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A SYSTEMATIC REVISION OF THE NORTH EASTERN ATLANTIC SHALLOW-WATER HAPLOSCLERIDA (PORIFERA, DEMOSPONGIAE), PART I: INTRODUCTION, OCEANAPIIDAE AND PETROSIIDAE

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ABSTRACT

The taxonomic history of the sponge order Haplosclerida is reviewed, with emphasis on literature concerning the Haplosclerida of the North Eastern Atlantic Ocean. The characters and their value for a phylogenetic classification are discussed. Two families are treated systematically: the Oceanapiidae, which have two representatives in the area, and the Petrosiidae, represented by one species. Emended diagnoses for the order, families, and genera are given.

INTRODUCTION

This publication is the first of a series dealing with the taxonomy, biogeography, and phylogeny of the shallow-water Haplosclerida (Porifera, Demospongiae) of the North Eastern Atlantic region. Taxonomically, the Haplosclerida are known to be one of the most difficult and unstable groups of the class Demospongiae (Burton, 1926b, 1930; Lévi, 1973; Wiedenmayer, 1977b; van Soest, 1980), and a sound classification of the order is still to be established.

This is due to a combination of factors: the paucity of characters which are available for taxonomic investigation, the pronounced variability of most of these characters, the large number of species involved, and the divergent views of authors concerning the systematic value of the characters.

Recent attempts to deal with the taxonomy of the Haplosclerida are largely based on a combination of in vivo study of the living animal and that of early preserved museum material. Such studies include those of Griessinger (1971, Mediterranean), Bergquist & Warne (1980, New Zealand), van Soest (1980, West Indies), and Desqueyroux-Faundez (1984, and in preparation, New Caledonia), all faunistically orientated. Apart from making important contributions towards a better classification of the Haplosclerida, these studies have contributed to a greater understanding of the ecophenotypic variation of the species.

The Haplosclerida are widely distributed around the world and they form an important element of marine sessile shallow- and deep-water communities. As such the group is well suited for biogeographic studies.

The present author has undertaken a taxonomic revision of the Haplosclerida of the North Eastern Atlantic region, an area with a rich sponge fauna and very interesting from a zoogeographical point of view. It is an area which has been thoroughly explored in the past, as evidenced by the many European expeditions and investigations, and the extensive literature.

Bathymetrically the study is confined to the continental platform, e.g. from 0 to ca. 200 m.

In this first part of the revision the taxonomic history of sponges, and of the Haplosclerida in particular, is briefly reviewed, the taxonomic value of the characters is discussed, and the families Oceanapiidae and Petrosiidae are treated systematically. Both families have only a few shallow-water representatives in the area: two Oceanapiid and a single Petrosiid species are reported.

MATERIAL AND METHODS

The material studied for the present paper consists for the greater part of museum specimens deposited in the collections of the British Museum (Natural History), London (BMNH), the Zoologisk Museum , København (ZMK), and the Zoölogisch Museum, Amsterdam (ZMA). Fresh material was collected by diving in Lough Ine, Ireland in June 1981, and by dredging near Bergen, Norway in August 1982.

For the study of the skeletal architecture two microscopical sections were prepared from the preserved specimens: one of the surface (to obtain a tangential view of the ectosomal skeleton), and one perpendicular to the surface (to examine the choanosomal skeleton). The sections were dried and mounted in Canada balsam on a microscopical slide.

Spicule sizes are based on 25 measurements of each spicule category. Only full-grown spicules were measured.

TAXONOMIC HISTORY OF THE HAPLOSCLERIDA

The order Haplosclerida (*nomen correctum* de Laubenfels, 1955, pro Haplosclerina Topsent, 1928) was created by Topsent in 1928 to include sponges with "exclusively diactinal megascleres of one kind, which are mostly oxea, sometimes strongyles. Microscleres are generally absent, but when present they are sigmas, toxas, microxeas or rhapides, never chelae, asters, discorhabds, or derived forms. The choanosomal skeleton is variable, but it is never provided with "echinating" spicules. Spongin may be important" (translation of Topsent, 1928: 66). Topsent included one family, the Haplosclerídae, with three sub-families: Gelliinae Ridley and Dendy, 1887 (all Haplosclerids with microscleres), the Renierinae Ridley, 1884 (with spicule-reinforced skeletons), and the Chalininae Ridley, 1884 (with spongin-reinforced skeletons).

Prior to Topsent Haplosclerid sponge species were widely distributed among different, and often remote taxonomic groups. As the development of the classification of the Haplosclerida runs parallel to the classification of the remaining sponges, it will be useful to briefly trace the most important stages which occurred prior to 1928.

The classification of sponges begins with Donati (1750), who discovered the spicules. He recognized sponges as "Piante-animali". Before that time several sponge species had been described by Imperato (1599), Plukenet (1691; first description of a fresh-water sponge), Sloane (1696), Tournefort (1700), Ray (1724), Marsigli (1725), and several others, but these are not officially recognized today, as they predate Linnaeus, 1758. Actually it was Aristotle who was the first to recognize Mediterranean bathsponges as animals.

The earliest authors whose species are recognized include Seba (1758), Pallas (1766), Linnaeus (1767), Müller (1776), Fabricius (1780), Esper (1791-94, 1798-1806), Lamarck (1813-14, 1816), and Montagu (1818). At the beginning of the 19th century several schemes had been more or less simultaneously produced by Grant (1825, 1826a, b, c, 1861), Nardo (1833, 1839), Hogg (1851), Johnston (1842), and Lieberkühn (1859). By the end of this period there was general agreement about classifying sponges into horny-, siliceous-, and calcareous sponges.

An important period began with Bowerbank (1864, 1866, 1874), Schmidt (1862, 1864, 1866, 1868, 1870), Gray (1867, 1872), and Carter (1875, 1884), who between them are generally considered to have laid the foundations of our present-day classifications.

Bowerbank (l.c., 1882) described a large number of species, for the greater part from British waters. Following previous authors he classified sponges according to the inorganic matter and the architecture of their skeleton into the Calcarea, Silicea, and Keratosa. However, his Calcarea are equivalent to Grant's (l.c.) Leuconida and his Silicea to Grant's Chalinida. He kept Grant's name for the Keratosa. Bowerbank's nomenclatorial change of available and accepted names has been criticized by later authors (cf. Vosmaer, 1886), and furthermore his classification of the lower taxonomic groups has been considered as very unnatural. Certainly it is true that with the Haplosclerida he placed closely related and even conspecific species in different classes. For instance, the mono-typic genus *Diplodemia*, erected for *D. vesicula* (Bowerbank, 1866) was included in the Silicea. *D. vesicula* (holotype present in the BMNH) consists of a cluster of gemmules situated on the inside of a shell, held together by a few spicule containing spongin fibres. As already suggested by Topsent (1894a), these gemmules appear to belong to *Haliclona oculata* (Pallas, 1766). This latter species, however, Bowerbank included in the Keratosa (as *Chalina oculata*).

Schmidt, a contemporary of Bowerbank, worked mainly on the Mediterranean fauna, and although his classification essentially utilizes the same characters, his system is considered to be a more natural one. Actually Schmidt was the first to emphasize the importance of a system reflecting evolutionary trends. In 1870 Schmidt divided the sponges into 13 families: the Hexactinellidae, Lithistidae, Halisarcinae-Gumminae, Ceraospongiae, Chalineae (containing Haplosclerids, pars), Renierinae (containing Haplosclerids, pars), Suberitinae, Desmacidinae, Chalinopsidinae, Ancorinidae, Geodinidae, and Calcispongiae. The major problem of this system is that closely related families like Chalineae and Renierinae are of the same taxonomic rank as, for example, the Calcispongiae. Later, in 1880, Schmidt largely improved this system by transferring the Chalineae, Renierinae, Suberitidinae, Dessacidinae, and Chalinopsidae, into the Monactinellidae, and the Ancorinidae and Geodinidae into the Tetractinellidae (Schmidt, 1880).

Gray's attempt to classify the sponges were again heavily critized, and Vosmaer (1886) even considered rejecting them altogether. However, Gray's original system (Gray, 1867) is the first in which two large divisions were created on the basis of reproductive patterns. His Sub-class the Poriphora-silicea was subdivided into the Section Malacosporae ("soft-spored" sponges), with reproduction by ova or gemmules, and the Section Chlamydosporae (sponges with "armed spores"), with "reproduction by a thick ovisac, strenghtened with siliceous spicules, the ovisac often at length becoming solid spheres formed of siliceous spicules radiating from a central point". (Gray, l.c.: 502-505). Vosmaer particularly criticized Gray's sub-Sections (Sub-Section I: Dictyospongiae, Sub-Section II: Spiculospongiae, Sub-Section III: Arenospongiae), as being unnatural. Gray's important contribution to sponge classification lies mainly in his recognition of discrete groups of species within the large, vaguely defined "genera" of his contemporaries. In addition he authored many Haplosclerid genera.

Carter (1884) completely ignored the other systems, and based his classification on the "condition" of the skeleton, dividing the class Spongida into eight orders, viz. Carnosa, Ceratina, Psammonemata, Rhaphidonemata (equivalent to Ridley's family Chalinidae (Ridley, 1884), cf. Lévi, 1956, and below), Echinonemata, Holorhaphidota (= Silicea), Hexactinellida, and Calcarea. His system has been disapproved by all later authors, and his classification was considered to be very unnatural and of little practical value.

By about 1884 the sponges were divided into the Calcarea, Hexactinellida, Cornea (with

Haplosclerids), Silicea (also containing Haplosclerids), and Carnosa (without skeleton) (cf. also Lévi, 1956).

In the following period the main sponge classifiers were Ridley (1884), Ridley & Dendy (1887), Vosmaer (1886), Sollas (1885, 1886, 1888), and Lendenfeld (1884, 1886, 1887, 1888). At the same time embryological studies were started by Schulze (1877, 1878, 1879, 1880, 1881), Delage (1892), and Maas (1893).

Vosmaer based his classification largely on that of Schmidt, which he considered to be the best and most natural. Vosmaer's classification of 1887 is the first in which all Haplosclerid species (together with non-Haplosclerids) are grouped into one family, viz. the Halichondridae (sub-order Halichondrina, order Cornacuspongiae).

Ridley (1884) stated that he did not follow any one author in his classification, but he did use a combination of previously known systems. He raised Schmidt's Monactinellidae and Tetractinellidae to the level of sub-order, and divided the sub-order Monactinellidae (order Silicea) into seven families: Chalinidae, Renieridae, Desmacidinidae, Ectyonidae, Axinellidae, and Suberitidae, Haplosclerids being found in the first three families. Ridley & Dendy (1887) apparently followed Vosmaer's earlier work. They retained the Halichondria and Clavulina in the Monaxonida, and kept the Homorrhaphidae, Heterorrhaphidae, Desmacidonidae, and Axinellidae as separate families.

Sollas (1888) erected the Demospongiae for siliceous sponges with monaxons, tetraxons, and triaxons as megascleres, with microscleres of different types, and either with skeletons of spicules, spicules with spongin, or only spongin.

Lendenfeld (1887) erected numerous Haplosclerid genera, but as he used the growth form as the main diagnostic character at genus level, many of his genera will quite certainly turn out to be invalid.

By the end of the early 1900's the sponges were classified into Calcarea, Hexactinellida, and Demospongiae (cf. also Lévi, 1956).

Hentschel's (1923) idea of dividing the Demospongiae into the Tetraxonida, Cornacuspongia, and Dendroceratida was taken up and developed by Topsent (1928). He divided the Class Demospongiae into two sub-classes: the Spiculispongia (comprising the orders Tetractinellida and Hadromerida) and Cornacuspongiae (comprising the orders Halichondrina, Poecilosclerina, Haplosclerina, Dictyoceratina, and Dendroceratina). Topsent's classification is still largely used today, with minor changes.

