

## Order Leucosolenida Hartman, 1958

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Leucosolenida Hartman (Calcarea, Calcaronea) is emended here to include nine families, and 42 genera. Leucosolenida seems to have evolved from the olynthus grade, a form that is probably present in the early stages of ontogenesis of all Leucosolenida, and subsists at the adult stage in *Leucosolenia*. Leucosolenida comprises a diverse group with several pathways of progressive 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).

**Keywords:** Porifera; Calcarea; Calcaronea; Leucosolenida; [Staurorrhaphidae]; Amphoriscidae; Grantiidae; Heteropiidae; Jenkinidae; Lelapiidae; Leucosoleniidae; Achramorphidae fam. nov.; Sycanthidae; Sycettidae; *Achramorpha*; *Amphiute*; *Amphoriscus*; *Anamixilla*; *Aphroceras*; *Ascute*; *Ascyssa*; *Breitfussia*; *Dermatreton*; *Grantessa*; *Grantia*; *Grantilla*; *Grantiopsis*; *Heteropia*; *Jenkina*; *Kebira*; *Lelapia*; *Leucandra*; *Leucandrilla*; *Leucascandra*; *Leucettaga*; *Leucilla*; *Leucosolenia*; *Megapogon*; *Paraheteropia*; *Paralelapia*; *Paraleucilla*; *Polejaevia*; *Sycandra*; *Sycantha*; *Sycetta*; *Sycettusa*; *Sycodorus*; *Sycon*; *Syconessa*; *Sycute*; *Sycyssa*; *Synute*; *Teichonopsis*; *Ute*; *Uteopsis*; *Vosmaeropsis*.

### DIAGNOSIS & SCOPE

#### Synonymy

Leucosolenida Hartman, 1958a: 108; Borojevic, 1967a: 192; Hartman, 1980b: 32; Hooper & Wiedenmayer, 1994: 449; Borojevic *et al.*, 2000: 210.

#### 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.

#### Scope

Leucosolenida represents a homogeneous group of sponges, in which are found all the possible modifications of the fundamental sponge bauplan, from asconoid to leuconoid, and including most of the intermediate stages of the progressive modifications of the associated skeleton. Consequently, the Leucosoleniida represents a single taxonomic unit that cannot be divided into two groups, according to homocoel or heterocoel grade of organization (Borojevic *et al.*, 2000: 210; Manuel, 2001: 132–140). The simplest forms correspond to the olynthus grade of organization, with a single tubular central cavity lined by choanocytes and are

found in the Leucosoleniidae. 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 characterised by a single central tube devoid of



**Fig. 1.** Diagram of the *Sycetta* type of organization. The arrow shows the direction of the water flow (after Borojevic *et al.*, 2000). Abbreviations: a, atrium; o, osculum; ps, pinacoderm and skeletal layer.

choanocytes, which corresponds to the atrium, from which tubes with a choanoderm radiate. This sponge has only an exhalant aquiferous system; the incurrent water flows directly into the radial tubes through inhalant pores. The first group of morphological characters used to define the Leucosolenida 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: (1) the growth and elongation of radial tubes which increases 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) (for details see Borojevic *et al.*, 2000: 211).

In typical species of this order and in fully-grown specimens, the main characteristic of each family is quite easily recognized. However for young specimens 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". A cladistic analysis using morphological and molecular characters is needed for understanding the phylogenetic relationships of the families and genera.

#### KEY TO GENERA

- (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 ..... *Acute*  
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*  
No 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 ..... *Dermatretton*
- (11) Presence of a distinct layer of subcortical pseudosagittal spicules ..... 12  
Absence of a distinct layer of subcortical pseudosagittal spicules ..... 17
- (12) Inarticulated choanoskeleton composed of the unpaired actines of subatrial spicules and the centripetal paired actines of subcortical pseudosagittal spicules ..... 13  
Articulated 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) Articulated 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  
Inarticulated choanoskeleton, or choanoskeleton composed of an external inarticulated 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 chactines (Achromorphidae fam. nov.) ..... 19  
With tangential atrial skeleton composed of triactines and/or tetractines ..... 20

(19) Syconoid organization .....	<i>Achramorpha</i>
Sylleibid or leuconoid organization .....	<i>Megapogon</i>
(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 diapasans .....	23
(22) Tubular sponge, syconoid or sylleibid organization, choanoskeleton with short, radially arranged tracts between the distal parts of the radial tubes .....	<i>Grantiopsis</i>
Massive sponge with a thick wall containing large diactines, choanoskeleton with long tracts in an approximately radial arrangement .....	<i>Kebira</i>
(23) Cortex composed of giant longitudinal diactines, which do not invade the choanoskeleton .....	<i>Paralelapia</i>
Giant diactines in the choanoskeleton .....	<i>Lelapia</i>
(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 .....	<i>Grantia</i>
Diameter of the osculum larger than that of the atrium: pedunculate calyciform sponge with a thin folded wall .....	<i>Teichonopsis</i>
(27) Septa with a specific skeleton of minute triactines within the atrial cavity .....	<i>Leucettaga</i>
No septa within the atrial cavity .....	28
(28) Cortex composed of triactines and possibly diactines, which protrude from the cortex making it hispid .....	<i>Leucandra</i>
Cortex with triactines and tetractines .....	<i>Leucandrilla</i>
(29) Leuconoid organization .....	<i>Aphroceras</i>
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 .....	<i>Synute</i>
(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 .....	<i>Sycute</i>
No tufts of radial diactines .....	<i>Ute</i>
(33) Longitudinal diactines present only in the atrial skeleton .....	<i>Sycodorus</i>
Longitudinal diactines present both in the atrial and the cortical skeleton .....	<i>Amphiute</i>
(34) Giant cortical tetractines (Amphoriscidae) .....	35
No giant cortical tetractines (Jenkinidae) .....	37
(35) Syconoid organization .....	<i>Amphoriscus</i>
Sylleibid or leuconoid organization .....	36
(36) Inarticulated choanoskeleton; scattered spicules occasionally between subcortical and subatrial layers .....	<i>Leucilla</i>
Choanoskeleton divided in two parts: the external part has an inarticulated organization, while the internal one is intercalated between the subatrial spicules and the atrial skeleton, and is supported by scattered triactines and/or tetractines .....	<i>Paraleucilla</i>
(37) Syconoid organization .....	38
Sylleibid or leuconoid organization .....	40
(38) Thin cortical skeleton, composed of one to several layers of triactines .....	<i>Breiffussia</i>
Reinforced cortical skeleton .....	39
(39) Skeleton reinforced with giant tangential triactines, which are also scattered in the choanoskeleton .....	<i>Anamixilla</i>
Reinforced skeleton with longitudinal diactines .....	<i>Uteopsis</i>
(40) Without scattered spicules in the choanoskeleton .....	41
With scattered spicules in the choanoskeleton, smaller than those of the cortex, and without defined position .....	<i>Polejaevia</i>
(41) Sponge growing as small individual tubes .....	<i>Jenkina</i>
Sponge forming a large cormus composed of copiously anastomosed and ramified tubes .....	<i>Leucascandra</i>

**FAMILY LEUCOSOLENIIDAE MINCHIN, 1900****Diagnosis****Synonymy**

Leucosoleniidae Minchin, 1900: 110; Hooper & Wiedenmayer, 1994: 491; Borojevic *et al.*, 2000: 215; Dendy & Row, 1913: 716 & 718; Homocoelidae Dendy & Row, 1913: 716; [in part] Burton, 1963: 136.

Leucosolenida 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.

**Scope**

Leucosoleniidae includes all the calcaronean homocoel sponges. In contrast to the Clathrinidae, which frequently form large massive corals, the Leucosoleniidae are most often small and creeping tubular sponges that only rarely form corals several centimetres large, such as *Leucosolenia complicata* (Montagu, 1818) or *Leucosolenia eleanor* Urban, 1905. Three genera have been recognized within the family: *Leucosolenia*, *Ascute* & *Ascyssa*.

**LEUCOSOLENIA BOWERBANK, 1864****Synonymy**

*Leucosolenia* Bowerbank, 1864: 164; Dendy & Row, 1913: 719; Burton, 1963 [in part]; Hooper & Wiedenmayer, 1994: 492; Borojevic *et al.*, 2000: 216.

**Type species**

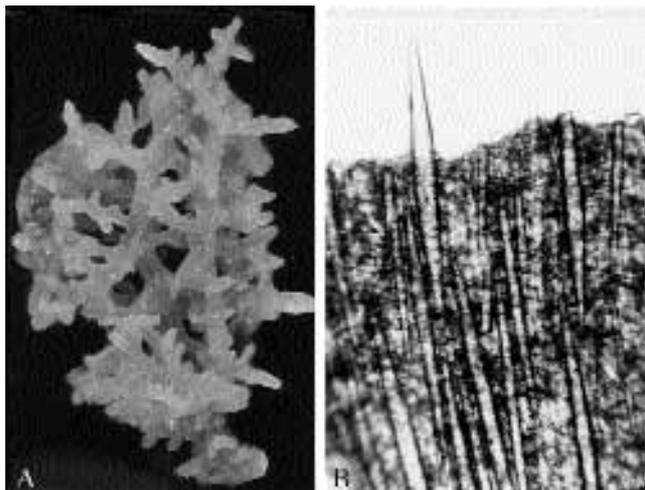
*Spongia botryoides* Ellis & Solander, 1786 (by original designation).

**Diagnosis**

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

**Scope**

*Leucosolenia* is morphologically very homogenous and consequently is presently considered cosmopolitan, and includes many species worldwide. The asconoid tubes may be creeping and only rarely branched, or be copiously ramified but not anastomosed;



**Fig. 2.** A, *Leucosolenia complicata* (Montagu, 1818) (3.5 cm high) from the Channel, MNHN C.1968.341. B, section of the wall of *Ascute* from Port Phillip Head (Australia), BMNH 1893.6.9.33 (after Borojevic *et al.*, 2000) (1 cm = 320  $\mu$ m).

they may form a large arborescent cornus, such as seen in *L. complicata* (Montagu, 1818). The cornus of *Leucosolenia* is always simple, without subdivisions or differentiation into regions with distinct functions, although in larger specimens the central and proximal tubes are usually wider than the distal ones. About 50 species have been described but all need thorough revision, in particular resolution of cosmopolitan cryptic species complexes.

**Distribution**

Found in all oceans.

**ASCUTE DENDY & ROW, 1913****Synonymy**

*Ascute* Dendy & Row, 1913: 729; Hooper & Wiedenmayer, 1994: 492; Borojevic *et al.*, 2000: 216; Burton, 1963: 182 [*Leucosolenia* in part].

**Type species**

*Leucosolenia uteoides* Dendy, 1893c (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.

