CONVENIENT GENERA OR PHYLOGENETIC GENERA ? EVIDENCE FROM CALLYSPONGIIDAE AND NIPHATIDAE (HAPLOSCLERIDA)

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Desqueyroux-Faúndez, R. 1999 06 30: Convenient genera or phylogenetic genera ? Evidence from Callyspongiidae and Niphatidae (Haplosclerida). *Memoirs of the Queensland Museum* **44**: 131-146. Brisbane. ISSN 0079-8835.

A taxonomic revision of all nominal genera in the haplosclerid Callyspongiidae and Niphatidae (Porifera: Demospongiae), is based exclusively on type species and discusses the taxonomic value of traditional characters. Of 27 available nominal genera in both families only 19 available genera are recognised. For some of them I tentatively propose subgenera (of *Callyspongia*), or synonymise them with other genera (e.g. –*Cladochalina*). Type species of 6 'chalinid' genera in the early literature of Lendenfeld 1886-1888 are comprehensively revised and their taxonomic status confirmed, as previously suggested by Burton in 1934, or changed, and some are illustrated for the first time. Morphometric characters important in defining a species group (genus or subgenus) include specific modifications to a specialised ectosomal skeleton, structure and distribution of choanosomal fibres, presence and width of the spongin sheath in the fibres, presence of foreign material and free spicules in the skeleton, and presence and amount of free spongin in the skeleton. General characters, only useful as a reference for identification of a species group, but not essential to establish their taxonomical status are also indicated. ❐ *Porifera, Demospongiae, Haplosclerida, Callyspongiidae, Niphatidae, generic revision, taxonomy, morphology.*

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The taxonomy of Haplosclerida is still controvertial as far as recognition, interpretation and definition of genera, subgenera and species groups are concerned. One reason for this is the small number of unequivocal taxonomic characters available (including secondary metabolite structures). The recognition of 'reliable' characters, which are discrete and consistent for a genus group, is a first condition for the construction of a classification based on natural affinities.

Recent revisions of Haplosclerida provided some new insights to the taxonomy of this group. A study of West Indian Haplosclerida, notably re-examination of the Duchassaing & Michelotti collection, lead Van Soest (1980) to propose a new classification of families and genera, and to erect three new families: Niphatidae, Petrosiidae and Oceanapiidae (pro Phloeodictyidae). A phylogeny of Haplosclerida was proposed, based principally on features of the ectosomal skeleton, and nearly completely disregarding microscleres.

A rival classification based on five descriptive criteria (colour, growth form, consistency, spicules and skeleton) was published by Bergquist (1980) and Bergquist & Warne (1980), who distinguished two orders (Haplosclerida and Nepheliospongida), and five families (Haliclonidae, Callyspongiidae, Adociidae, Nepheliospongiidae and Oceanapiidae (pro Phloeodictyidae).

The monophyly of Haplosclerida was supported by de Weerdt (1985, 1986, 1989), in a study of three families of Eastern Atlantic Haplosclerida: Oceanapiidae (pro Phlocodictyidae), Chalinidae and Petrosiidae. De Weerdt (1985, 1986, 1989) based her phylogeny principally on synapomorphies of skeletal architecture. Van Soest (1990) claimed that Bergquist (1980) emphasised some of the apomorphic characters shared by Nepheliospongida and Haplosclerida, while at the same time recognising Nepheliospongida (pro Petrosida) as a distinct order. Van Soest (1990) proposed to keep Nepheliospongida (pro Petrosida) within the Haplosclerida, as suborder or superfamily. Presently, the taxonomic position of Petrosida is still unresolved.

Sponge secondary metabolites also appear to be useful in characterising different groups of sponges (e.g. reviews by Bergquist & Wells, 1983; Van Soest & Braekman, 1999, this volume), and based on an analysis of sterols in Haplosclerida and Petrosida there is no chemotaxonomic support for a division of Haplosclerida into two orders (Fromont et al., 1994). A phylogeny of

TABLE 1. Callyspongiidae genera and their taxonomic assignments.

Genus	Type species	Original assignment	Actual assignment	Proposed subgenus assignment	Synonymy
Callyspongia Duchassaing & Michelotti, 1864	*C. fallax*	*C. fallax* Duchassaing & Michelotti, 1864	*C. (Callyspongia) fallax*	*Toxochalina, Spinosella, Chalinopora, Patuloscula, Euplacella*	*Cavochalina* Carter, 1885, *Placochalina* Lendenfeld, 1887, ?*Platychalina* Esper, 1797, *Ceraochalina* Lendenfeld, 1887, *Chalinella* Lendenfeld, 1887
Toxochalina Ridley, 1884	*T. folioides*	*Desmacidon folioides* Bowerbank, 1875	*C. (Toxochalina) folioides*		
Spinosella Vosmaer, 1885	*S. sororia*	*Tuba sororia* Duchassaing & Michelotti, 1864	*C. (Spinosella) sororia*		*Cladochalina* Schmidt, 1870
Chalinopora Lendenfeld, 1887	*C. typica*	*C. typica* Lendenfeld, 1887	*C. (Chalinopora) typica*		*Euchalina* Lendenfeld, 1887
Siphonochalina Schmidt, 1868	*S. coriacea*	*S. Coriacea* Schmidt, 1868	*Siphonochalina coriacea*		*Sclerochalina* Schmidt, 1868, *Siphonella* Lendenfeld, 1887, *Tuhulodigitus* Carter, 1881
Patuloscula Carter, 1882	*P. procumbens*	*P. procumbens* Carter, 1882	*C. (Patuloscula) procumbens*		
Euplacella Lendenfeld, 1887	*E. australis*	*E. australis* Lendenfeld, 1887	*C. (Euplacella) australis*		
Arenosclera Pulitzer-Finali, 1982	*A. heroni*	*A. heroni* Pulitzer-Finali, 1982	*A. heroni*		
Dactylia Carter, 1885	*D. chaliniformis*	*D. chaliniformis* Carter, 1885	*D. chaliniformis*		*Chalinopsis* Lendenfeld, 1886 *Chalinopsilla* Lendenfeld, 1888

Haplosclerida based on molecules of the 3-alkylpiperidine alkaloid types appears incongruent with the phylogenetic tree of haplosclerid families, probably because of the uncertainty in identification of species analyzed and also ignorance of metabolite occurrence throughout a range of taxa (Andersen et al., 1996). Straight-chain acetylene compounds of Haplosclerida are efficient markers for the whole order, and in some cases can be characteristic of certain genera and families (Van Soest et al., 1997), but these compounds are found among species of other orders, and their presence or absence is not an absolute indicator of phylogenetic relationships.

Moreover, difficulties encountered in the application of biochemical methods can also be attributed to the diversity of other organisms living within sponges (e.g. symbiotic cyanobacteria), making it arduous to identify the origin of chemical compounds in some instances (Bergquist & Wells, 1983). Consequently, chemotaxonomic data must be treated with caution, and these data are not considered in this present paper.

In this paper, therefore, I am constrained to using to relatively few 'reliable' morphometric characters traditionally described for Haplosclerida, but this raises three problems. 1) Superficially at least, some of these 'reliable' morphological characters appear to be lacking in some taxa included in the five recognised families of Haplosclerida: Chalinidae, Niphatidae, Callyspongiidae, Phloeodictyidae and Petrosidae. 2) Conversely there are a number of nominal taxa, doubtfully available or presently considered as synonyms, which are clearly distinct from each other in their respective 'reliable' characters. 3) Frequently characters have been difficult to differentiate because their variability occurred within very narrow bounds, especially related to the structure of fibres.

In order to clarify the status of these taxa I undertook a thorough analysis of the structural characters, especially at the skeletal level, in two families of Haplosclerida: Callyspongiidae and Niphatidae. I focused on the use of shared morphological characters as determinant tools to establish the taxonomic position of genera,