A period of refinement began with Burton (1926a, b, 1930, 1932, 1934a, b, c), and de Laubenfels (1936). Burton, who worked at the British Museum (Natural History), London, re-examined much of Bowerbank's material. His studies led him to emphasize the variability of taxonomic characters. He synonymized many of Bowerbank's species into a few, very variable species. Although his work on the Calcarea has great value because of its completeness with respect to literature data (Burton, 1963) it is certain that he carried the synonymisations too far, and thus his biogeographical theories are of doubtful value. Concerning the Haplosclerida, Burton (1932, 1934c) minimized the systematic value of the microscleres and the amount of spongin, emphasizing instead the importance of the presence or absence of a special dermal (ectosomal) skeleton. He abandoned the family Gelliinae (based purely on the presence of microscleres), and revived the genus *Adocia* Gray, 1867, with *Adocia simulans* (Johnston) as type-species. This genus was characterized by the presence of a dermal skeleton, as opposed to *Haliclona* Grant, 1835, which was characterized by the absence of a dermal skeleton. Later Burton (1959b) changed this viewpoint, and minimized both the taxonomic value of the microsclere complement and the presence of a special ectosomal skeleton. As a consequence he synonymized *Adocia* with *Haliclona*. This important change of view has not been adopted by later authors (cf. also Wiedenmayer, 1977b), but in the present author's opinion it is the only classification of this group which is not based on primitive characters. I largely agree with Burton's later classification, which will be explained later in this paper.

De Laubenfels (1936) created a highly artificial system which had practical use for the classification of families and subfamilies. He followed Burton (1934c) with respect to the value of a dermal skeleton, but he regarded the microscleres as an important character. De Laubenfels considered the presence of a dermal skeleton of such a great taxonomic significance that he restricted Topsent's definition of the order Haplosclerina for sponges lacking a dermal skeleton, and with spongin-reinforced skeletons. He placed sponges with a dermal skeleton, and with spicule-reinforced skeletons into the order Poecilosclerina, which he subdivided into four artificial groups: the Phorbasiformes (principal and auxiliary spicules diactinal), the Plocamiiformes (principal spicules diactinal, auxiliary spicules monactinal), the Myxilliformes (principal spicules monactinal, auxiliary spicules diactinal), and the Microcioniformes (principal and auxiliary spicules monactinal). Within the order Haplosclerina he created the families Haliclonidae and Callyspongiidae, and retained three other Haplosclerid families, viz. Spongillidae, Desmacidonidae, and Oscarellidae. *Adocia*, *Pellina*, *Orina*, *Sigmadocia*, *Toxadocia* (erected by de Laubenfels for species with a dermal skeleton and/or sigmas), genera which were hitherto considered to be Haplosclerid genera, were put in the family Adociidae (sub-family Crellininae) of the order Poecilosclerina, together with *Baikalospongia* (spined tylotes), for instance. It is evident that this classification is highly unnatural and not based on characters reflecting phylogenetic relationships. However, because of its comprehensive coverage of the literature this work has proved to have a practical application in sponge systematics (Lévi, 1956, Hechtel, 1965).

In 1956 Lévi proposed a new classification, based on a thorough study of larval structures of species representing the different higher taxa. He proposed to group the earlier established orders of the class Demospongiae which have an incubated parenchymella larvae (the Dendroceratida, Dictoyceratida, Haplosclerida, and Poecilosclerida) into the sub-class Ceractinomorpha. Sponges with different larval structures, e.g. sponges which are heterogenous with respect to this feature (the Homosclerophora, Tetractinellida, and Clavaxinellida) were put into the other sub-class, the Tetractinomorpha. At present the Haplosclerida are still classified in the sub-class Ceractinomorpha.

RECENT CLASSIFICATIONS OF THE HAPLOSCLERIDA

Hechtel (1965), who made a systematic study of the sponges of Jamaica, regarded the order Haplosclerida as comprising the family Haliclonidae, Desmacidonidae, Adociidae (placed by de Laubenfels (1936) in the Poecilosclerida (cf. above)), and Callyspongiidae. Hechtel allows for the presence of chelae in the Haplosclerida. They are common in the Desmacidonidae, but he also mentions the possibility of chelae in his definition of the Adociidae. Apart from the major change of including the Adociidae in the Haplosclerida again, Hechtel largely follows de Laubenfels.

The next important contribution concerning the recent classification of the Haplosclerida is that of Griessinger (1971), who worked in the Mediterranean. According to Griessinger two evolutionary trends are present within the Haplosclerida, viz. one verging towards a skeleton with spongin as the major reinforcing material, and one verging towards a skeleton which is reinforced by spicules. The first group is represented by the family Haliclonidae de Laubenfels, 1936; the second by the family Renieridae Ridley, 1884.

Griessinger recognized only these two families in the Haplosclerida, together with the Gelliidae Ridley & Dendy, 1887, although the latter is not included in his study. Actually it is far from clear what is Griessinger's opinion concerning the taxonomic value of the microscleres. On p. 100 (l.c.) he writes: "On admet ainsi chez les Haplosclérides deux familles: celle des Haliclonidae et celle des Renieridae; la première est charactérisée par une charpente bien organisée, la seconde par une charpente moins organisée; il semble que les Gelliidae (qui n'ont pas été étudiés dans ce travail) doivent aussi être classés en fonction de leur type de charpente et non plus distingués par la possession de microsclères (Burton, 1932-1934)." However, on p. 117 he writes: "Dans cette étude nous admettrons seulement les trois premières"; (Renieridae, Haliclonidae, Gelliidae)"; ... seules des espèces appartenant aux Renieridae et aux Haliclonidae ont été étudiées." From these remarks it is not possible to know if Griessinger considered the Gelliidae as a separate family or not.

The Haliclonidae sensu Griessinger are characterized by small oxea, which are regular in size and form, and a skeleton which is regular, with reduced spicule content and in which spongin may play an important role.

The Renieridae sensu Griessinger are characterized by large oxea, irregular skeletons, and reduced spongin.

The Haliclonidae comprise the genera *Haliclona*, *Chalinula*, *Adocia*, *Callyspongia*, and *Siphonochalina* (within the Mediterranean limits of Griessinger's study). The Renieridae comprise the genera *Reniera*, *Pellina*, *Rhizoniera*, and *Dendroxea*.

Griessinger's classification has been followed by Lévi (1973) who proposed to abandon the Gelliidae, and who mentioned the possibility that the maintenance of genera on the basis of their microsclere complement might be unnatural. In general, one speaks of the Griessinger-Lévi classification (cf. also van Soest, 1980). This classification has, however, been criticized by later authors (Wiedenmayer, 1977a, b, Bergquist & Warner, 1980, van Soest, 1980). The main criticisms of these authors is the fact that it is not possible to make a clear distinction between the two families, particularly with regard to the size and shape of the spicules, the regularity of the skeleton and the amount of spongin, which are such variable characters. Griessinger's classification is not adopted here as it does not agree with a phylogenetic system.

Wiedenmayer (1977a, b) abandoned the family Callyspongiidae, but erected the family Nepheliospongiidae Clarke, 1900 for the genera *Petrosia*, *Xestospongia*, *Cribrochalina*, *Hemigellius*, *Vagocia*, *Calyx*, *Rhizochalina*, *Oceanapia*, *Biminia*, and *Siphonodictyon*. This family is characterized by a stony structure, due to the strong development of megascleres in relation to fleshy parts and spongin, and with a skeleton consisting of thick ascending fibres, often in combination with a strong development of the secondary fibres. The ectosomal skeleton is often a thick, multilayered crust. Wiedenmayer related this family to the fossil family Heliospongidae Finks, 1960.

As a basis for his classification he used the general architecture of the skeleton, but he maintained the presence of an ectosomal skeleton as a character to define the family Adociidae, and he also kept microsclere bearing species in separate genera. Unlike Burton, Wiedenmayer (1977b: 79) proposed to widen the concept of the family Haliclonidae with respect to that of de Laubenfels (1936), and he agreed with Hechtel (1965) about including the Adociidae in the Haplosclerida instead of placing them in the Poecilosclerida.

The most recent classifications are those of Bergquist & Warne (1980), van Soest (1980), and Desqueyroux-Faundez (1984, and in the press).

Van Soest (l.c.) erected three new Haplosclerid families: Niphatidae, Petrosiidae (pro: Nepheliospongiidae), and Oceanapiidae, and retained the Haliclonidae and Callyspongiidae. He did not follow Wiedenmayer (l.c.) with respect to the family Nepheliospongiidae, because *Nepheliospongia* probably cannot be associated with *Petrosia* and other recent genera. Although van Soest maintained genera based on an ectosomal skeleton or microscleres, he strongly emphasized the possibility that these characters represent a primitive state, on which a phylogenetic classification cannot be based.

Bergquist (1980a) and Bergquist & Warne (1980) adopted the Oceanapiidae of van Soest as a separate family, but on the basis of reproductive characters they created a separate order, the Nepheliospongida for the families Nepheliospongiidae and Oceanapiidae.

They kept the families Haliclonidae, Adociidae, and Callyspongiidae in the order Haplosclerida. According to Bergquist & Warne (l.c.) the sponges of the Nepheliospongida are oviparous, whilst those of the Haplosclerida are viviparous. Furthermore the Nepheliospongida are characterized by some special biochemical properties, viz. a cyclopropene ring in the side chain of novel sterols. This view of creating a separate order on basis of such characters is not adopted by the present author. Ovipary is known to be the primitive reproductive pattern in sponges (also mentioned by Bergquist & Warne, l.c.), and consequently retention of it cannot be used in classification. The value of the biochemical character is difficult to weigh, since so few species have been investigated.

THE TAXONOMIC HISTORY OF HAPLOSCLERIDA OF THE NORTH EASTERN ATLANTIC REGION

The sponge fauna of the North Eastern Atlantic region, especially of the European coasts, is one of the best described in the whole world. The area has an extremely rich intertidal and subtidal flora and fauna, as the strong tidal currents in combination with a vast littoral area, and the presence of numerous sheltered "Loughs" create optimal conditions for marine benthic organisms.

It is therefore not surprising that the number of described Haplosclerid species is large, and that most of the sponges collected during the present study appear to conform to previously described forms.

One of the foremost authors of sponges for the area was Bowerbank, who described 42 Haplosclerid species under the generic names of *Chalina*, *Isodictya*, and *Halichondria* (Bowerbank, 1864, 1866, 1874, 1882). He was, however, one of the so-called "splitters" and although his descriptions and figures are good, it is evident that he described far more species than really existed. He received most of the material from other collectors, and his lack of knowledge of the living sponge may be one of the reasons why he described every variety as a separate species.

Bowerbank's material, which is largely incorporated in the collections of the British Museum (Natural History) (London), has been reexamined by Burton, the other important British author to deal with Haplosclerid sponges (Burton, 1926a, b, 1927, 1930, 1931a, b, c, 1931/32, 1932, 1934a, b, c, 1935a, b, 1947, 1948, 1956a, b, 1959a, b). Burton frequently mentioned the fact that the Haplosclerids are extremely difficult for taxonomic investigation, because of the simplicity of the skeleton and the few characters which are available in this group.

Lundbeck (1902, 1909) described several species, mainly from Norway and Greenland. In addition, species have been described by Johnston (1842, Britain), Schmidt (1870, Denmark, Greenland), Vosmaer (1882, 1885, Norway, Arctic), Fristedt (1885, Sweden), Topsent (1888, France), Arnesen (1903, Norway), Stephens (1912, Ireland), Hentschel (1916, 1929, Arctic), and several others. In total ca. 140 nominal species are described.