**Scope**

Two species have been allocated to *Ascute*: *A. uteoides* and *A. asconoides* (Carter, 1886b: 134) both restricted so far to the Australian fauna (Port Phillip Heads).

**Remarks on the type species**

*Leucosolenia uteoides* Dendy, 1893c.

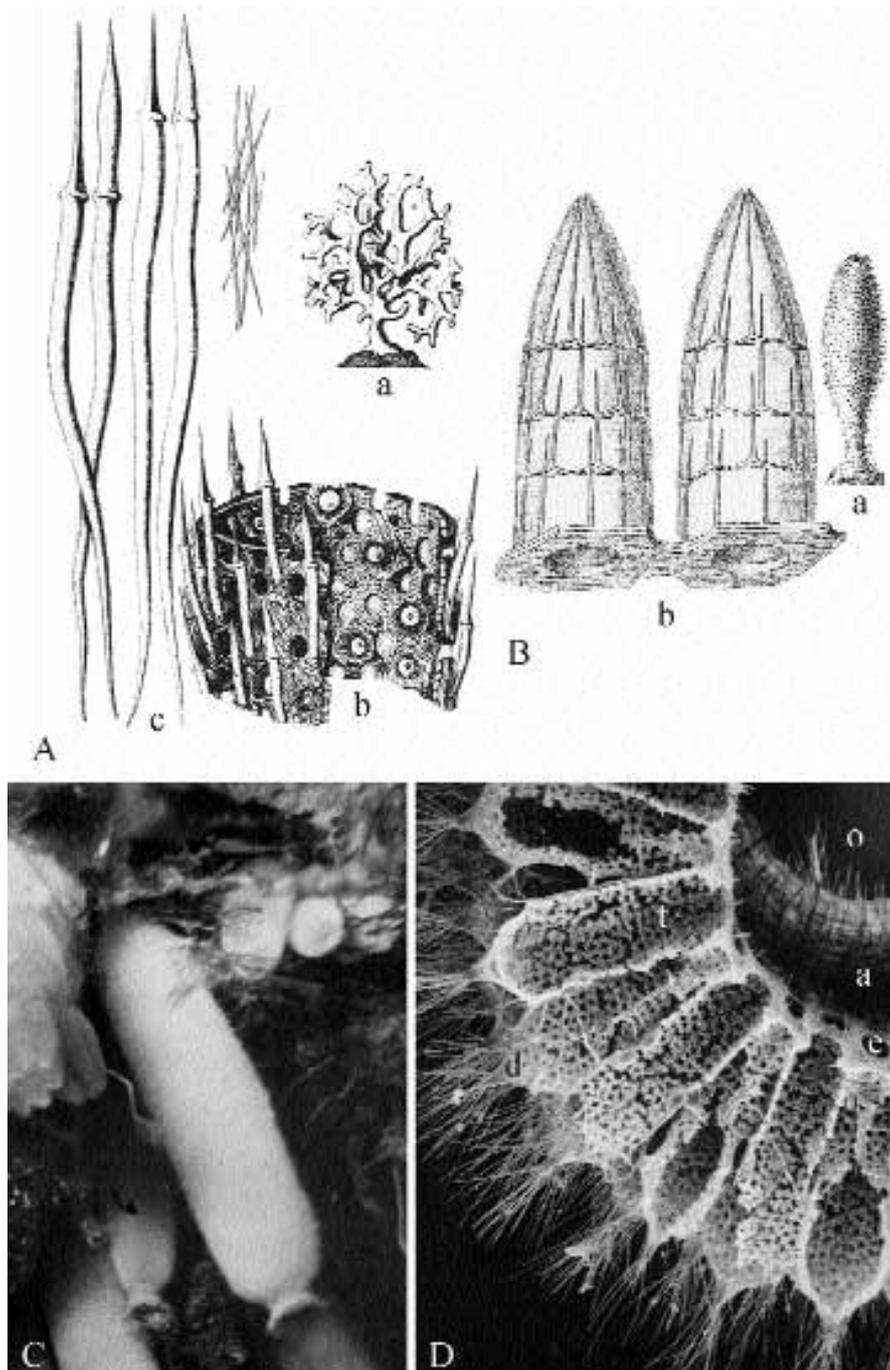
**Synonymy.** *Leucosolenia* Dendy, 1893c: 178; Burton, 1963: 183; *Ascute* Dendy & Row, 1913: 729; Hooper & Wiedenmayer, 1994: 492; Borojevic *et al.*, 2000: 216.

**Material examined.** Holotype BMNH 1893.6.9.33 – Port Phillip Heads.

**Remarks.** Dendy & Row (1913) placed the genus *Ascute* among sponges with basinuclate choanocytes. Re-examination of type material showed that it only has typical sagittal triactine and tetractine spicules that are organized in a pattern very similar to the skeleton of *Leucosolenia*, and quite different from the Clathrinidae (which are characterised by regular spicules). This genus, close to *Leucosolenia*, is placed in Leucosoleniidae until examination of new specimens will allow a re-evaluation of their cytology.

**ASCYSSA HAECKEL, 1872****Synonymy**

*Ascyssa* Haeckel, 1872: 48; Dendy & Row, 1913: 729; Borojevic *et al.*, 2000: 217; Burton, 1963: 38 [*Leucosolenia* in part].



**Fig. 3.** A, *Ascyssa troglodytes* Haeckel, 1872. a, external form. b, section of the wall. c, spicules (diactines) (after Haeckel, 1872). B, *Sycetta sagittifera* Haeckel, 1872. a, external form. b, schematic drawing of the skeleton of the radial tubes (after Haeckel). C, *Sycon ciliatum* (Fabricius, 1780) (7 cm high) from the Channel. D, *Sycon sycandra* Lendenfeld, 1885a, SEM section showing the organization of the aquiferous system (choanocyte chambers 375  $\mu\text{m}$  high) (abbreviations: a, atrium; d, distal cones; e, apopyle; o, oscule; t, tubes).

#### Type species

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

#### Diagnosis

Leucosolenidae with a skeleton composed entirely of diactines.

#### Scope

Haeckel (1872) described two species of *Ascyssa* from very few small specimens; representatives of this genus have not been found since. Given that 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.

**Distribution**

*A. acufera* is an Arctic species from Spitzberg and *A. troglodytes* is a NW Mediterranean species.

**FAMILY SYCETTIDAE DENDY, 1892****Synonymy**

Sycettidae Dendy, 1892a: 72; Dendy, 1913: 18; Dendy & Row, 1913: 742; Burton, 1963: 53; Hooper & Wiedenmayer, 1994: 498; Borojevic *et al.*, 2000: 217; Scyphidae de Laubenfels, 1936a: 196. [Syconidae] Haeckel, 1869 (*nomen oblitum*).

**Diagnosis**

Leucosolenida 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.

**Scope**

In Leucosolenida 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 Clathrinida. 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 of the genus *Sycon*, gives compactness to the sponge, simultaneously maintaining an efficient water circulation. Only two genera have been allocated to the family: *Sycetta* with only four species and *Sycon* which has a worldwide distribution with numerous species.

**SYCETTA HAECKEL, 1872****Synonymy**

*Sycetta* Haeckel, 1872: 240; Dendy, 1892a: 72; Dendy & Row, 1913: 743; Burton, 1963: 421; Hooper & Wiedenmayer, 1994: 499; Borojevic *et al.*, 2000: 217.

**Type species**

*Sycetta sagittifera* Haeckel, 1872 (by subsequent designation, Borojevic *et al.*, 2000).

**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.

**Scope**

*Sycetta*, as defined by Dendy & Row (1913), comprised three species described under the names *Sycetta primitiva* Haeckel, 1872, *S. sagittifera* Haeckel, 1872 and *Sycaltis conifera* Haeckel, 1872. However *Sycetta primitiva* is most likely a Calcinea (see discussion in the Levinellidae, Clathrinida). *Sycetta sagittifera*, as an originally included nominal species, was designated the type species of *Sycetta* by Borojevic *et al.* (2000: 218). This species displays all the characteristics of the genus as understood by Dendy (1893b), Dendy & Row (1913), and subsequent authors. Brøndsted (1931: 23) 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 characterised by the presence of diactines and the occasional coalescence of radial tubes, which, however, are not fused. Borojevic *et al.* (2000: 228) now placed *Tenthrenodes* Jenkin, 1908a in synonymy with *Sycantha* Lendenfeld, 1891. *Tenthrenodes primitivus* Brøndsted, 1931 is however much closer to a typical *Sycetta* and has been transferred to *Sycetta*. *Sycetta* (ex. *Tenthrenodes*) *primitiva* (Brøndsted, 1931) should be distinguished from *Sycettaga* (ex. *Sycetta*) *primitiva* Haeckel, 1872, which is now assigned to the family Levinellidae (Calcinea, Clathrinida).

**Distribution**

The type-species is from the Indian Ocean (Ceylon), *S. conifera* from the Adriatic and the other species from the Antarctic.

**SYCON RISSO, 1826****Synonymy**

*Sycon* Risso, 1826: 368; Dendy, 1892a: 72; Dendy & Row, 1913: 743; Burton, 1963: 51 [*Sycon*, 141; *Scypha* in part]; Hooper & Wiedenmayer, 1994: 499; Borojevic *et al.* 2000: 218; Manuel, 2001: 60, 101–104.

**Type species**

*Sycon humboldti* Risso, 1826 (by subsequent designation; Dendy, 1892a).

**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.

### Scope

The genus *Sycon* is cosmopolitan, and it is often considered to represent an archaetypal calcareous sponges. More than one hundred species have been described within this genus but the validity of all these is completely unknown, requiring a thorough revision. A recent cladistic analysis of morphological characters for 9 taxa have shown that this genus could be paraphyletic (Manuel, 2001: 101). 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, 1845a; *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 characterised by tangential triactine spicules. A group of small representatives of the genus arise from solid or tubular creeping stolons.

### Material examined

The type specimen is not known, and Haeckel's slide (named '*Sycon humboldtii* Risso, 1826', MNHN.C.1968.653) does not correspond to the description of the type-species.

### Reproduction

Asexual reproduction has been observed in some species with stolons. These stolons can produce terminal hollow spherical buds (e.g., *Sycon sycandra* Lendenfeld, 1885a), 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 and 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). Sexual reproduction has been extensively studied.

### Ecology

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 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.

### FAMILY GRANTIIDAE DENDY, 1892

#### Synonymy

Grantiidae Dendy, 1892a: 72; Dendy & Row, 1913: 757; de Laubenfels, 1936a: 193; Hooper & Wiedenmayer, 1994: 459; Borojevic *et al.*, 2000: 220.

#### Diagnosis

Leucosolenida in which there is always a cortex, supported by a skeleton of tangential spicules that can be diactines, triactines, tetractines, or any combination of these. 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.

