A revision of the supraspecific classification of the subclass Calcaronea (Porifera, class Calcarea)

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Borojevic R., Boury-Esnault N. & Vacelet J. 2000. — A revision of the supraspecific classification of the subclass Calcaronea (Porifera, class Calcarea). *Zoosystema* 22 (2) : 203-263.

ABSTRACT

A revision of all the genera of the subclass Calcaronea (Porifera, Calcarea) is given. In addition to the two previously described orders, Leucosoleniida Hartman, 1958 *emend.* and Lithonida Vacelet, 1981, we recognize a third one: the Baeriida. The order Leucosoleniida includes nine families, one of which is new (the Jenkinidae), and 42 genera of which four are new (*Breitfussia, Leucandrilla, Polejaevia* and *Syconessa*). The order Lithonida includes two families and six genera. The order Baeriida includes three families of which two are new (the Baeriidae and the Trichogypsiidae), and eight genera. The Leucosoleniida seem to have evolved from the olynthus grade, a form that is probably present in the early stages of ontogenesis of all Leucosoleniida and subsists at the adult stage in *Leucosolenia*. The Leucosoleniida comprises a diverse group with several pathways of progressing complexity of form, starting with sponges of a simple sycettid organization and leading to sponges with a complex aquiferous system and skeleton. Increase in size from the sycettid grade of organization may occur by two different processes: 1) the growth and elongation of radial tubes increasing the thickness of the sponge body (seen in the Sycettidae-Grantiidae line and the Heteropiidae), or 2) the growth of the central tube containing the atrial cavity which increases the length of the sponge body (seen in the Jenkinidae and the simple forms of Amphoriscidae). The sponges classified in the Baeriida and the Lithonida have very divergent forms that are represented by only a few living species. Identification keys and illustrations are provided for all the valid genera.

KEY WORDS
Porifera,
Calcaronea,
evolution,
generic definitions,
Baeriida,
Jenkinidae.

RÉSUMÉ

Révision de la classification supraspécifique de la sous-classe Calcaronea (Porifera, classe Calcarea).

Une révision de tous les genres de la sous-classe Calcaronea (Porifera, Calcarea) est faite. Le nouvel ordre Baeriida est proposé en addition aux deux ordres précédemment reconnus, Leucosoleniida Hartman, 1958 *emend.* et Lithonida Vacelet, 1981. L'ordre Leucosoleniida comprend neuf familles dont une nouvelle (Jenkinidae) et 42 genres, dont quatre nouveaux (*Breitfussia, Leucandrilla, Polejaevia* et *Syconessa*). L'ordre Lithonida comprend deux familles et six genres. L'ordre Baeriida comprend trois familles, dont deux nouvelles (Baeriidae et Trichogypsiidae) et huit genres. Les Leucosoleniida semblent avoir évolué à partir du stade olynthus. Cette forme est probablement présente dans les stades précoces de l'ontogenèse chez toutes les Leucosoleniida et subsiste à l'état adulte chez *Leucosolenia*. Les Leucosoleniida sont un groupe florissant dans lequel on reconnaît plusieurs lignées ayant un système aquifère et un squelette de complexité croissante à partir de l'organisation de type sycettide. La croissance en taille à partir du stade sycettide peut avoir lieu en suivant deux voies : 1) la croissance et l'élongation des tubes radiaires, qui accroissent l'épaisseur du corps de l'éponge et qui sont représentées par la lignée Sycettidae-Grantiidae et les Heteropiidae ; 2) la croissance du tube central contenant la cavité atriale qui accroît la longueur du corps, comme chez les Jenkinidae et les formes simples des Amphoriscidae. Au contraire, les Baeriida et les Lithonida sont des groupes très divergents, représentés seulement par un petit nombre d'espèces. Des clés d'identification et des illustrations sont données pour tous les genres considérés comme valides.

MOTS CLÉS
Spongiaires,
Calcaronea,
évolution,
définitions génériques,
Baeriida,
Jenkinidae.

SYSTEMATIC INDEX

Family JENKINIDAE n. fam.
  Genus *Breitfussia* n. gen.
  Genus *Jenkina* Brøndsted, 1931
  Genus **Leucascandra* Borojevic & Klautau, 2000
  Genus **Anamixilla* Poléjaeff, 1883
  Genus **Polejaevia* n. gen.
  Genus **Uteopsis* Dendy & Row, 1913

Family HETEROPIIDAE Dendy, 1892
  Genus **Syconessa* n. gen.
  Genus *Sycettusa* Haeckel, 1872
  Genus **Grantilla* Row, 1909
  Genus *Grantessa* Lendenfeld, 1885
  Genus *Heteropia* Carter, 1886
  Genus **Paraheteropia* Borojevic, 1965
  Genus *Vosmaeropsis* Dendy, 1892

Family AMPHORISCIDAE Dendy, 1892
  Genus *Amphoriscus* Haeckel, 1872
  Genus *Leucilla* Haeckel, 1872
  Genus *Paraleucilla* Dendy, 1892

Family STAURORRHAPHIDAE Jenkin, 1908
  Genus *Achramorpha* Jenkin, 1908
  Genus *Megapogon* Jenkin, 1908

Family LELAPIIDAE Dendy & Row, 1913
  Genus *Grantiopsis* Dendy, 1892
  Genus **Kebira* Row, 1909
  Genus **Paralelapia* Hôzawa, 1923
  Genus *Lelapia* Gray, 1867

Family *INCERTAE SEDIS*
  Genus *Sycyssa* Haeckel, 1872

Order BAERIIDA n. ord.
  Family BAERIIDAE n. fam.
    Genus *Baeria* Miklucho-Maclay, 1870
    Genus **Lamontia* Kirk, 1895
    Genus **Leucopsila* Dendy & Row, 1913
    Genus **Eilhardia* Poléjaeff, 1883

  Family TRICHOGYPSIIDAE n. fam.
    Genus *Trichogypsia* Carter, 1871
    Genus **Kuarrhaphis* Dendy & Row, 1913
    Genus **Leucyssa* Haeckel, 1872

  Family LEPIDOLEUCONIDAE Vacelet, 1967
    Genus **Lepidoleucon* Vacelet, 1967

Order LITHONIDA Vacelet, 1981
  Family MINCHINELLIDAE Dendy & Row, 1913
    Genus *Minchinella* Kirkpatrick, 1908
    Genus *Plectroninia* Hinde, 1900
    Genus **Monoplectroninia* Pouliquen & Vacelet, 1970
    Genus **Petrostroma* Döderlein, 1892
    Genus **Tulearinia* Vacelet, 1977

  Family PETROBIONIDAE Borojevic, 1979
    Genus **Petrobiona* Vacelet & Lévi, 1958

* Genus with only one described species.

INTRODUCTION

In a previous study (Borojevic *et al.* 1990), we revised the classification of Recent calcareous sponges belonging to the subclass Calcinea Bidder, 1898, in an attempt to redefine the currently recognized families and genera and to trace the possible evolutionary pathways in this subclass of the Calcarea. The present study is a continuation of this revision, extending it now to the Recent sponges belonging to the subclass Calcaronea Bidder, 1898.

The common characteristic of all representatives of the Calcarea is the presence of calcium carbonate spicules that have a basal diactine or triactine structure. Calcareous spicules are secreted into an intercellular space that is delimited by two or more cells. Although molecular evolutionary studies have identified a potential early common origin of the two subclasses of the Calcarea, there is no convincing molecular evidence for a close relationship between Calcarea and other sponges (Lafay *et al.* 1992; Cavalier-Smith *et al.* 1996; Borchiellini *et al.* 1999). To our knowledge, no study has been conducted on molecular phylogeny within the subclass Calcaronea, and the present revision is based on morphological and anatomical data.

Dendy & Row (1913) conducted the first major general revision of the Calcaronea in an attempt to classify all the described genera into the evolutionary pathways recognized at the time. Since then there have been several modifications of that proposal (Laubenfels 1936; Hartman 1958; Borojevic 1979; Vacelet 1991). But despite the recent description of new species and even higher taxa, and the availability of new information gathered from cell and developmental biology, genetics, biochemistry, as well as observations of morphology at both the microscopic and the ultrastructural level, there has been no overview of the classification that attempts to group all the described calcaronean genera so as to show the putative evolutionary development of the group, with the exception of Burton's (1963) "Revision of the Classification of the Calcareous Sponges". The fundamental rationale of the Burton's revision was to analyse the supposed great intraspecific variability of the Calcarea that has resulted in the merging of species and higher taxa, which had been previously recognized as distinct phylogenetic and taxonomic units, into a small number of "genera" and "species". This drastic decrease in lower systematic units has not been universally accepted (see discussion in Borojevic *et al.* 1990). Recent biochemical studies of the Calcarea have shown that slight morphological differences may correspond to large genetic differences, and that a full genetic separation of sympatric or allopatric populations is often associated with subtle or even undetectable differences as inferred by the more conventional morphological criteria (Solé-Cava *et al.* 1991; Klautau *et al.* 1994). Thus the classical taxonomy based on the morphological criteria is overconservative, and many specimens that had been classified as simple variations of the previously described and often cosmopolitan species, probably represent distinct taxonomic units.

In the present work we have tried to identify the taxonomic units that potentially represent monophyletic groups of species within the Calcaronea, and we have tried to identify all the possible evolutionary pathways, leading from the simplest Calcaronea, such as *Leucosolenia*, to the most complex, such as *Lelapia*. We present the more complex types of skeletal and tissue organization as deriving from simpler ones, and follow the conventional view that the simple "ascon" type of sponge organization is "primitive". This does not mean that we interpret the progressive increase of complexity as necessarily the true evolutionary pathway, but this cannot be reconstructed from morphological data alone.

Using this approach, we have confirmed the separation of sponges that we now group in the order Leucosoleniida from those belonging to the Lithonida, in agreement with the previously proposed classifications (Borojevic 1979; Vacelet 1991). We were also led to separate a group of sponges considered as "aberrant" by Dendy & Row (1913) from the Leucosoleniida, and propose the recognition of the Baeriida as a new order in Calcaronea for this group.

The scope of most of the genera is that proposed by Dendy & Row (1913), who provided very detailed descriptions of the genera, and discussed synonymy and correspondence with the previously described taxa extensively. The reader is referred to that revision for a detailed discussion on earlier synonymies.

An analysis of the proposed classification will reveal that many points are still uncertain. One of the major drawbacks of any attempt to prepare a general revision of calcareous sponges is the fact that our knowledge on this group is still very fragmentary. The largest collection of Calcarea ever studied is that described more than a century ago by Haeckel (1872), who analysed and reviewed most of the specimens collected up to his time. It is noteworthy that Haeckel proposed a large portion of the presently recognized genera, and in many cases new specimens have not since been found. The Indo-Pacific, Antarctic and Japanese Calcarea have received more attention, mostly during the period between the end of the last century and the first part of this century, but the fauna of calcareous sponges in many other regions remains very poorly known. A review of any collection, even from regions one would expect to be much studied such as the European coasts of the Atlantic or the Mediterranean, produces many new species that frequently belong to new higher taxa, indicating that our knowledge of the diversity of this group of sponges is very incomplete. The present revision aims at gathering and assessing the available data so as to guide the supraspecific identification of the Calcaronea, and propose a framework for future cellular and molecular studies, which should give new insights into the biology of this group. This

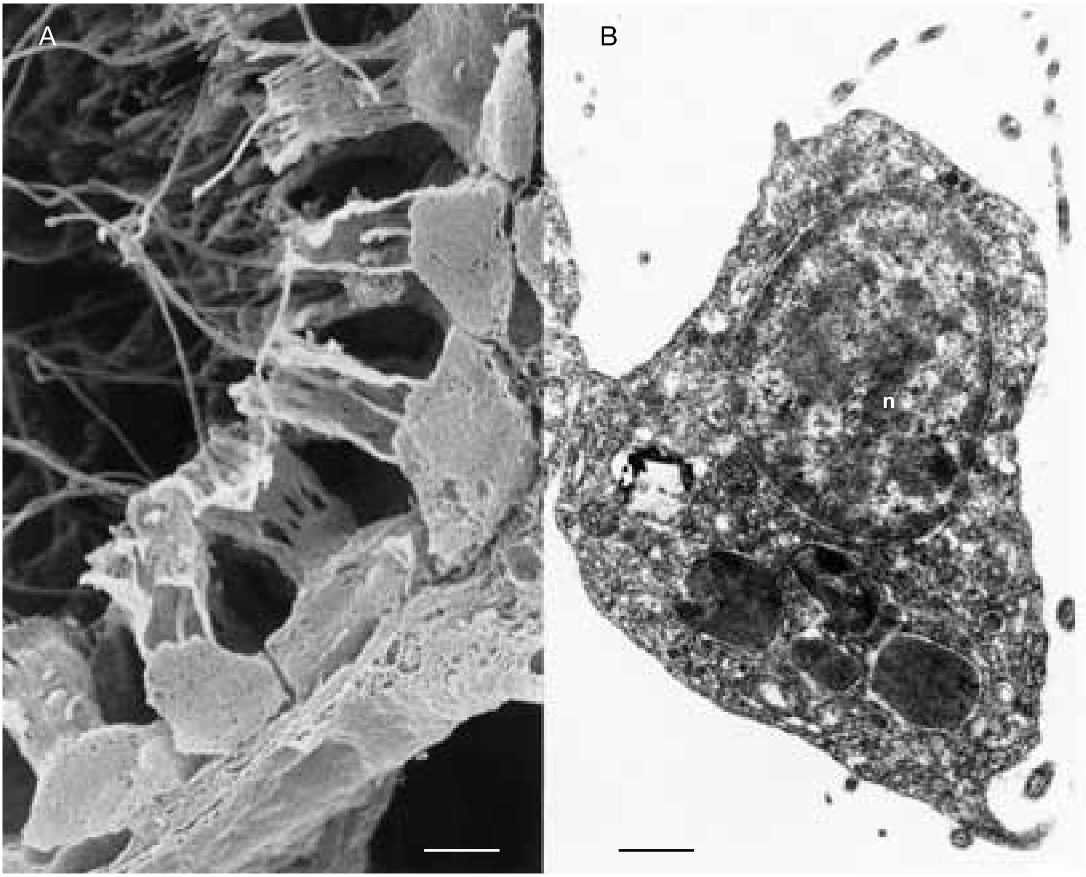

FIG. 1. —*Sycon sycandra*; **A**, SEM view of the choanoderm; **B**, a choanocyte showing the typical apical nucleus (**n**) of the Calcaronea (TEM). Scale bars: A, 3 µm; B, 0.7 µm.

approach will highlight the taxonomic questions which should be addressed in future morphological, genetic and molecular studies of the Calcarea. For all the terms of sponge morphology we refer the reader to Boury-Esnault & Rützler (1997).

ABBREVIATIONS USED

MNHN	Muséum national d'Histoire naturelle, Paris.
BMNH	Natural History Museum, London.

SYSTEMATICS

Class CALCAREA Bowerbank, 1864

DIAGNOSIS. — Marine Porifera in which the mineral skeleton is composed entirely of calcium carbonate. The skeleton is composed of free diactine, triactine, tetractine and/or polyactine spicules, to which can be added a solid basal calcitic skeleton with basal spicules either cemented together or completely embedded in an enveloping calcareous cement. The aquiferous system can be asconoid, syconoid, sylleibid or leuconoid. Members of the Calcarea are viviparous and their larvae are blastulae.

Subclass CALCARONEA Bidder, 1898

DIAGNOSIS. — Calcarea with diactines and/or sagittal triactines and tetractines, rarely also with regular spicules. In addition to the free spicules, there can be a non-spicular basal calcareous skeleton in which basal spicules are cemented together or completely embedded in an enveloping calcareous cement. In ontogeny, the first spicules to be produced are diactines in the settled larva. No information is available for the early

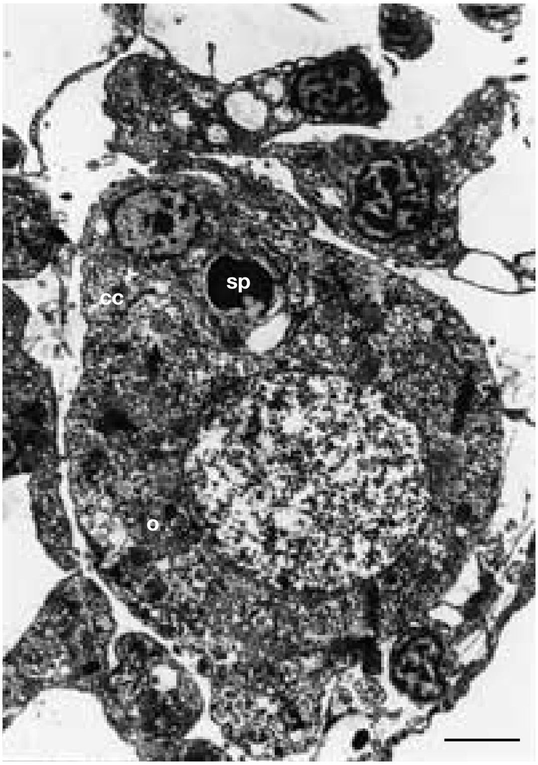

FIG. 2. — Fertilization in *Leucillla*. Transmission electron microscopy (TEM). Abbreviations: **cc**, choanocyte chamber; **o**, osculum; **sp**, spicule. Scale bar: 1 µm. (Courtesy Dr M.-F. Gallissian).

stages of postlarval development in the Baeriida and the Lithonida. Choanocytes are apinucleate and the basal system of the flagellum is adjacent to the apical region of the nucleus. The first stage in embryogenesis is a coeloblastula in which the flagella are internal and face into the central cavity. This blastula passes through a complex inversion, turning the flagellated pole of the blastomeres to the outside, and giving rise to an amphiblastula larva, in which the anterior pole is flagellated and the posterior pole is bare. After settlement, the flagellated cells give rise to choanocytes, and the large posterior aflagellated cells give rise to the other cell categories of the sponge, pinacocytes, porocytes, sclerocytes and to the amoeboid cells that are found between the choanoderm and the pinacoderm.

DESCRIPTION

Like the calcineans, calcaroneans are extremely variable in size, form, organization of the aquiferous system, and skeleton. Most of the representatives are known only from Recent seas. Isolated spicules, which may belong to calcaronean sponges have been reported from Early Cambrian reefs (James & Klappa 1983) and in Ordovician strata (Van Kempen 1978), but no unequivocal calcaronean fossils have yet been found (Reitner & Mehl 1995).

The aquiferous system in the Calcaronea can be asconoid, syconoid, sylleibid or leuconoid. Asconoid, syconoid, and sylleibid systems are found only in the Leucosoleniida. The leuconoid aquiferous system, such as that seen in the Leucosoleniida, can easily be derived from a syconoid type of organization, as these sponges retain traces of the radial organization of the skeleton and the usually clearly defined central atrium. However, the leuconoid systems in the Baeriida and the Lithonida bear no trace of an original tubular or radial organization, but are instead quite similar to the leuconoid aquiferous systems of the Demospongiae.

Calcaronean sponges have choanocytes with an apical, ovoid or pyriform nucleus. The basal flagellar roots are always in contact with the nuclear envelope at the apical pole of the nucleus. In many species, a glycocalyx layer is present between the microvilli which form the collar (Fig. 1). The interpretation of the localization of the nucleus within the choanocytes is often hampered by artefacts caused by handling of sponge collections and their fixation. Since this is one of the most distinctive characters distinguishing the Calcinea from the Calcaronea, sections of preserved material must be interpreted with caution (Vacelet 1964).

Despite the observed great diversity of body plan, our present knowledge of calcaronean biology, in particular their cell and skeletal morphology, indicates that there are a number of homologies among currently known species, and strongly supports the hypothesis of their common origin as well as a rather close relationship among all the sponges belonging to this subclass. Most notably, sponges in the Calcaronea have a typical fertilization process and a very particular pattern of embryogenesis and larval morphogenesis.

During fertilization, the spermatozoa are captured by choanocytes, which transform into a particular spermatozoon carrier cell containing the spermiocyst (Duboscq & Tuzet 1937, 1942; Vacelet 1964; Gallissian 1989; Gallissian &

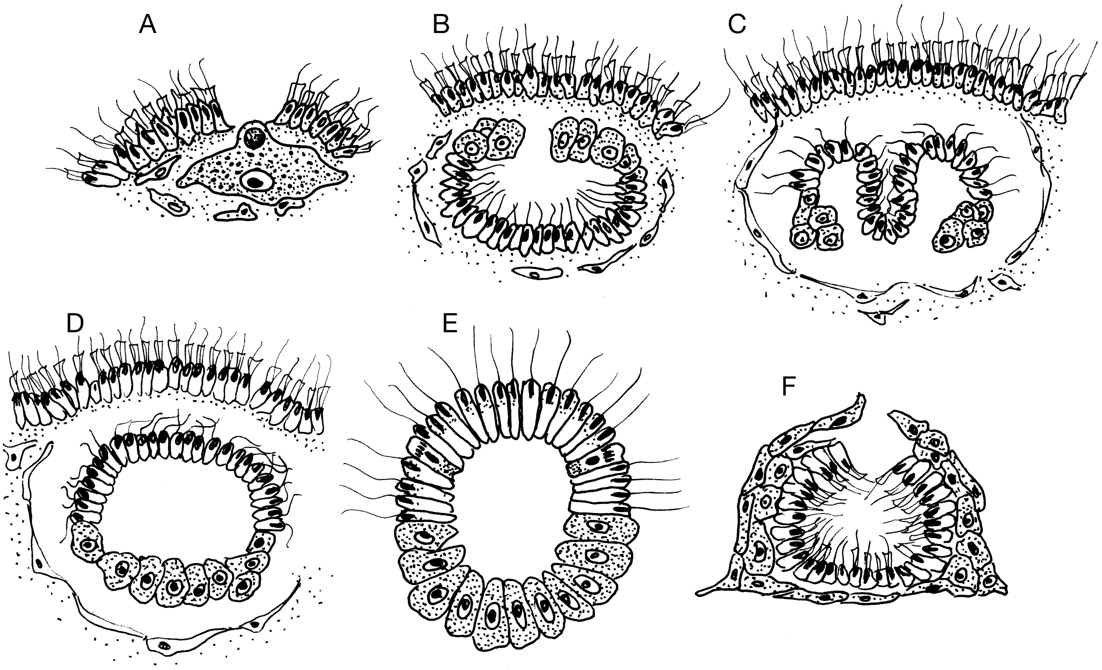

FIG. 3. — Diagram of the stomoblastula showing the phenomenon of inversion; **A**, fertilization; **B**, stomoblastula with the flagellum of the flagellated cells inside the blastocoel; **C**, inversion; **D**, amphiblatula with flagellae outside; **E**, mature free-swimming amphiblastula; **F**, young rhagon after metamorphosis.

Vacelet 1990). These cells migrate into the subchoanodermal space where they fertilize large mature oocytes. The entrance point of the carrier cell into the oocyte determines the symmetry of the future larva in the Leucosoleniida, but apparently not in a sponge that we currently classify in the Baeriida (Duboscq & Tuzet 1937, 1942). Only small differences were observed in the fertilization process in different species of the calcaronean sponges studied until now. There is only one report of a similar fertilization process in the rest of the Calcarea (Tuzet 1947) (Fig. 2).

The amphiblastula larva has large aflagellated cells at one end and small flagellated cells at the other. There are four "cellules en croix" which have the presumed function of photoreceptors (Duboscq & Tuzet 1941; Borojevic 1970; Amano & Hori 1992). At the early blastula stage the flagella are directed inwards into the primary blastocoel. Subsequently, in the stage called the stomoblastula, the aflagellated cells form an opening through which the flagellated blastula wall evaginates, inverting the larval wall and turning the flagella outwards. The larva closes again, delimiting a secondary blastocoel (Fig. 3). At this stage the larva is a typical amphiblastula with clearly marked poles: the flagellated pole corresponds to the anterior pole of the free-swimming larva, while the large aflagellated cells are restricted to the posterior pole (Fig. 4). After settlement, the large aflagellated cells give rise to pinacocytes, sclerocytes and to other amoeboid cells, while the flagellated cells differentiate into choanocytes (Amano & Hori 1993). The inversion of the early larva is unique and specific to the subclass Calcaronea, and is reminiscent of the morphogenesis of *Volvox* (Ivanov 1971). The amphiblastula larvae of the Calcaronea differ from all other sponge larvae. They are only superficially similar to the larvae of the Homoscleromorpha, which have been described as amphiblastula, but which are now termed "cinctoblastula" in order to underline these differences (Boury-Esnault *et al.* 1995). In the order Leucosoleniida, after the settlement of the larva, an asconoid tubular sponge is formed, which can remain at this stage of orga-

FIG. 4. — An amphiblastula larva (**a**) in the parental sponge. Scanning electron microscopy (SEM). Scale bar: 8 µm.

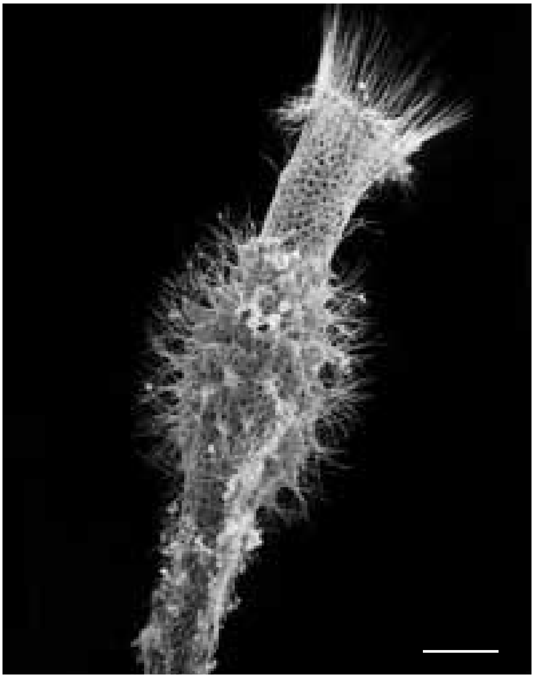

FIG. 5. — Young *Sycon sycandra* in the sycettid stage. Scale bar: 1.7 mm.

nization (e.g. *Leucosolenia*) or form radial outgrowths which give rise to the radial tubes of the syconoid grade of organization (Fig. 5) (Schulze 1875). The postlarval development of the other two orders of the Calcaronea is not known.