Topsent (1890, 1891, 1892, 1894a, 1896, 1899, 1928, France, North Atlantic), Lambe (1900, Greenland), Brøndsted (1914, 1916, 1932, 1933a, b, Greenland), Ferrer Hernandez (1916, Spain), Alander (1942, Sweden), Lilly *et al.* (1953, Ireland), Koltun (1959, Arctic) and Könnecker (1973, Ireland) reported or redescribed several species, but the descriptions given require the study of the original specimens to be sure of their identity, so most of these records must be considered unreliable.

As a basis for identification one is at present largely dependent on the work of Arndt (1935), and his Haplosclerid species descriptions are without doubt the best and most reliable which we have available.

SYSTEMATIC CHARACTERS

GROWTH FORM

Ecophenotypic variation is a common feature in sponges, and this includes the Haplosclerida where the growth form is very variable.

An example is the frequent occurrence of small, thin encrustations under intertidal stones, showing little variation in colour, which at first sight seem to be one and the same species. Most frequently these encrustations appear to be *Haliclona cinerea* (Grant, 1826d) and *H. rosea* (Bowerbank, 1866). They are almost indistinguishable in this form, and they can be regularly found growing together in several patches under the same stone.

Another example is *Haliclona oculata* (Pallas, 1766), a well-known circum-Atlantic species. Young specimens are finger shaped. Older sponges are branched and stalked, but there is a great variation in the degree of branching. The branches may remain isolated along their entire length, growing from a common basal stalk, or they may also coalesce to such a high degree that the shape of the sponges becomes almost flabellate. Commonly the growth form is intermediate between these two extremes.

In *Oceanapia* the form is a rather constant feature: all species which belong to this genus consist of a body from which arise fistular processes.

The high variability of the growth form is certainly one of the reasons why there are so many descriptions of species which are actually phenotypic variations of one and the same species.

The growth form, therefore, is a difficult although not completely unreliable character, best used after wide experience of studying the living sponges from different ecological and geographical localities.

SURFACE

The appearance and the texture of the surface is species-specific and shows little variation. At higher taxonomic level it has no importance, but it is certainly a very useful character for species identification.

CONSISTENCY

Contrary to Griessinger (1971), the present author thinks that the consistency is an objective feature, easy to describe, and species-specific. It is a very useful character for species identification (especially for living sponges), and furthermore, it is also characteristic at the family level, as already mentioned by Bergquist & Warne (1980). Generally the Petrosiidae are firm, sometimes stony, the Niphatidae tough, the Callyspongiidae elastic, the Oceanapiidae fibrous or crumbly, and the Haliclonidae are generally very fragile.

It is, however, difficult to judge the value of the different consistencies as characters for a phylogenetic classification. At present I consider it only as a useful, but rather equivocal character.

COLOUR

In some cases the colour may be a useful character in species identification, as has already been mentioned by Griessinger (1971) and Bergquist & Warne (1980). However, in my opinion it is superfluous to mention official colour codes as extra information. Some species show a greater variation in colour than others, and also the degree to which they fade in spirit is not the same in each species. The strict use of colour codes can invoke an undesirable tendency for splitting off "species" or subspecies. It is certainly a character to be described in species descriptions, but at a higher taxonomic level it has no value.

OTHER CHARACTERS OF THE LIVING SPONGE

Some species have certain peculiarities in their living state which can be of great use for identification purposes. *Haliclona cinerea* (Grant, 1826d), for example, has a specific sort of spongin, different from the spicula-connecting spongin, which appears as slimy threads when the sponge breaks or when it is removed from the substratum. The nature of these so-called "slime strands" (Jones, 1984) has been described by Topsent (1888, 1925) and Tuzet (1932). *Halicona viscosa* (Topsent, 1888) is very slimy and gives off a large amount of mucus when removed from the water. *Haliclona indistincta* (Bowerbank, 1866) is only slightly sticky. These characteristics are certainly worth mentioning in species descriptions, but they have no value at higher taxonomic level.

ECOLOGY

Some species are quite clearly confined to certain habitats. *Haliclona viscosa*, for instance, is always found in places with strong tidal currents but never in the upper intertidal region. It grows most frequently on vertical walls at a depth of 10-25 m. *Haliclona indistincta* is only found at the underside of intertidal stones; *Acervochalina loosanoffi* (Hartman, 1958) is an estuarine sponge (cf. also Fell, 1978).

For many of the species in the study area, however, the ecology is at present poorly known, mainly because of the taxonomic uncertainty surrounding Haplosclerid sponges, which has had a discouraging affect on further ecological investigation (cf. also "The MCS sponge Guide" produced by the Marine Conservation Society, England).

REPRODUCTION AND LARVAL STRUCTURES

The Haplosclerida reproduce mainly by vivipary (the Petrosiidae and Oceanapiidae by ovipary, according to Bergquist (1980a), and Bergquist & Warne (1980)), and the larvae are round or oval, generally incompletely ciliated and of different pigmentations.

The main studies of larval structures of Haplosclerid species are those of Carter (1874), Barrois (1876), Keller (1879), Delage (1892), Maas (1893), Meewis (1938, 1939a, b, 1941), Lévi (1956), Griessinger (1971), and Bergquist *et al.* (1979). Bergquist *et al.* (l.c.) give a review of different larval types for species assigned to *Chalinula* (= *Acervochalina*), *Reniera* (= *Haliclona*), *Adocia* (= *Haliclona*), *Callyspongia*, and *Haliclona*. They conclude that two different lines are distinguishable: one group represented by the "*Chalinula*" and *Reniera* larval types, the other by the *Callyspongia*, *Adocia*, and *Haliclona* larval types. *Reniera* and *Adocia* are synonymous with *Haliclona*, as it is impossible to define these three genera on distinctive and derived characters. The differences found in larval structures, as described in the literature and observed by the present author for *Acervochalina loosanoffi*, *Haliclona oculata*, *H. rosea*, and *Haliclona* n.sp. de Weerdt, in prep., are of minor importance.

AMOUNT OF SPONGIN

As mentioned earlier in this paper, the so-called Griessinger-Lévi classification of the Haplosclerida is based on the theory that two evolutionary trends were present in the group: one verging towards a spongin reinforced skeleton, the other one verging towards a spicula reinforced skeleton. The Haliclonidae and Renieridae are modern representatives. Both families are synonymized by the present author, in favor of the older name Haliclonidae.

Apart from the fact that there are no distinctive characters in the type species of *Haliclona* and *Reniera*, it is not possible to maintain families on basis of such a highly variable character as the amount of spongin present. Most Haliclonid species possess an intermediate amount of spongin. In some species there is a striking difference between the amount of spongin found at the periphery and that found in the inner and basal parts of the sponge. It is a difficult character to rely on, even at species level, but it is not without value.

BIOCHEMICAL PROPERTIES

The study of sponge biochemistry began with Bergmann (1949, 1962), Bergmann & Feeney (1950), and Bergmann *et al.* (1957). Since that time it has been Bergquist in particular, who has advocated the importance of a biochemical approach in sponge taxonomy (Bergquist & Hogg (1969), Bergquist & Hartman (1969), Bergquist (1978, a, b), Bergquist *et al.* (1980, 1984), and Evans & Bergquist (1977)). Other biochemical studies include those of Erdman & Thomson (1972), Voogt (1972), de Rosa *et al.* (1973), Cimino *et al.* (1975), Fattorusso *et al.* (1975), and Mattia *et al.* (1978).

Bergquist *et al.* (1980) suggest a possible relationship between the occurrence of 26-methyl sterols and oviparous reproduction patterns within the Ceractinomorpha. Bergquist (1980a) created the order Nepheliospongida, in which she included the Nepheliospongidae (with *Petrosia* and *Xestospongia*), and the Oceanapiidae (with *Oceanapia* and *Vagocia*), on the basis of the occurrence of novel sterols with a cyclopropane or cyclopropene ring in the side chain, in combination with oviparous reproduction. This view is not adopted here. The importance of biochemical characters in sponge taxonomy is difficult to assess, but they do not determine phylogenetic relationships by themselves. As far as the Haplosclerida are concerned, more evidence is needed before any decision on the classification of the group can be taken.

SPICULATION

MEGASCLERES

In the Haplosclerida only one type of megasclere occurs, viz. diactinal monaxones. These can be oxea or strongyles. Stylote modifications occur quite frequently, but they are never the original spicules. Except for some of the Petrosiidae, the Haplosclerida megascleres are usually of one size category. Individual variation in size and shape of the spicules is always present, but I do not agree with Bergquist & Warne (1980) that this intraspecific variation renders this character worthless.

According to Griessinger (1971) small spicules with a limited variation in size would be characteristic for the Haliclonidae, whilst large spicules with a high degree of variation would be characteristic for a family such as the Renieridae. Furthermore his definition of the Haliclonidae includes sponges with regular skeletons and a tendency towards spongin-reinforcing, and the Renieridae have irregular skeletons with a tendency towards spicule-reinforcement. That this is not a realistic classification may be evident from the following examples.

Haliclona oculata (Pallas, 1766, type-species of *Haliclona*) is the first and most obvious example. Its spicule size is evidently correlated to water temperature (Hartman, 1958, Griessinger, 1971), as northern populations have larger spicules than southern. Hartman gives size ranges from ca. 65 to ca. 170 µm for American populations (cf. Hartman, 1958). European specimens which were collected or studied during the present study appear to have comparable size ranges. As a mean, the spicule size ranges from 80 to 120 µm.

Haliclona aquaeductus (Schmidt, 1862, type-species of *Reniera*, but assigned to *Haliclona* by the present author) has a spicule size ranging from 130 to 180 µm.

Haliclona crassa (Topsent, 1925, assigned to *Reniera* by Griessinger, 1971) has a spicule range of 120 to 180 µm.

Haliclona simulans (Johnston, 1842, type-species of *Adocia*, but assigned to *Haliclona* by the present author) has exactly the same range in spicule size as *H. crassa*.

It is evident that the spicule size in combination with the variation is a character overlapping amongst the species.

To summarize, the form and size of the megascleres is a character which may be used at the species level, despite its individual variation, but an intimate knowledge of the species is necessary.

MICROSCLERES

There has been much disagreement in the past (de Laubenfels (1936), Burton, 1934b, 1959b, Bergquist & Warne, 1980, van Soest, 1980) about the systematic value of the microscleres within the Haplosclerida.

Although the function of the microscleres is still unknown, they represent important taxonomic characters in many sponge taxa, because of their large diversity in form and size (cf. also Dendy, 1921, 1924; Hartman, 1981).
Their presence or absence, and their structural characteristics may be of great help in developing a phylogenetic classification.

Haplosclerida possess relatively few microscleres. Simple sigmata and toxa are the most common forms, but microxea, microstrongyles, and rhaphides occur also. The sigmata and toxa show certain peculiarities, which are found only in the Haplosclerida and the Poecilosclerida. The sigmata are typically accolada-shaped, often centrotylote, and they lack the sharp curved points at their extremities. The toxa are of a typically straight form.

The rhaphides, on the other hand, are indistinguishable from non-Haplosclerid rhaphides. Furthermore they are widely distributed amongst all taxa, but they are always of a rather rare occurrence (Dendy, 1924), and only being found in a few Haplosclerid species.

This might be explained by the fact that they were originally present in one of the earliest ancestor species, and that they are slowly disappearing in the different lines. The other possibility is, of course, that of parallel evolution, i.e. that they have evolved independently in the different taxa, but this is highly improbable. An indication that rhaphides might be a primitive (symplesiomorph) character is the fact they are of the same size and shape in the different taxa (both the single rhaphides, and the trichodragmata).

It is here assumed that the sigmata and toxa of the Haplosclerida are a symplesiomorph character, i.e. that they have not developed just within the Haplosclerida, but that they were already in existence in an earlier stage of sponge evolution. In the circumstances, it is not possible to define Haplosclerid families or genera on the presence or absence of microscleres.

