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, Diaz & 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-HALICHONDRIA 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 Axinellidae 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 Axinellidae 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: families Axinellidae, Bubaridae, and perhaps some Desmoxyidae, but excepting the Raspallidiidae, 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 indiscernible 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 Spongiosorites; 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 Raspallidiids (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, Raspallidiidae, 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 (Raspalliid 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, Hemisterelliidae, Raspailiidae and Sigmanellidae), 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: Sigmanellidae and Poeciloscleridae). 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 *Rhiazinella* 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 homoplastic 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 Demospongeae 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.: *Demospongeae 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 Demospongeae (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 Poeciloscleridae, these groups show localization or categorization in them. For instance, in Myxillids stylole 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.

Isonitrioles are organic compounds found in *Axinella*, *Acanthella*, *Ciocalypta*, *Axinyssa*, "*Epipolais*", "*Stylotheta*", "*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 HALICHONDRIADA (s.l.)**

Although our revision will confine itself to the Halichondrida in the restricted sense (which will subsequently be named the family Halichondrididae) 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 Raspailiida or Hemisterellida 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): *Halichondria* 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*, *Hymenhabdia*, 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 sponginedveloped 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...
Raspailiids and Microcionids because of the converging habits found in these groups; absence of acanthostyles in the present family seems to 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 Piilocaulis- 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): Halichondrididae 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 apomorphic 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 Halichondridae 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.

CLADISTIC ANALYSIS OF THE HALICONDRIIDAE

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

Figs. 8-11.
Fig. 8. Axinella donnani Bowerbank, 1875, ZMA specimen from Indonesia (s.b. = 1 cm).
Fig. 9. Piilocaulis 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).
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 an 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 synapomorphy 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.

Fig. 12. Phylogenetic relationships of newly defined Halichondrid families (further explanations see text).
3. Reticulate choanosomal architecture: this is an ancestral character of a much larger group including the families Desmoxyidae, Axinellidae, but also probably the Pocilosclerida. For the Halichondridae and Dictyonellidae, its loss (3b) is considered a synapomorphy, thus uniting both families and making the Dictyonellidae the nearest outgroup of the Halichondridae.

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 Halichondridae causes a loss of reticulation and a more confused skeleton and leads to a higher spicular density: a synapomorphy of the family Halichondridae.

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 Halichondridae.

7. Haphazard arrangement of spicules: also related to the above is the confused arrangement of many single spicules: a synapomorphy of the family Halichondridae.

8. Finely conulose surface: without ectosomal skeletal covering, the type of choanosomal skeleton found in the Halichondridae 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 Halichondridae 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-Hymentiacidon; (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 aphyomorphic character state is formed by the parchment-like ectosome that sets Epipolitis apart: oxea arranged in a tangential felt-like mass; (possibly independently developed in the doubtful genus Pyliderma).

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 “organic skin”, leaving isolated rounded areas with ectosomal pallasides, 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 homoplastic occurrence of sinuous trichodragmata is found in Epipolitis; 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 Pocilosclerida family Desmacellidae (e.g. Dragnetella).

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-Epipolitis-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 Epipolitis 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 apomorphic character of Epipolitis.


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.


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).


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 assistance 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 ektosomal 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 ektosomal tangential crust. Relationships within the latter group are further determined by details of the ektosomal crust, which may consist of a paratangential arrangement of spicules (Topsentia, Petromica), a reticulation of spicule bundles (Amorphinopsis, Ciocalypta) or feltwork (Epipolais), or single spicules (Hymeniacidon, Halichon-

![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.](image)

dria). Spongosorites deviates rather strongly from the others in architecture and chemistry.

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 Raspailiidae. 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 (sub-
jective) 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 homoplastic 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 homoplastic, 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, Topsenia, Halichondria, Hymeniaidion, 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 Hymeniaidion) 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 successfully 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 Axinellid genus close to Axinella.

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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 oecosomal 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 *Leucophloius* belong to *Axinyssa*; however, the type species of that genus is assigned to *Ciocalypa*.

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 Raspailiidae.

Species examined: *Axinyssa topsentii* 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. gravierei* Topsent, 1893 (holotype, MNHN DT. 1873), *A. aculeata* Wilson (1925) (holotype USNM. 21341 (Fig. 19) and ZMA specimens from Indonesia), *A. apliesinoides* (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 *Leucophloius lewisi* Van Soest & Stentoff, 1988 ZMA 5401 which is now considered a junior synonym; holotype of *Dictyonella yuanae* 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 *Prostlyssia*) (holotype fragment MNHN DCl. 2954 examined). Geographical
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. adorna* 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 trichodragma, 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
Anacanthaea and Epipolasis (several species except the type species) to Myrmekioderma. Several species of Myrmekioderma reveal the presence of quantities of spongina, which may cause the spicules to be arranged in irregular thick tracts.

Synonyms:
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. niæa 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 sinusoidal.

