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The Nepheliospongiidae CLARKE 1900 (Demospongia, Upper Devonian to Recent), an ultraconservative, chiefly shallow-marine sponge family

By FELIX WIEDENMAYER¹⁾

ABSTRACT

The types of the late Devonian *Nepheliospongia avocensis* CLARKE, from Avoca, New York, are described. Though individual spicules are not preserved, growth form, apopores and skeletal architecture suggest that *Nepheliospongia* is a haplosclerid demosponge, closely related to the late Paleozoic Heliospongiidae FINKS (1960) and to some modern forms of the West Indies and of other regions (WIEDENMAYER 1977). Most genera of the Renieridae sensu LÉVI (1973, «Traité de zoologie») are transferred to the Nepheliospongiidae. *Reniera*, however, is very close to, if not congeneric with, *Haliclona*. It is therefore suggested that Renieridae RIDLEY should replace the junior synonym Haliclonidae DE LAUBENFELS.

The middle Cambrian genus *Hazelia* WALCOTT is regarded as directly ancestral to both *Nepheliospongia* and the Ordovician *Saccospongia*. Two major phylogenetic divisions, *Saccospongia* → Axinellida, and *Nepheliospongia* → Poecilosclerida + Haplosclerida + Keratosa, are accepted as collateral. The concept of phylogeny advanced by FINKS (1967, 1970), though modified, is preferred to that by REID (1970). Both views are discussed, with particular regard to the monaxonid sponges of the Burgess shale (middle Cambrian of western Canada) and to the Plakinidae. The lithistid demosponges are not considered, however.

Fossil records of nepheliospongiids and other non-lithistid demosponges are discussed in the perspective of ecologic evolution.

ZUSAMMENFASSUNG

Die Typusexemplare von *Nepheliospongia avocensis*, aus dem Oberdevon von Avoca, New York, werden neu beschrieben. Einzelne Spicula sind zwar nicht erhalten, doch weisen Habitus, Verteilung der Apoporen und Skelettbau auf eine Zugehörigkeit zu den haploscleriden Demospongien. *Nepheliospongia* ist mit den permo-karbonischen Heliospongiidae FINKS (1960) nah verwandt, ebenso mit einigen lebenden Gattungen Westindiens und anderer Gebiete (WIEDENMAYER 1977). Die meisten Gattungen der Renieridae sensu LÉVI (1973, «Traité de zoologie») werden den Nepheliospongiidae neu zugeordnet. *Reniera* ist jedoch als evolutiv fortschrittlicher Typ mit *Haliclona* nah verwandt, wenn nicht gar deren Untergattung. Damit wäre es sinnvoll, den jüngeren Namen Haliclonidae DE LAUBENFELS mit Renieridae RIDLEY zu ersetzen.

Die mittelkambrische Gattung *Hazelia* WALCOTT wird als direkter Vorfahre von *Nepheliospongia* betrachtet, aber auch von *Saccospongia* (Ordovicium, revidiert von FINKS 1967). Damit lassen sich zwei parallele Hauptströme der Entwicklung erkennen: *Saccospongia* → Axinellida und *Nepheliospongia* → Poecilosclerida + Haplosclerida + Keratosa. Von den neuesten Konzepten zur Phylogenetese der Demospongien wird das von FINKS (1967, 1970), zwar in modifizierter Form, jenem von REID (1970) vorgezogen. Beide Ansichten werden eingehend erörtert, mit Bezug auf die Monaxoniden des Burgess Shale (Mittelkambrium, westliches Kanada) und auf die Familie Plakinidae. Die lithistiden Demospongien werden allerdings von der Diskussion ausgeklammert.

Fossile Vorkommen von Nepheliospongiiden und anderer nicht lithistider Demospongien werden in Verbindung mit ökologischer Evolution besprochen.

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Introduction

In my monograph on the sponges of the western Bahamas (WIEDENMAYER 1977), I have postulated a direct phylogenetic link between a group of living haplosclerid sponges (*Petrosia* and related genera), of cosmopolitan but chiefly tropical and mediterranean distribution, and the Heliospongiidae FINKS (1960) of late Paleozoic age (Upper Carboniferous and Permian). In today's littoral and sublittoral zones of tropical seas, the Haplosclerida constitute one of the most important and diverse orders of the class Demospongea, to which most modern shallow-water sponges belong. Comparable to the Haplosclerida in diversity are the Keratosa (without proper spicules) and the Poecilosclerida. The three orders are closely related and are grouped today in the subclass Ceractinomorpha, together with the small order Halichondriida (for modern classification, current concepts of phylogeny, and their discussion, see LÉVI 1973 and WIEDENMAYER 1977; the latter contains a glossary of morphological terms for non-lithistid demosponges).

During a stay at the Carnegie Museum of Natural History in Pittsburgh, in the first half of 1975, I had the opportunity of surveying the E. B. Hall collection of fossil sponges. While looking through the type specimens of the Dictyospongiidae (extinct lyssacine Hexactinellida) from the Upper Devonian of central and southwestern New York State, which had been described by HALL & CLARKE (1899), I came upon the two syntypes of *Nepheliospongia avocensis* CLARKE 1900. These sponges, like *N. typica*, are from sand- and siltstones of deltaic facies and Famennian (Chautauquan) age (Chemung group according to CHADWICK 1935). They had been described in a separate publication (CLARKE 1900, together with *N. typica* CLARKE, the two syntypes of which are in the New York State Museum in Albany, but having been loaned to Dr. Robert Finks were not available for study to me in 1975), because CLARKE regarded this genus and family as belonging to the dictyonine Hexactinellida.

I have already critizised CLARKE's systematic interpretation on 4 points (WIEDENMAYER 1977, p. 112), denying any affinity of *Nepheliospongia* with the Hexactinellida. At the same time I have noted a singular similarity of the fossil sponge to the West Indian haplosclerid *Cribrochalina vasculum* (LAMARCK), both in gross morphology and structure of the skeleton. The only relevant difference is to be found in the presence of regularly arranged macroscopic skeletal oscules (larger apopores) on the exhalant surface of *Nepheliospongia avocensis*. *Cribrochalina vasculum* (Fig. 9) is lipostomous as a rule, i.e. the bowl-shaped specimens show the

inner (exhalant or gastral) surface not essentially different from the outer (inhalant or pleural) surface in structure. However, well differentiated macroscopic oscules occur in solid-ramose specimens of *Cribrochalina* (WIEDENMAYER 1977, Pl. 17; see Fig. 11).

Before seeing the types of *Nepheliospongia avocensis*, I had noted striking parallels in shape and structure between some living haplosclerids, chiefly of the genera *Xestospongia* and *Cribrochalina*, and the Pennsylvanian-Permian Heliospongiidae as described and illustrated by FINKS (1960). Despite this correspondence of morphological characters, including spicules, and of ecological affinity, I hesitated at first to include the living genera in the family Heliospongiidae, chiefly because of the unusual step of introducing a rather esoteric family name of fossil sponges into an order of living demosponges frequently dealt with in the modern literature. However, a re-examination of the type specimens of Heliospongiidae in the U.S. National Museum, simultaneously with my study of *Nepheliospongia avocensis*, convinced me that the three groups of sponges (from the Devonian, Pennsylvanian-Permian, and Recent, respectively) belonged to the same family. This requires that priority be given to the name Nepheliospongiidae.

Besides its phylogenetic implications, this revision may offer a more plausible alternative to the hitherto rather confused and conflicting views on familial placement of many Recent haplosclerid genera. This concerns chiefly the families Adociidae DE LAUBENFELS, the Gelliidae and Renieridae of French authors, besides some genera placed in other families, such as the Coelosphaeridae sensu DE LAUBENFELS. The presence or absence of peripheral specialization of the skeleton and of a simple complement of microscleres were probably overemphasized as systematic criteria in these instances, while habits and main skeletal structure appear to have been either excessively subdivided (by earlier authors) or neglected or misinterpreted (chiefly by BURTON). LÉVI (1973, based on GRIESSINGER 1972) arrived at similar conclusions. His use of the family Renieridae RIDLEY approximates in scope that of the modern Nepheliospongiidae as here understood. The question of subjective synonymy and of the respective merit of one name over the other will have to be discussed below.

Revision of *Nepheliospongia avocensis*

Class ***Demospongia*** SOLLAS 1885

Subclass ***Ceractinomorpha*** LÉVI 1953

Order ***Haplosclerida*** TOPSENT 1928

Family ***Nepheliospongiidae*** CLARKE 1900

Genus ***Nepheliospongia*** CLARKE 1900

Type species (by original designation and typonomy): *Nepheliospongia typica* CLARKE (1900, p. 189, Pl. 10, Fig. 1-3) (Upper Devonian, New York State). The two syntypes are in the New York State Museum, Albany, Nr. 2440/1 and 2.

Nepheliospongia avocensis CLARKE

(Fig. 1-7)

1900 *Nepheliospongia avocensis* CLARKE, Bull. New York State Mus. 39, p. 190, Pl. 10, Fig. 4; Pl. 11, Fig. 1.

Lectotype (here designated). - Carnegie Museum Nr. 7971, with Clarke's autograph label: "A large turbinate specimen with undulated or cinctured surface. Small patches of matrix are irregularly scattered over the wall." Cotton Hill near Avoca, New York.

Paralectotype. - Carnegie Museum Nr. 8001, with Clarke's autograph label: "This is doubtless a siliceous sponge but appears to be dictyonine rather than lyssacine; hence does not belong to the same order as the Dictyospongidae." Same locality as lectotype.

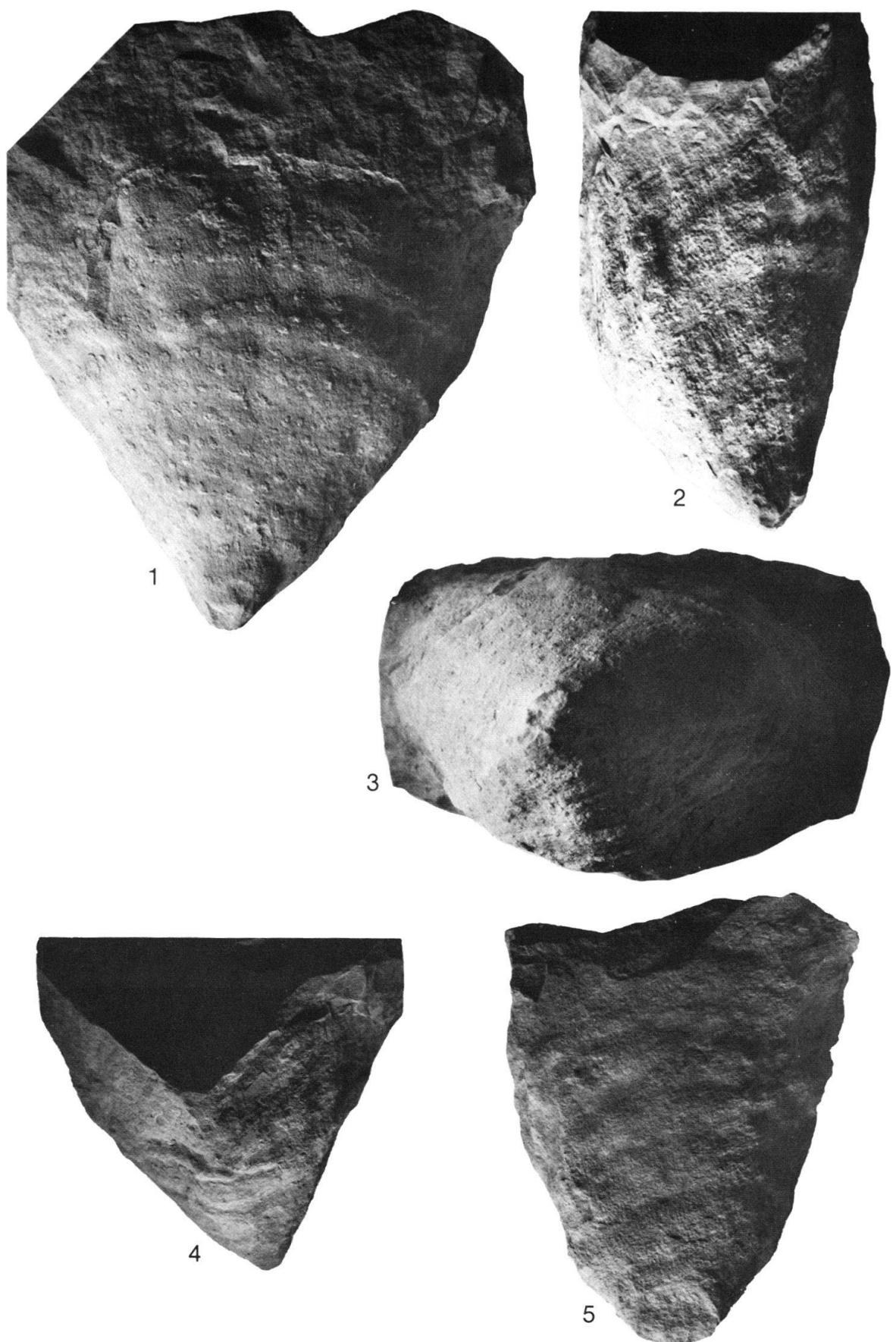
Description of the lectotype. - The side represented in CLARKE's figure seems to be essentially a gastral cast of a vase-shaped specimen. The "patches of matrix" are not irregularly scattered as stated by CLARKE. They are arranged preferentially in lines parallel to the rim of the cup and to the annular ridges and depressions in the wall. They are very probably fillings of larger skeletal apertures or oscules. A few are v-shaped, i.e. confluent towards the base. Many show a sharp line forming the rim, which is rounded in others, rarely surrounded by a pattern of concentric weaker lines. In some apertures the rim is stellate, with very short, weak radial grooves. Over most of the surface between the patches, the pattern is finely and vaguely imbricate, but in some areas there is a longitudinal striation. On the back (with respect to CLARKE's figure), near the base, depressions appear instead of patches.

The body wall at the upper end of the cast, where it disappears into the matrix, is 2 to 3 mm thick. On the upper left, with respect to CLARKE's figure (Pl. 11), a definite stratification is apparent, which, while still slightly oblique, is more parallel to the surface than on the figure. This stratification is so fine and contrasts so much with the coarser architecture elsewhere, that it is probably due to diagenesis. In other places, the oblique fracture across the wall has a coarsely granular appearance. This also applies to areas where parts of the body wall still cling to the inner cast, as in the upper middle with respect to CLARKE's figure, just below the rim, but more extensively on the reverse side (cf. Fig. 6).

