the recent sclerosponges is necessary to show the weight of the evidence against the existence of such a class, found in the soft parts of these sponges.

Ceratoporella, *Goreauiella*, *Stromatospongia*, *Hispidopetra* and *Astrosclera*:

These all share a single spicule type, viz. an acanthostyle with the thorns arranged in verticils. Such a characteristic spicule type is also found in a single non-sclerosponge genus: *Agelas*. This "enigmatic" group of species was recently raised to ordinal status, but has presumed axinellid affinities. *Astrosclera* is known to have unstable spicules, as specimens have been found without them or with only a few (Vacelet, 1977, 1981). This fact is given considerable weight in arguments presented below.

Acanthochaetetes (= *Tabulospongia*):

The spicules in the soft parts are tylostyles and

spirasters; this combination is characteristic of the genus *Spirastrella*, family Spirastrellidae, order Hadromerida.

Calcifibrospongia:

No material has been studied, but from Hartman's (1979) well-presented description it can be easily seen that the strongyle reticulation found in this form shows undeniable similarities with haplosclerids of the family Halicionidae.

The data given above are summarized in fig. 6. If we should wish to unite these forms into a single (sub-)class, comprising sclerosponges only, we are forced to admit:

- either that there has occurred an improbable number of parallel developments in spicule categories and combinations in Sclerospongiae on the one hand and Demospongiae on the other,
- or that all these spicules are primitive, occurring already in the (Cambrian?) common ancestor of both groups.

As several of these spicule types are quite unusual with only a limited distribution, such conclusions are hardly parsimonious. For this reason I strongly support Vacelet in his refutation of the Sclerospongiae as a class separate from the Demospongiae.

The next question to be solved is: has the basal calcareous skeleton been developed separately in each different line, or is it a primitive (ancestral) character of a large group of demosponge orders? *Merlia* does not provide us with an unequivocal answer to this. If parallel development is postulated, one might cite *Merlia* as an example of a living form in which the development of a basal skeleton is actually witnessed this very moment in time. Adversely, if it is assumed (as Vacelet, in press, has put forward) that the basal skeleton is primitive, shared with many fossil sponges (stromatopoids, chaetetids), then *Merlia* may be cited as an example of a sponge in the process of losing its calcareous base. However, three more arguments for the latter view can be put forward: firstly, the fossil record of sclerosponges

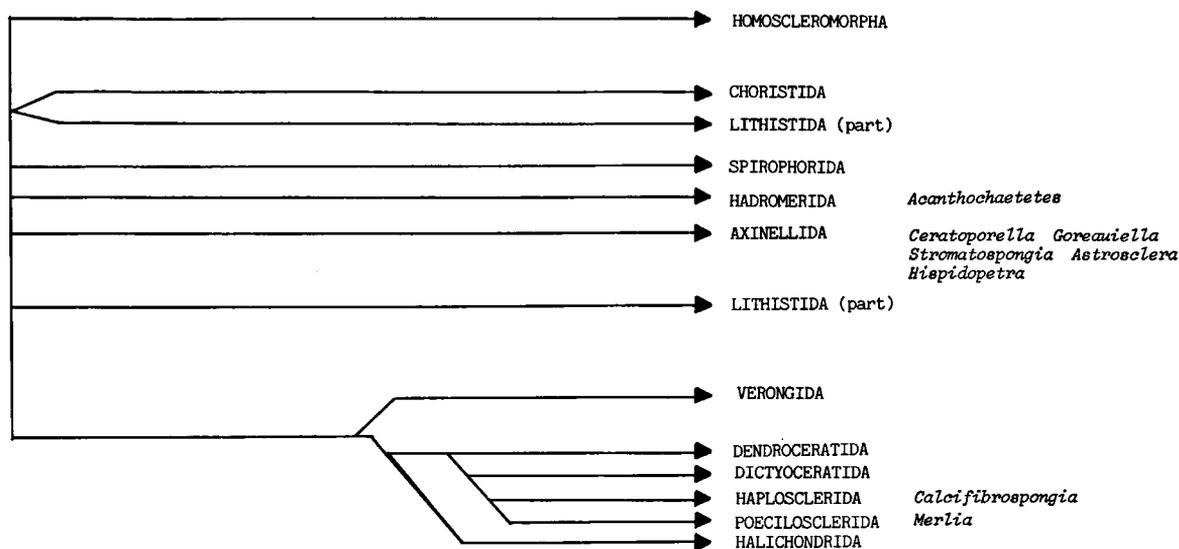


Fig. 6. Distribution of sclerosponge genera over the currently recognized demersponge orders (partly redrawn from Bergquist, 1978, fig. 8.8).