At the species level the microscleres, however, are a very useful character.

SKELETAL ARCHITECTURE

ECTOSOMAL SKELETON

The systematic value of the ectosomal skeleton has, like the microscleres, been given varying importance amongst authors, and it is therefore desirable to discuss this character at some length.

In the Haplosclerida several ectosomal skeletons occur, which differ in their degree of complexity. Generally they can be divided into the following categories (fig. 1):

1. A multilayered ectosomal crust, composed of an irregular and dense reticulation of mainly tangential spicules. This type is found in the Oceanapiidae and Petrosiidae (fig. 1a).
2. A regular, tangential reticulation of spicule tracts arranged in a circular pattern with rounded meshes. This structure is characteristic for the Niphatidae (it may also be found in some Petrosiidae) (fig. 1b).
3. A very regular, tangential reticulation of spongin fibres which is subdivided into at least two categories of larger and smaller meshes. This type of ectosomal skeleton is exclusive for the Callyspongiidae (fig. 1c).
4. An unilayered, very regular, isodictyal, continuous reticulation with three-sided meshes, composed of spicules which are bound by spongin at the nodes. This skeleton is common in the Haliclonidae, but it is also found in some Oceanapiid species (fig. 1d).
5. An unilayered, somewhat irregular, isotropic or subisotropic reticulation, interrupted by many openings but still forming a cohesive structure. In the open areas the dermal membrane is clearly visible, pierced by pores. This ectosomal skeleton is common in the Haliclonidae, and it is often found in species assigned to *Reniera* by Griessinger (1971) and van Soest (1980) (fig. 1e).

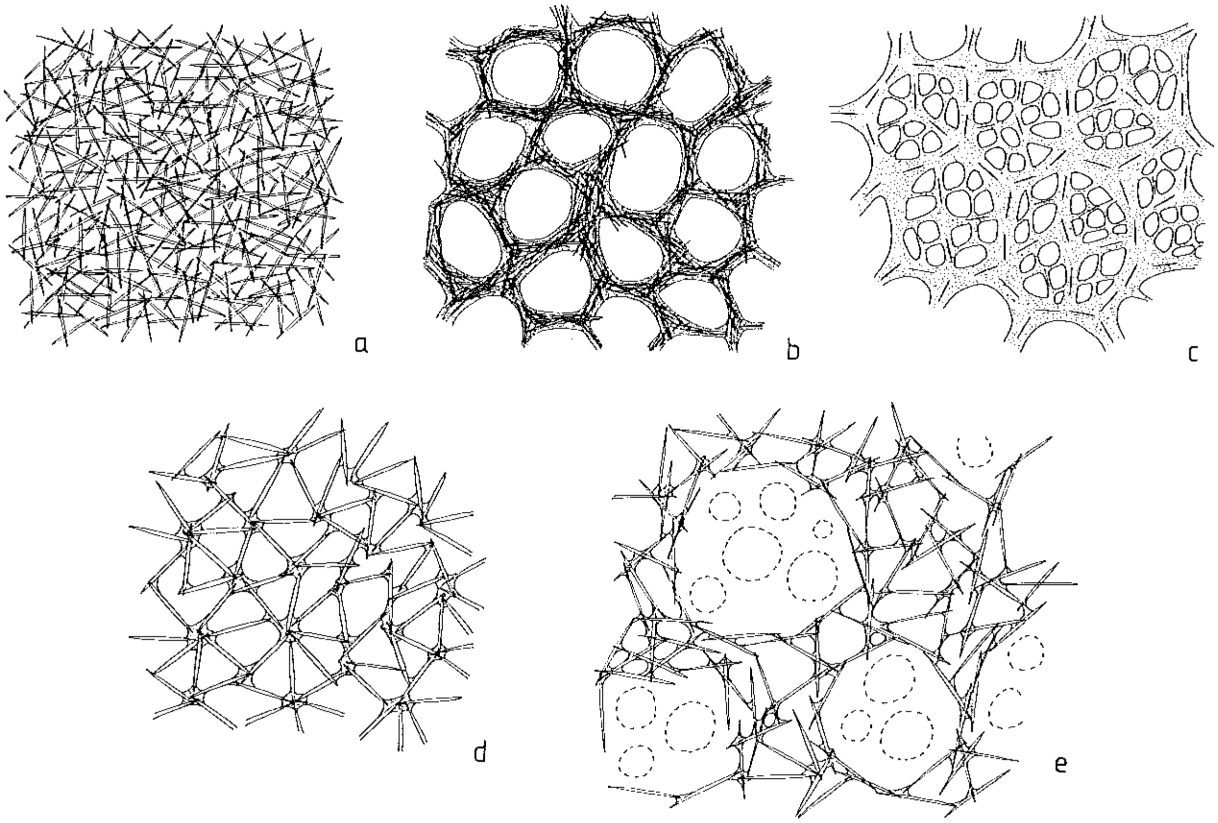


Fig. 1. Ectosomal skeletons in the Haplosclerida (see text) a. Oceanapiidae; b. Niphatidae; c. Callyspongiidae; d. Haliclonidae; e. Haliclonidae.

In order to judge the taxonomic value of these different ectosomal structures in a phylogenetic sense, it is necessary to compare the Haplosclerida with other groups, and then it is seen that similar structures occur in some of the Poecilosclerida. In the Myxillidae, Clathriidae, and Mycalidae we find an ectosomal crust which is quite similar to that of the Oceanapiidae and Petrosiidae.

It is still too premature to draw conclusions concerning the state of the ectosomal skeletons of the Haplosclerida, but it is here assumed that the ectosomal crust as found in the Oceanapiidae and Petrosiidae is a character which is shared with the Poecilosclerida, i.e. that this ectosomal skeleton was present in a common ancestor species of both the Haplosclerida and Poecilosclerida.

The remaining ectosomal skeleton types seem to be found only in the Haplosclerida, and they are interpreted by the present author as derived (apomorphic) character states which can be used as differentiating characters at the family level.

CHOANOSOMAL SKELETON

The choanosomal skeleton is here considered as the main distinguishing character at the generic level. The number of different choanosomal skeleton structures is too large to mention here, and will be described in detail when the different genera are treated. The most common choanosomal structures are the following (fig. 2):

Haliclonidae:

a. ladder-like, with uni-, pauci-, or multispicular ascending (primary) lines and

unispicular connecting (secondary) lines (*Haliclona*) (fig. 2a).
b. no clear distinction between primary and secondary lines, which are uni-paucispicular (*Acervochalina*) (fig. 2b).

Callyspongiidae:

A regular reticulation of primary and secondary spongin fibres which are cored by single spicules (*Callyspongia*) (fig. 2c).

Niphatidae:

Ladder-like with thich multispicular primary lines which are connected by paucispicular secondary lines (*Amphimedon*) (fig. 2d).

Oceanapiidae:

Irregularly disposed multispicular tracts, forming a subdermal tangential supporting system just below the surface, with an isotropic

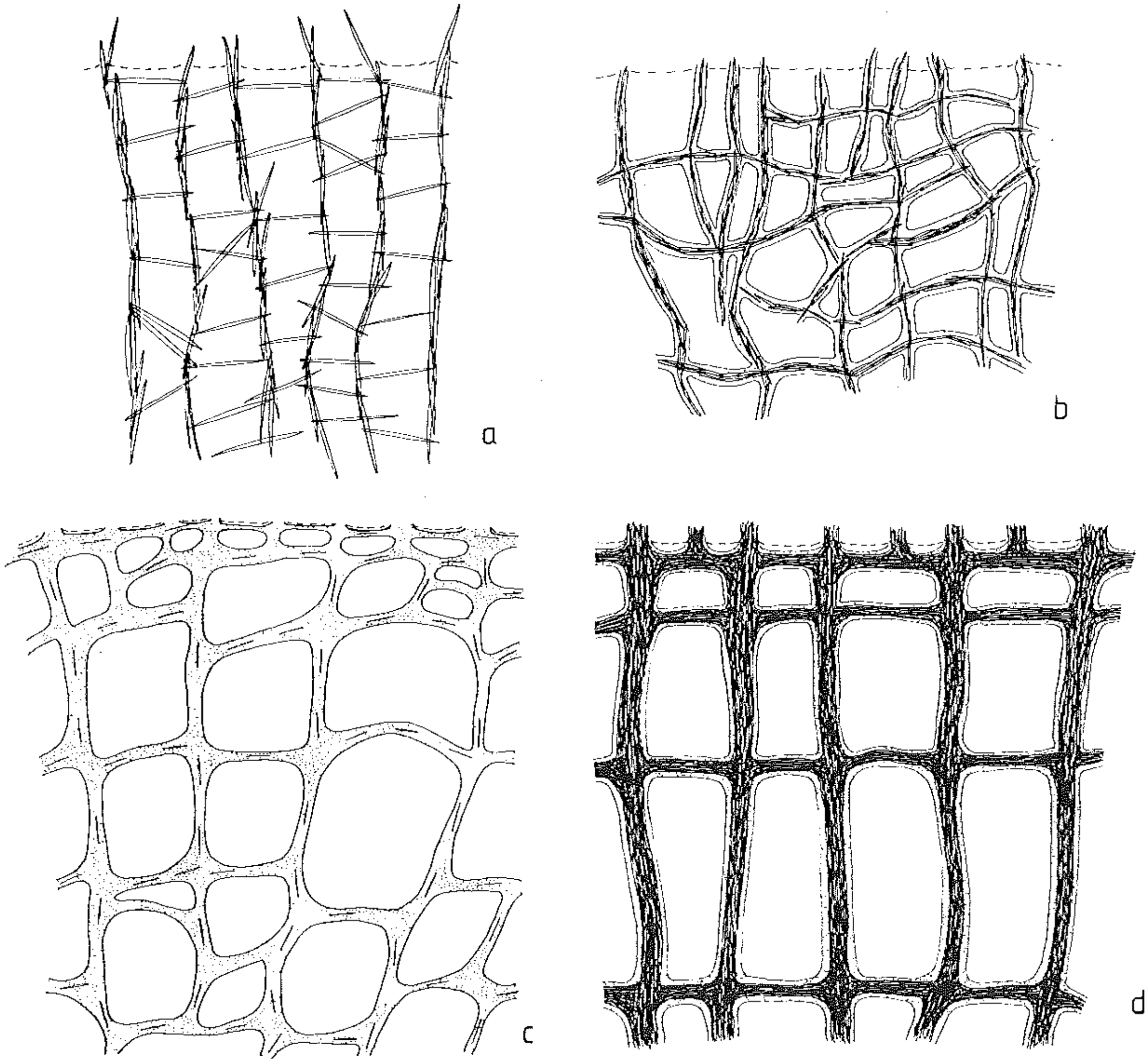


Fig. 2. Choanosomal skeletons in the Haplosclerida (see text) a. *Haliclona*; b. *Acervochalina*; c. *Callyspongia*; d. *Amphimedon*.

reticulation of single spicules lying in between the tracts (*Oceanapia*) (fig. 3b).

Petrosiidae:

Multispicular primary and secondary tracts which form a reticulate pattern with rounded meshes (*Petrosia*) (fig. 6a).

The choanosomal skeleton of *Amphimedon* is very similar to the skeletons found in some of the Desmacidonidae, Gray, 1876 (Poecilosclerida).

The taxonomic status of the Desmacidonidae is still doubtful, and some authors tend to include them in the Haplosclerida (de Laubenfels, 1936; Hechtel, 1965; Bergquist, 1965). Apart from the fact that many Desmacidonidae have styles for megascleres, the main difference between this family and the Haplosclerida is the presence of chelae in the Desmacidonidae. Chelae may, however, be unstable in certain cases. An example is *Isodictya palmata* Bowerbank (1866), type-species of *Isodictya*, which is conspecific with *Pachychalina excelsa* Schmidt (1870) and *P. schmidtii* Lundbeck (1902). The latter two species are described as having no chelae, and were presumed to be Haplosclerids in the past. Material of the three species has been studied by the present author, and it is certain that they are conspecific (also mentioned by Arndt, 1925).