Longitudinally oriented polygonal meshes are sometimes visible in the surface layer. Upon closer inspection, with strong tangential light, the structure is that of tiny scales overlapping longitudinally (Fig. 7). It may be interpreted as due to the imprints of the tips of spicular trabeculae, or, more likely, as negative casts of sediment infills of interstices, radiating obliquely to the surface. Here they may have been covered by a very thin layer of paratangentially placed spicules, and thus

Fig. 1-5. *Nepheliospongia avocensis* CLARKE. The two type specimens in the Carnegie Museum, Pittsburgh. Avoca, New York, Chemung stage (Famennian, upper Devonian).

1-4: Lectotype, CM 7971. 1: Side figured by CLARKE 1900, Plate 11. $\times \frac{1}{2}$. 2: Left side with respect to Figure 1. $\times \frac{1}{2}$. 3: Bottom view showing annular and vertical folds. $\times \frac{1}{2}$. 4: Reverse side with respect to Figure 1. $\times \frac{1}{3}$. 5: Paralectotype, CM 8001. Side figured by CLARKE 1900, Plate 10, Figure 4. $\times \frac{1}{2}$.





6



7

Fig. 6, 7. *Nepheliospongia avocensis*, Lectotype.

6: Detail of Figure 2. $\times 1$. 7: Detail of gastral surface (upper right center on Fig. 1), inclined to the right (annular constriction with apopore casts running diagonally from upper left to lower right). $\times 3$.

separated from the main sediment infill of the gastral concavity. Some annular stratification is barely evident here and there, the short trabeculae or interstices forming palisades. In a few smaller areas, probably representing the mesial layer of the body wall, some parallel longitudinal trabeculae or interstitial casts are revealed for up to 5 mm of their length.

In a few areas of the reverse side, the granular, brownish layer, i.e. the body wall, seems to be covered by a continuous, rather smooth sheet (dermal skeleton?). Also on the reverse side, near the rim, there is an area with often confluent lacunae (interstices limonitic, lacunae with grey sandy matrix). This lacunose layer may be situated between the main skeleton and the dermal layer (?), but the relationship is obscured by strong compression. Also, simulation of a lacunose layer present in the living sponge, by diagenetic separation and concentration of limonite, cannot be excluded.

No traces of spicules could be detected under the microscope.

Description of the paralectotype. - In this smaller vase-shaped specimen, the preserved surface seems to be pleural. Most of it is covered by a polygonal reticulum, which in better preserved areas consists of meshes with brown pigment. Here and there crowded brown spicules can barely be detected that seem to be monaxons. They seem to be packed in trabeculae as a rule, probably without definite orientation, but appear to be arranged in a prevalent direction in spots, indicating original disposition in palisades or sheets, or in brushes erect on the surface. In other areas, particularly above the base and near the rim, a prevalence and alignment of longitudinal trabeculae is visible, which provides for a striate appearance. At the broken rim, these trabeculae are seen to continue radially inward.

The surface layer, marked by brownish pigment, is about 1 mm thick. Below this is a thicker layer (3-4 mm) with a structure indistinctly radial around the base and imbricate above, at the broken rim, where the wall seems to be vaguely stratified.

Comparison with Nepheliospongia typica. - The two specimens, as described and illustrated by CLARKE, are considerably smaller than *N. avocensis*. Their pleural surface is smooth, lacking annular constrictions. Otherwise, the obconical hollow shape is not essentially different from that of *N. avocensis*. In the smaller syntype (NYSM 2440/2, CLARKE 1900, Pl. 10, Fig. 2, 3), the rim seems to be preserved intact, rounded, revealing a thickness of the body wall around 3 mm.

The meshes of the surface reticulum are apparently partly polygonal, partly quadrate, overall somewhat smaller than in *N. avocensis*, more regular, without axial elongation.

All this does not exclude the possibility that the two "species" are merely different growth stages or phenotypes of the same species. In the two localities concerned (*N. typica* is from Deyo basin, Naples, N.Y.), there is a difference in the sponge assemblage (the extreme proliferation of *Hydnoceras* at Cotton Hill, Avoca, is lacking at Naples), but the age of the two "species" is the same (CHADWICK 1935, p. 319).

The Heliospongiidae FINKS 1960

The anatomy of *Heliospongia* GIRTY, as described by GIRTY (1908) and KING (1933, 1943), was reinterpreted by FINKS (1960, p. 40f.) on the basis of exceptionally well preserved specimens (silicified and prepared with acid). He could demonstrate that the regularly arranged trabeculae of the skeleton are not the rays of single spicules (hexacts or tetracts), as GIRTY and KING believed, but that they consist of bundles of parallel oxeas. FINKS could even isolate and illustrate oxeas (1960, Pl. 3, Fig. 1) with a distinct axial canal. He concluded that *Heliospongia* is a demosponge with simple diactinal spiculation.

A further characteristic of *Heliospongia*, almost unique among fossil sponges, is the very regular skeletal architecture: ascending tracts divergent towards the surface, transverse tracts arranged in equally spaced, upwardly convex layers (I have called this style of architecture "radiate-accretive"). The aquiferous system is also exceptionally regular, with prosocochetes following the ascending trabeculae and fairly regularly spaced apochetes parallel to transverse tracts. A thin superficial crust of tangentially placed diacts is often present, with spicules surrounding skeletal ostia in concentric lines. Atria are well developed and the prevailing habit of the whole sponge is tubular and branching.

These characteristics essentially constitute the diagnosis given by FINKS (1960) for his family Heliospongiidae. He included the following genera: *Heliospongia* GIRTY (upper Pennsylvanian to lower Permian), *Coelocladia* GIRTY (middle to upper Pennsylvanian), and tentatively *Coelocladia* FINKS (upper Pennsylvanian to lower Permian). The latter differs from the first two genera in its less regular, more open skeletal architecture, with slender flattened tracts curving and anastomosing, more like partitions around alveoles. No spicules could be observed in this genus and FINKS did not exclude that it is a calcareous sponge. *Coelocladia* shares with both *Coelocladia*, and calcareous sponges similar in gross morphology, a pleural and gastral crust pierced by circular orifices.

However, some Recent sponges, already assigned by me (1977) to this family, show a corresponding alveolate structure of the main skeleton, such as *Xestospongia muta* (SCHMIDT; see Fig. 20), and the species of the genus *Siphonodictyon* (cf. RÜTZLER 1971). The modern species also have a distinct dense reticulum or spicular crust on the pleural surface as a rule, but such a feature is not developed on the inner surface (lining the lumina) of tubular species.

FINKS (1960) assigned the Heliospongiidae to the order Epipolasida SOLLAS, which he diagnosed as follows: "Megascleres exclusively monaxonic, but tylostyles absent; architecture commonly radiate; cortex or dermal specialization commonly present; spongin absent." However, in noting the difficulty of placing the Heliospongiidae unequivocally in one of the orders of demosponges, he discussed the possible merits of alternative placement among the other 4 orders with exclusively monaxonic megascleres, as defined by DE LAUBENFELS (1936): Haplosclerida, Poecilosclerida, Halichondriida, Hadromerida. The extremely uniform spiculation of the Heliospongiidae is said to be closest to the Haplosclerida, but inclusion of the fossil forms in this order is rejected by FINKS, on the grounds that it lacks the distinct dermal layer characteristic of heliospongiids. This trait and the presence of radiate architecture,

in which spongin probably had no part, makes the Epipolasida the best repository for the family, according to FINKS (1960, p. 42).

Continuing from here, FINKS noted the uncertainty among neontologists as to the phylogenetic significance and systematic delimitation of the orders of demosponges, particularly with regard to the Epipolasida. Already DE LAUBENFELS (1936, p. 157), in raising SOLLAS' family to the rank of an order, admitted that it might be polyphyletic, comprising genera with hadromerid affinity, and others derived from Choristida by loss of tetraxons (as was assumed by other authors before and after DE LAUBENFELS, cf. REID 1970, p. 71; LÉVI 1973, p. 598). The latter view, however (still following FINKS 1960, and assuming that the Heliospongiidae are indeed early Epipolasida) would be contradicted by the heliospongiids being at least as ancient as any of the known choristids, and probably having been exclusively monaxonic from their beginning, as their similarity with the Haplistiidae suggests.

Since DE LAUBENFELS 1936 several genera have been transferred from the Epipolasida to other orders, chiefly to the Axinellida, Hadromerida, and Halichondriida (cf. WIEDENMAYER 1977, p. 24, 172). The recent trend has been to eliminate the Epipolasida as a separate order altogether. Even the genera thought to be most representative by DE LAUBENFELS, having only oxeas, or at most a simple complement of small asters, *Jaspis*, *Epipolasis* and *Sollasella*, are said by BERGQUIST & HARTMAN (1969) to be probably closely related to the Choristida, on biochemical evidence. Another typical epipolasid genus, according to earlier systematic concepts, is *Spongisorites* TOPSENT (sensu TOPSENT 1900, i.e. only the type species *S. placenta* and related forms). Its recent placement among the Halichondriida by Italian and French authors is debatable, because of the presence in this genus of centrangle, centrotylote oxeas, which are probably atrophied tetracts (calthrops), as TOPSENT pointed out.

As the case may be, the structure of the foregoing 4 epipolasid genera is quite different from that of the Heliospongiidae (recte Nepheliospongiidae). These modern sponges have a very dense skeletal architecture, with spicules commonly packed in confusion. Their arrangement may be radial, but like in choristids, without condensation in definite, regularly anastomosing tracts. The size range of these spicules exceeds that indicated by FINKS (1960, p. 51) for various Heliospongiidae very considerably. The superficial specialization in Epipolasida, when present, is quite different from that in heliospongiids, being chiefly organic, i.e. a collagenous cortex, which may contain an ectochroite with microscleres.

Later, FINKS (1967, p. 1145, 1147, textfig. 4) grouped the Heliospongiidae - no longer regarded as Epipolasida - in proximity to the Rhizomorina, as their collateral offshoot, possibly developing in late Silurian or early Devonian time from forms close to *Haplistion*. The latter genus has a very similar architecture, but with bipolar rhizoclines instead of oxeas (for terminology of desmas, see REID 1970, p. 32f.). Again later, FINKS (1970, Fig. 3) interpreted the Heliospongiidae as an offshoot from the Cambrian *Hazelia* WALCOTT, from which the Haplistiidae and *Saccospongia* would have diverged as separate lines. While the latter two persisted or gave rise to groups persisting to Recent (the modern Rhizomorina from late Paleozoic haplistiids, the Clavixinellida and Ceractinomorpha from *Saccospongia*), the Heliospongiidae became extinct before the end of the Permian, according to FINKS.

Modern Nepheliospongiidae

I have included the Nepheliospongiidae (as a senior synonym of the Heliospongiidae) in the Haplosclerida and introduced them to neontology (WIEDENMAYER 1977, p. 111), on the grounds of pronounced similarities in habit and skeletal structure between some living genera (chiefly *Xestospongia*, *Cribrochalina* and *Petrosia*) and fossil ones (*Heliospongia*, *Coelocladia*, *Nepheliospongia*). As I have pointed out in that monograph, superficial (peripheral) specialization is rather common in the Haplosclerida, contrary to DE LAUBENFELS' belief. I consider it a more or less diataxic trait in general terms (but not in qualitative expression), cutting across limits between families, genera and even some species or forms. However, it seems to be more common and hence of better diagnostic value in the Nepheliospongiidae.

At the same time (WIEDENMAYER 1977, p. 78f.), I dismissed the presence of microscleres as being a diagnostic criterion, particularly on the family level, as DE LAUBENFELS had maintained, and emphasized instead architecture of the main skeleton, contrary to BURTON's view (e.g. 1932). This led me to abandon the family Callyspongiidae DE LAUBENFELS. I had maintained the family Adociidae DE LAUBENFELS provisionally and am now inclined to drop it too.

Inadvertently, I was largely in accord with the newest views of French colleagues (GRIESSINGER 1972, LÉVI 1973) on systematics of the Haplosclerida, though only in principal matters. Having completed the systematic part of the manuscript of my monograph (1977) in 1969, except for minor emendations up to 1976, I had noted in the introduction that the Nepheliospongiidae overlapped in scope with the Renieridae RIDLEY 1884 sensu GRIESSINGER and LÉVI to a significant degree.

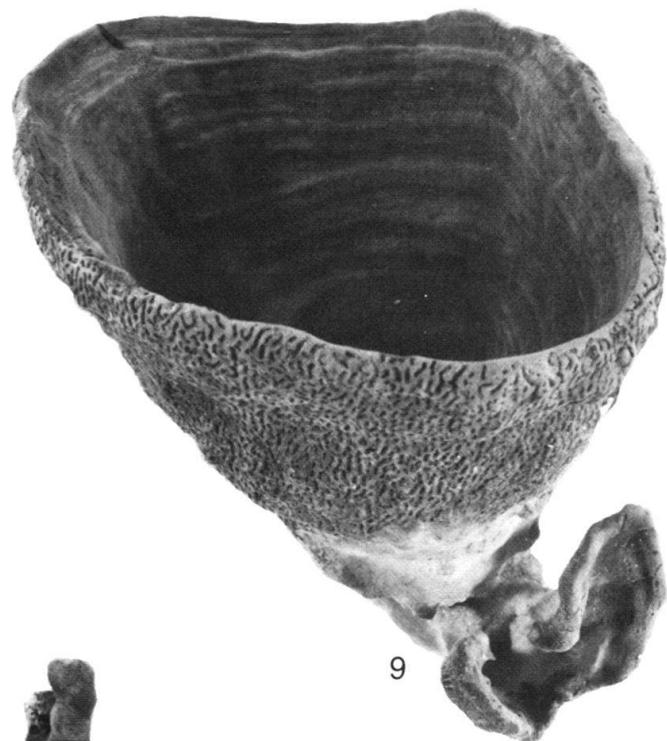
In the diagnosis of the Nepheliospongiidae (WIEDENMAYER 1977, p. 111), I emphasized the stiff and hard, occasionally friable consistency due to the proliferation of megascleres. Spongin is subordinate, agglutinating the diactines packed in plurispicular tracts as a rule. The prevailing architecture is radiate-accretive, but several modifications occur: reduction of either ascending or horizontal tracts, loss of orientation of tracts with respect to the surface, alveolate to densely isotropic (felted) structure. Accessory renieroid or isodictyal reticulation may occur interstitially. Diacts (oxeas to strongyles) are quite variable in size and proportions. Peripheral specialization, often a spicular crust, or latticed palisade of spicules, is common.