is quite extensive (the sclerosponge nature of many stromatoporoids and chaetetid tabulates seems to be firmly established, see e.g. Stel, 1978, cf. also Hartman et al., 1980); secondly, the number of living sclerosponges is quite low, pointing to a low strategic advantage of the basal calcareous skeleton, which in its turn supports the idea of it having been abandoned by most sponges for competitive reasons; thirdly, the cryptic habitat of living sclerosponges points in the same direction: it is probable that they have been pushed into unfavourable niches by modern reef building organisms (stony corals and non-sclerosponges). Vacelet's (in press) overall picture thus is consistent with the observed facts and represents the most acceptable hypothesis.

Some remarks on lithistid sponges are in order here. In many ways lithistids assume the same habit as sclerosponges, and it is likely that they represent a separate attempt of sponges to occupy the reef habitat. From the literature (e.g. Finks, 1970, cited in Hartman et al., 1980: 74) it could be concluded that lithistids appeared (in geological time) after the stromatoporoids, and thus could not with certainty be considered a parallel development (it

would be conceivable that they evolved from stromatoporoids by replacing the calcareous chamber walls by SiO_2 spicules). Adversely, it could be argued that the earliest (Middle Cambrian) stromatoporoids are doubtful sponges (Stearn, 1979), unequivocal ones being known only from the Middle Ordovician. This would mean that the lithistids could be considerably older, and may have been ancestral to the stromatoporoids. We will leave this question undecided here.

Lithistids have a limited distribution among the Demerspongiae, being confined mostly to astrophorid and spirophorid tetractinomorpha, a few probably unrelated sublithistids excepted. Those forms considered *incertae sedis* by Lévi (1973) on account of the lack of true tetracts quite likely just lost these spicules and are probably closely related. Just as the sclerosponges, the lithistids have been likewise driven to an unfavourable habitat (they are commonest in deep water beyond the reefs), due no doubt to competition with more successful reef builders.

SPHINCTOZOANS, MURRAYONIDS

These are "living fossils" described or redescribed recently by Vacelet (1970, 1977,

1979), assigned or formerly assigned to the class Calcarea. This class is well characterized by a number of synapomorphies (shared derived characters), the most important of which is the possession of triactine and tetractine CaCO_3 spicules. The origin of the group has never been satisfactorily clarified, because the fossil record is poor and the group shows few plesiomorphous characters.

The sclerosponge-like murrayonids give food to the assumption that such a synplesiomorphy of Calcarea and other sponges may be found in their common stromatoporoid origin, an idea advocated by Termier & Termier (1973). If this is rejected (as Vacelet, in press, apparently has done), then we have to assume that a basal calcareous skeleton has at least evolved twice independently from soft-bodied sponges (this is not entirely impossible, since there are quite large structural differences between different sclerosponge basal skeletons).

Where has the dialytine (soft bodied sponges with free calcareous spicules) structure come from? Until recently, this type of sponge was known from the Carboniferous onwards (Wendt, 1979, cited in Hartman et al., 1980: 170), but Van Kempen (1978) rather casually mentioned the occurrence of dialytine spicules from the Middle Cambrian of Australia. However, after careful restudy and reconsideration (photographs and comparisons with recent dialytine sponges), Van Kempen and I reached the conclusion that the spicules are not likely to be dialytine in origin. They probably represent tetractinellid spicules. In a forthcoming paper of Van Kempen the presence of these particular forms of spicules will be discussed in more detail. Consequently, it still stands that soft-bodied calcareous sponges came out of the blue, somewhere near the beginning of the Mesozoic, in which time inozoans and sphinctozoans were already well established (Wendt, 1979, cited in Hartman et al., 1980). The earliest sphinctozoans apparently developed in the Middle Cambrian (Pickett & Jell, 1983), so it is impossible to suggest any evolutionary sequence other than to point out that they appeared in the same period as lithistids, (?) tetractinellids and

probably stromatoporoids. Although Vacelet (1979) has shown that the only living sphinctozoan, *Vaceletia crypta*, has Demospongiae characters and lacks the Calcarea synapomorphies, nevertheless comparable fossil forms with typical Calcarea spicules have been described, which have to be attributed to the Calcarea, e.g. *Verticillites*.