The question of the place of the Desmacidonidae, and also, of course, of the Spongillidae (s.l.), which are still considered to be Haplosclerids by many authors, remains unsolved at the present time. However, it seems reasonable to consider the ladder-like choanosomal structure of *Amphimedon*, for example, as a synapomorphy for the Haplosclerida and these families. Within the Haplosclerida it is, therefore, a plesiomorph character, and the family Niphatidae should be defined on the basis of other, derived characters.

SYSTEMATIC DESCRIPTIONS

Phylum Porifera Grant, 1836
Subphylum Cellularia Reiswig & Mackie, 1983
Class Demospongiae Sollas, 1885
Subclass Ceractinomorpha Lévi, 1956

Order Haplosclerida Topsent, 1928

Ceractinomorpha with a reticulate skeleton of diactine monaxones as megascleres, and a microsclere complement, if present, of sigmata, toxa, microxea, microstrongyles, or rhaphides. Spongin present. Ectosomal skeleton, if present, tangential and unspecialized, i.e. composed of the same elements as the choanosomal skeleton.

Family Oceanapiidae van Soest, 1980

Definition: Haplosclerida with an ectosomal skeleton consisting of a tangential, subisotropic reticulation of single spicules: choanosomal skeleton a subisotropic reticulation of single spicules to which there is added an irregular system of spicule tracts.

Remarks: The ectosomal skeleton is often a thick, multilayered crust, which may be heavily reinforced by spongin. Fistular outgrowths are a common feature; they are always present in *Oceanapia*. Common microscleres are sigmata and toxa.

Genus *Oceanapia* Norman, 1869b

Rhizochalina Schmidt, 1870
Phloeodictyon Carter, 1882
Biminia Wiedenmayer, 1977b

Type-species: *Isodictya robusta* Bowerbank, 1866

Definition: Fistule bearing Oceanapiidae. Fistule walls supported by a longitudinal reticulation of spicule tracts, with a subisotropic reticulation of single spicules lying in between.

Remarks: The choanosomal skeleton of the main body is often a confused combination of reduced spicule tracts with minimal spongin. This type of skeletons is responsible for the pulpy consistency, which occurs in *Oceanapia* *robusta* (Bowerbank, 1866). Spongin may be highly developed in other species.

Oceanapia robusta (Bowerbank, 1866)
(fig. 3, pl. 1 fig. 1, pl. 2, fig. 1, 2)

Isodictya robusta Bowerbank, 1866: 304.
Desmacidon jeffreysii Bowerbank, 1866: 347; 1874: 157, pl. LXII, figs. 1-5; 1882: 170; Carter, 1882: 117; Fristedt, 1887: 442.
Gellius robustus; Gray, 1867: 538.
Biemna jeffreysii; Gray, 1867: 539.
Oceanapia jeffreysii; Norman, 1869b: 334.
Esperia jeffreysii; Schmidt, 1870: 77.

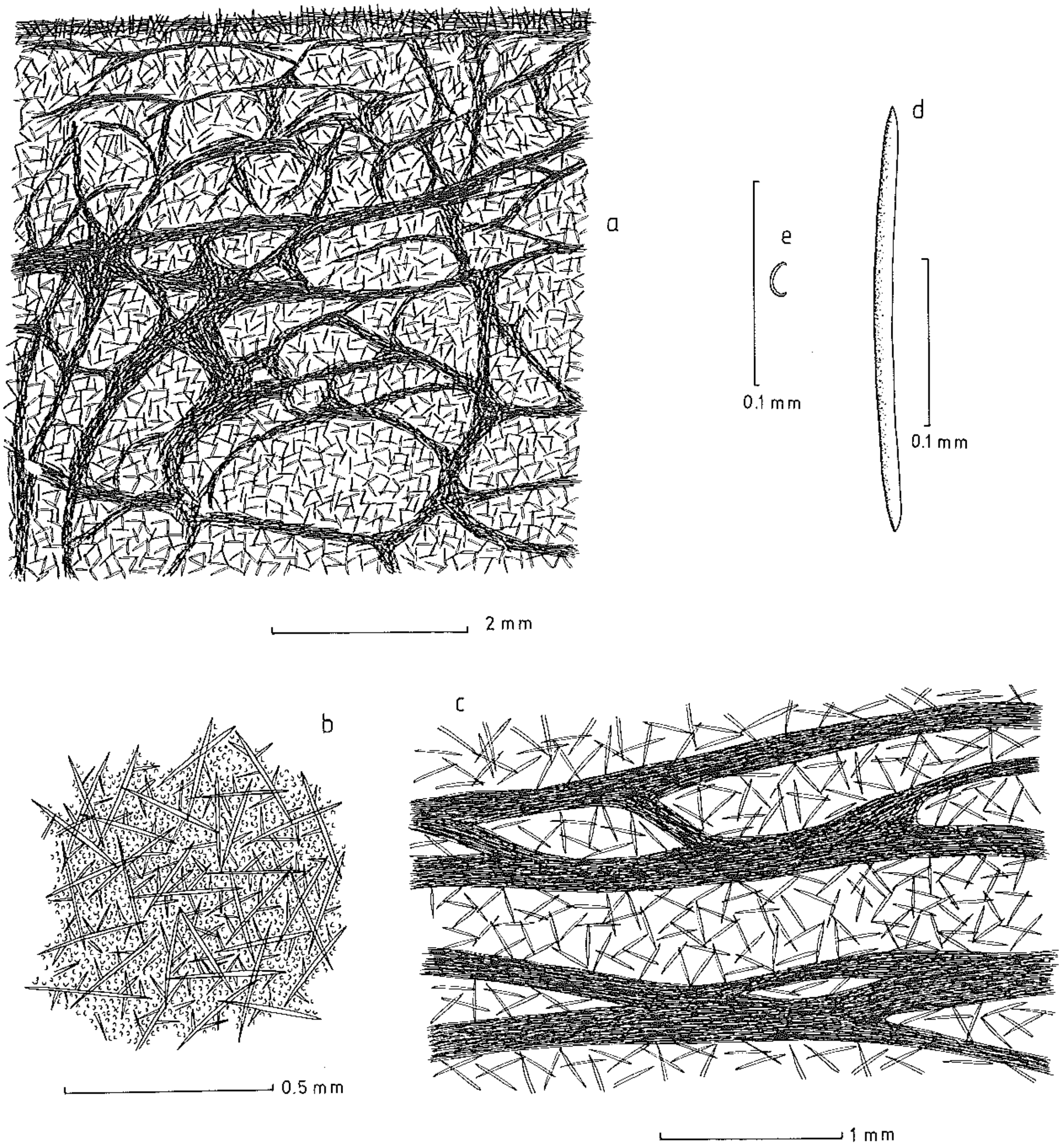
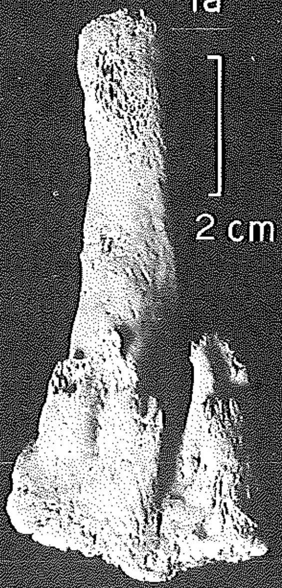
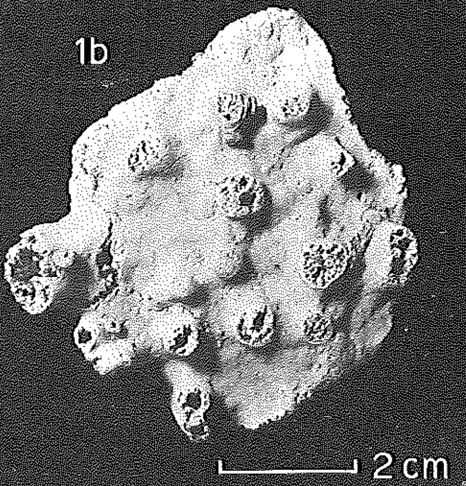


Fig. 3. *Oceanapia robusta*, a. choanosomal skeleton, b. tangential view of ectosome, c. fistular architecture, d. oxe, e. sigma.

1a



1b



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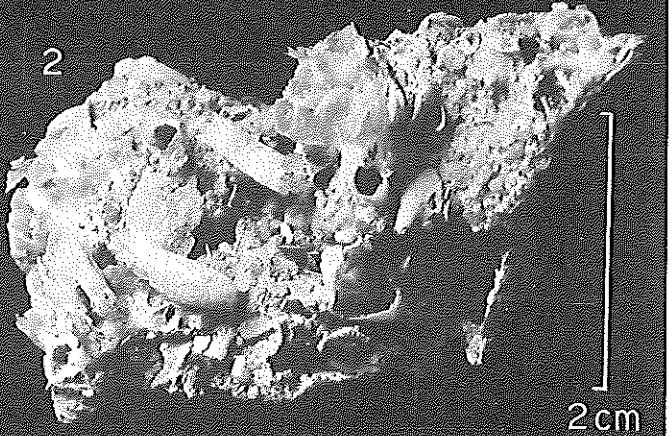

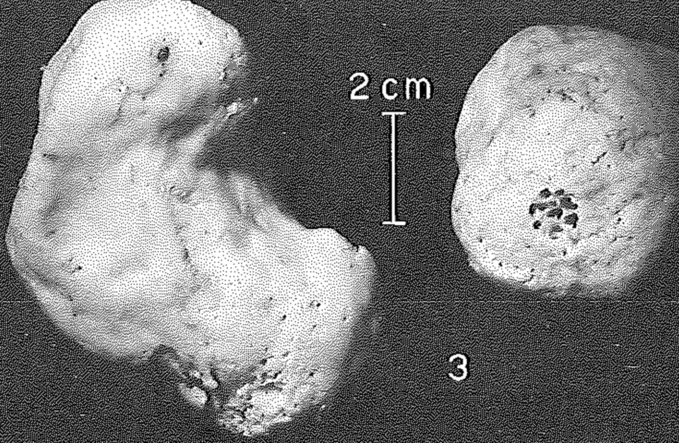

3

Reniera tubulosa Armauer Hansen, 1885: 4, pl. 1 fig. 12, pl. 6 fig. 4.
[non: *Reniera tubulosa* Fristedt, 1887 = *Haliclona rosea* (Bowerbank, 1866)].
Gelliodes cavicornis Topsent, 1892: 78, pl. 3 fig. 4, 9, pl. 9 fig. 12.
Oceanapia robusta; Lundbeck, 1902: 78, pl. 15 figs. 1-4; Arnesen, 1903: 8; Topsent, 1904: 228, pl. 5 fig. 15 & 16; Lundbeck, 1909: 434; Brøndsted, 1914: 483; Stephens, 1916: 233; 1917: 6; 1921: 6; Topsent, 1928: 319; Hentschel, 1929: 979; Arndt, 1935: 93, fig. 199.
[non: *Oceanapia robusta*, Ridley & Dendy, 1887 = *O. fistulosa* (Bowerbank, 1873), cf. van Soest, 1980: 86].

Type-locality: Shetland.

Material examined: Shetland: BMNH 1877.5.2.156, 1910.1.1.372, 373, 1930. 7.3.416, 1900.4.4.36-40. Britain: BMNH 1877.5.21.2040, 1930.7.3.414; Norway: ZMA POR. 3298 (58° 5′ N, 03° 20′ E), 45 fms., 14-X-1949, coll. H. F. van der Lee. Azores: ZMK, no reg.nr. (37° 57′ N, 31° 35′ W), 200 m, 1897, coll. E. Topsent.