Fig. 8-11. Modern nepheliospongiids from shallow water near Bimini, Bahamas, photographed in the dry state (cf. WIEDENMAYER 1977, Pls. 14-17). The specimens are deposited in the U.S. National Museum.

8: *Xestospongia subtriangularis* (DUCHASSAING). Form with slightly compressed, repent branches, with oscules along top side. $\times \frac{1}{3}$. Outer platform west of Turtle Rocks, reefoid environment, depth ca. 10 m. Large portions of the surface are beset by the epizoic zoantharian *Parazoanthus* sp. 9: *Cribrochalina vasculum* (LAMARCK). $\times \frac{1}{4}$. Same locality data as for Figure 8. Note *Parazoanthus* on pleural surface only, and gastral surface with annular and vertical folds but without oscules. 10: *Xestospongia tierneyi* (DE LAUBENFELS). $\times \frac{1}{3}$. Same locality data as for Figure 8. 11: *Cribrochalina dura* (WILSON). View from above. $\times \frac{1}{3}$. Note the bizarre habit, with arching, anastomosing and coalescent branches, and the presence of small oscules in contrast to *C. vasculum*. Outer platform west of Turtle Rocks, depth 5-6 m, rock pavement with brown algae, plexaurid and gorgoniid alcyonarians dominating.



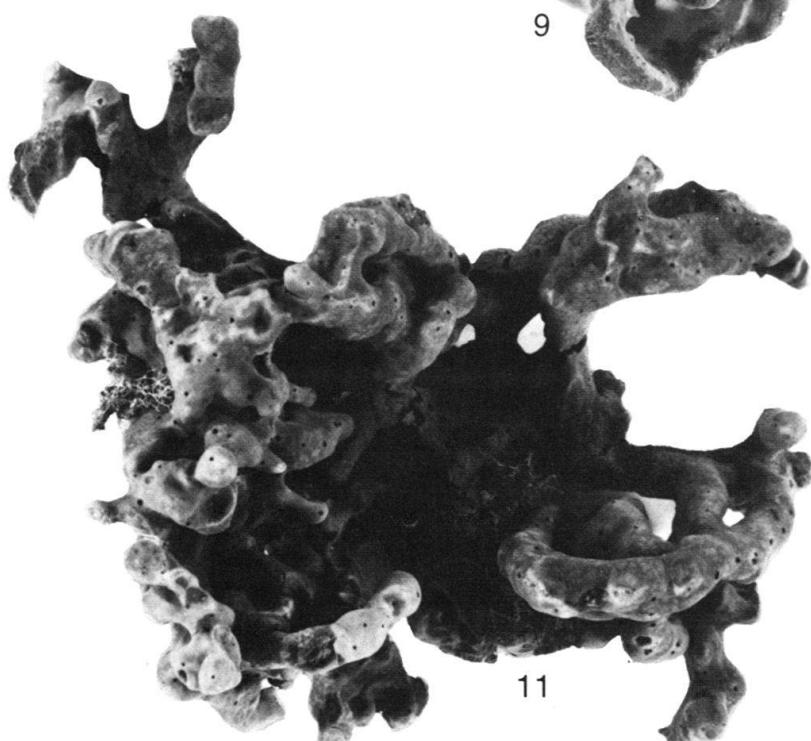
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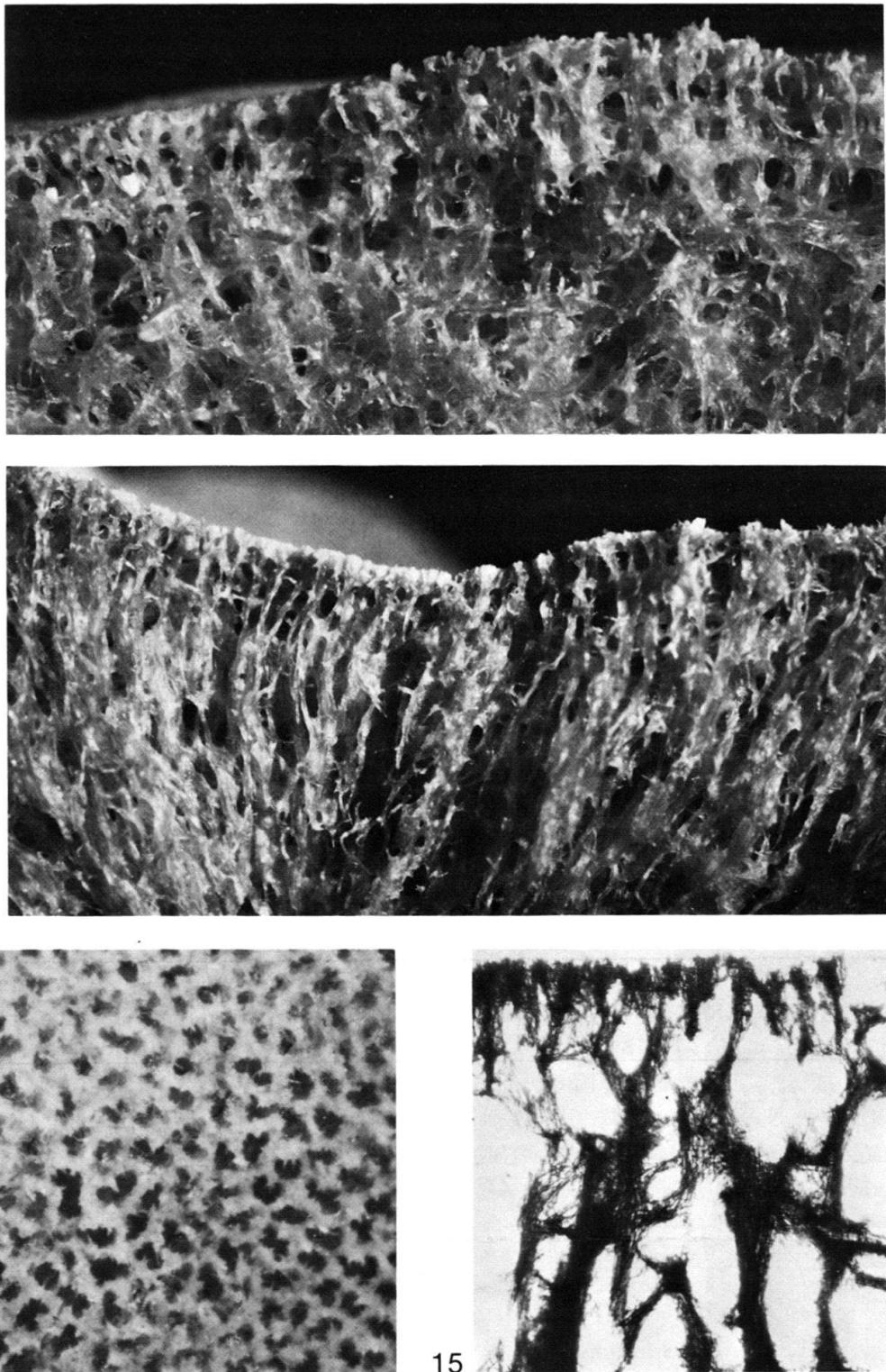


Fig. 12-15. Details of skeletal architecture in the living West Indian nepheliospongiid genus *Cribrochalanina*. (Same dry specimens as on Fig. 9, 11.)

12, 13: Fractures perpendicular to surface (above) of *C. vasculum* and *C. dura*, respectively, in reflected light. $\times 10$. 14: *C. dura*, surface in reflected light. $\times 40$. Note irregular latticework of peripheral spicular brushes. 15: Section perpendicular to surface (above), in transmitted light. $\times 25$. Note umbellate condensation of peripheral skeleton.

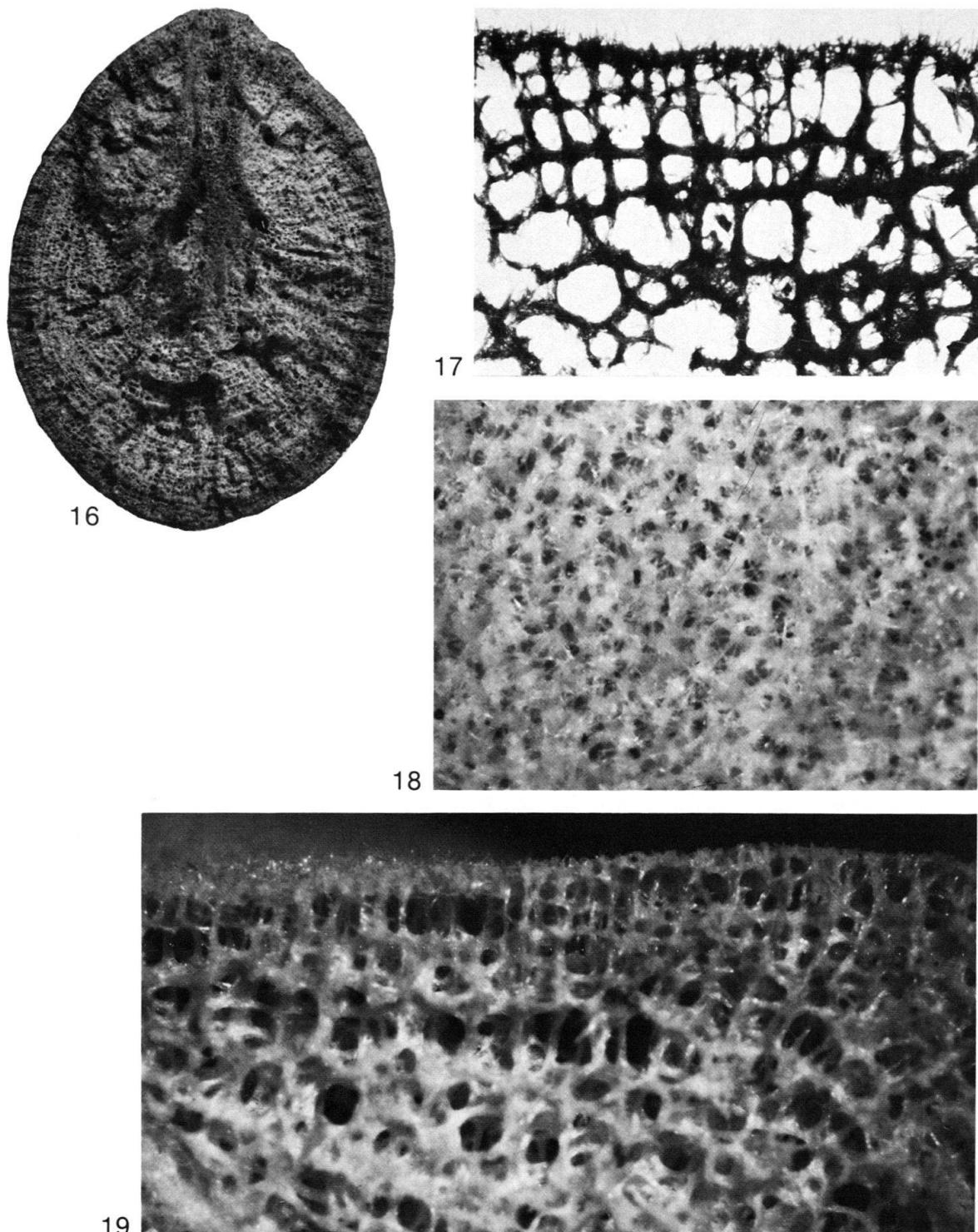
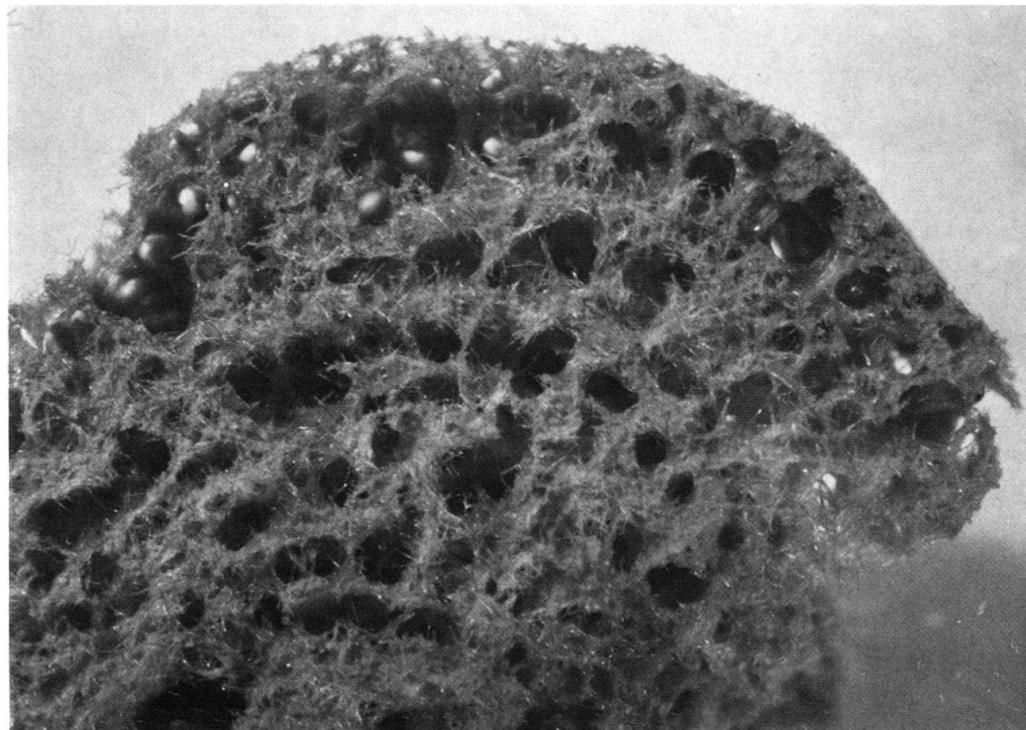
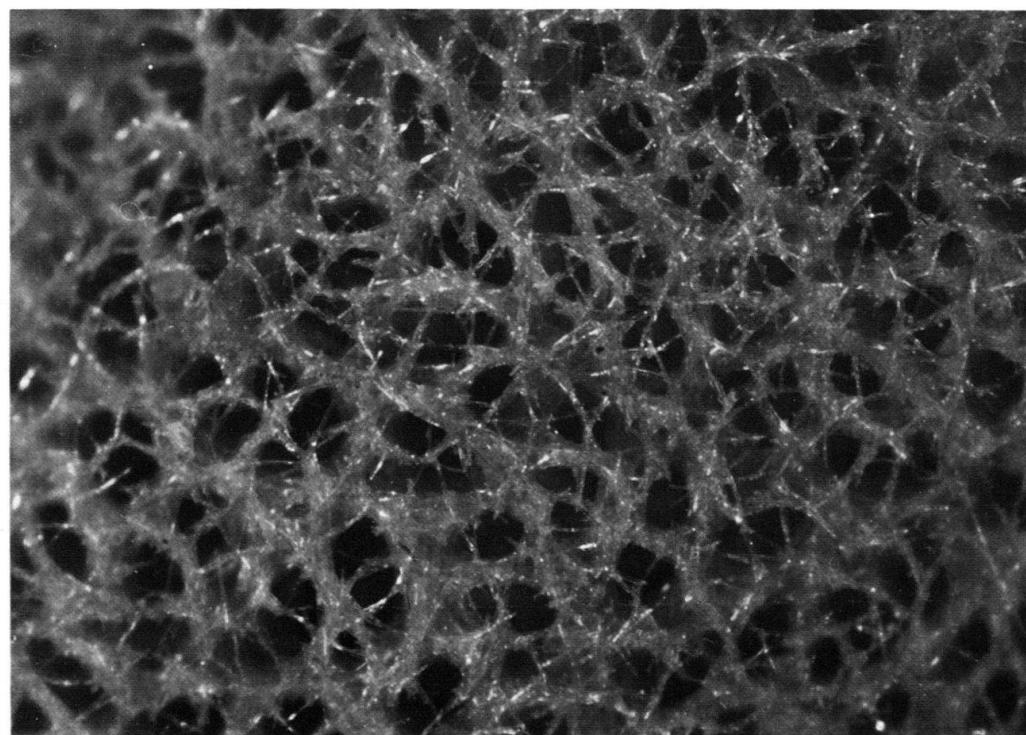