Order LEUCOSOLENIIDA Hartman, 1958 *emend.*

DIAGNOSIS. — Calcaronea with a skeleton composed of exclusively free spicules, without calcified non-spicular reinforcements. The aquiferous system is asconoid, syconoid, sylleibid or leuconoid. In the latter case, the radial organization around a central atrium can generally be detected by a well-formed atrial skeleton tangential to the atrial wall, and/or a subatrial skeleton consisting of subatrial tri- or tetractines with the paired actines tangential to the atrial wall and the unpaired actine perpendicular to it. The post-larval development passes (presumably always) through an olynthus stage.

DESCRIPTION

Like the calcinean order Clathrinida (Borojevic *et al.*, 1990), the Leucosoleniida represents a homogenous group of sponges, in which are found all the possible modifications of the fundamental pattern of the sponge body organization, from asconoid to leuconoid, and including most of the intermediate stages of the progressive modifications of the associated skeleton. Consequently, we consider that the Leucosoleniida represents a single taxonomic unit that cannot be divided into two groups, according to homocoel or heterocoel grade of organization as proposed by Hartman (1958).

The simplest forms correspond to the olynthus grade of organization, with a single tubular central cavity lined by choanocytes (family Leucosoleniidae) (Fig. 6). However, whereas in the Clathrinida, the olynthus form has given rise to several independent evolutionary lineages (see Borojevic *et al.* 1990) in the Leucosoleniida, the major and, as far as we are aware, sole evolutionary line from the homocoel to the heterocoel grade of organization passes through a sycettid grade of organization. *Sycetta* is characterized by a single central tube devoid of choanocytes, which

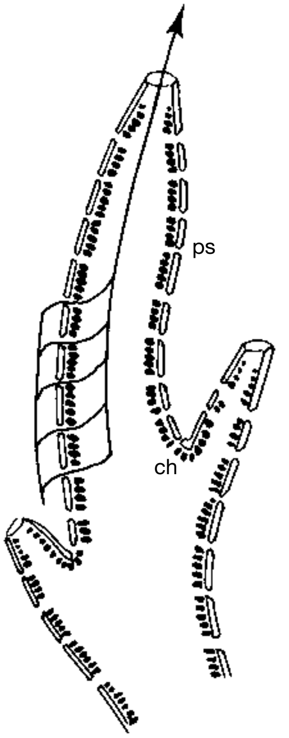

FIG. 6. — Diagram of an asconoid aquiferous system, such as is found in *Leucosolenia*. Abbreviations: **ps**, pinacoderm and the skeletogenous layer; **ch**, choanoderm. The arrow shows the direction of water flow.

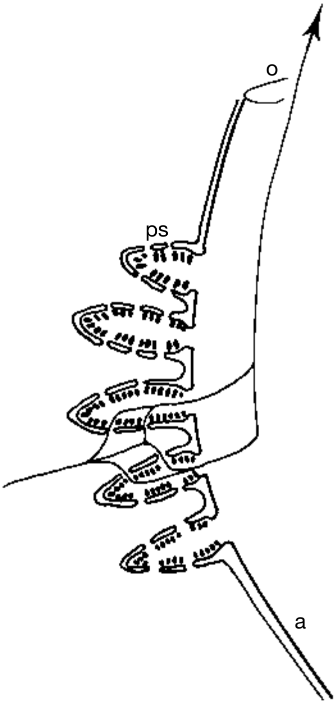

FIG. 7. — Diagram of the *Sycetta* type of organization of the sponge wall. Abbreviations: **ps**, pinacoderm and the skeletogenous layer; **a**, atrium; **o**, osculum. The arrow shows the direction of water flow.

corresponds to the atrium, from which tubes with a choanoderm radiate (Fig. 7). This sponge has only an exhalant aquiferous system; the incurrent water flows directly into the radial tubes through inhalant pores (Figs 7; 8).

The first group of morphological characters used to define the Leucosoleniida is the overall shape and the underlying skeletal support of the tubes. Increase in size from the sycettid grade of organization may occur by two different processes: the growth and elongation of radial tubes which increases the thickness of the sponge body, or the growth of the central tube containing the atrial cavity, which increases the length of the sponge body. Both processes can be observed in the Leucosoleniida:

A) the first process has given rise to two evolutionary pathways. The first is well-depicted by very young specimens of *Sycon*, as well as adult *Sycetta*, where the radial tubes are short and separate. At this stage they have an inarticulate choanoskeleton, i.e. the central atrial tube has a distinctive tangential skeleton, but the radial tubes perpendicular to the atrium are primarily supported by subatrial triactines whose paired actines are adjacent to the atrial skeleton, and the unpaired ones support the radial tube walls. The distal cones have peculiar small triactines.

The evolutionary lineages of the Sycettidae-Grantiidae and Heteropiidae bifurcate from this point. Whereas in the Sycettidae, this type of inarticulated organization is found only in very young specimens of *Sycon* and *Sycetta*, in the Heteropiidae, the inarticulate choanoskeleton is found in *Syconessa* and in *Sycettusa*, which also has distal cones that are fused into a continuous tangential cortical layer. In both families the elongation of radial tubes and their progressive coalescence result in a compact body that has a strictly radial organization, such as is found in

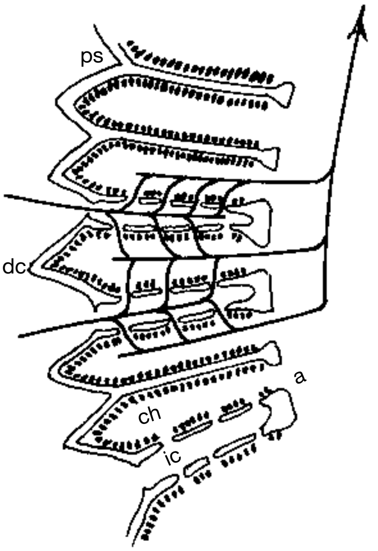

FIG. 8. — Diagram of *Sycon* type of sponge wall organization. Abbreviations: **ps**, pinacoderm and the skeletogenous layer; **ch**, choanoderm; **a**, atrium; **dc**, distal cones; **ic**, inhalant canals. The arrow shows the direction of water flow.

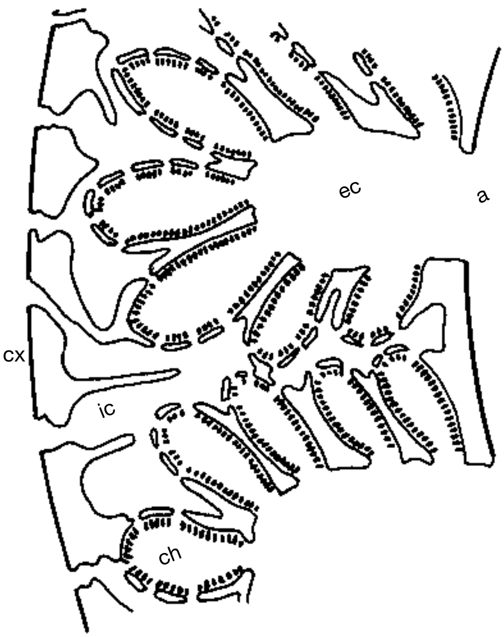

FIG. 9. — Diagram of the sylleibid type of aquiferous system organization, such as observed in *Polejaevia, Paralelapia,* and *Leucilla*. Abbreviations: **cx**, cortex; **ch**, choanoderm; **a**, atrium; **ic**, inhalant cavities; **ec**, exhalant cavities.

typical adult representatives of *Sycon* (Fig. 8) and *Grantessa*. The radial tubes are intercalated with narrow inhalant canals with an inhalant pore-bearing membrane devoid of skeleton.

Progressively, a common cortex covers the external part of the radial tubes and the openings of inhalant canals, i.e. the inhalant pores move to the cortical surface, and the cortex becomes supported by a specific skeleton. Such corticalization has given rise to a wide range of sponges with a solid body and with elaborate skeleton. The aquiferous system changes from long choanocyte chambers arranged radially around the central atrium, characteristic of the syconoid system (Fig. 8), to shorter elongate or ovoid choanocyte chambers arranged around radial exhalant cavities, such as observed in the sylleibid aquiferous system (Fig. 9), and to ovoid or spherical choanocyte chambers arranged between the inhalant and exhalant canals, such as observed in sponges with a typical leuconoid aquiferous system (Fig. 10). Sponges belonging to the latter evolutionary pathway usually have a typical articulate choanoskeleton, i.e. several rows of similar triactine spicules. In the first subatrial row, the paired actines are adjacent to the atrial skeleton and the unpaired actine is perpendicular to it, lying in the wall of the radial tube. This is the most common form of subatrial skeleton, and is easily recognized in all heterocoel Leucosoleniida. Although the spicules of the choanoskeleton can be irregularly scattered in massive sponges with a leuconoid aquiferous system such as *Leucandra*, the original orientation of many triactines with the unpaired angle turned to the atrium and the unpaired actine pointing distally, is frequently preserved. As indicated earlier, this evolutionary line has bifurcated quite early into two pathways that are distinguished by the presence or absence of pseudosagittal spicules in the distal part of the radial tubes. In both pathways, there is both increased corticalization, and progressive evolution of the syconoid organization into the leuconoid one (see descriptions of the families Grantiidae and Heteropiidae).

B) The second process has also given rise to two evolutionary pathways. The first one is analogous

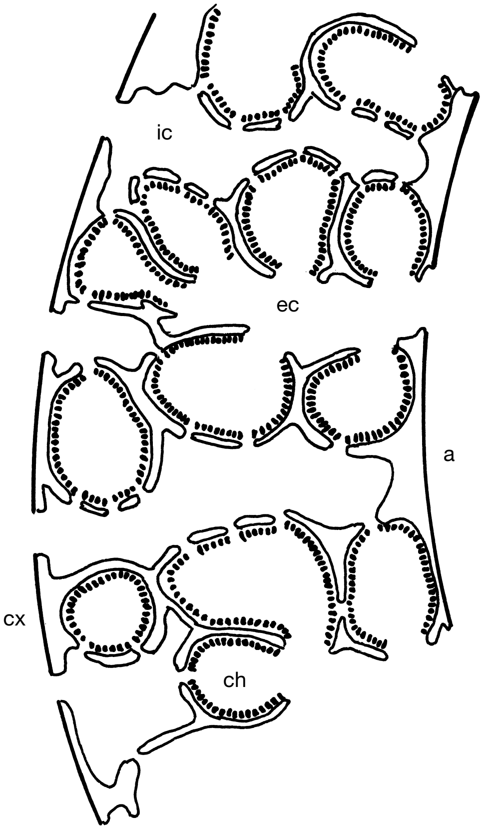

Fig. 10. — Diagram of the leuconoid type of aquiferous system organization, such as observed in many Calcaronea. Instead of a central atrial cavity there is a network of aquiferous exhalant canals that increase in size from the distal regions to the oscula. Abbreviations: **cx**, cortex; **ch**, choanoderm; **ic**, inhalant cavities; **ec**, exhalant cavities; **a**, atrium.

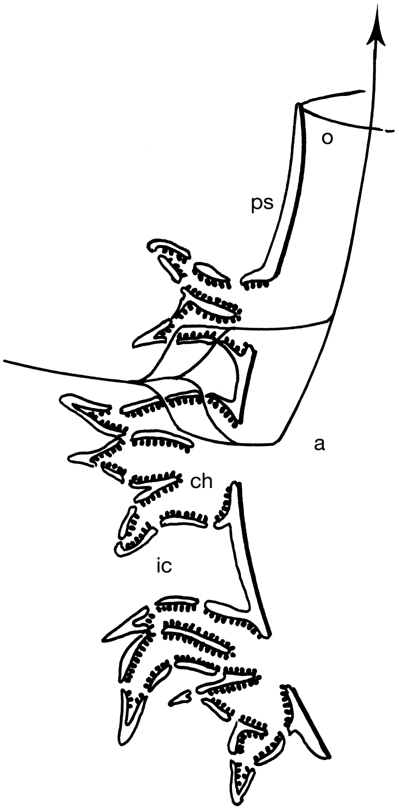

Fig. 11. — Diagram of the *Sycantha* type of sponge wall organization. Abbreviations: **ps**, pinacoderm and the skeletogenous layer; **ch**, choanoderm; **a**, atrium; **o**, osculum; **ic**, inhalant cavities. The arrow shows the direction of water flow.

to that of the Levinellidae in Calcinea (see Borojevic & Boury-Esnault 1986). During the longitudinal growth of the central tube, the radial outgrowths of the sycettid type of organization do not increase in length, but multiply. They can become grouped around the common cavities, each of them opening into the atrium. These groups of outgrowths are intercalated by shallow inhalant spaces. This organization, classified as "aberrant" by Dendy & Row (1913) in comparison with the typical *Sycon* form of growth, was described by Lendenfeld (1891) for the genus *Sycantha* (Fig. 11) and by Jenkin (1908a) for his genera *Tenthrenodes, Hypodictyon* and *Dermatreton*. A partial corticalization can occur in this evolutionary line by an increase of tangential triactine spicules in the distal parts of the fused radial tubes between the inhalant cavities so as to form a loose network such as observed in *Dermatreton*. Since this network does not provide sufficient mechanical support, the atrial skeleton takes over this function, and is thickened in order to provide the required rigidity. This evolutionary pathway has only given rise to a few sponges, which we group in the family Sycanthidae.

In the second evolutionary pathway, the short radial tubes retain their regular distribution on the central atrial tube and become covered by a true continuous cortex. The result is a sponge with a thin body surrounding a large atrial cavity,

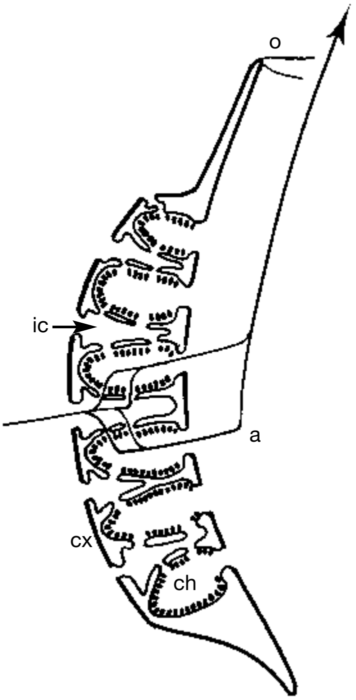

FIG. 12. — Diagram of the Jenkinidae type of the sponge wall organization. Abbreviations: **cx**, cortex; **ch**, choanoderm; **a**, atrium; **o**, osculum; **ic**, inhalant cavities.

with a rigid and well-developed atrial and cortical skeletons (Fig. 12). This morphology is found in several independent evolutionary lineages. In two families, the Jenkinidae and the simple forms of Amphoriscidae, a continuous and dense cortex is associated with an inarticulate choanoskeleton composed of only the unpaired actines of the subatrial spicules, and occasionally the actines of cortical or subcortical spicules (e.g. Amphoriscidae). In the basal region of these sponges, where the wall can be thicker, a number of subatrial or cortical spicules may be found at some distance from respectively the atrial or the cortical plane. Nonetheless, they clearly retain the morphology of cortical or subatrial spicules and never form an articulate choanoskeleton. Among the sponges with a thick wall and an articulate skeleton, the original syconoid organization of the thin-wall sponges can also result in a more elaborate sylleibid or an irregular alveolar leuconoid aquiferous system (Figs 9; 10).

The growth of the Jenkinidae is longitudinal. As these long tubular structures become fragile, large species form a complex cormus of branched and occasionally anastomosed tubes (e.g. *Anamixilla, Uteopsis, Leucascandra*), quite similar to the large cormi of *Leucosolenia* in the Calcaronea, and *Levinella* or *Leucaltis* in the Calcinea. Conversely, in the Amphoriscidae, large specimens of *Paraleucilla* can secondarily form massive bodies by a secondary thickening of the body wall rather than by the distal elongation of the original radial tubes, such as occurs in *Sycon*. The original inarticulate organization of the choanoskeleton is still clearly visible at least in the external part of the sponge. The thickening of the sponge wall may be caused by the insertion of new layers between the atrial and the subatrial skeletons, forming a subatrial area with a specific skeleton derived from subatrial, atrial or both types of spicules. Alternatively, the thickened body can be a consequence of multiple folding and coalescence of the originally thin sponge body wall.

It is conceivable that an inarticulate choanoskeleton can also be derived from an articulate one by the secondary reduction of the choanosome wall thickness. Dendy & Row (1913) favoured this possibility, concluding that both inarticulate and articulate types of choanoskeleton can coexist in the same genus, the former one being derived from the latter one. We find, like Brøndsted (1931), that there is a relative morphological and geographical homogeneity of sponges with an inarticulate choanoskeleton, and consequently consider this form of skeleton is a primary morphological characteristic. We have now tried to group those sponges with an inarticulate skeleton in separate taxa. However, we are aware that some species may be difficult to fit into the proposed system, and that the thickening of the originally thin choanosome may be a natural consequence of the growth of the sponge body.

The second group of morphological characters corresponds to the different patterns of spicules that participate in the composition of the skeleton in specific regions of the sponge wall. These characteristics can be used to subdivide the Leucosoleniida, into the families Grantiidae, Heteropiidae, Staurorrhaphidae and Lelapiidae. Since all these families derive from the sycettid

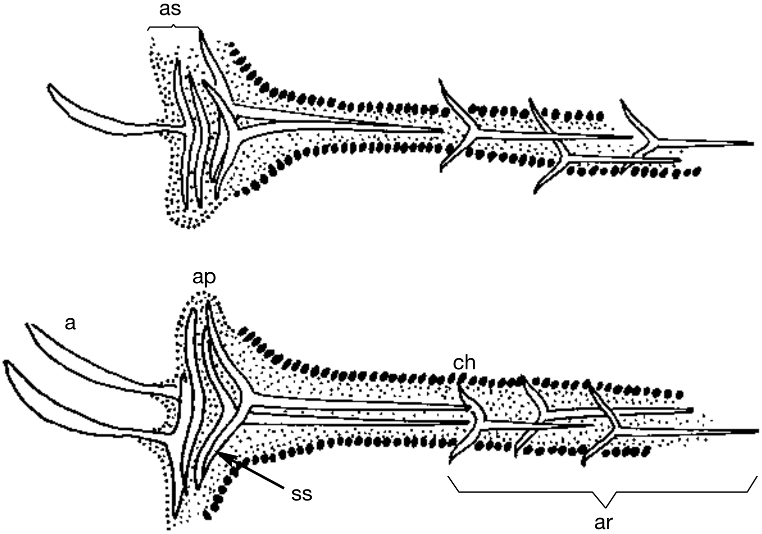

FIG. 13. — Diagram of the subatrial region of heterocoel Leucosoleniida. Abbreviations: **a**, atrium; **as**, atrial skeleton, composed of triactines and tetractines tangential to the atrial surface; **ap**, apopyle of the radial choanocyte chamber; **ss**, subatrial spicules; **ar**, articulate choanosomal skeleton; **ch**, choanoderm.

grade of organization mainly through the distal increase of their radial tube length and subsequent corticalization, they all still bear clear traces of the radial organization, in the tubes growing out from the central atrium. This is generally quite easily noted in the proximal subatrial skeleton, which is perpendicular to the atrial one, and indicates the original position of radial tubes (Fig. 13). Within each of these families, the genera are generally defined by the presence or absence of certain types of spicules (e.g. large diactines) in defined regions of the sponge. This division may be rather artificial, but it is convenient for classification of many sponges which belong to the heterocoel Leucosoleniida.

In typical species of this order and in fully-grown specimens, the main characteristic of each family is quite easily recognized. For example, giant cortical tetractines typify the Amphoriscidae and subcortical pseudosagittal spicules are typical of the Heteropiidae. However, this is not the case in young specimens, and their identification can be quite difficult. Furthermore, a particular spicule type can be rare in some specimens, or in certain regions of a sponge (Borojevic 1966). New spicule types can appear in families where they are not originally found, representing a secondary, rather than a primary and diagnostic, morphological characteristic (e.g. the cortical tetractines in *Leucandrilla,* which does not belong to Amphoriscidae). In a similar way, the normally thick sponge wall can be thin and supported only by a reduced choanoskeleton in young sponges, or in the suboscular region, causing a sponge belonging to the Grantiidae to appear similar to those in the Jenkinidae. It is always difficult to resolve such cases, and we can only agree with Dendy & Row (1913) in stating that "it must be frankly admitted that the boundary line… is by no means sharply defined". We hope that further studies will shed more light on the problematic cases.

Family LEUCOSOLENIIDAE Minchin, 1900

TYPE GENUS. — *Leucosolenia* Bowerbank, 1864 by original designation.

DIAGNOSIS. — Leucosoleniida with a cormus composed of frequently branched, but rarely anastomosed, asconoid tubes, and with a continuous choanoderm that lines all the internal cavities of the sponge. There is neither a common cortex covering the cormus, nor a delimited inhalant or exhalant aquiferous system.

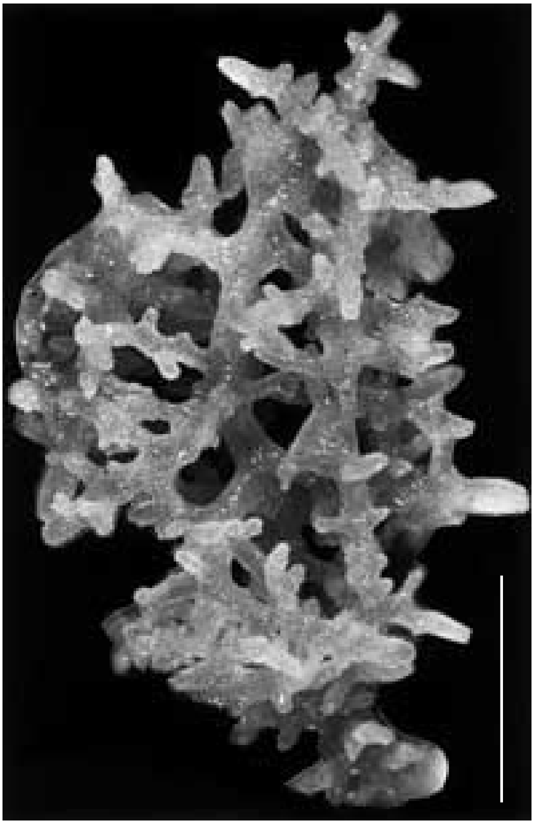

FIG. 14. — *Leucosolenia complicata* from the Channel Sea (Roscoff) MNHN C.1968,341. Scale bar: 1 cm.

FIG. 15. — Section of the wall of *Ascute*. Specimen from the Wilson collection collected near Port Philips Heads (Australia), BMNH 1983.6.9.33. Scale bar: 160 µm.

DESCRIPTION

The family Leucosoleniidae includes all the calcaronean homocoel sponges. In contrast to the Clathrinidae, which frequently form large massive cormi, the Leucosoleniidae are most often small and creeping tubular sponges that only rarely form cormi several centimetres large, such as *Leucosolenia complicata* (Montagu, 1818) or *Leucosolenia eleanor* Urban, 1905.

Genus *Leucosolenia* Bowerbank, 1864

TYPE SPECIES. — *Spongia botryoides* Ellis & Solander, 1786 by original designation.

DIAGNOSIS. — Leucosoleniidae in which the skeleton can consist of diactines, triactines and/or tetractines. There is no reinforced external layer on the tubes.

DESCRIPTION

While the genus *Leucosolenia* is morphologically very homogenous, it is nonetheless cosmopolitan and includes numerous species. The asconoid tubes may be creeping and only rarely branched, or be copiously ramified but not anastomosed; they may form a large arborescent cormus such as seen in *L. complicata* (Montagu, 1818). The cormus of *Leucosolenia* is always simple, without subdivisions or differentiations into regions with distinct functions, although in larger specimens the central and proximal tubes are usually wider than the distal ones (Fig. 14).

Genus *Ascute* Dendy & Row, 1913

TYPE SPECIES. — *Leucosolenia uteoides* Dendy, 1892 by original designation.

DIAGNOSIS. — Leucosoleniidae in which the skeleton can be composed of diactines, triactines and/or tetractines, with an outer layer that is supported by giant longitudinal diactines.

DESCRIPTION

Dendy & Row (1913) placed the genus *Ascute* among sponges with basinucleate choanocytes. We have examined the type specimen of *Leucosolenia uteoides* Dendy, 1892 (BMNH 1893. 6.9.33) and found that it only has typical sagittal triactine and tetractine spicules that are organized in a pattern very similar to the skeleton of *Leucosolenia* (Fig. 15), and quite different from the Clathrinidae, which are characterised by regular spicules. Since the appearance of the choanocytes may be considered altered by fixation (Vacelet 1964), we prefer to place this genus close to *Leucosolenia* until examination of new specimens and a revision of their cytology is possible. Only two species were described in this genus; both are from Australia: *A. asconoides* (Carter, 1886) and *A. uteoides* (Dendy, 1892).

Genus *Ascyssa* Haeckel, 1872

TYPE SPECIES. — *Ascyssa troglodytes* Haeckel, 1872 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Leucosoleniidae with a skeleton composed entirely of diactines.

DESCRIPTION

Haeckel (1872) described the two species of the genus *Ascyssa* from very few small specimens; representatives of this genus have not been found since. Since in the Calcaronea the first spicules to be secreted are diactines, these specimens may simply represent very young *Leucosolenia*, as suggested by Dendy & Row (1913). However, because Haeckel (1872) indicated that the specimen of *A. acufera* Haeckel, 1872 was sexually reproductive, this hypothesis is unlikely.

Family SYCETTIDAE Dendy, 1892

TYPE GENUS. — *Sycetta* Haeckel, 1872 by original designation.

DIAGNOSIS. — Leucosoleniida with a central atrial tube and perpendicular regularly arranged radial tubes lined by choanoderm. The distal cones of the radial tubes, which may be decorated with tufts of diactines, are clearly noticeable on the sponge surface. They are never covered by a cortex supported by tangential triactines and/or tetractines. The proximal skeleton of the radial tubes is composed of a row of subatrial triactines and/or tetractines, which are usually followed by only a few or several rows of triactines and/or tetractines. Distal pseudosagittal spicules are absent. A tangential layer of triactines and/or tetractines supports the atrial wall.

DESCRIPTION

In the Leucosoleniida, the transition from homocoel to heterocoel grade of organization apparently passes only through the sycettid-grade of organization (Dendy & Row 1913). The sycettid organization is essentially a sponge like *Leucosolenia* in which the median region of the single central tube is decorated with regularly arranged short and unbranched radial tubes. It is structurally analogous to the organization of simple Levinellidae from the Calcinea (Fig. 7). The transition from the homocoel to the heterocoel organization involves the progressive restriction of choanocytes to the radial tubes, while the central tube acquires the sole function of an exhalant atrium. In the Sycettidae the elongation of the radial tubes is concurrent with their partial or full longitudinal coalescence around the radial inhalant canals. This organization, typical in the genus *Sycon,* gives compactness to the sponge, simultaneously maintaining an efficient water circulation.