Description:

Shape and size: the sponge consists of a globular body with a diameter of 5 - 20 cm, with numerous thick, blind fistules, generally arising from the upper parts of the body and the sides. Diameter of the fistules 0.5 - ca. 3 cm. On the underside of the body a firm, root-like structure is present, with which the sponge is attached to the substratum. The interior of the body in preserved specimens is filled with a loose and pulpy material, yellowish-white in colour, which contracts into a hard, dark-yellow or brownish wax-like substance when the sponge is dried. The oscules are situated at the inner side of the body; they are circular, slightly elevated, and measure 2-3 mm.
Consistency: the exterior part of the body is slightly hard and firm, the interior part is fragile, the fistules are fragile and easily broken.
Surface: even, slightly hispid from projecting spicules.
Colour (alive and spirit): dirty white.
Ectosome: a compact, multilayered ectosomal crust consisting of closely-packed, mainly tangentially orientated spicules, with loosely scattered vertical spicules. The ectosome is supported by a system of branching and anastomosing, subdermal multispicular fibres.
Choanosome: the skeleton in the interior of the body consists of an irregular network of multispicular fibres of variable thickness, with many confused single spicules lying in between the fibres.
Fistules: thick, multispicular fibres, running longitudinally and sometimes anastomosing, with a loose, subisotropic reticulation of single spicules lying in between the fibres.
Spongin: sparse, nodal.
Spicules: straight or slightly bent, robust oxea, with a sharp, often mucronated point, 170-*220*-260 by 6-*8.5*-10 µm. Sigmata: thin, irregularly curved, sometimes accolade-shaped, 9.5-*12.5*-17 µm.

Ecology: in deeper water, on sandy bottom, 80-1700 m.
Distribution (fig. 4): E-Greenland (Fristedt, 1887, as *Desmacidon jeffreysii*, 130 fathms.); Iceland, Faroe (Lundbeck, 1902, 132-912 fathms.); Shetland (Bowerbank, 1866, 1874, 1882, as *Isodictya robusta* and *Desmacidon jeffreysii*, no record of depth); Norway (Armauer Hansen, 1885, as *Reniera tubulosa*, 1198 m; Arnesen, 1903; specimen in ZMA collection, 45 fathms.); Ireland (Stephens, 1916, 1917, 1921, 74-100 fathms.); Azores (Topsent, 1892, 1928, as *Gelliodes cavicornis*, 200 m).

Discussion

The above given description is compiled from studying Bowerbank's original material, which

Plate I.
fig. 1a. *Oceanapia robusta*, body with fragments of fistules (BMNH 1930.7.3.414).
fig. 1b. *Oceanapia robusta*, fistules (BMNH 1930.7.3.414).
fig. 2. *Oceanapia isodictyiformis* (holo-type, BMNH 1872.5.4.1).
fig. 3. *Petrosia crassa* (ZMA POR. 5675).

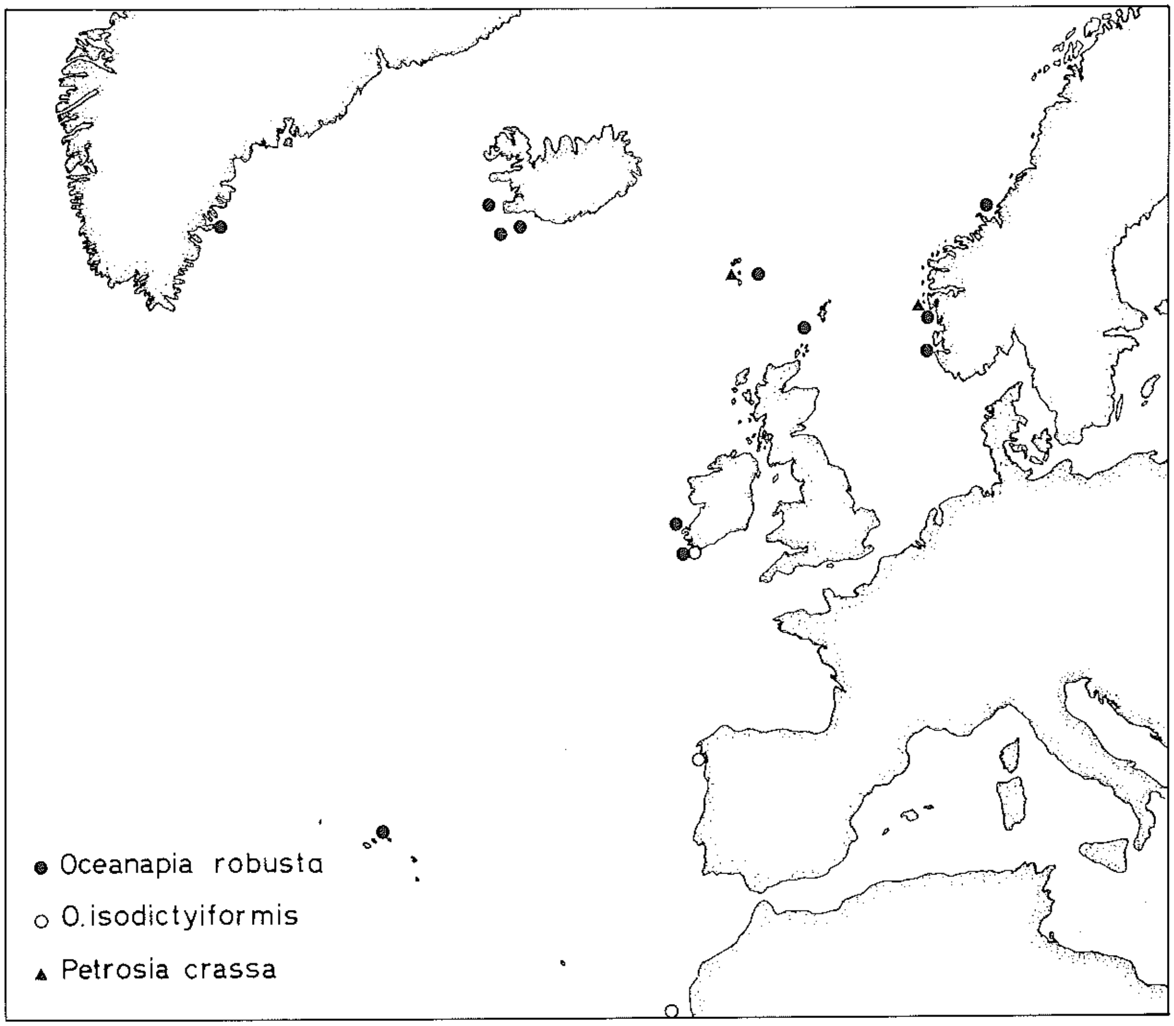

Fig. 4. Distribution of *Oceanapia robusta*, *O. isodictyiformis*, and *Petrosia crassa*.

consists of fragments of the body and the fistules and an interpretation of descriptions given by Bowerbank, Norman, and Lundbeck. No type-specimen could be detected in the BMNH material, nor could a specimen be found which agrees with Bowerbank's first description of *Isodictya robusta* and *Desmacion jeffreysii*.

Lundbeck (1902), who was the first to use the combination of *Oceanapia robusta* in his extensive description of the species, had the opportunity of studying both Armauer Hansen's material of *Reniera tubulosa* and Topsent's material of *Gelliodes cavicornis*. Undoubtedly he was right in his conclusion that both species conform to *O. robusta*. Topsent (1904), in a later paper dealing with sponges from the Azores, referred to the species as *O. robusta* instead of *G. cavicornis*, and explained why he agreed with Lundbeck's point of view. From a study of a microscopical slide of Topsent's *G. cavicornis* in the Paris Museum (MNHN D.T. 1061) it is apparent that the spicules are of a somewhat smaller size than those of the more northern specimens, but such size discrepancies are accepted today and this is no reason to regard Topsent's material as a separate species.

O. robusta has been reported from Australia by Ridley & Dendy (1887), but this record is in-

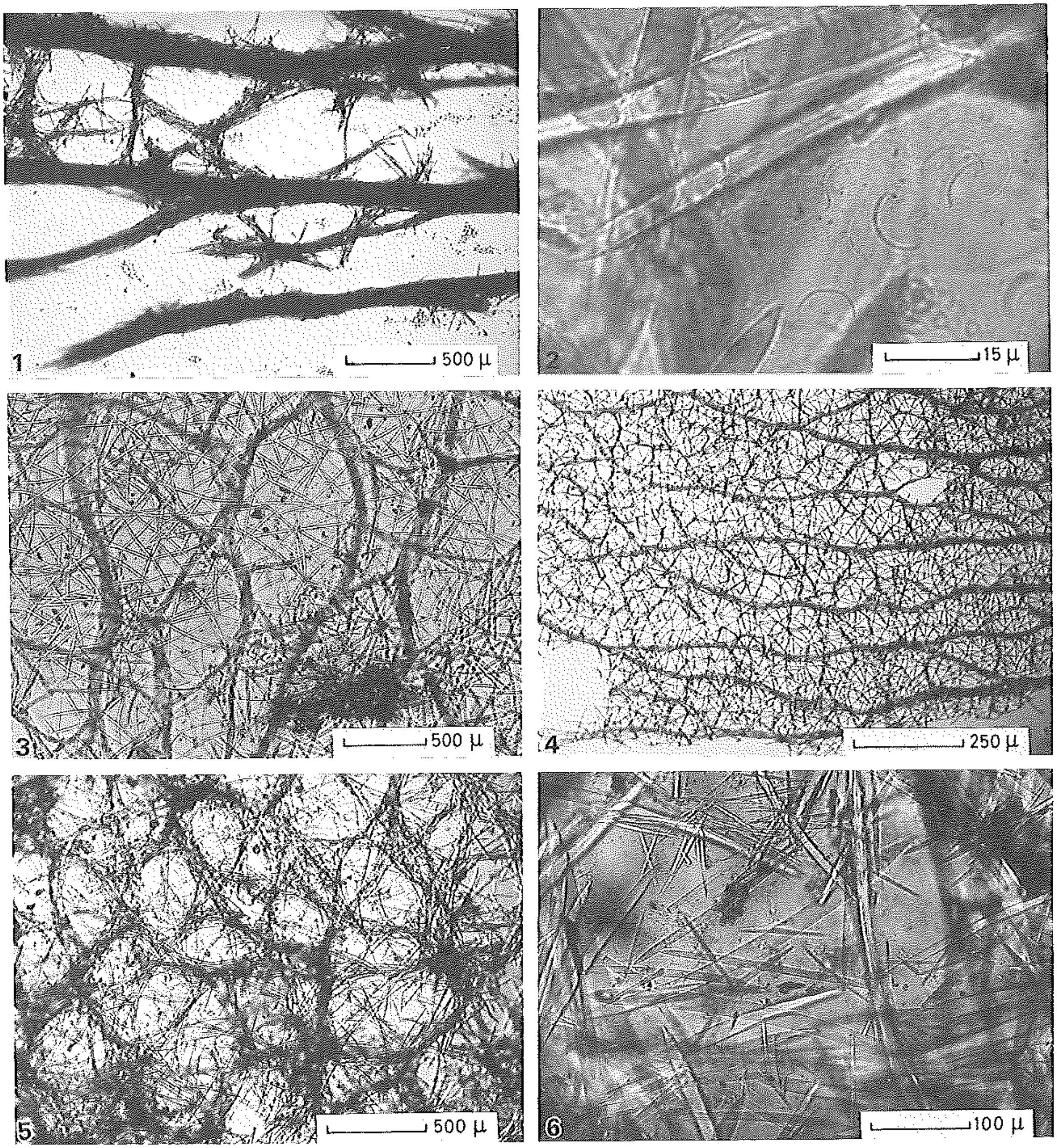

Plate II.
fig. 1. *Oceanapia robusta*, fistular architecture.
fig. 2. *Oceanapia robusta*, sigmata.
fig. 3. *Oceanapia isodictyiformis*, tangential view of ectosome.
fig. 4. *Oceanapia isodictyiformis*, fistular architecture.
fig. 5. *Petrosia crassa*, tangential view of ectosome.
fig. 6. *Petrosia crassa*, spicules.

correct. It is more likely that their species conforms to *Oceanapia fistulosa* (Bowerbank, 1873), as discussed by van Soest (1980) and de Weerdt & van Soest (1985).