#### Scope

Grantiidae has a central position among the Leucosolenida. 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 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. Twelve genera have been allocated to Grantiidae. While some of these are currently monospecific (e.g., *Teichonopsis*, *Sycute*, *Synute*), others (e.g., *Grantia*, *Leucandra*) include numerous species that occur throughout all the oceans.

### GRANTIA FLEMING, 1828

#### Synonymy

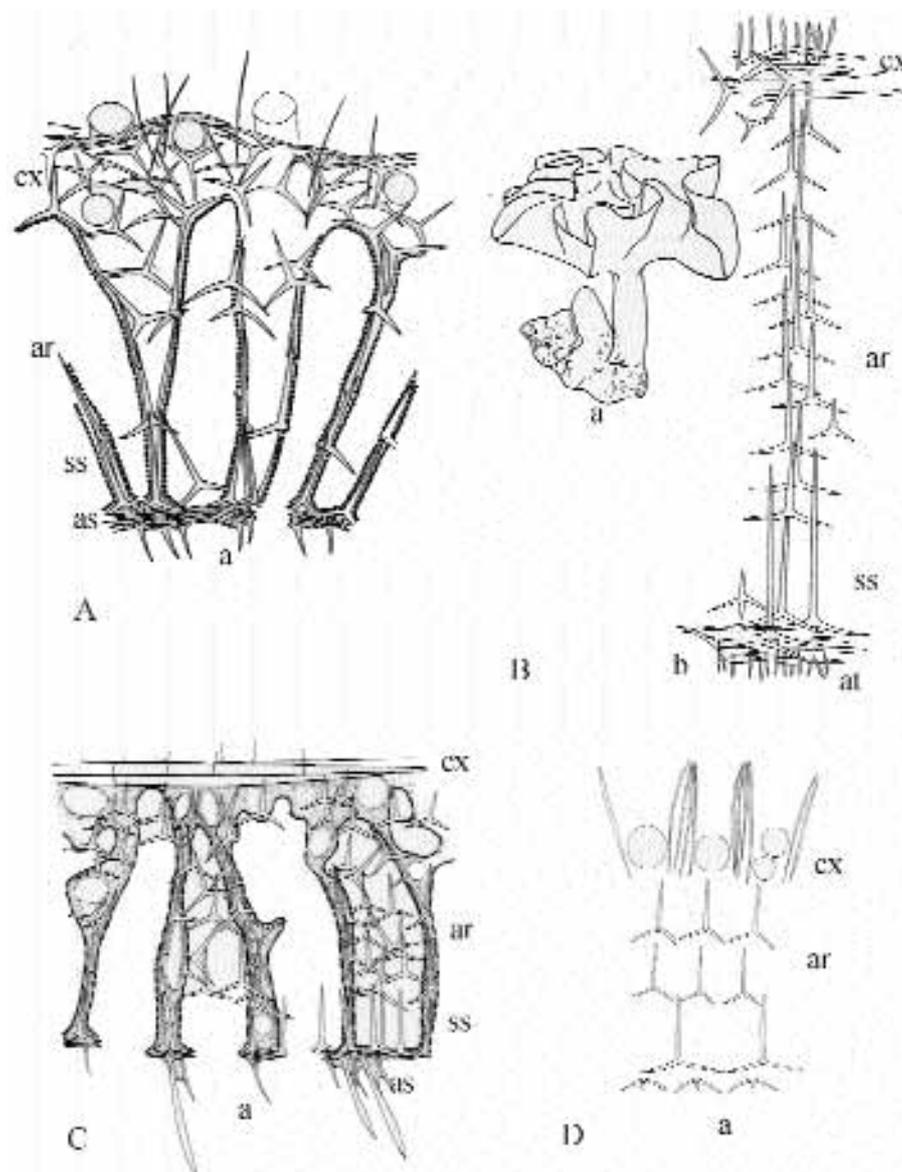
*Grantia* Fleming, 1828: 524; Dendy, 1892a: 73; Dendy & Row, 1913 : 759; Hooper & Wiedenmayer, 1994: 461; Borojevic *et al.*, 2000: 221.

#### Type species

*Spongia compressa* Fabricius, 1780 (by original designation).

#### Diagnosis

Grantiidae with syconoid organization. The cortex is composed of tangential triactines and/or tetractines, occasionally with



**Fig. 4.** A, *Grantia socialis* Borojevic, 1967b, diagram of a transverse section (after Borojevic, 1967b) (thickness 700  $\mu$ m) (abbreviations: a, atrium; ar, articulate choanosomal skeleton; as, atrial skeleton composed of tangential triactines and tetractines; cx, cortex; ss, subatrial spicules). B, *Teichonopsis labyrinthica* (Carter, 1878a). a, external form. b, diagram of a section at right angle to the surface (after Dendy, 1891) (abbreviations: at, atrium; ar, articulate choanosomal skeleton; cx, cortex; ss, subatrial spicules). C, *Ute gladiata* Borojevic, 1966b, diagram of a longitudinal section through the wall (after Borojevic, 1966b) (thickness 1000  $\mu$ m) (abbreviations: a, atrium; ar, articulate choanosomal skeleton; as, atrial skeleton; cx, cortex; ss, subatrial spicules). D, *Sycote dendyi* (Kirk, 1895), schematic representation of the skeleton (after Kirk, 1895) (abbreviations: a, atrium; ar, articulate choanosomal skeleton; cx, cortex).

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.

#### Scope

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.

#### SYCANDRA HAECKEL, 1872

##### Synonymy

*Sycandra* Haeckel, 1872: 370 pars; Dendy & Row, 1913: 749; Breitfuss, 1932: 246; Borojevic *et al.*, 2000: 222.

##### Type species

*Ute utriculus* Schmidt, 1870 (by subsequent designation; Dendy & Row 1913: 749).

**Diagnosis**

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

**Scope**

Dendy & Row (1913) retained Haeckel's genus *Sycandra* for a single species, *S. utriculus*, characterised 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. However, 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. This species has been recorded only from the Arctic and N Atlantic, from 20–860 m.

**TEICHONOPSIS DENDY & ROW, 1913****Synonymy**

*Teichonopsis* Dendy & Row, 1913: 761; Hooper & Wiedenmayer, 1994: 472; Borojevic *et al.*, 2000: 222.

**Type species**

*Teichonella labyrinthica* Carter, 1878a (by monotypy).

**Holotype**

BMNH 1955.11.2.104 – Fremantle, Australia.

**Diagnosis**

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

**Scope**

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 asymmetrical leaf, freely traversed by the water current that runs from the lower cortical to the upper atrial surfaces.

**Distribution**

SW Pacific: western and southern coasts of Australia.

**UTE SCHMIDT, 1862****Synonymy**

*Ute* Dendy & Row, 1913: 763; Borojevic, 1966b: 712; Hooper & Wiedenmayer, 1994: 471; Borojevic *et al.*, 2000: 222.

**Type species**

*Ute glabra* Schmidt, 1864 (by monotypy).

**Diagnosis**

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

**Scope**

Calcarea belonging to the genus *Ute* are among the most beautiful of calcareous sponges. They have a regular tubular form with a vitreous, smooth and shiny surface due to many longitudinal, parallel diactines. The relationship between the genera *Ute* and *Aphroceras* has been discussed previously (Borojevic, 1966b) but most of the species allocated to this genus require thorough revision.

**Distribution**

The type species is Mediterranean, whereas the other species (about 12) have been found in all the seas.

**SYCUTE DENDY & ROW, 1913****Synonymy**

*Sycute* Dendy & Row, 1913: 763; Borojevic *et al.*, 2000: 222; Kirk, 1895: 287 [as *Sycon dendyi*].

**Type species**

*Sycon dendyi* Kirk, 1895 (by monotypy).

**Diagnosis**

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

**Scope**

This genus has a single species described by Kirk (1895) under the name *Sycon*. Like *Sycon*, it is characterised by tufts of diactines that decorate the distal cones of the radial tubes, and like *Ute* it has longitudinal cortical giant diactines.

**Distribution**

SouthWest Pacific: New Zealand.

**SYNUTE DENDY, 1892****Synonymy**

*Synute* Dendy, 1892b: 1; Dendy, 1892a: 74; Dendy, 1893b: 174; Dendy & Row, 1913: 764; Hooper & Wiedenmayer, 1994: 471; Borojevic *et al.*, 2000: 222.

1166

Porifera • Calcarea • Calcaronea • Leucosolenida

**Type species**

*Synute pulchella* Dendy, 1892 (by monotypy).

**Holotype**

NMV G2404 – Port Phillip Heads.

**Diagnosis**

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

**Scope**

This genus is monospecific and only known from the southern Australian coasts.

**AMPHIUTE HANITSCH, 1894****Synonymy**

*Amphiute* Hanitsch, 1894b: 433; Dendy & Row, 1913: 754; Borojevic, 1965: 665; Borojevic *et al.*, 2000: 223.

**Type species**

*Amphiute paulini* Hanitsch, 1894b (by monotypy).

**Diagnosis**

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

**Scope**

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

**Material examined**

Holotype from the collection of the Zoological Museum of the University of Coimbra (Portugal).

**Distribution**

NE Atlantic: Iberian coasts and the Channel.

**SYCODORUS HAECKEL, 1872****Synonymy**

*Sycodorus* Haeckel, 1872: 375; Dendy & Row 1913: 764; Burton, 1963: 569; Borojevic *et al.*, 2000: 224.

**Type species**

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

**Diagnosis**

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

**Scope**

*Sycodorus* is a variation of the type of sponges belonging to the 'group' *Ute*, whose skeleton is provided with longitudinal diactines. They are characterised by the presence of longitudinal diactines that are restricted to the atrial tangential skeleton. The genus is currently monotypic.

**Distribution**

South Africa. The Mediterranean record is doubtful (Topsent, 1934b: 11).

**LEUCANDRA HAECKEL, 1872****Synonymy**

*Leucandra* Haeckel, 1872: 173; Dendy & Row, 1913: 768; Burton, 1963: 95; Hooper & Wiedenmayer, 1994: 464; Borojevic *et al.*, 2000: 224.