Genus *Sycetta* Haeckel, 1872

TYPE SPECIES. — *Sycetta sagittifera* Haeckel, 1872 by subsequent designation (this work).

DIAGNOSIS. — Sycettidae with a central atrial tube decorated with short, completely separate radial tubes. There is no defined inhalant aquiferous system. The skeleton of the radial tubes is composed of triactines and tetractines, and diactines may be found in the distal cones.

DESCRIPTION

The genus *Sycetta,* as defined by Dendy & Row (1913), comprised three species described under

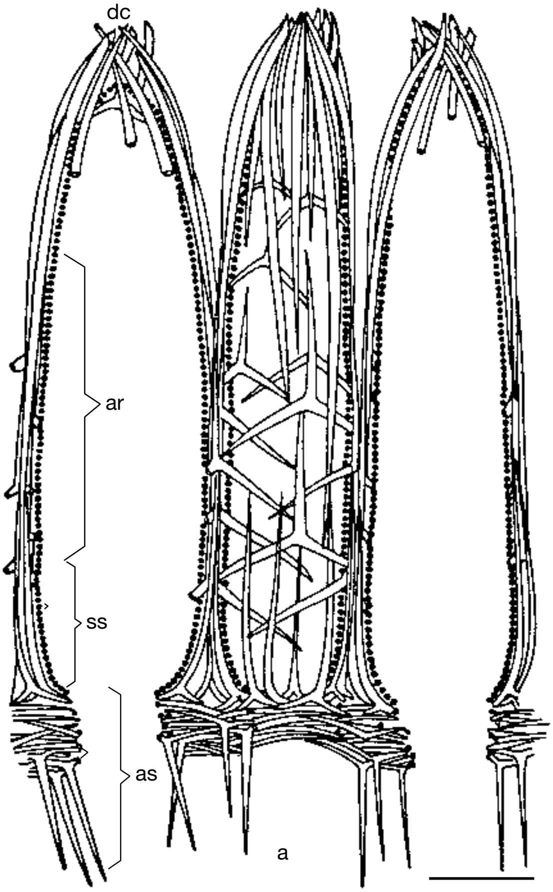

FIG. 16. — Diagram of a transverse section through the wall of *Sycon natalense* Borojevic, 1967. Abbreviations: **a**, atrium; **as**, atrial skeleton composed of tangential triactines and tetractines; **ss**, subatrial spicules; **ar**, articulate choanosomal skeleton; **dc**, distal cone, with a short tuft of diactines (from Borojevic 1967b). Scale bar: 100 µm.

the names *Sycetta primitiva* Haeckel, 1872, *S. sagittifera* Haeckel, 1872 and *Sycaltis conifera* Haeckel, 1872. Dendy & Row 1913 designated *Sycetta primitiva* as the type species. Haeckel (1872) characterized this species by the presence of regular, equiangular and equiradiate spicules, which are clearly described and represented as such in the corresponding figure. In the same figure, Haeckel (1872: vol. III, pl. 41) shows that the choanocytes are closer to the basinucleate than to the apinucleate type. Although Haeckel's descriptions may be taken with some reservation, and *S. primitiva* has not been observed since that time, the original description indicates quite clearly that this is a calcinean sponge, and should be classified as a typical member of the family Levinellidae (Borojevic & Boury-Esnault 1986). Haeckel (1872) classified *Sycetta primitiva* in the subgenus *Sycettaga*, and we propose to transfer it as a genus to the family Levinellidae, with a single species *Sycettaga* (*Sycetta*) *primitiva* Haeckel, 1872. *Sycetta sagittifera* being an originally included nominal species is designated here as the type species of *Sycetta*. This species displays all the characteristics of the genus as understood by Dendy (1893), Dendy & Row (1913), and subsequent authors.

Brøndsted (1931) described two sponges from the Deutsche Südpolar Expedition collection, *Sycetta antarctica* and *Tenthrenodes primitivus*. Whilst the former one is a typical *Sycetta*, the latter is characterized by the presence of diactines and the occasional coalescence of the radial tubes, which, however, are not fused. We have now placed the genus *Tenthrenodes* Jenkin, 1908 in synonymy with *Sycantha* Lendenfeld, 1891. *Tenthrenodes primitivus* Brøndsted, 1931 is however much closer to a typical *Sycetta* and we propose to transfer this species to the genus *Sycetta*. *Sycetta* (*Tenthrenodes*) *primitiva* (Brøndsted, 1931) should be distinguished from *Sycettaga* (*Sycetta*) *primitiva* Haeckel, 1872, which belongs now to the family Levinellidae. Dendy & Row (1913) specified that sponges in the genus *Sycetta* have no diactines, as all the sponges described in the genus up to their time were devoid of them. Their presence in *Sycetta primitiva* (Brøndsted, 1931) leads us to modify this point accordingly in the definition of the genus *Sycetta*.

Genus *Sycon* Risso, 1826

TYPE SPECIES. — *Sycon humboldtii* Risso, 1826 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Sycettidae with radial tubes partially or fully coalescent; distal cones are decorated by tufts of diactines. The inhalant canals are generally well-defined between the radial tubes and are often closed at the distal end by a membrane that is perforated by an ostium, devoid of a skeleton. There is no continuous cortex covering the distal ends of the radial tubes. Skeleton of the atrium and of the tubes composed of triactines and/or tetractines.

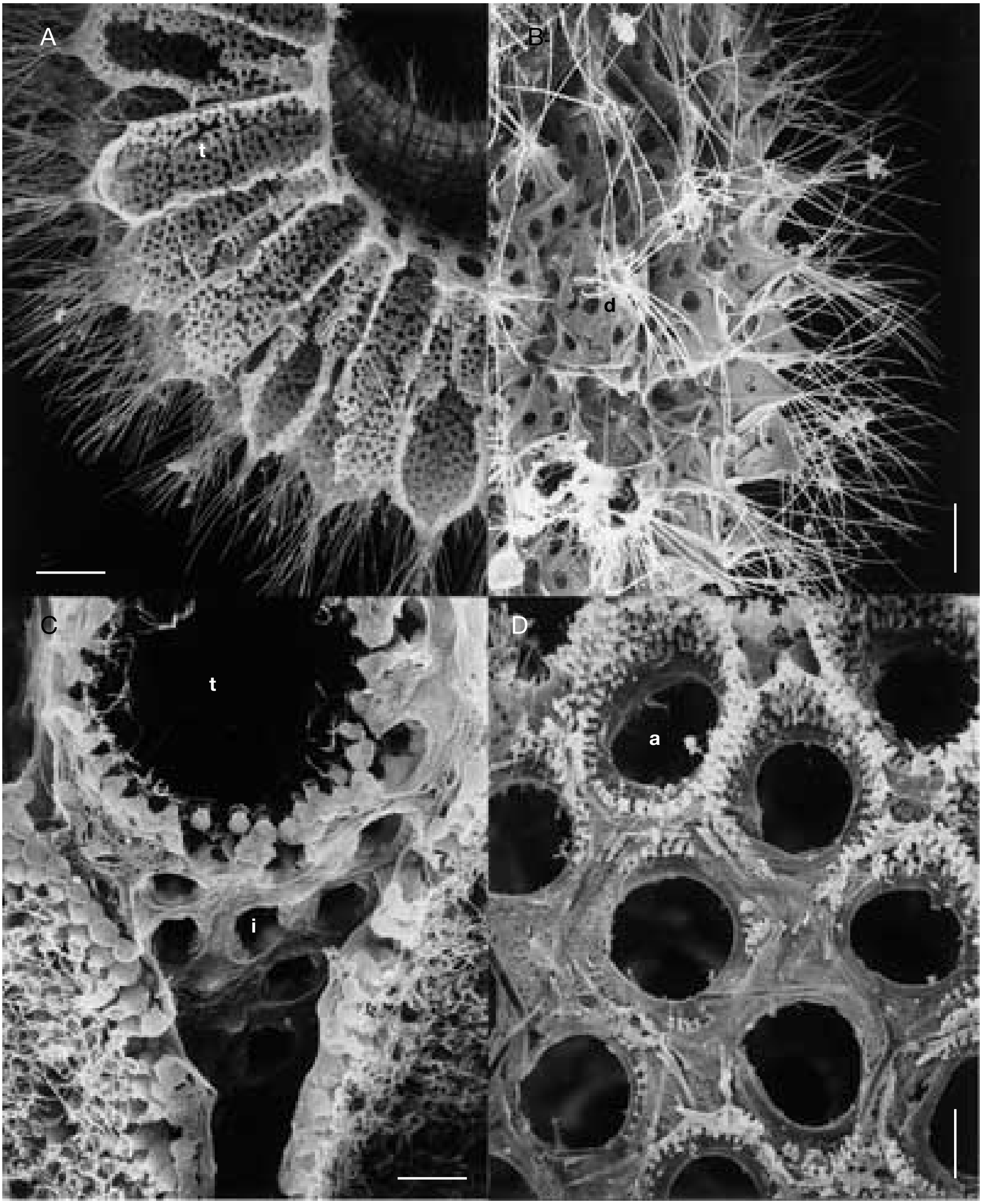

FIG. 17. — The organization of the aquiferous system in *Sycon sycandra* (SEM); **A**, tubes (**t**); **B**, distal chones (**d**); **C**, detail of tubes (**t**) and inhalant openings (**i**); **D**, apopyles (**a**). Scale bars: A, 160 µm; B, 65 µm; C, 13 µm; D, 43 µm.

DESCRIPTION

The genus *Sycon* is cosmopolitan, and it is often considered to be a perfect example of the calcareous sponges (Figs 16; 17). Many representatives have a simple radially organized body with a single osculum, occasionally with a short peduncle. Species that grow larger may be arborescent, with a peduncle and ramified body, each branch representing a complete syconoid organization. The radial tubes are generally simple, but in large specimens they can also be ramified. In this case, the branches remain parallel, and each branch ends by a peculiar terminal cone. In some species (e.g. *Sycon elegans* Bowerbank, 1845; *Sycon gelatinosum* Blainville, 1837), the distal cones have dense tufts of diactines, which terminate all at the same level, giving the external surface a smooth, tabulate appearance. This organization should not be misinterpreted as a cortex, which is always characterized by tangential triactine spicules.

A group of small representatives of the genus arise from solid or tubular creeping stolons. The stolons can produce terminal hollow spherical buds (e.g. *Sycon sycandra* Lendenfeld, 1885), which detach, and form propagules with a peculiar skeleton. They are usually hispid due to the presence of long diactines, which act as flotation devices and promote their subsequent anchorage, attachment to the substrate, and formation of the young sponge. These propagules can live for a long time in the water column, and are quite frequently collected in the mesopsammon. However, they cannot be identified as *Sycon* until they attach to the solid substrate and grow into the typical adult sponge. Alternatively, spherical propagules can be formed from the distal parts of the radial tubes through the constriction and subsequent detachment of the region just under the distal cones (e.g. *Sycon frustulosum* Borojevic & Peixinho, 1976).

Most species of *Sycon* are attached to hard substrates, but occasionally they can live on a soft bottom [e.g. *S. villosum* (Haeckel, 1872), *S. raphanus* (Schmidt, 1862)]. In this case, they are anchored by long and ornate spicules, which are not found on the specimens that are attached to hard substrates. Since all the other morphological characteristics are identical, and similar sponges can grow in close proximity on different substrata, we interpret the presence of these spicules to be a secondary adaptation to the type of substratum.

Sycon is a common genus which has been extensively studied. Following Laubenfels (1936), Burton (1963) revived the name *Scypha* Grant, 1821 which was described in the Flora of the British Plants, and which has recently been used by non-taxonomists. Since 1899, no taxonomist except Laubenfels and Burton has used this name and more than 25 works, and 10 authors have used the generic name *Sycon* since 1950. We wish to maintain the commonly used younger synonym to avoid confusion. As the rule 23.9.1.2 of reversal of precedence cannot be applied strictly, we refer the case to the Commission with an appropriate recommendation for a ruling under the plenary power (Art. 81). The use of the junior name is to be maintained while the case is under consideration (Art. 82).

Family GRANTIIDAE Dendy, 1892

TYPE GENUS. — *Grantia* Fleming, 1828 by original designation.

DIAGNOSIS. — Leucosoleniida in which there is always a cortex, supported by a skeleton of tangential spicules that can be diactines, triactines, tetractines, or any combination of them. The aquiferous system is either syconoid with radial and elongate choanocyte chambers, or sylleibid or leuconoid with elongate or spherical, scattered choanocyte chambers. The inhalant and exhalant aquiferous systems are always fully developed. The choanoskeleton is articulate, tubular in syconoid species, and contains few to several rows of triactines and/or tetractines, or is, in leuconoid species, arranged without apparent order. In the latter case, the choanoskeleton always preserves traces of the radial organization, particularly at the level of the subatrial triactines and/or tetractines. The atrial skeleton consisting of tangential triactines and/or tetractines is well-developed.

DESCRIPTION

The family Grantiidae has a central position among the Leucosoleniida. Its major characteristic is the development of a distinct cortex. The development of a cortex is quite progressive in the Grantiidae, and simple forms, such as *G. compressa* (Fabricius, 1780), clearly indicate their

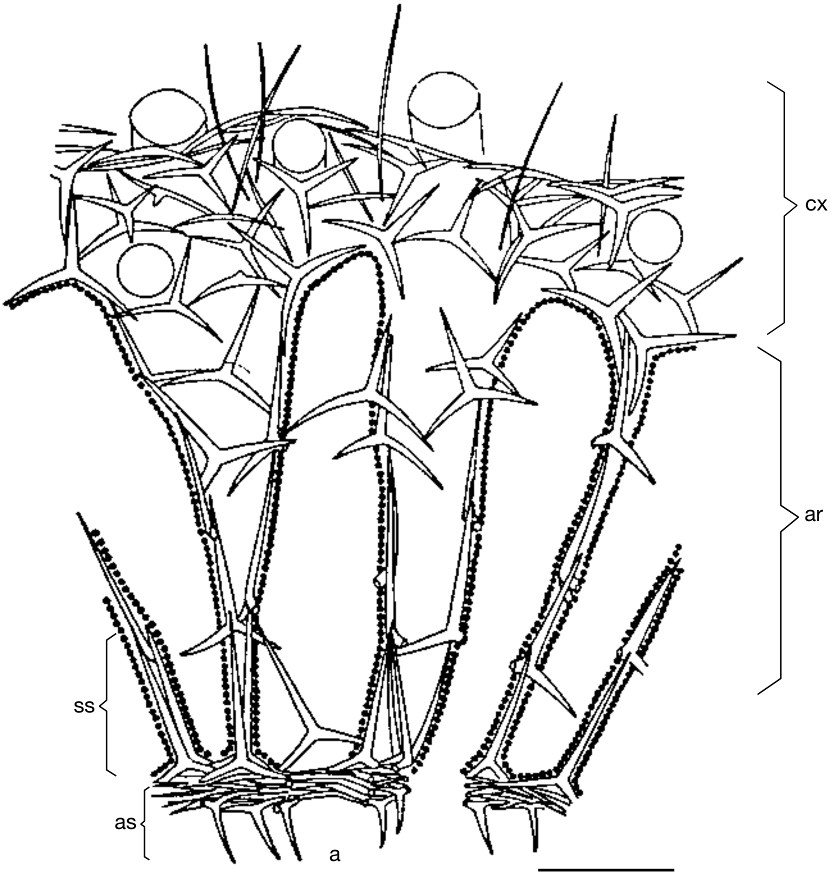

FIG. 18. — Diagram of a transverse section through the wall of *Grantia socialis* Borojevic, 1967. Abbreviations: **a**, atrium; **as**, atrial skeleton composed of tangential triactines and tetractines; **ss**, subatrial spicules; **ar**, articulate choanosomal skeleton; **cx**, cortex (from Borojevic 1967a). Scale bar: 100 µm.

proximity to *Sycon* by the presence of tufts of diactines at the end of their radial tubes. Indeed, in large *Sycon* species, the inhalant canals are partially closed by a membrane devoid of spicules. Formation of a specific skeleton in this membrane, with the production of tangential spicules which do not derive from those of the tubes, is a new feature which marks a major evolutionary step, and the boundary between the families Sycettidae and Grantiidae (Fig. 18).

The family Grantiidae is very large. While some of the genera were designated to include sponges with a very particular type of growth or skeleton, and consequently include only a single species (e.g. *Teichonopsis, Sycute, Synute*), others have a rather basic type of organization and skeleton, and include numerous species that are present throughout all the oceans (e.g. *Grantia, Leucandra*).

Genus *Grantia* Fleming, 1828

TYPE SPECIES. — *Spongia compressa* Fabricius, 1780 by original designation.

DIAGNOSIS. — Grantiidae with a syconoid organization. The cortex is composed of tangential triactines and/or tetractines, occasionally with small perpendicular diactines. Longitudinal diactines, if present, are not found exclusively in the cortex, but cross obliquely, at least a part of the choanosome and protrude from the external surface.

DESCRIPTION

Typical species of *Grantia* have long and regular radial tubes, which may be branched distally, and a relatively thin atrial and cortical skeletons. Diactines frequently protrude from the external surface of the sponge. Many species of *Grantia* that form small solitary tubes or large bushy sponges have been described from all oceans.

Genus *Sycandra* Haeckel, 1872

TYPE SPECIES. — *Ute utriculus* Schmidt, 1870 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Grantiidae with a large flattened body; the atrial cavity with a complex network of tissue tracts, supported by parallel diactines.

DESCRIPTION

Dendy & Row (1913) retained Haeckel's genus *Sycandra* for a single species *S. utriculus* that was characterized by a complex network of tissue tracts in the atrial cavity, supported by bundles of parallel diactines. Similar structures can be seen inside the atrial cavity of several large and flattened Grantiidae and Amphoriscidae. The surface of the opposite sides of the central atrial cavity can be close, touch and become coalescent (e.g. *Leucilla saccharata* Haeckel, 1872; *Amphiute lepadiformis* Borojevic, 1967). These regions thus become connected by tissue tracts supported by a skeleton that is derived from the atrial one, and which can contain modified atrial spicules. However, in other Sycettidae diactines are not normally present in the atrial skeleton, and the presence of an internal atrial network with a specific skeleton is a new morphological characteristic. Here we follow the opinion of Dendy & Row (1913) and consider that this character is sufficient to separate the genus from other Grantiidae.

Genus *Teichonopsis* Dendy & Row, 1913

TYPE SPECIES. — *Teichonella labyrinthica* Carter, 1878 by monotypy.

DIAGNOSIS. — Pedunculate calyciform Grantiidae with a syconoid organization and an expanded atrium. The thin wall is highly folded and the convoluted edge corresponds to the oscular margin.

DESCRIPTION

The separation of this genus from *Grantia* is justified because of its particular pattern of growth, through which the atrial cavity becomes wide open. As it grows the sponge wall becomes a highly folded asymmetric leaf, freely traversed by the water current that runs from the lower cortical to the upper atrial surface.

Genus *Ute* Schmidt, 1862

TYPE SPECIES. — *Ute glabra* Schmidt, 1864 by monotypy.

DIAGNOSIS. — Grantiidae with a syconoid organization. The cortex is supported by giant longitudinal diactines, and the choanoskeleton is articulate, composed of several rows of triactines with occasional tetractines. There are no radial fascicles of diactines.

DESCRIPTION

Calcarea belonging to the genus *Ute* are among the most beautiful calcareous sponges. They have a regular tubular form with a vitreous, smooth and shiny surface due to many longitudinal, parallel diactines (Fig. 19).

The relationship between the genera *Ute* and *Aphroceras* has been discussed previously (Borojevic 1966).

Genus *Sycute* Dendy & Row, 1913

TYPE SPECIES. — *Sycon dendyi* Kirk, 1895 by monotypy.

DIAGNOSIS. — Grantiidae with a syconoid organization. The cortex is supported by giant longitudinal diactines. The distal part of the choanocyte chambers is crowned by fascicles of radial diactines located between the longitudinal diactines.

DESCRIPTION

This genus has a single species. Like *Sycon*, it is characterized by tufts of diactines that decorate the distal cones of the radial tubes, and like *Ute* it has longitudinal cortical giant diactines.

Genus *Synute* Dendy, 1892

TYPE SPECIES. — *Synute pulchella* Dendy, 1892 by monotypy.

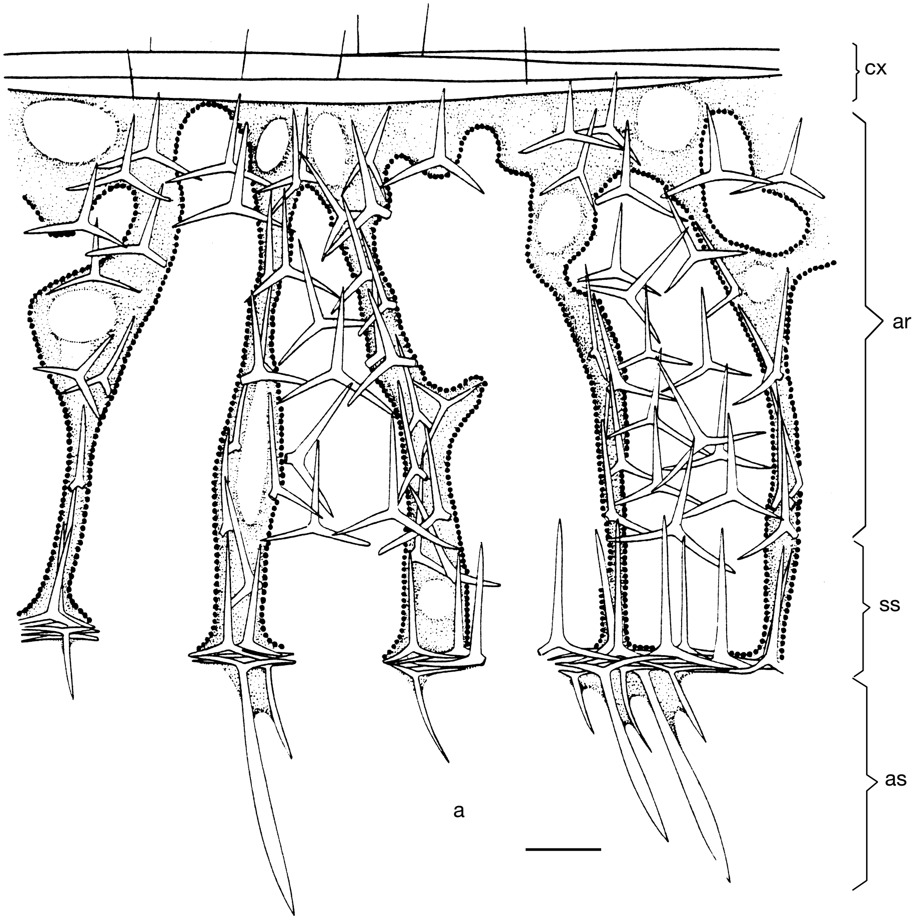

FIG. 19. — Diagram of a longitudinal radial section through the wall of *Ute gladiata* Borojevic, 1966. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicules; **ar**, articulate choanosomal skeleton; **cx**, cortex (from Borojevic 1966). Scale bar: 100 µm.

DIAGNOSIS. — Grantiidae with a cormus entirely made of fused syconoid units and surrounded by a common cortex with a special skeleton containing giant longitudinal diactines (Dendy 1892a).

DESCRIPTION

This genus is monospecific and only known from the southern Australian coasts. Its organization is reminiscent of colonial ascidians such as *Botryllus*.

Genus *Amphiute* Hanitsch, 1894

TYPE SPECIES. — *Amphiute paulini* Hanitsch, 1894 by monotypy.

DIAGNOSIS. — Grantiidae with a syconoid organization. Both cortical and atrial skeletons are supported by giant longitudinal diactines.

DESCRIPTION

These are syconoid sponges that form large cormi, which are supported in both the atrial and cortical surfaces by giant longitudinal diactines (Fig. 20). Their relationship with the family Heteropiidae has been discussed previously (Borojevic 1965).

Genus *Sycodorus* Haeckel, 1872

TYPE SPECIES. — *Sycandra* (*Sycodorus*) *hystrix* Haeckel, 1872 by subsequent designation (Dendy & Row 1913).

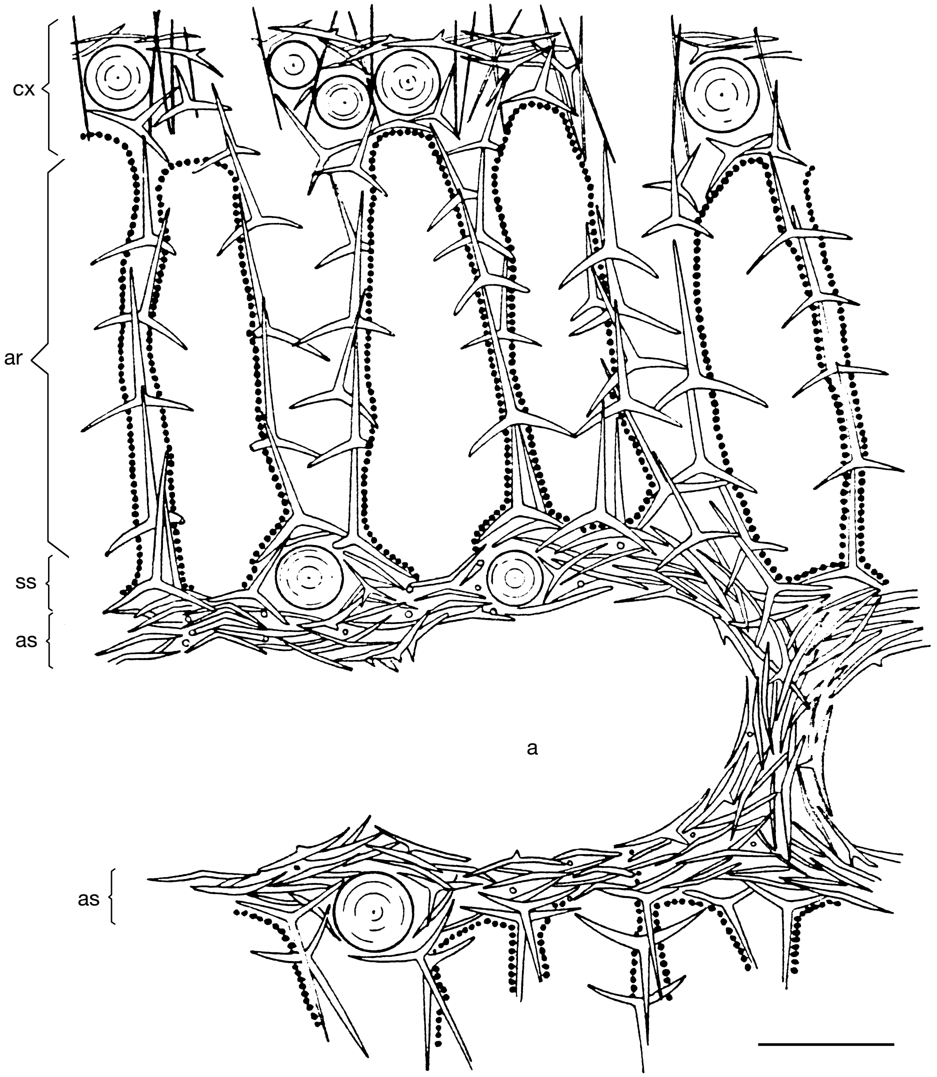

FIG. 20. — Diagram of a transverse section through the wall of *Amphiute lepadiformis* Borojevic, 1967. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicules; **ar**, articulate choanosomal skeleton; **cx**, cortex (from Borojevic 1967b). Scale bar: 100 µm.