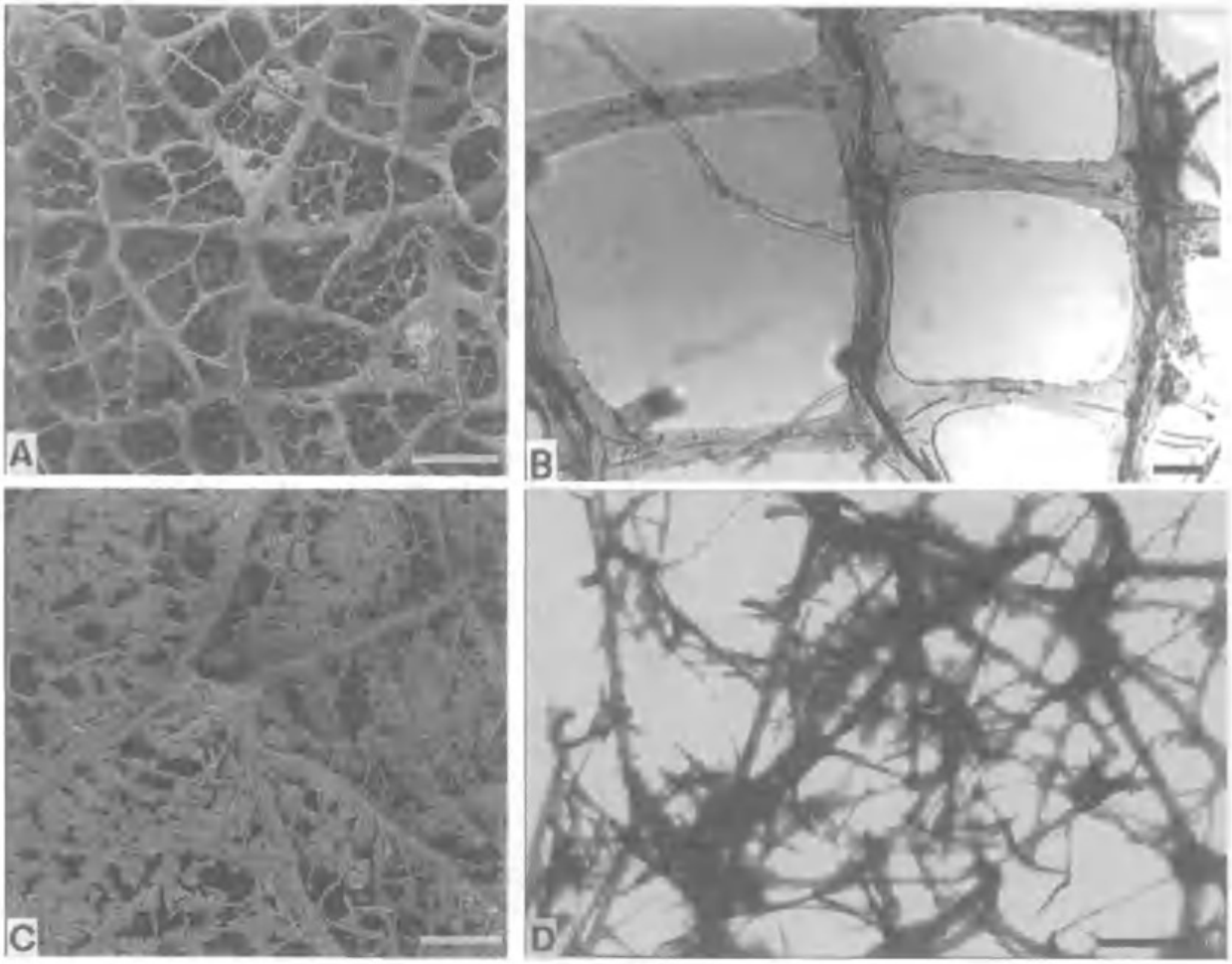

FIG. 1. *Callyspongia* and *Toxochalina*. A, B, *Callyspongia* Duchassaing & Michelotti, 1864. Type species *Callyspongia fallax* Duchassaing & Michelotti, 1864. St. Thomas. Schizolectotype BMNH1928:11:12:5. A, Ectosomal network. Large, triangular to polygonal meshes, subdivided in smaller secondary and tertiary meshes. B, Choanosomal regular meshes, longitudinal principal and transversal connecting fibres. (Scales bars A = 200µm; B = 8.2µm). C, D, *Toxochalina* Ridley, 1884. Type species *Desmacidon folioides* Bowerbank, 1875, Straits of Malacca, 'Bowerbank Collection'. Lectotype BMNH1887:5:21:2034. C, Ectosomal network, three types of meshes. D, Choanosomal network. (Scale bars C = 100µm; D = 20µm).

subgenera and/or groups of species in Haplosclerida.

I present here morphological evidence obtained exclusively from the study of type species of each nominal genus.

MATERIALS AND METHODS

Type material from the following Institutions was studied: BMNH, The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; IRSNB, Institut Royal de Sciences naturelles de Belgique, Brussels; ZMA, Zoological Museum, Amsterdam; MSNG, Museo de Storia Naturalle, Genova; AM, Australian Museum, Sydney; QM, Queensland Museum, Brisbane; MHNG, Muséum d'histoire naturelle, Geneva .

Described characters, and taxonomic relationships based on them, reflect my own critical observations. Consequently, character analyses were completed with the inclusion of remarks from the original author's descriptions. Specimens were studied by light and SEM microscopy. Lists of structural characters and character states of genera were established by comparing differences between genera. The following characters were used to compare genera: 1) variations in external morphology; 2) surface features; 3) type of ectosomal and choanosomal skeletons; 4) fibre structure and width variations of the spongin sheath; 5) presence of free spicules

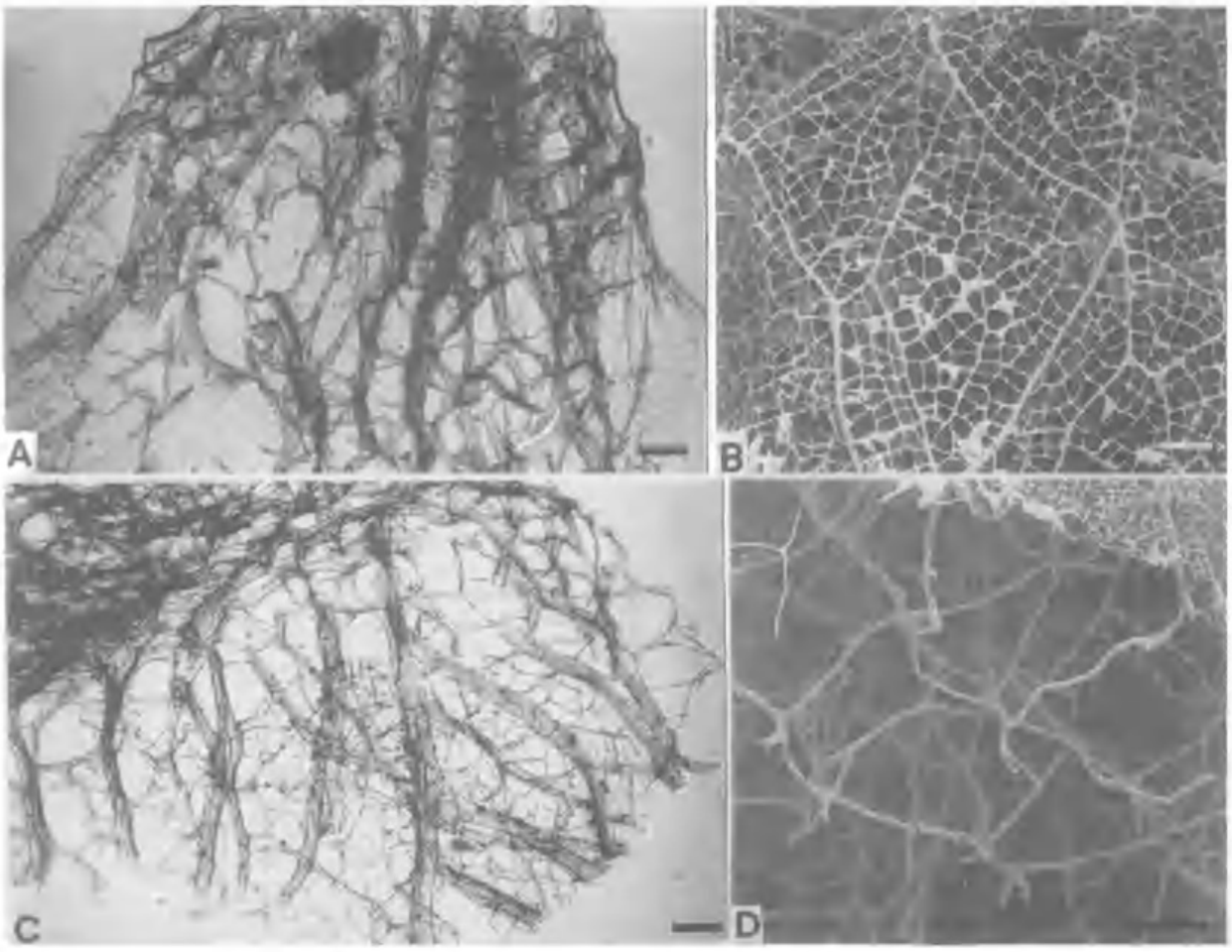

FIG. 2. *Spinosella (=Cladochalina)* and *Chalinopora (=Euchalina)*. A, C, *Spinosella* Vosmaer, 1885. Type species *Tuba sororia* Duchassaing & Michelotti, 1864. St. Thomas. Paralectotype, MUS. TORINO POR118. A, Longitudinal section through conular fascicle, surface at both sides of the figure. C, Three different sizes of triangular to polygonal ectosomal meshes and fasciculated subectosmal longitudinal fibres. (Scale bars A, C = 8.2µm). B, D, *Chalinopora* (=*Euchalina*) Lendenfeld, 1887. Type species *Chalinopora typica* Lendenfeld, 1887. Port Jackson, NSW. Syntype BMNH1886:8:27:411 (AMG3408, slide). B, Simple ectosomal network, one size of fine triangular to rectangular meshes. Conules not visible. D, Choanosomal network, fasciculated underlying longitudinal primary fibres. Fragment of surface on top. (Scale bars B = 200µm; D = 500µm).

in fibre meshes; and 6) amount of free spongin and type of spicules. Each character was checked for its presence or absence; and when present, each character was scored objectively as to the expresion of the character, with at least three different states recognised per character. In the present work only the three most significant ('reliable') characters are presented. Other allegedly 'inconsistent' or 'unreliable' characters, deemed by previous authors to have little or no taxonomic value at the supraspecific level (e.g. external morphology), are omitted from this work. A more complete, phylogenetic analysis of these taxa will is in progress (Desqueyroux-Faúndez, in prep.).

Whenever a character used in an original description was not sufficiently informative for the present work, a detailed description from a larger haplosclerid study was used (Desqueyroux-Faúndez, in prep.). In some cases, re-examination of type specimens did not closely follow the published description, or there was mistaken identification of type material by the original author, with the consequence that the actual concept of some genera had to be changed (e.g. *Hemigellius*).

Taxonomy and classification of families and genera are based on the most recently accepted classification of Porifera: Haplosclerida of Wiedenmayer, in Hooper & Wiedenmayer (1994).

