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PHYLOGENETIC CLASSIFICATION OF THE HALICHONDRIDS (PORIFERA, DEMOSPONGIAE)

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ABSTRACT

Using a multicharacter approach and numerical cladistic computer programs a phylogenetic analysis is made of a newly defined order Halichondrida (which includes all Halichondrida and parts of the Axinellida sensu Lévi, 1973), with emphasis on the newly defined family Halichondriidae (which includes the families Halichondriidae and Hymeniacidonidae sensu Lévi, 1973, and some genera formerly assigned to the Axinellidae and Desmoxyidae). The newly defined order consists of the "old" families Axinellidae/Bubaridae and Desmoxyidae, a "new" family Dictyonellidae (containing *Dictyonella, Acanthella, Liosina* and *Dactylella*), and the new concept of the family Halichondriidae. On the basis of numerous specimens, including many type and other original material from all parts of the world oceans, the latter group has been analyzed in depth. Next to classical morphological characters also biochemical data (secondary metabolites) were used. This resulted in the recognition of several discrete generic groups, viz. *Axinyssa* + *Collocalypta, Myrmekioderma* + *Didiscus, Spongosorites, Topsentia* + *Epipolasis* + *Petromica, Ciocalypta* + *Amorphinopsis*, and *Hymeniacidon* + *Halichondria*. A revision comprising definitions of and remarks on all genera, including all junior synonyms, of the newly defined Halichondriidae concludes the paper.

INTRODUCTION

The Halichondrids s.s., until very recently recognized as a separate order (*cf.* Lévi, 1973; Bergquist, 1978; Hartman, 1982) are a group heavily affected by the major changes of classification (based on reproductive strategies) introduced by Lévi (1953), which subsequently gained general acceptance. It has been argued elsewhere (e.g. Van Soest, 1987, 1990b; Diaz, *et al.*, 1990a), that reproductive strategies cannot be employed as synapomorphous characters at the subclass level and if used at lower levels are suspect as likely adaptive characters easily developed independently.

If reproductive strategies are abandoned as characters at the subclass-level, it is necessary to reevaluate the contents and the position of the Halichondrids. Characters of the sponges involved are discussed and evaluated, and a new classification based on (numerical) cladistic techniques is presented. For a general outline of these methods see Wiley (1981); for sponge examples see Van Soest (1987, 1990a and b).

The newly recognized valid families and genera and their junior synonyms are listed, defined, and illustrated, based on many type and other original specimens from all over the world oceans.

This study is the fourth part of a revision of the Halichondrids undertaken by Pomponi, Díaz & Van Soest. Preliminary papers on this revision have been published by Diaz *et al.* (1990a) and Pomponi *et al.* (1990), and a review of Central Atlantic representatives of the newly defined family Halichondriidae was made by Diaz *et al.* (in press).

AXINELLIDA-HALICHONDRIDA RELATIONSHIPS

To perform a cladistic analysis of the families and genera of the Halichondrids, it is necessary to find the nearest outgroups which enables character polarization (Watrous & Wheeler, 1980). Van Soest (in the press) and Diaz *et al.* (in the press) showed that Halichondrids and some Axinellida share many characteristics. Also, pre-Lévi (1953) classifiers (Topsent, Burton, De Laubenfels) associated Halichondrids with Axinellids, particularly the family Axinellidae. In fact, both were considered members of a single order Halichondrida Vosmaer, 1887 by Topsent and De Laubenfels, until the Axinellida were given separate ordinal status in 1955. Halichondrida *s.s.*, i.e. families Halichondriidae and Hymeniacidonidae *sensu* Lévi (1973), can be associated with Axinellida Lévi (1955) (in part only: familes Axinellidae, Bubaridae, and perhaps some Desmoxyidae, but excepting the Raspailiidae, Euryponidae, Rhabderemiidae, Trachycladidae, Sigmaxinellidae (= Hamacanthidae) and Hemiasterellidae), by a convincing series of intermediate genera and families. The major features of the Axinellida, i.e. axial condensation of the choanosomal skeleton and indiscriminate occurrence of styles and oxea, and the major features of Halichondrida, i.e. ectosomal tangential skeleton and confused choanosomal skeleton, intergrade nicely in the series of genera *Axinella* (Axinellida) - *Phakellia* (Axinellida) - *Acanthella* (?) - *Dictyonella* (?) - *Axinyssa* (?) - *Myrmekioderma* (?) - *Topsentia* (Halichondrida) - *Ciocalypta* (Halichondrida) - *Halichondria* (Halichondrida). In fact, the definitions of the "orders" Axinellida and Halichondrida apply only really well to the type genera *Axinella* and *Halichondria*, and it is only through other characters (e.g. sinuous spicules in *Phakellia* and *Acanthella*, and *Axinella cannabina* (Esper, 1794); telescoped endings of spicules in *Axinella*, *Dictyonella*, *Axinyssa* and *Spongosorites*; size ranges of oxea in *Myrmekioderma*, *Topsentia*, *Ciocalypta* and *Halichondria*), that typical genera are linked with intermediates. From these observations, it may be inferred that to provide definitions of two discrete groups (orders or suborders) encompassing all the associated genera is virtually impossible. It will not be attempted here; instead it will be shown below that the group of genera together comprising the presently recognized Axinellida *s.s.* and Halichondrida *s.s.* consists of four definable genus-groups which can conveniently be given family status.

The phylogenetic position of Raspailiids (including Euryponids) and Hemiasterellids has to be discussed briefly, since these have been considered close to Axinellidae in the past, and indeed showed up to be close in a recent phylogenetic exercise (Van Soest, 1987), based on possession of an axially condensed choanosomal skeleton. Ongoing cladistic analyses (Van Soest, 1990b), however, reveal the probable homoplasic nature of the axially condensed skeleton. Typical members of Axinellidae, Raspailiidae, Hemiasterellidae and Sigmaxinellidae share the axial condensation of the choanosomal skeleton; however, each of them also shares indubitable synapomorphous characters with widely different groups such as Hadromerids (Hemiasterellid asters) and Poecilosclerids (Raspailiid acanthostyles and Sigmaxinellid sigmata). There is no solution for this distribution of characters other than to assume that one or more homoplasic developments have occurred in the evolution of these groups. According to recent cladistic analyses (Van Soest, 1990b), it is more parsimonious to assume that axial condensation has developed in four different lines (Axinellidae, Hemiasterelliidae, Raspailiidae and Sigmaxinellidae), than to assume that asters, acanthostyles and sigmata have each developed independently in two separate lines (asters: Hadromerids and Hemiasterellids; acanthostyles: Raspailiids and Microcionids/Myxillids; sigmata: Sigmaxinellids and Poecilosclerids). Speculations about presence of any of those characters in unknown ancestors of the groups, and subsequent independent losses in several major lines, seem to be all equally (un-)parsimonious and unnecessary. These results are in support of Hooper (1990), who correctly pointed out the similarities of Raspailiids and Microcionids. Moreover, axial condensation of a sort is found in several Suberitid Hadromerids, viz. species of *Rhizaxinella* and the species originally described as *Phakellia lobata* Wilson, 1902. Comparisons of axially condensed species of all these groups show important architectural differences between various axial skeletons (see Van Soest, 1990b), testifying for the probable homoplasic nature of this type of supporting skeleton. The revised classification of the Hadromerid-Axinellid-Halichondrid-Poecilosclerid Demosponges is presented in Fig. 1 (after Van Soest, 1990b).

A problem remaining is the formal definition of the group comprising Axinellidae *s.s.* and Halichondrida (Lévi's (1973) families Axinellidae, Bubaridae, Desmoxyidae, Halichondriidae, and Hymeniacidonidae), which may be named Halichondrida (*s.l.*) because the present contents of this group largely conform to those of the similarly named group of Topsent and De Laubenfels. Although as argued above a convincing series of intermediates exists linking this group closely together, it seems nevertheless that easily recognizable synapomorphies are absent. Thus, we have to rely on underlying synapomorphies found in many but not all members of a taxon and unique combinations of characters not uniquely confined to the group. Possibly, biochemical compounds may turn out to provide strong (underlying) synapomorphies (Pomponi, *et al.*, in press).

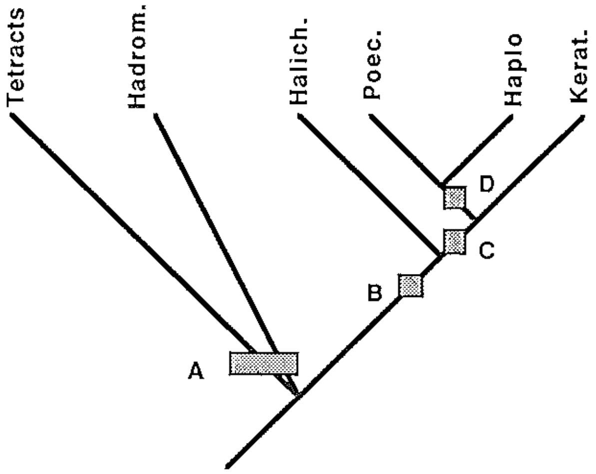

Fig. 1. Revised classification of the Demospongiae based on the reevaluation of major group synapomorphies (based on Van Soest, 1990b). Character A: (sub-)radiate architecture, B: anisotropic reticulation, C: taurin synthesis via cysteic acid, D: sigmatose microscleres.

Definition of the Halichondrida s.l.: *Demospongiae with a plumoreticulate skeletal architecture built of interchangeable styles and oxea and intermediate spicules, of widely diverging sizes, and not functionally localized.*

Remarks: The plumoreticulate skeletal architecture maybe a synapomorphy for a much wider group of Demospongiae (see Van Soest, 1990b). This character is progressively lost in the group formerly considered the order Halichondrida *sensu* Lévi. However, a basic plumoreticulate or plumose architecture is found even there with few exceptions.

Although the combination of styles and oxea is also found in a few Raspailiids and Poecilosclerids, these groups show localization or categorization in them. For instance, in Myxillids stylote choanosomal spicules are combined with ectosomal diactines; in the Raspailiid *Echinodictyum* choanosomal oxea are arranged into tracts which are echinated by (acantho-)styles. Indiscriminate occurrence of styles and oxea is not found. Localized spicules in *Didiscus*, *Myrmekioderma* and *Higginsia* are considered microscleres.

Sinuous longer or shorter diactinal spicules are found in *Axinella cannabina, Phakellia, Auletta, Bubaris, Acanthella, Dactylella*, some *Axinyssa* and some *Topsentia*. This distribution may be interpreted as retention of ancestral spicules, possibly related to lithistid spicules (through *Monocrepidium* and fossil genera such as *Cephalorhaphidites* and *Megaloraphium*), and thus constitute an underlying synapomorphy.

Isonitriles are organic compounds found in *Axinella, Acanthella, Ciocalypta, Axinyssa,* "*Epipolasis*", "*Stylotella*", "*Halichondria*", and "*Hymeniacidon*" (names between quote marks represent doubtful generic assignments) (personal communication Dr J. C. Braekman), and thus may turn out to be a good underlying synapomorphy, too.

RELATIONSHIPS WITHIN THE HALICHONDRIDA (*s.l.*)

Although our revision will confine itself to the Halichondrida in the restricted sense (which will subsequently be named the family Halichondriidae) and will not include at this moment Axinellidae/Bubaridae/Desmoxyidae, we will need to find the nearest outgroup of the group we wish to study further. So it is necessary to briefly discuss the contents of the Halichondrida s.l., for which purpose we considered the descriptions of an original 148 genera, of which 56 were later left out of consideration for their likely Raspailiid or Hemiasterellid nature. The remaining 92 nominal genera recognized within the newly defined Halichondrida could be subdivided among the following generic groups:

Family Axinellidae Ridley & Dendy, 1887 (emended) (Figs. 2-3, 8): *Halichondrida with axially condensed and extra-axially plumoreticulate choanosomal skeletons.*

Characteristically, oscules are star-shaped (Fig. 8) but in view of its (non-homologous?) occurrence outside the group that is a doubtful synapomorphy. Next to typical Axinellidae genera like *Axinella* (Figs. 2, 8), *Phakellia* and *Auletta*, the family Bubaridae with valid genera *Bubaris* (Fig. 3), *Monocrepidium, Hymerhabdia,* and *Cerbaris*, are here included based on the observation that the incrusting growth form is supported by an axially = basally condensed and an extra-axially = peripheral plumoreticulate skeleton.

Family Desmoxyidae Hallmann, 1917 (emended) (Figs. 4, 9): *Halichondrida with a reticulate-fasciculate choanosomal skeleton of spongin-enveloped tracts with a fleshy, corrugate/ridged surface.*

Genera included are *Higginsia* (with junior synonym *Desmoxya*), which possesses ectosomal centrotylote acanthoxea, and *Ptilocaulis* (Figs. 4, 9), which lacks this character but is very close in habit. Possibly, this group is more related to

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Figs. 2-7.

Figs. 2. *Axinella verrucosa* (Esper, 1794), A. longitudinal section showing axially condensed and extra-axially plumoreticulate skeleton (redrawn from Vosmaer, 1912: pl. 16 fig. 5) (scale bar (s.b.) = 1 cm), B. Spicules (s.b. = 100 µm).

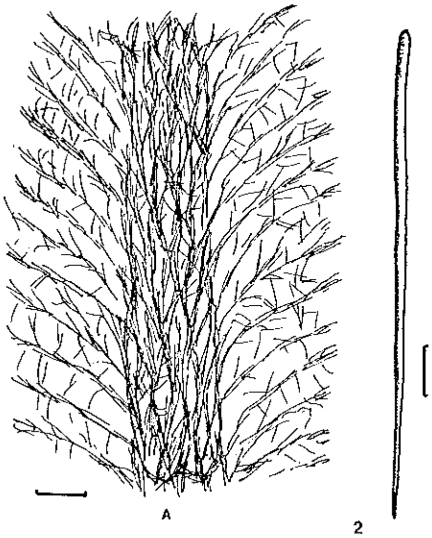
Fig. 3. *Bubaris vermiculata* (Bowerbank, 1866), choanosomal styles erect on a basal mass of sinuous strongyles (s.b. = 100 µm).

Fig. 4. *Ptilocaulis walpersi* (Duch. & Mich., 1864), A. longitudinal section showing reticulation of spongin-enforced tracts (s.b. = 1 mm), B. spicules (s.b. = 1 oo µm) (both redrawn from Zea, 1987: fig. 67).

Fig. 5. *Dictyonella obtusa* (Schmidt, 1868), A. dendritic spicule tracts (redrawn from Vosmaer, 1912: pl. 16 fig. 1) (s.b. = 1 mm), B. spicules (s.b. = 100 µm).

Fig. 6. *Scopalina lophyropoda* Schmidt, 1862, A. dendritic spicule tracts (redrawn from Schmidt, 1862; pl. 7 fig. 18) (s.b. = 100 µm), B. style (s.b. = 100 µm).

Fig. 7. *Acanthella acuta* Schmidt, 1862, A. dendritic spicule tracts (redrawn from Vosmaer, 1912: pl. 16 fig. 3) (s.b. = 1 mm), B. spicules (s.b. = 100 µm).



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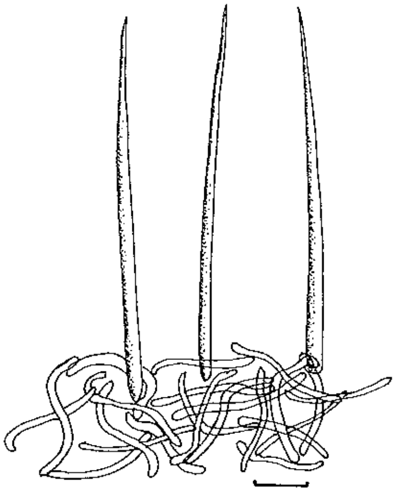

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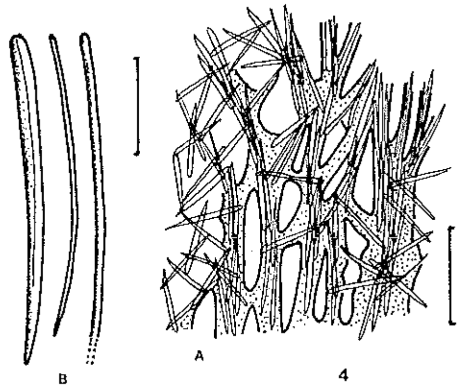

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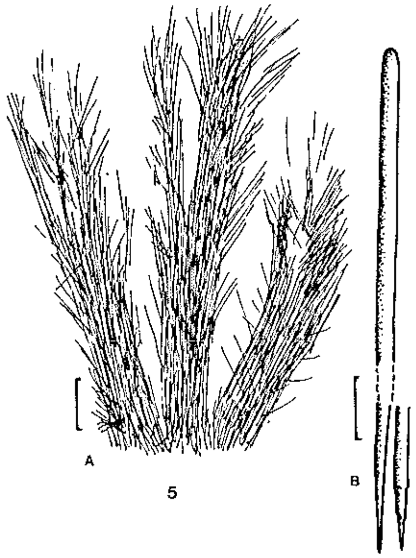

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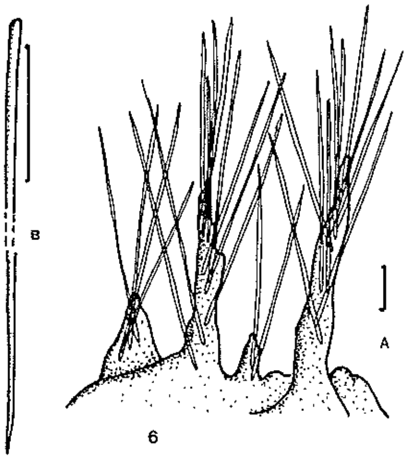

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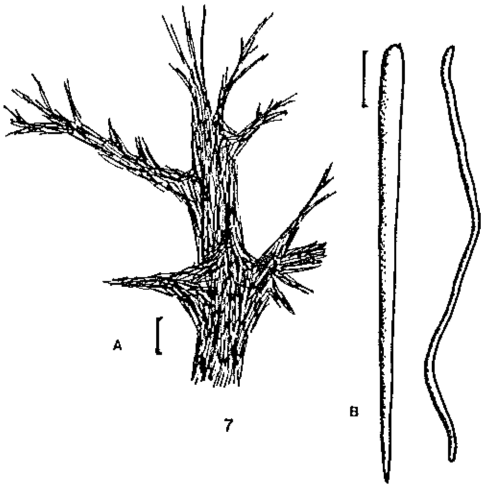

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Raspailiids and Microcionids because of the converging habits found in these groups; absence of acanthostyles in the present family seems to be preclude a more close association between these forms. Also there seem to be two distinct habits in *Higginsia* species: one more or less smooth with a cover of tightly packed microscleres (e.g. *Higginsia petrosioides* Dendy, 1905), the other *Ptilocaulis*- like possessing long styles. The latter may be related to the Euryponid *Halicnemia* which shares the microsclere morphology. A revision of *Higginsia* is necessary for evaluating the contents of the family Desmoxyidae.

Family Dictyonellidae, new family (Figs. 5-7, 10-11): *Halichondrida with spongin-enforced dendritic choanosomal spicule tracts and a fleshy conulose surface.*

Genera included are *Dictyonella* (Figs. 5, 10), *Scopalina* (Fig. 6), *Acanthella* (Fig. 7), *Dactylella*, *Tethyspira*, and *Liosina* (Fig. 11).

The presence of reticulate skeletons in Axinellidae and Desmoxyidae, and also in many Raspailiids and Poecilosclerids, is here interpreted as ancestral, be it that the particular development of this reticulate architecture in the different groups represent apomorphous states. The absence of a reticulate skeleton in Dictyonellidae and Halichondriidae is considered a synapomorphy for the two families, thus making the Dictyonellidae the sistergroup (or functional outgroup) of the Halichondriidae. Dictyonellidae and Desmoxyidae share the fleshy ectosome, which is also found in some Halichondriidae such as *Axinyssa* and *Hymeniacidon*, and this is hesitatingly considered an underlying synapomorphy of the three families. The absence of axial condensation of the skeleton is here interpreted as an ancestral character, which cannot be used as a synapomorphy. The resulting picture, which is admittedly rather weak, is graphically represented in Fig. 12.

Family Halichondriidae Vosmaer, 1887 (emended): *Halichondrida with a choanosomal skeleton consisting of (1) a high density of spicules arranged in (2) vague, ill-defined, directionless tracts, and of (3) spicules in confusion.*

Remarks: As is remarked above, the new concept of the family Halichondriidae includes the old families Halichondriidae and Hymeniacidonidae, as well as "Axinellid" genera such as *Myrmekioderma* and *Axinyssa*; moreover, also *Didiscus*, in the past regarded variously as Hadromerid or Poecilosclerid, but properly assigned recently by Díaz *et al.* (1987). A total of 46 nominal genera (see below) are considered to belong to this group. After examination of specimens of most type species (including many holotypes), and many other species assigned to these genera, we consider 12 genera as valid, with another 4 monotypical genera of doubtful status.

CLADISTISTIC ANALYSIS OF THE HALICHONDRIIDAE

We selected two representative species of each of the twelve valid genera and included some representatives of the outgroups (*Phakellia, Ptilocaulis, Dactylella* and *Dictyonella*). We submitted this group of 27 taxa to a formal character analysis. This involved drawing up a list of