**Type species**

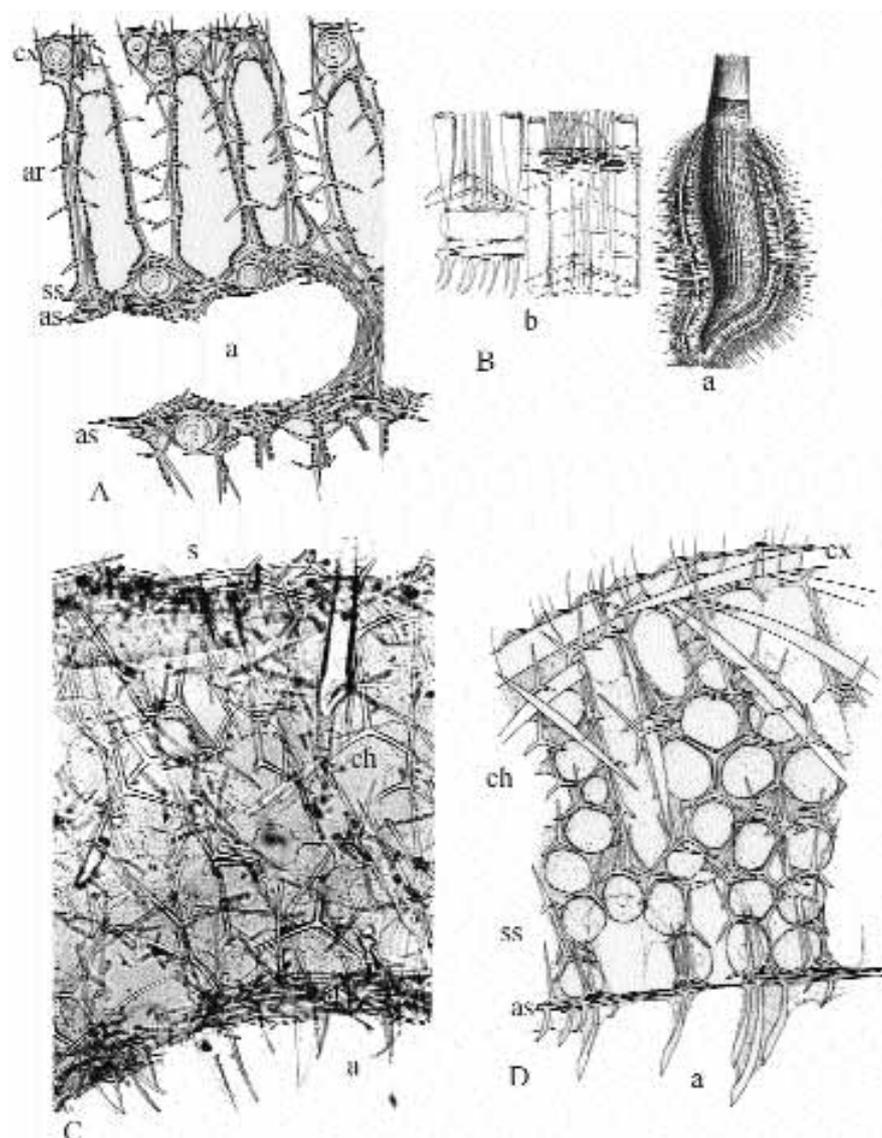
*Sycinula egedii* Schmidt, 1870 (by subsequent designation; Dendy & Row, 1913).

**Diagnosis**

Grantiidae with 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.

**Scope**

This is a very large genus containing many nominal species (about 70) for which *Leuconia* Grant 1833 has been frequently used. This name was rejected by Borojevic *et al.* (2000), who wrongly believed that it was preoccupied by a mollusc. *Leuconia* in fact predates the mollusc and is thus available for sponges, but its type species, *Spongia nivea* Grant, 1826, is transferred to the order Baerida. Initially *Leucandra* was defined primarily by negative characters, and included most of the leuconoid Calcarea. Dendy & Row (1913) narrowed this definition and thus succeeded in providing a more positive diagnosis for the taxon. In particular, they reallocated numerous leuconoid calcinean species to *Leucetta*. Borojevic *et al.* (2000) separated from *Leucandra* another group of species into the order Baerida, which has a particular skeletal organization and are classified in the genus *Leuconia*. At the same time, following Jenkin (1908a) and Brøndsted (1931), they allocated species with thin walls



**Fig. 5.** A, *Amphite lepadiformis* Borojevic, 1967b, diagram of a transverse section (after Borojevic, 1967b) (thickness 800  $\mu\text{m}$ ) (abbreviations: a, atrium; ar, articulate choanosomal skeleton; as, atrial skeleton; cx, cortex; ss, subatrial spicules). B, *Sycodorus hystrix* (Haeckel, 1872). a, section through holotype. b, section at right angles to surface (after Haeckel, 1872). C, *Leucandra aspera* (Schmidt, 1862), histological transverse section through the wall (after Borojevic *et al.*, 2000) (thickness 2300  $\mu\text{m}$ ) (abbreviations: a, atrium; as, atrial skeleton; ch, choanosomal skeleton; s, surface). D, *Aphroceras ensata* (Bowerbank, 1858), diagram of a transverse section through the wall (after Borojevic, 1966b) (thickness 1600  $\mu\text{m}$ ) (abbreviations: a, atrium; as, atrial skeleton; ch, choanosome; cx, cortex; ss, subatrial spicules).

and an inarticulated type of choanoskeleton into the family Jenkinidae; following Dendy (1913) they also allocated grantiid sponges with tetractines in the cortical skeleton into a new genus *Leucandrilla*. As pointed out by Dendy & Row (1913), *Leucandra* may 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 one that is scattered. Nonetheless, traces of the original radial organization are clearly preserved in the subatrial skeleton.

#### Distribution

*Leucandra* has numerous representatives in all oceans. The type species has been found in Arctic from littoral to 2000 m deep.

#### APHROCERAS GRAY, 1858

##### Synonymy

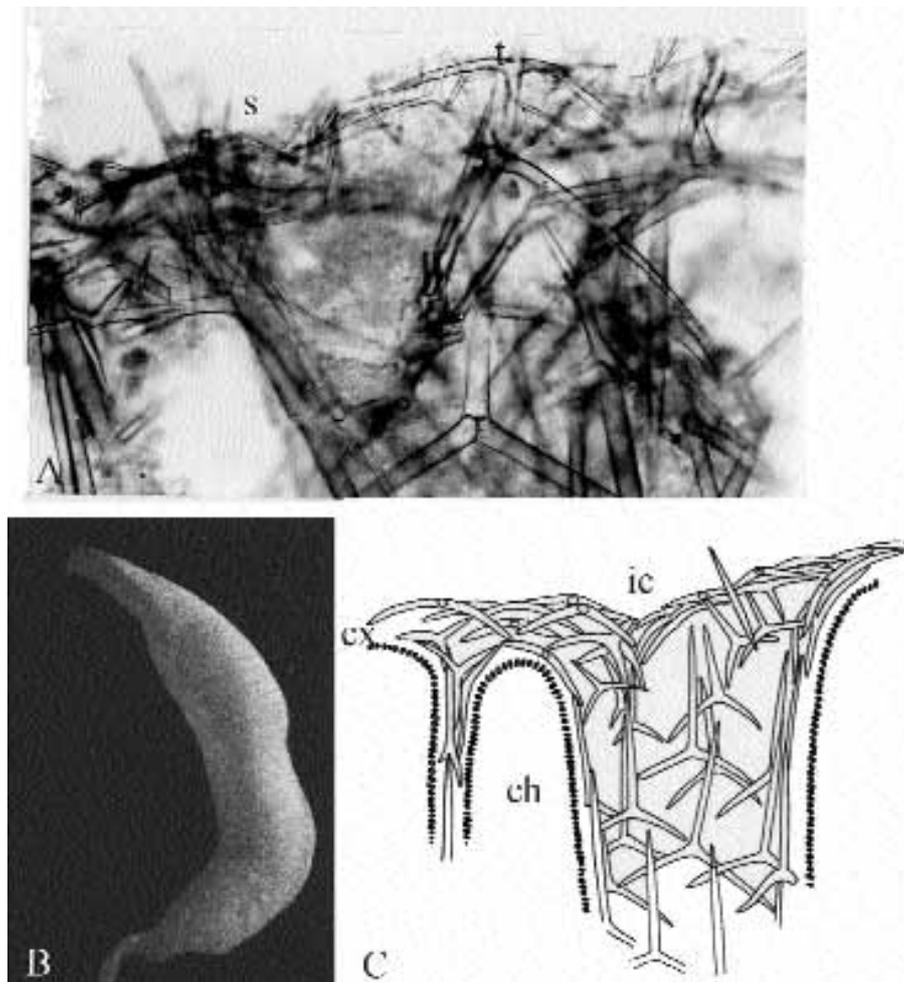
*Aphroceras* Gray, 1858a: 113; Dendy & Row, 1913: 776; Burton, 1963: 491; Borojevic, 1966b: 707; Hooper & Wiedenmayer, 1994: 460; Borojevic *et al.*, 2000: 225.

##### Type species

*Aphroceras alvicornis* Gray, 1858a (by monotypy).

##### Diagnosis

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



**Fig. 6.** A, *Leucandrilla wasinensis* (Jenkin, 1908), transverse section through the holotype (BMNH 1908.9.25.59) (after Borojevic *et al.*, 2000) (1 cm = 170  $\mu$ m) (abbreviations: s, surface; t, tetractine). B, *Dermatretion hodgsoni* Jenkin, 1908, holotype (after Jenkin, 1908) natural size. C, diagram of the *Dermatretion* wall organization (after Borojevic *et al.*, 2000) (abbreviations: ch, choanoderm; cx, cortex; ic, inhalant cavities).

### Scope

*Aphroceras* is differentiated from *Leucandra* by the presence of internal longitudinal diactines in the cortex. Borojevic (1966b) showed that the number of these spicules can be quite variable, ranging from a continuous dense layer to only very rare spicules, or even absent completely. In the latter case, it is not possible to distinguish this sponge from a typical *Leucandra*. However, for the time being, this genus is retained until a precise revision of all species of *Aphroceras*, *Leucandra* and *Ute* is undertaken (Borojevic, 1966b).

### Distribution

About 10 species have been described worldwide. *Aphroceras alcicornis* is an Indo-Pacific species (Hooper & Wiedenmayer, 1994: 461) described from Hong-Kong.

### LEUCANDRILLA BOROJEVIC, BOURY-ESNAULT & VACELET, 2000

### Synonymy

*Leucandrilla* Borojevic *et al.*, 2000: 226.

### Type species

*Leucilla wasinensis* Jenkin, 1908a (by original designation).

### Diagnosis

Grantiidae with leuconoid organization. In addition to triactines the cortex contains tetractines, with the apical actines turned into the choanoderm. The articulated 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.

### Material examined

Type specimen BMNH 1908.9.25.59; other material, BMNH 1936.3.4.537. Not *Leuconia wasinensis* (Burton, 1963: 363).

### Scope

*Leucandrilla* is differentiated from *Leucandra* by the presence of tetractines in the cortical skeleton. 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 (1987b) 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 allocated to Grantiidae. In particular, they have a completely articulated choanoskeleton, reminiscent of the grantiid organization, which is absent in Amphoriscidae. While Dendy (1913) proposed that these sponges should be included in *Leucandra*, Borojevic *et al.* (2000) proposed to allocate them in a separate genus in Grantiidae. It should be noted that the cortical tetractines are a secondary character, corresponding to a modification of normal cortical triactines, while cortical tetractines of Amphoriscidae are a primary character, marking an independent evolutionary line.