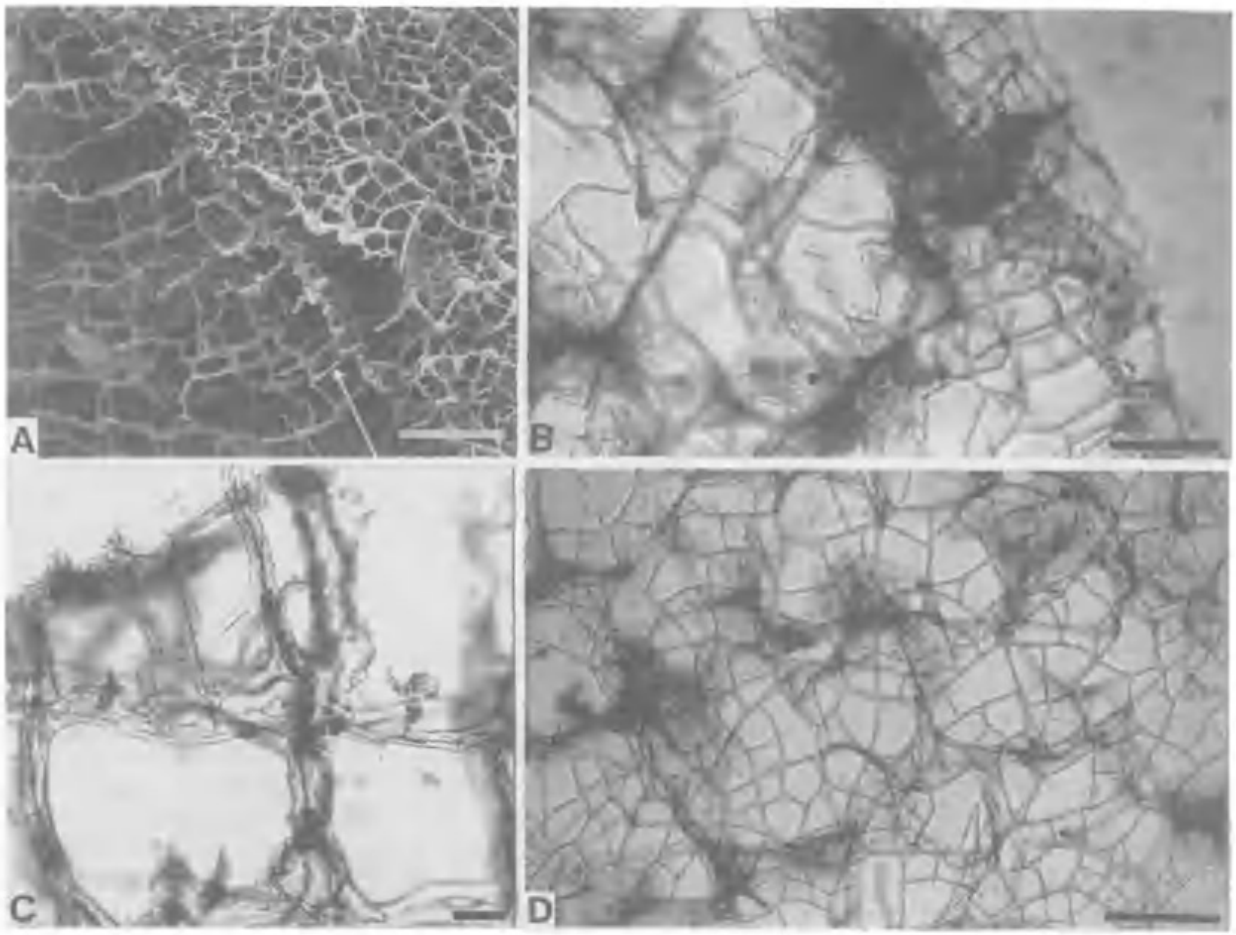

FIG. 3. *Ceraochalina (=Chalinella)* and *Tubulodigitus*. A, C, *Ceraochalina* Lendenfeld, 1887. Type species *Ceraochalina typica* Lendenfeld, 1887. Port Phillip, Victoria. Holotype BMNH1886:8:27:439. A, Transverse section of ectosomal network with one size of triangular meshes, subectosomal longitudinal fibres, intercalate short longitudinal fibres, small meshes and transverse fibres (arrow). C, Longitudinal section of surface, intercalate fibres and transversal fibres with echinating oxea. (Scale bars A = 500μm; C = 8.2μm). B, D, *Tubulodigitus* Carter, 1881. Type species *Tubuludigitus communis* Carter, 1881. Bass Strait. Neotype BMNH-1889:1:21:1. B, Longitudinal section through ecto and choanosomal skeleton. D, Transverse section of ectosomal skeleton, with one size of meshes. (Scale bars B, D = 20μm).

Modification of this classification in this work, and actual taxonomic assignments are indicated in each case (Table 1). Terminology for descriptive morphological characters is taken from Boury-Esnault & Rützler (1997). New morphometric terms were introduced and defined, when necessary.

SYSTEMATICS

A list of the major 'reliable' characters and their character states is presented as follows.

CHARACTER 1. *Ectosomal skeleton.* 1(1), Tangential, regular network, three sizes of large triangular to polygonal meshes subdivided in smaller secondary and tertiary meshes (triple ectosomal network). Inconspicuous conules formed by free end of only one longitudinal primary fibre (*Callyspongia*, Fig. 1A; *Toxochalina*, Fig. 1C). 1(2), Tangential regular network around a conspicuous central conule, with three sizes of large triangular to polygonal meshes subdivided in smaller secondary and tertiary meshes (triple ectosomal network). Central conspicuous conule produced by ends of the fascicle branches of longitudinal primary fibres (*Spinosella (= Cladochalina)*, Figs 2A, C). 1(3), One size of fine triangular to rectangular meshes (simple ectosomal network) over confusely fasciculated underlying longitudinal primary fibres. Conules not visible (*Chalinopora* (=*Euchalina*), Fig. 2B, D). 1(4), One size triangular

TABLE 2. Niphatidae genera and their taxonomic assignments.

Genus	Type species	Original assignment	Actual assignment	Proposed subgenus arrangement	Synonymy
Gelliodes Ridley, 1884	*G. fibulata*	*Axos fibulatus* Carter, 1881	*Gelliodes fibulata*		
Microxina Topsent, 1916	*M. charcoti*	*M. charcoti* Topsent, 1916	*Microxina charcoti*		
Niphates Duchassaing & Michelotti, 1864	*N. erecta*	*N. erecta* Duchassaing & Michelotti, 1864	*Niphates erecta*		
Dasychalina Ridley & Dendy, 1887	*D. fragilis*	*D. fragilis* Ridley & Dendy, 1886	*Pachychalina (Dasychalina) fragilis*	*Dasychalina*	
Pachychalina Schmidt, 1868	*P. rustica*	*P. rustica* Schmidt, 1868	*Pachychalina rustica*		
Amphimedon Duchassaing & Michelotti, 1864	*A. compressa*	*A. compressa* Duchassaing & Michelotti, 1864	*Amphimedon compressa*		*Hemihaliclona* Burton, 1937
Hemigellius Burton, 1932	*G. rudis*	*Gellius rudis* Topsent, 1901	*Hemigellius rudis*		
Cribrochalina Schmidt, 1870	*C. infundibulum*	*C. infundibulum* Schmidt, 1870	*Cribrochalina infundibulum*		
Haliclonissa Burton, 1932	*H. verrucosa*	*H. verrucosa* Burton, 1932	*Haliclonissa verrucosa*		

meshes (simple ectosomal network); isolated underlying longitudinal fibres connected by 2-3 transverse fibres with echinating brushes of oxeas. Intercalate longitudinal fibres present to form small subectosomal meshes (*Ceraochalina*, Fig. 3A, C (= *Chalinella*); *Siphonochalina*, Fig. 4A (= *Sclerochalina*, Fig. 4B, D; *Siphonella; Tubulodigitus*, Fig. 3B, D). 1(5), One size rounded meshes (simple ectosomal network); isolated underlying subectosomal ends of longitudinal primary fibres profusely divided to form uniform tangential network of poorly delimited unispicular fibres (*Patuloscula*, Fig. 5A, B). 1(6), One size rounded meshes (simple ectosomal network); ends of longitudinal primary fibres connected by three tangential successive layers of parallel fibres, echinated by numerous surface spicular brushes of oxeas. In longitudinal section subectosomal meshes appear smaller than choanosomal (peripheral condensation) (*Euplacella*, Fig. 5D). 1(7), Tangential irregular network of fragmentary unispicular fine fibres, one size rounded meshes (simple ectosomal network); string of foreign material (*Arenosclera*, Figs 6A). 1(8), Tangential irregular meshes; fine aspicular fibres finely cored by foreign material. No distinction between primary and secondary fibres (*Dactylia*, Figs 6C, D; *Chalinopsilla*, Fig. 7A). 1(9), Tangential irregular fibre network of secondary multispicular fibres, interrupted by ends of longitudinal primary fibres (ramified spines or conules); free oxeas and sigmas abundant (*Gelliodes*, Fig. 7B). 1(10), Strong free unordered oxea network, interrupted by ends of longitudinal primary fibres (brushes of spicules or strong spines); microscleres (sigma or microxea) abundant or scarce (*Microxina*, Fig. 8A; *Niphates*, Fig. 8C). 1(11), Tangential irregular network of abundant free oxeas and fibres interrupted by strong ends of longitudinal primary

TABLE 3. Presence of ectosomal and choanosomal characters and their distribution amongst genera of Callyspongiidae.