Fig. 16-19. Details of skeletal architecture in the living West Indian nepheliospongiid *Xestospongia subtriangularis* (dry specimens).

16: Transverse fracture through a branch from the Florida Reef Tract, supplied by Dr. K. Rützler (U.S. National Museum). $\times 2$. Note radiate-accretive architecture, regularity of aquiferous system, terete atrium from oscule above branching towards the axial portion. 17-19: Same specimen as Figure 8. 17: Section perpendicular to surface (above), in transmitted light. $\times 25$. The periphery is constituted by spicular brushes mixed with paratangentially arranged tracts and spicules. 18: Surface in reflected light. 19: Fracture perpendicular to surface (above), in reflected light. $\times 20$.



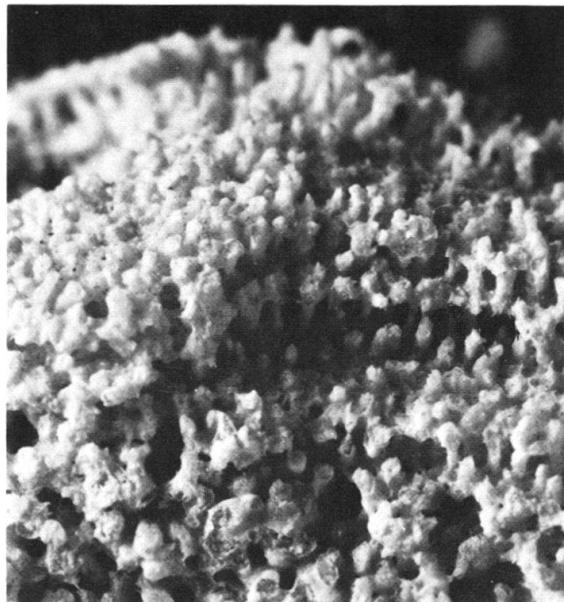
20



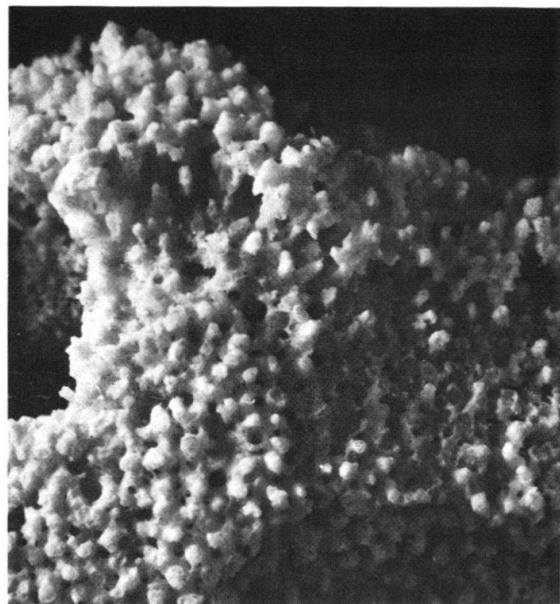
21

Fig. 20, 21. Skeletal structure in the living West Indian nepheliospongiid *Xestospongia muta* (for habitus, see WIEDENMAYER 1977, Pl. 15, and cover of Symposium volume which contains FINKS 1970 and REID 1970). From a dry specimen, same locality data as for Figure 8.

20: Section perpendicular to outer surface (above), showing alveolate structure. $\times 10$. 21: Outer surface, with periphery partly visible in depth, in reflected light. $\times 20$. Note in both figures the coarse isotropic reticulation of the periphery grading into a superficial layer of paratangentially strewn spicules.



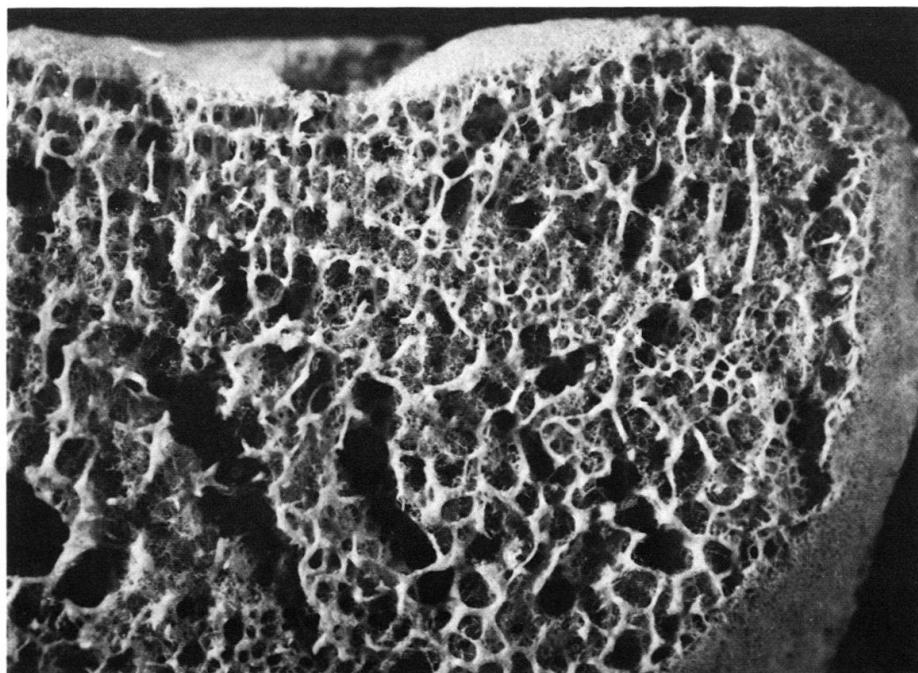
22



23

Fig. 22, 23. *Heliospongia excavata* KING, from the Pennsylvanian of Texas. Specimen USNM 127580a, illustrated by FINKS 1960, Plate 1, Figure 5. Details from the portion of the latter closest to FINKS' adjacent Figure 3, photographed by G. A. Cooper, U.S. National Museum. $\times 5$.

22: View in perspective showing regular arrangement of 'floors' and ascending stout spicular pillars.
 23: The same portion tilted forward to show the commonly rounded apertures of variable size in two successive 'floors'.



24

Fig. 24. A modern Mediterranean nepheliospongiid, *Petrosia ficiformis* (POIRET). Dry fragment from Rovinj, Istria, Yugoslavia, depth 2 m, collected by K. RÜTZLER, U.S. National Museum. Section perpendicular to surface, in reflected light. $\times 6$. Curving surface above and to the right, in perspective. Tightly reticulate 'floors' curving to the right and forward. Note the interstitial isodictyal reticulation, which is typical of *Petrosia*. For further details, see RÜTZLER 1965, p. 40.

I then included the following genera: *Petrosia*, *Xestospongia*, *Cribrochalina*, *Hemigellius*, *Vagocia*, *Calyx*, *Rhizochalina*, *Oceanapia*, *Biminia*, and *Siphonodictyon*.

GRIESSINGER (1972) and LÉVI (1973) gave a similar diagnosis of the Renieridae, stressing the generally larger size and variability of oxeas in comparison with the Haliclonidae. The latter are further contrasted with greater development of spongin relative to spicules. As a rule, the geometric arrangement of fibers or tracts, both in main and peripheral skeleton, would not be essentially different in the two families (the only marine families left in the Haplosclerida by LÉVI). The exceptions are the combinations of ascending plurispicular tracts or parallel lamellae with an interstitial isodictyal reticulation, typical of some Renieridae, and on the other hand an exclusively or chiefly isodictyal architecture in *Haliclona* (thus restricted by GRIESSINGER 1972, but not by LÉVI 1973).

The latter type, said to be relatively rare, is regarded by GRIESSINGER and LÉVI as primitive in evolution, ancestral to the styles of architecture developed along parallel lines in the Renieridae and in the Haliclonidae. The traits common to both families, i.e. variable degree of peripheral specialization, range of habits, and presence of microscleres in some forms, are considered as indications of parallel evolution. No paleontological evidence is cited in favour of such assumptions, however. As will be discussed below, the paleontological evidence actually points to a trend which is virtually the reverse of what would be expected according to LÉVI's (and GRIESSINGER's) view.

The following genera are included in the Renieridae by LÉVI (1973, p. 620): *Reniera* SCHMIDT (not NARDO, a nomen nudum), *Pellina* SCHMIDT, *Pachychalina* SCHMIDT, *Petrosia* VOSMAER, *Rhizochalina* SCHMIDT, *Oceanapia* NORMAN, *Rhizoniera* GRIESSINGER, *Cladocroce* TOPSENT, *Calyx* VOSMAER, and *Gellius* GRAY (the latter is probably meant to include *Hemigellius* and *Vagocia*). GRIESSINGER (1972) also included *Haliclonissa* BURTON and his own *Dendroxea*.

The difference between this list of the Renieridae and mine of the Nepheliospongiidae is partly due to a zoogeographical difference of approach: that of the French authors being oriented on the traditional chief preoccupation with the Mediterranean, and the Eastern and Northern Atlantic; my list reflecting the concern for shallow-water sponges of tropical seas, but, more significantly, also for fossil sponges.

The question arises, whether the two family names under consideration are synonyms (which is of course a subjective matter), in which case Renieridae would have priority.

In view of GRIESSINGER's revision, I admit that I misinterpreted the West Indian sponge which I described as *Haliclona* (*Reniera*) *aquaeductus* in 1977 (p. 87), and that it should receive another name, probably one of the synonyms that I have listed there. That the West Indian sponge is a *Reniera*, however, is still beyond doubt. The styles of skeletal architecture in *Reniera* and *Haliclona* are close, and the proportions of spongin to spicules and of spicules to choanosome probably intergrade. I am equally in doubt about the diagnostic value of size of spicules and their degree of uniformity in distinguishing *Haliclona* and *Reniera*. The West Indian *Reniera* "*aquaeductus*" has spicules in the size range of *Haliclona* sensu GRIESSINGER. Incidentally, the West Indian sponges grouped by me in the subgenus *Amphimedon*,

based on a style of architecture distinct from *Haliclona* and *Reniera*, show extreme variability of spicule size (as do *Spinosella* and *Callyspongia*). Thus the spicules of *H.(A.) compressa* and *H.(A.) viridis* (both included in *Reniera* by GRIESSINGER) largely overlap in size with those in mediterranean Renieras, but *H.(A.) complanata* (DUCHASSAING) has small, almost vestigial oxeas.

The skeletal architecture of *Reniera* is rather remote from that of typical nepheliospongiids, being quite flimsy in comparison. The ascending tracts are paucispicular as a rule, i.e. comprising single or paired, usually overlapping oxeas. Plurispicular tracts, with 3 to 5 adjacent or rather overlapping oxeas, occur exceptionally, in *Reniera aquaeductus* and the related *R. crassa* and *R. perlucida*, but are still flimsy in arrangement of the component oxeas. Though there is a similarity in this group with e.g. *Hemigellius pachyderma* (a modern nepheliospongiid, see BURTON 1932, p. 273; WIEDENMAYER 1977, Fig. 87) in main skeletal structure, the compactness of ascending tracts and the dense ectosomal spicular crust of the latter are distinct traits proper to the Nepheliospongiidae, which are lacking in Renieras, including the *aquaeductus* group.

I would be prepared to elevate *Haliclona* s.s., *Reniera* and *Amphimedon* (which I interpreted as congeneric subgenera in 1977) to the rank of genera, but not to distribute them among two different families. Even if the group of *Reniera aquaeductus* were to be included in the Nepheliospongiidae on less strict taxonomic standards, the naming and hence definition of this group after a phylogenetically and ecologically advanced, taxonomically marginal genus would hardly be compatible with taxonomic practice.