(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 Compagnieen und dem Gummineen stehende Gattung, wo die Sarcode-Substanz ein hochst 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 oxeas. 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 Topsenia. 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 Israeli 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 palisade-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 Heteroxyla 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 revétantes, sans microsclères, à choanosome à peu près asciculeux, 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.
Type species (monotypy): N. atina De Laubenfels, 1954 190, fig. 127 (holotype USNM 22974 reexamined).

Figs. 22-23.
Fig. 22. Axinella (= Axinyna) 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. Colloclayptia 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).
See for details of this synonymization Bergquist, 1965: 177.

The genus Raspaigella Schmidt, 1868 has been used for species of Myrmekiaderma, e.g. by Burton (1939) and Vacelet & Vasseur (1971), but the type species (monotypy), R. brumne Schmidt, 1868, is a Halichondria (see also there).

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

Species examined: Myrmekiaderma granulata (Esper, 1794) (ZMA specimens (Fig. 28) from Indonesia; holotype of Neoprosopa 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. dendi (Burton, 1959) (ZMA specimens from Indonesia), M. speleae Pulitzer-Finali, 1983 (as Raphisia) (holotype in Mus. Genova PTR D.18; Aegean specimens collected by E. Voultisadou-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 Myrmekiaderma-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 Myrmekiaderma. 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 Myrmekiaderma, 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. oxecata Hechtel, 1983 (holotype YPM 8969 from Brazil; holotype fragment

Figs. 24-27.

Fig. 24. Myrmekiaderma 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. sinusous trichodragnata (s.b. = 25 µm) (B-C after Van Soest & Stentoft, 1988: fig. 43).

Fig. 25. Anacanthaea (= Myrmekiaderma) nisea 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. sinusous trichodragnata (found in the BMNH type specimen) (s.b. = 25 µm).

Fig. 26. Callites lacazei sensu Tsurnamal, 1969 (= probably Myrmekiaderma speleae (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. Heteroeca (?) = Myrmekiaderma) 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).
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-Halicordia-
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 choanosome qui ressemble durement fasciculée, irrégulière, pourvue d’oxes et de microrhobdes plus ou moins centrotylotes, ces derniers parsemant la chair et s’accumulant dans la couche externe de l’écorce en un feuillage tangentiel, à la façon de ceux de l’ectochrote des Erylas."
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 (1Topsent, 1892) (specimens identified by Pulitzer-Finali, 1983; specimen in ZMA from Norway), S. ruetzleri (Van Soest & Stenotoft, 1988) (as ?Halicordia) (type specimens in ZMA, HBOI specimens, Fig. 34)), S. siliquaria Van Soest & Stenotoft, 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
Type species (original designation): Anisoxyla glabra Topsent, 1989: 234 (type slide MNHN D.T.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 centstroylote 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:


(Fig. 47)

Type species (original designation); A. tenuispinosa Topsent, 1927: 6 (type slide MNHN D.T. 1190 reexamined). Topsent: “Spongosoritidæ à spicules de deux sortes, les uns monactinaux, plus grands, représentant les éléments principaux, d’une charpente vaguement halichondroïde, lâche, sans spongine, les autres diactinaux, de petite taille et de rôle accessoire, épars et nombreux.”.

Topsent claims there are acanthoxea among the small oxoe (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 Anisoxyla 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 Anisoxyla 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

Figs. 31-35.
Fig. 31. Didiscus placospongoides (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 oxeyta Hechtel, 1985, 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 ruetsleri (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).
assigned to this genus, but only the type species conforms to *Topsentia*.

(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 halichondroïde, d’où s’élevent 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 *Ciocalypta*.**” (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 *Cirexanthia*).

(Fig. 49)

Type species (monotypy): *O. annandalei* Ferrer Hernandez, 1922: 9, figs. 8-9, pl. I (see Fig. 49) (no material examined).

Ferrer-Hernandez: “Axinellidos con esqueleto formado por fibras espiculosas ascendentes, que terminan en pinceles de espículas 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*.

(Fig. 50)


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 ectsosomal skeleton, and the oxea-styles-strongyles of 350-1300 by 9-19 μm are in confusion; some spongion 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 brasiliensis* 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. halichondroides* (type in BMNH (Fig. 46), specimens from Aldabra in MNHN DCI. 361), *T. dura* Lindgren, 1897 as *Halichon-
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 sub-tropical 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 ektosomal 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 ektosome. 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 ektosome, sinuous trichodragmata) must be considered homoplasic or plesiormorphous.

The parchment-like skin resembles that of Halichondria latrunculoides Ridley & Dendy, 1886, type of the monotypic genus Pyoderma Kirkpatrick, 1908 (see Fig. 82b). However, the soft consistency with loose spicule tracts, and absence of microscleres, make it unlikely that both are congeneric. Pyoderma 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 spication 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).
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: ‘Desmanthidiae in which the skeleton is formed of monocrepid desmas of the common type, separate or joined together, and of monaxon megascleres.