To date three species have been allocated to *Leucandrilla*: the type-species, *L. wasinensis* (Jenkin, 1908b), *L. intermedia* (Row, 1909), and *L. lanceolata* (Row & Hôzawa, 1931).

#### Distribution

The type locality of the type species is East Africa (Wasin). All three species are from the Indo-Pacific region.

#### LEUCETTAGA HAECKEL, 1872

##### Synonymy

*Leucettaga* Haeckel, 1872: 127; Dendy & Row, 1913: 777; Burton, 1963: 114; Borojevic *et al.*, 2000: 227.

##### Type species

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

##### Diagnosis

Grantiidae (?) with leuconoid organization. The skeleton is composed only of 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.

##### Scope

Dendy & Row (1913) retained the genus *Leucettaga* with a single species, *Leucetta loculifera* Haeckel, 1872, for the sponge described as one of the subspecies of *Leucetta 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. The presence of atrial tracts is considered as a distinctive character for the genus *Sycandra*, and consequently Borojevic *et al.* (2000) retained 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 at all, in which a skeleton composed of

only triactines is quite unusual. The precise classification of this genus will only be possible from detailed histological examination of new specimens. It was described from Pacific Ocean.

#### FAMILY SYCANTHIDAE LENDENFELD, 1891

##### Synonymy

Sycanthidae Lendenfeld, 1891: 192; Borojevic *et al.*, 2000: 229.

##### Type genus

*Sycantha* Lendenfeld, 1891 (by original designation).

##### Diagnosis

Leucosolenida with 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.

##### Scope

Borojevic *et al.* (2000) allocated two genera to Sycanthidae, both of which are derived from sponges with a sycetid type of organization and have a particular type of growth form. 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., *Dermatretion*). 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 from the National Antarctic Expedition collections, Jenkin (1908a) proposed the genera *Tenthrenodes*, *Hypodictyon* and *Dermatretion* 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).

Consequently, Borojevic *et al.* (2000) considered that *Tenthrenodes* and *Hypodictyon* are synonyms of *Sycantha*, while they retained *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.

#### SYCANTHA LENDENFELD, 1891

##### Synonymy

*Sycantha* Lendenfeld, 1891: 235; *Hypodictyon* Jenkin, 1908a; Borojevic *et al.*, 2000: 228; Topsent, 1934b: 10 [as *Sycon*]; Burton, 1963: 67 [as *Sycon*]; Dendy & Row, 1913: 795 [as *Sycon*]. Taxonomic decision for synonymy: Borojevic *et al.* (2000).

##### Type species

*Sycantha tenella* Lendenfeld, 1891 (by monotypy).

##### Diagnosis

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

##### Scope

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, 1908a) 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), it is retained in *Sycon*. As pointed out by Dendy & Row (1913), the sponge described as *Tenthrenodes scotti* Jenkin, 1908a has tangential spicules at the distal parts of the radial tubes. This species has the organization typical of the Sycanthidae and belongs to *Dermatreton* as it is understood now (Borojevic *et al.*, 2000). *Sycantha* (ex. *Hypodictyon*) *longstaffi* (Jenkin, 1908a) is apparently one of the typical representatives of the genus. As discussed under the family Achramorphidae fam. nov., the presence of the subatrial spicules with a lone centrally directed apical actine, is common in many Leucosolenida, and does not merit the separation of the genus *Hypodictyon* from *Sycantha*. Two species have been allocated to this genus so far.

##### Distribution

The type locality of the type species is Trieste (Adriatic), and the second species comes from the Antarctic.

#### DERMATRETON JENKIN, 1908

##### Synonymy

*Dermatreton* Jenkin, 1908b: 23 [in part]; Borojevic *et al.*, 2000: 229; Dendy & Row, 1913: 789 [as *Grantia*]; Burton, 1963: 487 [as *Grantia*].

##### Type species

*Dermatreton hodgsoni* Jenkin, 1908a (by subsequent designation; Borojevic *et al.*, 2000).

##### Diagnosis

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

##### Material examined

Holotype BMNH 1907.8.6.74 and fragment of the holotype MNHN-LBIM C 1968.42.

##### Scope

*Dermatreton* contains two species with a loose cortex covering the distal parts of fused radial tubes, which 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) did not designate a type species for the genus, with Borojevic *et al.* (2000) subsequently designating *D. hodgsoni* as the type species, with a second species included (*Dermatreton* (ex. *Tenthrenodes*) *scotti*). A third nominal species, *Dermatreton chartaceum*, was allocated to *Breitfussia*.

##### Distribution

Both species live in Antarctica.

#### FAMILY JENKINIDAE BOROJEVIC, BOURY-ESNAULT & VACELET, 2000

##### Synonymy

Jenkinidae Borojevic *et al.*, 2000: 229.

##### Diagnosis

Leucosolenida with syconoid, sylleibid or leuconoid organization. The thin wall surrounding the large atrial cavity is supported by tangential atrial and cortical skeletons, and essentially an inarticulated 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.

##### Scope

Jenkinidae presently contains 6 genera (*Breitfussia* Borojevic *et al.*, 2000, *Jenkina* Brøndsted, 1931, *Leucascandra* Borojevic *et al.*, 2000, *Anamixilla* Poléjaeff, 1883, *Polejaevia* Borojevic *et al.*, 2000, and *Uteopsis* Dendy & Row, 1913), all characterised by an inarticulated choanoskeleton (Borojevic *et al.*,

2000). 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 inarticulated skeleton into the genus *Jenkina*. However, a primary inarticulated 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, 1987b). Dendy (1913), and Dendy & Row (1913) underlined the differences between the *Leucilla* that have an inarticulated type of choanoskeleton and which derive from *Amphoriscus*, and those with an articulated skeleton, by transferring the former group to the genus *Leucandra* (now allocated to *Leucandrilla* Borojevic *et al.*, 2000). This implies that the inarticulated type of choanoskeleton, and not the cortical tetractines, is the primary characteristic of Amphoriscidae. Borojevic *et al.* (2000) considered that an inarticulated 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 strategy, and is not a secondary reduction of the thickness of the sponge wall during its evolution. Consequently, sponges with this organization should be separated from those with a massive type of growth form, as observed in Grantiidae. While in Amphoriscidae the cortical skeleton is always supported by large tetractines, in 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 inarticulated skeleton that becomes articulated when the sponge is fully grown. Conversely, Jenkinidae are characterised by an inarticulated skeleton in fully-mature sponges. As mentioned previously the growth of these long tubular sponges into a large branched corium, such as observed in *Leucascandra*, *Anamixilla* and *Uteopsis*, is a consequence of the restriction of their radial growth, and this is unique to the Leucosolenida.

#### **BREITFUSSIA BOROJEVIC, BOURY-ESNAULT & VACELET, 2000**

##### **Synonymy**

*Ebnerella* (in part) Breitfuss, 1896: 429; *Breitfussia* Borojevic *et al.*, 2000: 230.

##### **Type species**

*Ebnerella schulzei* Breitfuss, 1896 (by original designation).

##### **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.

##### **Scope**

The species included by Lendenfeld (1891) in *Ebnerella* belongs now to the genus *Amphoriscus*, and *Ebnerella* is thus a junior synonym of *Amphoriscus*. Among the species described

latter by Breitfuss (1896) in *Ebnerella*, *E. kuekenthali* belongs to the family Heteropiidae, with only *E. schulzei* remaining in Jenkinidae and which has been allocated to a new genus *Breitfussia* by Borojevic *et al.* (2000). Two other species, with an inarticulated choanoskeleton, were allocated to *Breitfussia* by Borojevic *et al.* (2000): *Breitfussia* (ex. *Grantia*) *vitiosa* (Brøndsted, 1931), and *Breitfussia* (ex. *Dermatreton*) *chartacea* (Jenkin, 1908a).

##### **Distribution**

*Breitfussia* is known only from cold Arctic and Antarctic waters.

#### **JENKINA BRØNDSTED, 1931**

##### **Synonymy**

*Jenkina* Brøndsted, 1931: 33; de Laubenfels, 1936a: 196; Hooper & Wiedenmayer, 1994: 464; Borojevic *et al.*, 2000: 230.

##### **Type species**

*Leucandra hiberna* Jenkin, 1908a (by subsequent designation; de Laubenfels, 1936a).

##### **Diagnosis**

Jenkinidae with a simple tubular body and 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.

##### **Scope**

Brøndsted (1931) proposed the genus *Jenkina* for a group of sponges described by Jenkin (1908a: 14) and by himself from Antarctica. These sponges are well-characterised by an inarticulated 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 a precise revision of all species included in *Breitfussia* and *Jenkina* is essential to better understand the scope of both genera.

##### **Distribution**

Antarctica, from 380–390 m depth.

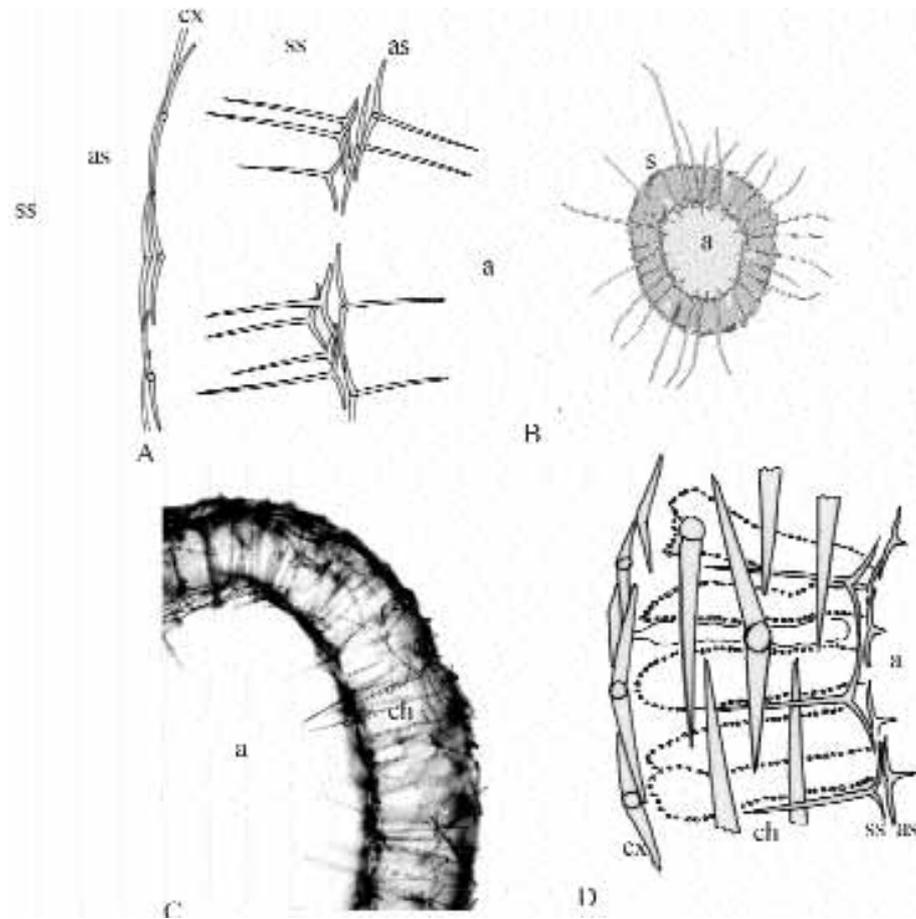
#### **LEUCASCANDRA BOROJEVIC & KLAUTAU, 2000**

##### **Synonymy**

*Leucascandra* Borojevic & Klautau, 2000: 199.