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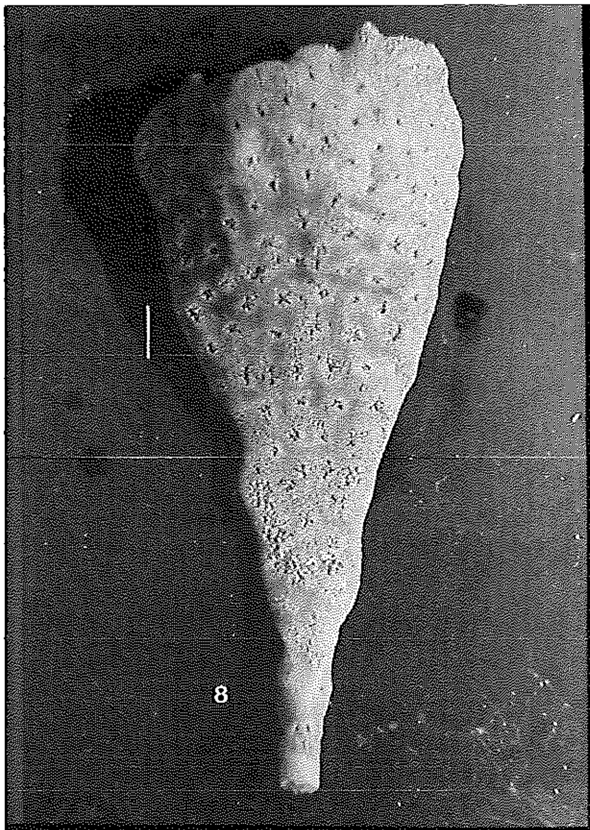
Figs. 8-11.
Fig. 8. *Axinella donnani* Bowerbank, 1875, ZMA specimen from Indonesia (s.b. = 1 cm).
Fig. 9. *Ptilocaulis walpersi* (Duch. & Mich., 1864), ZMA specimen from Curaçao (s.b. = 1 cm) (photo L. A. van der Laan).
Fig. 10. *Dictyonella obtusa* Schmidt, 1868, ZMA specimen from Marseille (s.b. = 1 cm) (photo L. A. van der Laan).
Fig. 11. *Liosina paradoxa* Thiele (1903), ZMA specimen from Indonesia (s.b. = 1 cm) (photo H. van Brandwijk).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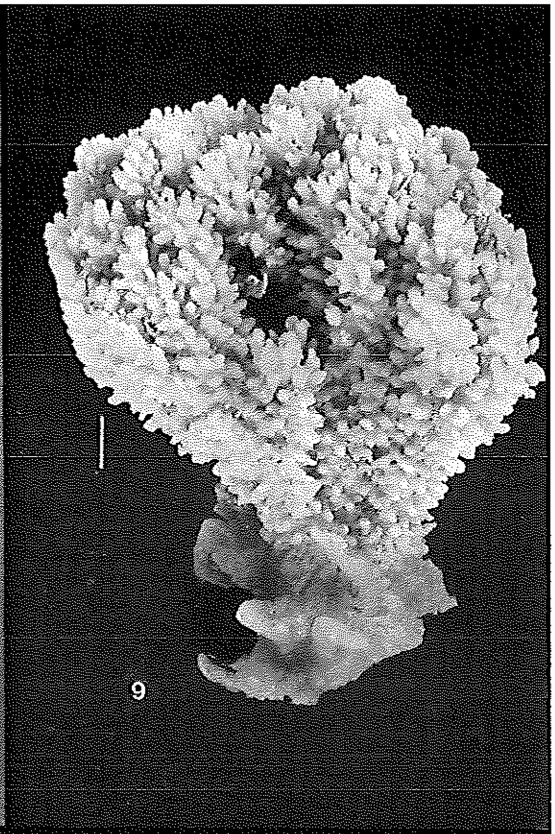
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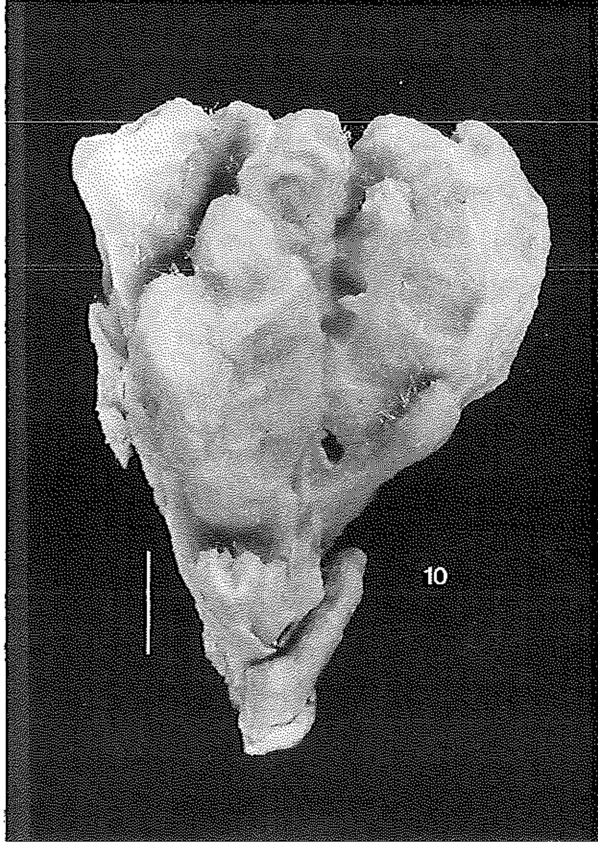
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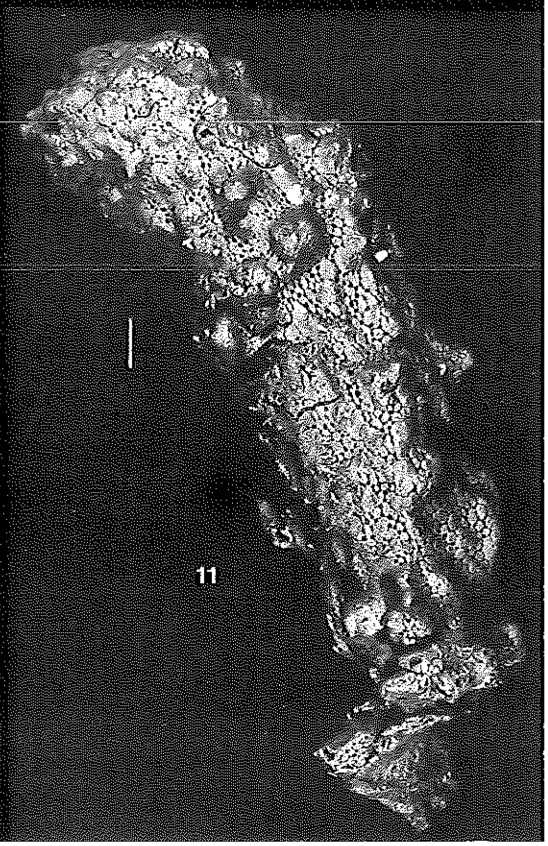
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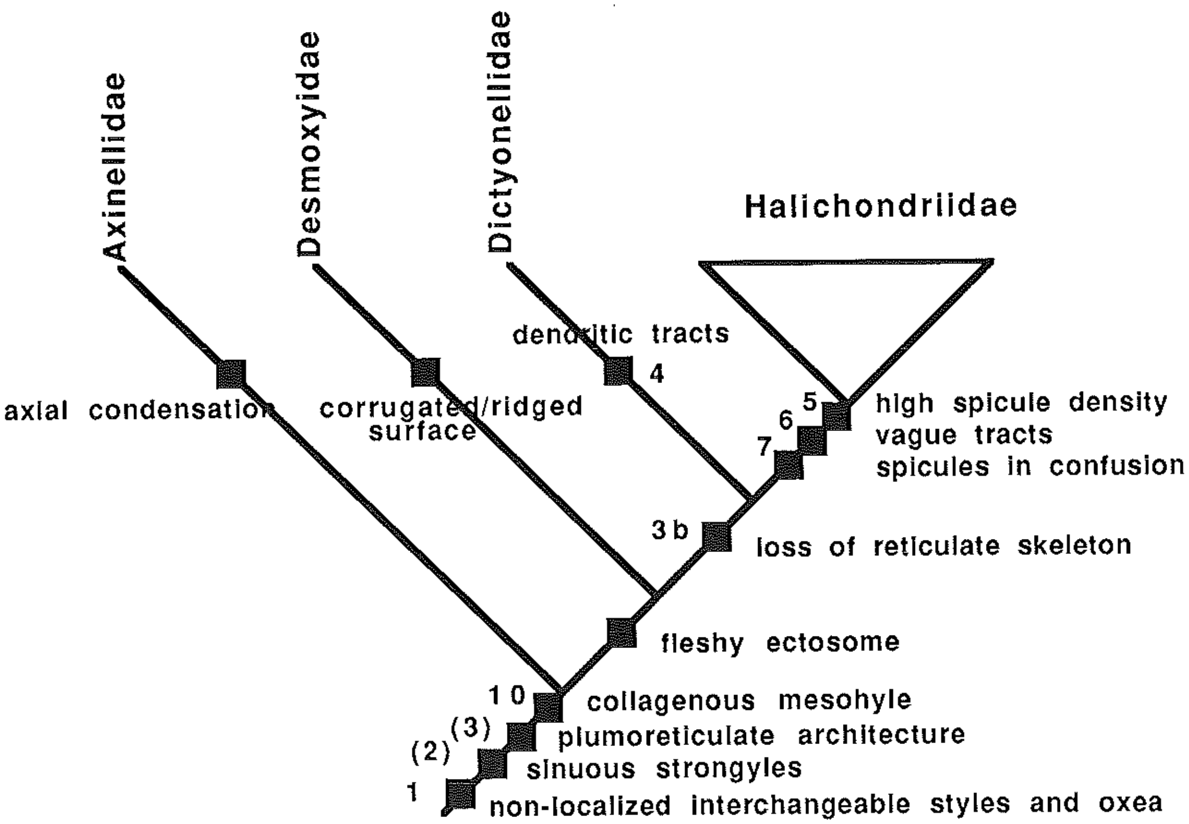


Fig. 12. Phylogenetic relationships of newly defined Halichondrid families (further explanations see text).

26 characters (see below) and tabulating the distribution of these characters and their states over the taxa, thus constructing a taxon-character matrix. Where it appeared necessary, it was decided to use a multi-state coding because of the obvious interdependent nature of many characters/states. The necessity to develop transformation-series hypotheses in the case of multistate characters seriously complicates this type of analysis; however these complications were preferred over a strict binary coding, which has serious philosophical setbacks. Subsequently the taxon-character matrix has been evaluated without computer assistance, and also treated with three different computer programs all constructing Wagner-Trees in which relationships between taxa and their hypothetical ancestors are computed, viz. MacClade 2.1 (Maddison & Maddison, 1987), Tree Tools 2.5 (Ellis, 1987) and Phylip 3.0 (which necessitated transformation of the multistate character matrix into a additive-binary one using the "Factor" option, after which "Mix", and Dollo parsimony algorithms were used) (Felsenstein, 1987).

Synapomorphic characters used in the cladistic analysis of relationships in the Halichondriidae:

1. *Occurrence of a combination of oxea, styles and modifications of these*: this is a synamorphy of the order Halichondrida.
2. *Sinuous spicules*: these occur in some Bubaridae, Axinellidae, Dictyonellidae, and Halichondriidae; however, the distribution within these groups is restricted to a small number of species and genera, and within a species the proportion of sinuous spicules may be quite small (e.g. in *Dactylella* and *Topsentia*). The presence of these spicules is here considered an underlying synapomorphy of the order Halichondrida.

3. *Reticulate choanosomal architecture*: this is an ancestral character of a much larger group including the families Desmoxyidae, Axinellidae, but also probably the Poecilosclerida. For the Halichondriidae and Dictyonellidae its loss (3b) is considered a synapomorphy, thus uniting both families and making the Dictyonellidae the nearest outgroup of the Halichondriidae.
4. *Spongin-enforced perpendicular tracts*: these consist of long somewhat wavy spicules, and often follow a dendritically anastomosing course ending at the surface and causing a more or less pronounced conulose exterior: a synapomorphy of the family Dictyonellidae.
5. *High spicular density*: the reduced spongin in the Halichondriidae causes a loss of reticulation and a more confused skeleton and leads to a higher spicular density: a synapomorphy of the family Halichondriidae.
6. *Vague spicule tracts*: loss of spongin and reticulation has left only a vague organization of central confused elements and equally vague tracts radiating to the surface: a synapomorphy of the family Halichondriidae.
7. *Haphazard arrangement of spicules*: also related to the above is the confused arrangement of many single spicules: a synapomorphy of the family Halichondriidae.
8. *Finely conulose surface*: without ectosomal skeletal covering, the type of choanosomal skeleton found in the Halichondriidae results in groups of spicules sticking out (often at diverging angles) beyond the ectosome, producing a finely conulose surface: this is a synapomorphy of the genera *Axinyssa* and *Collocalypta*.
9. *Ectosomal skeletal strengthening*: the remaining Halichondriidae have some sort of ectosomal skeleton (and if not they are so obviously related to forms that possess it, that the subsequent loss is a likely assumption): a strong synapomorphy of all genera except *Axinyssa* and *Collocalypta*. The strengthening occurs in several forms: (9b) the ectosomal skeleton may consist of a mass of spicules arranged more or less vertically, mostly tightly packed, erected on a base of larger tangential spicules: a synapomorphy of the genera *Myrmekioderma* and *Didiscus*; (9c) the ectosome may consist of a tangential arrangement of bundles of spicules or single ones, a synapomorphy for the genus group *Ciocalypta-Amorphinopsis-Halichondria-Hymeniacidon*; (9d) a possible variant of this is an utterly confused crust as found in the genus *Topsentia*; (9e) a recognizable variant is also the detachable ectosome of *Hymeniacidon* and *Halichondria*; (9f) a doubtful apomorphous character state is formed by the parchment-like ectosome that sets *Epipolasis* apart: oxea arranged in a tangential felt-like mass; (possibly independently developed in the doubtful genus *Pyloderma*).
10. *Collagenous mesohyle*: most Axinellidae and Dictyonellidae show a highly collagenous choanosome apart from the variable presence of recognizable spongin (in the form of fibres or enveloping or binding spicule tracts); this collagenous choanosome is lost in all genera except in *Axinyssa, Collocalypta, Myrmekioderma* and *Didiscus*, and its loss (10b) is considered a strong synapomorphy for the remaining Halichondrids.
11. *Meandering surface grooves*: deep surface grooves, sinuously curving or meandering, roofed over by "organic skin", leaving isolated rounded areas with ectosomal pallisades, form a distinct synapomorphy of *Myrmekioderma* and *Didiscus*.
12. *Sinuous trichodragmata*: these are a synapomorphy of *Myrmekioderma*, where there are normally several size categories. An assumed homoplasic occurrence of sinuous trichodragmata is found in *Epipolasis*; the dragmata are definitely slimmer and much more curved in that genus (arranged around the megascleres and keeping these presumably together). Outside the Halichondrida sinuous trichodragmata are found in the Poecilosclerid family Desmacellidae (e.g. *Dragmatella*).
13. *Discorhabds*: strong synapomorphy of *Didiscus*; since they develop from thin oxea they may be homologous with the smallest category of megascleres of other genera, but in view of their small size this is left undecided.
14. *Choanosomal tracts of spicules strengthened by some spongin running more or less parallel with the surface*: a synapomorphy for *Spongosorites*.
15. *Colour-change*: from yellow or orange to brown or black, when exposed to air or any other medium containing free oxygen (aerophobic): a synapomorphy of *Spongosorites*.
16. *Topsentins*: secondary metabolites found only in *Spongosorites*.
17. *Progressive loss of spongin*: presumably in two stages all genera (excepting those of the genus groups *Axinyssa-Collocalypta* and *Myrmekioderma-Didiscus* and also *Spongosorites*) exhibit loss of spongin; most genera retain some binding the spicules (17b), but in the genus group *Topsentia-Epipolasis-Petromica* loss of spongin is virtually total resulting in a notable brittle fragile consistency (17c).
18. *Absence of true styles*: a "weak" synapomorphy (18b) setting *Topsentia* and *Epipolasis* apart from *Petromica*.
19. *Presence of desmata*: possibly an ancestral character setting *Petromica* apart; maybe inadmissible, if possession of desmata turns out to be a retained ancestral character.
20. *Trichodragmata draped around the spicules*: an apomorphous character of *Epipolasis*.
21. *Ectosomal small styles*: a synapomorphy of the genus group *Amorphinopsis-Ciocalypta*.
22. *Bundles of longer oxeotes 'echinated' by small styles*: a synapomorphy of *Amorphinopsis*.
23. *Axially arranged fistule architecture*: a "weak" synapomorphy of *Ciocalypta*; in *Petromica* the axial strengthening skeleton is found in the wall of the

fistules, rather than in the centre, but in other respects it is similar; in certain fistulose *Topsentia* and *Halichondria* arrangements are more or less the same as in *Ciocalypta*.

24. *Tufted larvae*: a synapomorphy of *Halichondria*.
25. *Vivipary*: a synapomorphy of the genera *Halichondria* and *Hymeniacidon*; this is certainly an adaptive character, easily developed anew (occurs in such widely diverging groups as Hexactinellida, Calcarea, Homosclerophorida, Poecilosclerida, Haplosclerida and Keratosa).
26. *Styles with tylote swellings*: a synapomorphy of *Hymeniacidon*.

RESULTS

Treatment of the taxon-character matrix by the computer programs yielded several equally parsimonious trees, which differed however only marginally from each other. Among them was one tree which was identical to the one made without computer assistence and it was decided to adopt this as the most likely representation of phylogenetic relationships of the Halichondrid genera and the outgroup-families.

The inferred relationships between the genus groups which have been preliminary suggested already in a previous paper (see Diaz, *et al.*, in press), are here formally presented in the cladogram of Fig. 13. In short, the Halichondriidae consist of three major genus groups: one comprising two genera which are characterized by a finely conulose surface, and which retain still an 'Axinellid' type of collagenous choanosome; furthermore two genera with characteristically grooved surfaces and heavy ectosomal protective skeleton; they, too, retain a collagenous mesohyl; and, finally, a group of eight genera which have lost the collagenous nature of the organic choanosome and are characterized by having some sort of ectosomal tangential crust. Relationships within the latter group are further determined by details of the ectosomal crust, which may consist of a paratangential arrangement of spicules (*Topsentia, Petromica*), a reticulation of spicule bundles (*Amorphinopsis, Ciocalypta*) or feltwork (*Epipolasis*), or single spicules (*Hymeniacidon, Halichondria*). *Spongosorites* deviates rather strongly from the others in architecture and chemistry.

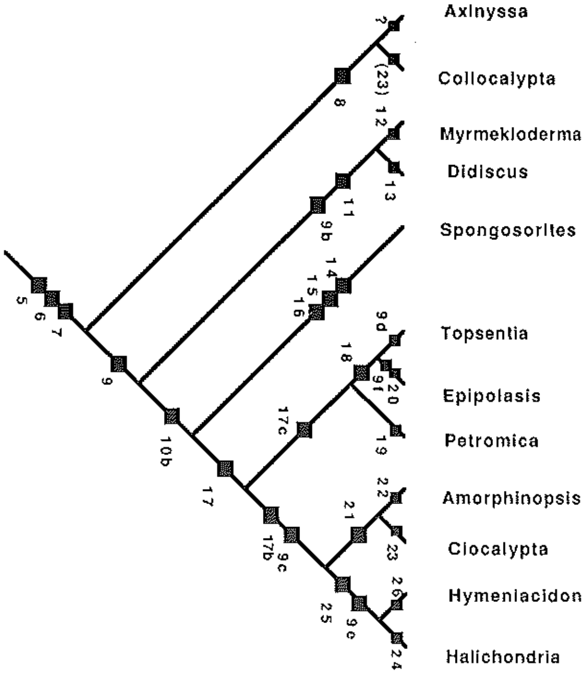


Fig. 13. Phylogenetic relationships of the valid genera of the newly defined family Halichondriidae; numbers with black boxes refer to synapomorphic characters listed and discussed in the text.

DISCUSSION

Although a formal analysis of relationships within the whole order Halichondrida s.l. has not yet been completed it is proposed here to adopt above presented results into a formal classification of the order into four families, one of which (Desmoxyidae) may turn out to be more related to Raspailiids. It is furthermore proposed to assign Raspailiids, Rhabderemiids, and Euryponids for the time being as a discrete group to the Poecilosclerida (partly in accordance with suggestions made by Hooper, 1990), but the relationships with this group as well as with *Agelas* have to be reevaluated. Trachycladids are considered Hadromerida on account of similarities of their microscleres with spirasters.

Below, the recognized genera and their (subjective) synonyms will be defined. In a forthcoming monograph of the West Indian Halichondriidae (see Diaz *et al.*, in press) the new classification will be adopted at the species level.

Characters considered to be of low value as synapomorphies (if used are considered 'weak') or assumed to be homoplasic are:
Shape: most Halichondriidae tend to be 'amorphous', connected no doubt to the low grade of skeletal organization. Certain characteristic shapes, such as fistulose forms with a massive base buried in the sediment are definitely homoplasic, as these habits do not concur with other character distributions, and moreover are also known in several other Demospongiae orders (e.g. *Oceanapia* in Haplosclerida and *Coelosphaera* in Poecilosclerida). Striking similarities between "*Ciocalypta*"-like forms in different genera (*Ciocalypta, Topsentia, Halichondria, Hymeniacidon, Petromica, Collocalypta*) (see e.g. Wells *et al.*, 1960: Figs. 47, 49, 50, 51) are here considered the product of environmental pressure on growth form and general low grade skeletal organization in the Halichondrids.

Spicule morphology: the spicules in this group share with their outgroups an 'indifference' with regard to the exact shapes of the spicules, especially the apices, but also the curvature and axial canal width. These characters are assumed to be partly ancestral (plesiomorphic), partly easily developed independently. Emphasis on stylote vs. oxeote nature of the spicules is only made occasionally (e.g. in distinguishing *Amorphinopsis* and *Ciocalypta,* or *Halichondria* and *Hymeniacidon*) and considered 'weak'. In fact, it is not so much the nature itself of the spicules but rather the absence of one or more of the usual forms we are using. Spicule malformations and centrotylote condition are found in several groups within and outside the Halichondriidae, and it does apparently not point to close relationship. The frequent occurrence in some, e.g. in *Spongosorites* is however noteworthy. Spicule size categories seem to occur in most genera and can only be succesfully employed as apomorphy in distinguishing species. A special category of small styles, however, is regarded as a synapomorphy of *Amorphinopsis*.

A REVISION OF THE GENERA PRESENTLY ASSIGNED TO THE HALICHONDRIIDAE

Family Halichondriidae Vosmaer, 1887 (emended)

Halichondrida with a choanosomal skeleton consisting of a high density of spicules arranged in vague, ill-defined, directionless tracts and of spicules in confusion.

Genus group *Axinyssa-Collocalypta*:

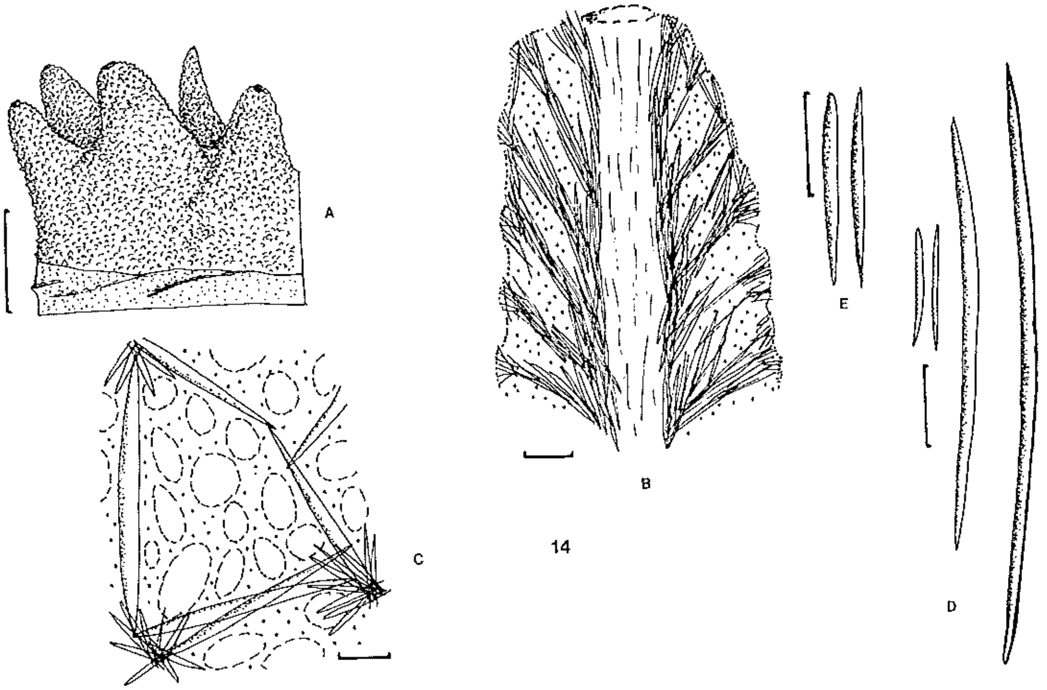
Halichondriidae with choanosomal spicule tracts protruding slightly beyond the organic ectosome producing a finely conulose surface pattern.

Genus *Axinyssa* Von Lendenfeld, 1897: 116 Figs. 14-22

Type species (monotypy): *A. topsenti* Von Lendenfeld, 1897: 116, pl. 10 figs. 134-144 (Holotype ZMB 2971 (Fig. 14), reexamined; holotype fragments in BMNH 1908:9:24:145 (Fig. 17) and slide 1897:3:25:70 reexamined).

Definition (emended): Halichondriidae of the genus group *Axinyssa-Collocalypta* with vague choanosomal tracts ending at the surface in regularly distributed spicule brushes producing a regularly spaced conulation.

Remarks: This is a common genus in tropical waters. The type species has smaller stylote oxeotes in the surface brushes, and this has led authors in the past to recognize a separate genus (*Pseudaxinyssa*) for species similar to *A. topsenti*, but without clearly differentiated spicule size categories. In view of the common occurrence of these in various Halichondrid genera, this is considered superfluous.
The well known North Australian *Pseudaxinyssa stipitata* Bergquist & Tizard, 1967 is not an *Axinyssa* but probably belongs to an Axinelid genus close to *Axinella*.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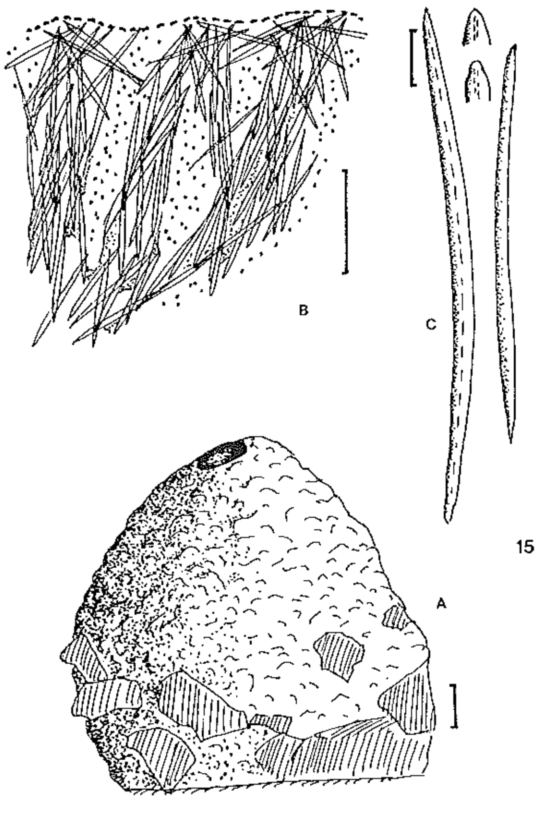
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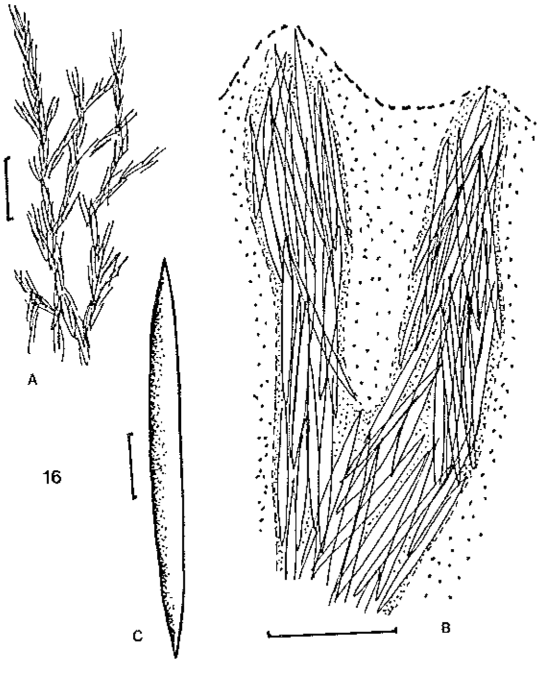
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Synonymy:

Genus *Pseudaxinyssa* Burton, 1931:350
(Figs. 16, 18)
Type species (original designation): *Axinyssa tethyoides* Kirkpatrick, 1903: 245, pl. V fig. 12, pl. VI fig. 8 (holotype reexamined)
Burton: "Axinellidae of massive form in which the skeleton is composed of vertically ascending fibres of oxea of one sort only, the fibres branching and anastomosing throughout their length and ending at the surface in small tufts which project to a greater or lesser extent".
Remarks: The holotype specimen of Kirkpatrick (Fig. 18) is incorporated in the collections of the British Museum (reg. no. 1902:11:16:25), and has been reexamined. It has a dendritic reticulation of spongin-bound (?) tracts. In many ways the specimen is quite unusual: it is black, has a coarse organic skin, large quantities of choanosomal organic (?foreign) material; the spicule tracts are often quite discrete and seem to be unattached to the organic parts. Possibly, the specimen is not a healthy representative of the species as no other, similar specimens have ever been described.