Genus	Ectosomal meshes	Subectosomal fibres	Longitudinal intercalate ectosomal fibres	Parallel connecting ectosomal fibres
Callyspongia	three sizes	isolated	absent	absent
Toxochallina	three sizes	isolated	absent	absent
Spinosella	three sizes	fasciculated	absent	absent
Ceraochalina (=*Chalinella*)	one size	isolated	present	absent
Chalinopora (=*Euchalina*)	one size	fasciculated	absent	absent
Siphonochalina (=*Sclerochalina, Siphonella, Tubulodigitus*)	one size	isolated	absent	absent
Patuloscula	one size	isolated	absent	present
Euplacella	one size	isolated	absent	present (3 layers)
Arenosclera	one size	absent	absent	absent
Dactylia (=*Chalinopsilla*)	one size	absent	absent	absent

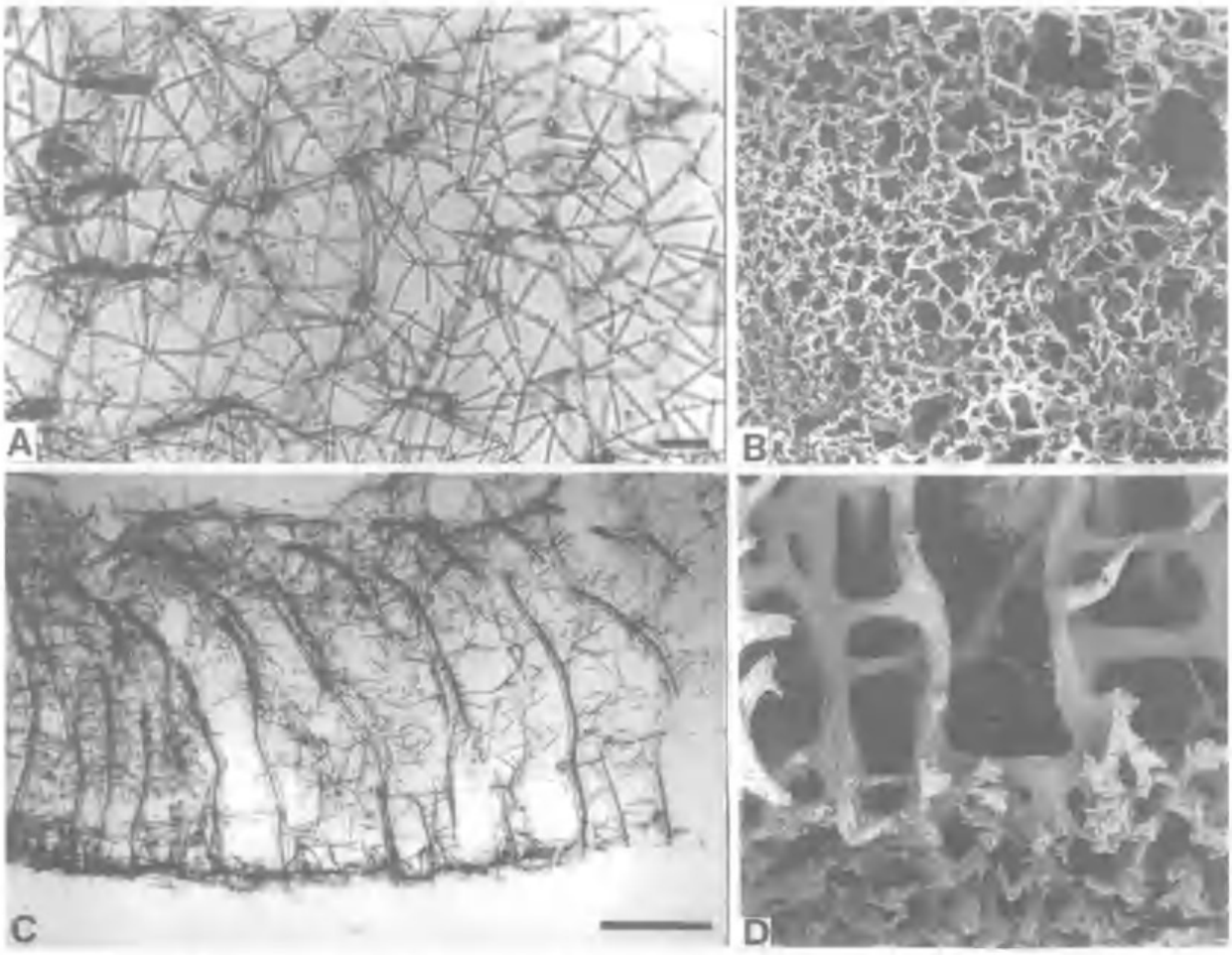

FIG.4. *Siphonochalina and (=Slerochalina).* A, C, *Siphonochalina* Schmidt, 1868. Type species *Siphonochalina coriacea* Schmidt, 1868. La Calle, 'Lacaze-Duthier' collection. Syntype MNHN LBIM DT77. A, Dense tangential network of fine unispicular fibres with uniform meshes of only one type. C, Longitudinal section through choanosomal and ectosomal networks. Parallel, strong primary fibres with large spongin sheath. Ectosomal skeleton at the base of the figure (Scale bars A = 8.2µm; C = 20.0µm). B, D, *Sclerochalina* Schmidt, 1868. Type species *Sclerochalina asterigena* Schmidt, 1868. La Calle, 'Lacaze-Duthier' collection. Holotype MNHN LBIM DT 89-11. B, Simple ectosomal network with one size of triangular to rectangular small meshes. D, Longitudinal section through subectosomal and surface regions. Isolated parallel, strong longitudinal fibres, abundant spongin, surface below. (Scale bars B = 500µm; D = 100µm).

fibres (aculeations, prickles or stings) (*Dasychalina*, Fig. 9A). 1(12), Tangential regular fibre network with uniform rounded meshes. Ends of longitudinal primary fibres barely protruding (*Amphimedon*, Fig. 9C). 1(13), Perpendicular ill-defined extremely irregular network of spicule brushes in between the ends of primary fibres, riddled by aquiferous orifices (*Pachychalina*). 1(14), Tangential dense irregular network of free oxeas and sigmas forming continuous layer over ends of primary fibres (*Hemigellius*, Fig. 10B). 1(15), Perpendicular ends of longitudinal primary fibres expanded as strong continuous palisade of free oxeas (strongly hispid crust) (*Cribrochalina*, Fig. 10D). 1(16), Perpendicular ends of longitudinal primary fibres expanded to form wart-like elevations (verrucose surface), abundant free oxeas in between (*Haliclonissa*).

CHARACTER 2. *Choanosomal skeleton.* 2(1), Regular network of longitudinal parallel strong primary fibres, regularly connected by short secondary fibres to form empty rectangular very regular meshes. Large spongin sheath present (*Callyspongia* Fig. 1B; *Ceraochalina* (= *Chalinella)*, Fig. 3C; *Siphonochalina*, Fig. 4C). 2(2), Strong irregular network with large triangular to irregular meshes, poorly oriented; compact multispicular primary fibres irregularly

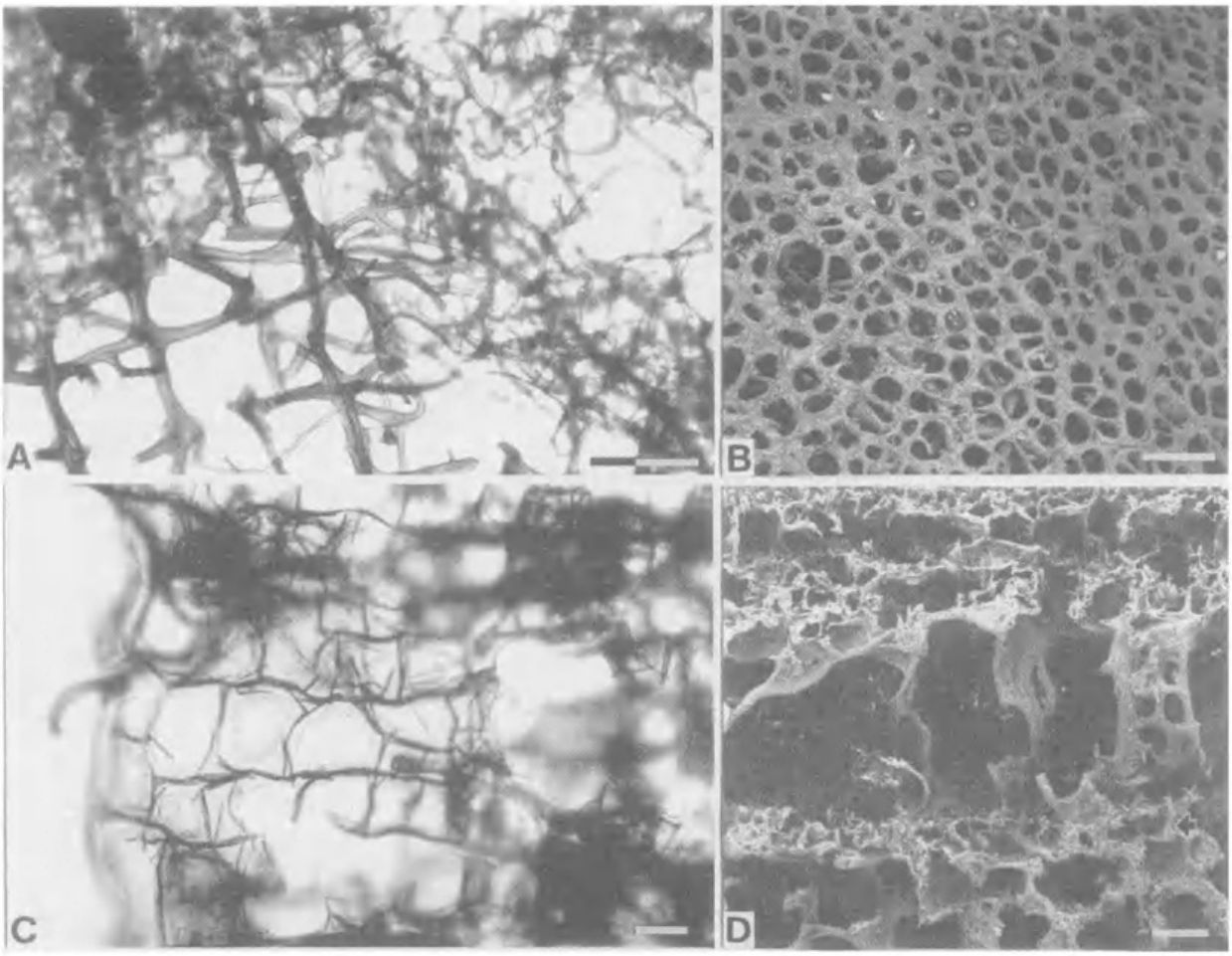

FIG. 5. *Patuloscula* and *Euplacella*. A, B, *Patuloscula* Carter, 1882. Type species *Patuloscula procumbens* Carter, 1882, Grenada, West Indies. Syntypes BMNH:1845:5:12:13, 15, 16. A, Longitudinal section, choanosomal region, isolated parallel subectosomal ends of primary longitudinal fibres at the base of the figure. B, Transverse section, continuous ectosomal layer, one size rounded meshes of poorly delimited unispicular fibres (simple network). (Scale bars A = 20μm; B = 500μm). C, D, *Euplacella* Lendenfeld, 1887. Type species *Euplacella australis* Lendenfeld, 1887. Torres Straits, Qld. Lectotype BMNH1886:8:27:591. C, Choanosomal network, paucispicular primary fibres with large spongin sheath, surface at left. D, Longitudinal section through triple ectosomal layer or 'peripheral condensation', with surface brushes of oxea, three layers indicated by arrows. (Scale bars C = 8.2μm; D = 200μm).