DIAGNOSIS. — Grantiidae with a syconoid organization. Only the atrial skeleton is supported by giant longitudinal diactines.

DESCRIPTION

Sycodorus is a variation of the type of sponges belonging to the "group" *Ute*, whose skeleton is provided with longitudinal diactines. They are characterized by the presence of longitudinal diactines that are restricted to the atrial tangential skeleton.

Genus *Leucandra* Haeckel, 1872

TYPE SPECIES. — *Sycinula egedii* Schmidt, 1870 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Grantiidae with a sylleibid or leuconoid organization. Longitudinal large diactines, if present, are not restricted to the cortex, but lie obliquely across the external part of the sponge wall and protrude from the surface of the sponge.

DESCRIPTION

This is a very large genus containing many species (Fig. 21). Initially it was defined primarily by negative characters, and included most of the leuconoid Calcarea. Dendy & Row (1913) narrowed the definition of the genus, and succeeded in giving it a more positive and circumscribed definition. In particular, they clearly perceived the difference between *Leucetta* and *Leucandra*, the first step required to separate a large group of leuconoid Calcinea from the genus *Leucandra*. In the present study we separate another group of leuconoid sponges, which have a particular skeletal organization and had been classified as *Leucandra,* into the order Baeriida. At the same time, following Jenkin (1908a) and Brøndsted (1931), we separate the sponges with thin walls and an inarticulate type of choanoskeleton into the family Jenkinidae, and following Dendy (1913), we separate grantiid sponges with tetractines in the cortical skeleton into the new genus *Leucandrilla*.

As pointed out by Dendy & Row (1913), *Leucandra* can be derived from grantiid sponges by a progressive substitution of the syconoid aquiferous system by a sylleibid or a leuconoid organization, and a concomitant replacement of the choanoskeleton of the tubes with a scattered one. Nonetheless, traces of the original radial organization are clearly preserved in the subatrial skeleton.

Several authors have considered *Leuconia* Grant, 1841 as a senior synonym of *Leucandra*. As shown by Vosmaer (1887) and Dendy (1893), *Leuconia* has to be rejected, being previously used for a genus of mollusks. *Leucandra* Haeckel, 1872 being a valid synonym is the valid name of the taxon.

Leucandra has numerous representatives in all oceans.

Genus *Aphroceras* Gray, 1858

TYPE SPECIES. — *Aphroceras alcicornis* Gray, 1858 by monotypy.

DIAGNOSIS. — Grantiidae with a leuconoid organization. The cortex is supported, at least in part, by giant longitudinal diactines.

FIG. 21. — A transverse section through the wall of *Leucandra aspera* (Schmidt, 1862) (light micrograph). Abbreviations: **a**, atrium; **as**, atrial skeleton; **ch**, choanosome; **cx**, cortex. Scale bar: 230 µm.

DESCRIPTION

Aphroceras is differentiated from *Leucandra* by the presence of internal longitudinal diactines in the cortex (Fig. 22). In a previous study (Borojevic 1966), it was shown that the number of these spicules can be quite variable, ranging from a continuous dense layer to only very rare spicules, or even absence. In the latter case, it is not possible to distinguish this sponge from a typical *Leucandra*. However, we retain this genus at present, as we feel that the typical *Aphroceras* are easy to identify. Dendy & Row (1913) pointed out that *Aphroceras* probably derives directly from *Leucandra* by a secondary acquisition of longitudinal internal diactines, and not from *Ute* by a modification of the syconoid

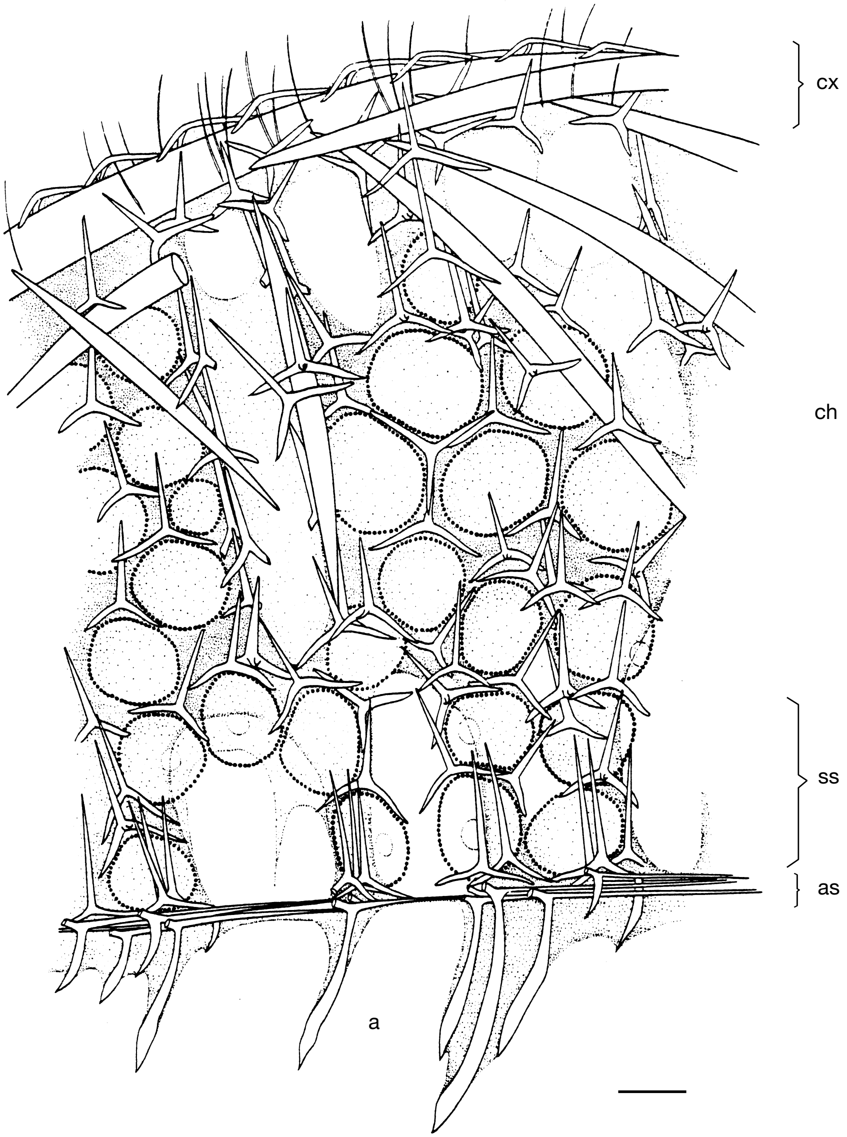

FIG. 22. — Diagram of a transverse section through the wall of *Aphroceras ensata* (Bowerbank, 1858). Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicules; **ch**, choanosome; **cx**, cortex (from Borojevic 1966). Scale bar: 100 µm.

aquiferous system into the leuconoid one. Our studies on *A. ensata* (Bowerbank, 1858) (Borojevic 1966), however, point to a close relationship between *Ute* and *Aphroceras*.

Genus *Leucandrilla* n. gen.

TYPE SPECIES. — *Leucilla wasinensis* Jenkin, 1908 BMNH 1908.9.25.59 by original designation. Not *Leuconia wasinensis* BMNH 1936.3.4.537, in Burton (1959).

DIAGNOSIS. — Grantiidae with a leuconoid organization. In addition to triactines the cortex contains tetractines, with the apical actines turned into the choanoderm. The articulate choanoskeleton is supported by subatrial triactine spicules, and numerous rows of choanosomal triactines and/or tetractines, with apical actines of cortical tetractines in the distal region.

DESCRIPTION

Leucandrilla is differentiated from *Leucandra* by the presence of tetractines in the cortical skeleton (Fig. 23). Like *Aphroceras*, which is distinguished from *Leucandra* by the presence of cortical diactines, the separation between *Leucandrilla* and *Leucandra* is not clear-cut. Dendy (1913), Dendy & Row (1913) and Borojevic & Boury-Esnault (1987) have already pointed out that some of the sponges with cortical tetractines that had been classified among Amphoriscidae are not very different from a typical *Leucandra*, but are quite distinct from *Leucilla,* and should consequently be classified in the Grantiidae. In particular they have a complete articulate choanoskeleton, reminiscent of the grantiid organization, which is absent in Amphoriscidae. While Dendy (1913) proposed that these sponges should be included in *Leucandra,* we now propose to isolate them in a separate genus in the family Grantiidae, analogous with the recognized separation of *Aphroceras*. It should be noted that we consider the cortical tetractines in this genus to be a secondary character, corresponding to a modification of normal cortical triactines, while cortical tetractines of the family Amphoriscidae are a primary character, marking an independent evolutionary line.

In addition to *L. wasinensis* (Jenkin, 1908b), which we propose to be the type species of the genus *Leucandrilla*, other sponges that had been classified in the genus *Leucandra,* such as *L. intermedia* (Row, 1909) and *L. lanceolata* (Row & Hôzawa, 1931), also belong to this genus.

FIG. 23. — *Leucandrilla* organization. Section made on the type specimen from Jenkin (1908b) (BMNH 1908.9.25.59). The cortex contains tetractines (**t**), with the apical actines turned into the choanoderm. Scale bar: 150 µm.

Genus *Leucettaga* Haeckel, 1872

TYPE SPECIES. — *Leucetta* (*Leucettaga*) *loculifera* Haeckel, 1872 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Grantiidae (?) with a leuconoid organization. The skeleton is composed of only triactines, arranged without apparent order in the cortex and in the choanosome. The atrium is crossed by numerous septa, which possess a special skeleton containing minute triactines.

DESCRIPTION

Dendy & Row (1913) retained the genus *Leucettaga* with a single species, *Leucetta* (*Leucettaga*) *loculifera* Haeckel, 1872 for the sponge described as one of the subspecies of *L. pandora* Haeckel, 1872, based on the presence of spicular tracts in the atrium whose skeleton is quite different from that of the sponge wall. Sponges described by Haeckel (1872) under *L. pandora* are quite heterogeneous, containing the most divergent forms of spicules. The drawing representing the sponge wall organization (Haeckel 1872: table 22, 3b and c) shows quite an unusual structure, and is difficult to interpret. We have considered the presence of atrial tracts that have a specific skeleton as a distinctive character for the genus *Sycandra*, and consequently we retain the genus *Leucettaga* in the scope proposed by Dendy & Row (1913). However, this sponge is so incompletely described that it is quite doubtful whether it belongs to the family Grantiidae, in which a skeleton composed of only triactines is quite unusual. The precise classification of this genus will only be possible after the examination of new specimens.

Family SYCANTHIDAE Lendenfeld, 1891

TYPE GENUS. — *Sycantha* Lendenfeld, 1891 by original designation.

DIAGNOSIS. — Leucosoleniida with an irregular syconoid organization, and the skeleton primarily supported by triactine spicules, with occasionally diactines in the distal cones. The large central atrium bears numerous short radial tubes lined by choanoderm. Radial tubes are grouped and fused proximally, each group communicating through a wide opening with the atrial cavity. The distal free or coalescent cones are intercalated by large inhalant spaces, which often reach the external surface of the atrial skeleton. When coalescent, distal cones can have tangential triactines, but there is no continuous cortex covering the choanosome and delimiting the inhalant cavities externally.

DESCRIPTION

We propose to include a small group of Leucosoleniida, which are derived from sponges with a sycettid type of organization and have a particular type of growth, in the family Sycanthidae, in a similar scope to the subfamily Sycanthinae proposed by Lendenfeld (1891). In these sponges, a thin wall surrounds a large atrial cavity that has numerous short radial tubes, which are not regularly distributed on the central atrium but form groups which communicate with the central atrial cavity by a large opening. Distally, the grouped radial tubes bear individual cones (e.g. *Sycantha*), which may become coalescent and protected by tangential spicules similar to those present in the radial tubes (e.g. *Dermatreton*). Despite the presence of these spicules, a continuous cortex is not formed, but rather a loose cortical network perforated by large openings of the inhalant cavities covers the distal regions of the radial tubes. The inhalant spaces left between the groups of radial tubes are quite large, and can reach the external face of the atrial wall, giving the external side of the sponge a honeycombed appearance. Lendenfeld (1891) observed that the radial tubes communicate among themselves in the proximal region, and that the water flow passes from one tube to another through pores, before reaching the atrial cavity. Dendy (1892b), and subsequently Jenkin (1908a) who had the opportunity to examine the type specimen described by Lendenfeld (1891), refuted this interpretation. Both Jenkin (1908a) and Dendy & Row (1913) considered *Sycantha tenella* Lendenfeld, 1891 as an aberrant species of *Sycon*. However, having observed sponges with a similar type of growth in the National Antarctic Expedition collections, Jenkin (1908a) proposed the genera *Tenthrenodes*, *Hypodictyon* and *Dermatreton* for sponges with chambers that are fused in the proximal region, in an almost identical manner to that in the genus *Sycantha* (Dendy & Row, 1913). We thus consider that *Tenthrenodes* and *Hypodictyon* are synonyms of *Sycantha,* while we retain the genus *Dermatreton* for sponges with linked choanocyte chambers that have developed an external tangential meshwork that is supported by tangential spicules, corresponding topologically to a cortex, but differing from it by the fact that it does not delimit an inhalant aquiferous system externally.

Genus *Sycantha* Lendenfeld, 1891

TYPE SPECIES. — *Sycantha tenella* Lendenfeld, 1891 by monotypy.

DIAGNOSIS. — Sycanthidae that have fused radial tubes with free distal cones decorated by diactine spicules.

DESCRIPTION

Only Lendenfeld (1891) observed *Sycantha tenella* from a specimen collected in the northern part of the Adriatic Sea, and he gave quite a detailed description of this species. *Tenthrenodes antarcticum* (Jenkin, 1908) is similar to pedunculate small *Sycon* species; the description of the linked type of radial tubes is not fully convincing, and following Dendy & Row (1913) we propose to keep it in the genus *Sycon.* As pointed out by Dendy & Row (1913), the sponge described as *Tenthrenodes scotti* Jenkin, 1908 has tangential spicules at the distal parts of the radial tubes. This species has the organization typical of the Sycanthidae and belongs to the genus *Dermatreton* as we understand it now. Sycantha (*Hypodictyon*) *longstaffi* (Jenkin, 1908) is apparently one of the typical representatives of the genus. As discussed under the family Staurorrhaphidae, the presence of the subatrial spicules with a lone centrally directed apical actine, is common in many Leucosoleniida, and does not merit the separation of the genus *Hypodictyon* from *Sycantha.*

Genus *Dermatreton* Jenkin, 1908

TYPE SPECIES. — *Dermatreton hodgsoni* Jenkin, 1908 by subsequent designation (this work).

DIAGNOSIS. — Sycanthidae with coalescent radial tubes whose distal parts are supported by tangential triactines that form a loose meshwork perforated by large inhalant cavities.

DESCRIPTION

We use the genus *Dermatreton* in the manner proposed by Jenkin (1908a). The loose cortex, which covers the distal parts of fused radial tubes, is in the form of a meshwork with broad openings formed by the inhalant spaces. As such it cannot give sufficient mechanical rigidity to the sponge, and consequently the atrial skeleton is thickened and rigid. Jenkin (1908a) has not designated the type species of the genus. Among the originally included species we designate *D. hodgsoni* as the type species. Similar morphology is observed in *Dermatreton* (*Tenthrenodes*) *scotti* (Fig. 24). The description and illustrations of *Dermatreton chartaceum* suggest that it should be included in the genus *Breitfussia.*

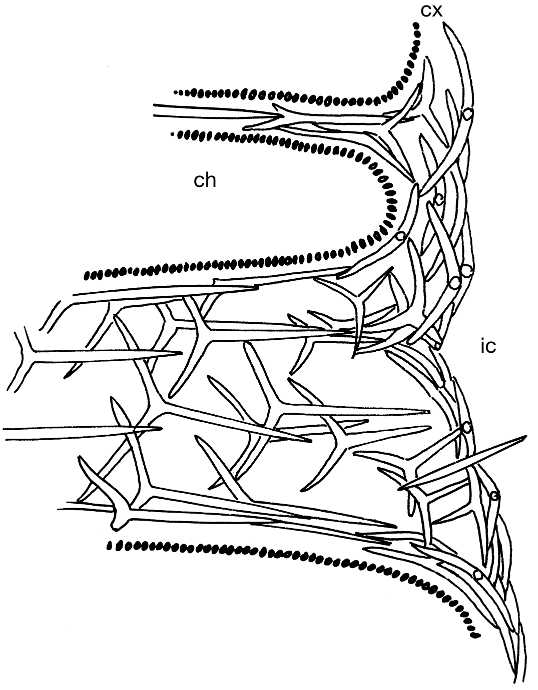

FIG. 24. — Diagram of the *Dermatreton* type of sponge wall organization. Abbreviations: **ch**, choanoderm; **ic**, inhalant cavities; **cx**, cortex.

Family JENKINIDAE n. fam.

TYPE GENUS. — *Jenkina* Brøndsted, 1931 by original designation.

DIAGNOSIS. — Leucosoleniida with a syconoid, sylleibid or leuconoid organization. The thin wall surrounding the large atrial cavity is supported by tangential atrial and cortical skeletons, and essentially an inarticulate choanoskeleton consisting of unpaired actines of the subatrial triactines and/or tetractines, and occasionally with small radial diactines. The proximal part of the large radial diactines that protrude from the external surface, or the tangential triactines scattered irregularly in the cortex, may also form the choanoderm. Large cortical tetractines or subcortical pseudosagittal triactines are not present.

DESCRIPTION

We propose the family Jenkinidae for a group of sponges characterized by an inarticulate choanoskeleton (Fig. 25). Dendy & Row (1913) considered this character not to be relevant at the generic level, and only Brøndsted (1931) proposed separating the leuconoid sponges with an inarticulate skeleton into the genus *Jenkina*. However, a primary inarticulate type of choanoskeleton is a characteristic of the family Amphoriscidae, in which it is always associated with the presence of large cortical tetractines (Borojevic & Boury-Esnault 1987). Dendy (1913) and Dendy & Row (1913) underlined the difference between the sponges of the genus *Leucilla* that have an inarticulate type of choanoskeleton and which derive from *Amphoriscus*, and those with an articulate skeleton, by transferring the former group to the genus

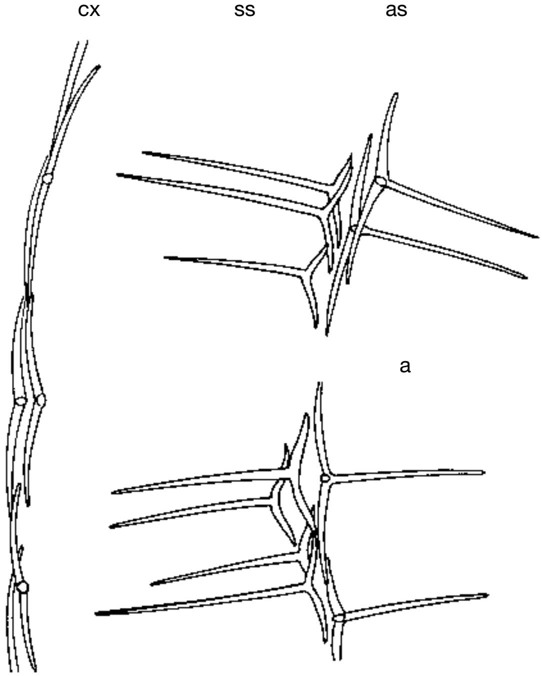

FIG. 25. — Diagram of the Jenkinidae-type of skeleton. Abbreviations: **a**, atrium; **as**, atrial spicules; **ss**, subatrial spicules; **cx**, cortex.

Leucandra (placed now into the new genus *Leucandrilla*). They thus implied that the inarticulate type of the choanoskeleton, and not the cortical tetractines, is the primary characteristic of the family Amphoriscidae. We now consider that the inarticulate type of sponge wall organization, with a thin choanoderm and well-defined atrial and cortical skeletons, is a consequence of a particular type of growth, and is not a secondary reduction of the sponge wall thickness during evolution. Consequently, sponges with this organization should be separated from those with a massive type of growth as is observed in the Grantiidae. While in the Amphoriscidae the cortical skeleton is always supported by large tetractines, in the Jenkinidae it can be thin (e.g. *Jenkina, Leucascandra*), or reinforced by large diactines or triactines (e.g. *Uteopsis* and *Anamixilla*, respectively). It should be emphasized that young specimens of Grantiidae, and the suboscular region of adult Grantiidae in which the sponge grows longitudinally, can have an inarticulate skeleton that becomes an articulate one when sponge is fully grown. Conversely, the Jenkinidae are characterized by an inarticulate skeleton in the fully-grown sponges. As mentioned previously the growth of these long tubular sponges into a large branched cormus such as observed in *Leucascandra, Anamixilla* and *Uteopsis* is a consequence of the restriction of their radial growth, and this is unique in the Leucosoleniida.

Genus *Breitfussia* n. gen.

TYPE SPECIES. — *Ebnerella schulzei* Breitfuss, 1896.

DIAGNOSIS. — Jenkinidae with a simple tubular body and syconoid organization. The choanoskeleton is reduced to the unpaired actines of the subatrial triactines, and occasionally contains the proximal part of radial diactines.

DESCRIPTION

In the system proposed by Lendenfeld (1891), and followed by Breitfuss (1896), the genus *Ebnerella* of the subfamily Amphoriscinae was characterized by an inarticulate skeleton, containing diactines, triactines and/or tetractines. The species included by Lendenfeld (1891) in this genus belongs now to the genus *Amphoriscus* and *Ebnerella* is thus a junior synonym of *Amphoriscus*. Among the species described by Breitfuss (1896) in *Ebnerella*, *E. kuekenthali* belongs to the family Heteropiidae (*Sycettusa*), but a new name is needed for *E. schulzei*. In addition, species with an inarticulate choanoskeleton, described under the genus *Grantia* or *Dermatreton*, should be included in the new genus *Breitfussia* as now defined, such as *Breitfussia* (*Grantia*) *vitiosa* (Brøndsted, 1931) and *Breitfussia* (*Dermatreton*) *chartacea* (Jenkin, 1908). *Breitfussia* is known only from cold Arctic or Antarctic waters.

Genus *Jenkina* Brøndsted, 1931

TYPE SPECIES. — *Leucandra hiberna* Jenkin, 1908 by subsequent designation (Laubenfels 1936).

DIAGNOSIS. — Jenkinidae with a simple tubular body and a sylleibid or leuconoid organization of the aquiferous system. The choanoskeleton is composed of the unpaired actine of subatrial spicules and, occasionally, the proximal part of radial diactines that cross the sponge wall.

FIG. 26. — Specimen of *Leucascandra caveolata* Borojevic & Klautau from New Caledonia (Poindimié, 30 m) (Photo P. Laboute) (from Borojevic & Klautau 2000). Scale bar: 1.4 cm.

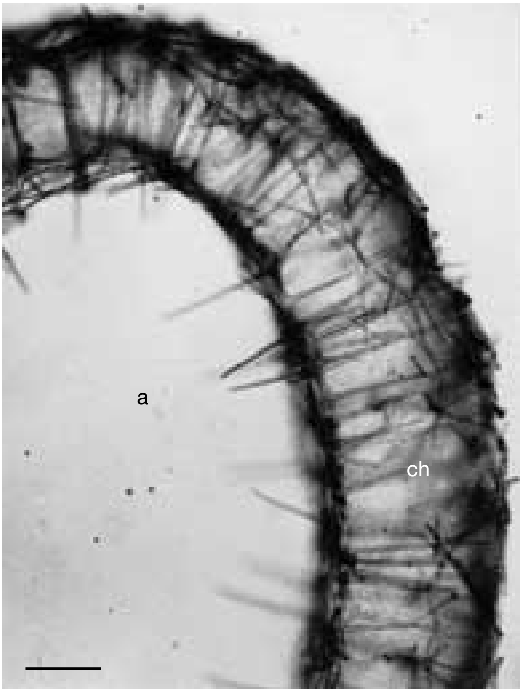

FIG. 27. — *Leucascandra* organization. Transverse section through the sponge wall; the choanoskeleton is composed of only subatrial triactines and the atrial skeleton contains triactines and tetractines. Abbreviations: **a**, atrial skeleton; **ch**, choanoskeleton. Scale bar: 40 µm.

DESCRIPTION

Brøndsted (1931) proposed the genus *Jenkina* for a group of sponges described by Jenkin (1908a) and by himself from Antarctica. These sponges are well-characterized by an inarticulate choanoskeleton that contains unpaired actines of subatrial spicules and occasionally radial diactines, which cross the thin choanoderm and protrude from the external surface of the sponge. The thin choanosome frequently lacks a typical leuconoid aquiferous system, and some doubt remains about the division between the genera *Breitfussia* and *Jenkina.*

Genus *Leucascandra* Borojevic & Klautau, 2000

TYPE SPECIES. — *Leucascandra caveolata* Borojevic & Klautau, 2000 by monotypy.

DIAGNOSIS. — Jenkinidae with a complex cormus composed of copiously branched and anastomosed tubes. Each tube has a thin wall with a rather irregular alveolar type of leuconoid aquiferous system, and an inarticulate choanoskeleton that is supported only by unpaired actines of subatrial triactines. Both cortical and atrial skeletons consists of a thin layer of tangential triactines and/or tetractines.