Remarks: The family Desmanthidiae 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.


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 stylocle megaascleres.

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 stylole megascleres and a characteristic semi-transparent parchment-like, fistular habit.

Remarks: So far, the tendency is found among many authors 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*.

Genus *Leucophlebus* Carter, 1883: 323.

Type species (monotypy): *Leucophlebus 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.

Genus *Leucophlebus* Carter, 1883: 323.

Type species (monotypy): *Leucophlebus 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.
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 Fiji. 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 Leucolephous 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 collection labeled Leucolephous 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 spong 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 Leucolephous) (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 oxetes “echinates” by small styles.

Remarks: The choanosomal megascleres are mostly oxetes although apices may be blunt, occasionally stylopetes. The peripheral parts include smaller oxetes 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 (= Stiphonodictyon).

Synonyms:
(Fig. 64)
Type species (monotypy): P. siemensis Topsent, 1923: 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 spéciﬁque en se plaçant debout, solitaires ou par groupes, le long des oxes tangentielle 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 siemensis (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 alabrensis 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.
Remarks: two genera *Halichondria* and *Hymeniacidon* were formerly considered the type genera of two distinct lines within the Halichondrida, 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 styloite 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 *Ciocalypta* De Laubenfels, 1936: 134. (Fig. 73)

Type species (monotypy): *Ciocalypta amorpha* 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* (= *Epitopola*) *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 palisade-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. trichodragma (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 (s.b. = 10 µm), D. desma (s.b. = 100 µm) (all redrawn from Van Soest & Zea, 1986: figs. 2-5).
Genus *Cioxeamastia* De Laubenfels, 1942: 265. (Fig. 78)

Type species (monotypy): *C. polyaclypta* 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 *Ciocalepta* of the *Halichondriidae* also has fistules, but these are coarser than those of *Cioxeamastia*. The spiculation of *Ciocalepta* 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 kiegel- und zotzenförmigen Ausstülpungen 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; toptypical 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 épais, remarquable cor- ice, pourvu de spicules abondants et echevêtés en toutes directions sans son épaisseur, et fortement adhérent au chaonosome; cavités préparées très réduites.'"

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. *Ciocalepta 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. *Amorphopis excavus* 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. *Amorphopis excavus* 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. *Amorphopis excavus* 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. *Prostyliusa siamensis* Topsent (1925) (= *Amorphopis excavus* 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).
Fig. 65. *Epipolaxis sulensis* (Wilson, 1925), holotype USNM 21297 from the Philippine region (s.b. = 1 cm).

Fig. 66. *Petronica 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.

(Fig. 83)
Type species: T. glaberrima Burton, 1931: 138, figs. 3-4 (holotype reexamined).
Burton: “Ha polyscleridae 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 Raspailiella Schmidt, 1868: 25
(Fig. 77, 84)
Type species (monotypy): R. brumnea Schmidt, 1868: 25 (type specimens reexamined).
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 temporarley stored in the Museum 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.

Type species: S. borealis Miklucho Maclay, 1870: 13.
Remark: We have not seen the original description. Kolun (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 Halichon-
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*.

(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 *Uritisia* (see below).

(Fig. 89)
Burton: “Axinellidae with skeleton composed of unusually slender styli, arranged mainly in an irregular (sub-halichondroid) manner, but frequently forming whispy-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): *Batella corticata* Thiele, 1905: 438, fig. 58 (type slide reexamined).
Burton: “Close to *Rhaphoxia* 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; spongion 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*.

(Fig. 91)
Von Lendenfeld: “*Heterorrhaphidae of very soft texture,*

Figs. 69-73.
Fig. 69. *Halichondria panicea* (Pallas, 1776), A. tangential view of ectsosomal skeleton (redrawn from Hartman, 1958: fig. 9) (s.b. = 100 µm), B. spicules (s.b. = 100 µm).
Fig. 70. *Halichondria bouverbanki* Burton (1930), tangential view of ectsosomal skeleton (redrawn from Hartman, 1958: fig. 8) (s.b. = 100 µm).
Fig. 71. *Halichondria lutca* 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. *Ciocalapata* (= *Halichondria*) gibbs 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).
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.

(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. perplexis (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 bowserbanki Burton (1930), ZMA specimen from SW Netherlands (s.b. = 1 cm) (photo L. A. van der Laan).
Fig. 77. Raspagella (= 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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De Laubenfels, see Laubenfels.


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).


Figs. 87-93.

Fig. 87. Hymeniacidon caruncula Bowerbank, 1866 (= H. perleisii (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. Naiuldra (Hymeniacidon) maja 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 styloides (s. b. = 25 µm) (all made from the USNM holotype).

Fig. 89. Raphidostyla (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. Batella (= Hymeniacidon) corticata Thiele (1905), spicules (redrawn from Thiele, 1905: fig. 58) (s. b. = 50 µm).

Fig. 91. Stylostella (= 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. Thielea (= 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).