split up to form connective fibres. Spongin sheath absent from all types of fibres, present only at fibre nodes. (*Toxochalina*, Fig. 1D). 2(3), Irregular confused network of multispicular fasciculated longitudinal primary fibres, irregularly split up to form short connective fibres. Empty meshes of only one type but of different sizes. All fibres with narrow spongin sheath (one 25 % of fibre diameter) (*Chalinopora* (= *Euchalina*), Fig. 2D). 2(4), Strong network of stout longitudinal paucispicular, primary fibres and irregular short connecting fibres, irregular empty meshes. Fibres with large spongin sheath (*Euplacella*, Fig. 5C; Patuloscula, 5A). 2(5), Strong dense network of longitudinal primary fibres gathered to form fibrofascicles and split up to form free secondary fibres. Irregularly elongate to roundish meshes, always subdivided by tertiary finer fibres (*Spinosella (= Cladochalina*), Fig. 2C). 2(6), Aspicular network of longitudinal divergent primary fibres and perpendicular connecting fibres, abundantly cored by foreign material. Irregular to rectangular empty meshes (*Dactylia* (= *Chalinopsilla*), Fig. 7C). 2(7), Intricate network of undifferentiated meshes and fibres with no preferential direction, not clearly distinguishable,abundantly cored by foreign material (*Arenosclera*, Fig. 6B). 2(8), Regular network of longitudinal primary fibres and short connecting fibres, isotropic to elongate

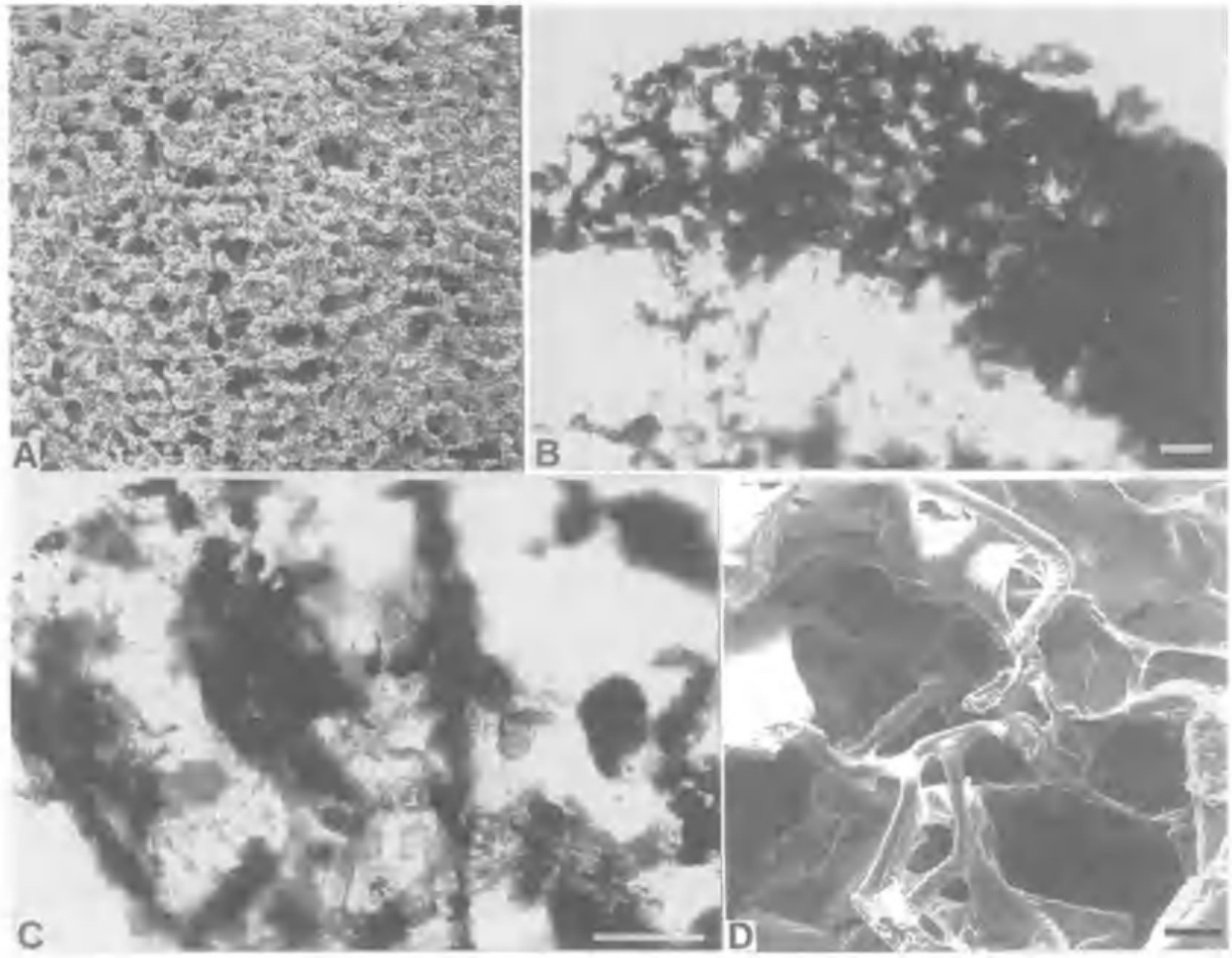

FIG. 6. *Arenosclera* and *Dactylia*. A, B, *Arenosclera* Pultizer-Finali, 1983. Type species *Arenosclera heroni* Pultizer-Finali, 1982. Heron Island, GBR, Qld. Holotype MSNG 46949. A, Tangential, irregular network of string of foreign material, one size rounded meshes (simple ectosomal network). B, Longitudinal section through ectosomal and choanosomal networks. (Scale bars A = 200μm; B = 8.2μm). C, D, *Dactylia* Carter, 1885. Type species *Dactylia chaliniformis* Carter, 1885. Port Phillip Heads, Victoria. Holotype BMNH 1886:12:15:196. C, Ectosomal network, abundant foreign material. D, Fine aspicular ectosomal fibres, finely cored by foreign material. (Scale bars: C = 20μm; D = 50μm).

meshes. Abundant free spicules (*Cribrochalina*, Fig. 10C). 2(9), Diffuse longitudinal primary fibres, tight and ill-defined meshes, abundant free spicules. Spongin abundant: free and coring the fibres (*Amphimedon*, Fig. 9D. 2(10), Poorly defined meshes with numerous free spicules in between the fibres; longitudinal primary fibres divergent, intermingled. Spongin inconspicuous (*Haliclonissa*). 2(11), Strong compact, multispicular primary fibres split up to form non connecting secondary fibres lacking orientation, irregular meshes, scattered spicules (*Dasychalina*, Fig. 9B). 2(12), Open and loose, formed by compact longitudinal primary fibres and abundant free secondary fibres, oxeas and sigmas, irregular meshes, free spicules (*Gelliodes* Fig. 7D). 2(13), Confused compact formed by abundant unordered strong spicules, no clear fibres or meshes. No visible spongin. Abundant sigmas (*Hemigellius*). 2(14), Confused, irregular lacuna with thick longitudinal primary fibres repeatedly divided to form isolated finer free ramifications, abundant free spicules, no clear meshes (*Pachychalina*, Fig. 10A). 2(15), Abundantly ramified with long thick non oriented fibres, large meshes and free spicules, no visible spongin, abundant microxea (*Microxina*, Fig. 8B). 2(16), Radiating longitudinal fasciculate primary fibres, connecting secondary fibres regularly distributed to form rounded to irregular meshes. Free spicules abundant (*Niphates*, Fig. 8D)