##### **Type species**

*Leucascandra caveolata* Borojevic & Klautau, 2000 (by monotypy).



**Fig. 7.** A, Diagram of the Jenkinidae-type of skeleton (after Borojevic *et al.*, 2000) (abbreviations: a, atrium; as, atrial skeleton; cx, cortex; ss, subatrial spicules). B, *Jenkinia hiberna* (Jenkin, 1908), diagram of a section through the holotype (after Jenkin 1908) (abbreviations: a, atrium; s, surface). C, *Leucascandra caveolata* Borojevic & Klautau, 2000, histological transverse section through the wall (100  $\mu$ m thick) (after Borojevic *et al.*, 2000) (abbreviations: a, atrium; ch, choanoderm). D, *Anamixilla torresi* Poléjaeff, 1883, diagram of a transverse section through the wall of the holotype (abbreviations: a, atrium; as, atrial skeleton; ch, choanoderm; cx, cortex; ss, subatrial spicules).

### 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 inarticulated choanoskeleton that is supported only by unpaired actines of subatrial triactines. Both cortical and atrial skeletons consist of a thin layer of tangential triactines and/or tetractines.

### Scope

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

### Description of the type species

*Leucascandra caveolata* Borojevic & Klautau, 2000.

**Synonymy.** *Leucascandra caveolata* Borojevic & Klautau, 2000: 199; Borojevic *et al.*, 2000: 231.

**Material examined.** Holotype MNHN LBIM C 1999-05 – New Caledonia (with many other specimens).

**Description.** The holotype forms a large cormus of about 10 cm high of a rather loose network composed of delicate tubes, the larger ones attaining nearly 1 cm in diameter. The smaller ones (about 2 mm in diameter) rise perpendicularly from the larger ones. They are ramified at the distal part, and occasionally anastomosed, bearing a naked osculum at the end. They are brown in color, and the wall of the tubes is supported by a thin cortex, composed only of triactines, and a parallel atrial skeleton composed of tetractines. In both layers, most spicules are arranged in parallel, with the unpaired angle directed towards the osculum. The thin choanosome is only supported by the unpaired actines of the subatrial triactines. All the spicules are of a similar thickness.

### Distribution

This sponge is common on the east and south coasts of New Caledonia, in the littoral zone 15–30 m depth. The type locality is the 'Passe de Nakéty' 20 m depth.

**ANAMIXILLA POLÉJAEFF, 1883****Synonymy**

*Anamixilla* Poléjaeff, 1883: 50; Dendy, 1893b: 177; Dendy & Row, 1913: 766; Hooper & Wiedenmayer, 1994: 460; Borojevic *et al.*, 2000: 232.

**Type species**

*Anamixilla torresi* Poléjaeff, 1883 (by monotypy).

**Diagnosis**

Jenkinidae with 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.

**Material examined**

Holotype. BMNH 1884.11.22.28 – ‘Challenger’. Fragment of holotype. MNHN LBIM C 1968.29. Other material: MNHN LBIM C 1968.140 – ZMA ‘Siboga’ expedition (slide).

**Scope**

In *Anamixilla* large triactines form a thick cortex and apparently invade the choanosome. A similar phenomenon has been 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, 1930c, but re-examination of a specimen of this species (BMNH 1929.8.30.6) shows that it does not belong to the genus *Anamixilla*.

**Distribution**

Indo-Malayan archipelago and W Pacific, Great Barrier Reef.

**POLEJAEVIA BOROJEVIC, BOURY-ESNAULT & VACELET, 2000****Synonymy**

[*Polejna*] (in part) Lendenfeld, 1891: 110; *Polejaevia* Borojevic *et al.*, 2000: 232.

**Type species**

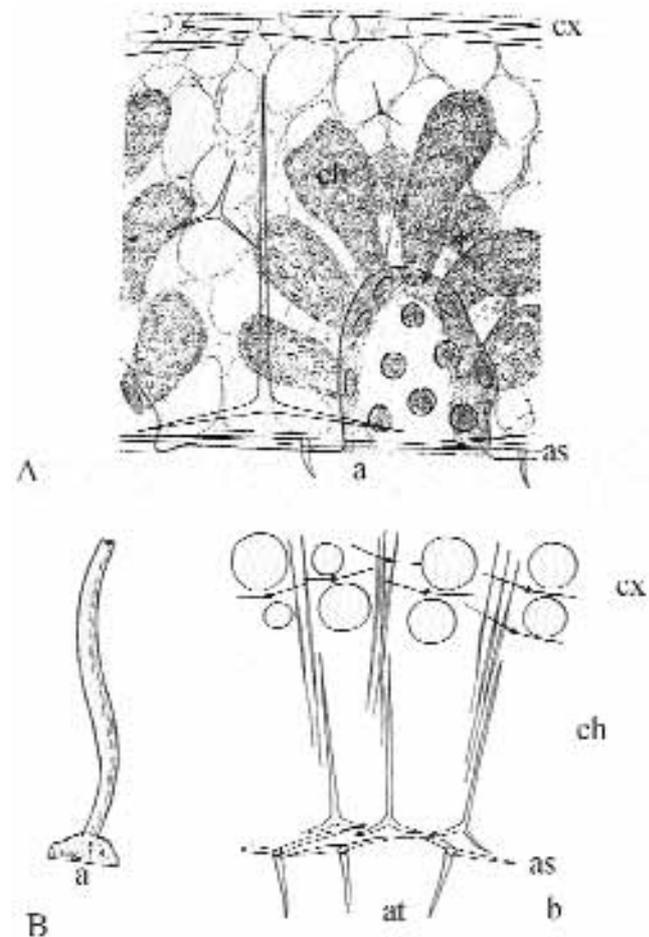
*Polejna telum* Lendenfeld, 1891 (by monotypy).

**Diagnosis**

Jenkinidae with 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.

**Scope**

In the system proposed by Lendenfeld (1891), *Polejna* Lendenfeld, 1885a was used for sylleibid sponges with triactines and tetractines. The type species of *Polejna*, described originally as *Leucilla uter* Poléjaeff, 1883, is in fact a good species of *Leucilla* (Borojevic & Boury-Esnault, 1987b). *Polejna* is thus a junior synonym of *Leucilla*. Subsequently, Lendenfeld (1891) described a new species from the Adriatic, *Polejna telum* Lendenfeld, 1891, that Borojevic *et al.* (2000) considered to be different from Amphoriscidae, and subsequently placed in Jenkinidae. A new name has been proposed for Jenkinidae with a sylleibid organization and triactines and tetractines, such as *Polejna telum*, as *Polejaevia* (Borojevic *et al.*, 2000). The position of *Polejaevia* in Jenkinidae is somewhat dubious, however, since small choanosomal triactines have been described from it and are represented in the illustration of the type species (Lendenfeld, 1891: 112), distinguishing it from typical Jenkinidae. The size and distribution of the triactines is also quite unusual, and as they are not reminiscent of the articulated choanoskeleton of the tubes of the Grantiidae – thus, classification of *P. telum* in *Leucandra* is impossible. Lendenfeld (1891) suggested that the triactines might be young cortical triactines. Secondary



**Fig. 8.** A, *Polejaevia telum* (Lendenfeld, 1891), diagram of a transverse section (after Lendenfeld, 1891) (abbreviations: a, atrium; as, atrial skeleton; ch, choanocyte chambers; cx, cortex). B, *Uteopsis argentea* (Poléjaeff, 1883). a, external form (3 cm high). b, section at right angle to surface (after Poléjaeff) (abbreviations: at, atrium; as, atrial skeleton; ch, choanocyte chambers; cx, cortex).

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. The genus should be maintained in the Jenkinidae until histological evidence can be evaluated from new material. The description of *Leucandra mawsoni* Dendy, 1918 suggests that it might belong to *Polejaevia*. Borojevic *et al.* (2000) examined specimens (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.

#### Distribution

Adriatic Sea, close to Lesina.

#### UTEOPSIS DENDY & ROW, 1913

#### Synonymy

*Uteopsis* Dendy & Row, 1913: 766; Burton, 1963: 145; Hooper & Wiedenmayer, 1994: 473; Borojevic *et al.*, 2000: 233.

#### Type species

*Ute argentea* Poléjaeff, 1883 (by monotypy).

#### Diagnosis

Jenkinidae with 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.

#### Material examined

BMNH 1929.6.18.14 and fragment from the 'Siboga' expedition (ZMA collection): MNHN LBIM C1968.25.

#### Scope

*Uteopsis* is well described and illustrated by Poléjaeff (1883: 43). It is characterised by an inarticulated choanoskeleton and a thick cortex composed of giant longitudinal diactines and triactines. It is a currently a monospecific genus.

#### Distribution

Indo-Pacific region, type locality being Two-fold Bay (New South Wales, Australia).

#### FAMILY HETEROPIIDAE DENDY, 1892

#### Synonymy

Heteropiidae Dendy, 1892b: 75; Dendy, 1893b: 238; Dendy & Row, 1913: 750; Hôzawa, 1916: 1; Borojevic, 1965: 669;

Hooper & Wiedenmayer, 1994: 474; Borojevic & Klautau, 2000: 197; Borojevic *et al.*, 2000: 233.

#### Diagnosis

Leucosolenida with 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.

#### Scope

Heteropiidae, as presently understood by Borojevic *et al.* (2000), contains seven genera. It is characterised by the presence of a layer of subcortical pseudosagittal spicules. At 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. This position is clearly observed for the distal triactines of the radial tubes in sycon-like sponges that are now allocated to *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 sycetid 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, *S. syconiformis* (Borojevic, 1967b), the choanoskeleton is inarticulated, or has only a few spicules in the proximal part of the choanoskeleton. The corticalisation of such a sponge can lead both to the genus *Sycettusa*, which is characterised by a thin body wall with the choanosome devoid of its own skeleton, and to *Grantessa*, in which the choanoskeleton is articulated. 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.