Contrary to the opinion of Borojévič (1979), these data and observations may be interpreted in such a way that the origin of the Calcarea from early demosponge-stromatoporoid-sphinctozoan stock is made plausible through a series of presumed steps: First, it is suggested that primitive Sphinctozoa-like sponges evolved from stromatoporoids by losing their siliceous spicules. The tendency to lose the siliceous spicules is observed in the recent *Astrosclera*; most other demosponge-sclerosponges have feebly developed spicules compared to their non-sclerosponge relatives (compare spicule sizes of *Merlia* with those of most biemnids, those of *Acanthochaetetes* with spirastrellids). Hereafter a progressive loss of the basal calcareous skeleton occurred, unrelated to the loss of spicules, in the same way as it is assumed to have happened in demosponge sclerosponges, and indeed is witnessed in *Merlia* and in the murrayonids *Murrayona* and *Paramurrayona*. Finally, the resulting total loss of a supporting skeleton would in some cases have been compensated by the development of a new type of support, the calcareous triactine or tetractine spicules, in a form similar to that of certain demosponge SiO_2 spicules (calthrops). It is conceivable that the ability of making SiO_2 spicules was lost along the way and that the ability of making a certain type of spicule was retained.

HOMOSCLEROPHORIDA

Dialytine Calcarea show similarities with Homosclerophorida, which have always been considered independently acquired*, but it may

* Möhn (1984) in a recent major revision of the classification of the Porifera, apparently considers these similarities as primitive, since he clearly states them to be homologous in both groups, but at the same time he considers Calcarea as the oldest and most original sponge group.

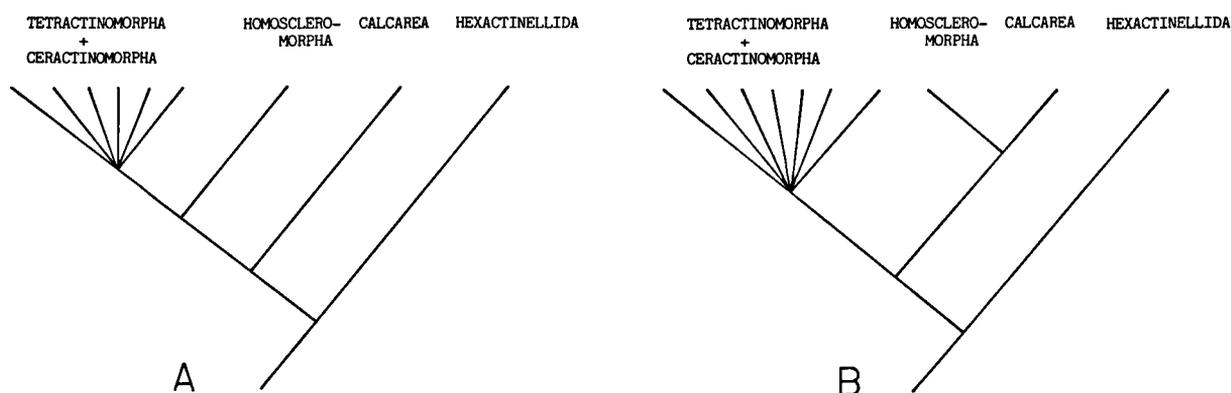


Fig. 7. Diagrams representing overall phylogenetic relationships of major sponge taxa. A: Currently accepted view with classes Hexactinellida, Calcarea and Demospongiae (Tetractinomorpha + Ceractinomorpha + Homoscleromorpha). B: suggested view based on the idea that hypercalcified skeletons were developed only once and on the assumption that similarities of Calcarea and Homoscleromorpha are homologous.

be worth while to reconsider this. Some of these similarities are: calthrops-like spicule form and amphiblastula larva. Donadey (1979) noted several corresponding cytological phenomena, which might well turn out to be genuine homologies. Possibly, the large choanocyte chambers in both groups may be a homologous feature as well.