As to the nomenclatorial aspect, it might be objected that I am trying to replace a commonly used family name (Renieridae) with a junior synonym and nomen oblitum (for a discussion of article 23b of the International Code of Zoological Nomenclature in connection with sponges, see WIEDENMAYER 1977, p. 52). RIDLEY's name was used chiefly by TOPSENT (e.g. 1928). The distinction was made by RIDLEY & DENDY (1887) within the Homorrhaphidae (essentially comprising the Haplosclerida without microscleres) of the Renierinae with "spicules never completely enveloped in horny fibre", and of the Chalininae with "a considerable amount of spongin present, typically forming a thick sheath around the fibres." In my opinion, the renierid and chalinid structural types (cf. WIEDENMAYER 1977, glossary) intergrade, hence the genera possessing them should be merged in one family. Common to these genera is the flimsy organization of the skeleton, hence their comparatively weak consistency, which reflects adaptation to low-energy environments – probably late in haplosclerid evolution. There are several exceptions to this rule among the chalinid sponges, such as the chiefly tropical genera *Callyspongia* (= *Siphonochalina*), *Spinosella*, *Niphates*, which share a tough though resilient consistency and a preference for high energy environments. But these are probably rather primitive, relatively close to the Nepheliospongiidae.

I regard the Nepheliospongiidae as the ancestral root stock of the chalinid and renierid genera, as probably older than upper Devonian and as ranging to Recent with a considerable number of surviving genera (others could probably be included with further revisions). Their structural stability, reached through packing of diacts

in trabeculae and thickening of body walls, may be one of the simplest if not most archaic modes of adaptation to high-energy environments.

I do not regard the Nepheliospongiidae as a synonym of the Renieridae, but I am transferring most of the genera from the latter (sensu LÉVI) to the former, except for *Reniera*, *Pachychalina* and *Pellina*. I do not condemn the use of the name Renieridae, however, and suggest that it should be treated as a senior synonym of the Haliclonidae. DE LAUBENFELS obviously introduced the latter to replace the Chalininae RIDLEY, a name based on an objective synonym of *Haliclona*. His definition and discussion of the Haliclonidae (DE LAUBENFELS 1936, p. 37) leaves no doubt that he included *Reniera*, which he regarded as a synonym of *Haliclona*. Having noted that French authors continued to use *Reniera* and Renierinae, he proceeded to 'eliminate' *Reniera* with one of his favorite acts of nomenclatorial juggling (DE LAUBENFELS 1957, discussed in WIEDENMAYER 1977, p. 87). Though the name Chalinidae would not have been invalid, its decline since 1928 (when TOPSENT still used it for a subfamily) and the common use of the Haliclonidae to the present day (e.g. American and Russian authors; LÉVI 1973) make the senior synonym obsolete (cf. ICZN art. 40a). There are no nomenclatorial objections, however, to regarding the Renieridae as a valid senior synonym of the Haliclonidae.

Records, evolution, paleoecology

The ancestry of the Nepheliospongiidae (= Heliospongiidae) in *Hazelia* WALCOTT, as postulated by FINKS (1970), is quite plausible. The establishment by DE LAUBENFELS (1955) of a proper family for virtually every genus of the demosponges from the Burgess shale described by WALCOTT (1920) is more or less arbitrary and mostly academic, particularly with respect to placement among various orders. DE LAUBENFELS (1955, p. E69/70) vaguely admits to this, in placing his family Leptomitidae within the Lyssakida. However, the classes Demospongea, Hexactinellida and Heteractinida were probably already differentiated (FINKS 1970, p. 3), contrary to DE LAUBENFELS' belief. Those genera showing the most pronounced similarity with modern Haplosclerida in skeletal architecture, i.e. *Wapkia*, *Hazelia*, and probably *Tuponia*, differ in possessing diacts extremely variable in shape, often huge. *Tuponia* and *Hazelia* (especially the type species) have such spicules arranged in ascending tracts, which may be somewhat plumose in *Hazelia*. In both these genera, there are also smaller diacts, arranged in transverse anastomoses in *Tuponia*, but in various less geometrical styles in *Hazelia*.

Hazelia palmata WALCOTT (1920, p. 282) has crooked, rather loosely branching and vaguely anastomosing thick tracts, with smaller diacts either strewn interstitially, peripherally, or forming palisades on the outer edges of the tracts (the arrangement in the thin body wall is unclear due to strong compression of the fronds in the bedding plane), and arranged in distal fringes. This skeletal architecture is suggestive of the modern nepheliospongiid *Haliclonissa* BURTON (1932, p. 270), which is much more massive, however, with tracts perpendicular to the surface, and has uniformly small oxeas. This similarity is more likely a case of homoeomorphy.

H. nodulifera WALCOTT (1920, p. 287) is quite similar to *H. palmata*, but has a subisodictyal structure (in one plane or on the surface?). The interstitial nodes may be an artefact of preservation, with sediment squeezed out after burial.

H. delicatula WALCOTT (1920, p. 284) has a denser, finer structure, with smaller, more uniform oxeas. There seems to be a main skeleton, with tracts similar to those in *H. palmata*, but finer, more undulating, and a peripheral reticulum. The latter may be anisodictyal, with meshes elongated in axial direction (WALCOTT 1920, Pl. 70, Fig. 1b, 1f), thus suggestive of *Nepheliospongia avocensis*; or vaguely subisodictyal, with meshes fringed by radially oriented free oxeas (WALCOTT 1920, pl. 70, Fig. 1c, d), inviting comparison with the surface of *Cribrochalina* (see Fig. 14).

The specimen figured by WALCOTT (1920, Pl. 70, Fig. 1c, d) as *H. delicatula* and the two specimens illustrated under the same name by WALCOTT (1920, Pl. 90) make it likely that the species is composite. The latter two specimens are especially suggestive of *Nepheliospongia*. The smaller, cup-shaped (stenoproct) specimen (Pl. 90, Fig. 2) has regularly arranged orifices, like in the lectotype of *N. avocensis*, but because of strong compression and inferred thinness of the body wall, it is not clear whether these are apopores only (as in *N. avocensis*), prosopores only, or both of equal size (as in the modern nepheliospongiid *Cladocroce*). The larger specimen (Pl. 90, Fig. 4) is probably a widely caliculate (amblyproct) specimen with a narrow base, not a platyproct one with a mammillate center, as WALCOTT assumed. Both specimens display some annular stratification of the (main?) skeleton next to the prevailing ascending tracts.

Hazelia mammillata WALCOTT (1920, Pl. 90, Fig. 3) seems to be remarkably advanced, being platyproct (plate-shaped) with mammillate elevations and apical oscules, having a relatively thick body wall with a lacunose (alveolate), rather rigid structure, as the surface and the preservation (resistance to diagenetic compression) imply.

Species such as *H. delicatula* s.l. seem to have had the potential to evolve into nepheliospongiids. Hazelias were probably not predominantly frondose (in the shape of fans or ribbons) in life, as WALCOTT's descriptions might suggest, but chiefly vase-shaped to tubular (occasionally branching) or caliculate to concave-frondose. Only *H. mammillata* was probably sprawling or encrusting. The preservation of some specimens (WALCOTT 1920, Pl. 70, Fig. 1e, g) suggests that tubular to vase-shaped forms may already have had body walls comparable to *Nepheliospongia* in thickness. However, their consistency must have been limp to resilient (with the probable exception of *H. mammillata*), judging from lithofacies and preservation.

WALCOTT (1920, p. 219, 265) gave some consideration to the manner of preservation and to the habitat of the sponges in the Burgess shale and of the North American Cambrian in general. He argued that the sponges were carried into the Wapta pool or bay (the site where the Burgess shale was deposited) by currents, settled on and eventually became embedded in the toxic ooze, which was devoid of benthos. This view is still supported by many writers (cf. DUNBAR 1960, p. 124; OKULITCH & NELSON 1957, p. 763), but the nature of the habitat of these sponges is still open to speculation. WALCOTT (1920) assumed that they lived in shallow, clear water connected with the open sea. This habitat may well have been above wave base (cf. DUNBAR 1960, p. 124), or at least stirred by currents, as in the late middle to early upper Cambrian Metis shale of Quebec (cf. DAWSON as quoted by WALCOTT 1920, p. 265).

According to OKULITCH & NELSON (1957, p. 763), Cambrian sponges of North America were found embedded in shale at 8 localities, in limestone at only one locality. WALCOTT (1920, p. 281) reported *Hazelia* also from the bedded limestone overlying the Burgess shale (i.e. in the base of the Eldon formation). OKULITCH & NELSON (1957) aptly remarked: "That the sponges are found in shaly sediments does not necessarily mean that they preferred only, or at least died in, muddy water. It could also indicate that the sponges lived in other environments, but that the muds were the only media capable of preserving a delicate monactinellid skeleton." But even assuming that these sponges preferred calcareous substrates, it is most likely that these were calcilutitic. Though somewhat firmer than argillaceous muds on the sea floor, pure calcareous muds are still soft and susceptible to stirring in their top layer, even in sheltered subtidal situations, by occasional strong winds (cf. description of "whitings" in the lee of Andros Island, Bahamas, by CLOUD 1962).

Reefs or reefoid environments (except for stromatolites) were rare in North America during the middle Cambrian, and associated coarser carbonate sediments (calcareous, shelly facies) certainly absent at or near the sponge bearing localities. The last Archaeocyatha died out before the deposition of the Burgess shale (FINKS & HILL 1967, Fig. 9.1A). The reconstruction of the middle Cambrian sea floor reproduced in KUMMEL (1961, p. 181, Fig. 7-3), with the Burgess shale fauna swarming amidst thickets of *Archaeocyathus*, is therefore quite misleading.

Sponges attached to shells (cf. WALCOTT 1920, Pl. 71, Fig. 3) or other hard objects are exceptional in these faunas. Not only the Hexactinellida but also some Monaxonida of the Burgess shale probably had anchoring spicules. The feathery fringe of *Wapakia* may have served the same purpose, at least in part. Other sponges, especially *Hazelia*, may have had fleshy rhizomatous structures, with loose spicules, like the modern West Indian *Siphonodictyon siphonum* and *Xestospongia tierneyi*, which were torn off when the sponges were broken loose (by storms?) and transported to the Wapta pool. Many of the frondose specimens of *Hazelia palmata* are preserved in a lacerated state which may mean that they were either torn upon detachment or that they drifted for some time prior to settling. WALCOTT's observation on these fronds, that "some show irregular arrangement as though there had been a change in position of the frond and a new direction given to the increased growth", could be interpreted in favour of episodic stirring of the substrate.

It is perhaps no coincidence that one of the few species regularly colonizing subtidal unstable sediment bottoms in the West Indies, even with a high proportion of mud (e.g. the "archaic" bottom facies west of Andros, cf. CLOUD 1962, Pl. 2, Fig. H), and without attachment to other organisms or debris, is the nepheliospongiid *Siphonodictyon siphonum* (DE LAUBENFELS). It consists of clusters of fingerlike pipes and fistules piercing the sediment surface, without fleshy parts except for the atrial lining, connected within the sediment by a mass or layer of mucous choanosome. This fleshy base has excavating properties, and the genus comprises forms inhabiting coral heads (RÜTZLER 1971).

Considering the degree of differentiation of the middle Cambrian sponges within three major classes, it could be argued that some of these sponges had undergone evolution from ancestors adapted to other niches, particularly hard substrates, that could have existed in early Cambrian reefs. The extinction of the archaeocyathids

may have forced such sponges to adapt to soft substrates, muddy water or sediment at least episodically stirred into suspension. The *Hazelias* could be such types. Their dense main skeleton, caliculate-frondose to tubular, occasionally plate-like (encrusting?) habit, commonly narrow base and relatively thick body walls in some forms could be traits inherited from ancestors that lived in reef environments. On the other hand, the peripheral reticula or mats of fine spicules could have been characters acquired in the new environment, for keeping coarser debris in suspension from entering the incurrent system.

The habitat of the sponges of the Famennian of New York State was one of shifting hydrodynamic conditions, being situated at the distal fringe of the Catskill delta, with shales, siltstones and sandstones interfingering (cf. DUNBAR 1960, Fig. 139, 140). The stratigraphically highly sporadic distribution (usually at shale/sandstone interfaces) and the virtually exclusive dominance of the Protospongioidea (cf. FINKS 1960, Fig. 1; CLARKE 1920) make it difficult to place the extremely rare *Nepheliospongia* as to its habitat. The rather delicate, thinwalled Dictyospongiidae of the Famennian give the impression of a preference for sheltered muddy bottom, and may have inhabited chiefly the areas of deposition of grey to blue shales around Lake Erie and further north (Ontario). Dictyospongiidae are known from the Chagrin shale of this age near Cleveland, Ohio (some undescribed ones are deposited in the Cleveland Museum). Perhaps the famous dictyospongiid colonies of New York State were marginal, episodic extensions that were preserved due to high sedimentation rates associated with turbidite layers.

Nepheliospongia had apparently already evolved considerably with respect to *Hazelia*, strengthening its body wall by reducing the oxeas of the main skeleton to the same size as the peripheral ones, and by packing them in reticulate trabeculae. This trend is likely to have started within *Hazelia*. Considering the specific differentiation in the Cambrian genus, other forms of *Nepheliospongia* probably existed in the Famennian. Though seemingly better suited for this periodically shifting environment than the Dictyospongiidae, *Nepheliospongia*, being so rare here, seems to have preferred other environments, most likely associated with high-energy carbonates. Such carbonate environments, with reefs, at least temporarily connected with the Appalachian province, were present in the Michigan basin in the middle Devonian (DUNBAR 1960, p. 186), but were followed in the upper Devonian by the Antrim black shale. The widespread shallow-water carbonate facies of the Cordilleran province persisted into Famennian time, but was marked by regression and erosion, and hence progressive reduction of faunas, including stromatoporoids (DUNBAR 1960, p. 182; McLAREN, NORRIS & CUMMING 1970, p. 616). No direct marine connection existed between Iowa, the easternmost extension of the Cordilleran province, and the Appalachian province (cf. DUNBAR 1960, Fig. 139). The late Devonian spirifer *Theodossia hungerfordi* migrated from Eurasia to Iowa, but failed to reach the Appalachian province (DUNBAR 1960, p. 183 and Fig. 154).

Paleozoic sponges were probably more eurytopic than brachiopods, and capable of more extensive migration. Already in the middle Cambrian, the sponges of British Columbia and Quebec were quite similar, although the late Cambrian seaways across the continent were probably not yet in existence. Such connections existed in the late Cambrian, late Ordovician, probably Silurian, and Mississippian

time, but the sponges were probably not dependent on them to colonize suitable areas opened by transgressions on either side of the continent. The pronounced conservatism of the Nepheliospongiidae and the cosmopolitan distribution, wide niche differentiation and bathymetric range of its modern representatives make it likely that this group was always extremely eurytopic. This evolutionary trend, adaptability without radical morphological changes, was probably already characteristic of the middle Cambrian Hazeliidae, as we have seen. Other conservative groups of sponges, however, have been specialized from the start and have either modified and restricted this trait gradually (modern sclerosponges, pharetronids, sphinctozoans), or drastically changed their bathymetric range (Titusvilliidae CASTER, upper Devonian to Recent; cf. CASTER 1941).