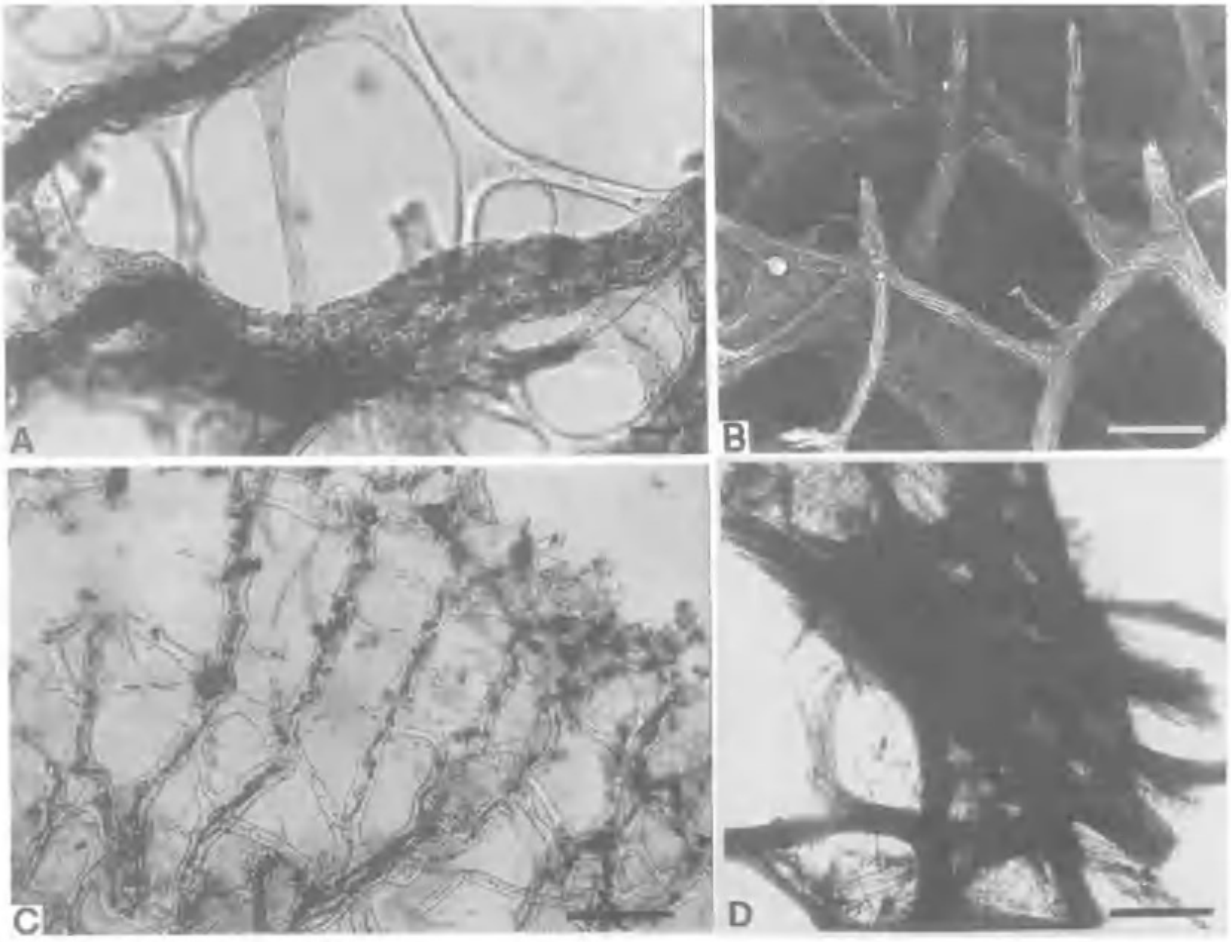

FIG. 7. *Chalinopsilla* and *Gelliodes*. A, C, *Chalinopsilla* Lendenfeld, 1888. Type species *Chalinopsilla dichotoma* Lendenfeld, 1886. West Coast of Australia. Lectotype BMNH1886:8:27:62. Schizolectotype: AM-G 8960 (MNHNLBIM DCL2061). A, Fine aspicular ectosomal fibres, abundantly cored by foreign material. C, Aspicular network abundantly cored by foreign material, divergent primary longitudinal fibres, and perpendicular connecting fibres. (Scale bars A = 8.2μm; C = 20μm). B, D, *Gelliodes* Ridley, 1884. Type species *Axos fibulatus* Carter, 1881. Bass Strait, Victoria. Syntype BMNH: 1882:2:23:202. B, Tangential view of surface, protruding ectosomal spines, from ends of longitudinal primary fibres (conules). D, Choanosomal skeleton of compact primary fibres and free secondary fibres. Free spicules abundant (Scale bars B = 500μm; D = 20μm).

CHARACTER 3. *Primary fibre structure*. 3(1), Strong longitudinal, pauci to multispicular primary fibres (5-15 or more spicules), parallel to divergent, regular in width, isolated, not ramified or moderately ramified, not fasciculate. Spicules sparsely distributed at center of fibre. Large spongin sheath, at least 66 % of fibre diameter (*Callyspongia*; *Patuloscula*; *Ceraochalina* (=*Chalinella*). 3(2), Strong large irregular spongin sheath cored by 3-5 spicules, some of them fused as observed by the presence of 2 or 3 central spicule rows; short, slender secondary fibres regularly split up from primaries (*Euplacella*). 3(3), Multispicular primary fibres densely cored; spongin sheath absent, only with nodal spongin; secondary fibres of the same type. Unispicular tertiary fibres with very scanty spongin (*Toxochalina*). 3(4), Ascending parallel radially distributed primary fibres extending from internal to external sponge wall. Fibres paucispicular (3-5 spicules), not ramified. Subectosomal longitudinal intercalate fibres present (*Siphonochalina* (=*Sclerochalina*; *Siphonella*; *Tubulodigitus*). 3(5), Aspicular to paucispicular primary fibres radiating from the sponge base to form fibrofascicles, surface conules and finer secondary and tertiary fibres. Large spongin sheath (*Spinosella* (=*Cladochalina*)). 3(6), Multispicular primary fibres with very narrow spongin sheath, less than 33 % of fibre diameter, or absent;

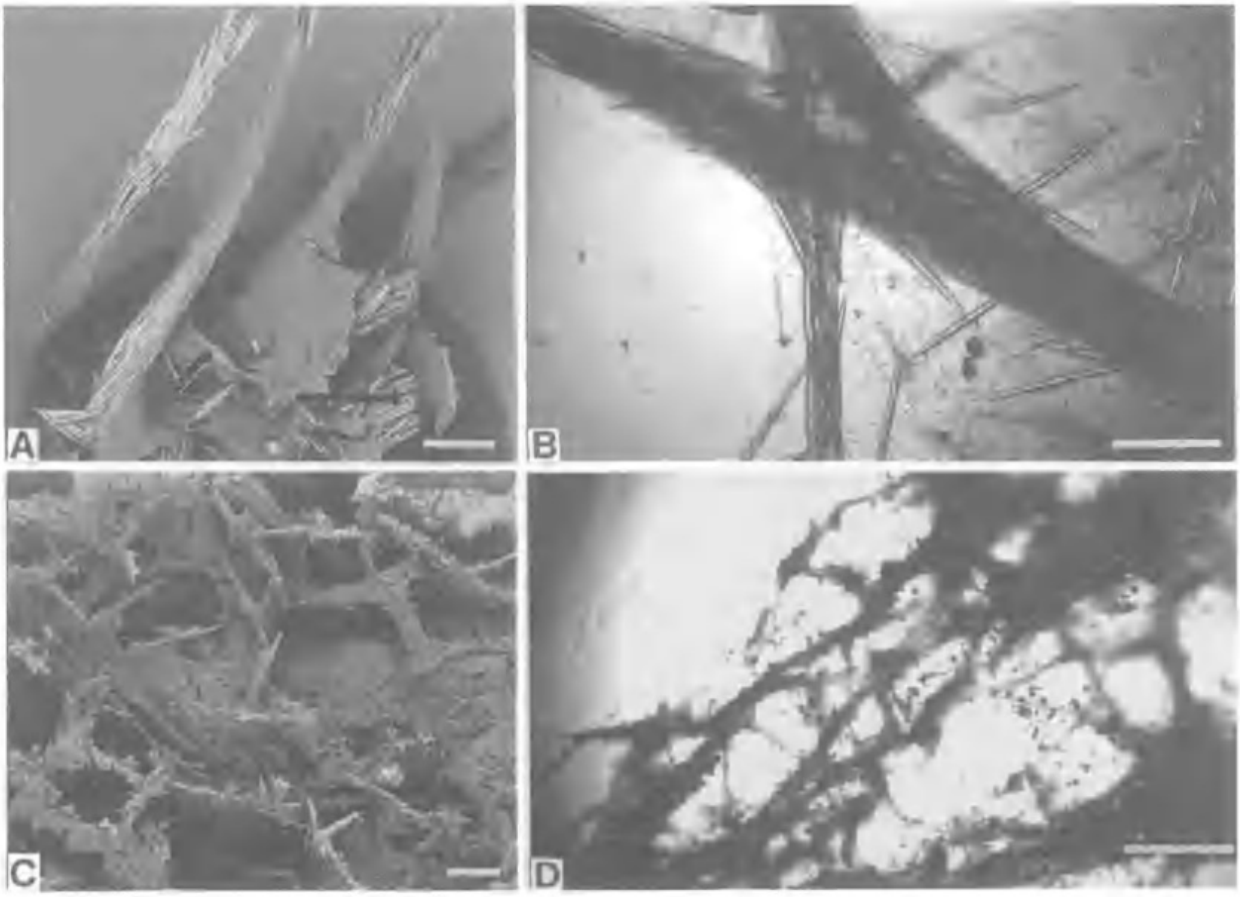

FIG. 8. *Microxina* and *Niphates*. A, B, *Microxina* Topsent, 1916. Type species *Microxina charcoti* Topsent, 1916. Antarctica. Holotype MNHN LBIM DT692, schizoholotype BMNH1926:10:26:339a. A, Ectosomal network of strong end brushes of primary fibres (strong spines), microxeas (arrows) in between. B, Strong ramified choanosomal tracts, abundant microxea. (Scale bars A = 500µm; B = 20µm). C, D, *Niphates* Duchassaing & Michelotti, 1864. Type species *Niphates erecta* Duchassaing & Michelotti, 1864. St.Thomas. Paralectotype MUS.TORINO POR51; ZMA POR1633. C, Ectosomal network, tangential section. Strong free unordered oxea network, interrumpted by ends of primary fibres, brushes of spicules. D, Choanosomal network, fasciculated primary fibres, secondary fibres and rounded meshes. (Scale bars: C = 200µm; D = 20µm).

secondary fibres of the same type (*Chalinopora* (=*Euchalina*)). 3(7), Primary and secondary fibres not clearly differentiated. All fibres lacking preferential direction. Spicules and foreign material variably present. Thicker fibres cored only by foreign debris, or both foreign debris and proper spicules. Thinner tracts with sparse spicules or uncored. Proper spicules absent if foreign material abundant (*Arenosclera*). 3(8), Aspicular, primary fibres isolated longitudinal, not ramified, slightly branched to form short, fine, aspicular, amber-like, connecting fibres. All fibres with abundant foreign material (*Chalinopsilla*). 3(9), Multispicular, inconspicuous, plumose, anastomosing, radially ascending primary fibres producing diffuse irregular secondary fibres *(Amphimedon)*. 3(10), Strong, regular, well-defined multispicular and radially ascending primary fibres not ramified. Spongin sheath narrow or missing. Short interconnecting fibres of the same structure (*Cribrochalina*). 3(11), Very stout compact, multispicular, primary fibres split up to form paucispicular secondary fibres. No visible spongin sheath (*Dasychalina*). 3(12), Very stout, compact, ascending, radiating, branching and anastomosing, splitting up to produce irregularly oriented, secondary fibres. No distinct spongin sheath except at bifurcation points (*Gelliodes*). 3(13), Pauci to multispicular longitudinal primary fibres, divergent, diffuse, isolated and rarely ramified. Connecting fibres not defined, only abundant free spicules (*Haliclonissa*). 3(14), Confused, compact primary tracts, with no clear fibres, only strong abundant