DESCRIPTION

In the Clathrinida, tubular sponges frequently form a large cormus composed of ramified and anastomosed tubes (e.g. *Clathrina, Ascandra, Ascaltis, Leucascus, Leucaltis*). In the Leucosoleniida, this growth form is quite rare. While the Jenkinidae from cold Antarctic or Arctic waters grow as small solitary tubes, those from warmer waters can form large complex cormi. The genus *Leucascandra* is thus characterized by a tendency to form a large cormus composed of extensively branched and anastomosed tubes (Fig. 26), an inarticulate choanoskeleton, and a thin cortex (Fig. 27).

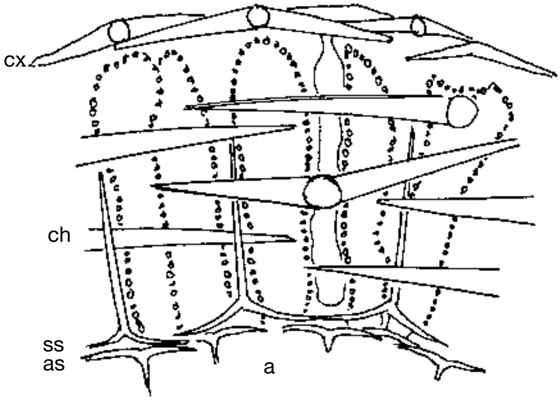

FIG. 28. — Diagram of a transverse section through the wall of *Anamixilla torresi* Poléjaeff, 1883. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicule; **ch**, choanosome; **cx**, cortex (from Poléjaeff 1883).

Genus *Anamixilla* Poléjaeff, 1883

TYPE SPECIES. — *Anamixilla torresi* Poléjaeff, 1883 by monotypy.

DIAGNOSIS. — Jenkinidae with a syconoid organization. The thick cortex is supported by many layers of triactines. The choanoskeleton is composed of the unpaired actine of the subatrial spicules, and giant tangential triactines similar to those in the cortex but lying scattered in the choanosome.

DESCRIPTION

In *Anamixilla*, large triactines form a thick cortex and apparently invade the choanosome (Fig. 28). A similar phenomenon is observed in the Lelapiidae, in which the reduction of the classical choanoskeleton is concomitant with its partial substitution by large cortical diactines. Large diactines have been observed in the oscular region of *A. irregularis* Burton, 1930. We have examined the specimen deposited in the British Museum (BMNH 1929.8.30.6) and found that it does not belong to the genus *Anamixilla*.

Genus *Polejaevia* n. gen.

TYPE SPECIES. — *Polejna telum* Lendenfeld, 1891 by monotypy.

DIAGNOSIS. — Jenkinidae with a sylleibid organization. The cortex is supported by a layer of large tangential triactines. The choanoskeleton is composed of the unpaired actines of the subatrial triactines, and of rare small scattered triactines.

DESCRIPTION

In the system proposed by Lendenfeld (1891), the genus *Polejna* Lendenfeld, 1885 was used for sylleibid sponges with triactines and tetractines. The type species of *Polejna*, described originally as *Leucilla uter* Poléjaeff, 1884 is in fact a good species of *Leucilla* (Borojevic & Boury-Esnault 1987). *Polejna* is thus a junior synonym of *Leucilla*. Subsequently, Lendenfeld (1891) described in Adriatic a new species in the genus, *Polejna telum* Lendenfeld, 1891, that we consider to be different from Amphoriscidae and place now in the family Jenkinidae. A new name is thus required for the Jenkinidae with a sylleibid organization and triactines and tetractines such as *Polejna telum*, for which we propose *Polejaevia*.

The position of *Polejaevia* in the family Jenkinidae is somewhat dubious, since small choanosomal triactines have been described in it and are represented in the illustration of the type species, distinguishing it from typical Jenkinidae. The size and distribution of the triactines is quite unusual, and as they are not reminiscent of the articulate choanoskeleton of the tubes of the Grantiidae, classification of *P. telum* in the genus *Leucandra* is impossible. Lendenfeld (1891) suggested that the triactines might be young cortical triactines. Secondary spicules may be found in the choanosome in the absence of any other skeleton, as seen in the genus *Leucettusa* Haeckel, 1872 (Borojevic *et al.* 1990). On the other hand, the organization of *Polejaevia* can be understood to be quite similar to *Anamixilla*: while in the former the additional triactines in the choanosome are new spicules, in *Anamixilla* the cortical spicules apparently invade the choanoskeleton. We propose that the genus should be maintained in the Jenkinidae until new specimens are examined.

The description of *Leucandra mawsoni* Dendy, 1918 suggests that it might belong to *Polejaevia*. We have examined the specimens deposited in the British Museum (BMNH 20.12.9.95) and found that this species is a calcinean sponge, belonging to the genus *Leucascus*. Hence *Polejaevia telum* is the only known species belonging to this genus.

Genus *Uteopsis* Dendy & Row, 1913

TYPE SPECIES. — *Ute argentea* Poléjaeff, 1883 by monotypy.

DIAGNOSIS. — Jenkinidae with a syconoid organization. The cortex is thick and is supported by giant longitudinal diactines. The choanoskeleton is reduced to the unpaired actines of the subatrial spicules and smaller distal radial diactines.

DESCRIPTION

Uteopsis is well-described and illustrated by Poléjaeff (1883). It is characterized by an inarticulate choanoskeleton and a thick cortex composed of giant longitudinal diactines and triactines.

Family HETEROPIIDAE Dendy, 1892

TYPE GENUS. — *Heteropia* Carter, 1886 by original designation.

DIAGNOSIS. — Leucosoleniida with a syconoid or leuconoid organization. The choanoskeleton is composed of a proximal layer of subatrial triactines and a distinct distal layer of pseudosagittal triactines and/or pseudosagittal tetractines, often separated by an intermediate layer that is supported by several rows of triactines and/or tetractines. The atrial skeleton is well-developed.

DESCRIPTION

The family Heteropiidae is characterized by the presence of a layer of subcortical pseudosagittal spicules. At a first glance, these spicules may seem to be sagittal triactines with the paired actines adjacent to the cortex, and the unpaired actine turned inwards in a position symmetrical to that of the subatrial spicules. However, as indicated by Poléjaeff (1883) and Dendy & Row (1913), both the length and the form of the paired actines in these spicules are unequal. The longer paired actine is perpendicular to the cortex, while the shorter one as well as the unpaired actine are adjacent to the cortex (Fig. 29). This position is clearly observed for the distal triactines of the radial tubes in sycon-like sponges that we now place in the genus *Syconessa*. This indicates that the formation of pseudosagittal spicules precedes the formation of a cortex and appears early in the evolution of the Heteropiidae, immediately after the acquisition of the sycettid type of organization. The evolutionary pathway of the Heteropiidae, well-represented by the genus *Syconessa,* diverges from sponges that are very similar to *Sycon.* In the type species *Syconessa syconiformis* (Borojevic, 1967a), the choanoskeleton is inarticulate, or has only a few spicules in the proximal part of the choanoskeleton. The corticalization of such a sponge can lead both to the genus

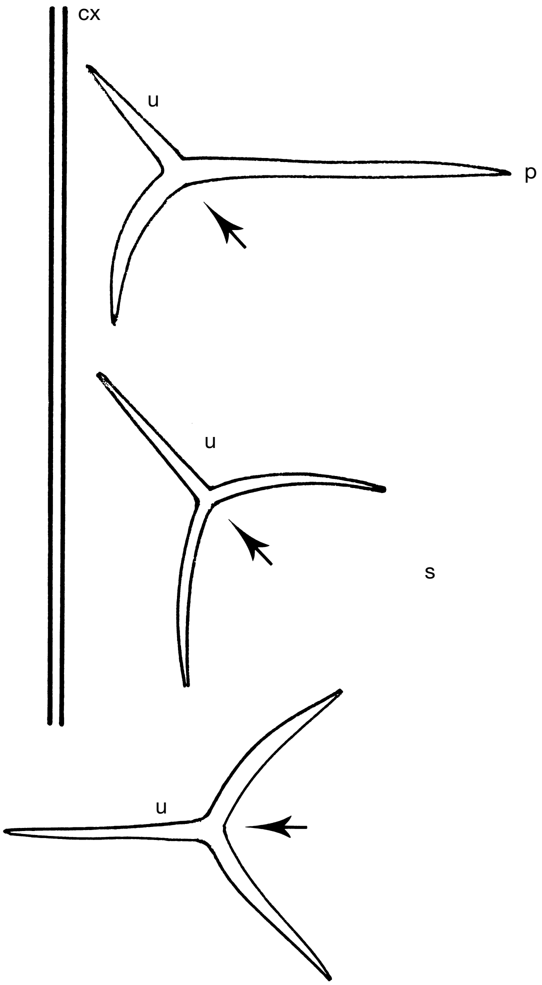

FIG. 29. — Diagram of one parasagittal (**p**) and two sagittal (**s**) spicules in Heteropiidae. The arrow indicates the unpaired angle, and **u** indicates the unpaired actine. The double line represents the cortex (**cx**). Note that the two paired actines of the parasagittal spicules are of quite different sizes, and they are always in a subcortical position with the longer paired actine directed inwards.

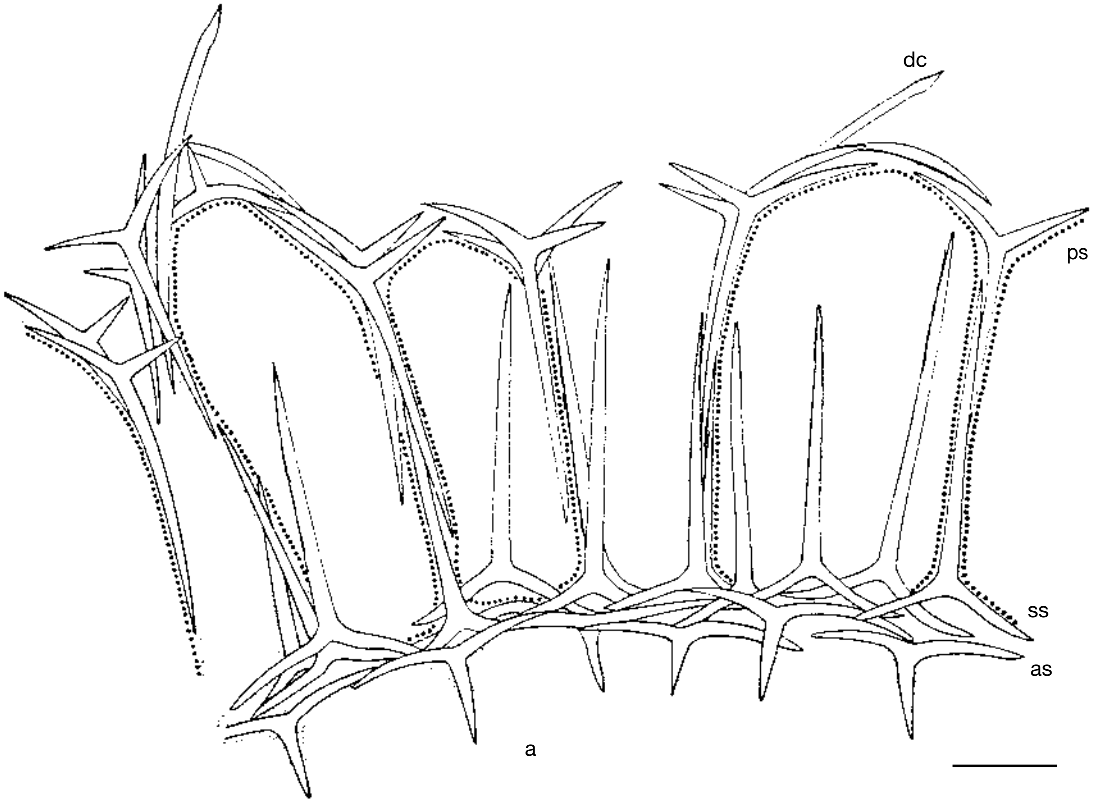

FIG. 30. — Diagram of a transverse section through the wall of *Syconessa syconiformis* (Borojevic, 1967a). Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicule; **ps**, parasagittal spicules; **dc**, distal cones (from Borojevic 1967b). Scale bar: 50 µm.

Sycettusa, which is characterized by a thin body wall with the choanosome devoid of its own skeleton, and to *Grantessa*, in which the choanoskeleton is articulate. It should be noted that several species of *Grantessa* have a very thin and/or poorly defined cortex, and the distal cones of the radial tubes are still decorated by tufts of diactines (e.g. *Grantessa ramosa* Haeckel, 1872), clearly showing their relationships to sponges with a sycon-like organization.

Corticalization has apparently arisen several times in the Leucosoleniida. In the family Heteropiidae, corticalization associated with the maintenance of the choanoskeleton of the tubes that is reduced to subatrial and subcortical spicules has given rise to the genus *Sycettusa*, whilst the corticalization associated with the thickening of the choanosome has produced *Grantessa*. The subsequent transition to the leuconoid type of organization is seen in the genus *Vosmaeropsis*. Similar progression is observed among the Leucosoleniida that lack pseudosagittal spicules, in which the first route has given rise to the Jenkinidae and the Amphoriscidae, and the second the Grantiidae.

The family Heteropiidae contains a series of genera that are analogous to those of the family Grantiidae, the sole difference being the presence of subcortical pseudosagittal spicules. In any calcaronean sponge with a strong cortex, some subcortical spicules may be in the position and have the shape of pseudosagittal spicules, due to the restriction of their growth by the rigidity of the cortical skeleton. They should not be interpreted as an indication that the sponge belongs to the family Heteropiidae (see discussion on *Amphiute paulini* Hanitsch, 1894 *in* Borojevic 1965: 665-670). Consequently, the regular presence of a distinct layer of subcortical pseudosagittal spicules resembling the continuous layer composed exclusively of these spicules found in *Grantessa*, should be interpreted as an indication that the sponge belongs to the Heteropiidae, whilst isolated pseudosagittal spicules should be understood to be the secondary modification of subcortical spicules that is found in some representatives of the Grantiidae. We are aware that this distinction is often unclear, and a search for complementary cytological or biochemical criteria should be undertaken to identify those features that could distinguish the Grantiidae from the Heteropiidae, to allow the correct classification of some of the problematic cases.

Genus *Syconessa* n. gen.

TYPE SPECIES. — *Grantessa syconiformis* Borojevic, 1967 by original designation.

DIAGNOSIS. — Heteropiidae with short radial tubes supported by a skeleton composed of a proximal row of subatrial triactines and distal pseudosagittal triactines, with occasional tube spicules. The paired actines of proximal subatrial spicules are adjacent to the atrial skeleton, while the unpaired actine is in the wall of the radial tube. The shorter paired actine and the unpaired actine of the distal pseudosagittal spicules support the distal cones, while the longer paired actine is inside the wall of the radial tube.

DESCRIPTION

As discussed by Dendy & Row (1913) and by Borojevic (1965, 1967a), the pseudosagittal spicules are derived from the spicules of the distal tubes rather than from the cortical spicules. In *Syconessa*, distinct pseudosagittal spicules can be seen at the distal part of the radial choanocyte chambers, where their unpaired actine and the shorter paired actine participate in the skeleton of the distal cones, while the centripetal longer paired actine of pseudosagittal triactines support the external part of the radial tubes (Fig. 30). This genus is the starting point of the evolutionary line of the Heteropiidae. We now propose the new genus *Syconessa* for sponges with a syconoid type of organization and a layer of pseudosagittal spicules in the distal part of their choanocyte chambers, but without a cortex. Dendy & Row (1913) pointed out that *Sycon ensiferum* Dendy, 1892 also has triactines that have a typical form of pseudosagittal spicules in the distal part of radial tubes, rendering the species almost indistinguishable from *Grantessa*. We have examined the slides of this species in the British Museum (BMNH 93.6.9.6a, 25.11.1.1746/47), and found that indeed this sponge belongs to the genus *Sycon*, despite the occasional presence of spicules of the pseudosagittal type.

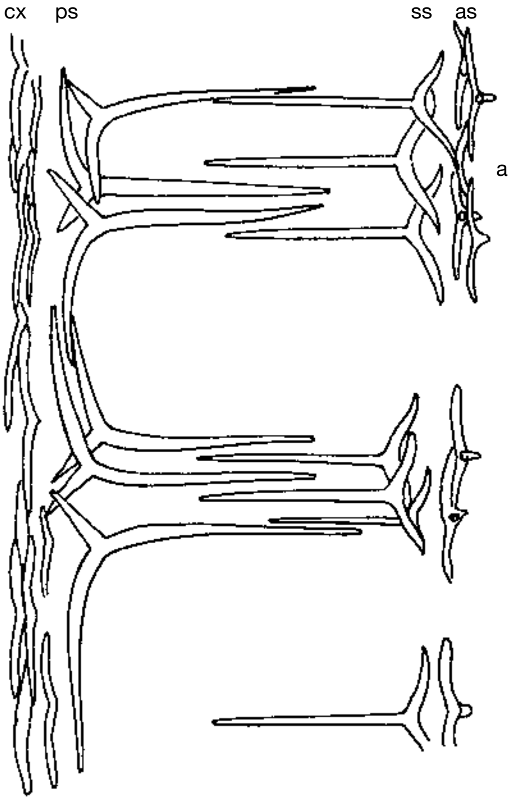

FIG. 31. — Diagram of the *Sycettusa* inarticulate skeleton. Abbreviations: **a**, atrium; **as**, atrial spicules; **ss**, subatrial spicules; **ps**, parasagittal subcortical spicules; **cx**, cortex.

Genus *Sycettusa* Haeckel, 1872 *emend.*

TYPE SPECIES. — *Sycetta* (*Sycettusa*) *stauridia* Haeckel, 1872 by monotypy.

DIAGNOSIS. — Heteropiidae with a syconoid organization. Atrial and cortical skeletons are formed by tangential triactines and/or tetractines. The choanoskeleton is inarticulate, and is composed of unpaired actines of the subatrial triactines, and of centripetal actines of the pseudosagittal subcortical triactines.

DESCRIPTION

We propose to divide the genus *Grantessa* (as defined by Dendy & Row 1913) into two groups: one with an inarticulate choanoskeleton, to be called *Sycettusa,* and the other with an articulate choanoskeleton, to be called *Grantessa*. As stated earlier, we consider that the former genus evolved by the corticalization of sponges with an inarticulate skeleton similar to *Syconessa syconiformis* (Borojevic, 1967), thereby maintaining this characteristic of the choanoskeleton (Fig. 31). The sponges assembled in the genus *Sycettusa* can be divided into two groups, one common in the Arctic region and the other in the Indo-Pacific. The relationship between these two groups remains to be established. The Arctic group includes *Sycettusa* (*Sycaltis*) *glacialis* (Haeckel, 1872), *S. (Ebnerella) kuekenthali* (Breitfuss, 1896), *S.* (*Ebnerella*) *lanceolata* (Breitfuss, 1898), *S. (Amphoriscus) murmanensis* (Breitfuss, 1898), *S. (Amphoriscus) thompsoni* (Lambe, 1900) and *S. (Ebnerella) nitida* (Arnesen, 1901). The Indo-Pacific group includes *S. stauridia* Haeckel, 1872, *S.* (*Sycortis*) *sycilloides* (Schuffner, 1877), *S. (Amphoriscus) poculum* (Poléjaeff, 1883), *S. (Grantessa) simplex* (Jenkin, 1908b), *S. (Grantessa) glabra* (Row, 1909) and *S. (Grantessa) hastifera* (Row, 1909).

Haeckel (1872) proposed the subgenus *Sycettusa* for the single species *S. stauridia* from the Red Sea, which is a typical syconoid Heteropiidae with an inarticulate choanoskeleton, and we retain this genus and species name in the same combination.

Genus *Grantilla* Row, 1909

TYPE SPECIES. — *Grantilla quadriradiata* Row, 1909 by monotypy.

DIAGNOSIS. — Heteropiidae with a syconoid organization. The skeleton of the tubes is inarticulate, composed of subatrial triactines, and subcortical pseudosagittal triactines and tetractines.

DESCRIPTION

The vast majority of Heteropiidae have only pseudosagittal triactines in the subcortical skeleton. The genus *Grantilla* has been proposed for the single species *G. quadriradiata* Row, 1909, with pseudosagittal tetractines. Other morphological characteristics are quite similar to *Sycettusa*.

Genus *Grantessa* Lendenfeld, 1885

TYPE SPECIES. — *Grantessa sacca* Lendenfeld, 1885 by monotypy.

DIAGNOSIS. — Heteropiidae with a syconoid organization and an articulate choanoskeleton. A thin cortex is formed by triactines but lacks longitudinal large diactines. The distal part of the radial tubes is frequently decorated by tufts of radially arranged diactines, indicating a close relationship to the genus *Syconessa*.

DESCRIPTION

We include in the genus *Grantessa* s.s. the syconoid Heteropiidae with articulate choanoskeletons (Fig. 32). We consider that they are derived from sponges similar to *Syconessa,* in which the increase of radial tubes had generated the articulate choanoskeleton. *Grantessa* are common in warm seas, and often grow as large arborescent or bushy cormus.

Genus *Heteropia* Carter, 1886

TYPE SPECIES. — *Aphroceras ramosa* Carter, 1886 by monotypy.

DIAGNOSIS. — Heteropiidae with a syconoid organization, an articulate choanoskeleton, and where the cortical skeleton consists of longitudinal large diactines, with occasionally tangential triactines and perpendicular small diactines.

DESCRIPTION

Heteropia in the family Heteropiidae corresponds to the same grade of skeletal complexity than *Ute* in the family Grantiidae.

Genus *Paraheteropia* Borojevic, 1965

TYPE SPECIES. — *Amphiute ijimai* Hôzawa, 1916 by monotypy.

DIAGNOSIS. — Heteropiidae with a syconoid organization, an articulate choanoskeleton, and with both cortical and atrial skeletons containing longitudinal diactines.

Description

Paraheteropia in the family Heteropiidae corresponds to the same grade of skeletal complexity than *Amphiute* in the family Grantiidae.

Genus *Vosmaeropsis* Dendy, 1892

TYPE SPECIES. — *Heteropia macera* Carter, 1886 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Heteropiidae with a sylleibid or leuconoid organization. The choanoskeleton is composed of proximal subatrial triactine spicules and an irregular layer of scattered triactines and tetractines.

Description

The genus *Vosmaeropsis* most often has a typical leuconoid grade of organization, and corresponds closely to the genus *Leucandra* in the family Grantiidae. When the sponge wall is thick, the skeleton has a tendency to be irregular, with the progressive loss of traces of the radial organization. While the layer of subatrial triactines or tetractines in general is well-preserved, and the proximal part of the choanoskeleton is supported exclusively by unpaired actines of these spicules, the distal layer of the choanoskeleton, that is supported by centripetal rays of pseudosagittal subcortical spicules, becomes blurred by the invasion by other choanosomal spicules. Alternatively, the pseudosagittal subcortical spicules and the facing subatrial spicules can retain their original relationship, and the thickening of the wall can be obtained by insertion of new spicules between the subatrial spicules and the atrial skeleton, such as observed in *Vosmaeropsis hozawai* Borojevic & Klautau, 2000. This is similar to the secondary thickening of the sponge wall in the genus *Paraleucilla*. In these cases, the distinction between *Vosmaeropsis* and *Leucandra* is very difficult.

Family AMPHORISCIDAE Dendy, 1892

TYPE GENUS. — *Amphoriscus* Haeckel, 1870 by original designation.

DIAGNOSIS. — Leucosoleniida with a syconoid, sylleibid or leuconoid organization, and a distinct cortex supported by tangential tetractines whose centripetal apical actines cross the outer part of or the whole of the choanosome. Tangential triactines and small tetractines may be also present in the cortex. The choanoskeleton typically is inarticulate, composed of the apical actines of cortical tetractines and the unpaired actines of subatrial spicules. In species with a thick wall scattered triactines and/or tetractines may be also present, either among the spicules of the inarticulate choanoskeleton, or forming a distinct subatrial layer. An atrial skeleton is always present.

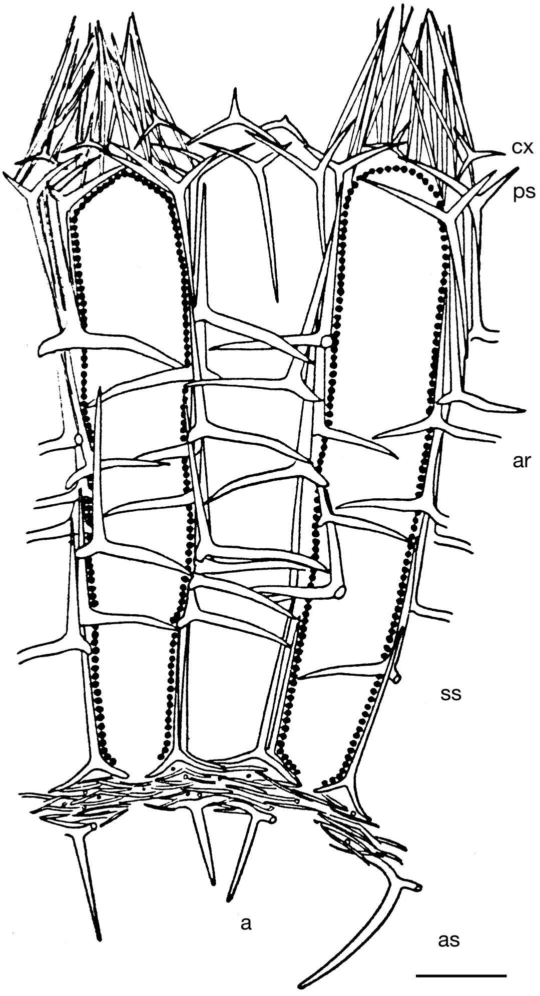

FIG. 32. — Diagram of a transverse section through the wall of *Grantessa ramosa* (Haeckel, 1872). Abbreviations: **a**, atrium; **as**, atrial skeleton; **ar**, articulate choanosomal skeleton; **ss**, subatrial spicule; **ps**, parasagittal spicules; **cx**, cortex (from Borojevic 1967a). Scale bar: 100 µm.