The distribution of *O. robusta* therefore seems to be restricted to the northern part of the North Eastern Atlantic Ocean, viz. from E-Greenland, Iceland, and Norway down to the Azores (37° N). It has not been reported from the Mediterranean, nor from the western side of the Atlantic Ocean.

Oceanapia isodictyiformis (Carter, 1882) (n. comb.)
(fig. 5, pl. 1, fig. 2, pl. 2, fig. 2, 3)

Phloeodictyon isodictyiforme Carter, 1882: 122.
? *Phloeodictyon nodosa* George & Wilson, 1919: 152, Pl. 62, figs. 29, 30, 32, Pl. 66, fig. 63.
? *Pellina nodosa*; Van Soest, 1980: fig. 29, pl. XIII, 2.
(for further synonymy of *Pellina nodosa* cf. Van Soest, 1980: 80)

Type-locality: Vigo, Spain.

Material examined: Holotype: BMNH 1872.5.4.1 (Saville Kent collection No. 15, dredged by vessel "Norna", 1870, Vigo Bay, Spain). Tenerife: ZMA POR. 5792 (11-XI-1979, coll & don. T. Cruz). Ireland: ZMA POR. 5794 (Lough Ine, Co. Cork, Ireland, 27-VI-1981, 12 m, coll. W. H. de Weerdt & R. W. M. van Soest).

Description:

Shape and size: the holotype consists of a firm piece of agglomerated shell-detritus, 4.5 × 2.5 × 2 cm, completely overgrown by and inter-

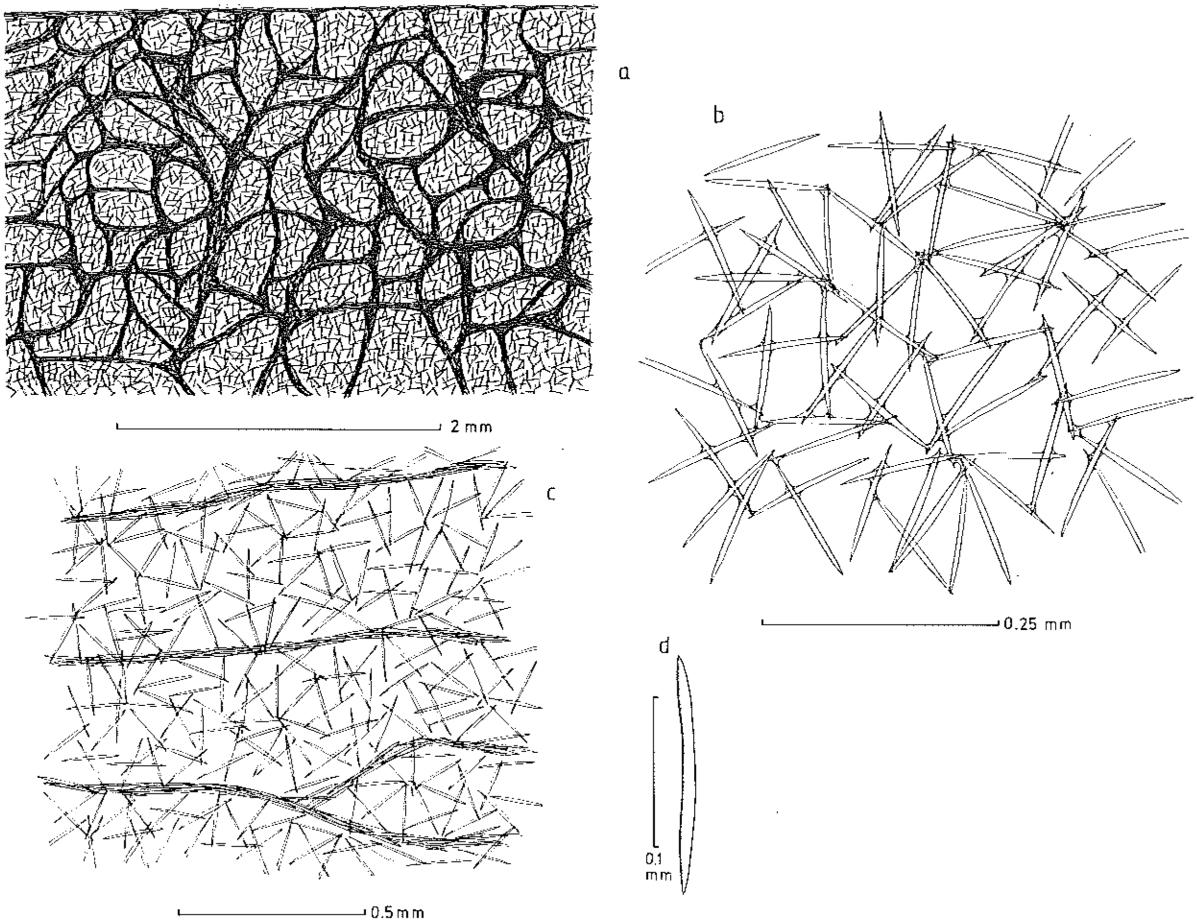

Fig. 5. *Oceanapia isodictyiformis*, a. choanosomal skeleton, b. tangential view of ectosome, c. fistular architecture, d. oxe.

mixed with the body of the sponge. At the surface of the sponge there are numerous partly broken off very fragile fistules. They are 1-2 mm in diameter and 15 mm long. ZMA POR. 5792 consists of a basal part of 7 mm in diameter from which one fistule, 2 cm long and 2 mm thick arises. Some small shell fragments are incorporated into the basal part. ZMA POR. 5794 consists of small fistules attached to some minute body fragments.

Consistency: fragile.

Surface: even.

Colour: the holotype (dried) is yellow-brown, the ZMA specimens (spirit) are white. The colour alive is fawn (Carter, 1882).

Ectosome: the ectosome of the body is a regular, unilayered reticulation of intercrossing oxea, which are bound by a little amount of spongin at the nodes. The fistules are composed of longitudinal pauci-multispicular tracts, with the interstices completely filled with a rather dense, isotropic reticulation of single spicules.

Choanosome: the choanosomal skeleton consists of a dense reticulation of multispicular tracts, and a rather dense, subisotropic reticulation of single spicules lying in between the tracts.

Spongin: sparse, nodal.

Spicules: slightly curved oxea, evenly tapering towards a sharp point, 120-*142*-160 by 4-*7*-10 μm.

Ecology: shallow water, growing on shell-detritus on the seabed and on the undersides of stones.

Distribution (fig. 4): Atlantic coast Spain (Carter, 1882, shallow-water); Tenerife (specimen ZMA collection, shallow-water); S-E Ireland (specimens ZMA collection, 12 m; ?Beaufort Harbour (Atlantic coast North America; George & Wilson, 1919, as *Phloeodictyon nodosa*, no record of depth);? Caribbean (van Soest, 1980, as *Pellina nodosa*).

Discussion:

Carter's original material and the specimens in the ZMA collection conform in every respect to *Phloeodictyon nodosa*, as described by George & Wilson (1919: 152) and van Soest (1980, as *Pellina nodosa*). A possible synonymy of the two species is only suggested here, as a thorough comparison of material is beyond the scope of the present study. *O. isodictyiformis* is a very distinctive species characterized by its skeletal architecture and its ability to incorporate shell-detritus and grains into the body, and it is therefore surprising that there are only two new Atlantic records of the species. The Irish record is the first North Atlantic record since Carter's description of the species. It might have been overlooked because of its cryptic habit but this seems unlikely. Possibly *O. isodictyiformis* is a very rare species.

Discussion of the genus *Oceanapia*.

Following Burton (1934), Bergquist & Warne (1980), and van Soest (1980), I consider *Rhizochalina* and *Phloeodictyon*, two microsclere-lacking genera, to be synonyms of *Oceanapia* for reasons given earlier, which needs no further discussion here (cf. also de Weerdt & van Soest, 1985). However, I propose to include here also the genus *Biminia* Wiedenmayer, 1977b in *Oceanapia* (a possible synonymy of the genera was already suggested by van Soest, 1980 and de Weerdt & van Soest, 1985). Wiedenmayer established *Biminia* for two Oceanapüd species with toxa and sigmata, viz. *Oceanapia toxophila* Dendy (1922), the type-species of *Biminia*, and *Biminia stalagmitica* Wiedenmayer (1977b). Hooper (1984) has recently described a third species, *Biminia macrotoxa*. A fragment of *O. toxophila* is incorporated in the ZMA collection (ZMA POR. 1709, Siboga expedition Stat. 310). It has oxea which are somewhat shorter and thicker than the sizes given by Dendy (the ZMA specimen: 270 × 15 μm, Dendy: 300 × 12 μm), but there is no doubt about its identity. The presence of toxa is considered a primitive character, as was mentioned earlier in this paper, and for this reason the genus *Biminia* cannot be maintained. The fourth *Oceanapia* species which is known to posses toxa is *Oceanapia* spec. nov. de Weerdt & van Soest

(1985) (off West Africa). The four species conform in every respect to *Oceanapia*.

Other Oceanapiid species reported from the area are *Oceanapia elongata* (Lundbeck, 1902), *Oceanapia irregularis* (Lundbeck, 1902), and *Oceanapia tuber* (Lundbeck, 1902, not *O. tuber* sensu Burton, 1956 = *O. fistulosa* (Bowerbank)). However, these are deep-water species and therefore beyond the scope of the present study.

Discussion of the family Oceanapiidae.

The Oceanapiidae consist of the following genera: *Oceanapia* Norman, 1869b (type-species *O. robusta* (Bowerbank, 1866); *Pachypellina* sensu van Soest, 1980 (not Burton, 1934b = *Xestospongia* by virtue of its type-species *P. fistulata* Kirkpatrick, 1907; *Calyx* Vosmaer, 1883 (monotypic genus, type-species *C. nicaensis* (Risso, 1826), *Foliolina* Schmidt, 1870 (monotypic genus, type-species *F. peltata* Schmidt, 1870), and *Vagocia* (type-species *Gellius arcuarius* Topsent, 1913).
Van Soest (1980) included *Pellina* in the Oceanapiidae, but de Weerdt & van Soest (1985) changed this, since the type-species of *Pellina*, *Halichondria semitubulosa* Lieberkühn (1859), lacks Oceanapiid-caracters. Instead it conforms completely with *Haliclona* (also de Weerdt, in prep.).
Of the five Oceanapiid genera, *Oceanapia* has the widest geographical (and perhaps bathymetrical) distribution, with representatives in all parts of the world. *Foliolina peltata* Schmidt (1870) is reported from West-Africa and the West Indies (Burton, 1956; de Weerdt & van Soest, 1985), *Calyx nicaensis* Vosmaer (1883) is restricted to the Mediterranean, whilst *Pachypellina* sensu van Soest, 1980 has representatives in the West Indies (*P. podatypa* (de Laubenfels, 1934)), the Cape Verde Islands (*P. tufa* (Ridley & Dendy, 1887), and the Mediterranean (*P. parietalis* (Topsent, 1893)). It is a doubtful Oceanapiid.