Genus *Axinomimus* De Laubenfels, 1936: 163.
(Fig. 22)
Type species (monotypy): *Axinella paradoxa* Ridley & Dendy, 1886:482, 1887: pl. XXV fig. 4 (holotype reexamined). De Laubenfels: "The spicules are oxeas only and the construction is so nearly radiate that inclusion in this family (i.e. Sollasellidae) seems justified, but it deviates from typical members of the family in the direction of the family Axinellidae in as much as the spicules are more or less vaguely arranged in plumose tracts. The rubbery consistency is very noteworthy."
Remarks: The type specimen BMNH 87:5:2:68 from near Tristan da Cunha in the South Atlantic is a rubbery lobate mass with conulose surface; no ectosomal skeleton; choanosomal skeleton consists of confused loose spicules arranged mostly in vague radiating tracts; oxea on average 870 by 22 µm.

Several species assigned to *Trachyopsis* are here considered members of *Axinyssa*; however, the type species of that genus is considered a *Topsentia*.
Several species assigned to the genus *Leucophloeus* belong to *Axinyssa*; however, the type species of that genus is assigned to *Ciocalypta*.
The genus name *Rhaphisia* Topsent, 1892, has been used in connection with *Axinyssa* specimens by some authors (e.g. De Laubenfels). The type species of *Rhaphisia* (monotypy), viz. *R. laxa* Topsent, 1892, however, is a clear *Haliclona* (see De Weerdt & Van Soest, 1986; De Weerdt, 1987).
The genus name *Phycopsis* Carter, 1882, has been used for at least one species of *Axinyssa*, but the type of that genus, *P. hirsuta* Carter, 1883, is a spinous Raspailiid.

Species examined: *Axinyssa topsenti* Von Lendenfeld (1897) (holotype in the Berlin Museum (Fig. 14), fragments in BMNH (Fig. 17)), *A. tethyoides* Kirkpatrick (1903) (holotype in BMNH (Figs. 16, 18), *A. gravieri* Topsent, 1893 (holotype, MNHN DT. 1873), *A. aculeata* Wilson (1925) (holotype USNM. 21341 (Fig. 19) and ZMA specimens from Indonesia), *A. aplysinoides* (Dendy, 1922 as *Halichondria* (Fig. 16)) (holotype BMNH.1921:11:7:31 and ZMA specimens from Indonesia (Fig. 20)), *A. ambrosia* (De Laubenfels, 1934 as *Raphisia*) (holotype USNM. 22445, holotype of *Leucophloeus lewisi* Van Soest & Stentoft, 1988 ZMA 5401 which is now considered a junior synonym; holotype of *Dictyonella yumae* Pulitzer-Finali, 1986 Mus. Genova CE 47694; ZMA specimens from Curaçao (Fig. 21) and Puerto Rico)), *A. fenestratus* Ridley, 1884 (holotype, BMNH 82:2:23:253; ZMA specimens from Indonesia), *A. valida* (Thiele, 1899 as *Phycopsis*) (holotype, Mus. Basel no. 154; ZMA specimens from Indonesia), *A. radiata* (Lévi & Lévi, 1983 as *Prostylyssa*) (holotype fragment MNHN DCl. 2954 examined). Geographical

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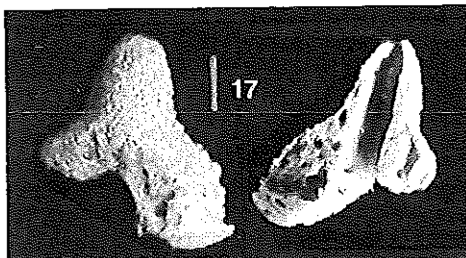
Figs. 14-16.
Fig. 14. *Axinyssa topsenti* Von Lendenfeld, 1897, A. Habit (redrawn from Lendenfeld, 1897: pl. 10 fig. 134) (s.b. = 1 cm), B. longitudinal section of one of the oscular cones to show skeletal architecture (s.b. = 1 mm), C. tangential view of ectosome showing spicule brushes and single oxea (redrawn from Lendenfeld, 1897: pl. 10 fig. 144) (s.b. = 100µm), D. spicules (s.b. = 100 µm).
Fig. 15. *Axinyssa aplysinoides* (Dendy, 1922), A. Habit (redrawn after Dendy, 1922: pl. 3 fig. 3) (s.b. = 1 cm), B. Cross section showing confused spicule tracts with ill-developed spicule brushes (s.b. = 1 mm), C. spicules (s.b. = 100 µm).
Fig. 16. *Axinyssa tethyoides* Kirkpatrick, 1903 (type of *Pseudaxinyssa*), A. skeletal architecture (redrawn from Kirkpatrick, 1903: pl. 6 fig. 8) (s.b. = 1 mm), B. peripheral endings of choanosomal spicule tracts enveloped in spongin coat (s.b. = 0.5 mm), C. oxea (s.b. = 100 µm).



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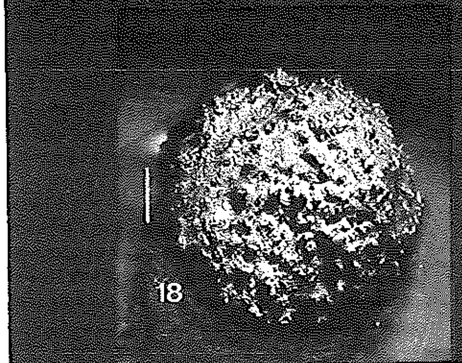

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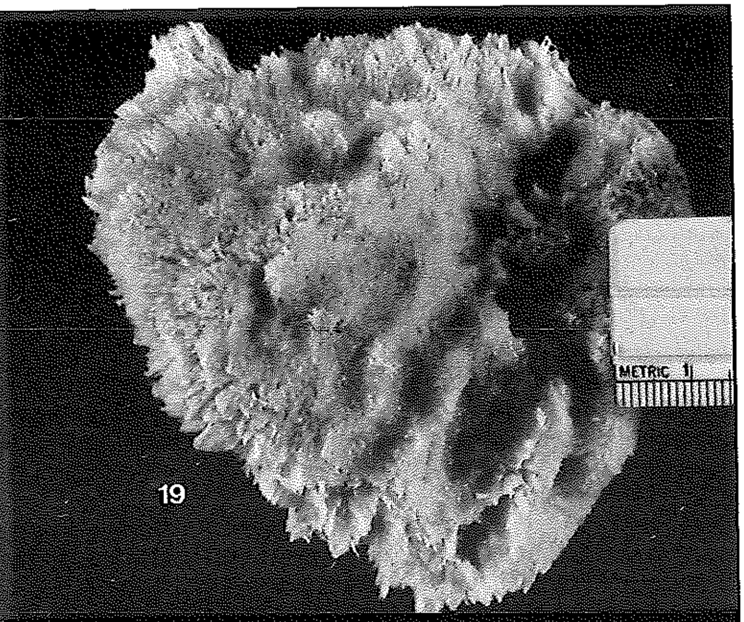

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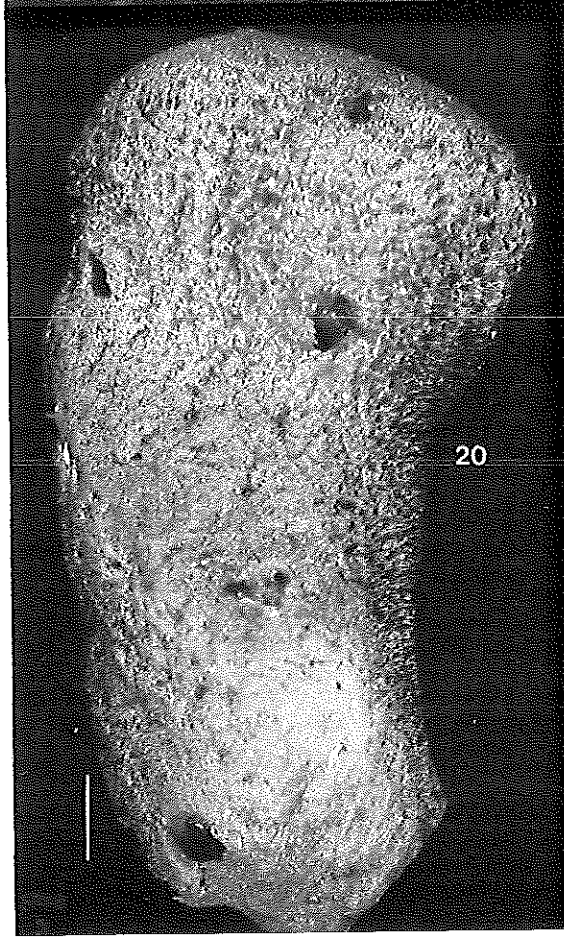

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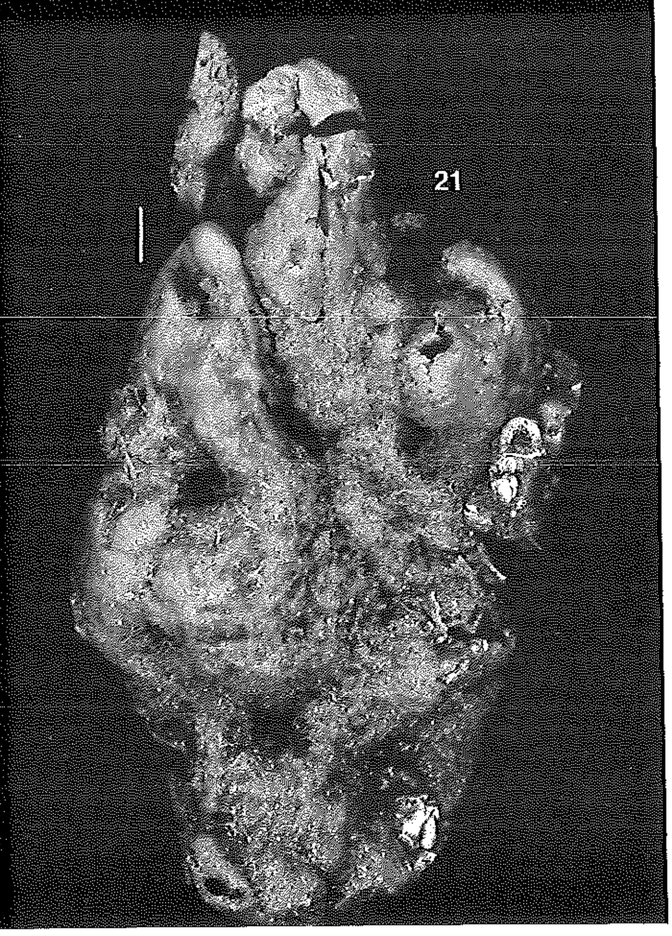

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distribution: probably confined to the tropical regions of the three oceans.

Genus *Collocalypta* Dendy, 1905: 199.
Fig. 23

Type species: *Collocalypta digitata* Dendy, 1905: 199, pl. VII fig. 6, pl. XIII figs. 1-2. (Holotype BMNH 1907:2:6:89 reexamined).

Definition: Halichondriidae of the genus group *Axinyssa-Collocalypta*, with *Ciocalypta*-like fistulose habit and architecture but without ectosomal skeleton and with highly collagenous choanosome.

Remarks: So far only two species have been assigned to this genus, viz. the type species and *C. aderma* Lévi & Vacelet, 1958. Some doubt as to the generic distinctness of *Collocalypta* and *Ciocalypta* seems justified. The central column of spicules with diverging spicule tracts carrying the ectosome is present in both. Conceivably the present species are *Ciocalypta* having lost the ectosomal skeleton (which also is assumed to have occurred in some *Halichondria* species). On the other hand, the fistular habit seems a clear adaptation to life on sandy bottom and there may well be no other way to build a fistule with the confused spicular arrangement found in the Halichondriidae. Hence the occurrence of similar fistules in unrelated *Petromica, Coelocalypta* (= *Topsentia*) and *Ciocalapata* (= *Halichondria*).

Species examined: *C. digitata* (holotype and ZMA specimens from Indonesia).
Geographic distribution: India, Indonesia, Eastern Atlantic.

Genus group *Myrmekioderma-Didiscus*:

Halichondriidae with sinuous surface grooves and ectosomal skeletal strengthening of palissade-like arranged smaller spicules erected on a crust of tangential larger megascleres.

Remark: The remaining Halichondriid genera are all characterized by an ectosomal strengthening skeleton; in most this takes the form of a tangential spicule arrangement (which may occasionally be absent, e.g. in some *Topsentia* or *Halichondria*), while in the present genus group species have variously arranged crust-like ectosomes, which consist at least partly of semi-erect (non-tangential) spicules on top of a layer of tangential spicules.

Genus *Myrmekioderma* Ehlers, 1870:32.
Figs. 24-30

Type species (monotypy): *Alcyonium granulatum* Esper, 1794: 71, pl. XXIV (holotype not examined, possibly lost).

Definition (emended): Halichondriidae of the genus group *Myrmekioderma-Didiscus* with one or more categories of trichodragmata, the larger of which are sinuously curved.

Remark: As a distinguishing feature of the genus the possession of an acanthose smaller category of megascleres has been traditionally used. However, recent studies of the variability of the acanthose condition of these spicules in the type species and in Caribbean representatives has revealed that the spination may be weak or even absent in many individuals. This led to the assignment of species of the genera

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Figs. 17-21.
Fig. 17. *Axinyssa topsenti* Von Lendenfeld, 1897, BMNH type fragment 1908:9:24:145 from Zanzibar, photographed from outer and inner side (s.b. = 0.5 cm).
Fig. 18. *Axinyssa tethyoides* Kirkpatrick, 1903, holotype BMNH 1902:11:16:25 from the Natal coast (s.b. = 1 cm).
Fig. 19. *Axinyssa aculeata* Wilson, 1925, holotype USNM 21341 from the Philippine region (s.b. = 1 cm).
Fig. 20. *Axinyssa aplysinoides* (Dendy, 1922), ZMA specimen from Indonesia (s.b. = 1 cm) (photo H.. van Brandwijk).
Fig. 21. *Axinyssa ambrosia* (De Laubenfels, 1934), ZMA specimen from Curaçao (s.b. = 1 cm) (photo H. van Brandwijk).

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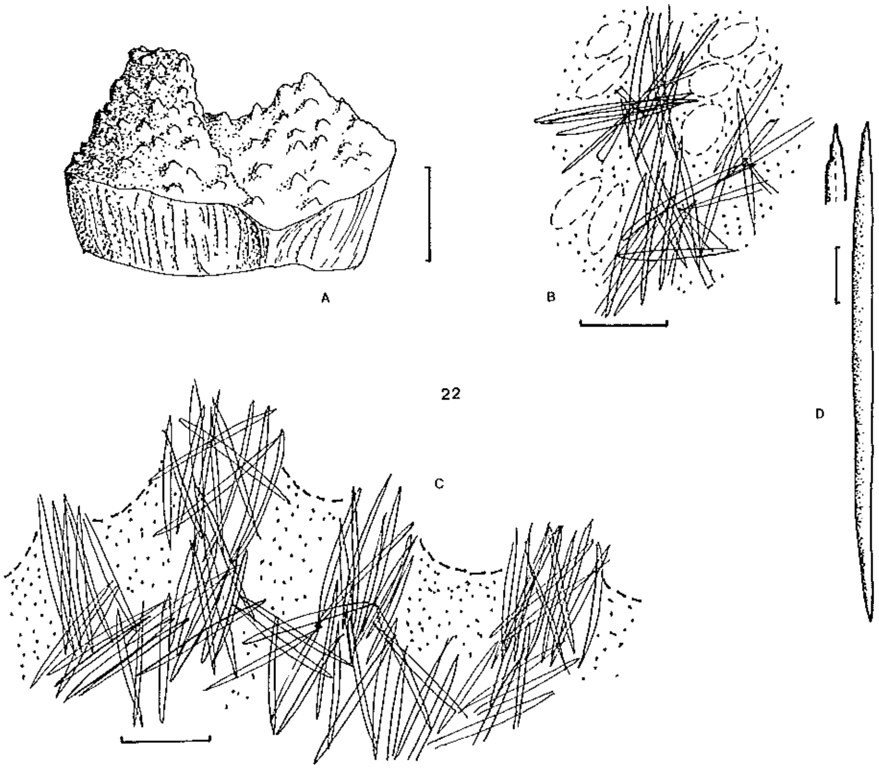

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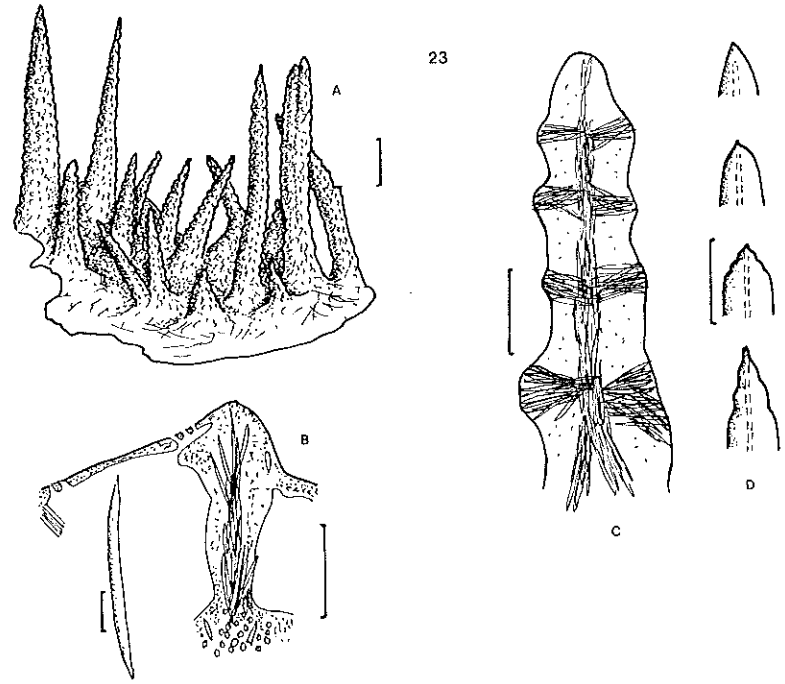


Anacanthaea and *Epipolasis* (several species except the type species) to *Myrmekioderma*. Several species of *Myrmekioderma* reveal the presence of quantities of spongin, which may cause the spicules to be arranged in irregular thick tracts.

Synonyms:

Genus *Acanthoxifer* Dendy, 1905:157.
Type species (monotypy): *A. ceylonensis* Dendy, 1905: 157, pl. IX fig. 5 (holotype not examined).
See for details of this synonymization: Bergquist, 1965: 177.

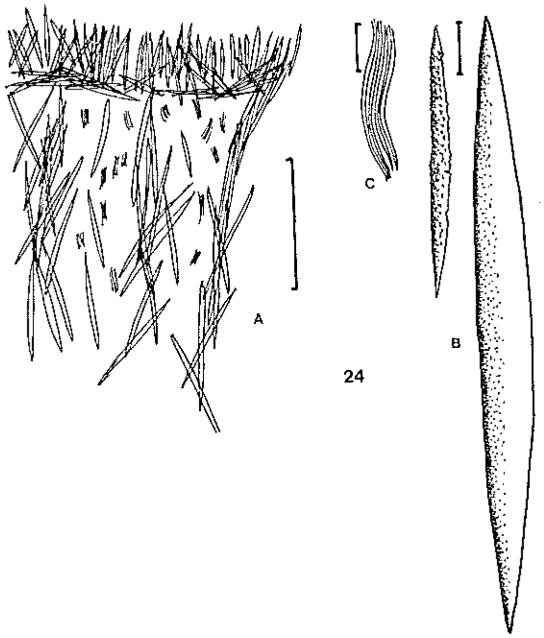
Genus *Anacanthaea* Rowe, 1911: 329.
(Fig. 25)
Type species (monotypy): *A. nivea* Rowe, 1911: 329, pl. 38 fig. 17, text-fig. 14 (holotype fragment BMNH reg. no. 1912:2:1:54 reexamined)
Rowe: "Heteroxyinae in which the oxea are not differentiated into two forms, and without spines on them. There are no microscleres."
Remarks: The external surface of the upright-lamellar specimen has the characteristic grooves (Rowe's pl. 38 fig. 17) making polygonal areas; brushes of smooth oxea form a cortical skeleton; oxea are 350-430 by 6-10 µm with stair-stepped apices; not mentioned in the original description but nevertheless present are two sizes of trichodragmata (20 and 110 µm), the larger of which is sinuous.

?Genus *Callites* Schmidt, 1868: 16.
(Fig. 26)
Type species (monotypy): *Callites lacazii* Schmidt, 1868: 16, pl. III fig. 2 (microscopic slide in BMNH reexamined).
Schmidt: "Eine auf der Grenze zwischen den Compagineen und den Gummineen stehende Gattung, wo die Sarcode-Substanz ein höchst unregelmässiges Gerüst oder Fachwerk, auch Gänge und Röhren bildet, jedoch keine die Gummineen charakterisierende Rindenschicht. Es sind Kieselgebilde vorhanden".
Remarks: The identity of Schmidt's species remains uncertain, because the description focusses on what can only be abnormally developed spicules, polyaxone proliferations of malformed, crooked oxea. The British Museum (Nat. Hist.) holds a spicule slide preparation with a label in Schmidt's handwriting. The slide contains oxeote spicules in three categories: 443-680/12-15 µm, 196-320/4-9 µm, and 80-121/1-2 µm; there are a few malformations, blunt or stair-stepped apices with wide axial canals, etc. No rhaphides have been found, and coupled to the three size categories of oxea the most likely genus for it would be *Topsentia*. However, in the absence of a type specimen (Topsent, 1945; Desqueyroux, pers. comm.) it is proposed here to consider the genus and the species *incertae sedis*, although Tsurnamal (1969) claimed the rediscovery of the species in Israelian waters. Tsurnamal's material (Fig. 26) clearly belongs to the genus *Myrmekioderma* through its possession of a confused skeleton of oxeote spicules of three size categories, a complement of flexuous rhaphides, and a palissade-like arrangement of smaller oxea in the ectosomal crust. It is assumed here, that Tsurnamal's material belongs to *Myrmekioderma spelea* (Pulitzer-Finali, 1983). If Schmidt's species would at any time be proven to be identical to this species, than *Myrmekioderma* Ehlers, 1870 will become a junior synonym of *Callites* Schmidt, 1868.

?Genus *Heteroxya* Topsent, 1904: 133.
(Fig. 27)
Type species (monotypy): *H. corticata* Topsent, 1904: 133, pl. I fig. 15, pl. XII figs. 22-23 (holotype slide MNHN DT. 905 reexamined).
Topsent: "Tethyidae revêtantes, sans microsclères, à choanosome à peu près aspiculeux, à ectosome en revanche différencié en une écorce solide armée d'oxes de deux sortes, disposés verticalement: les uns tres nombreux et serrés, les autres, solitaires, déterminant le hispidation de la surface".
Remark: no mention is made of surface grooves; no trichodragmata have been found in the slide; the holotype (Fig. 27) is described as a hispid plaque of 2 mm thick; oxea are 1600-2000 by 35, and acanthoxea are 235-420 by 11-23 µm. Conclusion: reexamination of the holotype is necessary.