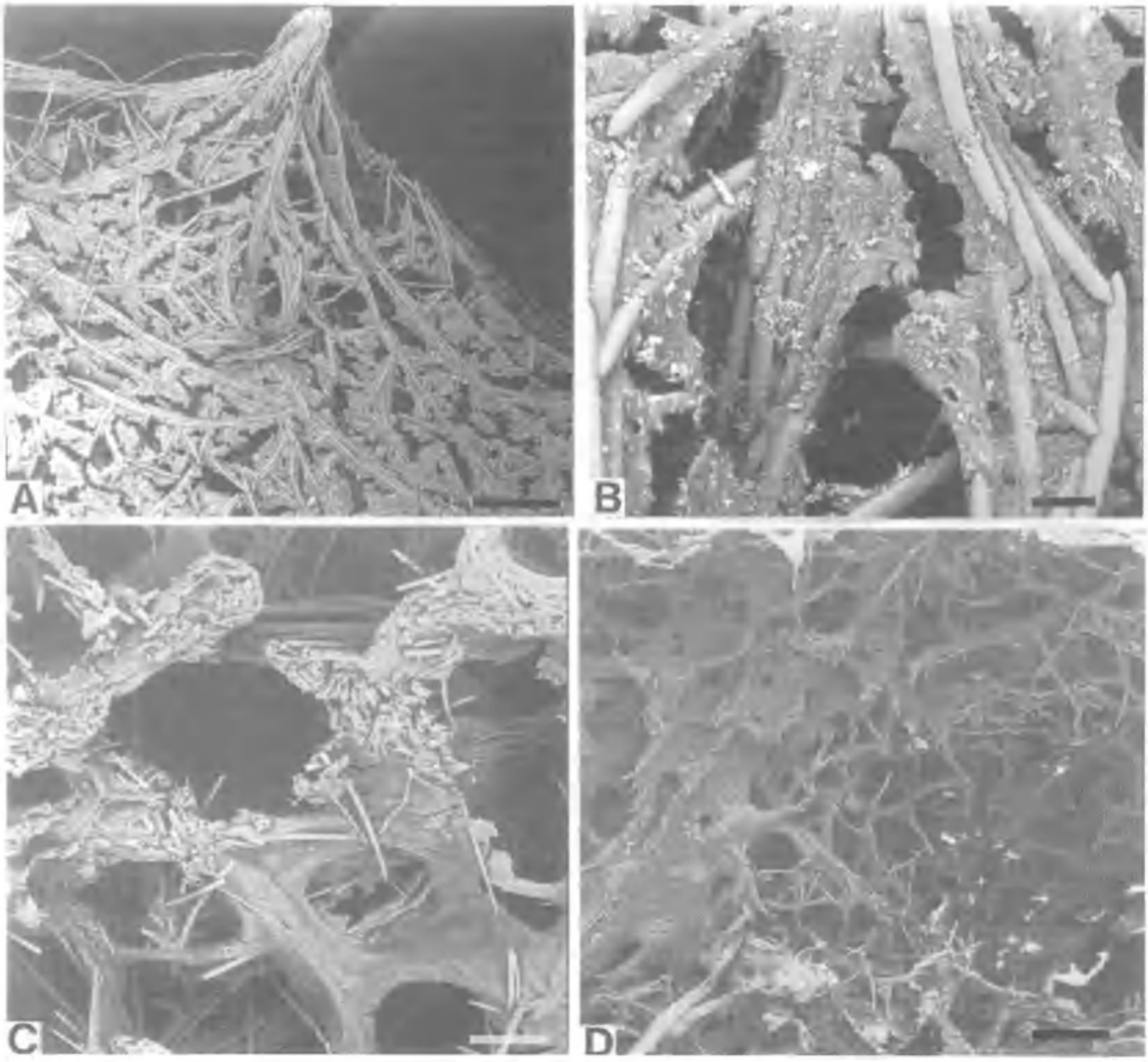

FIG. 9. *Dasychalina* and *Amphimedon. A, B, Dasychalina* Ridley & Dendy, 1886. Type species *Dasychalina fragilis* Ridley & Dendy, 1886. 'Challenger' Collection, Philippine Islands. Schizotype BMNH1887:2:170. A, Surface aculeations, spines or prickles, from ends of primary fibres, abundant free oxeas in between. B, Strong spicules, choanosomal fibres without distinct sheath of spongin (Scale bars A = 500μm; B = 50μm). C, D, *Amphimedon* Duchassaing & Michelotti, 1864. Type species *Amphimedon compressa* Duchassaing & Michelotti, 1864. St. Thomas. Lectotype MUS.TORINO POR.35; Schizoparalectotype BMNH1928:11:12:42. C, Tangential, regular ectosomal network with uniform rounded meshes, barely protruding ends of primary fibres. D, Choanosomal skeleton, plumose, anastomosing primary fibres, irregular secondary fibres, abundant spongin (Scale bars C = 50μm; D = 200μm).

spicules, unordered and cemented by no visible scarce spongin (*Hemigellius*). 3(15), Very stout, multispicular primary longitudinal, irregularly ascending, compact, large, occasionally fasciculated, without spongin sheath (*Microxina*). 3(16), Pauci to multispicular primary longitudinal fibres, diffuse, abundantly branched to form fibrofascicles, and pauci-to multispicular secondary connecting fibres. Spongin dominant between loose spicules, inside the fibres or free in meshes (*Niphates*). 3(17), Thick, irregular and compact multispicular primary fibres, with no preferential orientation; spongin sheath absent. Free spicules abundant. Thinner ill defined multispicular secondary fibres (*Pachychalina*).

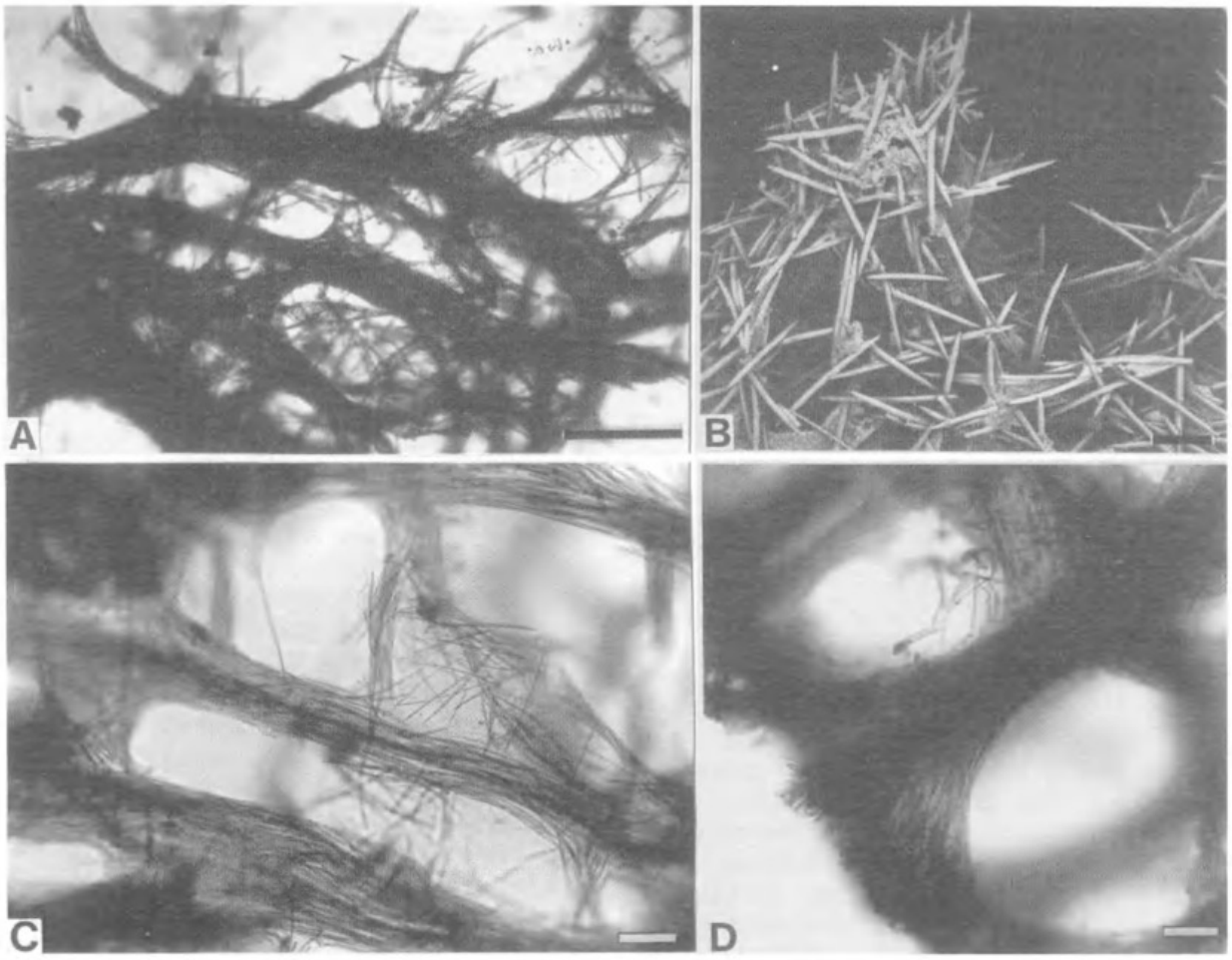

FIG. 10. *Pachychalina, Hemigellius, Cribrochalina*. A, *Pachychalina* Schmidt, 1868. Type species *Pachychalina rustica* Schmidt, 1868. La Calle, 'Lacaze-Duthier' collection. Syntype MNHN LIBM DT47. Confused, irregular, lacunar choanosomal network, thick longitudinal primary fibres, repeatedly divided to form isolated finer free ramifications, abundant free spicules. (Scale bar = 20μm). B, *Hemigellius* Topsent, 1901. Type species *Hemigellius rudis* Topsent, 1901. Antarctica, 'Belgica' Expedition. Holotype RBINSC POR033. Ectosomal skeleton, tangential dense, unordered network of free oxeas and sigmas, no clear fibres or meshes, no visible spongin. (Scale bar = 200 μm). C, D, *Cribrochalina* Schmidt, 1870. Type species *Cribrochalina infundibulum* Schmidt, 1870. West Indies. Lectotype BMNH1870:5:3:165. C, Longitudinal section through choanosomal elongate meshes, abundant free spicules. (Scale bar = 8.2μm). D, Longitudinal section through ectosomal and subectosomal skeleton, ectosomal palisade (crust) at left. (Scale bar = 8.2μm).