In the Pennsylvanian, the Nepheliospongiidae are preserved in a relatively wide range of morphotypes in high-energy carbonates for the first time in the stratigraphic column. Their importance within such communities (chiefly of shelly facies and patch reefs, cf. FINKS 1960, Fig. 6, 7 and p. 22f., 47f.; 1970, p. 19f.) increased somewhat in the Permian, probably due to higher differentiation of shallow-water niches and immigrant forms from other regions. The older forms (*Coelocladia spinosa*, *Heliospongia excavata*) were confined to shallow but relatively quiet shelf facies (calcareous shales and argillaceous limestone). Reefs were then absent in the Texas region, hence the Pennsylvanian forms were not necessarily more stenotopic than the Permian ones. Most of the latter ranged from shallow-water shales into reefs and reefoid environments; only *Coelocladia philoconcha* was apparently confined to patch-reef facies.

FINKS (1960, p. 19) makes no mention in heliospongiids of tough rhizomes with extensions of main skeletal strands, as in the modern genera *Rhizochalina*, *Oceanapia*, *Biminia*, *Rhizoniera*, hence this feature may have been produced later in the evolution of the Nepheliospongiidae.

At this point, we should remember that the discovery of the Heliospongiidae and their skeletal structure by FINKS was fortuitous, based on some exceptionally well preserved specimens. Were it only for the normally calcified specimens (FINKS 1960, Pl. 3, Fig. 2-4), this group would probably still be ranged among the non-lithistid tetractinellids. On the other hand, if the apparent trend of increasing adaptation of the Nepheliospongiidae to high-energy carbonate environments should prove to be real and world-wide, the probability is high that coeval or subsequent populations are too poorly preserved for recognition or are still awaiting discovery. The probable morphological convergence of some nepheliospongiids and pharetronids in habit and gross aspects of skeletal structure would tend to veil any further records of the older group even more.

After the breakdown of reefs in early Triassic time, the reef communities of the upper Triassic were marked by proliferation of calcareous algae, of the ischyrosponges (all sponges with rigid calcareous skeletons, TERMIER & TERMIER 1975), and by the emergence of scleractinian corals (NEWELL 1972). The nepheliospongiids, if not completely forced out by new competing groups, may have been severely decimated and confined to rarefied niches not usually preserved in sediments. Any populations inhabiting the carbonate platforms so widespread in the Tethys at that time, would not have had a chance of preservation in the prevailing intertidal

conditions. Some of the alpine basinal shales, marls, and marly limestones of upper Triassic age, which yielded numerous exceptionally well preserved rigid Calcarea (DIECI et al. 1970, 1974; WENDT 1974) are apparently devoid of siliceous sponges. The ischyrosponges of such beds are believed to have lived in reefs and reefoid environments and to have been swept into adjacent basinal deposits (VEIZER & WENDT 1976, p. 559). Nepheliospongiids, if equally transported, may not have withstood the mechanical stress involved, or the microenvironment at the site of burial in mud may have been selectively preservative for aragonite skeletons and inimical to siliceous spicules. (The latter, however, is counterindicated by the frequent tuffaceous intercalations in the Cassian beds). Ischyrosponges found in their biotope are almost invariably recrystallized. The absence of records of nepheliospongiids in the Jurassic may be attributed to the same causes, i.e. rarity, confinement to restricted niches, and failure to be recognizably preserved (for lists of localities of shallow-water sponges, see WENDT 1976, VEIZER & WENDT 1976).

A special environment is preserved in the sponge bioherms of the upper Jurassic of Southern Germany, usually regarded as of slightly deeper water than coral reefs. The frame-building lithistids and hexactinellids are commonly more or less corroded and penecontemporaneously "mummified" by coats of microspherical blue-green algae (BEHR & BEHR 1976). Nepheliospongiids, if present, would thus have had a far better chance of preservation than in other Mesozoic settings. These sponge faunas have been monographed by KOLB 1910, and SCHRAMMEN 1936, and nothing therein is comparable to nepheliospongiids.

The isolated spicules preserved in the basinal bedded limestone between the South German sponge mounds suggest that some modern types (families or even genera) of non-lithistid demosponges already existed then, as some diagnostic spicule types imply: sterrasters (of Geodiidae) and oxyspherasters to pycnasters (of Chondrillidae or *Placospongia*) have been described and illustrated by REIF (1967) and SCHINDEWOLF (1967). The erection of the genus *Rhaxella* for the special spicule type known as rhax, so abundant in these deposits, still plentiful in the upper Cretaceous (cf. REIF 1967, p. 95, with distribution and references) has to be reconsidered. *Rhaxella* is probably either a post mortem artefact, as SCHRAMMEN (1936b, p. 68) assumed, or a fragment from the axial portion of a *Placospongia*. The rhax is not comparable to the sterrasters of the Geodiidae, in my opinion. REIF (1967) gave a new record of rhaxes from the Eocene of Barbados and vaguely compared this spicule type with the selenaster of *Placospongia* (cf. VOSMAER & VERNHOUT 1902; WIEDENMAYER 1977, Fig. 77). The latter affinity is very likely, because of the plentiful occurrence of rhax spicules in a Pleistocene or subrecent reef core from the Atlantic coast of Panama taken by Dr. Ian Macintyre (U.S. National Museum; personal communication by Dr. Klaus Rützler, ibidem). Dr. Rützler was able to produce rhaxes experimentally by corroding selenasters in fluoric acid. The selenasters in the peripheral plates and in the axial region of modern *Placospongias* occupy about 50% of the biomass. This proportion may have been considerably higher in fossil forms, which could explain the huge quantities of rhaxes in some upper Jurassic beds, which are sometimes rock-forming.

Other types of spicules might be taken to indicate the presence in the upper Jurassic of modern shallow-water groups of demosponges, besides non-lithistid

tetractinellids. Thus styles and tylostyles (REIF 1967, Pl. 12) suggest the presence of Clavaxinellida. A slender tylote (REIF, Pl. 12, Fig. 20) might have belonged to an early poecilosclerid.

Unequivocal records of Poecilosclerida, through special types of microscleres (chelae, toxae, diancistra) are known in the Cretaceous of Northern Germany (SCHRAMMEN, 1936a, p. 169, with additional references).

FINKS (1960, p. 42; Pl. 2, Fig. 7, 10, 11; Pl. 7, Fig. 1-3) pointed out the pronounced similarity between the late Paleozoic Nepheliospongiidae and *Pharetratospongia strahani* SOLLAS 1877 from the Cretaceous of England, chiefly in spiculation and skeletal architecture. The differentiation in structure of the excurrent and incurrent surface in SOLLAS' sponge is not incompatible with including it in the Nepheliospongiidae. The reticulum of the outer surface is quite like that in *Nepheliospongia*, in *Cribrachalina* and in *Siphonodictyon*. The round apopores piercing the smooth, dense inner surface are reminiscent of the excurrent surface of *Coelocladia spinosa* (cf. FINKS 1960, Pl. 7, Fig. 4). The modern West Indian *Xestospongia tierneyi* (Fig. 10) also has a dense, smooth layer of tangentially arranged diacts lining the atrium. Though FINKS later obviously abandoned any thought of close phyletic ties between *Pharetratospongia strahani* and his Heliospongiidae, his point that the Cretaceous sponge was siliceous and only diagenetically calcified is here upheld. Its inclusion in the pharetronids by DE LAUBENFELS (1955) is not warranted. I fail to see any justification in assigning to *Pharetratospongia* forms from the upper Triassic (DIECI, ANTONACCI & ZARDINI 1970, p. 98; WENDT 1974, p. 503, 507, 509), which, except for very rare monaxonic spicules, have an aragonitic skeleton typical of pharetronids.

Phylogenetic and systematic implications

The middle Ordovician was the time of marked diversification of demosponges (FINKS 1970, p. 6f.). This was possibly due to the emergence of a wealth of new niches in shallow water, when reefs and associated shallow-water communities flourished again following the scarcity and impoverished nature of reefs from middle Cambrian to lower Ordovician (NEWELL 1972). This adaptive radiation produced a remarkably advanced type, *Saccospongia laxata* (cf. FINKS 1967), already close to modern Axinellida and sublithistids in skeletal structure. FINKS (1970, p. 8, Fig. 5) suggested that *Saccospongia* may have been the common root of the modern Clavaxinellida and Ceractinomorpha. It seems at least as plausible that the earliest nepheliospongiids were then already in existence. A separation of two lines (*Saccospongia* → Axinellida, and earliest nepheliospongiids → Ceractinomorpha with the possible exception of Halichondriida) seems likely even before the middle Ordovician, if we assume that *Saccospongia* arose independently from *Hazelia*.

No attempt is made here to discuss phylogeny of demosponges in a comprehensive context. The matter has been treated exhaustively by REID (1963, 1970) and FINKS (1967, 1970), in which publications some rather controversial issues were raised. It must be noted, however, that these authors did not categorically dismiss each other's line of evidence, but each presented alternatives which he considered more plausible. Some confrontations were altogether avoided. These divergences of opinion concern chiefly the phylogenetic distribution of tetraxons (primitive versus

advanced as megascleres, continuous versus disjunct) and the position of the Homosclerophora (primitive and ancestral to all other orders, versus terminal). I have discussed these opinions in my monograph (1977, p. 19f.) in the context of classification, but only on the basis of the earlier accounts. Those of 1970 came to my attention too late for proper consideration.

What makes the issues so complex and the lines of reasoning so tortuous is the rarity of paleontological records in the Paleozoic (cf. REID 1970, p. 71), particularly of those miracles of preservation which document rather delicate structural types. Microscleres from demosponges are practically unknown in the Paleozoic.

With these fundamental handicaps acknowledged, I tend to side with FINKS on early stages of demosponge phylogeny, chiefly on the evidence afforded by the monaxonids from the Burgess shale. The important point made by REID (1970, p. 72) has to be conceded, that the lower Carboniferous choristids (which FINKS took as evidence for emergence of the tetraxonic megasclere from monaxonic ancestors) were differentiated to such a degree that their roots must be assumed to be several times older. With equal right the remarkable differentiation of the monaxonids in the Burgess shale can be interpreted as an indication of a long history going back to the Precambrian. Nevertheless, the triaene, also known beginning in the lower Carboniferous, might still be a comparatively late development, given its ectosomal specialization, large size and absence in the early Paleozoic record. This means that very large megascleres must have been developed in monaxonic stocks long before tetraxons of comparable size appeared. WALCOTT noted the following spicule lengths: up to 5 mm in *Hazelia palmata*; up to 6 cm in *Wapchia grandis*; up to 12 cm in *Tuponia lineata*. It could be argued that these middle Cambrian sponges were not demosponges, as REID (1970, p. 71) tentatively pointed out. The only alternative that comes to mind is that they were specialized hexactinellids, in which monaxonic prostalia took over completely, or which were comparable to the Dictyospongiidae, except for lack of hexacts. In view of the evolutionary trends of Hexactinellida (FINKS 1960, p. 10; 1970), this is not very likely (but see below, p. 914).

In his suggested phylogeny, REID (1970, p. 78, Fig. 5) pictures the common root stock of the Demospongea as consisting of primitive microspiculate sponges closely allied to the modern Homosclerophora (Plakinidae), which he regards as their conservative offshoot, independent from all other lines of demosponges. The subsequent specialization of the Plakinidae would include the amphiblastula of *Plakina* and lophate spicules. REID's phylogenetic scheme is a development of the hypothesis of SCHULZE and DENDY (cf. REID 1970, p. 64).

This primitive microspiculate group is assumed to have comprised forms with radiate spicules (microcalthrops and meristic variants ranging from diacts to polyacts) and other forms with monaxons only. The former would have formed an astrotetraxonid radical stock, the latter a sigmatomonaxonid one. REID (1970, p. 78) is not committed on the nature of the supposed primitive monaxons. In one alternative he considers that they might correspond to the diacts in modern plakinids. These diacts are invariably centrally inflated, centrangulate or centrotylote, and grade into triacts. The reduced nature of these diacts is implied by many writers, including REID (1970, p. 64).

There are no modern plakinids with diacts only (though *Diactinolopha* SARÀ 1960 has lophodiacts dominating, with a complement of smaller, intergrading, simple diacts and triacts). Some forms have larger lophocalthrops distinct in size from smaller diacts to calthrops (*Placinolopha* TOPSENT), or even triaenes with short rhabds (*Plakinastrella* SCHULZE), but this hardly corresponds to a separation of megascleres, and there are not traces of a more advanced skeletal structure (e.g. radiate).

From an interpretation of REID's phylogenetic scheme (1970, Fig. 5) it would seem that he considers that only the ancestral microspiculate sponges existed in the Precambrian and perhaps also the early Cambrian. I think that all monaxonids known from the Burgess shale would thus have to be ruled out as early members of the "sigmatomonaxonid stock": they are far too remote in spiculation and structure to fit in here, especially in view of the phylogenetic implications of Figure 1 in REID (1970, p. 64). These cannot be negated altogether, however abstract DENDY's concept was. Disregarding the microsclere "series", which have no paleontological foundation, the formation of oxeote and monactinal megascleres would be an advanced if not terminal trait with respect to evolution, according to DENDY.

REID did not rule out that some modern monaxonids descended from Cambrian groups with megascleres, which never possessed tetraxons. This possibility is accounted for in his scheme (1970, p. 79), with "other stocks?" placed between the radical dichotomy. The scheme, however, gives the impression that all modern sigmatomonaxonids (Haplosclerida, Poecilosclerida, Halichondriida, Keratosa, monaxonic lithistids) are derived from the radical stock with monaxonic microscleres only.