Genus *Neoprosypa* De Laubenfels, 1954: 189.
Type species (monotypy): *N. atina* De Laubenfels, 1954: 190, fig. 127 (holotype USNM 22974 reexamined).

Figs. 22-23.
Fig. 22. *Axinella* (= *Axinyssa*) *paradoxa* (Ridley & Dendy, 1886), A. habit (redrawn from Ridley & Dendy, 1887: pl. 25 fig. 4) (s.b. = 1 cm), B. tangential view of ectosome (s.b. = 0.5 mm), C. cross section of peripheral region (s.b. = 0.5 mm), D. spicules (s.b. = 100 µm) (B-D made from the BMNH type specimen).
Fig. 23. *Collocalypta digitata* (Dendy, 1905), A. habit (redrawn from Dendy, 1905: pl. 7 fig. 6) (s.b. = 1 cm), B. cross section of peripheral region (s.b. = 1 mm), with as inset a typical spicule (s.b. = 100 µm) (both redrawn from Dendy, 1905: pl. 13 figs. 1-2), C. longitudinal section of apex of fistule to show architecture (s.b. = 0.5 mm), D. spicule apices (s.b. = 50 µm).



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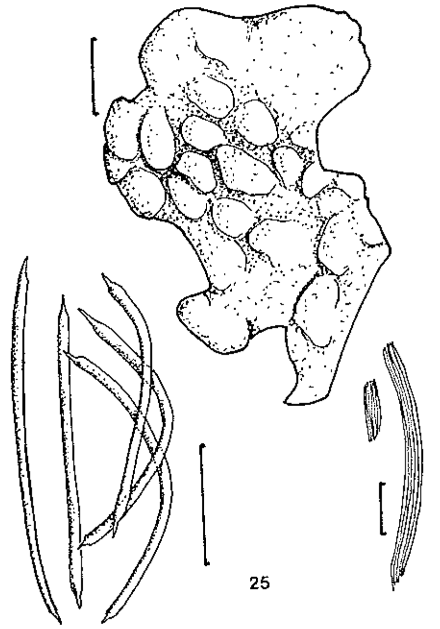
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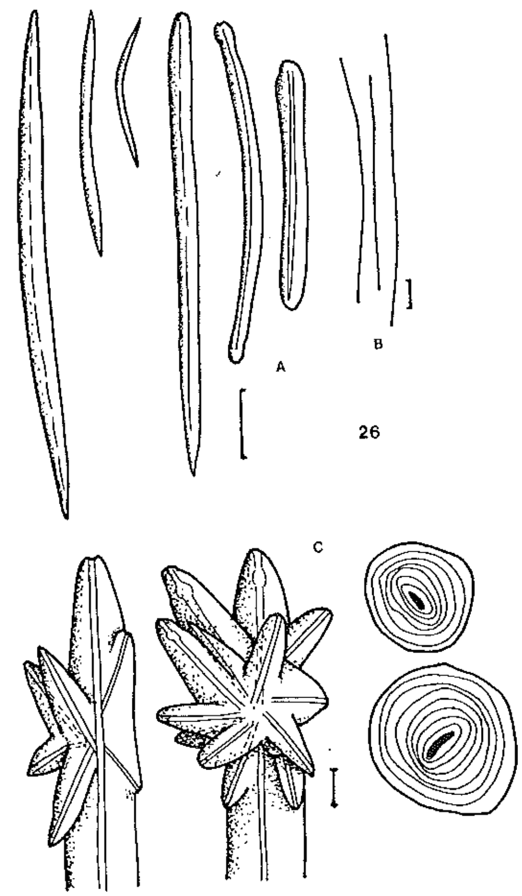

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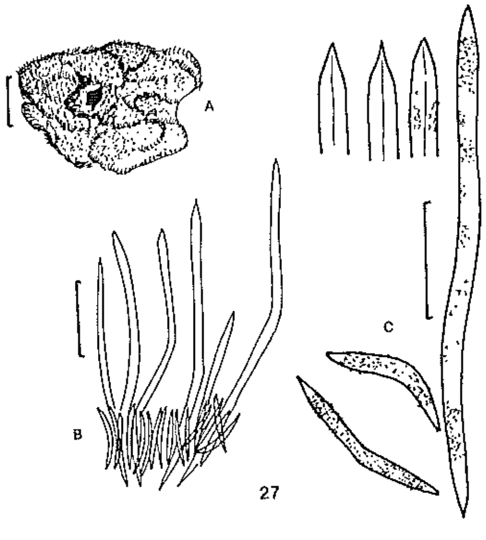

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See for details of this synonymization Bergquist, 1965: 177.

The genus *Raspaigella* Schmidt, 1868 has been used for species of *Myrmekioderma*, e.g. by Burton (1959) and Vacelet & Vasseur (1971), but the type species (monotypy), *R. brunnea* Schmidt, 1868, is a *Halichondria* (see also there).

The genus *Epipolasis* De Laubenfels, 1936 has been used for species of *Myrmekioderma*, *e.g.* by Díaz *et all.* (1987) and Van Soest & Stentoft (1988), but the type species (original designation), *Spongosorites suluensis* Wilson (1925) has unique characters which make it necessary to uphold it as a separate genus (see also there).

Species examined: *Myrmekioderma granulata* (Esper, 1794) (ZMA specimens (Fig. 28) from Indonesia; holotype of *Neoprosypa atina*), *M. styx* De Laubenfels, 1953 (holotype USNM 23400; HBOI specimens (Fig. 24); ZMA specimens including the holotype (Figs. 29-30) and paratypes of *Epipolasis reiswigi* Díaz *et al.* 1987 which is a junior synonym of *M. styx*), *M. rea* De Laubenfels, 1934 (as *Anacanthaea*) (holotype USNM 22301; HBOI specimens; ZMA specimens), *M. tulearensis* (Vacelet, Vasseur & Lévi, 1976) (holotype MNHN.D.JV.20), *M. dendyi* (Burton, 1959) (ZMA specimens from Indonesia), *M. spelea* Pulitzer-Finali, 1983 (as *Raphisia*) (holotype in Mus. Genova PTR D.18; Aegean specimens collected by E. Voultsiadou-Koukoura).

Geographical distribution: tropical and subtropical parts of all three oceans, Mediterranean; not known from the East Pacific.

Genus *Didiscus* Dendy, 1922: 135
Figs. 31-32, 36-40

Type species (monotypy): *D. placospongioides* Dendy, 1922: 135, pl. 7 fig. 10, pl. 18 fig. 3 (holotype BMNH 11:7:112 reexamined).

Definition (emended): Halichondriidae of the *Myrmekioderma-Didiscus* genus-group with discorhabds.

Remarks: The discorhabds tend to be arranged peripherally perpendicular to the surface; this arrangement is assumed to be homologous to that of the palissade of small oxeotes of *Myrmekioderma*. The genus has been associated with *Latrunculia* (Hadromerida) on account of the similarity of the microscleres. This similarity is non-homologous, the 'discorhabds' of *Latrunculia* are streptasters/spirasters, while those of *Didiscus* can be traced back to centrotylote microxea. In some cases microxea of a size equal to that of the discorhabds and ornamented with small spines are found as abnormal variations of the discorhabds; these are quite similar to acanthose microxea found in *Myrmekioderma*, though much smaller.

For a review of all species and a phylogenetic analysis of the genus see Hiemstra & Van Soest (in press).

Synonyms: none.

Species examined: *D. placospongioides* Dendy, 1922 (holotype, Fig. 31), *D. aceratus* (Ridley & Dendy, 1886 as *Latrunculia*) (ZMA specimens from Indonesia), *D. oxeata* Hechtel, 1983 (holotype YPM 8969 from Brazil; holotype fragment

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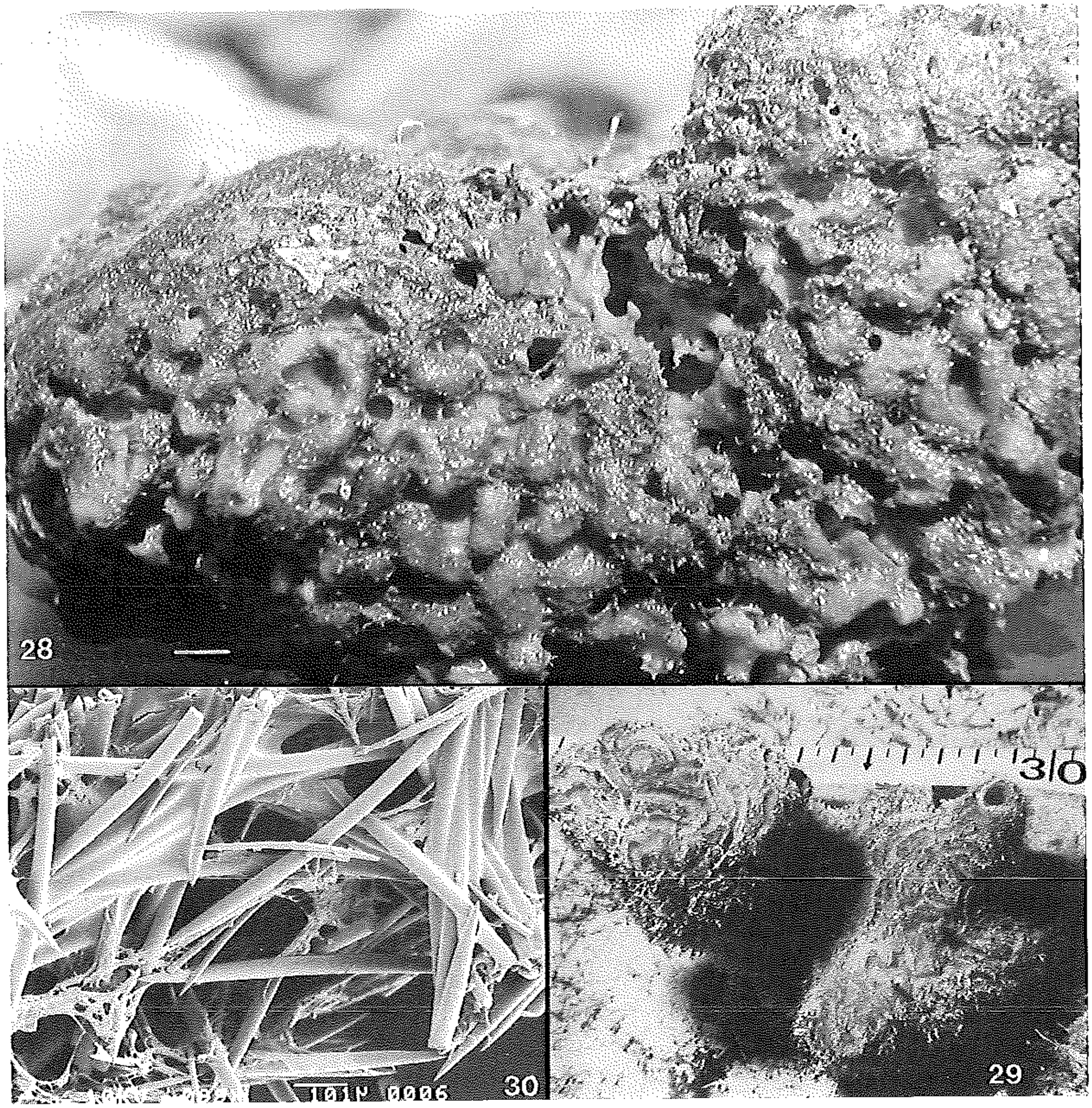
Figs. 24-27.

Fig. 24. *Myrmekioderma styx* De Laubenfels (1953), A. cross section of peripheral region to show ectosomal palissade (redrawn from Díaz *et al.*, 1990a) (s.b. = 1 mm), B. megascleres (s.b. = 50 µm), C. sinuous trichodragmata (s.b. = 25 µm) (B-C after Van Soest & Stentoft, 1988: fig. 43).

Fig. 25. *Anacanthaea* (= *Myrmekioderma*) *nivea* Row, 1911, A. habit (redrawn from Row, 1911: pl. 38 fig. 17) (s.b. = 1 cm), B. megascleres (redrawn from Row, 1911: fig. 14), C. sinuous trichodragmata (found in the BMNH type specimen) (s.b. = 25 µm).

Fig. 26. *Callites lacazei* sensu Tsurnamal, 1969 (= probably *Myrmekioderma spelea* (Pulitzer-Finali, 1983), A. megascleres (s.b. = 100 µm), B. rhaphides (s.b. = 10 µm), C. malformed spicules (s.b. = 10 µm) (all redrawn from Tsurnamal, 1969: fig. 26).

Fig. 27. *Heteroxya* (? = *Myrmekioderma*) *corticata* Topsent, 1904, A. habit (s.b. = 1 cm), B. cross section of peripheral region (s.b. = 0.5 mm), C. acanthoxea (s.b. = 100 µm) (all redrawn from Topsent, 1904: pl. 1 fig. 15, pl. 12 figs. 22-23).



Figs. 28-30.
Fig. 28. *Myrmekioderma granulata* (Esper, 1794), ZMA specimen from Indonesia (s.b. = 1 cm).
Fig. 29. *Epipolasis reiswigi* Díaz *et al.*, 1987 (= *Myrmekioderma styx* De Laubenfels, 1953), holotype in situ in reefs of Los Roques, Venezuela (photo E. Weil).
Fig. 30. *Myrmekioderma styx* De Laubenfels, 1953, SEM photo of choanosomal skeletal arrangement (photo F. Hiemstra).

of *D. habanensis* Alcolado, 1984 (junior synonym) in USNM; holotype (ZMA 4889) (Figs. 36-39) and paratypes (ZMA 4890-4892) of *D. flavus* Van Soest, 1984 (junior synonym); HBOI specimens from Jamaica (Fig. 32), ZMA specimens from Curaçao and Colombia), *D. anisodiscus* Vacelet & Vasseur, 1971 (ZMA specimens from Indonesia) (Fig. 40), *D. styliferus* Tsurnamal, 1968 (holotype from Tel-Aviv Museum, Mediterranean specimen of Pulitzer-Finali, 1983 examined in Mus. Genova), *D. verdensis* Hiemstra & Van Soest, in press (holotype and paratypes in ZMA from Cape Verde Islands). Geographical distribution: tropical and subtropical parts of all three oceans; not known from the East Pacific; occurrence in North Australia (Pulitzer-Finali, 1982) is doubtful.

Genus group *Spongosorites-Topsentia-Epipolasis-Petromica-Ciocalypta-Amorphinopsis-Halichondria-Hymeniacidon*:
Halichondriidae which have lost the collagenous nature of the choanosome.

Genus *Spongosorites* Topsent, 1896: 117.
Figs. 33-35, 41-44

Type species (monotypy): *S. placenta* Topsent, 1896: 117 (type slide MNHN DT.904 reexamined).

Definition (emended): Halichondriidae with a smooth, flaky crust of paratangentially arranged, relatively thin spicules, and a choanosomal utterly confused skeleton which is traversed by spongin-enforced tracts running more or less parallel to the surface. Most species show an aerophobic colour-change from yellow to greyish brown or black.

Remarks: The emended diagnosis is based on reexamination of the type slide in MNHN (D.T.904) and on a specimen of the MNHN collection identified by Prof. Lévi; the type specimen (Fig. 33) itself seems to be lost. Emphasis in the past has been put to the frequent malformations or centrotylote conditions in the smaller category of oxeotes, but this is not a consistent character; moreover, it is also infrequently found in other genera, e.g. *Topsentia*. For that reason, *Spongosorites* has often been considered a senior synonym of the latter genus (e.g. a MNHN specimen identified by Topsent himself as *S. placenta*, D.T.1116, is a *Topsentia*). However, the two are clearly distinct in architecture, spicule sizes and shapes, and especially in the aerophobic properties. All chemically examined species reveal the presence of topsentin (Fig. 34B), a biochemical compound apparently confined to the genus. Unfortunately, the specimen upon which the first report of topsentin (Bartik *et al.*, 1987) was based, was erroneously identified as a *Topsentia*. Those true *Topsentia* species examined so far, did not reveal the presence of topsentin. The phylogenetic relationships of the genus are uncertain; it stands rather isolated through lack of distinct synapomorphies with other genera.

Synonyms:

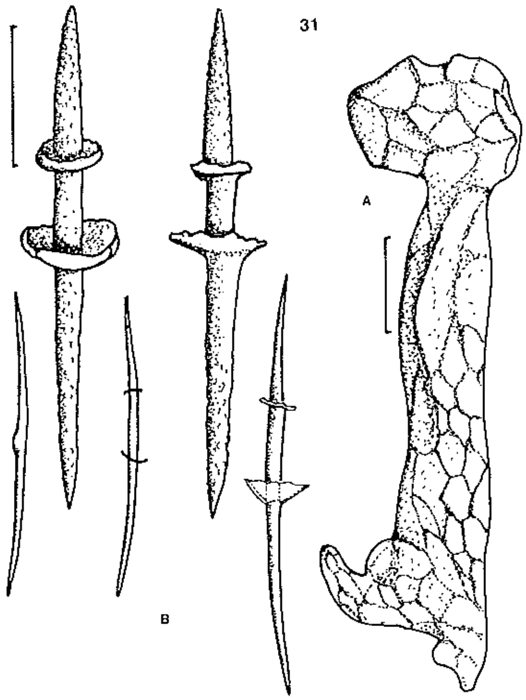
Genus *Aponastra* Topsent, 1927: 5
(Fig. 35)
Type species (monotypy): *A. dendyi* Topsent, 1927: 5 (type slide reexamined).
Topsent: "Spongosoritidae à ectosome différencié en écorce, à charpente choanosomique grossièrement fasciculée, irrégulière, pourvue d'oxes et de microrhabdes plus ou moins centrotylotes, ces derniers parsemant la chair et s'accumulant dans la couche externe de l'écorce en un feutrage tangentiel, à la façon de ceux de l'ectochrote des *Erylus*."
Remarks: the type species (Fig. 35) is described as black, and has spicules 500 by 16-20 and 45-145 by 2-7 µm. A slide of the type specimen has been examined (MNHN D.T. 2865) and it conforms completely to *Spongosorites*, possibly to *S. placenta*.

Species examined: *S. placenta* Topsent, 1896 (type slide and topotypical specimen from the North Atlantic, in MNHN) (Fig. 33), *S. intricata* (Topsent, 1892) (specimens identified by Pulitzer-Finali, 1983; specimen in ZMA from Norway), *S. ruetzleri* (Van Soest & Stentoft, 1988) (as *?Halichondria*) (type specimens in ZMA, HBOI specimens, Fig. 34)), *S. siliquaria* Van Soest & Stentoft, 1988 (type specimens in ZMA, Figs. 42-44), *S.* spec. (ZMA specimen from Indonesia), *S.* n. spec. (HBOI specimens, Fig. 41).
Geographical distribution: tropical, subtropical and temperate regions of all three oceans.

Genus-group *Topsentia-Epipolasis-Petromica*:

Halichondriidae without any spongin resulting in an utterly confused arrangement of spicules.

Genus *Topsentia* Berg, 1899: 77.
Figs. 45-55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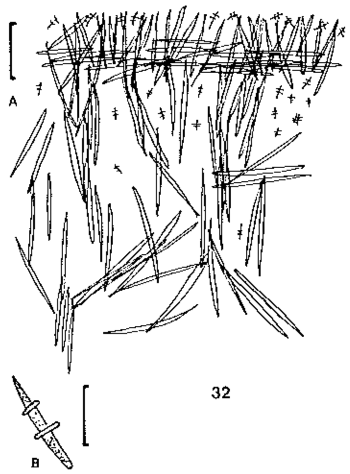
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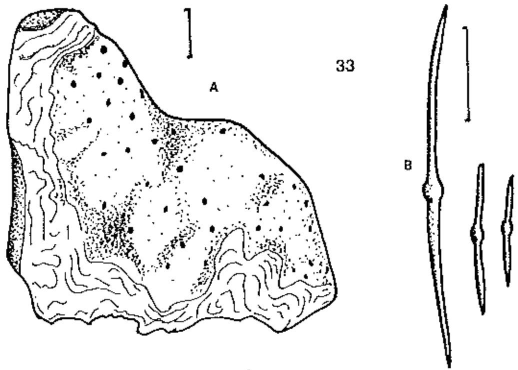
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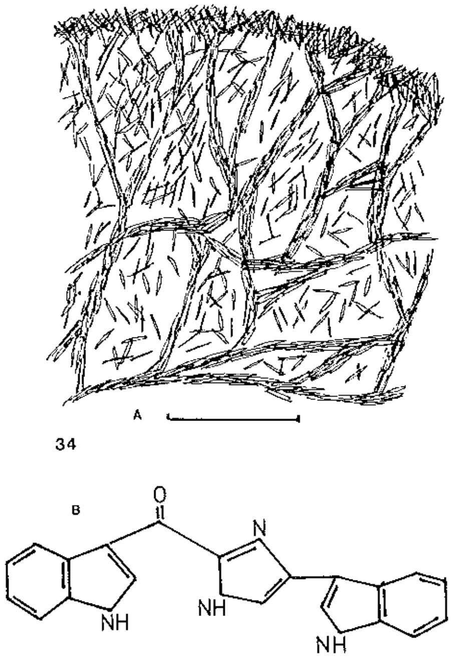
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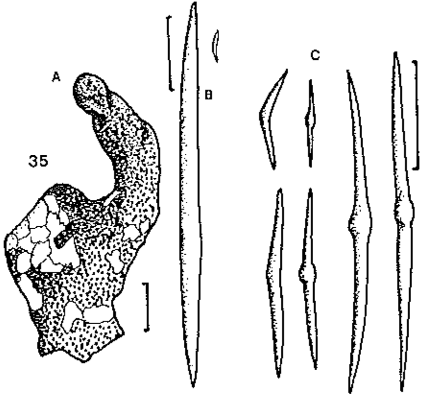
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Type species (original designation): *Anisoxya glabra* Topsent, 1989: 234 (type slide MNHN DT.1169 and topotypical specimen examined).

Definition (emended): Halichondriidae of the *Topsentia-Epipolasis-Petromica* genus-group with an utterly confused ectosomal crust.

Remarks: This is a decidedly brittle-siliceous type of sponge, which is also characterized by lacking bright colours (one bright yellow species excepted), dirty rosy white or greenish drab colouration being favoured. Many representatives also have lost their ectosomal crust-like specialization (no doubt due to absence of distinct smaller size categories of megascleres), in stead of which they have an utterly confused peripheral skeleton (Fig. 45) with individual spicules sticking out for a short distance producing an optically smooth, but rough-to-the-touch surface. The absence of a distinct crust is here merely interpreted as independent loss. Occasionally, spicules maybe sinuous or twisted, showing similarities with non-Halichondriid genera as *Bubaris* and *Dactylella*. Occasionally, the smaller category of (peripheral) oxea is centrotylote or malformed as is found quite commonly in *Spongosorites*. The present genus has indeed been confused or synonymized quite often with the latter genus, but both are clearly distinct morphologically as well as biochemically (see under *Spongosorites*).
Topsentia differs from the closely related genus *Epipolasis* in the absence of rhaphides, and in the presence of unique secondary metabolites (Pomponi *et al.*, 1990).

Synonyms:

Genus *Allosclera* Topsent, 1927: 6.
(Fig. 47)
Type species (original designation); *A. tenuispinosa* Topsent, 1927: 6 (type slide MNHN D.T. 1190 reexamined).
Topsent: "Spongosoritidae à spicules de deux sortes, les uns monactinaux, plus grands, représentant les éléments principaux, d'une charpente vaguement halichondroide, lâche, sans spongine, les autres diactinaux, de petite taille et de rôle accessoire, épars et nombreux."
Topsent claims there are acanthoxea among the small oxeotes (65-120 by 1-2 µm), but we could not find these in the type slide; the monactinal spicules are more definitely strongyloxea (350-500 by 7-10 µm). Later (1904), Topsent assigned some specimens of the type series of *Topsentia glabra* to the present "species"; this confusing action appears unnecessary as both "species" are probably synonymous.

Genus *Anisoxya* Topsent, 1898: 234 (type slide examined, MNHN D.T.1169).
Type species (monotypy): *A. glabra* Topsent, 1898: 234.
Preoccupied: this is an objective junior homonym of *Anisoxya* Mulsant, 1856.