Description

The family Amphoriscidae is well-characterized by a distinct subcortical layer exclusively support-

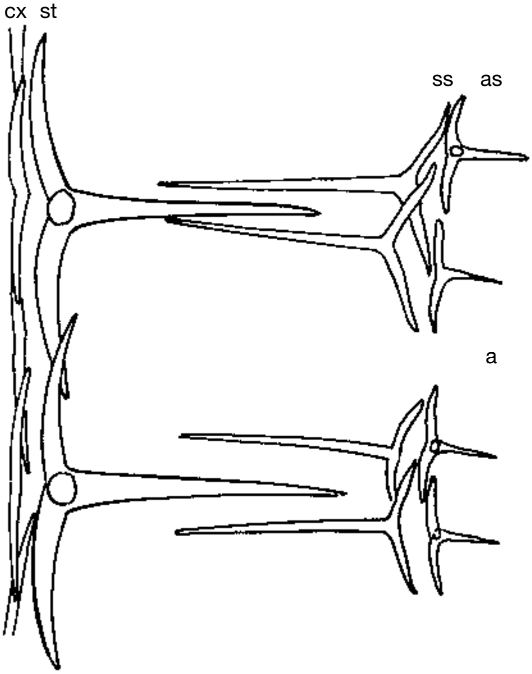

FIG. 33. — Diagram of the Amphoriscidae type of inarticulate choanoskeleton (*Amphoriscus* or *Leucilla*). Abbreviations: **a**, atrium; **as**, atrial spicules; **ss**, subatrial spicules; **st**, subcortical tetractines; **cx**, cortex.

ed by the apical actines of giant cortical tetractines. In species of *Leucilla* that have a leuconoid organization and a thick wall, the choanoskeleton is disorganized, unlike the simpler syconoid genus *Amphoriscus* (Fig. 33). We understand this to indicate that the simple inarticulate choanoskeleton is a primitive condition. This is an argument against the derivation of the Amphoriscidae from the typical Grantiidae, by reduction of the choanoskeleton and the secondary presence of the apical actines of cortical triactines. The regular presence of subatrial triactines in the Amphoriscidae clearly indicates that they derive from a *Sycetta* type of organization through the precocious development of a cortical skeleton reinforced by giant tetractines. Since the articulate skeleton of the tubes, typical of adult specimens of *Sycon* and *Grantia,* is not found in the Amphoriscidae, the origin of this family lies closer to the Jenkinidae than to Grantiidae. However, it is impossible to decide whether these two families have a common origin or have evolved independently.

In most Leucosoleniida, the thickening of the choanosome is associated with the growth of new spicules in the central part of the choanoskeleton, and with the increasing distance between the cortical skeleton on one side, and the atrial and subatrial skeletons on the other (e.g. *Grantessa ramosa*, Fig. 32). In the Amphoriscidae, the sponge wall can thicken through the addition of a new layer between the atrial and subatrial skeletons, and the subatrial and cortical skeletons strictly maintain their close primary relationship (Fig. 33). The invasion of the choanoskeleton by spicules derived from the inner atrial skeleton in *Paraleucilla* is analogous to the invasion of the choanoskeleton from the outer cortical skeleton in the Jenkinidae (e.g. *Anamixilla* and *Uteopsis*). In both families, the primary inarticulate choanoskeleton is preserved, despite the progressive thickening of the sponge wall and the necessity to introduce new skeletal structures to support it.

Genus *Amphoriscus* Haeckel, 1870

TYPE SPECIES. — *Ute chrysalis* Schmidt, 1864 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Amphoriscidae with a syconoid organization of the aquiferous system. Scattered spicules in the choanosome are always absent.

DESCRIPTION

Amphoriscus is a well-characterized genus, and contains several species of solitary sponges with beautiful vitreous transparent walls. The genus is found in all the oceans.

Dendy & Row (1913) kept the genus *Syculmis* Haeckel, 1872 for Amphoriscidae with a root-tuft of diactines and anchoring tetractines. We had the opportunity to observe similar anchoring structures in the families Sycettidae and Jenkinidae, and we do not feel that this character calls for the creation of a special genus; we propose the inclusion of the sponge described as *Syculmis synapta* by Haeckel (1872), in the genus *Amphoriscus.*

Genus *Leucilla* Haeckel, 1872

TYPE SPECIES. — *Leucilla amphora* Haeckel, 1872 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Amphoriscidae with a sylleibid or leuconoid organization. The choanoskeleton is formed primarily by the apical actines of giant cortical triactines and the unpaired actines of subatrial triactines or tetractines. It may contain dispersed spicules, but a typical articulate choanoskeleton is always absent.

DESCRIPTION

The genus *Leucilla* is quite close to *Amphoriscus,* and most species have a sylleibid aquiferous system. The simple species of *Leucilla*, such as *L. amphora* Haeckel, 1872, always have a thin sponge wall and an inarticulate choanoskeleton, which is reduced to the apical actines of cortical tetractines and to the unpaired actines of subatrial triactines or tetractines (Fig. 34). In specimens of *Leucilla* that build a thicker wall, scattered triactines or tetractines can be found in the choanosome, but they clearly derive from the cortical or the subatrial skeleton. There is no primary choanoskeleton derived from radially arranged spicules, and *Leucilla* species have never any structures reminiscent of the articulate arrangement of the choanoskeleton.

A group of sponges that have the organization typical of *Leucandra,* has been described under the genus *Leucilla.* Tetractines are present in their cortical skeleton, but their apical actines do not represent the main support of the choanoskeleton, which is typically articulate and clearly reminiscent of a grantiid organization with many rows of choanosomal triactines. Dendy & Row (1913) placed them in the genus *Leucandra* and we now include these sponges in the genus *Leucandrilla.*

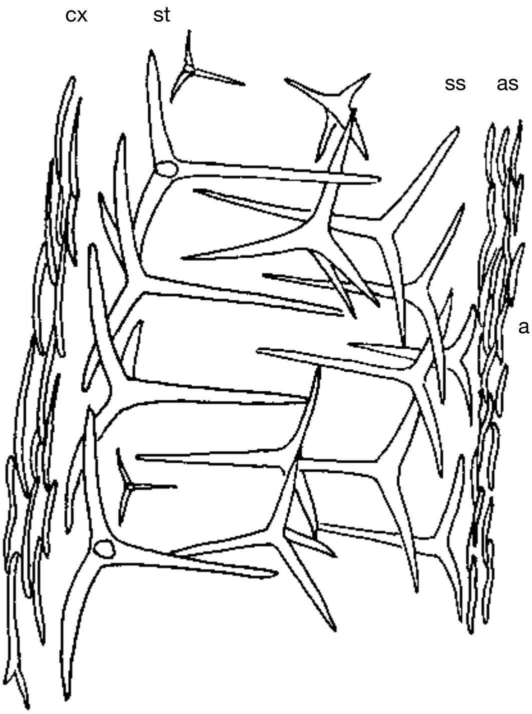

FIG. 34. — Diagram of a transverse section through the wall of *Leucilla*. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicule; **st**, subcortical tetractines; **cx**, cortex.

Genus *Paraleucilla* Dendy, 1892

TYPE SPECIES. — *Leucandra cucumis* Haeckel, 1872 by monotypy.

DIAGNOSIS. — Amphoriscidae with a leuconoid organization. The thick wall is divided into two regions. The outer region is supported by the skeleton which remains essentially inarticulate, with the apical actines of cortical tetractines pointed inwards, and a layer of triactines and/or tetractines with the unpaired actine pointed outwards. The inner region of the choanoskeleton is intercalated between the original subatrial skeleton and the atrial one, and it is supported by large triactines and/or tetractines, that are scattered in disarray, and whose form is similar to the spicules found in the outer layer of the choanoskeleton, or inside the atrial skeleton. Since the original subatrial layer still remains in the outer part of the choanosome, facing the cortical tetractines, there are no typical subatrial spicules adjacent to the atrial skeleton.

DESCRIPTION

Some leuconoid Amphoriscidae are massive sponges, with a folded, and thickened body. In these cases, the inarticulate organization is retained only in the outermost layer of the choanosome, which has a typical inarticulate skeleton consisting of the apical actines of cortical tetractines. Subatrial triactines or tetractines maintain their original position with their unpaired angle directed towards the atrium and their unpaired actine pointed towards the cortex (Fig. 35). The

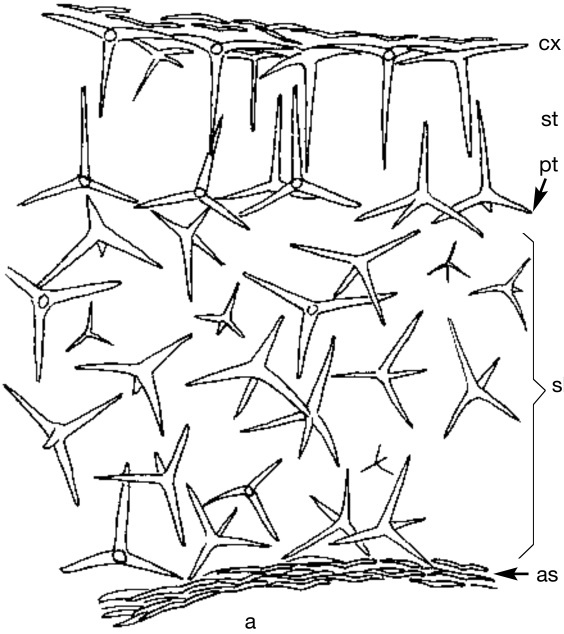

FIG. 35. — Diagram of a transverse section through the wall of *Paraleucilla*. Abbreviations: **a**, atrium; **as**, atrial skeleton; **sl**, secondary subatrial layer inserted between the atrial skeleton and the primary subatrial spicules, derived from the primary subatrial skeleton; **pt**, primary tetractines indicating the original position of the subatrial skeleton; **st**, subcortical tetractines; **cx**, cortex.

latter spicules, however, are far from the surface of the atrium or larger exhalant canals, since a thick layer supported by numerous scattered irregular triactines and/or tetractines is intercalated in between. This inner layer never has any traces of a radial structure, and is clearly a new acquisition due to the intense growth of the sponge in this region. This structure had been well-described in *Leucandra cucumis* Haeckel, 1872, but the outermost inarticulate layer was erroneously interpreted as containing only inhalant cavities. In specimens that we have observed, the outer layer contains the choanosome, although the lack of scattered spicules, that are present in the inner part of the wall gives an impression of loose cavities.

Dendy (1892b) proposed the genus *Paraleucilla* for Haeckel's species *Leucandra cucumis*. He afterwards abandoned this idea and included the species in the genus *Leucilla* (Dendy, 1893), but subsequently returned to use the genus (Dendy & Row 1913) in order to underline the particular organization of the subcortical region. After examination of the material listed below, we have found that other sponges classified in the genus *Leucilla* showed the organization typical of *Paraleucilla* in which we now classify them: *Paraleucilla* (*Leucilla*) *saccharata* Haeckel, 1872, (material studied MNHN-LBIM-C1968-681; BMNH 86.6.7.64 and 25.11.1.690a), *Paraleucilla* (*Leucilla*) *crosslandi* Row, 1909 (material studied BMNH 1954.2.24.25), *Paraleucilla* (*Leucilla*) *proteus* Dendy, 1913 (material studied BMNH 20.12.9.60a), *Paraleucilla* (*Leucilla*) *princeps* Row & Hôzawa, 1931 (material studied BMNH 25.11.1.90a).

Family STAURORRHAPHIDAE Jenkin, 1908

TYPE GENUS. — *Achramorpha* Jenkins, 1908 by original designation.

DIAGNOSIS. — Leucosoleniida with a continuous cortex covering all the choanosome. Cortical tetractines are absent. The organization of the aquiferous system is syconoid, sylleibid or leuconoid. A tangential atrial skeleton is present only in the oscular region. In the atrial cavity, only the paired actines of subatrial chiactines support the atrial surface, while the apical actine is bent and points into the atrial cavity, making its surface hispid.

DESCRIPTION

The Staurorrhaphidae have been proposed by Jenkin (1908a) to include sponges with chiactines ("cruciform" spicules), which are tetractines whose apical actine is bent so that it follows the same line as the unpaired actine, but in the opposite direction (Fig. 36). These spicules are found in the atrial wall: the paired actines are adjacent to the atrial surface, the apical actine is free in the atrial cavity giving the atrial surface a hispid appearance, and the unpaired actine lies in the wall of the radial tubes. Since the same sponges have no tangential spicules in the atrial skeleton, Jenkin (1908a) proposed that chiactines originate from the atrial tetractines. However, as pointed out by Dendy & Row (1913), chiactines have a typical subatrial origin and position. In several other genera of Leucosoleniida, subatrial tetractines are found with the apical actine curved either in the direction of the unpaired actine, thus pointing towards the distal end of the radial tube, or in the opposite direction, pointing into the atrium, such as the case of chiactines. Solely the presence of chiactines would not justify the creation of the family Staurorrhaphidae. However, in sponges included in this family the atrial skeleton is reduced to the region immediately adjacent to the osculum, and in the sponge body there are no atrial tangential tri- or tetractines. As indicated by Dendy & Row (1913), this is an unusual modification of the skeletal organization among the Leucosoleniida and justifies the separation of the two genera, *Achramorpha* and *Megapogon,* from other Leucosoleniida. Since in most sponges the atrial cavity is echinated or hispid, probably as a protection from invading organisms, in the Staurorrhaphidae the subatrial tetractines have apparently taken over this function, forming a long apical actine bent towards the atrial cavity. The family Staurorrhaphidae is thus characterized simultaneously by the absence of the atrial tangential skeleton and the presence of subatrial tetractines that are chiactines. All the known species in the Staurorrhaphidae have rather a thin wall with either an inarticulate skeleton, or only a few scattered spicules in the choanoskeleton. Both genera of Staurorrhaphidae are known only from Antarctica.

Genus *Achramorpha* Jenkin, 1908

TYPE SPECIES. — *Achramorpha nivalis* Jenkin, 1908 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Staurorrhaphidae with a syconoid organization.

Genus *Megapogon* Jenkin, 1908

TYPE SPECIES. — *Leuconia crucifera* Poléjaeff, 1883 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Staurorrhaphidae with a sylleibid or leuconoid organization.

Family LELAPIIDAE Dendy & Row, 1913

TYPE GENUS. — *Lelapia* Gray, 1867 by original designation.

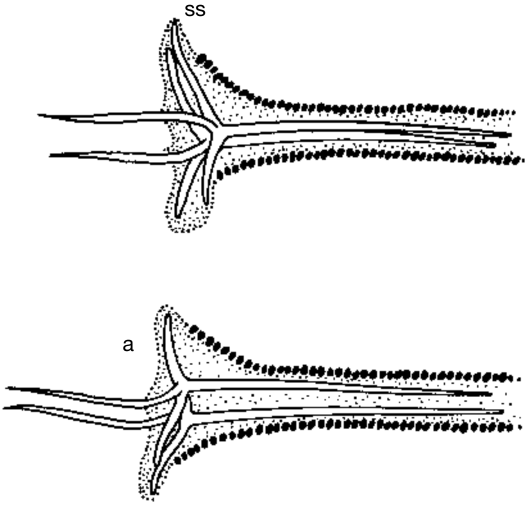

FIG. 36. — Diagram of the subatrial skeleton of the Staurorrhaphidae. Note the absence of the atrial skeleton, and the presence of the apical actines of the subatrial tetractines that point inwards into the atrial cavity. Abbreviations: **a**, atrium; **ss**, subatrial spicules.

DIAGNOSIS. — Leucosoleniida with a syconoid, sylleibid or leuconoid organization. The choanoskeleton contains typical subatrial spicules in the proximal region, associated with spicular tracts, consisting of modified triactines arranged in parallel, which traverse either radially or obliquely the choanosome. The cortex contains tangential triactines and occasionally large longitudinal diactines and/or small perpendicular diactines.

DESCRIPTION

The family Lelapiidae is characterized by spicular fibres or tracts, that are not found in other Leucosoleniida. These tracts contain triactines with reduced paired actines (nail-spicules) or diapasons (tuning-fork spicules), which replace the typical choanoskeleton. This feature attracted a lot of attention in the past, since it is similar to the type of skeleton found in "the Pharetronida", and was understood to be an indication of the relationship between the Lelapiidae and the fossil Calcarea. Two lines of evolution can be distinguished in this family. In the *Grantiopsis-Kebira* line the fibres are formed by the "nail-spicules", while in the *Paralelapia-Lelapia* line they are formed by diapasons. In both lines, the simplest sponges are quite reminiscent of the Grantiidae, while in the most complex ones the cortical skele-

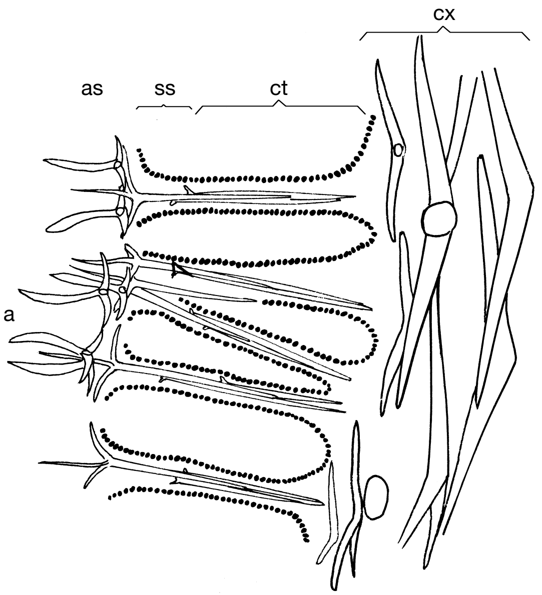

FIG. 37. — Diagram of a transverse section through the wall of *Grantiopsis*. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicules; **ct**, choanosomal spicule tracts composed of nail-like triactines; **cx**, cortex.

ton participates progressively in the reinforcement of the choanoskeleton, replacing the typical meshwork of choanosomal triactine spicules. The two types of modifications of the typical tangential triactines that participate in the spicule tracts are apparently related to the mechanical and spatial constraints of these linear structures. Similar modifications are found in the genus *Guancha* in the Calcinea, where the same constraints inside the peduncle induce either the reduction of the paired actines or their curvature into the diapason form (Borojevic *et al.* 1990). Consequently, we consider that the Lelapiidae belong to the Leucosoleniida, where they represent a rather specialized and well-delimited family, but that they do not have a close relationship with other calcareous sponges related to the fossil groups, such as the Lithonida and Murrayonida, which have diapasons. The Lelapiidae are characteristic of the Indo-Pacific region.

Genus *Grantiopsis* Dendy, 1892

TYPE SPECIES. — *Grantiopsis cylindrica* Dendy, 1892 by monotypy.

DIAGNOSIS. — Lelapiidae with a syconoid or sylleibid organization. The cortex is composed of tangential triactines, and occasionally has an external layer of small diactines perpendicular to the surface. The proximal layer of the choanoskeleton is composed of subatrial triactines and/or tetractines, whose unpaired actines are associated with modified triactines that have very reduced paired actines. These modified triactines are either isolated or form short bundles joined by an organic material, and support the external part of the choanosome.

DESCRIPTION

Grantiopsis has a particular skeleton that is characterized by triactines with reduced paired actines in the wall of the tubes. As is typical for triactines of the tubes, they are associated proximally with the unpaired actines of subatrial triactines. In *Grantiopsis* species that have a thin wall, such as young *G. fruticosa* Dendy & Frederick, 1924, the triactines occasionally occur singly; but in sponges with a thicker wall, such as *G. cylindrica*, they form distinct bundles (Fig. 37). Their reduced paired actines give them a form similar to diactines. They are parallel and tightly bound by an organic material that is more resistant to dissolution with sodium hypochlorite (which is used usually to dissociate calcareous spicules) than other parts of the skeleton. The nature of this material is unknown. The organization of their choanoskeleton is quite similar to a typical *Grantia* in which the articulate skeleton of radial tubes is substituted by spicular tracts formed of nail-shaped triactines. These tracts are much more developed and conspicuous in *Kebira*, clearly pointing to the origin of the Lelapiidae from sponges like the Grantiidae, in which *Grantiopsis* had previously been classified.

Genus *Kebira* Row, 1909

TYPE SPECIES. — *Kebira uteoides* Row, 1909 by monotypy.

DIAGNOSIS. — Lelapiidae with a leuconoid organization. The choanoskeleton has large diactines and spicule tracts consisting of triactines with rudimentary paired actines. The atrial and cortical skeletons are composed of triactines and diactines.

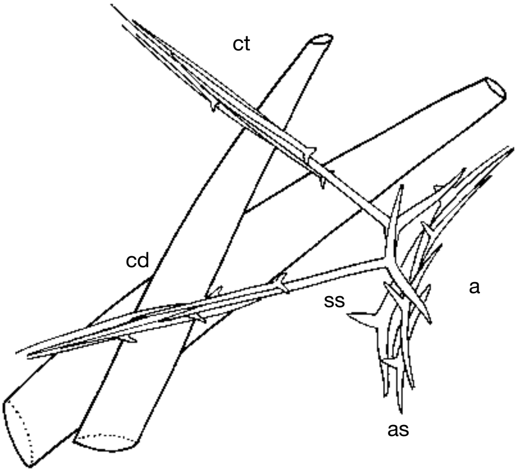

FIG. 38. — Diagram of the subatrial region of the *Kebira* skeleton. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ss**, subatrial spicules; **ct**, choanosomal spicule tracts composed of nail-like triactines; **cd**, choanosomal diactines.

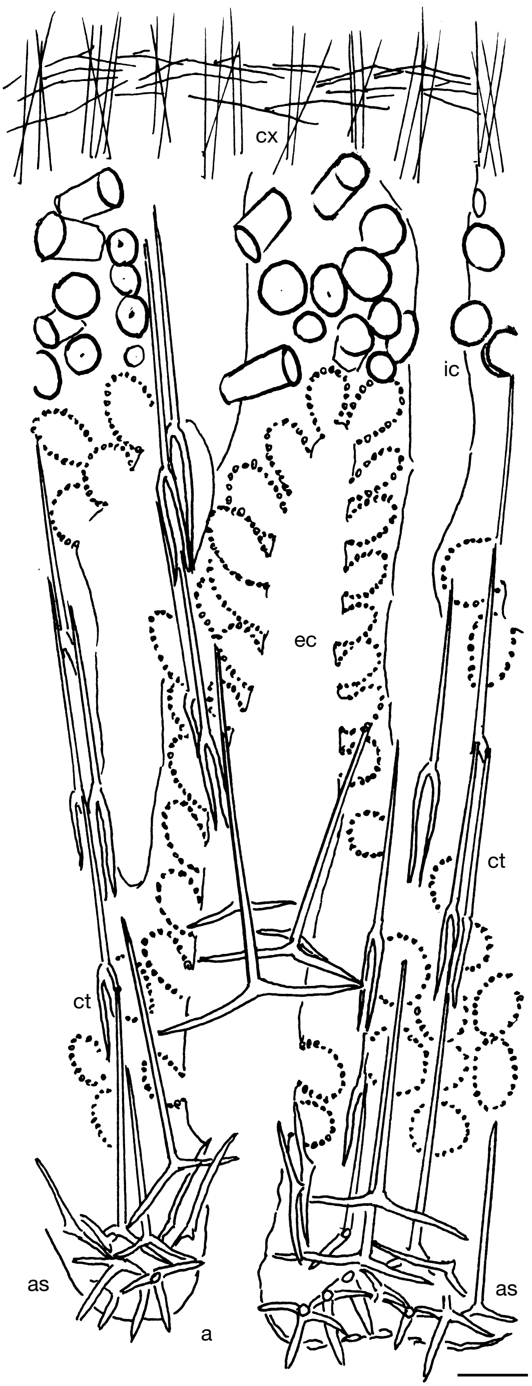

FIG. 39. — Diagram of a cross-section through the wall of *Paralelapia nipponica* Hara, 1894. Abbreviations: **a**, atrium; **as**, atrial skeleton; **ct**, choanosomal spicule tracts formed of tuning-fork-shaped triactines; **cx**, cortex; **ec**, exhalant canal; **ic**, inhalant canal. Scale bar: 60 µm (from Hôzawa 1923).

DESCRIPTION

Kebira is clearly related to *Grantiopsis* with which it shares the nail-form triactines, with reduced paired actines, that are bundled in long tracts. It has a thick wall and a leuconoid organization. The choanoskeleton is supported by giant diactines and multispicular tracts, which most often maintain the radial organization. The atrial surface is supported by tangential triactines (Fig. 38). Although Row (1909) and Ilan & Vacelet (1993) do not specifically mention subatrial spicules, we have examined the specimens studied by the latter authors, and found that each choanosomal tract of spicules is anchored at the atrial surface or at the surface of larger exhalant canals, in a single subatrial spicule, just as is observed in *Grantiopsis* (Fig. 37). Both *Grantiopsis* and *Kebira* lack the classical articulate choanoskeleton composed of triactine or tetractine spicules. In the thick-walled *Kebira*, large diactines, apparently derived from the cortical ones, participate in the formation of the skeleton of the choanosome, in addition to the spicular tracts.

Genus *Paralelapia* Hôzawa, 1923

TYPE SPECIES. — *Lelapia nipponica* Hara, 1894 by monotypy.

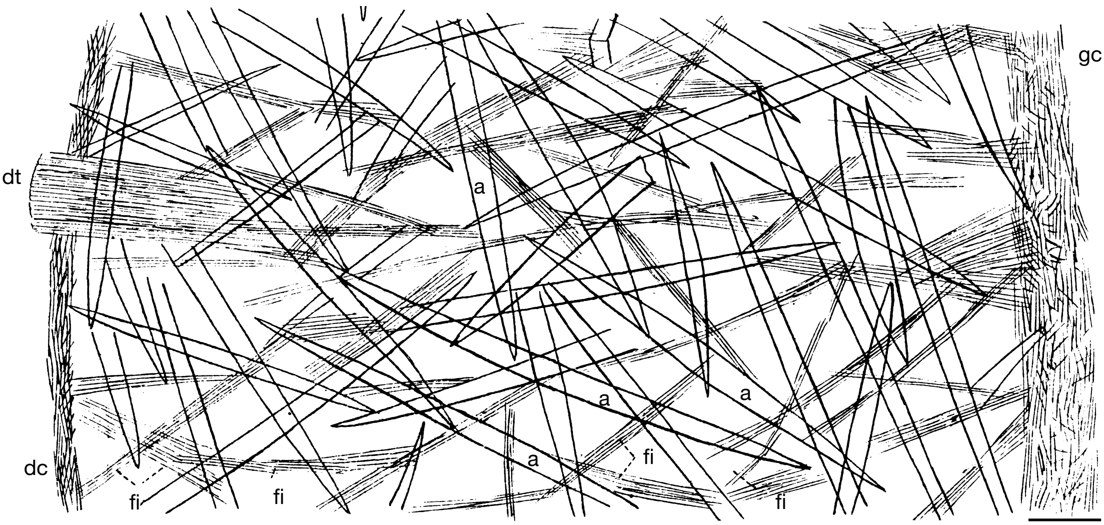

FIG. 40. — Skeletal arrangement in a longitudinal section of *Lelapia australis* Gray, 1867. Abbreviations: **a**, atrium; **dc**, dermal cortex; **dt**, dermal tuft of triactines and slender diactines; **fi**, spicular fibres formed of tuning-fork-shaped triactines; **gc**, atrial cortex. Scale bar: 350 µm (from Dendy 1894).