The calthrops-like spicule form was considered primitive by many older spongologists because of its similarity to large tetractine spicules as orthotriaenes, and to astrose microscleres found in tetractinellids and maybe also in hexactinellids. The more recent view emphasizes the monaxone spicule as primitive, because of its wider distribution among sponges in general. This matter is left here undecided, except for the suggestion that the calthrops may be a synapomorphy for Calcarea and Homosclerophorida.

Homosclerophorida, in his view, represent the oldest line in the Demospongiae. This view clearly violates the principle of parsimony, because both groups are small in diversity, with few taxa, and without extensive fossil record. Next to this, there are many smaller and larger inconsistencies in Möhn's new system, while the dazzling number of newly proposed subkingdoms, phyla, subphyla and classes seems unprecedented. The discussion of these proposals, however, is beyond the scope of the present paper, which is intended only to explore some of the possible consequences of the acceptance of the polyphyly of the Sclerospongiae.

The amphiblastula larva found in Calcarea and Homosclerophorida is similar in structure and function, but according to Tuzet (1948) this must be considered as a parallel development because the embryology in both cases differs substantially. I am not certain of the weight of these differences. The similarities and limited distribution among sponges as a whole make the assumption of a parallel development hard: it seems too much of a coincidence. The simpler type of larva found in *Clathrina* is quite naturally explained as a reduction of the amphiblastula.

A further corroboration of shared ancestry of Calcarea and Homosclerophorida may be found in the fact that in Homosclerophorida indeed some sponges are known without any skeleton at all (e.g. *Oscarella*). These are here assumed to be a testimony in favour of the hypothesis that two successive, but unrelated reduction processes from some stromatoporoid-sphinctozoan stock to the naked stage have indeed occurred at a certain moment in the evolution of these assorted groups of sponges. *Verticillites*, *Vaceletia*, and murrayonids are examples of relicts of lines that have diverged from this evolutionary sequence.

The many dissimilarities and perhaps the doubtful homology of some of the similarities together contribute to the assumption that any common ancestor of Calcarea and Homo-

sclerophorida (if there has been one at all) lived at least as far back as Devonian times. If the present suggestions would eventually be substantiated by new corroborating evidence (reexamination of embryology, new fossils, revision of the Homosclerophorida), its consequence would be that the Calcarea would have to be incorporated in the Porifera system at the same level as the Homosclerophorida (at present: subclass). In view of the increasing evidence of calcareous and siliceous skeletal material being employed in the same sponge, this seems acceptable. A tentative diagram of the presumed phylogenetic relationships is presented in fig. 7B.