Genus *Trachyopsis* Dendy, 1905: 147.
(Fig. 46)
Type species (monotypy): *T. halichondrioides* Dendy, 1905: 147, pl. X fig. 10 (holotype reexamined).
Dendy: "Renierinae in which the main skeleton is composed of a dense irregular network of oxea, while the surface is protected by similar (or perhaps more slender) spicules arranged in dense vertical brushes, which support the pore-bearing membrane."
Remarks: The type specimen (BMNH reg. no. 1907:2:1:44) has been reexamined and found to be like *Topsentia*, but lacking a clear categorization of the short and thick oxea, all oxea being more or less close to 600-700 by 30-35 µm. The consistency is hard and compact, due to the extremely dense and irregular arrangement of the oxea in the choanosome; the peripheral regions are relatively well-organized. Several other species have been

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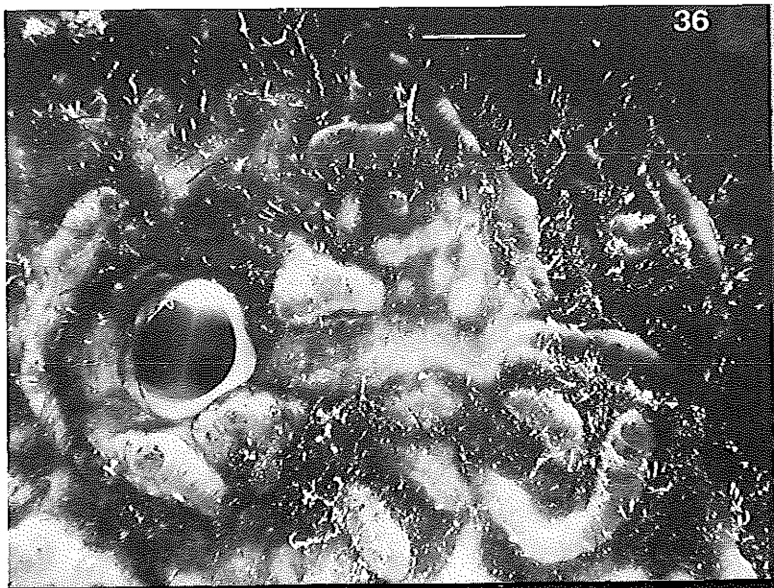
Figs. 31-35.
Fig. 31. *Didiscus placospongioides* (Dendy, 1922), A. habit (s.b. = 1 cm), B. discorhabds in various stages of development (s.b. = 25 µm) (all redrawn from Dendy, 1922: pl. 7 fig. 10, pl. 18 fig. 3).
Fig. 32. *Didiscus oxeata* Hechtel, 1983, A. cross section of peripheral region to show ill-developed ectosomal palissade (s.b. = 0.5 mm), B. discorhabd (s.b. = 50 µm) (all redrawn from Díaz *et al.*, 1990a).
Fig. 33. *Spongosorites placenta* Topsent, 1896, A. habit (s.b. = 1 cm), B. spicules (s.b. = 100 µm) (all redrawn from Topsent, 1904: pl. 10 fig. 6, pl. 12 fig. 21).
Fig. 34. *Spongosorites ruetzleri* (Van Soest & Stentoft, 1988), A. cross section of peripheral region to show directionless spicule tracts (redrawn from Díaz *et al.*, 1990a) (s.b. = 0.5 mm), B. topsentin (redrawn from Bartik *et al.*, 1987).
Fig. 35. *Aponastra* (= *Spongosorites*) *dendyi* Topsent, 1927, A. habit (redrawn from Topsent, 1928: pl. 3 fig. 24) (s.b. = 1 cm), B-C. spicules (s.b. = 100 µm).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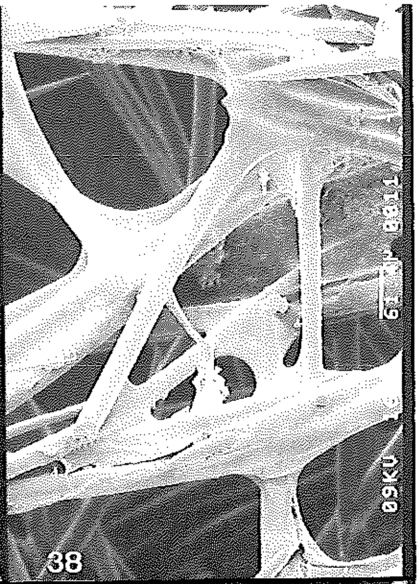
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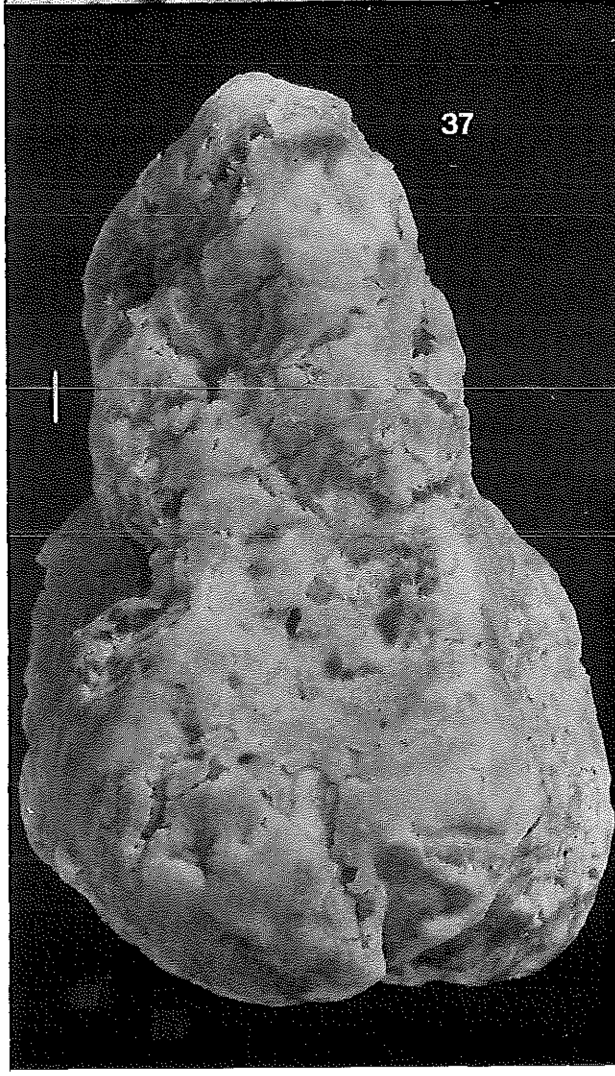
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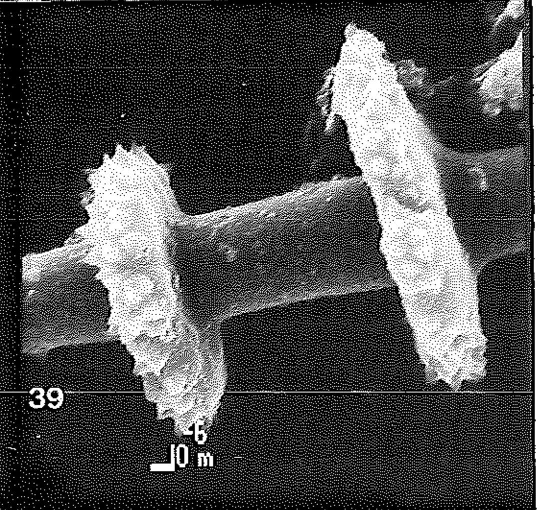
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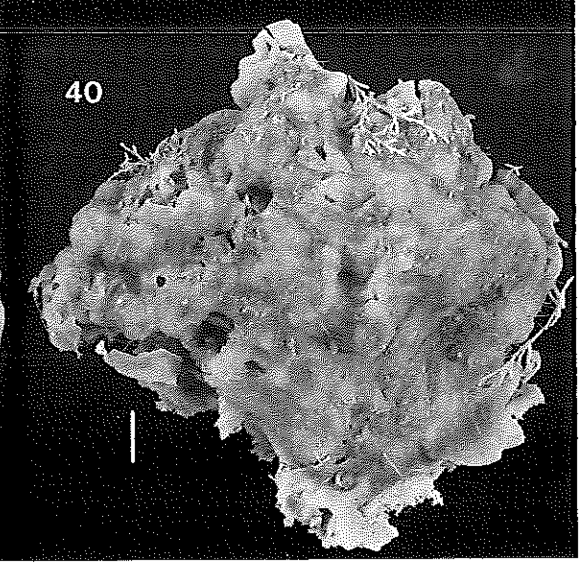
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assigned to this genus, but only the type species conforms to *Topsentia*.

Genus *Coelocalypta* Topsent, 1928: 167.
(Figs. 48, 53)
Type species (monotypy): *C. porrecta* Topsent, 1928: 167, pl. II fig. 6, pl. VI fig. 4.
Topsent: "Axinellides sans microsclères, composées comme les *Ciocalypta* d'un corps massif, de structure halichondroide, d'où s'élèvent des processus digitiformes aquifères. Ces processus sont creux; leur paroi, faite surtout d'une couche relativement épaisse où des spicules libres se placent debout très près les uns des autres, est soutenue par une assise interne spiculofibreuse, plus mince, équivalente à la colonne axiale de ceux des *Ciocalypyta*." (Fig. 48)
Remarks: The type species resembles *Ciocalypta penicillus*, although it is more solid and the 'fistules' are thicker (Fig. 53); the colour of topotypical specimens collected recently appeared to be strikingly yellow. The oxea of the holotype are 280-1000 by 4-50 µm; specimens from the Caribbean assigned to this species (Van Soest & Stentoft, 1988) have a larger upper limit to spicule size; they are not conspecific. All known specimens have oxeotes as the only spicules. Some doubt exists over the generic differences between this species and the genus *Ciocalypta*, because the habit and the internal fistule architecture of the two are similar. The view is taken here that both features are subject to environmental demands and constitute convergent developments (compare also *Petromica, Ciocalapata* and *Cioxeamastia*).

?Genus *Oxeostilon* Ferrer Hernandez, 1922: 10.
(Fig. 49)
Type species (monotypy): *O. annandalei* Ferrer Hernandez, 1922: 9, figs. 8-9, pl. I (see Fig. 49) (no material examined).
Ferrer-Hernandez: "Axinellidas con esqueleto formado por fibras espiculosas ascendentes, que terminan en pinceles de espiculas normales a la superficie y la cual atraviesan. Oxeas predominantes y dobladas en angulo y estilos probablemente derivados de aquellas por reduccion total o parcial de una actina o radio."
Remarks: The specimen is described as a smooth plaque, with skeletal tracts. On that basis it is possible that it is a *Spongosorites*. However, spicules sizes are a bit on the large side: 320-400 by 5 and 400-800 by 12 µm, and therefore we assume that this is a *Topsentia*.

Genus *Laminospongia* Pulitzer-Finali, 1983: 546.
(Fig. 50)
Type species (monotypy): *L. subtilis* Pulitzer-Finali, 1983: 547, fig. 59, 59bis. Holotype: Genova Museum reg. no. 47175 (reexamined).
Pulitzer-Finali: "Hymeniacidonidae of laminar form, with a halichondroid skeleton of oxeas to styles variously modified".
Remarks: The consistency of the type specimen is described as firm, it has a *Halichondria*-like but not separable ectosomal skeleton, and the oxea-styles-strongyles of 350-1300 by 9-19 µm are in confusion; some spongin is found binding single spicules.

Species examined: *Topsentia glabra* (Topsent, 1898) (Fig. 47) (type slide, topotypical specimen MNHN DT.1389), *T. ophiraphidites* (De Laubenfels, 1934) (Figs. 45, 51-52) (holotype USNM 22334; holotype (FCLR coll. no. 125 from Venezuela) and paratypes (ZMA 5839-5840 from Curaçao) of *T. roquensis* Díaz *et al.*, 1987, which is now considered a junior synonym; holotype of *Spongosorites sinuatus* Pulitzer-Finali, 1986 Mus. Genova no. 47961 which is considered a junior synonym; holotype YPM 8988 of *Halichondria braziliensis* Hechtel, 1983 from Brazil, which is considered a junior synonym), *T. porrecta* (Topsent, 1928 as *Coelocalypta*) (type in MNHN and topotypical specimens in ZMA (Figs. 48, 53)), *T.* n.sp. Díaz *et al.*, in press (Caribbean specimens identified as *T. porrecta* by Van Soest & Stentoft, 1988 in ZMA; HBOI specimens from Bahamas (Fig. 54)), *T. halichondrioides* (type in BMNH (Fig. 46), specimens from Aldabra in MNHN DCl. 361), *T. dura* (Lindgren, 1897 as *Halichon-*

Figs. 36-40.
Fig. 36. *Didiscus oxeata* Hechtel (1983), in situ (Curaçao reefs) photograph of surface showing grooves (s.b. = 0.5 cm) (photo G. van Moorsel).
Fig. 37. *Didiscus flavus* Van Soest, 1984 (= *D. oxeata* Hechtel, 1983), holotype from Curaçao reefs (s.b. = 1 cm) (photo L. A. van der Laan).
Fig. 38. *Didiscus oxeata* Hechtel (1983), SEM photo of choanosomal arrangement (photo F. Hiemstra).
Fig. 39. *Didiscus oxeata* Hechtel (1983), SEM photo of discorhabd (photo L. A. van der Laan).
Fig. 40. *Didiscus anisodiscus* Vacelet & Vasseur (1971), ZMA specimen from Indonesia (s.b. = 1 cm) (photo L. A. van der Laan).

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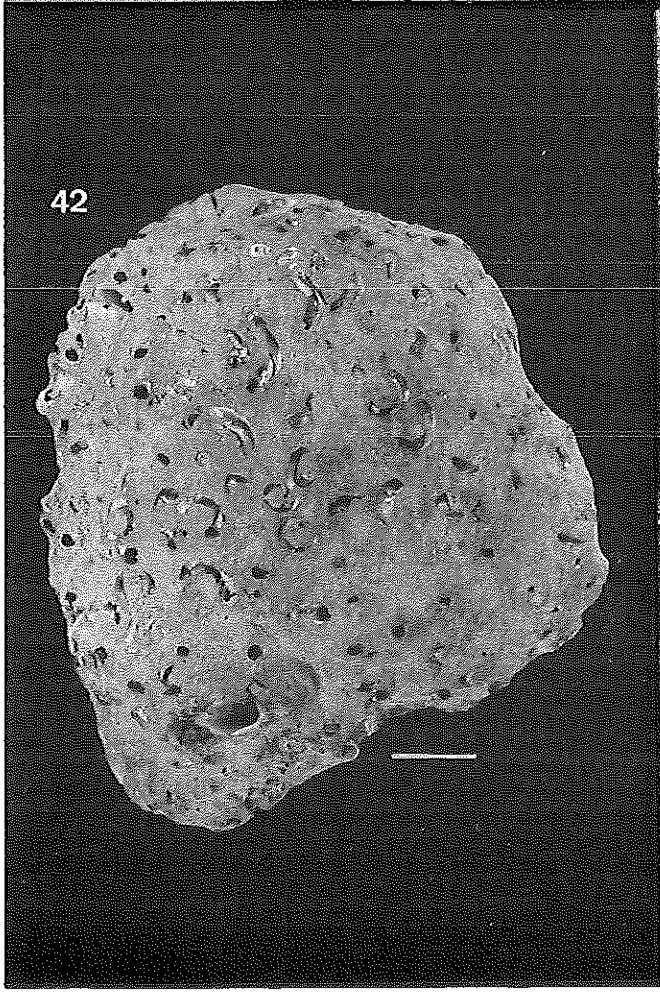

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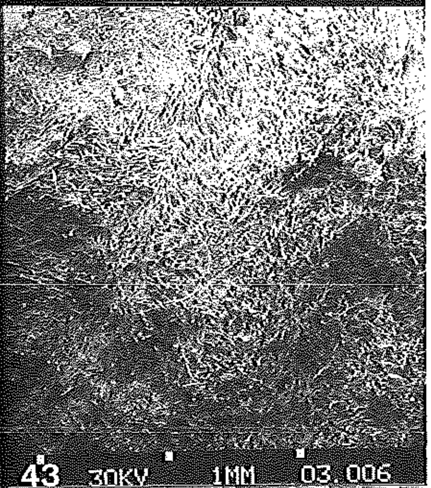

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dria) (ZMA specimens from Indonesia), *T. manaarensis* (Dendy, 1905 as *Spongosorites*) (ZMA specimens from Indonesia), *T. bubarioides* (Lévi & Lévi, 1983 as *Spongosorites*) (MNHN holotype DCl. 2933), *T.* n.spec. (HBOI specimens), *T. subtilis* (Pulitzer-Finali, 1983 as *Laminospongia*, holotype, Fig. 50), *T. aurantiaca* (Schmidt, 1862 as *Reniera*), type specimen LMJG 15630 (Fig. 55) from Mus. Geneva.
Geographical distribution: tropical and subtropical parts of all oceans.

Genus *Epipolasis* De Laubenfels, 1936: 162.
Figs. 56, 65

Type species (original designation): *Spongosorites suluensis* Wilson, 1925: 331, pl. 38 (fig. 8), pl. 48 (fig. 3) (holotype USNM 21297 reexamined).

Definition (emended): Halichondriidae of the genus-group *Topsentia-Epipolasis-Petromica* with a parchment-like feltwork of tangential oxea, and (sinuous) trichodragmata.

Remarks: So far this genus is known only by the type specimen of its type species and one West Indian specimen (Harbor Branch collection). The type is a flabellate specimen with sides differing in ectosomal skeletal strengthening: outer side with parchment-like skin, inner (oscule-bearing) side with palissade-like periphery. The West Indian specimen is massive and only shows the parchment-type ectosome. The genus has been misinterpreted by Van Soest & Stentoft (1988) and Díaz *et al.* (1987), who assigned *Myrmekioderma* species without acanthose oxea to this genus; the similarities between the two (size range of large oxeotes, palissade-like ectosome, sinuous trichodragmata) must be considered homoplasic or plesiomorphous.

The parchment-like skin resembles that of *Halichondria latrunculioides* Ridley & Dendy, 1886, type of the monotypic genus *Pyloderma* Kirkpatrick, 1908 (see Fig. 82b). However, the soft consistency with loose spicule tracts, and absence of microscleres, make it unlikely that both are congeneric. *Pyloderma* is tentatively assigned to *Halichondria*.

Species examined: *E. suluensis* (Wilson, 1925 as *Spongosorites*) (type specimen, Figs. 56, 65), *E.* n.sp. (HBOI specimen from Bahamas).
Geographic distribution: Philippine region, Bahamas.

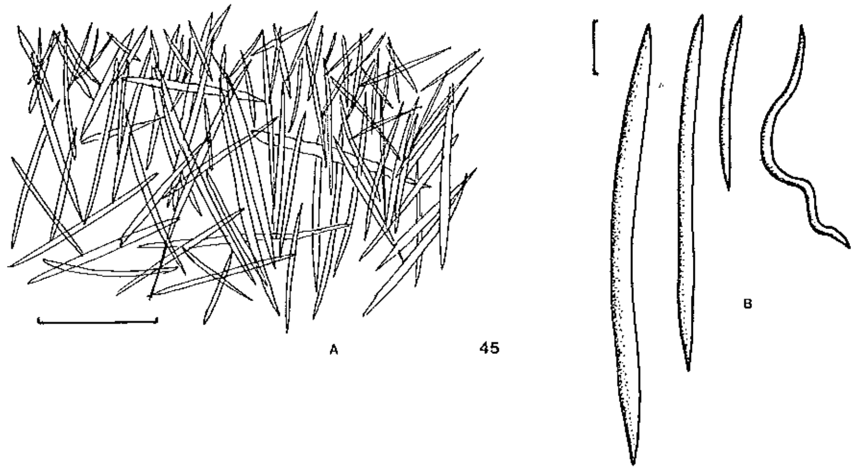
Genus *Petromica* Topsent, 1898: 216.
Figs. 57-59, 66

Type species (monotypy): *P. grimaldi* Topsent, 1898: 216, 1904: 64, pl. 5 figs. 2-4, pl. 8 fig. 6 (Fig. 57) (holotype not examined).

Definition (emended): Halichondriidae of the genus-group *Topsentia-Epipolasis-Petromica*, with sublithistid basal skeleton.

Remarks: These are whitish massive or fistulose forms. The growth form of one of the three species so far recorded, is similar to that of *Ciocalypta* or to that of *Topsentia porrecta* and there is an outside possibility that all these are closely related; however, the supporting ("axial") skeleton of the fistules of *Petromica ciocalyptoides* is found in the walls of the fistules rather than in the centre. The confused spiculation of oxeotes, and or styles in combination with desmata, however, is shared with non-fistulose *Petromica* species.

Figs. 41-43.
Fig. 41. *Spongosorites ruetzleri* (Van Soest & Stentoft, 1988), Bahamas specimen from the Harbor Branch collection.
Fig. 42. *Spongosorites siliquaria* (Van Soest & Stentoft, 1988), ZMA holotype from Barbados (s.b. = 1 cm) (photo L. A. van der Laan).
Fig. 43. *Spongosorites siliquaria* (Van Soest & Stentoft, 1988), macroscopic SEM photo of surface (photo N. Stentoft).
Fig. 44. *Spongosorites siliquaria* (Van Soest & Stentoft, 1988), detailed SEM photo of surface (photo N. Stentoft).



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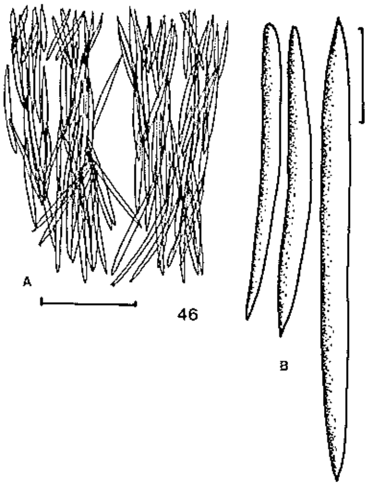

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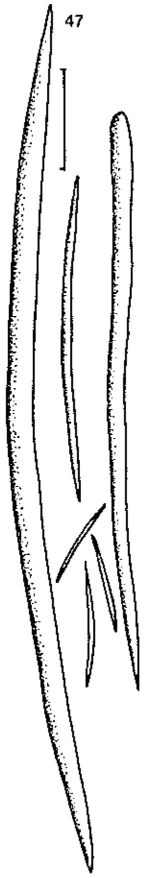

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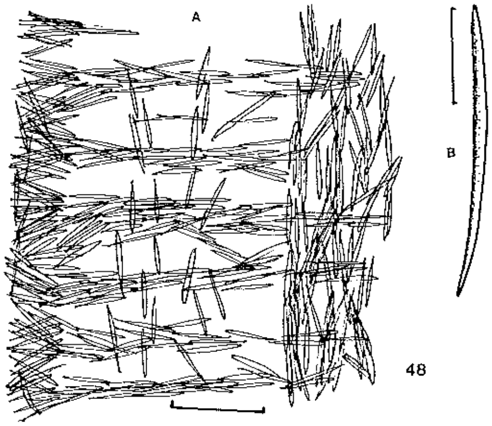

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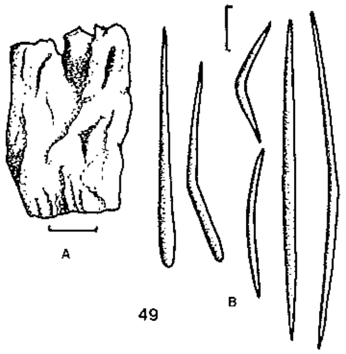

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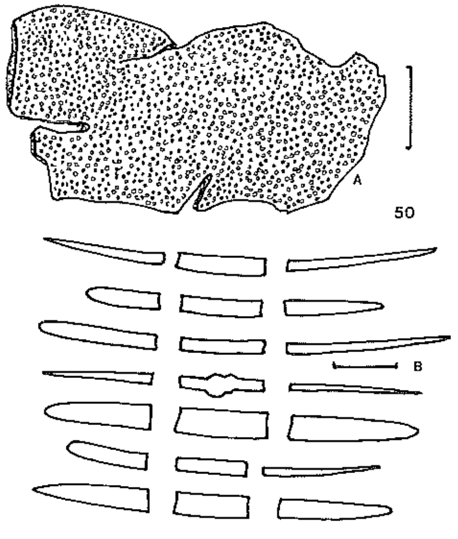

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Synonymy:

Genus *Monanthus* Kirkpatrick, 1903: 176.
(Fig. 58)
Type species (monotypy): *M. plumosus* Kirkpatrick, 1903: 176, pl. IV figs. 6-7 (Fig. 58) (holotype not examined).
Kirkpatrick: "Desmanthidae in which the skeleton is formed of monocrepid desmas of the common type, separate or joined together, and of monaxon megascleres.
Remarks: The family Desmanthidae shows architectural similarities with *Bubaris* (they are thin hairy crusts), but *Monanthus plumosus* is described and figured (Fig. 58) as an elaborate sponge with plumose columns of oxea and styles and isolated desmata. Burton (1929) described different growth forms of this species, one of which shows distinct tube-like fistules.

Species examined: *Petromica ciocalyptoides* (Van Soest & Zea, 1986, as *Monanthus*) (holotype in the Leiden Museum, paratype specimens in ZMA).
Geographical distribution: Azores, Caribbean and South East Africa.

Genus group *Ciocalypta-Amorphinopsis-Halichondria-Hymeniacidon*: Halichondriidae with a distinct ectosomal tangential reticulation of spicule tracts, bundles or single spicules.