DIAGNOSIS. — Lelapiidae with a sylleibid organization of the aquiferous system. The thick cortex is composed of an external layer of triactines and an internal layer of giant longitudinal diactines. The choanoskeleton is composed of radially arranged loose tracts of diapasons, originating proximally from unpaired actines of typical subatrial triactines. A well-developed atrial skeleton consists of tangential tri- and tetractines.

DESCRIPTION

The relationship of *Paralelapia* to *Lelapia* is quite similar to that of *Grantiopsis* and *Kebira.* In *Paralelapia*, the sylleibid aquiferous system and the organization of the choanoskeleton clearly have a radial organization, reminiscent of the Grantiidae. The loose spicular tracts are associated proximally with the subatrial spicules, and the cortical skeleton is well-separated from the choanoskeleton (Fig. 39).

Genus *Lelapia* Gray, 1867

TYPE SPECIES. — *Lelapia australis* Gray, 1867 by monotypy.

DIAGNOSIS. — Lelapiidae with a leuconoid organization. The cortex is formed by external layers of triactines; it may also have an internal layer of large longitudinal diactines, as well as radial thin diactines or microdiactines. The choanoskeleton has radially or subradially arranged spicule tracts consisting of diapasons, and large scattered diactines that are similar to the cortical ones. The atrial skeleton is composed of tangential triactine spicules.

DESCRIPTION

Lelapia antiqua Dendy & Frederick, 1924 and *L. australis* represent a series of modifications from *Paralelapia* (Dendy & Frederick 1924). As in *Kebira*, the choanoskeleton is reduced to spicule tracts, that are progressively invaded by the cortical diactines, which lead to the formation of a thick and rigid sponge wall (Fig. 40).

Family *INCERTAE SEDIS*

Genus *Sycyssa* Haeckel, 1872

TYPE SPECIES. — *Sycyssa huxleyi* Haeckel, 1872 by monotypy.

DIAGNOSIS. — Leucosoleniida (?) with a syconoid organization. The skeleton consists of diactines only.

DESCRIPTION

This species has been described using two specimens collected by Haeckel in the Adriatic; it was never found since. The absence of all the radiate spicules is quite remarkable. This condition is

KEY OF GENERA OF LEUCOSOLENIIDA

1. Homocoel organization: all the internal cavities are lined by the choanoderm 2

— Heterocoel organization; with separate choanocyte chambers and an exhalant aquiferous system devoid of choanocytes, with or without a separate inhalant system 4

2. Skeleton contains only diactines .... *Ascyssa*

— Skeleton composed of diactines, triactines and/or tetractines 3

3. Giant longitudinal diactines forming a continuous layer on the external surface.... *Ascute*

— No giant longitudinal diactines .... *Leucosolenia*

4. Skeleton composed exclusively of diactines .... *Sycyssa*

— Skeleton composed of diactines, triactines and/or tetractines 5

5. Sponge body composed of a central atrial tube bearing, at least in its median region, radial tubes lined with choanoderm and ending in conspicuous distal cones that are frequently crowned by tufts of radial diactines 6

— Sponge body covered by a cortex supported by tangential spicules 10

6. Elongate radial tubes regularly arranged around the central tube are completely separate from one another; no inhalant aquiferous system, the incurrent water enters directly through pores into the radial choanocyte chambers .... *Sycetta*

— Radial tubes are coalescent at least in their proximal region 7

7. Radial tubes are parallel and regularly arranged and are occasionally ramified in their distal part. Radial tubes are coalescent for most of their length, with inhalant canals in between that open to the outer surface between the distal cones through ostia .. 8

— A thin sponge wall consisting of the atrial skeleton supporting irregularly grouped short radial tubes that are coalescent or fused proximally, with free distal cones; each group of tubes communicates through a common opening with the atrial cavity; large irregular inhalant cavities are left between the groups of radial tubes, and frequently reach the outer surface of the central atrial tube .... *Sycantha*

8. The atrial cavity contains an internal tissue network supported by a skeleton of parallel bundles of diactines .... *Sycandra*

— No network inside the atrial cavity 9

9. Pseudosagittal spicules are present in the distal cones of the radial tubes .... *Syconessa*

— Absence of pseudosagittal spicules in the distal cones .... *Sycon*

10. The whole sponge is covered by a continuous cortex supported by tangential spicules 11

— Only the grouped distal cones are covered by a cortical network supported by tangential triactines, leaving large openings to the inhalant cavities, and giving to the external surface a honeycombed aspect .... *Dermatreton*

11. Presence of a distinct layer of subcortical pseudosagittal spicules 12

— Absence of a distinct layer of subcortical pseudosagittal spicules 17

12. Inarticulate choanoskeleton composed of the unpaired actines of subatrial spicules and the centripetal paired actines of subcortical pseudosagittal spicules 13

— Articulate choanoskeleton, containing few to several rows of tube spicules, which are more or less scattered between the subatrial and subcortical spicules 14

13. Pseudosagittal spicules are triactines only .... *Sycettusa*

— Pseudosagittal spicules are tetractines and triactines .... *Grantilla*

14. Sylleibid or leuconoid organization .... *Vosmaeropsis*

— Syconoid organization 15

15. Without large longitudinal diactines in the cortical or atrial skeleton ...... *Grantessa*

— With large longitudinal diactines in the cortical or atrial skeleton 16

16. Longitudinal diactines in the cortical skeleton only .... *Heteropia*

— Longitudinal diactines in the cortical and atrial skeleton .... *Paraheteropia*

17. Articulate choanoskeleton, with at least some trace of the tube organization; the majority of spicules have the unpaired actine pointing towards the outer surface of the sponge 18

— Inarticulate choanoskeleton, or choanoskeleton composed of an external inarticulate layer supported by apical actines of cortical tetractines, and an internal layer of scattered triactines and/or tetractines, without any apparent order 34

18. Without a tangential atrial skeleton substituted by subatrial chiactines .... (Staurorrhaphidae) 19

— With tangential atrial skeleton composed of triactines and/or tetractines 20

19. Syconoid organization .... *Achramorpha*

— Sylleibid or leuconoid organization .... *Megapogon*

20\. Spicular tracts in the choanoskeleton .... (Lelapiidae) 21

— No spicular tracts .... (Grantiidae) 24

21\. Spicular tracts made of "nail-shaped" triactines, with highly reduced paired actines .. 22

— Spicular tracts made of diapasons 23

22\. Tubular sponge, syconoid or sylleibid organization, choanoskeleton with short, radially arranged tracts between the distal parts of the radial tubes .... *Grantiopsis*

— Massive sponge with a thick wall containing large diactines, choanoskeleton with long tracts in an approximately radial arrangement .... *Kebira*

23\. Cortex composed of giant longitudinal diactines, which do not invade the choanoskeleton .... *Paralelapia*

— Giant diactines in the choanoskeleton .... *Lelapia*

24\. Absence of longitudinal diactine in the atrial and/or cortical skeleton 25

— Presence of longitudinal diactines in the atrial and/or cortical skeleton 29

25\. Syconoid organization 26

— Sylleibid or leuconoid organization 27

26\. Diameter of the osculum smaller than that of the atrium .... *Grantia*

— Diameter of the osculum larger than that of the atrium: pedunculate calyciform sponge with a thin folded wall .... *Teichonopsis*

27\. Septa with a specific skeleton of minute triactines within the atrial cavity ... *Leucettaga*

— No septa within the atrial cavity 28

28\. Cortex composed of triactines and possibly diactines, which protrude from the cortex making it hispid .... *Leucandra*

— Cortex with triactines and tetractines .... *Leucandrilla*

29\. Leuconoid organization .... *Aphroceras*

— Syconoid organization 30

30\. Sponge with individual syconoid tubes or an arborescent cormus composed of separate tubes 31

— Massive cormus composed of coalescent syconoid units, covered by a common cortex... *Synute*

31. Longitudinal diactines present only in the cortex 32

— Longitudinal diactines present in the atrial skeleton 33

32. Tufts of thin radial diactines decorate the distal parts of the radial tubes, and cross the cortex between the longitudinal diactines .... *Sycute*

— No tufts of radial diactines .... *Ute*

33. Longitudinal diactines present only in the atrial skeleton.......................... *Sycodorus*

— Longitudinal diactines present both in the atrial and the cortical skeleton ... *Amphiute*

— No giant cortical tetractines .... (Jenkinidae) 37

35. Syconoid organization .... *Amphoriscus*

— Sylleibid or leuconoid organization 36

36. Inarticulate choanoskeleton; scattered spicules occasionally between subcortical and subatrial layers .... *Leucilla*

— Choanoskeleton divided in two parts: the external part has an inarticulate organization, while the internal one is intercalated between the subatrial spicules and the atrial skeleton, and is supported by scattered triactines and/or tetractines .... *Paraleucilla*

37. Syconoid organization 38

— Sylleibid or leuconoid organization 40

38. Thin cortical skeleton, composed of one to several layers of triactines .... *Breitfussia*

— Reinforced cortical skeleton 39

39. Skeleton reinforced with giant tangential triactines, which are also scattered in the choanoskeleton .... *Anamixilla*

— Reinforced skeleton with longitudinal diactines .... *Uteopsis*

40. Without scattered spicules in the choanoskeleton 41

— With scattered spicules in the choanoskeleton, smaller than those of the cortex, and without defined position .... *Polejaevia*

41. Sponge growing as small individual tubes .... *Jenkina*

— Sponge forming a large cormus composed of copiously anastomosed and ramified tubes .... *Leucascandra*

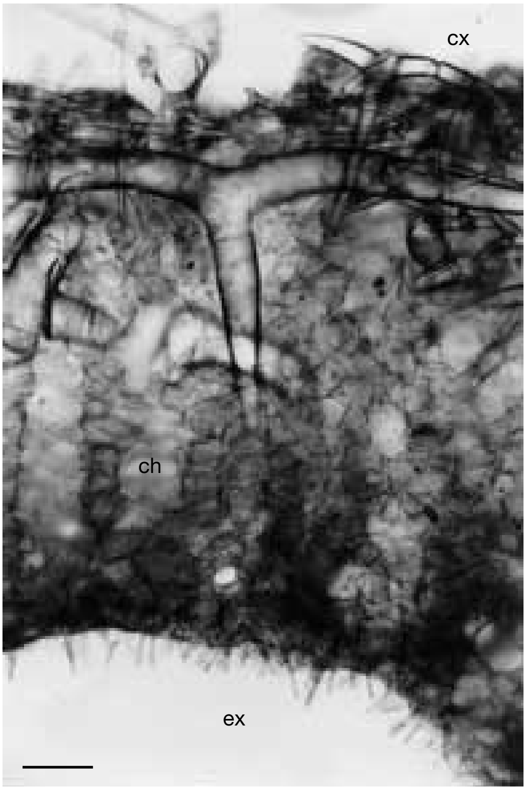

FIG. 41. — Transverse sections through the wall of *Baeria johnstoni* (Carter, 1871) (light micrograph). Abbreviations: **ex**, large exhalant canals; **ch**, choanosome; **cx**, cortex. Scale bar: 230 µm.

FIG. 42. — Transverse sections through the wall of *Baeria nivea* (Johnston, 1842) (light micrograph). Abbreviations: **ex**, large exhalant canals; **ch**, choanosome; **cx**, cortex. Scale bar: 230 µm.

similar to that seen in the family Trichogypsiidae in the order Baeriida. However, no other characteristics of the Baeriida are present, and the organization of *S. huxleyi* is otherwise quite similar to other grantiid sponges with a syconoid choanosome, in particular to *Sycodorus hystrix* Haeckel, 1872, as pointed out by the author. At present we are unable to decide what the relationship of this sponge is to other Calcaronea. However, we believe that it is closer to the Leucosoleniida than to the Baeriida.

Order BAERIIDA n. ord.

DIAGNOSIS. — Leuconoid Calcaronea with the skeleton either composed exclusively of microdiactines, or in which microdiactines constitute exclusively or predominantly a specific sector of the skeleton, such as choanoskeleton or atrial skeleton. Large or giant spicules are frequently present in the cortical skeleton, from which they can partially or fully invade the choanoderm. In sponges with a reinforced cortex, the inhalant pores can be restricted to a sieve-like ostia-bearing region. Dagger-shaped small tetractines (pugioles) are frequently the sole skeleton of the exhalant aquiferous system. Although the skeleton may be highly reinforced by the presence of dense layers of microdiactines in a specific region, an aspicular calcareous skeleton is not present.

DESCRIPTION

Dendy & Row (1913) already wrote that "aberrant genera [such] as *Leucopsila, Baeria, Kuarraphis, Leucyssa* and *Trichogypsia* can only be included in the Grantiidae provisionally. The difficulty of arranging the genera probably arises from the fact that great gaps exist in the family owing to extinction of intermediate forms". This

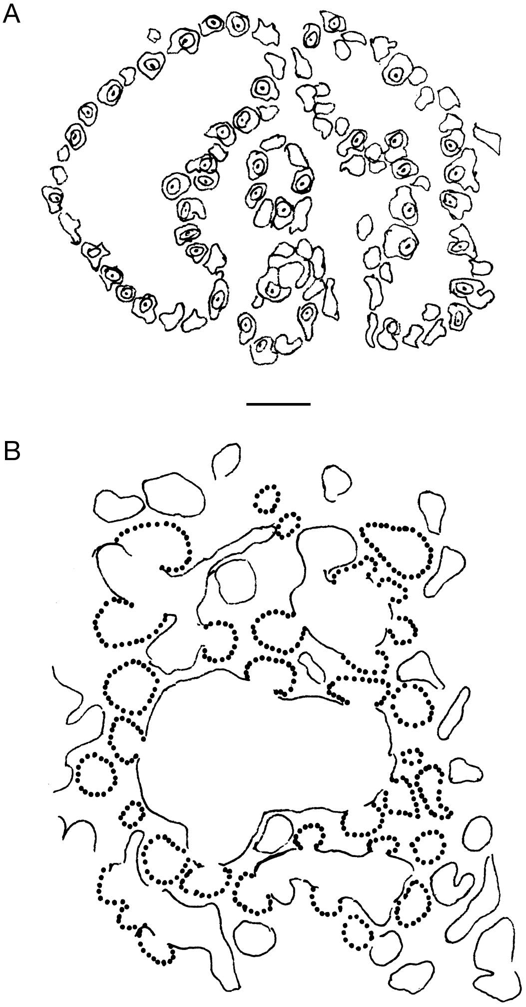

FIG. 43. — Diagram of the formation of choanocyte chambers of diamorphies during the process of reconstitution from dissociated cells; drawing from original micrographs by Peixinho (1980); **A**, pre-sycon stage of *Grantia compressa*; **B**, pre-leucon stage in *Baeria nivea*. Scale bar: A, 26 µm; B, 45 µm.

statement clearly outlines the major arguments for separating the above-named sponges from the Leucosoleniida. We now propose to create a new order, the Baeriida in the Calcaronea, for a group of sponges with quite a distinct type of organization, in which no traces of radial symmetry can be observed, and which apparently has not followed the sycettid pathway of evolution.

The aquiferous system of the Baeriida is always leuconoid, with choanocyte chambers distributed irregularly throughout the sponge wall and often arranged in groups around large exhalant canals (Figs 41; 42). No true atrial skeleton, reminiscent of the central tube, is found in the exhalant aquiferous system, nor does a clear subatrial skeleton indicate the original position of the radial tubes. We found no sponges with an asconoid or syconoid type of aquiferous system, which could be included in this order. The postlarval development of the Baeriida is not known, and the presence of an early olynthus stage in their development has not been established. It is noteworthy that a comparison of the morphogenesis of diamorphs, obtained after dissociation and reaggregation of *Sycon vigilans* and *Grantia compressa* (representing the Leucosoleniida) and *Baeria* (*Leuconia*) *nivea* (representing the Baeriida) (Sarà *et al.* 1974; Peixinho 1980) have disclosed clear differences. During morphogenesis both *Sycon* and *Grantia* pass through the olynthus stage, acquiring a sycettid grade of organization by the subsequent formation of radial tubes, similar to the postlarval development of the Leucosoleniida. Conversely, *Baeria* does not pass through olynthus and sycettid stages during morphogenesis, but develops a leuconoid type of aquiferous system by the formation of a rhagon, similar to that described for the Demospongiae by Lévi (1956) (Fig. 43). Consequently, we assume that in the Baeriida, as in the Demospongiae, the development of the aquiferous system involves the formation of spherical choanocyte chambers, simultaneous with the formation of the inhalant and exhalant aquiferous systems.

Apart from these aspects of the aquiferous system and the associated skeleton, the Baeriida are characterized by having two distinct categories of spicules, which correspond to the megascleres and microscleres in Demospongiae. Small spicules (most frequently microdiactines) are found throughout the sponge and giant spicules are limited to the cortical region (e.g. *Baeria johnstoni* and *Lamontia zona*), or invade the choanosome from the cortex and form a scattered skeleton throughout the body (e.g. *Baeria nivea*). One or several types of very small spicules may be present. A very particular type of tetractine termed "unicorvo-cruciform" by Bowerbank (1864), "kreuzförmigen Vierstrahlern" by Haeckel (1872), "dagger-shaped tetracts" by Grant (1826), Dendy (1892b) and Kirk (1895), or harpoon-like tetractines by more recent authors is found in the skeleton of exhalant surfaces. We propose to name these spicules "pugioles" (*pugiolus*, in Latin small dagger). Typical pugioles are found in *Baeria* and *Lamontia*. They constitute the exhalant canal skeleton, in which the paired actines are adjacent to the canal surface, the unpaired actine is perpendicular to it lying inside the adjacent tissue, and the apical actine is free in the canal lumen (Figs 44; 45). Consequently, they have the main axis (the one passing through the unpaired angle of the basal triactine system) perpendicular to the exhalant canal surface, as opposed to atrial spicules in the Leucosoleniida where this axis is parallel to the atrial surface oriented longitudinally with the unpaired angle in most of the cases turned towards the osculum. The position and function of pugioles are not unlike those of the equally "cruciform" large spicules named chiactines (Jenkin 1908a) that are characteristic of the family Staurorrhaphidae. We consider that this is a consequence of the same need for reinforcement and protection of the surface of the exhalant system. In both cases, the atrial surface is devoid of skeleton, and consequently is bald and exposed to invasion. Chiactines are modified subatrial spicules and thus participate both in forming the proximal part of the choanoskeleton and in the protection of the atrial cavity through long apical actines bent centripetally across the atrial surface of the sponge. However, pugioles are present only in the Baeriidae, where they point their apical actine towards the inside of the atrium. Apparently, they are derived from spicules that were tangential to the surface of exhalant canals, but which have subsequently acquired the particular position and orientation observed in *Baeria johnstoni* and *B. nivea*.

The second type of small spicules are microdiactines, often termed "Stäbchen-Mörtel" (Haeckel 1872) or "mortar spicules" (Dendy 1892b) (Fig. 45). These spicules apparently derive from small triactines, in which one of the paired actines is rudimentary, giving the spicule a lanceolate-like shape. Similar spicules can be found among sponges in the Leucosoleniida, but in the Baeriida they may be the sole spicule type present, or can constitute a specific part of the skeleton, either alone or as its major component, such as choanoskeleton (e.g. *Baeria, Lamontia, Eilhardia, Lepidoleucon*) or atrial skeleton (e.g. *Leucopsila*).

There may also be small triactines with two short or rudimentary paired actines, bent together to form a club-shaped spicule, often with a more or less pronounced hole adjacent to the centre of the spicule; these are the "needle-eye" spicules seen in the genus *Kuarraphis* and in *Baeria ochotensis*.

Baeria gladiator Dendy, 1892 also has typical trichodragmas. To our knowledge, this is the only calcareous sponge with this type of microdiactine.

The external skeleton of the Baeriida may have a thick and continuous layer of reinforced cortical spicules that obstructs the free flow of inhalant water and causes the inhalant pores to be restricted to a specific cribriform region (e.g. *Lamontia, Lepidoleucon*).

In the subclass Calcaronea, continuous evolutionary lineages with all the intermediate forms are observed in Leucosoleniida, suggesting a recent evolutionary radiation. In contrast, the Baeriida and Lithonida are represented by well-characterized and very distinct genera, with no intermediate forms, suggestive of long-term evolution in which a small number of only the most specialized forms are conserved. Similarly, in the subclass Calcinea, all the transitional forms are found in Clathrinida but not in Murrayonida (Borojevic *et al.* 1990).

Family BAERIIDAE n. fam.

TYPE GENUS. — *Baeria* Miklucho-Maclay, 1870 by original designation.

DIAGNOSIS. — Baeriida with a choanoskeleton consisting of giant triactines, and/or of tetractines in no particular order, and/or of very numerous microdiactines. No traces of radial organization can be seen in the choanoskeleton. The cortical skeleton consists of triactines, giant diactines, and/or numerous microdiactines, and occasionally the basal actines of cortical giant tetractines. The choanoskeleton consists of scattered spicules similar to those observed in the cortex, to which numerous microdiactines can be added, or which can be entirely replaced by microdiactines. The exhalant aquiferous system is formed by ramified canals that have no tangential skeleton, being loosely or densely covered by harpoon-shaped pugioles and/or microdiactines.

FIG. 44. — Pugioles (**p**) in an exhalant canal (**ex**) of *Baeria nivea* (Johnston, 1842). Scale bar: 90 µm.

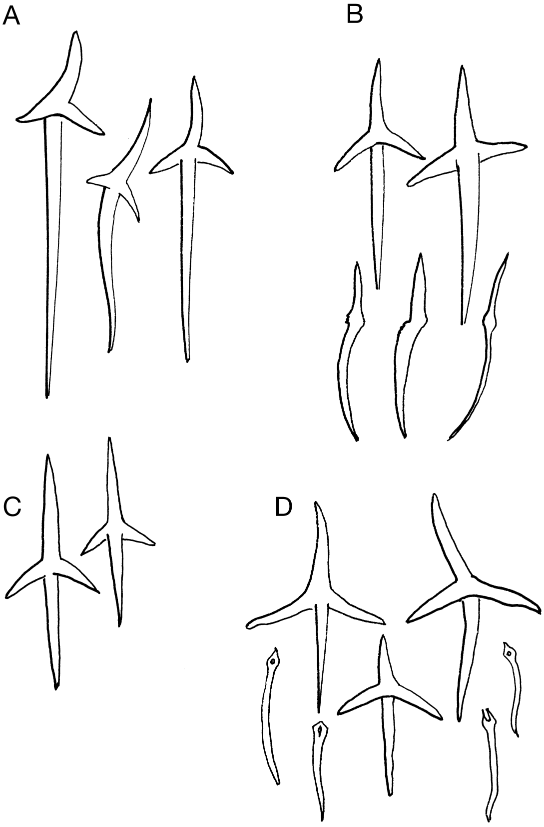

FIG. 45. — Diagram of pugioles and microdiactines; **A**, *Baeria gladiator*; **B**, *Lamontia zona*; **C**, *Baeria nivea*; **D**, *Baeria ochotensis.*

Genus *Baeria* Miklucho-Maclay, 1870

TYPE SPECIES. — *Baeria ochotensis* Miklucho-Maclay, 1870 by monotypy.

DIAGNOSIS. — Baeriidae in which the choanoskeleton consists of giant triactines and/or tetractines, lying without apparent order, and of very numerous microdiactines. A cavity equivalent to the atrium, localized only under the oscula, has a skeleton supported by tangential triactines. All the other exhalant canals have a skeleton composed of harpoon-shaped pugioles.

DESCRIPTION

In the genus *Baeria* we include the hitherto described species *B. nivea* (Grant, 1826), *B. johnstoni* (Carter, 1871), *B. ochotensis* Miklucho-Maclay, 1870, *B. gladiator* (Dendy, 1892) and *B. prava* (Breitfuss, 1898), which bear a number of similarities. They all have a choanoskeleton containing numerous microdiactines (“mortar spicules”), and very large triactines or tetractines that lie scattered without any apparent order. The cortical skeleton consists of triactines and microdiactines, which are different in size and form from those in the choanosome. The atrium is always limited to the space immediately below the osculum, and the oscular area contains a dense layer of sagittal triactines. However, the exhalant canals of all sizes are devoid of a tangential skeleton and contain only pugioles (Fig. 44). In *Baeria johnstoni* an additional type of very small tetractine is found in the choanosome.

Although Haeckel (1872) has represented the microdiactines of all these species as smooth and equally acerate on both ends, we have observed that in *B. nivea* and *B. johnstoni* the microdiactines are clearly hastate in form, with one long and one short actine, the shorter one having an angular twist close to the centre of the spicule. Dendy & Row (1913) reported that after re-examination of Haeckel's preparations of *B. ochotensis,* many of microdiactines were found to have a "needle-eye" form. These correspond to tiny triactines, with two very much reduced paired actines bent to lie approximately parallel, which can be slightly swollen and fused at the end (Fig. 45); such spicules can be observed in the Lithonida. Some of these spicules have their distal ends free, thus corresponding exactly to diapasons. Similar spicules are found in *Kuarraphis* Dendy & Row, 1913, which we place also in the Baeriida. In the original description of *Kuarraphis* (*Leucyssa*) *cretacea*, Haeckel (1872) indicated that the "needle-eye" spicules were found in *Baeria ochotensis* although they were not figured in its description.

B. johnstoni and *B. nivea* have previously been included in the genera *Spongia, Grantia, Leucandra* and *Leuconia.* The first three genera are now used in a different context, and the last one has been shown to be invalid (Dendy 1893; Dendy & Row 1913). The genus *Baeria* has been proposed previously by Dendy & Row (1913) for *B. ochotensis*, and the present definition of the genus is quite close to the one proposed by those authors.

Genus *Lamontia* Kirk, 1895

TYPE SPECIES. — *Lamontia zona* Kirk, 1895 by monotypy.

DIAGNOSIS. — Baeriidae in which the choanoskeleton consists of microdiactines. Cortical and atrial skeletons have triactines and tetractines, and the cortex is pierced by large diactines. A specialized ostia-bearing zone, located below the osculum, leads the incurrent water flow to inhalant cavities.

DESCRIPTION

Lamontia is a particular sponge, which bears a number of similarities with *Baeria*. The choanoskeleton is composed of microdiactines, and there are pugioles in the skeleton of the exhalant aquiferous system. It is distinguished by a special ostia-bearing zone and large diactines, which make the sponge hispid.