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REFERENCES

- BERGQUIST, P. R., 1978. Sponges: 1-268, pls. 1-10 (Hutchinson University Library, London).
- , in press. Poriferan relationships. Proc. Syst. Ass. Symposium "On origin and relationships of lower invertebrates", London, Sept. 1983.
- BOROJEVIĆ, R., 1979. Evolution des Calcarea. In: C. LÉVI & N. BOURY-ESNAULT eds., Biologie des Spongiaires. Colloques int. Cent. natn. Rech. scient., 291: 527-530.
- DENDY, A., 1922. Report on the Sigmatotetraxonida collected by H.M.S. "Sealark" in the Indian Ocean. Trans. Linn. Soc. London, (2, Zool.) 18: 1-164, pls. I-XVIII.
- DONADEV, C., 1979. Contribution à l'étude cytologique de deux Homosclerophoridés: *Oscarella lobularis* (Schmidt) et *Plakina trilopha* Schulze. In: C. LÉVI & N. BOURY-ESNAULT eds., Biologie des Spongiaires. Colloques int. Cent. natn. Rech. scient., 291: 165-172.
- HARTMAN, W. D., 1972. *Ceratoporella* (Porifera: Sclerospongiae) and the chaetetid "corals". Trans. Conn. Acad. Arts Sci., 44: 133-148.
- , 1979. A new sclerosponge from the Bahamas and its relationship to Mesozoic stromatoporoids. In: C. LÉVI & N. BOURY-ESNAULT eds., Biologie des Spongiaires. Colloques int. Cent. natn. Rech. scient., 291: 467-474.
- HARTMAN, W. D. & T. F. GOREAU, 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. Symp. zool. Soc. London, 25: 205-243.
- & —, 1975. A Pacific tabulate sponge, living representative of a new order of sclerosponges. Postilla, 167: 1-21.
- HARTMAN, W. D., J. WENDT & F. WIEDENMAYER, 1980. Living and fossil sponges. Sedimenta, 8: 1-274 (University of Miami, Florida).
- KEMPEN, TH. M. G. VAN, 1978. Anthaspidellid sponges from the Early Paleozoic of Europe and Australia. Neues Jahrb. Geol. Paläont. Abhandl., 156: 305-337.
- KIRKPATRICK, R., 1908. On two new genera of recent pharetronid sponges. Ann. Mag. nat. Hist., (8) 2: 503-515, pls. XIII-XV.
- LÉVI, C., 1973. Systématique de la classe de Demospongiaria (Demosponges). In: P. P. GRASSÉ ed., Traité de zoologie. Anatomie, systématique, biologie. Tome 3, fascicule 1. Spongiaires: 577-631 (Masson, Paris).
- MÖHN, E., 1984. System und Phylogenie der Lebewesen. Band 1: i-xxxv, 1-884, pls. 1-318 (Schweizerbart, Stuttgart).
- PICKET, J. P. & P. A. JELL, 1983. Middle Cambrian Sphinctozoa (Porifera) from New South Wales. Mem. Ass. Australas. Palaeontols., 1: 85-92.
- POULIQUEN, L., 1972. Les Spongiaires des grottes sous-marines de la région de Marseille. Téthys, 3: 717-758.
- PULITZER-FINALI, G., 1972. Report on a collection of sponges from the Bay of Naples, I. Sclerospongiae, Lithistida, Tetractinellida, Epipolasida. Pubbl. Staz. zool. Napoli, 38 ("1970"): 328-354.
- , 1983. A collection of Mediterranean Demospongiae (Porifera) with, in appendix, a list of the Demospongiae hitherto recorded from the Mediterranean Sea. Annali Mus. civ. Stor. nat. Giacomo Doria, 84: 445-621.
- SOEST, R. W. M. VAN, 1984. Marine sponges from

- Curaçao and other Caribbean localities. Part III. Poecilosclerida. *Stud. Fauna Curaçao*, 199: 1-167, pls. I-X.
- STEARNS, C. W., 1979. Stromatoporoids and related organisms. *Fossil Cnidaria int. Newsletter*, 8 (1): 49-50.
- STEL, J. H., 1978. Studies on the palaeobiology of favositids: 1-247 (Ph.D. Thesis, University of Groningen).
- TERMIER, H. & G. TERMIER, 1973. Stromatopores, Sclérosponges et Pharétrones: Les Ischyrospongia. *Annls. Mines Géol.*, 26: 285-297.
- TUZET, O., 1948. Les premiers stades du développement de *Leucosolenia botryoides* Ellis et Solander et de *Clathrina (Leucosolenia) coriacea* Mont. *Annls. Sci. nat., (Zool.)* 11: 103-113.
- VACELET, J., 1970. Les Éponges Pharétronides actuelles. *Symp. zool. Soc. London*, 25: 189-204.
- , 1977. Éponges Pharétronides actuelles et Sclérosponges de Polynésie française, de Madagascar et de La Réunion. *Bull. Mus. natn. Hist. nat. Paris*, (3) 444 (Zool. 307): 345-368.
- , 1979. Description et affinités d'une Éponge Sphinctozoaire actuelle. In: C. LÉVI & N. BOURY-ESNAULT eds., *Biologie des Spongiaires. Colloques int. Cent. natn. Rech. scient.*, 291: 483-493.
- , 1980. Squelette calcaire facultatif et corps de régénération dans le genre *Merlia*, Éponges apparentées aux Chaetétidés fossiles. *C. R. Acad. Sci. Paris, (D)* 290: 227-230, pl. I.
- , 1981. Éponges hypercalcifiées ("Pharétronides", "Sclérosponges") des cavités des récifs coralliens de Nouvelle-Calédonie. *Bull. Mus. natn. Hist. nat. Paris, (4)* 3 (A, 2): 313-351.
- , in press. Coralline sponges and the evolution of the Porifera. *Proc. Syst. Ass. Symposium "On origin and relationships of lower invertebrates"*, London, Sept. 1983.

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