Corticalisation has apparently arisen several times in the Leucosolenida. In Heteropiidae corticalisation associated with the maintenance of the choanoskeleton of the tubes that is reduced to subatrial and subcortical spicules has given rise to *Sycettusa*, whilst the corticalisation associated with the thickening of the choanosome has produced *Grantessa*. The subsequent transition to the leuconoid type of organization is seen in *Vosmaeropsis*. Similar progression is observed among the Leucosolenida that lack pseudosagittal spicules, in which the first route has given rise to the Jenkinidae and the Amphoriscidae, and the second the Grantiidae. 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 are found in some representatives of the Grantiidae. Complementary cytological or biochemical criteria should be undertaken to understand the limits between Grantiidae and Heteropiidae, to resolve these problematic cases.

**SYCONESSA BOROJEVIC, BOURY-ESNAULT & VACELET, 2000****Synonymy**

*Syconessa* Borojevic *et al.*, 2000: 235. *Grantessa* [in part] Borojevic, 1967b: 6.

**Type species**

*Grantessa syconiformis* Borojevic, 1967b (by original designation).

**Holotype**

MNHN LBIM C. 1968.239

**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. Syconoid type of organization.

**Scope**

As discussed by Dendy & Row (1913) and by Borojevic (1965, 1967b), 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 actines of pseudosagittal triactines support the external part of the radial tubes, but without cortex. *Syconessa* is the starting point of the evolutionary line of Heteropiidae. 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*. Despite the occasional presence of spicules of the pseudosagittal type, in *Sycon ensiferum*, and after examination of slides BMNH 93.6.9.6a, 25.11.1.1746/47 Borojevic *et al.* (2000) found that this species belongs to *Sycon*.

**Distribution**

New Caledonia, Baie de St Vincent, Ile Testard Sud.

**SYCETTUSA HAECKEL, 1872****Synonymy**

*Sycettusa* Haeckel, 1872: 236; Burton, 1963: 139; Borojevic *et al.*, 2000: 235.

**Type species**

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

**Diagnosis**

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

**Scope**

Borojevic *et al.* (2000) divided the genus *Grantessa* (as defined by Dendy & Row, 1913) into two groups: one with an inarticulated choanoskeleton, to be called *Sycettusa*, and the other with an articulated choanoskeleton, to be called *Grantessa*. The former genus apparently evolved by the corticalisation of sponges with an inarticulated skeleton similar to *Syconessa syconiformis* (Borojevic, 1967b), thereby maintaining this characteristic of the choanoskeleton. Haeckel (1872) proposed the subgenus *Sycettusa* for the single species, *S. stauridia* from the Red Sea, which is a typical syconoid Heteropiidae with an inarticulated choanoskeleton, and Borojevic *et al.* (2000) retained the genus and species names in the same combination.

**Distribution**

The 12 species allocated to *Sycettusa* can be divided into two groups, one common in the Arctic region and the other in the Indo-Pacific. The Arctic group includes *Sycettusa* (ex. *Sycaltis*) *glacialis* (Haeckel, 1872), *S.* (ex. *Ebnerella*) *kuekenthali* (Breitfuss, 1896), *S.* (ex. *Ebnerella*) *lanceolata* (Breitfuss, 1898a), *S.* (ex. *Amphoriscus*) *murmanensis* (Breitfuss, 1898a), *S.* (ex. *Amphoriscus*) *thompsoni* (Lambe, 1900) and *S.* (ex. *Ebnerella*) *nitida* (Arnesen, 1901). The Indo-Pacific group includes *S. stauridia* Haeckel, 1872, *S.* (ex. *Sycortis*) *syccilloides* (Schuffner, 1877), *S.* (ex. *Amphoriscus*) *poculum* (Poléjaeff, 1883), *S.* (ex. *Grantessa*) *simplex* (Jenkin, 1908b), *S.* (ex. *Grantessa*) *glabra* (Row, 1909), *S.* (ex. *Grantessa*) *hastifera* (Row, 1909).

**GRANTILLA ROW, 1909****Synonymy**

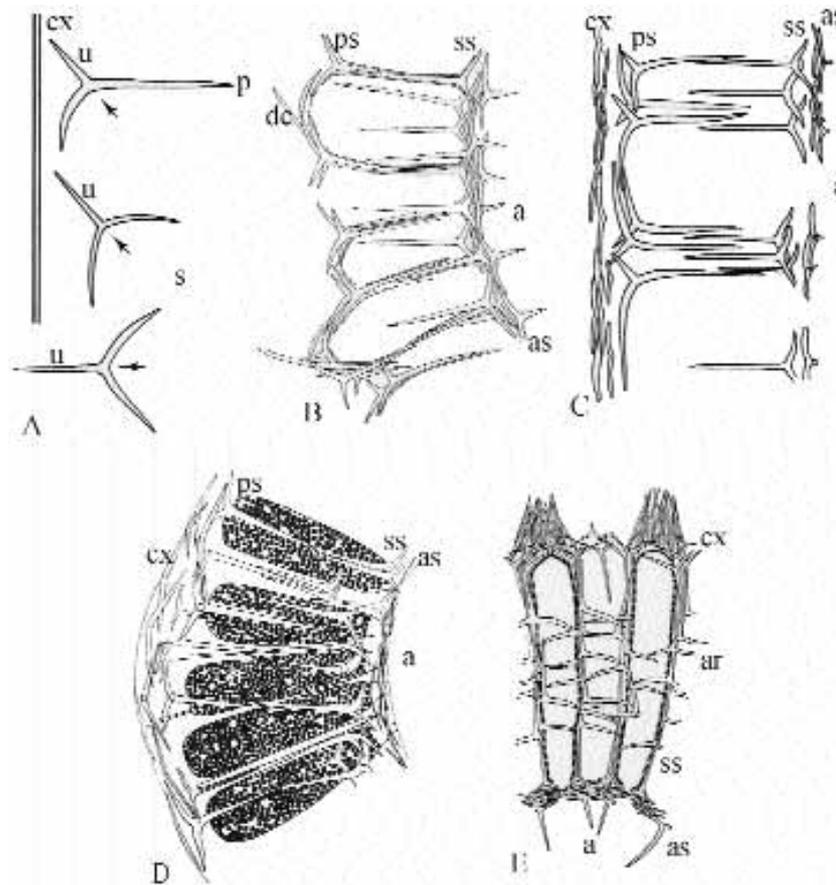
*Grantilla* Row, 1909: 198; Dendy & Row, 1913: 756; Borojevic *et al.*, 2000: 236.

**Type species**

*Grantilla quadriradiata* Row, 1909 (by monotypy).

**Diagnosis**

Heteropiidae with syconoid organization. The skeleton of the tubes is inarticulated, composed of subatrial triactines, and subcortical pseudosagittal triactines and tetractines.



**Fig. 9.** A, Heteropiidae, diagram of one parasagittal and two sagittal spicules (the arrow indicates the unpaired angle and the double line represents the cortex. 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) (from Borojevic *et al.*, 2000) (abbreviations: cx, cortex; p, parasagittal spicule; s, sagittal spicules; u, unpaired actine). B, *Syconessa syconiformis* (Borojevic, 1967b), diagram of a transverse section through the wall of the holotype (260  $\mu\text{m}$  thick) (after Borojevic, 1967b) (abbreviations: a, atrium; as, atrial skeleton; dc, distal cones; ps, parasagittal spicules; ss, subatrial spicules). C, *Sycettusa*, diagram of the inarticulate skeleton (after Borojevic *et al.*, 2000) (abbreviations: a, atrium; as, atrial skeleton; cx, cortex; ps, parasagittal subcortical spicules; ss, subatrial spicules). D, *Grantilla quadriradiata* Row, 1909, diagram of a transverse section at right angle to the surface (after Row, 1909) (abbreviations: a, atrium; as, atrial skeleton; ch, choanocyte chambers; cx, cortex; ps, parasagittal spicules; ss, subatrial spicules). E, *Grantessa ramosa* (Haeckel, 1872), diagram of a transverse section through the wall (800  $\mu\text{m}$  thick) (after Borojevic, 1967b) (abbreviations: a, atrium; ar, articulate choanosomal skeleton; as, atrial skeleton; cx, cortex; ss, subatrial spicules).

### Scope

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*.

### Distribution

Red Sea.

### GRANTESSA LENDENFELD, 1885

### Synonymy

*Grantessa* Lendenfeld, 1885a: 1098; Dendy & Row, 1913: 751; Hooper & Wiedenmayer, 1994: 475; Borojevic *et al.*, 2000: 236.

### Type species

*Grantessa sacca* Lendenfeld, 1885a (by monotypy).

### Diagnosis

Heteropiidae with syconoid organization and an articulated 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*.

### Scope

Borojevic *et al.* (2000) included in the genus *Grantessa sensu stricto* the syconoid Heteropiidae with articulated choanoskeletons. They are derived from sponges similar to *Syconessa*, in which the increase of radial tubes had generated the articulated choanoskeleton. *Grantessa* often grows as large arborescent or bushy cornus.

**Distribution**

Tropical Indo-Pacific area.

**HETEROPIA CARTER, 1886****Synonymy**

*Heteropia* Carter, 1886b: 92; Dendy & Row, 1913: 754; Burton, 1963: 77; Hooper & Wiedenmayer, 1994: 477; Borojevic *et al.*, 2000: 236.

**Type species**

*Aphroceras ramosa* Carter, 1886b, by monotypy.

**Diagnosis**

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

**Scope**

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

**Distribution**

The type species has been described from the N Atlantic. The other species have been described from Indo-Pacific and Atlantic areas.

**PARAHETEROPIA BOROJEVIC, 1965****Synonymy**

*Paraheteropia* Borojevic, 1965: 670; Borojevic *et al.*, 2000: 236.

**Type species**

*Amphiute ijimai* Hôzawa, 1916 (by monotypy).

**Diagnosis**

Heteropiidae with syconoid organization, an articulated choanoskeleton, and with both cortical and atrial skeletons containing longitudinal diactines.

**Scope**

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

**Distribution**

NW Pacific, Japanese coast.

**VOSMAEROPSIS DENDY, 1892****Synonymy**

*Vosmaeropsis* Dendy, 1892b: 76; Dendy & Row, 1913: 755; Hooper & Wiedenmayer, 1994: 477; Borojevic & Klautau, 2000: 198; Borojevic *et al.*, 2000: 237.

**Type species**

*Heteropia macera* Carter, 1886b (by subsequent designation; Dendy & Row, 1913).

**Diagnosis**

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

**Material examined**

BMNH 1887.7.12.19 from Wilson collection, S Coast Australia (fragment MNHN LBIM C1968.8).