Genus group *Ciocalypta-Amorphinopsis*:
Halichondriidae possessing small ectosomal styles next to a complement of oxeote or stylote megascleres.

Genus *Ciocalypta* Bowerbank, 1862: 1105.
Fig. 60, 67

Type species (monotypy): *C. penicillus* Bowerbank, 1864: 179 (holotype BMNH 1877:5:21: 1069 reexamined) (Fig. 60).

Definition (emended): Halichondriidae of the genus-group *Ciocalypta-Amorphinopsis*, with predominantly stylote megascleres and a characteristic semi-transparent parchment-like, fistular habit.

Remarks: So far, the tendency is found among spongologists to confine the use of this genus name to typically fistulose forms, although many authors dealing with Indonesian sponges (Dendy, 1889; Kieschnick, 1896; Sollas, 1902; Thiele, 1903; Hentschel, 1912) disregarded growth form and included *Topsentia*-like and *Amorphinopsis*-like non-fistulose sponges in *Ciocalypta*. Since several apparently closely related fistulose, style-bearing species are in existence, it is here proposed to restrict the use of *Ciocalypta* to these, and to assign oxeote fistulose forms to *Topsentia* or *Halichondria*, excepting those bearing desmata which go to *Petromica*.

Synonyms:

Genus *Leucophloeus* Carter, 1883: 323.
Type species (monotypy): *Leucophloeus massalis* Carter, 1883: 323, pl. XIV fig. 15A-B (not examined).
Remarks: The true nature of this genus remains uncertain due to the fact that we have not been able to trace the original Carter specimen from West-Australia. Other specimens incorporated in the British Museum (reg. no. 1857:1:2:29 and 1886:12:15:82) described by Carter

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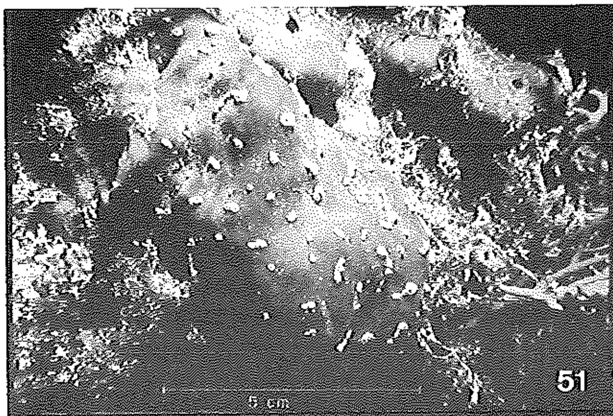
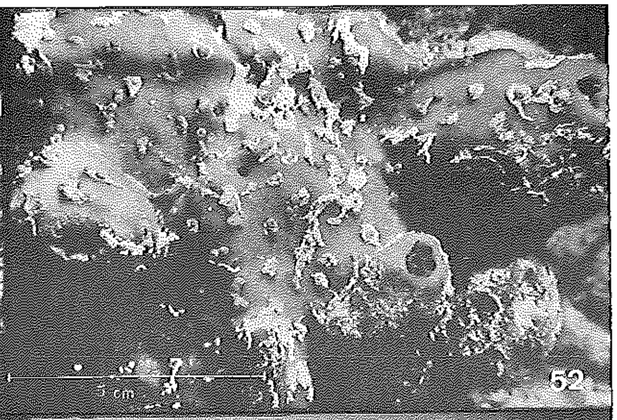
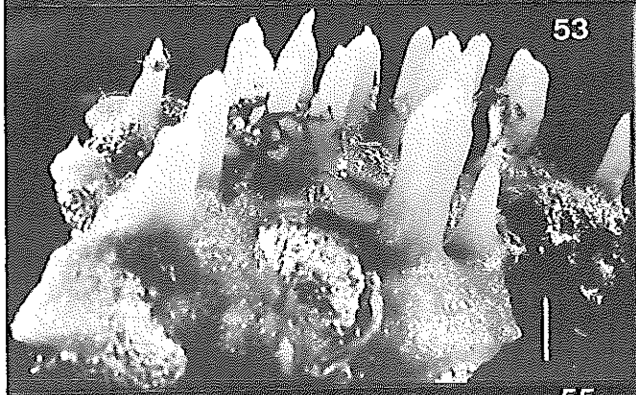
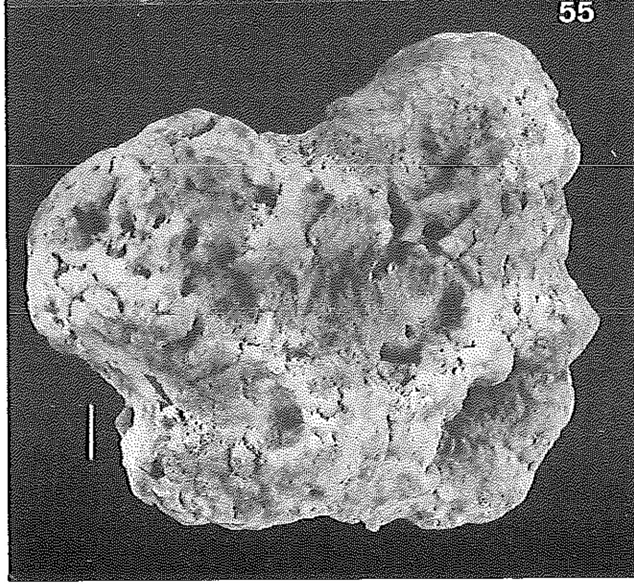
Figs. 45-50.
Fig. 45. *Topsentia ophirhaphidites* (De Laubenfels, 1934), A. cross section of peripheral region (redrawn from Díaz *et al.*, 1990) (s.b. = 0.5 mm), B. spicules (s.b. = 100 µm).
Fig. 46. *Trachyopsis* (= *Topsentia*) *halichondrioides* Dendy, 1922, A. cross section of peripheral region (made from BMNH holotype) (s.b. = 0.5 mm), B. oxea (s.b. = 100 µm).
Fig. 47. *Topsentia glabra* (Topsent, 1900), spicules (redrawn from Topsent, 1904: pl. 13 fig. 1) (s.b. = 100 µm).
Fig. 48. *Coelocalypta* (= *Topsentia*) *porrecta* Topsent, 1928, A. longitudinal section of fistule half, showing central supporting axis and brush-like ectosomal strengthening (s.b. = 0.5 mm), B. spicule (s.b. = 100 µm).
Fig. 49. *Oxeostilon* (? = *Topsentia*) *annandalei* Ferrer-Hernandez (1922), A. habit (s.b. = 1 cm), B. spicules (s.b. = 100 µm) (both redrawn from Ferrer-Hernandez, 1922: pl. 1 lower figure and figure on page 10).
Fig. 50. *Laminospongia* (= *Topsentia*) *subtilis* Pulitzer-Finali (1983), A. habit (s.b. = 2 cm), B. spicules (s.b. = 50 µm) (both redrawn from Pulitzer-Finali, 1983: figs. 59 and 59 bis).









Figs. 51-55.

Figs. 51-52, *Topsentia roquensis* Díaz *et al.* (1987) (= *T. ophirhaphidites* (De Laubenfels, 1934)), type specimens *in situ* in the reefs of Los Roques, Venezuela (s.b. = 5 cm) (photo E. Weil).

Fig. 53. *Topsentia porrecta* (Topsent, 1928), topotypical specimen from Boavista, Cape Verde Islands (s.b. = 1 cm) (photo F. Verbiest).

Fig. 54. *Topsentia* n. spec. Díaz *et al.* (in press), Bahama type specimens from the Harbor Branch collection.

Fig. 55. *Reniera* (= *Topsentia*) *aurantiaca* Schmidt (1862), Mus. Geneva holotype from the Adriatic (s.b. = 1 cm) (photo L. A. van der Laan).

(1886) and Dendy (1896) under this name from viz. New Zealand and South-Australia (examined due to the courtesy of Miss S.M. Stone) do not seem to conform exactly to the type description, but belong to a species of *Ciocalypta*. An unregistered dry specimen from the Bowerbank collection, labeled under the name *Leucophloeus massalis* Australia and bearing the numbers 706 and 31, has the characters described by Carter, viz. a thick white crust over a fibrous axially condensed choanosomal reticulation. The fragmentary specimen has a smooth but furrowed surface, and is hesitatingly assigned to *Ciocalypta*. A microscopic slide in the BMNH colection labeled *Leucophloeus massalis* SE Australia (1862:12:15:454) also seems to conform to Carter's description (thick crust of irregularly reticulated bundles of megascleres, carried by dendritically branched choanosomal vague tracts with variable spongin binding the spicules); however, the spicules are oxea and it may be from a species similar to *Topsentia porrecta*.

Species examined: *Ciocalypta penicillus* Bowerbank, 1862 (holotype in BMNH (Fig. 60) and topotypical specimens in BMNH and ZMA (Fig. 67)), *C. massalis* (Carter, 1886 as *Leucophloeus*) (topotypical specimens in BMNH), *Ciocalypta* spec. (Indonesian specimen in ZMA).
Geographical distribution: temperate, subtropical and tropical parts of all oceans.

Genus *Amorphinopsis* Carter, 1887: 77.
Figs. 61-64, 68
Type species (monotypy): *A. excavans* Carter, 1887: 77, pl. V figs. 12-15 (Fig. 61) (holotype not examined).

Definition (emended): Halichondriidae of the genus-group *Ciocalypta-Amorphinopsis*, with an ectosomal skeleton of thick bundles of oxeotes "echinated" by small styles.

Remarks: The choanosomal megascleres are mostly oxeotes although apices may be blunt, occasionally stylotes. The peripheral parts include smaller oxeotes and styles. Unfortunately, the type specimen of *A. excavans* seems to be no longer extant (pers. comm. Miss S.M. Stone), so we can only rely on the excellent redescriptions of Annandale (1919) (Fig. 62), who claims to have seen the type. The alleged excavating nature of this species (claimed also by Thomas, 1978) is not corroborated by recent findings of the species. We examined some of Thomas' material (MUS. Tervuren reg. no. 1355), but the identification seems dubious; probably, it concerns specimens of the genus *Aka* (= *Siphonodictyon*).

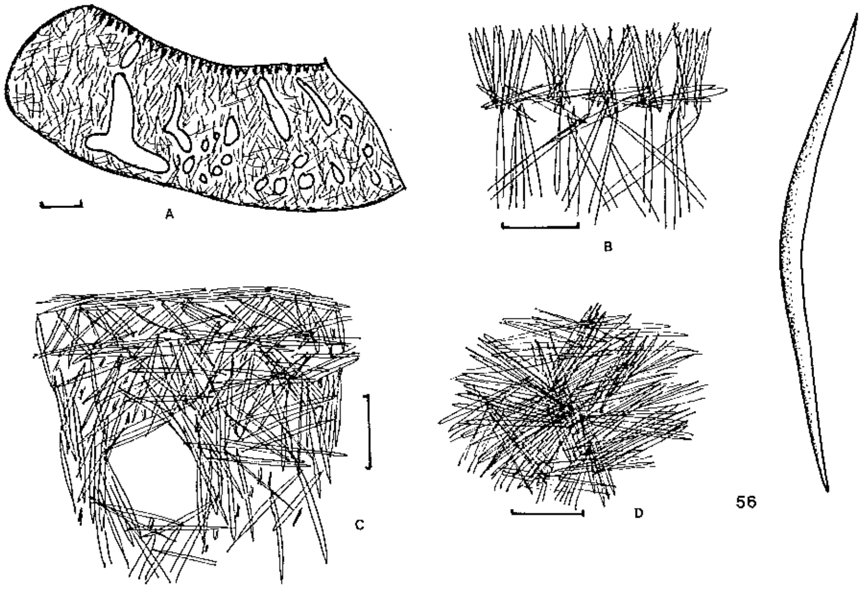
Synonyms:

Genus *Prostylissa* Topsent, 1925: 208.
(Fig. 64)
Type species (monotypy): *P. siamensis* Topsent, 1925: 208, figs. 1-2 (Fig. 64) (holotype reexamined).
Topsent: "Axinellidae à charpente composée d'oxes inégaux. De petits styles, qui s'ajoutent à l'intérieur en proportion relativement faible, deviennent nombreux dans l'ectosome et constituent à cette membrane une protection spéciale en se plaçant debout, solitaires ou par groupes, le long des oxes tangentielles qui la soutiennent."
Remarks: The type specimen (examined in MNHN, DT. 34; type slide: DT. 1885) is ramose, which is an unusual growth form of the normally massive species; skeletal details (detachable crust, confused choanosome, oxea of 300-1050 by 40 µm, and styles of 180-300 by 7-10 µm) agree completely with *A. excavans*.

Species examined: *A. excavans* Carter, 1887 (type of *Prostylissa siamensis* (Fig. 64); ZMA specimens from Indonesia (Fig. 63)), *A. subacerata* (Ridley & Dendy, 1886 as *Hymeniacidon*) (holotype in BMNH 1887:5:57, ZMA specimens from Indonesia), *A. foetida* (Dendy, 1887 as *Hymeniacidon*) (holotype in BMNH, ZMA specimens from Indonesia (fig. 68); specimen described as *A. foetida* by Lévi, 1961 in MNHN; holotype of *Halichondria aldabrensis* Lévi, 1961 MNHN no. DCl. 363 which is considered a junior synonym); *A.* spec. (ZMA specimens from Indonesia).
Geographical distribution: Indo-West Pacific tropical region.

Genus group *Halichondria-Hymeniacidon*:

Halichondriidae with an ectosomal skeleton consisting of a thin, tangential, detachable membrane charged with single spicules or vague bundles, supported by choanosomal columns traversing subdermal lacunae; larval strategy, where known, consists of internal fertilization and incubation of larvae.



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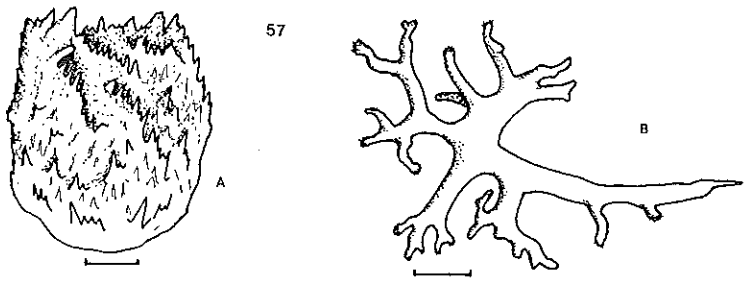

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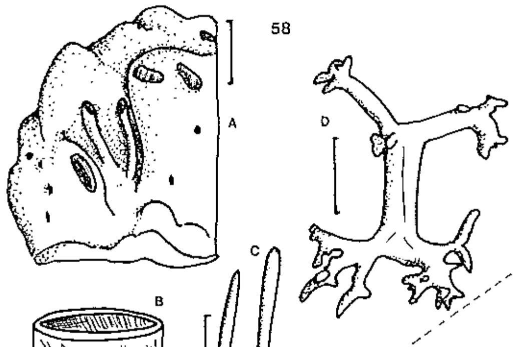
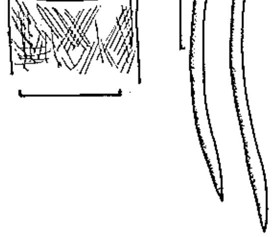

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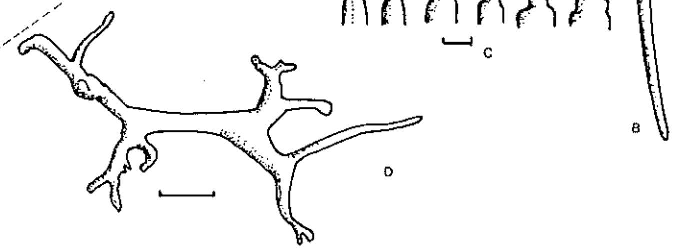


59

Remarks: two genera *Halichondria* and *Hymeniacidon* were formerly considered the type genera of two distinct lines within the Halichondriida, viz. the oxea-line and the style-line. Apart from the fact that ancestral forms quite likely already possessed both spicule-types, and that their possession cannot be used as synapomorphies, it is quite clear from their skeletal architecture that they are very close and can only be kept apart by assuming that the loss of oxea in *Hymeniacidon* is an apomorphous development. *Halichondria* can be characterized on their tufted larvae (known from at least two members, see e.g. Wapstra & Van Soest, 1987). Some monotypical genera belonging in this genus group have doubtful status; they have tentatively been synonymized with the two main genera.

Genus *Halichondria* Fleming, 1828: 520.

Figs. 69-83

Type species (original designation): *Spongia panicea* Pallas, 1766 (type specimen probably lost).

Definition: Halichondriidae of the genus group *Halichondria-Hymeniacidon* with tufted larvae.

Remarks: It is assumed here, that all *Halichondria* species have larvae similar to those of *H. panicea* and *H. bowerbanki* (see Topsent, 1911; Wapstra & Van Soest, 1987). Some *Halichondria*-like species (e.g. two undescribed Caribbean forms) have stylote modifications or even clear styles in their spicule complement, next to oxea, so "loss of styles" cannot be considered a synapomorphy; the majority of the species, however, possess exclusively sharp-pointed oxea of an intermediate to small size when compared to other members of the family.

Many *Halichondria*-species have lost partly or wholly their ectosomal skeleton, and their descriptions sound very much like e.g. *Axinyssa* on paper, however, this loss is here interpreted as having independently occurred here and there in the genus.

Synonymy:

?Genus *Ciocalapata* De Laubenfels, 1936: 134.
(Fig. 73)

Type species (monotypy): *Ciocalypta amorphosa* Ridley & Dendy, 1886: 479, 1887:175, pl. XL fig. 9 (holotype reexamined).

De Laubenfels: "Halichondriidae like *Ciocalypta* but with both oxea and styles."

Remarks: The type and only species is described as massive amorphous, with a rough tufted surface, which has a delicate dermal reticulation. Examination of a type fragment (BMNH 1887:5:2:56) (Fig. 73) revealed two sizes of oxea (1700 by 20 and 600-750 by 8 µm) and one size of styles (1400/28 µm). It is very probably not a typical *Halichondria* but in the absence of further specimens and similar species, it is considered closely related and falls probably within the definition. Possibly it is an atypical *Biemna*.

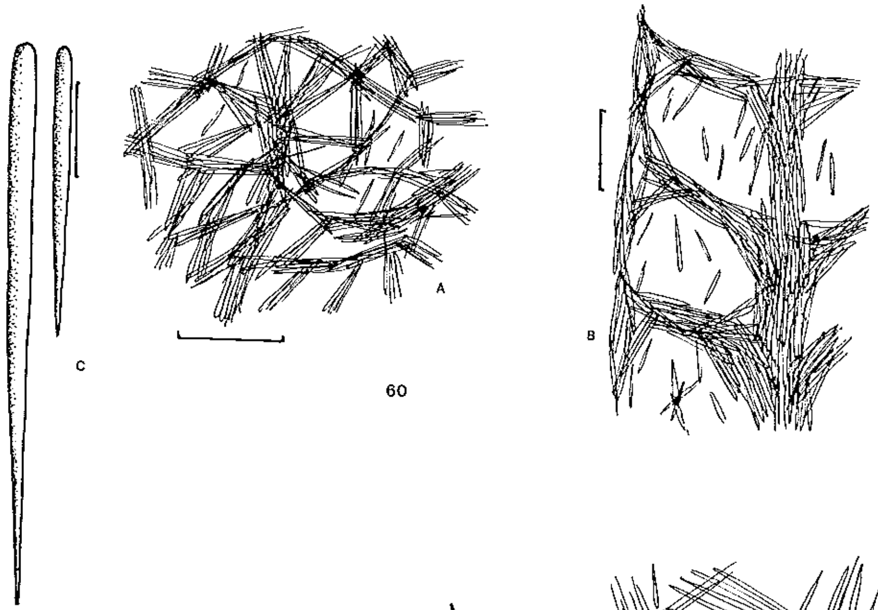
Figs. 56-59.

Fig. 56. *Spongosorites* (= *Epipolasis*) *suluensis* Wilson (1925), A. cross section to show overall structure (redrawn from Wilson, 1925: pl. 48 fig. 3) (s.b. = 1 cm), B. cross section of "upper" peripheral region to show palissade-like brushes (s.b. = 0.5 mm), C. cross section of "lower" peripheral region to show tangential crust (s.b. = 0.5 mm), D. tangential view of "lower" surface to show feltwork of tangential oxea (s.b. = 0.5 mm), E. megascleres (s.b. = 100 µm), F. trichodragmata (s.b. = 50 µm) (B-F made from the USNM type specimen).

Fig. 57. *Petromica grimaldi* Topsent (1898), A. habit (s.b. = 1 cm), B. desma (s.b. = 50 µm) (both redrawn from Topsent, 1904: pl. 5 fig. 5, pl. 8 fig. 6).

Fig. 58. *Monanthus* (= *Petromica*) *plumosus* Kirkpatrick (1903), A. habit of the var. *tubulata* (s.b. = 1 cm), B. section of oscular tube (s.b. = 0.5 cm), C. spicules (s.b. = 100 µm), D. desma (s.b. = 100 µm) (all redrawn from Kirkpatrick, 1903: fig. 6).

Fig. 59. *Monanthus* (= *Petromica*) *ciocalyptoides* Van Soest & Zea (1986), A. cross section of basal mass to show subectosomal desmata (s.b. = 1 mm), B. strongylotes (s.b. = 100 µm), C. apices of strongylotes ((sb. = 10 µm), D. desma (s.b. = 100 µm) (all redrawn from Van Soest & Zea, 1986: figs. 2-5).



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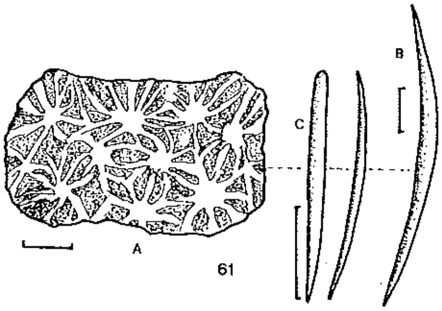

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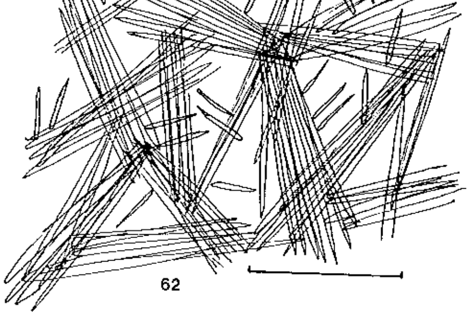

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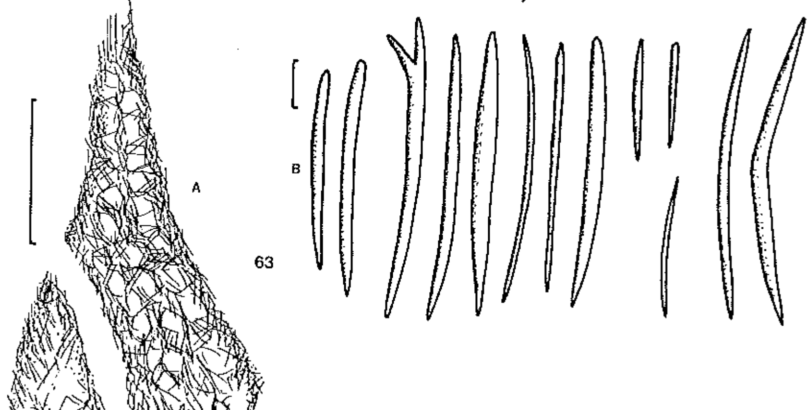

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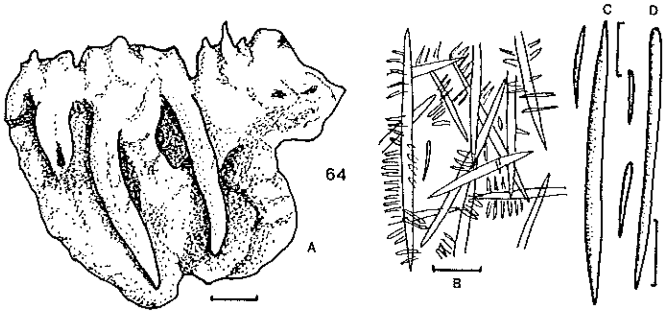


64

Genus *Cioxeamastia* De Laubenfels, 1942: 265.
(Fig. 78)

Type species (monotypy): *C. polycalypta* De Laubenfels, 1942: 265 (Fig. 78) (holotype reexamined).

De Laubenfels: "Halichondriidae with spiculation and most other characters quite typical, but differs in possessing conspicuous closed fistules, closely resembling those that characterize the genus *Polymastia* of the family Suberitidae. The genus *Ciocalypta* of the Halichondriidae also has fistules, but these are coarser than those of *Cioxeamastia*. The spiculation of *Ciocalypta* is not typical of its family."