If such hypothetical primitive monaxonids (with an incipient differentiation of megascleres?) coexisted with the known Canadian Cambrian faunas, they must have lived in other areas and/or habitats, or we would expect them to have been preserved with the Burgess fauna. As was discussed above (p. 904), muddy bottoms, whether calcilutitic or argillaceous, must have prevailed in middle Cambrian shallow seas, and both hexactinellids (protospongiids) and megaspiculate monaxonids were probably adapted to such habitats. Since the primitive microspiculate sponges sensu REID would not have been much different in gross morphology, habit, and ecology from modern Plakinidae, one would have to assume that they could only survive firmly attached to hard substrates or other benthos, and that they probably lived only in clear waters. Such conditions were then present only in the sparse reefs (chiefly of stromatolites) and along the coasts of the Precambrian shields. Any separation from the megaspiculate monaxonids would have been in effect more geographical than ecological. The presence of a Paleoatlantic and marked Cambrian provincialism (HALLAM 1972) could be considered as favouring such a view.

Since such littoral and reefoid environments were particularly subject to paleogeographic evolution, any sponges living here would be expected to evolve markedly over long periods (WIEDENMAYER 1974). One might argue that the conservative line of modern Plakinidae was one of the first benthonic groups to have migrated to deep water, where lack of competitors and of paleogeographic revolutions allowed them to remain inert in evolution. But then, later in their history, many modern

plakinid genera must be assumed to have migrated to the shallow-water habitats they occupy at present: this is a rather unlikely development.

A further problem with 3 primitive stocks of microspiculate sponges, which supposedly had in common diacts, formed as reduced calthrops or triacts, is the radical difference in rate of evolution. Why did the 'astrotetraxonid' and 'sigmomonaxonid' stocks start explosive expansion almost simultaneously, supposedly through adaptive radiation in the Ordovician, with several subsequent parallel trends, while the Plakinidae remained almost unchanged since the Precambrian? Apart from the unlikely chance that suitable, unchanged niches were always available for the Plakinidae, I find it difficult to believe that such a pronounced range of meristic variants would be preserved so long without going off in two or more directions. There is not even a clear trend in reduction of teracts to diacts, i.e. in their mutual proportion. Why was this proportion left unchanged in the Plakinidae, while on the other hand the separation of forms with monaxons only from a stock with monaxons and tetraxons occurred so early, producing a radical dichotomy followed by simultaneous expansion?

The other alternative (REID 1970, p. 78) is that "the most primitive spicules were monaxons, and radiate spicules arose from assembled monaxons which became their rays. This might happen, for instance, if a number of monaxon units were formed within one scleroblast, like trichites, but united in radial groups." This alternative might answer some of the questions raised above, but brings new problems.

If the primitive monaxons are believed to have united crosswise, intersecting at the same point, only stauracts and hexacts would have been formed next to polyacts. If the primitive monaxons are thought to have united distally, it must be asked why not only random meristic variants were formed, i.e. why certain fundamental geometric types (the calthrops and possibly the hexact) emerged. If the triacts and diacts so characteristic of Plakinidae are reduced calthrops, why are they so ubiquitous in this family, and not the augmented variants (pentacts to polyacts)? This would mean that such proportions of reduced versus augmented forms (next to calthrops) would probably have been similar in early Plakinidae, and that reduction, which is commonly associated with an evolutionary trend, would have persisted from Precambrian to Recent.

The alternative may be considered, that the diacts of the first Plakinidae were more fundamental in evolution, though still derived, i.e. formed by merging of primitive monacts at their heads. Since merging preferentially along one axis would have been unlikely, the commonly centrangulate morphology of diacts in modern Plakinidae might be cited in favour of this view. The uniformly high angle of the two actines in such spicules and their intergrading with triacts (with one actine reduced) are not indicative of such a primitive condition.

Derivation of diactinal megascleres from such microxeas would be unlikely, and centrangulate oxeas are rare in modern non-plakinid sponges (e.g. *Spongisorites*). A coexistence of primitive, undifferentiated monaxons (raphides), monacts (microstyles) and meristic diacts to polyacts in primitive microspiculate sponges is hardly compatible with parsimony in early stages of evolution. Microstyles are quite rare in modern sponges. It might be argued that the presence of microstyles in the earliest

demosponges can be implied from the early appearance of stylote megascleres (in the Ordovician *Saccospongia*). Actually, stylote megascleres are quite archaic and are known from other classes of sponges. *Pirania*, from the Burgess shale, though not a demosponge, has tylostyles and is possibly an early receptaculitid (FINKS & HILL 1967, p. 339). Sclerosponges, now generally believed to be related to the fossil stromatoporoids, have proper styles, and Paleozoic stromatoporoids probably also had them (HARTMAN & GOREAU 1970, Fig. 8, 15).

Regardless of whether megascleres and microscleres of later demosponges had common ancestors among primitive undifferentiated spicule types, or whether they arose independently, I prefer to think that monaxons were inherently adaptable to either a diactinal or a monactinal condition, primarily on the megascleric level. Such trends might have been reversible to some degree, depending on changes in skeletal structure, possibly also on more obscure features of evolution, like histological, cytological differentiation, and changes in non-skeletal gross morphology of choanosome and ectosome. This might explain the ubiquitous occurrence of styles s.l. in orders of the Tetractinomorpha (the Hadromerida and Axinellida, rarely in the Astrophorina and Spirophorina) and of the Cercatinomorpha (the Halichondriida and Poecilosclerida, rarely in the Haplosclerida).

The phylogenetic concept of REID, as I have pointed out before (WIEDENMAYER 1977, p. 20), is built on the primacy of diagnostic criteria (on the ordinal level) based on fundamental types of microscleres (except for the desmas of lithistids, which are treated in analogous fashion). Types of skeletal structure are subordinate to these criteria. With FINKS, the rank of these diagnostic standards is at least equal, if not inverse.

It should be admitted that both the lithistid and sublithistid conditions appeared independently in separate lines of descent. I do not feel competent to elaborate on the divergence of opinion, between FINKS and REID, concerning the phylogeny and classification of lithistid groups. However, I still fail to be convinced by the antecedence (fundamental dichotomy) of lines of microsclere evolution over phylogenetic lines based on megascleres and skeletal architecture. Apart from the improbability of the Homosclerophora constituting the earliest demosponges, it should suffice to recapitulate here 4 points, drawing partly on what I wrote in 1977.

Summary and conclusions

1. A primitive homosclerophorid root stock, ancestral to all demosponges and similar to the modern Plakinidae in spiculation, as postulated by REID, is unlikely on two counts:
 - a. The enormous difference in rate of evolution between the plakinid line and the two collateral radical stocks of demosponges could only be explained by a deep separation in ecologic affinity, i.e. extreme stenotopic versus eurytopic overall trend. The only viable pattern of such early and persistent niche segregation, that of deep versus shallow water, is counterindicated by the occurrence of most modern plakinids in shallow water.

b. The diversity of the middle Cambrian monaxonids suggests that their ancestors, which probably already possessed monaxonic megascleres, must have lived in the Precambrian. The common ancestry of *Saccospongia* and of the nepheliospongiids and hence of the modern Axinellida and Ceractinomorpha, i.e. of all 'sigmatomonaxonid' orders, in *Hazelia* is quite plausible.

2. A phylogenetic line *Hazelia* → *Saccospongia* → Clavixinellida is more consistent with LÉVI's classification on the basis of embryological criteria (LÉVI 1956) than with REID's scheme (REID 1970, p. 79). The latter shows the Hadromerida ('clavulids') and the Hemiasterellidae, i.e. Axinellida with euasters ('astraxinellids') as collateral offshoots of the Astrophorina, each apparently separate since pre-Carboniferous time.

The axinellid families with microrhabds and the Desmacellidae (= Sigmaxinellidae) were disregarded by REID. Microrhabds are ubiquitous, but the Desmacellidae would have to be included among the lines derived from REID's 'sigmatomonaxonid' stock. BERGQUIST & HARTMAN (1969) have noted that the Axinellida, as previously defined, are probably polyphyletic on biochemical evidence. Some genera (*Auletta* and *Phakellia*) have apparent poecilosclerid affinity. Desmacellids and hemiasterellids were not considered. Typical Axinellida are the families Axinellidae, Raspailiidae and Desmoxyidae. The order thus restricted, is distinct from all others, also from the Hadromerida. The superorder Clavixinellida is therefore questioned by BERGQUIST & HARTMAN. These authors found the Ceractinomorpha to be rather homogeneous in free amino acid patterns (which implies collateral evolution of their orders), while the Tetractinomorpha are said to be much more heterogeneous. The Axinellida, though apparently polyphyletic as still construed (e.g. LÉVI 1973), are nevertheless said to be intermediate between the Ceractinomorpha and Tetractinomorpha. (LÉVI 1956, though including the Clavixinellida in the Tetractinomorpha, granted a fundamental difference between the Tetractinellida and the Clavixinellida.)

Given the divergences between the system of LÉVI and that of BERGQUIST & HARTMAN, one might argue that either embryological or biochemical characters were subject to convergence over long periods of evolution. However, one important point of agreement stands out: *Tethya* is a hadromerid genus. This means that true euasters occur in the 'clavulids' and may have intergraded with spirasters in evolution. This is corroborated by the genus *Timea* (since the genus is not among the problematic ones regarding all other morphological traits, I fail to see a distinction of true euasters and pseudieuasters, hence a composite nature; cf. REID 1970, p. 81). It should also be pointed out in this context, that BERGQUIST & HARTMAN (1969, p. 263, 264) found *Chondrilla* (which has oxyspherasters only) to be close to *Tethya* in its free amino acid patterns.

If preference is given to BERGQUIST & HARTMAN (1969) over LÉVI (1956) in considering that the Hadromerida and true Axinellida are probably fundamentally separate orders, one could say that the presence of euasters in the biochemically related genera *Tethya* and *Chondrilla*, and the corticate structure of both is indicative of closer ties between the Hadromerida and the Astrophorina. The ambiguous nature of the epipolasids (with both choristid and hadromerid traits) would tend to

support this view. Perhaps the Hemiasterellidae, once tested for free amino acid patterns, might corroborate this.

Though this view is similar to the scheme of REID (1970, Fig. 5) in the later development of groups, it is not so in the supposed early separation of stocks, since we would not have mutual exclusion of euasters and spinispiras. The stock of such a widened astrophorid superorder might be envisaged as monaxonid, not corticate, with confused or radiate structure, without or with unknown microscleres capable of evolving into euasters, streptasters, spinispiras and sigmaspires. Its ancestors could well be forms like *Hamptonia* and *Choia* WALCOTT (1920). Triaenes were possibly developed in some of their descendants as anchoring spicules (anatriaenes) similar to such spicules in the modern *Tetilla radiata* (cf. BRIEN 1973, p. 145) and to the basalia in many hexactinellids (where the recurved clads are meristic, however), independently of tetraxonic megascleres in the choanosome. This interpretation would be in accord with FINKS' view on evolution of tetraxons on the meglasclere level and neutral as regards any pre-Carboniferous occurrences. Perhaps DE LAUBENFELS (1955, p. E70, under 'Leptomitidae') was right at least in part, in that some of the Cambrian sponges were yet undifferentiated as to class, ancestors both to non-protospongoid or marginally protospongoid Hexactinellida and to Tetractinomorpha. Perhaps some modern lyssakine hexactinellids should be tested for free amino acid patterns.

3. The Ordovician ancestry of typical modern Axinellida, if not of other 'Clavax-inellida' in *Sacospongia* is quite plausible on morphological grounds. Oxeas and microrhabds of modern forms do not necessarily mean that *Sacospongia* had microrhabds, or that hypothetical ancestors with a complement of oxeas (from which the heloclonid desmas of *Sacospongia* could be derived) should be contemplated. What little is known of spiculogenesis favours the view that the transitions between diacts and styles could have been reversible in evolution (even within the Hadromerida, as *Tethya* and some 'epipolasids' seem to indicate).

Following REID, the styles (including tylostyles), which are the virtually exclusive megascleres of the Hadromerida ('clavulids') would be homologous with the monaxonid megascleres of the Astrophorina (Geodiidae etc.). If the Hadromerida and the Spirophorina (Craniellidae) are collateral offshoots from primitive Astrophorina, why did the Hadromerida develop only tylostyles (which are quite rare in the Astrophorina and Spirophorina), retaining a few euasters, and these almost exclusively of newly formed spinispiras (with the exception of *Placospongia*, where spherasters (pycnasters) occur next to selenasters; see VOSMAER & VERNHOUT 1902, Pl. 4); and why did the Craniellidae inherit only oxeas and triaenes (very rare styles and subtylostyles occur in *Cinachyra*) but no euasters? The tylostyles of the Hadromerida cannot be regarded as reduced triaenes, given the basal position of tylos in peripheral portions of the sponge, as opposed to the distal position of the cladomes of triaenes.

4. As I have already hinted with the sigmata of the Desmacellidae and euasters of some Hadromerida, I cannot accept a mutual exclusion and equal diagnostic value of all fundamental types of microscleres (sensu DENDY) on such a high taxonomic level (subclasses or superorders), as DENDY and REID assumed. Granted

that some of these types provide excellent clues to phylogeny, I tend to agree with LÉVI (1955, p. 85), who noted that various morphological types differ greatly in their importance in taxonomy. This is partly corroborated by the findings in SIMPSON (1968, p. 113) that toxæ in poecilosclerids are secreted in different ways by distinct special cell types, and that, conversely, raphides of *Tedania*, which approximate some microcionid toxæ in morphology, are secreted in a manner similar to palmate isocheiae in microcionids.

5. The nepheliospongiid line is here regarded as collateral with the line *Saccospongia*-Axinellida, both issuing from *Hazelia*. Since the latter already shows advanced traits in some forms, the Nepheliospongiidae must be at least as old as *Saccospongia*. If the desmacellids are true Axinellida, as LÉVI assumed, sigmata s.s. must have been present in both lines from an early stage. As a concession to the principle of parsimony in evolution and to high diagnostic value of sigmatoscleres (the closest to a truly ancestral dichotomy sensu DENDY, REID), the presence of sigmata in common ancestors (*Hazelia*) is more likely than independent emergence of these spicules in both lines.

The primary offshoots of the nepheliospongiid parent line may have been the Poecilosclerida and the Haplosclerida. They may have issued about simultaneously and relatively late, perhaps coinciding in time with and caused by the revolutions around the Triassic/Jurassic boundary (early phases of central Atlantic plate tectonics, submergence of local shallow basins, pantethyan collapse of carbonate platforms, emergence of scleractinian corals, decline of ischyrosponge reefs).