Family Petrosiidae van Soest, 1980

Definition: Haplosclerida with an ectosomal skeleton consisting of an isotropic reticulation of single spicules or spicule tracts, and a choanosomal skeleton verging towards an isotropic reticulation of spicule tracts, in which primary and secondary tracts are indistinct.
Remarks: The above definition is unchanged from that given by van Soest (1980), and needs no alteration. Petrosiid species are often of a stony structure. Spongin may be present in moderate quantities.

Genus *Petrosia* Vosmaer, 1885

Strongylophora Dendy, 1905

Definition: Petrosiidae with a tangential ectosomal unispicular reticulation and basically a lamellate-isotropic choanosomal skeleton of thick spicule tracts, with an interstitial unispicular reticulation. There are at least two distinct size categories of strongylote or oxeote spicules.
Remarks: This definition differs only slightly from the definition given by van Soest (1980).

Type-species: *Spongia ficiformis* Poiret, 1789.

Petrosia crassa (Carter, 1876)
(Fig. 6, pl. 1, fig. 3, pl. 2, fig. 5, 6)

Reniera crassa Carter, 1876: 312.
Petrosia crassa; Lundbeck, 1902; 54, pl. 4, figs. 7-9, pl. 12, fig. 5 [non: *Petrosia crassa*; Topsent, 1904; nec: Topsent, 1928 = *P. ficiformis* (Poiret, 1789)].

Type-locality: Faroe

Material examined: Norway: ZMA POR. 5675 (Saengsbokt, Bergen, 26-VIII-1982, coll. W. H. de Weerdt c.s., dredge, 600-350 m).

Description

Shape and size: the ZMA material consists of four specimens and four small fragments. The largest specimen has an irregular roundish, massive shape, with a length of 9 cm and a thickness of 4-5 cm. The other specimens are of a somewhat smaller size, but they have the same irregular massive form. Oscules few, large

(8-10 mm), circular, slightly concave, and with conspicuous openings of the canal system. The diameter of these openings varies from 1-3 mm.
Consistency: very firm, but somewhat crumbly.
Surface: smooth, but rough to the touch.
Colour (alive and spirit): dirty white with a yellowish tinge.
Ectosome: the ectosomal skeleton consists of an irregular reticulation of loosely organized single spicules, which is partially obscured by the close proximity of the underlying peripheral spicule tracts of the choanosome.
Choanosome: the choanosomal skeleton consists of a regular, strong reticulation of multispicular primary and secondary fibres, which form a circular pattern with rounded meshes.
Spongin: minimal, nodal.
Spicules: three size categories of oxea are distinguishable in the ZMA specimens: the largest oxea measure 304 - *322* - 353 by 12.2 - *16.3* - 19 µm, the middle sized measure 100 - *135* - 200 by 2.6 - *5.0* - 7.7 µm, and the smallest are 53 - *80* - 98.5 by 1.9 - *2.8* - 4.6 µm. The oxea of all categories are evenly and slightly curved, with a rather short but very sharp point. No strongyles were found.

Ecology: in deeper water.

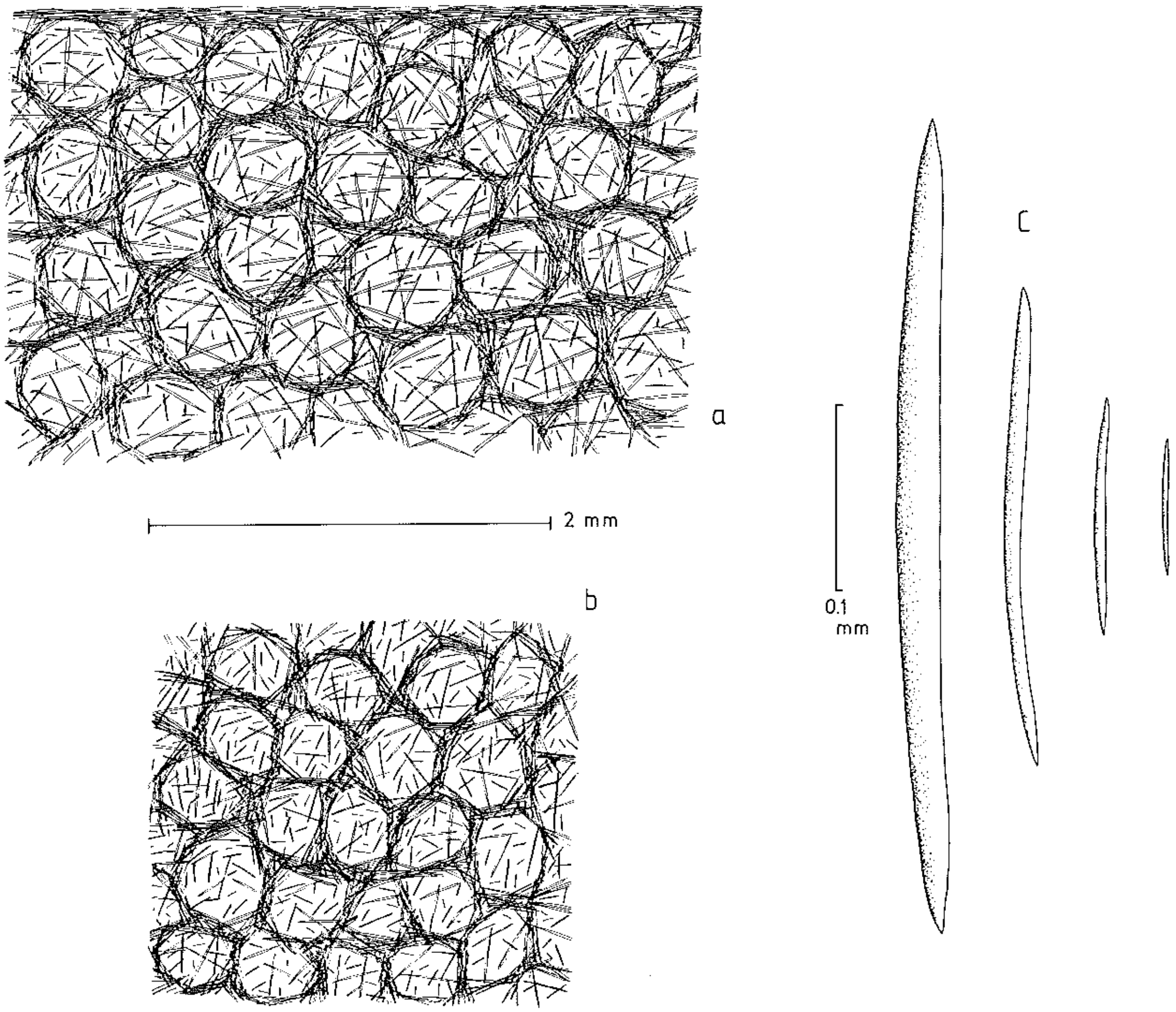

Fig. 6. *Petrosia crassa*, a. choanosomal skeleton, b. tangential view of ectosome, c. oxe.

Distribution (fig. 4): Faroe (Carter, 1876, as *Reniera crassa*); Norway (Lundbeck, 1902; specimens in ZMA collection).

Discussion: *Petrosia crassa* is very similar to *Petrosia ficiformis* Poiret, 1789), and a possible synonymy of the two species has been suggested already by Topsent (1928: 324). According to Lundbeck (1902: 55) two distinct species are involved, the main differences being the larger spicule size and thinner fibres of *P. crassa*. In table 1 spicules sizes of the two species are given. It is apparent that the species are hardly distinguishable on the basis of these characters, both species being very variable. Unfortunately the available material of *P. crassa* is too limited to enable a thorough comparison of the two species, but it is quite certain that the two species, if not conspecific, are closely related. The main differences are given in table 2.

Geographically the species are well separated: *P. crassa* is only known from its type-locality, the Faroe, and Norway, and it is quite possible that it is a rather rare, and

Table 1. Spicule sizes of *Petrosia crassa* and *P. ficiformis*

Reference	*Petrosia crassa*	*Petrosia ficiformis*
Lundbeck, 1902 (as *P. crassa*)	200-350 x 17 170 x 7 80	
Carter, 1876 (as *Reniera crassa*)	340 x 18 24	
ZMA POR. 5675	304-353 x 12.2-19 100-200 x 2.6-7.7 53-98.5 x 1.9-4.6	
Topsent, 1892 (as? *P. clavata*)		300-350 x 23
Topsent, 1904 (as *P. crassa*)		350 x 23 380 x 30 360 x 23 330 x 18 330 x 23 75-170 x 3-7 microstrongyles: 35 x 22
Topsent, 1928 (as *P. dura*)		220 x 8-10 80 x 8 52 x 3
Topsent, 1928 (as *P. crassa*)		280 x 13
de Weerdt & van Soest, 1985 (as *P. ficiformis*)		240 x 10-15 120-200 x 1.5-2.5 140 x 7.5 45 x 1 50 x 3.5 65 x 5

Table 2. Characteristics of *Petrosia crassa* and *P. ficiformis*

	Petrosia crassa	*Petrosia ficiformis*
form	irregular massive	fig-shaped, massive, repent ramose,flabelliform
oscules	large, few, with conspicuous canal-openings	small, more abundant, regularly distributed
colour	dirty white with yellowish tinge	dirty white with yellowish tinge, purplish, mottled with brown spots
consistency	very firm, somewhat crumbly	firm, but also somewhat elastic
surface	smooth, but rough to the touch	smooth, but rough to the touch
spicules	oxea of different size categories 200-350 by ca. 17 µm 100-200 by 3-8 µm 20-100 by 2-5 µm strongyles present	oxea of different size categories 200-380 by 10-30 µm 80-200 by 2-8 µm 50-70 by 1-5 µm strongyles abundant
ectosome	multispicular fibres with rounded meshes smallest spicules not predominant	irregular, dense, smallest spicules most abundant in ectosome
choanosome	multispicular fibres with rounded meshes	irregular, in places rounded meshes, in places tracts.
spongin	very little	variable
distribution	?Arctic-Atlantic	Mediterranean-Atlantic

predominantly deep-water species with an Arctic-Atlantic distribution. *P. ficiformis* is frequently recorded from the Mediterranean and Macaronesian islands (Azores, Cape Verde Islands, Madeira and the Canary Islands) (Topsent, 1892, as ?*Petrosia clavata*, 1894b; 1904, as *P. dura*; 1928, as *P. crassa* and *P. dura*; Vosmaer, 1835, as *P. ficiformis*; Lévi, 1957, Sarà, 1958, 1971-72; Sarà & Siribelli, 1962, as *P. ficiformis*; Rützler, 1965, as *P. ficiformis*; Vacelet, 1969, as *P. dura*; Boury-Esnault, 1971, as *P. ficiformis*; Sica & Zollo, 1978, as *P. ficiformis*; Mattia *et al.*, 1978, as *P. ficiformis*; Pulitzer-Finali, 1983, as *P. ficiformis*; and de Weerdt & van Soest, 1985, as *P. ficiformis*). Recently, in the summer of 1984, fresh material of *P. ficiformis* was collected near Banyuls, Mediterranean, by Drs. F. van Lent, and according to her observations it was one of the most common species in the area. *P. ficiformis* apparently is a common, shallow-water species with a Mediterranean-Atlantic distribution.

Discussion of the family Petrosiidae

The family Petrosiidae consist of the following genera: *Xestospongia* de Laubenfels, 1932 (type-species *X. diprosopata* de Laubenfels, 1932), and *Petrosia* Vosmaer, 1883 (type-species *P. ficiformis* Poiret, 1789).

Strongylophora Dendy, 1905 (type-species *S. durissima* Dendy, 1905) is here synonymized with *Petrosia*. It was defined on basis of peculiar kidney-shaped microstrongyles (cf. van Soest, 1980: 114), but on this basis the genus cannot be maintained.

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