Remarks: The type specimen from 66°N 80°W (USNM 22691, reexamined) is described as being subspherical with about 50 closed fistules each 4 mm high, 1-3 mm in diameter; the ectosome is said to be not detachable, but it is definitely tangential; oxea vary from 200-700 by 4-12 µm. It is likely that this specimen belongs to *Halichondria (Eumastia) sitiens* (Schmidt, 1870), which is a circum-Arctic species.

Genus *Eumastia* Schmidt, 1870: 42.
(Fig. 79)

Type species (monotypy): *E. sitiens* Schmidt, 1870: 42, pl. V fig. 12 (type material not examined).

Schmidt: "Unterscheidet sich von *Pellina* durch die kegel- und zottenförmigen Ausstulpungen der Haut, die sich sogar verzweigen können, und deren Basen ein unregelmässigen Labyrinth von zusammenhängenden Räumen bilden." (Fig. 79)

Remarks: The species is described as bearing cone-shaped papillae on a massive basis; topotypical specimens possess a detachable ectosomal membrane and subdermal lacunae; the skeleton consists of irregular tracts and spicules in confusion; oxea are (400-) 690 µm (by 7-10 µm).

Genus *Halichondriella* Burton, 1931: 137.
(Fig. 80)

Type species (monotypy): *H. corticata* Burton, 1931: 137, fig. 2 (holotype reexamined).

Burton: "Haploscleridae with spicules of one size only; main skeleton composed of long slender fibres running vertically to the surface and merging into a subdermal palissade of oxea with scattered spicules between the fibres; dermal skeleton a delicate tangential reticulation of oxea." (Fig. 80)

Remarks: The type specimen (BMNH 1931:10:28:25, reexamined) is an atypical *Halichondria panicea*, with relatively feeble oxea size (due no doubt to the fact that it had been growing under artificial circumstances in the Trondheim (Norway) aquarium).

Genus *Menanetia* Topsent, 1896: 115.
(Fig. 81)

Type species (monotypy): *M. minchini* Topsent, 1896: 116 (type slide reexamined).

Topsent: "Renierinae à ectosome epais, remarquable coriace, pourvu de spicules abondants et echevêtrés en toutes directions sans son épaisseur, et fortement adhérent au choanosome; cavités préporales très reduites."

Remarks: A slide of the type specimen (DT. 2099) has been reexamined; this conforms in many details with *Halichondria*, probably *H. panicea*, although the reduced state of subdermal cavities and the heavy ectosomal skeleton are somewhat atypical (Fig. 81). Similar specimens have been described as *Halichondria topsenti* De Laubenfels, 1936 from the same area; quite likely, these forms are growth forms of *H. panicea* from exposed habitats (see also Vethaak *et al.*, 1982). Van Soest (1980), on the suggestion of De Laubenfels (1936: 70) doubtfully accepted *Menanetia* as a Haplosclerid (synonym of *Adocia*).

?Genus *Pyloderma* Kirkpatrick, 1908: 51.
(Fig. 82)

Type species (monotypy): *Halichondria latrunculioides* Ridley & Dendy, 1886:326, 1887: pl. I figs. 5, pl. XLVI fig. 5 (holotype reexamined).

Figs. 60-64.

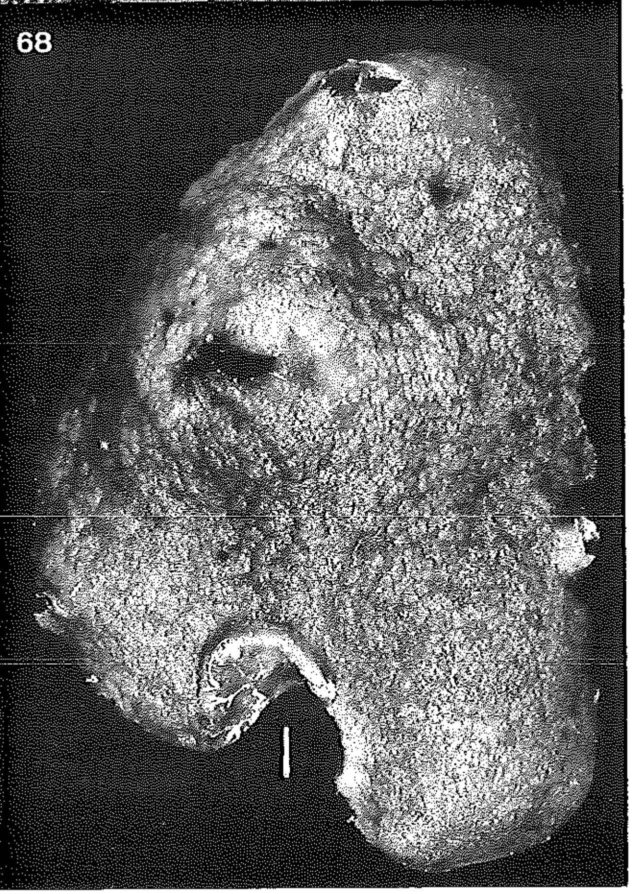
Fig. 60. *Ciocalypta penicillus* Bowerbank (1864), A. tangential view of surface skeleton (s.b. = 0.5 mm), B. longitudinal section through fistule showing axial support (s.b. = 05 mm), C. spicules (s.b. = 100 µm) (all made from the BMNH holotype).

Fig. 61. *Amorphinopsis excavans* Carter (1887), A. habit of holotype (s.b. = 1 mm), B. large megascleres (s.b. = 100 µm), C. small style (s.b. = 100 µm) (all redrawn from Carter, 1887: pl. 5 figs. 13-15).

Fig. 62. *Amorphinopsis excavans* Carter (1887), tangential view of the surface skeleton of a ZMA specimen from Indonesia to show spicule tracts and "echinating" small styles (s.b. = 0.5 mm).

Fig. 63. *Amorphinopsis excavans* var. *digitifera* Annandale (1913), A. longitudinal section through a digitiform process (s.b. = 1 cm), B. spicules (s.b. = 100 µm) (both redrawn from Annandale, 1913: figs. 4-5).

Fig. 64. *Prostylissa siamensis* Topsent (1925) (= *Amorphinopsis excavans* Carter, 1887), A. habit (s.b. = 1 cm), B. tangential view of surface skeleton (s.b. = 100 µm), C. spicules (s.b. = 100 µm) (all redrawn from Topsent, 1925: figs. 1-2).



Figs. 65-68.

Fig. 65. *Epipolasis suluensis* (Wilson, 1925), holotype USNM 21297 from the Philippine region (s.b. = 1 cm).

Fig. 66. *Petromica ciocalyptoides* (Van Soest & Zea, 1986), photographed in situ in the reefs of the Colombian Caribbean (s.b. = 5 cm) (photo S. Zea).

Fig. 67. *Ciocalypta penicillus* Bowerbank (1864), ZMA specimen from Lundy Island, SW Britain, collected by Dr W. H. de Weerdt (s.b. = 1 cm) (photo L. A. van der Laan).

Fig. 68. *Amorphinopsis foetida* (Dendy, 1889), ZMA specimen from Indonesia (s.b. = 1 cm) (photo H. van Brandwijk).

Kirkpatrick: "Renierinae with a parchment-like, easily separated dermal membrane in which are situated closely packed tangential oxea, and with distinct round or oval pore areas."

Remarks: the type specimen (type fragment BMNH 1887:5:2:197 reexamined) is described as erect-lobose, pear-shaped, surface uneven, soft, spongy; the dermal membrane is very dense (Fig. 82B), not like typical *Halichondria*, and the choanosomal skeleton consists of irregular tracts and loose oxea of 700-1250 by 22-31 µm. If more species with similar ectosomal characters would be found, then this genus could be considered valid.

Genus *Trachyopsilla* Burton, 1931: 138.
(Fig. 83)

Type species: *T. glaberrima* Burton, 1931: 138, figs. 3-4 (holotype reexamined).

Burton: "Haploscleridae with skeleton of oxea only, of variable size; main skeleton halichondroid, with loose fibres running vertically to the surface, and ending in brushes, and with a loose tangential layer of spicules associated with outer ends of these spicules."

Remarks: The type specimen (BMNH reg. no. 1931:10:28:77, reexamined) very probably conforms to *Halichondria panicea*; the 'brushes' are the skeletal columns on which the tangential ectosomal skeleton rests (Fig. 83). Oxea are 240-340 by 4-8 µm.

Genus *Raspaigella* Schmidt, 1868: 25.
(Fig. 77, 84)

Type species (monotypy): *R. brunnea* Schmidt, 1868: 25 (type specimens reexamined).

Schmidt: "...erinnert an *Raspailia*; es stehen je doch die Nadel nich so hervor wie bei jener Gattung, indem sie nur an einzelnen Stellen in unregelmässigen Bündeln bis zur Oberfläche und wenig über dieselbe herausragen. Auch löst sich die Oberflachenschichte stellenweise in Form einer Membran ab. Das innere hat nicht die bei *Raspailia* so deutliche Horngefüge. Die Nadeln liegen meist der längsachse der Äste parallel. Ihrer sind zwei Sorten: eine an beiden Enden allmählig zugespitzte von wechselnder Grösse herrscht vor. Die andere ist stumpf-spitz."

Remarks: The alleged type specimens (LMJG 15524 and 15350) of this species (Fig. 77) have been rediscovered in the collections of the museum in Graz (Desqueyroux, personal communication); they are now temporarily stored in the Musée d'Histoire de Genève. The sponge has limp branches (reminding strongly of *Halichondria bowerbanki*) and a definite ectosomal tangential *Halichondria* skeleton (Fig. 84). Oxea are in two size categories: 410-600 by 7-10 µm and 150-260 by 3-6 µm.

Genus *Spuma* Miklucho Maclay, 1870: 13.

Type species: *S. borealis* Miklucho Maclay, 1870: 13.

Remark: We have not seen the original description. Koltun (1959: 206) claims the type species is a junior synonym of *Eumastia sitiens* Schmidt, 1870.

The genus *Amorphina* Schmidt, 1870 has been generally assumed to be a junior synonym of *Halichondria*; however, the type species, *A. grossa*, is a *Haliclona*.

Species examined: *Halichondria panicea* (Pallas, 1766) (ZMA specimens from all over W Europa) (Figs. 69, 74), *H. bowerbanki* Burton, 1930 (ZMA specimens from all over W Europa) (Figs. 70, 76), *H. gibbsi* (Wells *et al.*, 1960 as *Ciocalypta*) (USNM holotype 23666, from North Carolina (Fig. 72), ZMA specimen from Bonaire), *H. tyleri* (Bowerbank, 1875) (as *Ciocalypta*) (holotype BMNH 1930:7:3:32 from South East Africa), *H. melanodocia* De Laubenfels, 1936 (USNM type specimen, ZMA specimens from the Caribbean); holotype of *Aponastra modesta* Pulitzer-Finali, 1986 from Mus. Genova no. 47688, which is considered a junior synonym), *H. magniconulosa* Hechtel, 1965 (USNM paratype specimen 24499, ZMA specimens from the Caribbean (Fig. 75), *H. lutea* Alcolado, 1984 (USNM type fragment, ZMA fragment from Venezuela (Figs. 71, 85), *H.* n. spec. (HBOI specimens from Venezuela); *H.* n. spec. Díaz *et al.*, in press (USNM holotype from Florida, (= *H. panicea sensu* Little, 1963)).

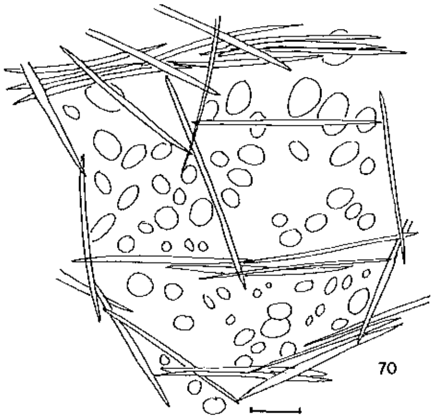
Geographical distribution: This seems to be a truly cosmopolitan genus, although it is definitely more common in temperate and cold waters than in tropical regions.

Genus *Hymeniacidon* Bowerbank, 1862: 1112.
Fig. 86-93

Type species (original designation): *Hymeniacidon caruncula* Bowerbank, 1864: 191, pl. XXXV fig. 372 (holotype not examined) (Fig. 87a). This is generally considered a junior synonym of *Spongia sanguinea* Grant (1829) and *Spongia perlevis* Montagu, 1818, so the definitive name of the type species is *Hymeniacidon perlevis* (Montagu, 1818).

Definition: Halichondriidae of the genus group *Halichondria-Hymeniacidon* which have lost their oxeote spicules, retaining styles and stylotes.

Remarks: The tangential ectosomal skeleton is normally less well-developed than in *Halichon-*



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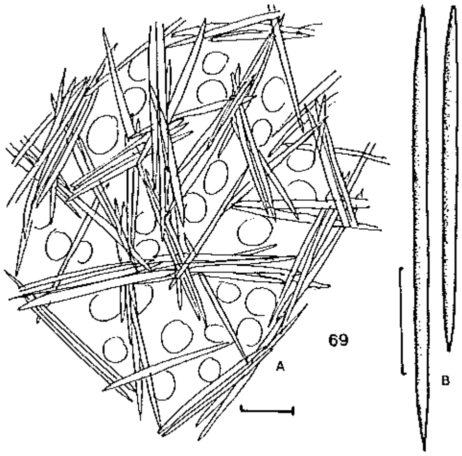

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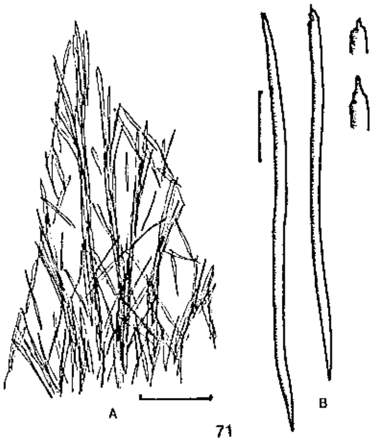

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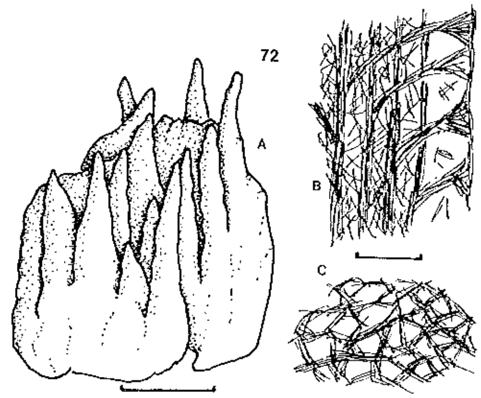

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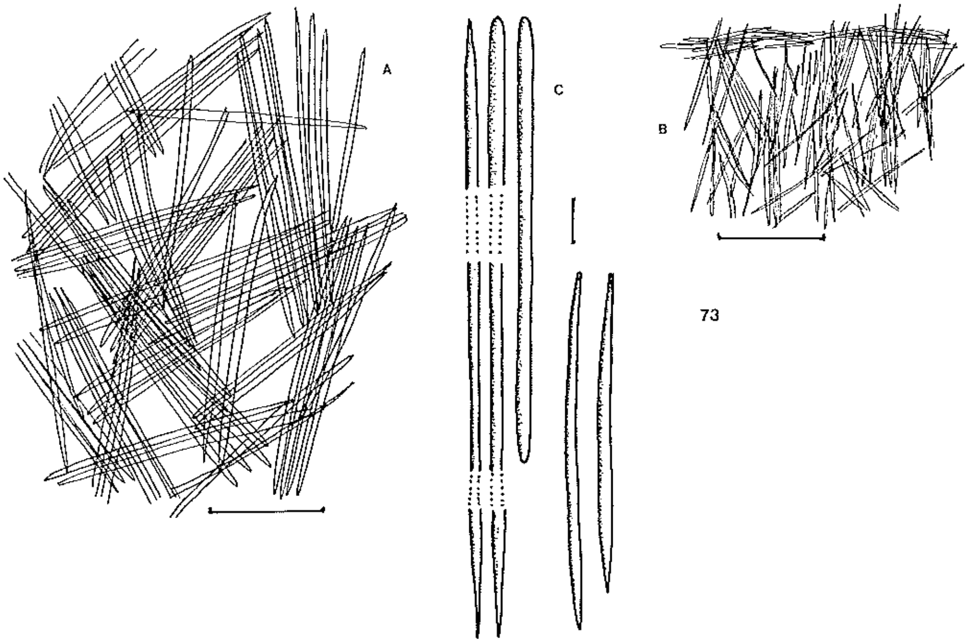


73

dria, and there is a decidedly fleshy consistency in the type and many other species.

Synonymy:

Genus *Amorphilla* Thiele, 1898: 44.
Type species (original designation): *Hymeniacidon sanguinea* (Grant, 1829). This designation makes the genus an objective junior synonym, as it is also the type of *Hymeniacidon*.

Genus *Nailondra* De Laubenfels, 1954: 182.
(Fig. 88)
Type species: *N. maza* De Laubenfels, 1954: 182, fig. 121 (holotype reexamined).
De Laubenfels: "Halichondriidae with strongyles and styles; structure like *Halichondria*."
Remarks: The specimen (USNM 23083, reexamined) is described as amorphous, soft like "soggy bread"; it has a definite tangential skeleton and subdermal spaces. The spicules are described as styles and strongyles. Although the majority are oxeotes with notable narrowing of the blunt apex, there are also some true styles, including ones with a faint tylote swelling. Size of larger category of spicules: 540-630/12 µm. In the *Halichondria*-like architecture, this species is close to *Uritaia* (see below).

Genus *Rhaphidostyla* Burton, 1935: 651.
(Fig. 89)
Type species (original designation): *R. kitchingi* Burton, 1935: 652 (holotype reexamined).
Burton: "Axinellidae with skeleton composed of unusually slender styli, arranged mainly in an irregular (sub-halichondroid) manner, but frequently forming whisp-like bundles, running towards the surface; spicules characterized by a series of abrupt narrowings ending in a point, at the distal end."
Remarks: Burton assigned also a series of Mediterranean *Dictyonella* species to his genus; the type specimen of *R. kitchingi* (BMNH reg. no. 1934:9:26:79, reexamined) is unlike the Mediterranean species in its lack of spongin, its possession of vague disoriented spicule tracts, and the small size of the styles. *Rhaphidostyla* has also been misinterpreted by Van Soest & Weinberg, 1981, who assigned *Tethyspira spinosa* Topsent, 1891, erroneously to *Rhaphidostyla incisa*. In a paper in press, Van Soest has rectified this error and proposed to abandon the use of *Rhaphidostyla* in favor of *Hymeniacidon* (for the type species *R. kitchingi*) and *Dictyonella* (for the other assigned species).

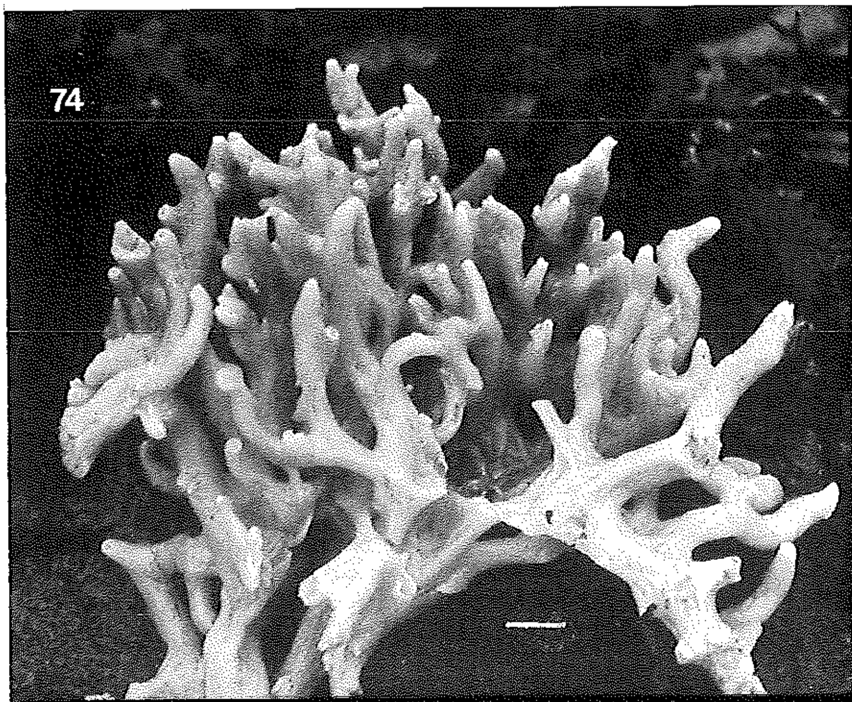
Genus *Rhaphoxiella* Burton, 1934: 554.
(Fig. 90)
Type species (monotypy): *Batzella corticata* Thiele, 1905: 438, fig. 58 (type slide reexamined).
Burton: "Close to *Rhaphoxya* Hallmann, but differs in having a tangential dermal layer of short strongyla, not recorded by Thiele, about half the length of the principal megascleres."
Remarks: The BMNH holds a slide (BMNH reg. no. 1908.9:24:15a, reexamined) of the type specimen (which is in the Berlin Museum); this shows an ectosomal tangential reticulation of loose spicules, and choanosomal vague tracts and low spicular density; spongin seems to be absent; spicules are styloids, oxeotes and strongyloids with variable apices. It is an atypical *Hymeniacidon*.

Genus *Stylohalina* Kirk, 1909: 539.
Type species (monotypy): *S. conica* Kirk, 1909: 539, pl. 25.
Remarks: The original description has not been seen, but Bergquist (1970) considers this a junior synonym of *Hymeniacidon*.

Genus *Stylotella* Von Lendenfeld, 1888: 185.
(Fig. 91)
Type species (monotypy): *S. digitata* Von Lendenfeld, 1888: 185. This is generally considered a junior synonym of *Hymeniacidon agminata* Ridley, 1884: 466, holotype BMNH 81:10:21:347 (see Hallmann, 1914: 349).
Von Lendenfeld: "Heterorrhaphidae of very soft texture.

Figs. 69-73.
Fig. 69. *Halichondria panicea* (Pallas, 1776), A. tangential view of ectosomal skeleton (redrawn from Hartman, 1958: fig. 9) (s.b. = 100 µm), B. spicules (s.b. = 100 µm).
Fig. 70. *Halichondria bowerbanki* Burton (1930), tangential view of ectosomal skeleton (redrawn from Hartman, 1958: fig. 8) (s.b. = 100 µm).
Fig. 71. *Halichondria lutea* Alcolado (1984), A. longitudinal section of apex of one of the digitate processes (s.b. = 1 mm), B. spicules (s.b. = 100 µm).
Fig. 72. *Ciocalypta* (= *Halichondria*) *gibbsi* Wells, *et al.* (1960), A., habit (redrawn from Wells, *et al.*, 1960: fig. 47) (s.b. = 1 cm), B. longitudinal section of fistule half (s.b. = 1 mm), C. tangential view of surface skeleton (same scale as B) (B and C made from the USNM holotype).
Fig. 73. *Ciocalapata* (? = *Halichondria*) *amorphosa* (Ridley & Dendy, 1886), A. tangential view of surface skeleton (s.b. = 0.5 mm), B. cross section of peripheral region (s.b. = 1 mm), C. spicules (s.b. = 100 µm) (all made from the BMNH holotype).