As primitive types among the Haplosclerida, we could imagine structurally strong genera (though with variable proportion of spicules versus spongin), peripheral specialization, prevailing ramosæ, stenoproct, euryproct, fistulose to 'coelosphaerid' habits, such as *Callyspongia* (= *Siphonochalina*, related to *Siphonodictyon*), *Spinosella*, *Pachychalina*, *Niphates*, *Pellina* and other 'adociids' sensu DE LAUBENFELS.

As poecilosclerids with primitive traits in the above sense, I would consider the Coelosphaeridae (sensu LÉVI 1973, not DE LAUBENFELS 1936). The pulpous choanosome with few spicules, and the corticate, highly spiculiferous, papillate to fistulose ectosome are suggestive of the nepheliospongiids *Siphonodictyon*, *Oceanapia*, *Rhizochalina* and *Biminia*. *Neofibularia* (cf. HARTMAN 1967; BERGQUIST & HARTMAN 1969, p. 250), a myxillid with strong development of diactinal megascleres, with simple microrhabds and sigmata (no chelæ), similar to *Xestospongia muta* in habit and structure, could be cited as a primitive poecilosclerid. The Crellidae (cf. LÉVI 1973, p. 612; TOPSENT 1928, p. 229), with chiefly diactinal megascleres, dense peripheral crust, and firm consistency, could be regarded as somewhat less primitive: acanthose condition and peripheral specialization of diacts, isolated acanthostyles and generally platyproct habit would be advanced traits.

The Keratosa are pictured by REID (1970, Fig. 5) as a line parallel to the Haplosclerida and Poecilosclerida, replenished in iterative fashion by these, but possibly of independent origin from the 'sigmatomonaxonid' radical stock. FINKS (1967) assumed a relatively late (Permian?) issue of the Keratosa from the Sigmatosclerophora (Haplosclerida, Poecilosclerida + Desmacellidae). BERGQUIST & HARTMAN

(1969) noted a fundamental dichotomy within the Keratosa, which is not congruent with the conventional morphological distinction of Dendroceratida and Dictyoceratida: the Verongiidae are separate in free amino acid patterns from the relatively homogeneous group Dendroceratida + Spongiidae + Dysideidae + Poecilosclerida without *Agelas*. A further case of incongruence of skeletal morphology and biochemical traits should be pointed out: *Aiolochroia crassa* (HYATT) (see WIEDENMAYER 1977) has a dendritic skeleton, but biochemical properties (as implied from the necrotic change of color) like the Verongiidae. *Smenospongia* WIEDENMAYER (1977) has similar chemical traits, but a prismatic (and fibrofasciculate) architecture like in some Haplosclerida and Spongiidae (cf. WIEDENMAYER 1977, Fig. 82, 83). This might indicate convergence of some biochemical traits in evolution.

On morphological grounds, the Dendroceratidae might have issued directly and early from the hazeliid-nepheliospongiid parent line, considering that dendritic architecture prevails in *Hazelia palmata* and in some modern nepheliospongiids (*Cladocroce*, *Calyx*, *Dendroxea*). For the Dictyoceratida, a derivation from the Haplosclerida is more likely, in view of prismatic and fibrofasciculate architecture being frequent in both orders, especially in conjunction with development of spongin fibers in the latter.

For the Halichondriida, regarding which BERGQUIST & HARTMAN (1969) remained uncommitted, I could see a line independent since the early Paleozoic, as REID (1970, Fig. 5) conceived. However, an ancestry in forms of the Burgess shale (*Halichondrites*) is again most plausible, considering the similarities in extreme size range of monaxons and in architecture with modern Halichondriidae.

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REFERENCES

BEHR, K., & BEHR, H.J. (1976): *Cyanophyten aus oberjurassischen Algen-Schwamm-Riffen*. - Lethaia 9/3, 283-292.
 BERGQUIST, P.R., & HARTMAN, W.D. (1969): *Free amino acid patterns and the classification of the Demospongiae*. - Marine Biol. 3/3, 247-268.

BRIEN, P. (1973): *Les Démospanges. Morphologie et reproduction*. In: GRASSÉ, P.P. (Ed.): *Traité de zoologie, anatomie, systématique, biologie* (tome III/1, p. 133-461). - Masson, Paris.

BURTON, M. (1932): *Sponges*. In: *Discovery Reports* (vol. 6, p. 237-392). - Cambridge University Press.

CASTER, K. E. (1941): *The Titusvilliidae; Paleozoic and Recent branching Hexactinellida*. - *Palaeontographica amer.* 2/12.

CHADWICK, G. H. (1935): *Faunal differentiation in the Upper Devonian*. - *Bull. geol. Soc. Amer.* 46, 305-342.

CLARKE, J. M. (1900): *Dictyonine hexactinellid sponges from the Upper Devonic of New York*. - *Bull. New York State Mus.* 39/8, 187-194.

— (1920): *The great glass-sponge colonies of the Devonian; their origin, rise, and disappearance*. - *J. Geol.* 28, 25-37.

CLOUD, P. E. (1962): *Environment of calcium carbonate deposition west of Andros Island, Bahamas*. - *Prof. Pap. U.S. geol. Surv.* 350.

DIECI, G., ANTONACCI, A., & ZARDINI, R. (1970): *Le spugne cassiane (Trias medio-superiore) della regione dolomitica attorno a Cortina d'Ampezzo*. - *Boll. Soc. paleont. ital.* 7/2 (1968), 94-155.

DIECI, G., RUSSO, A., & RUSSO, F. (1974): *Nota preliminaria sulla microstruttura di spugne aragonitiche del Trias medio-superiore*. - *Boll. Soc. paleont. ital.* 13, 99-107.

DUNBAR, C. O. (1960): *Historical geology. Second edition*. - Wiley & Sons, New York.

FINKS, R. M. (1960): *Late Paleozoic sponge faunas of the Texas region. The siliceous sponges*. - *Bull. amer. Mus. nat. Hist.* 120/1.

— (1967): *The structure of Saccospongia laxata Bassler (Ordovician) and the phylogeny of the Demospongiae*. - *J. Paleont.* 41/5, 1137-1149.

— (1970): *The evolution and ecologic history of sponges during Paleozoic times*. In: FRY, W. G. (Ed.): *The biology of the Porifera* (Symposia of the Zoological Society of London 25, p. 3-22). - Academic Press, London.

FINKS, R. M., & HILL, D. (1967): *Porifera and Archaeocyatha*. In: HARLAND, W. B. et al. (Ed.): *The fossil record* (p. 333-345). - Geol. Soc. London.

GIRTY, G. H. (1908): *On some new and old species of Carboniferous fossils*. - *Proc. U.S. natl. Mus.* 34, 281-303.

GRIESSINGER, J. M. (1972): *Étude des Réniérides de Méditerranée (Démospanges Haplosclérides)*. - *Bull. Mus. natl. Hist. nat. Paris* (3), 3 (1971), 97-182.

HALL, J., & CLARKE, J. M. (1899): *A memoir on the Paleozoic reticulate sponges constituting the family Dictyospongidae*. - *Mem. New York State Mus.* 2 (1898).

HALLAM, A. (1972): *Continental drift and the fossil record*. - *Sci. American* 227/5 (Nov.), 56-66.

HARTMAN, W. D. (1967): *Revision of Neofibularia (Porifera, Demospongiae), a genus of toxic sponges from the West Indies and Australia*. - *Postilla Peabody Mus. nat. Hist.* 113.

HARTMAN, W. D. & GOREAU, T. F. (1970): *Jamaican coralline sponges: their morphology, ecology and fossil relatives*. In: FRY, W. G. (Ed.): *The biology of the Porifera* (Symposia of the Zoological Society of London 25, p. 205-243). - Academic Press, London.

KING, R. H. (1933): *A Pennsylvanian sponge fauna from Wise County, Texas*. - *Bull. Univ. Texas* 3201, 75-85.

— (1943): *New Carboniferous and Permian sponges*. - *Bull. geol. Surv. Kansas* 47, 1-36.

KOLB, R. (1910): *Die Kieselspongen des Schwäbischen Weissen Jura*. - *Palaeontographica* 57, 142-254.

KUMMEL, B. (1961): *History of the earth. An introduction to historical geology*. - Freeman, San Francisco and London.

LAUBENFELS, M. W. DE (1936): *A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera*. - *Publ. Carnegie Instn. Washington* 467 (Pap. Tortugas Lab. 30).

— (1955): *Porifera*. In: MOORE, R. C. (Ed.): *Treatise on invertebrate paleontology. E. Archaeocyatha and Porifera* (p. E21-E112). - Univ. Kansas Press.

— (1957): *A problem in taxonomy: the sponge genus Reniera*. - *Syst. Zool.* 6, 156-159.

LÉVI, C. (1955): *Les Clavaxinellides, Démospanges Tétractinomorphes*. - *Arch. Zool. expér. gén.* 92, Notes Rev., 78-87.

— (1956): *Étude des Halisarca de Roscoff. Embryologie et systématique des Démospanges*. - *Arch. Zool. expér. gén.* 93, 1-181.

- (1973): *Systématique de la classe des Demospongiaria (Demosponges)*. In: GRASSÉ, P. P. (Ed.): *Traité de zoologie. Anatomie, systématique, biologie* (tome III/1, p. 577-631). - Masson, Paris.
- MC LAREN, D. J., NORRIS, A. W., & CUMMING, L. M. (1970): *Devonian faunas*. In: DOUGLAS, R. J. W. (Ed.): *Geology and economic minerals of Canada* (p. 614-622). - Geol. Surv. Canada (Ottawa).
- NEWELL, N. D. (1972): *The evolution of reefs*. - Sci. American 226/6 (June), 54-65.
- OKULITCH, V. J., & NELSON, S. J. (1957): *Sponges of the Paleozoic*. In: LADD, H. S. (Ed.): *Treatise on marine ecology and paleoecology. Vol. 2, Paleoecology* (p. 763-759). - Mem. geol. Soc. Amer. 67/2.
- REID, R. E. H. (1963): *A classification of the Demospongia*. - N. Jb. Geol. Paläont. [Mh.] 4, 196-207.
- (1970): *Tetraxons and demosponge phylogeny*. - In: FRY, W. G. (Ed.): *The biology of the Porifera* (Symposia of the Zoological Society of London 25, p. 63-89). - Academic Press, London.
- REIF, W. E. (1967): *Schwammspicula aus dem Weissen Jura Zeta von Nattheim (Schwäbische Alb)*. - Palaeontographica (A), 127, 85-102.
- RIDLEY, S. O. (1884): *Spongiida*. In: *Report on the zoological collections made in the Indo-Pacific during the voyage of H.M.S. 'Alert', 1881-2* (part 1, p. 366-482; part 2, p. 582-630). - Brit. Mus. nat. Hist.), London.
- RIDLEY, S. O., & DENY, A. (1887): *Report on the Monaxonida collected by H.M.S. Challenger during the years 1873-1876*. In: *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-1876* (Zoology, 20/59). - H.M.S.O., London, Edinburgh, Dublin.
- RÜTZLER, K. (1965): *Systematik und Ökologie der Poriferen aus Litoral-Schattengebieten der Nordadria*. - Z. Morph. Ökol. Tiere 55, 1-82.
- (1971): *Bredin-Archbold-Smithsonian Biological Survey of Dominica: burrowing sponges, genus Siphonodictyon Bergquist, from the Caribbean*. - Smithson. Contr. Zool. 77.
- SARÀ, M. (1960): *Diactinolopha, genere nuovo di Plakinidae per D. moncharmonti sp. n. rinvenuta nel golfo di Napoli (Demospongiae)*. - Annu. Ist. Mus. Zool. Univ. Napoli 12/4.
- SCHINDEWOLF, O. H. (1967): *Analyse eines Ammoniten-Gehäuses*. - Abh. Akad. Wiss. Lit. Mainz, math.-natw. Kl., 1976/8.
- SCHRAMMEN, A. (1936): *Die Kieselspongien des Oberen Jura von Süddeutschland*. - Palaeontographica 84 (1936a), 149-194; 85 (1936b), 1-114.
- SIMPSON, T. L. (1968): *The structure and function of sponge cells: new criteria for the taxonomy of poecilosclerid sponges (Demospongiae)*. - Bull. Peabody Mus. nat. Hist. 25, 1-141.
- SOLLAS, W. J. (1877): *On Pharetrospongia strahani Sollas, a fossil holorhaphidote sponge from the Cambridge "coprolite" bed*. - Quart. J. geol. Soc. London 33, 242-255.
- TERMIER, H., & TERMIER, G. (1975): *Rôle des éponges hypercalcifiées en paléoécologie et en paléobiogéographie*. - Bull. Soc. géol. France (7), 17/5, 803-819.
- TOPSENT, E. E. A. (1900): *Étude monographique des spongaires de France. III. Monaxonida (Hadromerina)*. - Arch. Zool. expér. gén. (3), 8, 1-331.
- (1928): *Spongaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert I^e de Monaco*. - Résult. Camp. sci. Albert I Monaco 74.
- VEIZER, J., & WENDT, J. (1976): *Mineralogy and chemical composition of Recent and fossil skeletons of calcareous sponges*. - N. Jb. Geol. Paläont. [Mh.] 1976/9, 558-573.
- VOSMAER, G. C. J., & VERNHOUT, J. H. (1902): *The Porifera of the Siboga-Expedition. I. The genus Placospongia*. In: WEBER, M. (Ed.): *Uitkomsten op zoologisch, botanisch, oceanographisch en geologisch Gebied, verzameld in Nederlandsch Oost-Indie 1899-1900, aan boord H. M. Siboga* (Monogr. VIa). - Brill, Leiden.
- WALCOTT, C. D. (1920): *Middle Cambrian Spongiae*. In: *Cambrian geology and paleontology* (IV/6). - Smithson. misc. Collect. 67/6, 261-364.
- WENDT, J. (1974): *Der Skelettbau aragonitischer Kalkschwämme aus der alpinen Obertrias*. - N. Jb. Geol. Paläont. [Mh.] 1974/8, 498-511.
- (1976): *Der Skelettbau mesozoischer und rezenter Kalkschwämme*. - Zbl. Geol. Paläont., Teil II, 1976/5-6, 321-325.
- WIEDENMAYER, F. (1974): *Recent marine shallow-water sponges of the West Indies and the problem of speciation*. - Verh. natf. Ges. Basel 84/1, 361-375.
- (1977): *Shallow-water sponges of the western Bahamas*. - Birkhäuser, Basel (Experientia Supplementa 28).