Genus *Leucopsila* Dendy & Row, 1913

TYPE SPECIES. — *Leuconia stilifera* Schmidt, 1870 by monotypy.

DIAGNOSIS. — Baeriidae in which the cortex is formed by tangential triactines and microdiactines. The choanoskeleton is composed almost exclusively of irregularly scattered giant tetractines, and numerous microdiactines. Both the cortical and atrial surfaces are covered by a dense layer of microdiactines. While in the cortex microdiactines overlay the continuous layer of tangential triactines, they are the sole skeleton of the exhalant aquiferous system.

DESCRIPTION

Like *Baeria, Leucopsila* has a massive body, with an irregular leuconoid aquiferous system organized around exhalant canals that are distributed in the choanosome in the form of an anastomosing network. The organization of the skeleton is similar in *Leucopsila stilifera* (Schmidt, 1870) and *Baeria johnstoni* (Carter, 1871); the major distinction between the two being the replacement of pugioles in the skeleton of the exhalant system of *Leucopsila* by microdiactines.

Leucopsila is a large sponge that has been reported only from arctic and subarctic waters, both from the Atlantic and Pacific regions (Schmidt 1870; Haeckel 1872; Hôzawa 1919).

Genus *Eilhardia* Poléjaeff, 1883

TYPE SPECIES. — *Eilhardia schulzei* Poléjaeff, 1883 by monotypy.

DIAGNOSIS. — Calyciform Baeriidae with inhalant ostia on the inner surfaces, and oscula on the outer surfaces. The ostia-bearing surface is supported by a thin layer of tangential triactines and scattered microdiactines. The skeleton of the exhalant system and of the choanoskeleton is composed of large triactines and microdiactines. The cortical skeleton consists of giant longitudinal and small diactines as well as tangential triactines.

DESCRIPTION

Eilhardia schulzei Poléjaeff, 1883 is quite an unusual calcareous sponge, with a calyciform body in which the inhalant surface is the inner one, and exhalant surface the outer one. Its internal organization is similar to other Baeriidae. Poléjaeff (1883) has given a very

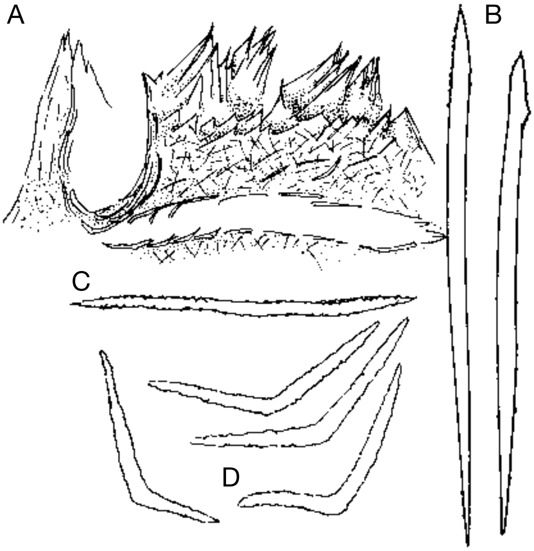

FIG. 46. — *Trichogypsia villosa* (Carter, 1871); **A**, a diagram of a transverse section of the body wall, showing a pit-like cavity and a canal parallel to the external surface that bears conules containing very densely arranged parallel diactines; **B**, diactines of the cortical conules; **C**, diactines of the internal reticular skeleton; **D**, diactines that line the pit-like cavity.

detailed description and beautiful illustration of this sponge.

Family TRICHOGYPSIIDAE n. fam.

TYPE GENUS. — *Trichogypsia* Carter, 1871 by original designation.

DIAGNOSIS. — Baeriida with a skeleton entirely formed by diactine spicules.

DESCRIPTION

We propose to put sponges that have affinities with the Baeriidae, but that have only diactine spicules in the family Trichogypsiidae. As discussed above, one of the characteristics of the Baeriida is the presence of small "mortar-shaped" diactines that make up either all of, or a large part of a specific portion of the skeleton. The Trichogypsiidae have large diactines, which are probably not homologous with "mortar-shaped" diactines. It is difficult to establish whether the absence of triactine spicules is a primitive condition or is a consequence of a secondary reduction of the skeleton. In the Leucosoleniida, diactines are the first spicules to be secreted, but it is not known if this is also true for the Baeriida. All the Trichogypsiidae are very poorly known, having been described in early studies from a small number of specimens; there are no recent studies that provide a detailed description of their cytology or biology. Up to now, the Trichogypsiidae have been only described from boreal or arctic regions.

Genus *Trichogypsia* Carter, 1871

TYPE SPECIES. — *Trichogypsia villosa* Carter, 1871 by subsequent designation (Dendy & Row 1913).

DIAGNOSIS. — Trichogypsiidae with a skeleton composed of spined diactines.

DESCRIPTION

Haeckel (1872) described two subspecies that were subsequently raised by Dendy & Row (1913) to the species level: *Trichogypsia* (*Leucyssa*) *incrustans* Haeckel, 1872 and *T. villosa* Carter, 1871. He pointed out the similarity of both the external form and the organization of the aquiferous system to *Baeria nivea*, but we have no information on the internal organization of the choanoderm or the choanoskeleton. We have examined the slide prepared from the original specimen, described by Carter (1871) (BMNH 1870.10.1.9). It contains a fragment of an encrusting sponge with a thick cortex elevated in conules. The cortex is supported by very densely packed parallel diactines, arranged in bunches in the conules. A large, deep cavity present at the surface is surrounded by a particular skeleton composed of bent diactines. A canal parallel to the surface is connected to this cavity. Both the canal surface and the internal skeleton consist of straight or slightly curved spiny diactines that form a rather loose network (Fig. 46).

Genus *Kuarrhaphis* Dendy & Row, 1913

TYPE SPECIES. — *Leucyssa cretacea* Haeckel, 1872 by monotypy.

DIAGNOSIS. — Trichogypsiidae with a skeleton composed exclusively of small perforated needle-eye diactines.

Description

Dendy & Row (1913) proposed the genus *Kuarraphis* for a sponge described by Haeckel (1872) that is characterized by the presence of only needle-eye spicules. The sponge is encrusting, has a leuconoid organization without an atrium, and has irregular exhalant canals. Haeckel (1872) pointed out the similarity of the choanosome and the skeleton of this sponge with those described by him in the "subgenus *Leucomalthe*", which comprises the species that we place now in the Baeriidae. As indicated by Dendy & Row (1913), the "needle-eye" spicules are similar to diapasons, and are also found in *Baeria ochotensis*.

Genus *Leucyssa* Haeckel, 1872

Type species. — *Leucyssa spongilla* Haeckel, 1872 by monotypy.

Diagnosis. — Trichogypsiidae (?) with a skeleton composed only of smooth diactines.

Description

The external shape of this sponge, which has a pedunculate cormus with a large clathrate body of anastomosed tubes, is quite different from both the Baeriida and Leucosoleniida, and is rather common among the Clathrinida. However, *Eilhardia* also has quite an unusual shape, and it is possible that our knowledge of only a very small number of sponges in the Baeriida gives the impression of a great divergence of the observed forms. We place this sponge among the Baeriida, following Haeckel's (1872) description of the rather irregular alveolar choanosome supported by a dense skeleton of small diactines, scattered without order.

Family Lepidoleuconidae Vacelet, 1967

Type genus. — *Lepidoleucon* Vacelet, 1967 by monotypy.

Diagnosis. — Baeriida with a leuconoid organization and with an irregular outer layer of scales derived from triactines. The choanoskeleton is exclusively composed of scattered microdiactines. The ostia are localized in a special area where the triactines are not transformed into scales.

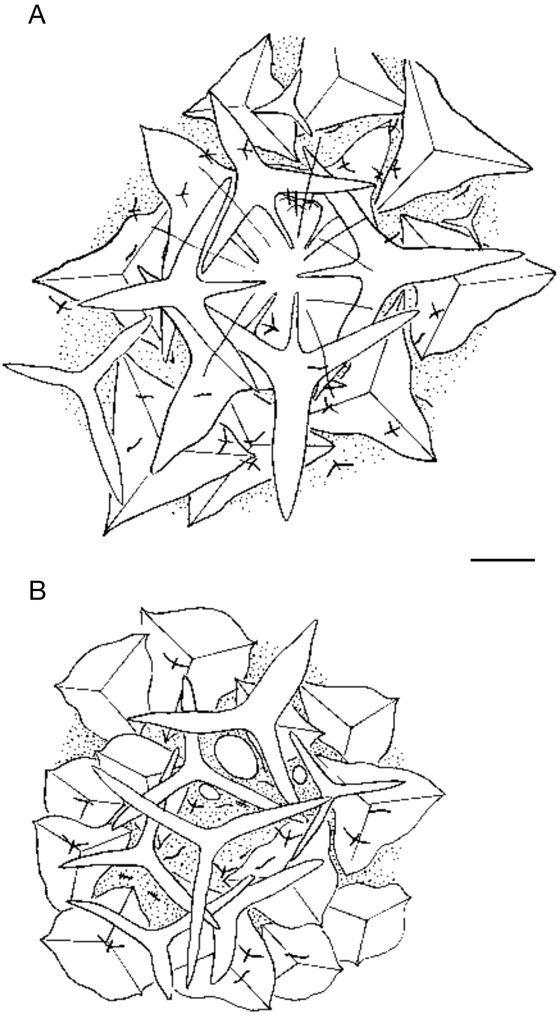

Fig. 47. — Diagram of the organization of *Lepidoleucon inflatum* Vacelet, 1967; **A**, osculum; **B**, inhalant area. Scale bar: 75 µm (from Vacelet 1967a).

Description

The Lepidoleuconidae is characterized by the formation of triangular scales in the cortex. Haeckel (1872) reported similar spicules in *Leucetta trigona* described from a single dried specimen from South Africa. As the description of this species is quite incomplete it is possible that it could belong to the family Lepidoleuconidae. The organization of the skeleton in the Lepidoleuconidae is similar to that of other Baeriida, and in particular to *Baeria johnstoni* and *Eilhardia schulzei* in

KEY OF GENERA OF BAERIIDA

1. Skeleton composed of only diactines ....(Trichogypsiidae) 2

— Skeleton composed of diactines, triactines and/or tetractines................................. 4

2. Microdiactines are the "needle-eye" type.. *Kuarrhaphis*

— Lanceolate diactines with spines on one or both ends, or smooth diactines 3

3. Lanceolate spiny diactines .... *Trichogypsia*

— Smooth diactines .... *Leucyssa*

4. Sponge with a specialized inhalant zone bearing pores 5

— Sponge without a specialized inhalant zone .... (Baeriidae) 6

5. Cortex composed of scales derived from triactines .... *Lepidoleucon*

— Cortex composed of triactines and tetractines and sometimes diactines; pugioles are present in the atrial skeleton .... *Lamontia*

6. Calyciform sponges with inhalant ostia localized on the inner surface and oscula on the outer surface .... *Eilhardia*

— not calyciform sponges 7

7. Atrial skeleton with pugioles .... *Baeria*

— Atrial skeleton with microdiactines .... *Leucopsila*

which the choanoskeleton consists solely of microdiactines, and to *Lamontia,* which also has the ostia-bearing inhalant area.

Genus *Lepidoleucon* Vacelet, 1967

TYPE SPECIES. — *Lepidoleucon inflatum* Vacelet, 1967 by monotypy.

DIAGNOSIS. — Same definition as the family (Fig. 47). The single osculum has a circlet of modified tetractines.

Order LITHONIDA Vacelet, 1981

DIAGNOSIS. — Calcaronea with reinforced skeleton consisting either of linked or cemented basal actines of tetractines, or of a rigid basal mass of calcite. Diapason spicules are generally present and the canal system is leuconoid.

DESCRIPTION

The families Lelapiellidae (Calcinea), Lepidoleuconidae (Baeriida) and Lelapiidae (Leucosoleniida) are now excluded from this order.

Family MINCHINELLIDAE Dendy & Row, 1913

TYPE GENUS. — *Minchinella* Kirkpatrick, 1908 by original designation.

DIAGNOSIS. — Lithonida with a choanoskeleton consisting of a primary network of tetractines cemented or linked together in a variety of ways.

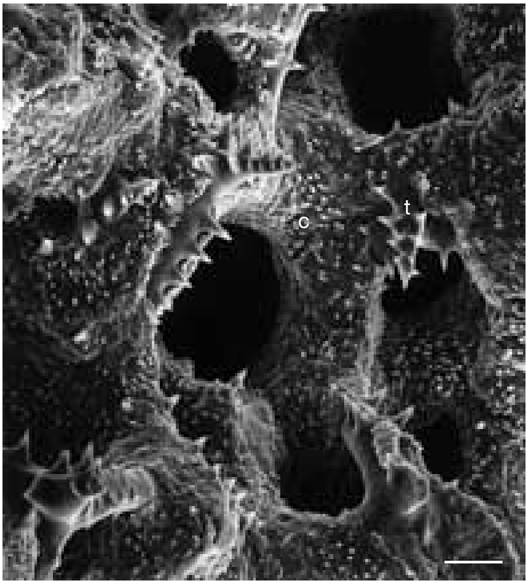

FIG. 48. — Surface view of the skeleton in *Minchinella lamellosa* Kirkpatrick, 1908, showing the progressive embedding of the tetractine framework (**t**) in a calcareous cement (**c**) (SEM). Scale bar: 31 µm (from Vacelet 1991).

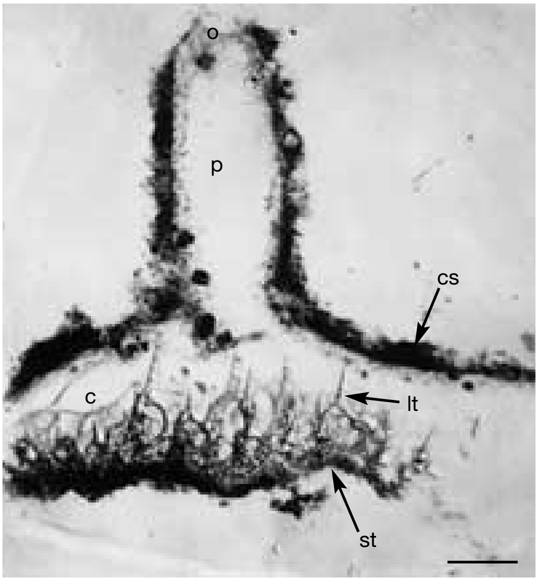

FIG. 49. — Transverse section of *Plectroninia hindei* Kirkpatrick, 1900 (light micrograph). Abbreviations: **p**, papilla; **o**, osculum; **c**, choanosome; **cs**, cortical skeleton; **lt**, large fused tetractines of the choanoskeleton; **st**, small fused tetractines of the choanoskeleton. Scale bar: 330 µm (from Pouliquen & Vacelet 1970).

DESCRIPTION

Vacelet (1981) provided an identification key of the known Recent species. The family includes several fossil genera, whose definitions have to be revised.

Genus *Minchinella* Kirkpatrick, 1908

TYPE SPECIES. — *Minchinella lamellosa* Kirkpatrick, 1908 by monotypy.

DIAGNOSIS. — Minchinellidae in which the choanoskeleton consists of tetractines cemented together into a rigid network by their basal actines and subsequently embedded in an enveloping cement (Fig. 48). The cortical skeleton is composed of triactines, diapasons, and diactines.

Genus *Plectroninia* Hinde, 1900

TYPE SPECIES. — *Plectroninia halli* Hinde, 1900 by monotypy.

DIAGNOSIS. — Minchinellidae with a choanoskeleton composed of tetractines, the basal actines of which are fused with the basal actines of adjacent spicules, while the apical actines remain free and point outward. This choanoskeleton is made up of two layers, an outer layer of large tetractines and a basal layer of small tetractines. The cortical skeleton consists of free spicules arranged tangentially. A perioscular circlet of tetractines, and rarely of triactines, is usually present.

DESCRIPTION

The genus *Plectroninia*, which was erected for fossil sponges, is difficult to distinguish from several other fossil genera, such as *Bactronella* Hinde, 1884; *Porosphaera* Steinmann, 1878; *Tretocalia* Hinde, 1900; *Porosphaerella* Welter, 1910; *Sagittularia* Welter, 1910. The type species of *Plectroninia*, *P. halli* Hinde, 1900 from the mid-Miocene, was turbinate in shape and was probably free-living on a muddy sand bottom (Pickett, pers. comm.). It was therefore quite different from the Recent species first allocated to this genus by Kirkpatrick (1900) (Figs 49-51). Kirkpatrick concluded that his specimen of *P. hindei* was a juvenile that had not reached its ultimate shape. The relationships of the Recent species, which are encrust-

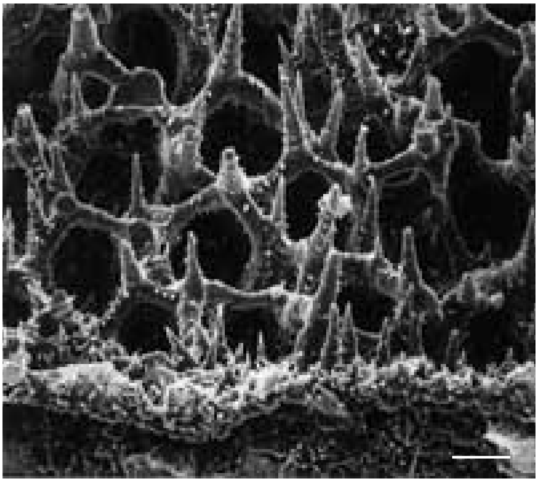

FIG. 50. — View of the choanoskeleton of *Plectroninia* sp., showing two layers of tetractines fused by their basal actines (SEM). Scale bar: 50 µm (from Vacelet 1991).

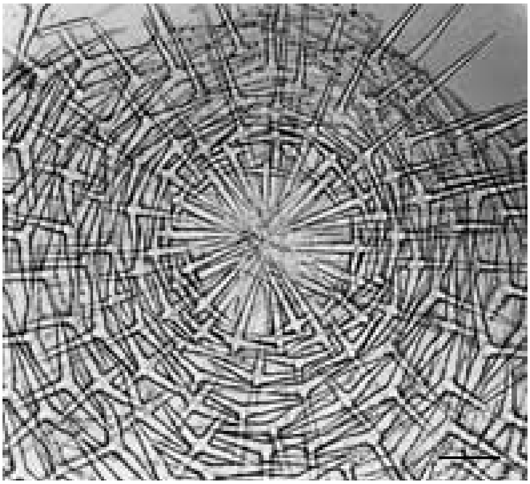

FIG. 51. — Cortical skeleton and osculum of *Plectroninia vasseuri* Vacelet, 1967b. Scale bar: 66 µm (from Vacelet 1967b).

ing, with the massive *Petrostroma* Döderlein, 1892 are also unclear at present.

This genus contains 12 known Recent species that have an unusually large depth distribution, being known from shallow water caves down to 1600 m in depth.

Genus *Monoplectroninia* Pouliquen & Vacelet, 1970

TYPE SPECIES. — *Monoplectroninia hispida* Pouliquen & Vacelet, 1970 by monotypy.

DIAGNOSIS. — Minchinellidae in which the choanoskeleton is composed of a basal layer made of one category of small tetractines cemented together by their basal actines, while their apical actine remains free and points outward. The cortical skeleton consists of free spicules.

Genus *Petrostroma* Döderlein, 1892

TYPE SPECIES. — *Petrostroma schulzei* Döderlein, 1892 by monotypy.

DIAGNOSIS. — Minchinellidae with tetractines fused by their basal actines forming radial lines that are linked by smaller tetractines, which are fused by their basal actines. The cortical skeleton consists of free spicules.

DESCRIPTION

The genus *Petrostroma* has not been found since it was originally described by Döderlein (1892) and then redescribed again by Döderlein (1898). It is difficult to distinguish this genus from *Plectroninia*. The existence of ascending radial lines in the main framework of large tetractines of the single known species may be a function of its massive shape as compared with encrusting Recent *Plectroninia*. Although these may represent different growth forms, we continue to separate the two genera, pending a revision that includes the fossil Minchinellidae. For illustration, see Döderlein 1898.

Genus *Tulearinia* Vacelet, 1977

TYPE SPECIES. — *Tulearinia stylifera* Vacelet, 1977 by monotypy.

DIAGNOSIS. — Minchinellidae (?) with a basal skeleton consisting of tetractines with basal actines that are interwoven but are not cemented, and with underlying layers of triactines linked in the same way.

DESCRIPTION

This genus may represent the first step in the process of the spicule linkage that is characteristic of Minchinellidae (Fig. 52). However, its inclusion in this family is questionable because the actine tips are only slightly modified, and true zygosis and diapasons are absent.

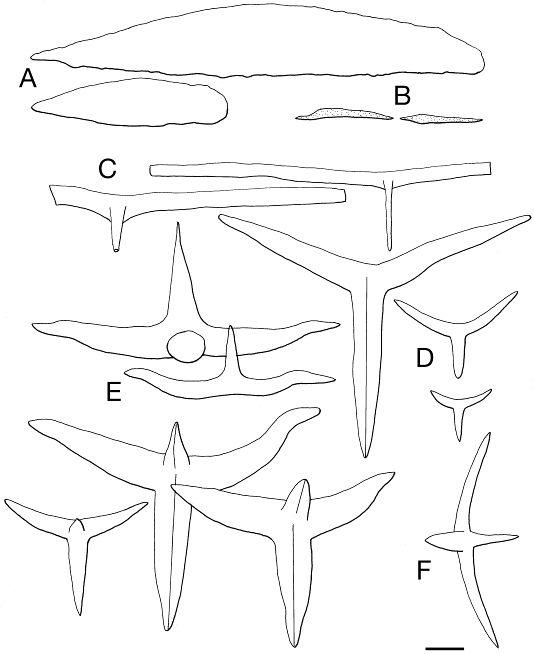

Fig. 52. — Diagram of dissociated spicules of *Tulearinia stylifera* Vacelet, 1977 (light micrograph); **A**, superficial diactines; **B**, microdiactines; **C**, perioscular triactines; **D**, triactines; **E**, tetractines from the basal network; **F**, tetractine from canals. Scale bars: A, D, E, 50 µm; B, C, 15 µm; F, 20 µm (from Vacelet 1977).

Family PETROBIONIDAE Borojevic, 1979

TYPE GENUS. — *Petrobiona* Vacelet & Lévi, 1958 by monotypy.

DIAGNOSIS. — Lithonida in which the basal skeleton is a solid mass. The living tissue is located between the crests and spines of the basal skeleton. The choanoskeleton and cortical skeleton consist of free spicules that may be trapped within the rigid skeleton.

Genus *Petrobiona* Vacelet & Lévi, 1958

TYPE SPECIES. — *Petrobiona massiliana* Vacelet & Lévi, 1958 by monotypy.

DIAGNOSIS. — Same definition as the family.

DESCRIPTION

The genus is known by a single species, which is the only member of the Calcarea that is provided with survival structures ("pseudogemmules")

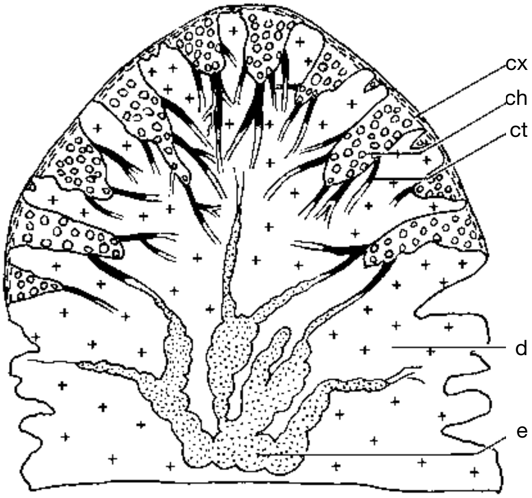

Fig. 53. — Diagram of the organization of *Petrobiona massiliana* Vacelet & Lévi, 1958. Abbreviations: **cx**, cortical skeleton; **ch**, choanosome; **ct**, tracts of storage cells; **d**, solid calcareous skeleton; **e**, parasitic excavating sponge (from Vacelet 1964).

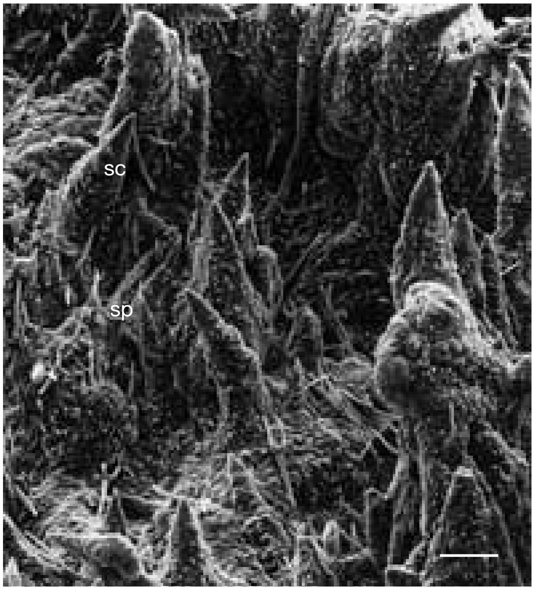

Fig. 54. — Surface view of the solid calcareous skeleton of *Petrobiona massiliana*, showing terminal spines of the sclerodermites (**sc**) and partially entrapped spicules (**sp**) (SEM). Scale bar: 50 µm (from Vacelet 1991).

KEY OF GENERA OF LITHONIDA

1. Skeleton including a solid mass of calcite .... *Petrobiona*

— Skeleton without a solid mass of calcite 2

2. Basal skeleton made of uncemented tri- and tetractines interlaced by their basal actines .... *Tulearinia*

— Basal skeleton made of tetractines cemented in a rigid network 3

3. Rigid network of tetractines embedded in a cement .... *Minchinella*

— Rigid network of tetractines not embedded in a cement 4

4. Basal skeleton made of a single category of tetractines .... *Monoplectroninia*

— Basal skeleton made of two categories of tetractines 5

5. Basal skeleton forming a thin basal layer .... *Plectroninia*

— Basal skeleton with ascending radial lines .... *Petrostroma*

enclosed within the calcareous skeleton (Vacelet 1964, 1990) (Fig. 53). The skeleton is formed by a solid mass of calcite consisting of elongated sclerodermites that form a series of crests between which lies the living tissue. Spicules trapped within the massive skeleton do not dissolve (Fig. 54). The massive skeleton differs in microstructure from that of *Murrayona* in the Calcinea. The species is known from both living and fossil specimens from Pleistocene strata in the Mediterranean.

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Submitted on 4 May 1999;
accepted on 6 October 1999.