74



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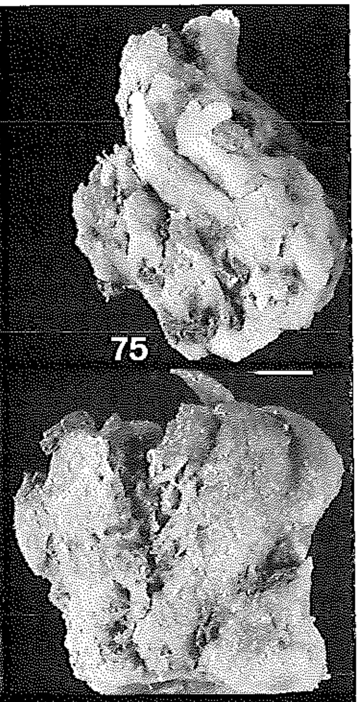

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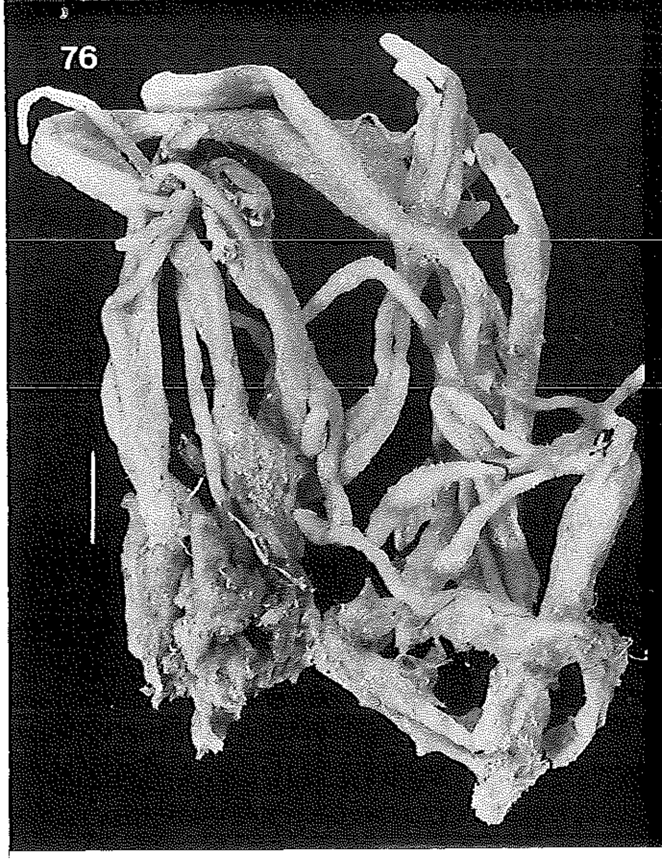

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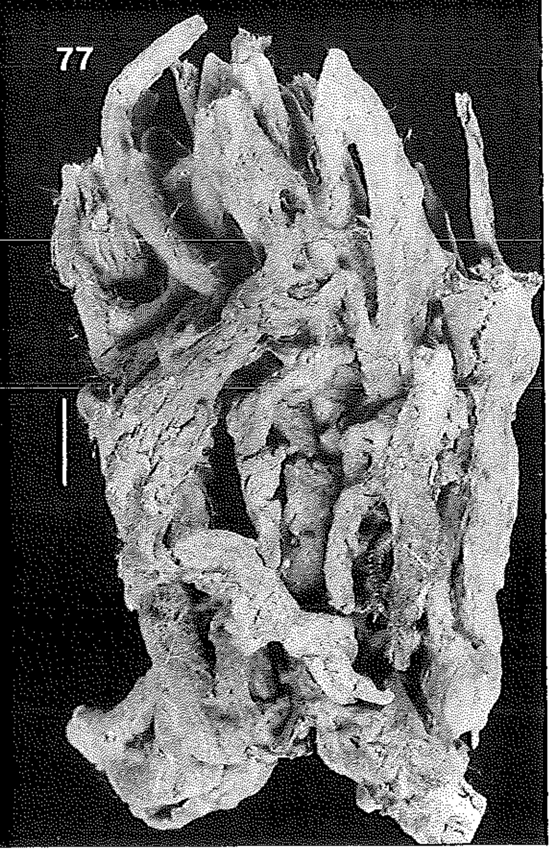

Megasclera styli; in bundles and scattered. No microsclera."

Remarks: The type is described as having branches and digitate processes; surface smooth; the ectosome has "horizontally disposed spicules", and the choanosome is "occupied entirely by a dense mass of longitudinally disposed spicules"; the only spicules are styles of 250 by 4 µm.

Genus *Thieleia* Burton, 1932: 329.

(Fig. 92)

Type species (monotypy): *Hymeniacidon rubiginosa* Thiele, 1905: 421, fig. 44 (paratype reexamined).

Burton: "Main skeleton composed of delicate strands of spicules running vertically to the surface and connected to each other by irregularly arranged masses of single spicules. At the surface the ends of the strands diverge to form dense brushes of spicules the apices of which project slightly beyond the dermis. There is no special dermal skeleton unless the dense brushes formed from the ends of the strands of the main skeleton can be regarded as such."

Remarks: The type is described as a flat crust, no detachable skin, with an organic skin stretched over the skeletal reticulum. The BMNH holds a fragment (08:9:24:133a, reexamined) from a paratype specimen from the Berlin Museum; this largely conforms to *Hymeniacidon*, the alleged absence of a dermal skeleton is a matter of grade, rather than a true absence.

Genus *Uritaia* Burton, 1932: 198.

(Fig. 93)

Type species (monotypy): *Uritaia halichondrioides* Burton, 1932: 199, pl. 7 figs. 3-4, text-fig. 4 (not examined).

Burton: "Axinellidae with skeleton composed of two categories of smooth styli; main skeleton a halichondroid reticulation of large styli, with a few small styli scattered between; dermal skeleton formed of brushes of smaller styli set at right angles to surface with numerous styli of similar size lying horizontally and scattered between them".

Remarks: Burton compares his new genus to *Amorphilla* and *Hymeniacidon* and found them to differ in the more halichondroid nature of the ectosomal skeleton. Since this is generally less well developed in *Hymeniacidon* species that difference seems hardly worth erecting a separate genus.

Species examined: *H. perlevis* (Montagu, 1818) (ZMA specimens from all over Europe (Fig. 86, 87)), *H. heliophila* (Parker, 1910) (USNM and ZMA specimens from Florida, West Indies, and North Carolina), *H. caerulea* Pulitzer-Finali, 1986 (USNM and ZMA specimens from the Caribbean), *H. corticata* (Thiele, 1905) (type slide from BMNH), *H. rubiginosa* (Thiele, 1905) (type fragment from BMNH), *H. kitchingi* (Burton, 1935) (type (BMNH) and ZMA specimens from the British Isles).

Geographic distribution: Temperate, subtropical and tropical regions of all oceans; not in (ant-)arctic regions.

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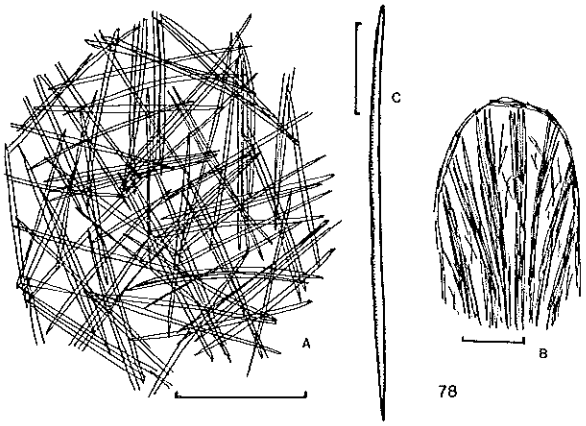
Figs. 74-77.

Fig. 74. *Halichondria panicea* (Pallas, 1776), ZMA specimen from SW Netherlands (s.b. = 1 cm).

Fig. 75. *Halichondria magniconulosa* Hechtel (1965), ZMA specimens from Curaçao (s.b. = 1 cm) (photo L. A. van der Laan).

Fig. 76. *Halichondria bowerbanki* Burton (1930), ZMA specimen from SW Netherlands (s.b. = 1 cm) (photo L. A. van der Laan).

Fig. 77. *Raspaigella* (= *Halichondria*) *brunnea* Schmidt (1868), one of the Mus. Geneva type specimens (LMJ G 15350/o) (s.b. = 1 cm) (photo L. A. van der Laan).



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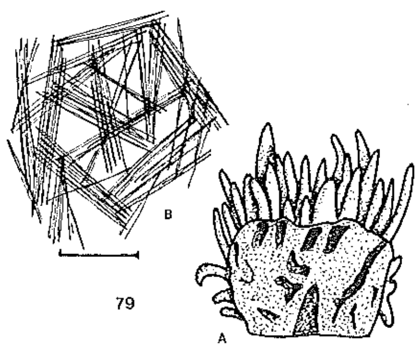

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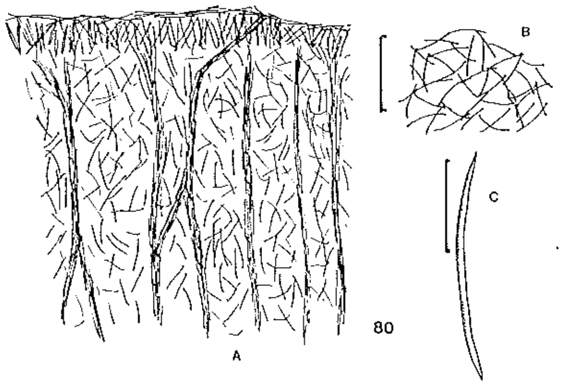

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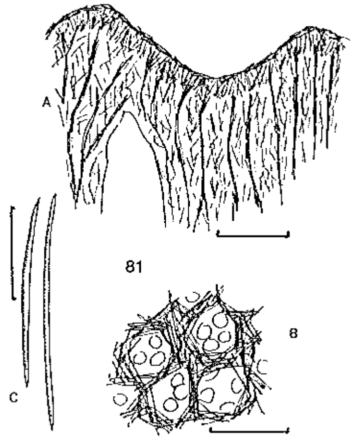

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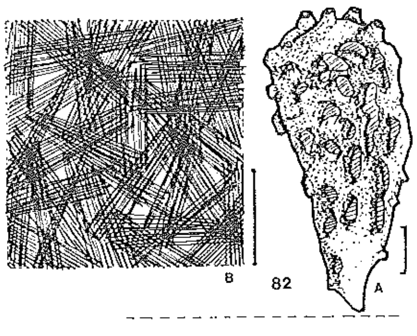

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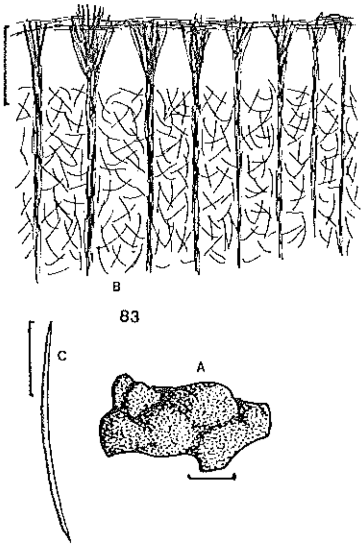

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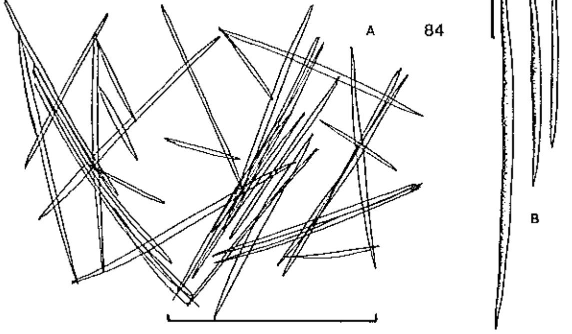

84

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Fig. 78-84.

Fig. 78. *Cioxeamastia* (= *Halichondria*) *polycalypta* De Laubenfels (1942), A. tangential view of surface skeleton (s.b. = 0.5 mm), B. longitudinal section of papilla (s.b. = 1 mm), C. oxea (s.b. = 100 µm).

Fig. 79. *Eumastia* (= *Halichondria*) *sitiens* Schmidt (1870), A. habit (redrawn from Schmidt, 1870: pl. 5 fig. 12) (no scale given by Schmidt), B. tangential view of surface skeleton of a ZMA specimen from the northern North Sea (s.b. = 0.5 mm).

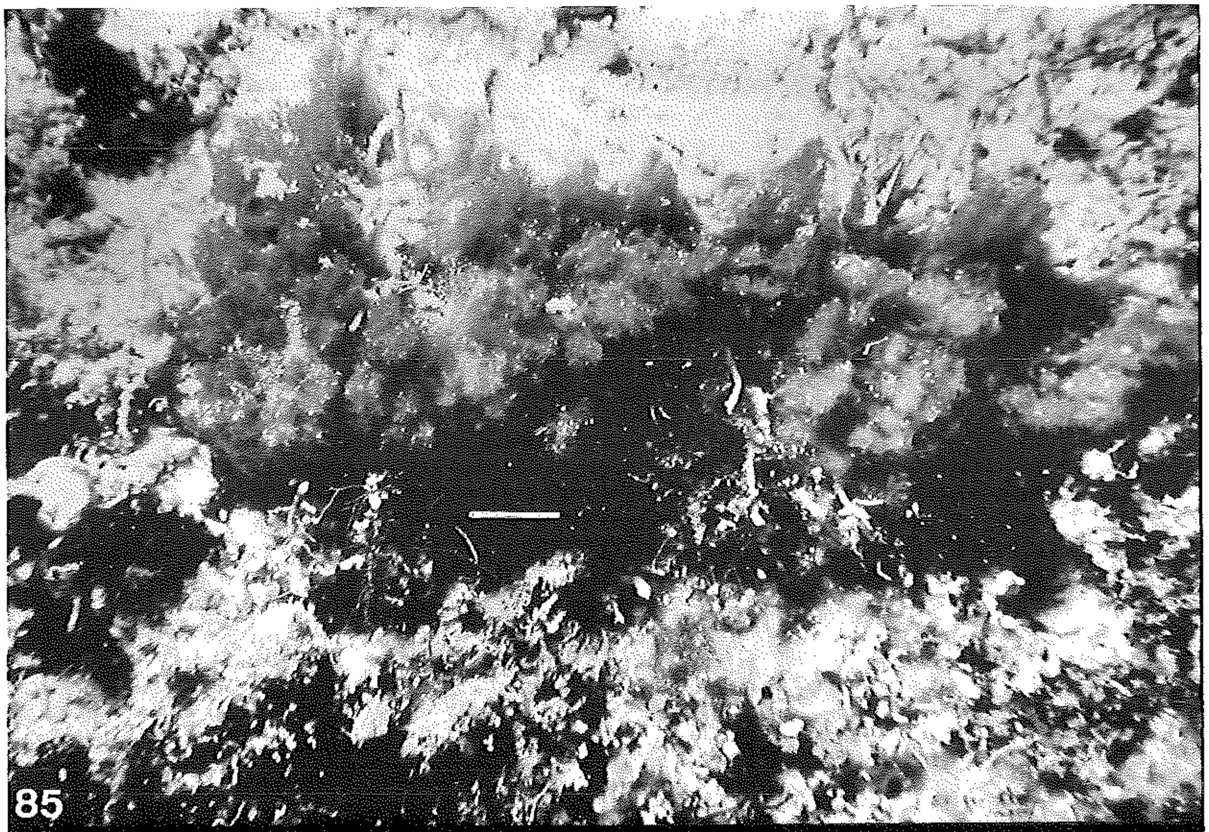
Fig. 80. *Halichondriella* (= *Halichondria*) *corticata* Burton (1931), A. cross section of peripheral region (s.b. = 0.5 mm), B. tangential view of surface skeleton (same scale), C. oxea (s.b. = 100 µm) (all redrawn from Burton, 1931: fig. 2).

Fig. 81. *Menanetia* (= *Halichondria*) *minchini* Topsent (1896), A. cross section of peripheral region (s.b. = 1 mm), B. tangential view of ectosomal skeleton (s.b. = 0.5 mm), C. oxea (s.b. = 100 µm) (all made from slide of MNHN type specimen).

Fig. 82. *Pyloderma* (? = *Halichondria*) *latrunculioides* (Ridley & Dendy, 1886), A. habit (s.b. = 1 cm), B. tangential view of surface skeleton showing a feltwork of oxea (s.b. = 1 mm) (both redrawn from Ridley & Dendy, 1887: pl. 1 fig. 5 and pl. 46 fig. 5).

Fig. 83. *Trachyopsilla* (= *Halichondria*) *glaberrima* Burton (1931), A. habit (s.b. = 1 cm), B. cross section of peripheral region (s.b. = 0.5 mm), C. oxea (s.b. = 100 µm) (all redrawn from Burton, 1931: figs. 3-4).

Fig. 84. *Raspaigella* (= *Halichondria*) *brunnea* Schmidt (1868), A. tangential view of surface skeleton (s.b. = 0.5 mm), B. oxea (s.b. = 100 µm) (made from one of the Mus. Geneva type specimens).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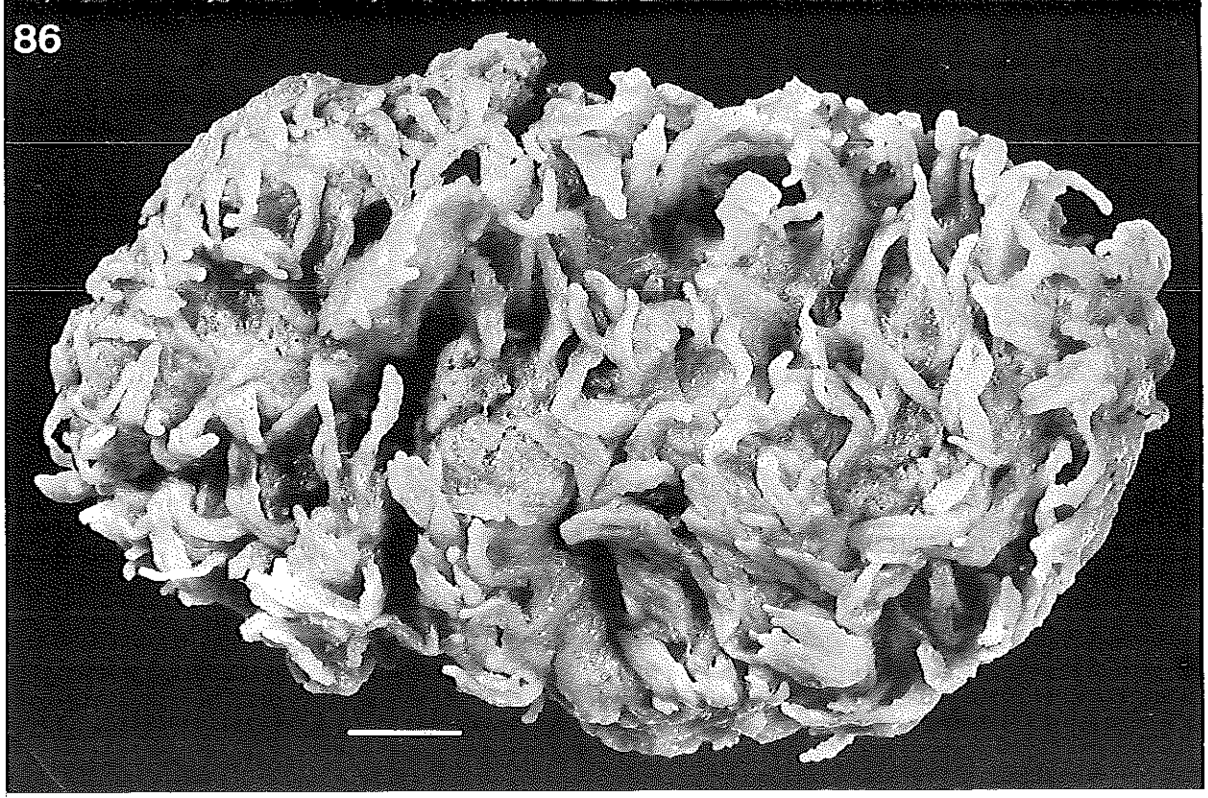
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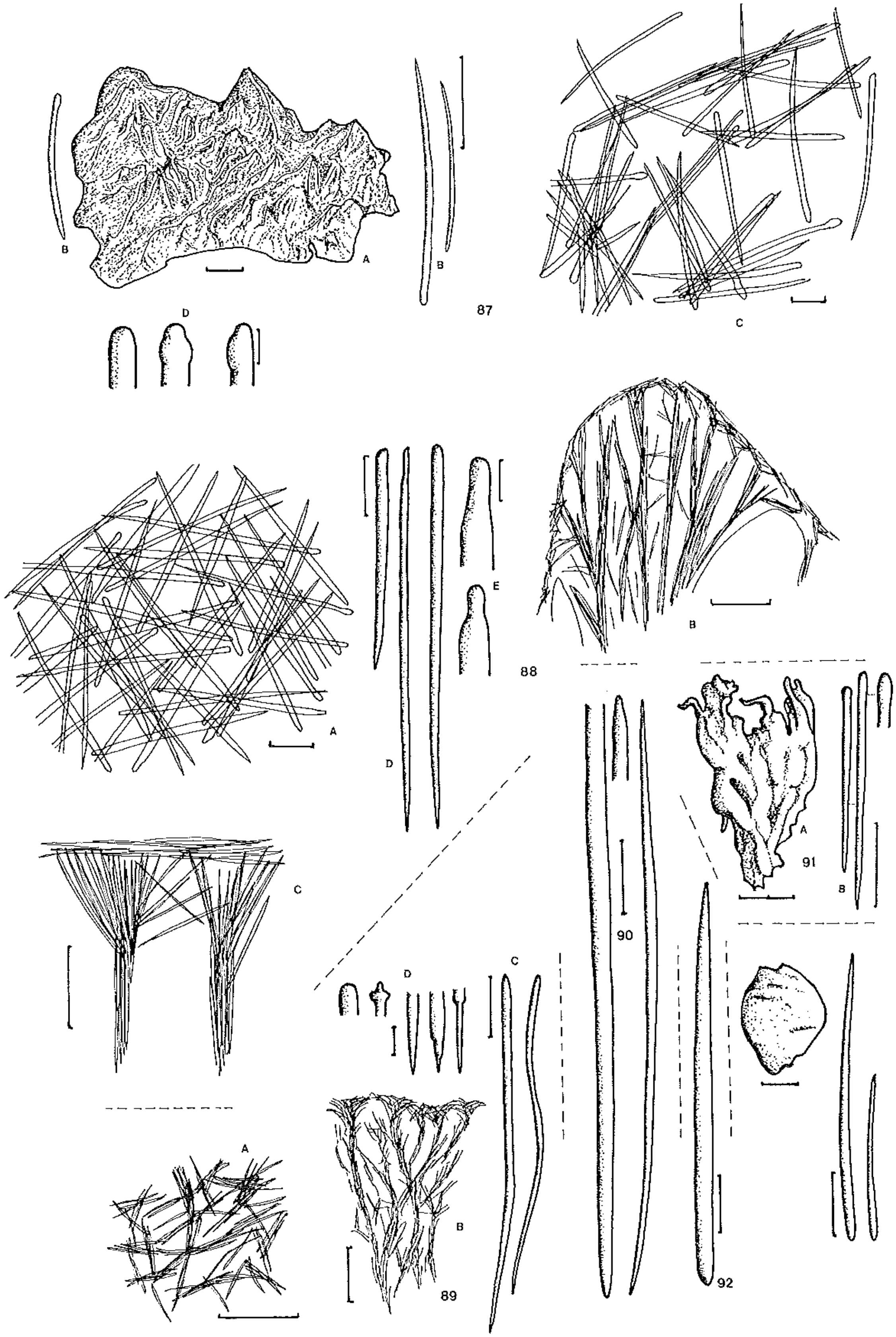
Figs. 85-86.

Fig. 85. *Halichondria lutea* Alcolado (1984), photographed in situ in the reefs of Los Roques, Venezuela (s.b. = 1 cm) (photo E. Weil).

Fig. 86. *Hymeniacidon perlevis* (Montagu, 1818), ZMA specimen from SW Netherlands (s.b. = 1 cm) (photo L. A. van der Laan).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Figs. 87-93.

Fig. 87. *Hymeniacidon caruncula* Bowerbank, 1866 (= *H. perlevis* (Montagu, 1818)), A-B. habit and spicules (redrawn from Bowerbank, 1874: pl. 32 fig. 1) (s.b. = 1 cm; s.b. spicules = 100 µm), C. tangential view of ectosomal skeleton (s.b. = 100 µm), D. blunt apices of styles to show faint tylote swellings) (s.b. = 10 µm).

Fig. 88. *Nailondra* (? = *Hymeniacidon*) *maza* De Laubenfels (1954), A. tangential view of ectosomal skeleton (s.b. = 100 µm), B. cross section of peripheral region (s.b. = 1 mm), C. detail of B (s.b. = 0.5 mm), D. spicules (s.b. = 100 µm), E. blunt apices of stylotes (s.b. = 25 µm) (all made from the USNM holotype).

Fig. 89. *Rhaphidostyla* (= *Hymeniacidon*) *kitchingi* Burton (1935), A. tangential view of surface skeleton (s.b. = 0.5 mm), B. cross section of peripheral region (s.b. = 1 mm), C. spicules (s.b. = 50 µm), D. apices of spicules (s.b. = 10 µm) (all made from the BMNH holotype).

Fig. 90. *Batzella* (= *Hymeniacidon*) *corticata* Thiele (1905), spicules (redrawn from Thiele, 1905: fig. 58) (s.b. = 50 µm).

Fig. 91. *Stylotella* (= *Hymeniacidon*) *agminata* Von Lendenfeld (1888), A. habit (s.b. = 1 cm), B. spicules (s.b. = 100 µm), (both redrawn from Ridley, 1884: pl. 41 fig. E and pl. 53 fig. f).

Fig. 92. *Thieleia* (= *Hymeniacidon*) *rubiginosa* (Thiele, 1905), spicule (s.b. = 50 µm) (redrawn from Thiele, 1905: fig. 44).

Fig. 93. *Uritaia* (= *Hymeniacidon*) *halichondrioides* Burton (1932), A. habit (s.b. = 1 cm), B. spicules (s.b. = 100 µm) (both redrawn from Burton, 1932: pl. 7 fig. 3 and text-fig. 4).

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