DISCUSSION

In both Callyspongiidae and Niphatidae studied here, 'reliable' generic characters matched structural differences within the group: ectosomal skeleton, choanosomal skeleton structure, and fibre structure. It is therefore important to determine the presence of these characters and their stability amongst genera, in order to use them as diagnostic characters.

In Haplosclerida the essential concept of 'genus' taxon is often misinterpreted or confused. Citations of genera as: "*Petrosia* Vosmaer 'sensu' Ridley & Dendy, 1887", or "*Callyspongia* Duchassaing & Michelotti, 1864, 'sensu' Burton, 1932" (Wiedenmayer, 1977), have no special validity or status in formal taxonomy. These terms have often a very different meaning than the one given by the original author. It is clear that this kind of citation should be avoided, particularly if it is not based on personal re-examination of type material. Such citations result in a new concept of the genus, an unnecessary widening of the generic concept without corroboratory evidence from the type specimen, and where 'sensu' the new author gives a new subjective diagnosis of the genus - all of which tend to become 'fixed' in the literature with their tacit acceptance by

contemporary authors. It is true that these modifications certainly make genera more 'convenient' for taxonomic identification of species, particularly in cases where the original concept of the genus is clouded or questionable. However, they omit the phylogeny and frequently lead to very heterogeneous taxa.

The question is then: do we accept genera or subgenera for their 'convenience', or do we have to find evidence for phylogenetically valid taxa ? What are the characters to consider when we split or fuse a nominal genus into an actual genus?

Some of the genera studied here are difficult to delimit, because of the large variability in their structural characters. For example *Callyspongia*, the type genus of Callyspongiidae, shares its habit with other genera of the same family: the lectotype of *Callyspongia*: *C. fallax*, has been described as massive, repent and lobate (Van Soest, 1980), but many species (including the type species) vary in habit from massive, ramose, lobate, repent to tubular. Today the genus is contains species with a great diversity and variability in growth forms, such that the concept of 'shape' has little taxonomic importance at the supraspecific level in this case. Nevertheless, *Callyspongia* exhibits a typical skeleton with a very stable fibre structure. Hooper & Wiedenmayer (1994) include 16 nominal genera as synonyms of *Callyspongia*, and Wiedenmayer (1989) included 21 nominal generic synonyms of *Callyspongia*. This is symtomatic of the biggest problem in Haplosclerida whereby the formulation of exact definitions and delimitation of generic boundaries is nearly impossible. Large revisions of problematic genera, following a strict interpretation of the genus' original concept, lead in some cases to the creation of genera with similar characters, or conversely to merge genera displaying some mutual characters ('splitting' versus 'lumping'). In the present work comparisons between type species of accepted generic synonyms of *Callyspongia* provided a clear mandate to differentiate them, based on their ectosomal features, whereas in some cases differences in their choanosomal skeletons were so minor as to be inconsequential.

So far, differences between type species of genera considered as synonyms of *Callyspongia* by Hooper & Wiedenmayer (1994) are too subtle to retain them as available genera (e.g. *Ceraochalina*; *Chalinella*; *Chalinopora*; *Euchalina*) whereas, conversely, the existence of several species showing consistent similarities in some of their characters confirm the potential validity of some of their nominal species groups, for which 'convenient' subgenera may be appropiate and 'useful' for classification (although perhaps not always phylogenetically sound taxa). A similar solution was adopted for a revision of the large family Microcionidae, with 73 nominal genera included (Hooper, 1996).

Tentative conclusions summarised in Tables 1 and 2 provide a convenient, practical classification, but they require confirmation from other sources using more objective methods (e.g. molecular studies).

Skeletal characters analyzed here were very often difficult to objectively differentiate, because variability occurred between very narrow limits, especially concerning the choanosomal skeleton and the structure of fibres and their variations. In these cases it is necessary to determine character priority in generic diagnoses as a first intent to delimit problematic genera.

The next stage in this analysis, an objective interpretation of characters and the distribution of character states amongst taxa, in a phylogenetic framework, should incorporate some of the more variable morphometric characters of Haplosclerida (e.g. habit, texture, surface ornamentation and aquiferous system). Authors have discarded these features as being 'not useful' at the generic level (e.g. Van Soest, 1980), but certainly some higher taxa such as *Cribrochalina* (Niphatidae) can be defined by a 'sticky texture', reflecting consistency in both skeletal and chemical characters, whereas in others this feature is completely inconsistent and discarded. Work is continuing in this regard (Desqueyroux-Faúndez, in prep.).

CONCLUSIONS

Grouping genera of Callyspongiidae and Niphatidae appears to be feasible using the structural characters defined above. Differences between genera are stable, consistent and deemed to be diagnostically important at the generic level.

In Callyspongiidae (Table 3), two groups of genera are distinguished, based on comparison of the form and size of ectosomal meshes with the structure of underlying longitudinal fibres: 1) Genera with three different sizes of triangular ectosomal meshes: *Callyspongia*, *Toxochalina* and *Spinosella* (=*Cladochalina*). 2) Genera with one size of ectosomal meshes: *Chalinopora* (=*Euchalina*), *Ceraochalina* (=*Chalinella*), *Siphonochalina* (=*Sclerochalina*, *Siphonella*,

Tubulodigitus), *Patuloscula*, *Euplacella*, *Arenosclera* and *Dactylia (=Chalinopsilla)*.

Furthermore, in this first group of genera this ectosomal character is associated with (linked to) the choanosomal character comprising 'fasciculated or isolated subectosomal longitudinal fibres'. In contrast, the character comprising the 'presence of transversal subectosomal connecting fibres' appears only in some genera displaying one size of meshes: *Siphonochalina* (=*Sclerochalina*, *Siphonella*, *Tubulodigitus*); *Patuloscula*. Similarly, *Ceraochalina* (=*Chalinella*), with one size of meshes, presents a different modification of subectosomal isolated longitudinal fibres in the form of 'presence of intercalate fibres and small subectosomal meshes', whereas *Euplacella* has one size of meshes and isolated longitudinal fibres, but it represents a modification of this character with three successive and isolated layers of ectosomal skeleton. This is considered here to represent different degrees in the development of the ectosomal layer, similar to those observed in genera of Phloeodictyidae (*Oceanapia* (=*Rhizochalina*). *Arenosclera* appears to be atypical of Callyspongiidae, having an irregular and disorganised skeleton without proper fibres and fibres strongly cored by foreign material. Wiedenmayer (1989) considered that the presence/absence of foreign material in fibres is a poorly correlated feature and only occurs as a gradual transition within some species of Callyspongiidae, with no clear boundaries between present/ absent. Nevertheless, there is a precedent for recognising a subgeneric taxon with incorporated detritus in the skeleton in Microcionidae (*Clathria* (*Wilsonella*)) (Hooper, 1996), as this feature was consistent within the species group and corroborated by the consistent morphological features. In this regard *Arenosclera* might form a 'convenient' and phylogenetically valid subgenus in group 2 Callyspongiidae.

In Niphatidae, the ectosomal skeleton appears to be a stable ans supraspecific character at the generic level, and in this regard two groups can be distinguished. 1) Genera with tangential ectosomal skeleton that may be formed by: a) a fibre network interrupted by ramified ends of longitudinal fibres (*Gelliodes*) or by barely protruding ends of longitudinal fibres (*Amphimedon*); b) a network of free oxea, interrupted by ends of longitudinal fibres, or spicule brushes with additional sigma or microxea (*Microxina*, *Niphates*); or c) both a fibre network and free oxeas interrupted by ends of longitudinal fibres or aculeations (*Dasychalina*). 2) Genera with perpendicular ectosomal skeletons that may be formed by: a) spicule brushes and ill-defined ends of longitudinal fibres (*Pachychalina*); b) a spicule palisade and expanded ends of longitudinal fibres *(Cribrochalin*a); or c) free spicules issued from the expanded ends of longitudinal fibres or wart-like conules (*Haliclonissa*).

Although, the characters used here appear to be useful to genus groups amongst Callyspongiidae and Niphatidae, their treatment is equivocal in the absence of data about their potential interrelations. Further studies on these two families is still necessary prior to accepting these criteria for a definitive classification. Nevertheless the present analysis provide a positive beginning towards a resolution of a very difficult and slightly chaotic group of sponge taxa.

ACKNOWLEDGEMENTS

For many years, Professor Claude Lévi (MNHN) helped me to understand the taxonomy of Haplosclerida. John Hooper (QM) and Rob van Soest (ZMA) assisted me with their valuable time encouraging this work in taxonomic discussions. I thank many colleagues from different institutions, for providing constructive comments on this manuscript and assisting me to obtain type material studied in this work: Philippe Willenz (IRSNB), Clare Valentine (BMNH), Valter Raineri and Enrico Borgo (MSNG). Technical work was undertaken at MHNG and I am grateful to J. Wüest (SEM), C. Ratton (photography) and I. Juriens (histology). Thanks to both reviewers who greately improved my manuscript.

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