**Scope**

*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 of other choanosomal spicules. Alternatively, the pseudosagittal subcortical spicules and the facing subatrial spicules may retain their original relationship, and the thickening of the wall may 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.

**Distribution**

The type locality of the type species is Bass Strait; the other species have been described from the Mediterranean, both sides of the Atlantic, and the Indo-Pacific region.

**FAMILY AMPHORISCIDAE DENDY, 1892****Synonymy**

Amphoriscidae Dendy, 1892b: 76; Dendy, 1893b: 242; Dendy & Row, 1913: 781; Borojevic & Boury-Esnault, 1987b: 39; Hooper & Wiedenmayer, 1994: 451; Borojevic *et al.*, 2000: 237.

**Diagnosis**

Leucosolenida with syconoid, sylleibid or leuconoid organization, and a distinct cortex supported by tangential tetractines whose centripetal apical actines cross the outer part or the whole of the choanosome. Tangential triactines and small tetractines may be also present in the cortex. The choanoskeleton is typically inarticulated, composed of 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 inarticulated choanoskeleton, or forming a distinct subatrial layer. An atrial skeleton is always present.

**Scope**

Amphoriscidae is well characterised by a distinct subcortical layer exclusively supported 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*. The simple inarticulated choanoskeleton is a primitive condition. The regular presence of subatrial triactines in the Amphoriscidae clearly indicates that they are derived from a *Sycetta*-type of organization through the precocious development of a cortical skeleton reinforced by giant tetractines. Since the articulated 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 Leucosolenida, 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 sub-atrial skeletons on the other (e.g., *Grantessa ramosa*). 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. 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 inarticulated choanoskeleton is preserved, despite the progressive thickening of the sponge wall and the necessity to introduce new skeletal structures to support it. Three genera have been allocated to Amphoriscidae: *Amphoriscus*, *Leucilla* and *Paraleucilla*.

**AMPHORISCUS HAECKEL, 1870****Synonymy**

*Amphoriscus* Haeckel, 1870a, b: 238; Burton, 1963: 146; Borojevic & Boury-Esnault, 1987b: 38; Hooper & Wiedenmayer, 1994: 452; Borojevic *et al.*, 2000: 238.

**Type species**

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

**Diagnosis**

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

**Scope**

*Amphoriscus* is a well-characterised genus, and contains several nominal species (about 12) of solitary sponges with beautiful vitreous transparent walls. Dendy & Row (1913) kept the genus *Syculmis* Haeckel, 1872 for Amphoriscidae with a root-tuft of diactines and anchoring tetractines. Similar anchoring structures are present in the families Sycettidae and Jenkinidae, but this character seems to be homoplastic and Borojevic *et al.* (2000) proposed the inclusion of the species described as *Syculmis synapta* by Haeckel (1872) in *Amphoriscus*.

**Distribution**

The genus is found in all the oceans.

**LEUCILLA HAECKEL, 1872****Synonymy**

*Leucilla* Haeckel, 1872: 132; Dendy & Row, 1913: 783; Borojevic & Peixinho, 1976; Borojevic & Boury-Esnault, 1987b: 29; Hooper & Wiedenmayer: 452; Borojevic *et al.*, 2000: 239.

**Type species**

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

**Diagnosis**

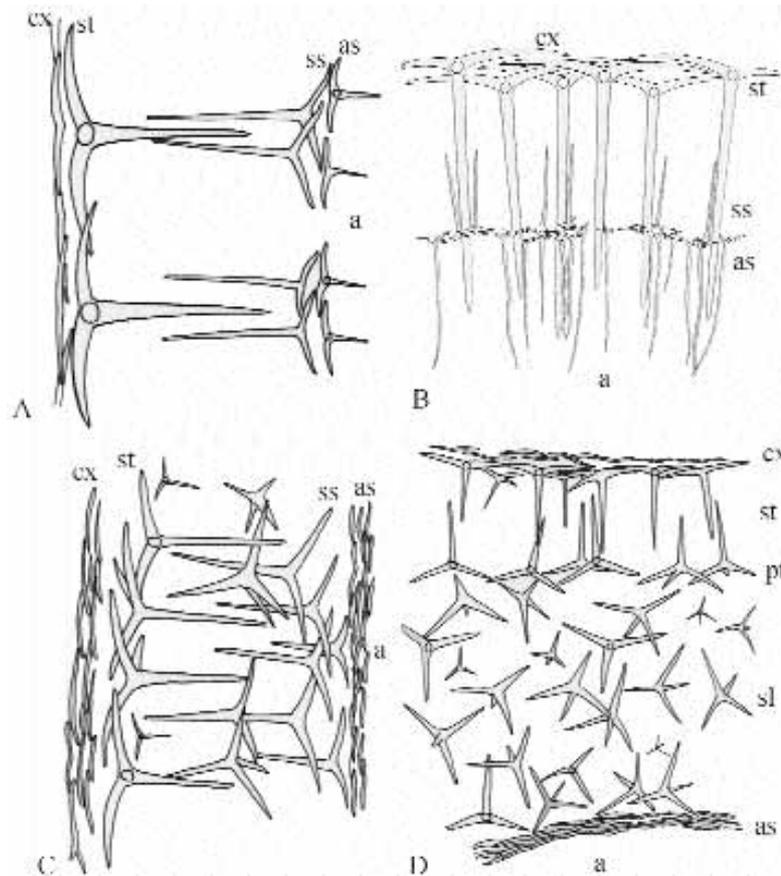
Amphoriscidae with sylleibid or leuconoid organization. The choanoskeleton is formed primarily by the apical actines of giant cortical triactines and the unpaired actines of subatrial triactines or tetractines. It may contain dispersed spicules, but a typical articulated choanoskeleton is always absent.

**Material examined**

MNHN LBIM C 1969.663 (Haeckel slide). Other material. Dakar (Sénégal), rocky shores, MNHN LBIM C.DAK.221, 226, 239, 240, 240, 241, 287, 294, 303, 317, 324.

**Scope**

*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 inarticulated choanoskeleton, which is reduced to the apical actines of cortical tetractines and to the unpaired actines of subatrial triactines or tetractines. 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 never have any structures reminiscent of the articulated arrangement of the choanoskeleton.



**Fig. 10.** A, Amphoriscidae, diagram of the type of inarticulated skeleton (after Borojevic *et al.*, 2000) (abbreviations: a, atrium; as, atrial skeleton; cx, cortex; ss, subatrial spicules; st, subcortical tetractines). B, *Amphoriscus chrysalis* (Schmidt, 1864), section at right angle to the surface (after Haeckel, 1872) (abbreviations: a, atrium; as, atrial skeleton; cx, cortex; ss, subatrial spicules; st, subcortical tetractines). C, *Leucilla*, diagram of a transverse section through the wall (after Borojevic *et al.*, 2000) (abbreviations: a, atrium; as, atrial skeleton; cx, cortex; ss, subatrial spicules; st, subcortical tetractines). D, *Paraleucilla*, diagram of a transverse section through the wall (after Borojevic *et al.*, 2000) (abbreviations: a, atrium; as, atrial skeleton; cx, cortex; pt, primary tetractines indicating the original position of the subatrial skeleton; sl, secondary subatrial layer inserted between the atrial skeleton and the primary subatrial spicules; st, subcortical tetractines).

### Distribution

Five species are now recognized in *Leucilla*: *L. amphora* (type locality West Indies, and also found on African coast of NE Atlantic), *L. uter* Poléjaeff, 1883 (which has an apparent circum-tropical distribution, West Indies and Indo-Pacific tropical waters), *L. nuttingi* (from California, NE Pacific), *L. echina* (from Norway, Bergen, NE Atlantic), and *L. endoumensis* Borojevic & Boury-Esnault, 1986 (from Mediterranean).

### PARALEUCILLA DENDY, 1892

#### Synonymy

*Paraleucilla* Dendy, 1892b: 116; Dendy & Row, 1913: 778; Burton, 1963: 116; Borojevic *et al.*, 2000: 239; Haeckel, 1872: 206 [as *Leucandra cucumis*].

#### Type species

*Leucandra cucumis* Haeckel, 1872 (by monotypy).

### Diagnosis

Amphoriscidae with leuconoid organization. The thick wall is divided into two regions. The outer region is supported by the skeleton which remains essentially inarticulated, 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.

### Material examined

MNHN LBIM C.1968.676 (Haeckel slide from the holotype). MNHN LBIM C.1968 681, *Leucandra cucumis*. BMNH 86.6.7.64 and 25.11.1.690a, *Leucilla saccharata* Haeckel, 1872. BMNH

1954.2.24.25, *Leucilla crosslandi* Row, 1909. BMNH 20.12.9.60a, *Leucilla proteus* Dendy, 1913. BMNH 25.11.1.90a, *Leucilla princeps* Row & Hôzawa, 1931.

### Scope

Some leuconoid Amphoriscidae are massive sponges, with a folded, and thickened body. In these cases, the inarticulated organization is retained only in the outermost layer of the choanosome, which has a typical inarticulated 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. The 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 inarticulated layer was erroneously interpreted as containing only inhalant cavities. In specimens that have been observed by Borojevic *et al.* (2000), 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, 1893b), but subsequently returned to use the genus (Dendy & Row, 1913) in order to underline the particular organization of the subcortical region. After re-examination of other material Borojevic *et al.* (2000) allocated four other species to *Paraleucilla*: *P. saccharata* (Haeckel, 1872), *P. crosslandi* (Row, 1909), *P. proteus* (Dendy, 1913), and *P. princeps* (Row & Hôzawa, 1931).

### Distribution

All species studied so far are from Indo-Pacific region, most of them in the vicinity of Australian coasts.

### FAMILY ACHRAMORPHIDAE FAM. NOV.

#### Synonymy

[Staurorrhaphidae] Jenkin, 1908a: 29 (*nomen nudum*); Hooper & Wiedenmayer, 1994: 495; Borojevic *et al.*, 2000: 240.

#### Diagnosis

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

#### Scope

Achramorphidae fam. nov. is here erected to replace Staurorrhaphidae Jenkin, 1908a because there is no genus

'*Staurorrhaphis*' and thus the family name is a *nomen nudum*. Staurorrhaphidae was proposed by Jenkin (1908a) to include sponges with chiacines ('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. 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 chiacines originate from the atrial tetractines. However, as pointed out by Dendy & Row (1913), chiacines have a typical subatrial origin and position. In several other genera of Leucosolenida, 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 chiacines. Solely the presence of chiacines would not justify the creation of the family Achramorphidae. 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 Leucosolenida and justifies the separation of *Achramorpha* and *Megapogon*, from other Leucosolenida. Since in most sponges the atrial cavity is echinated or hispid, probably as a protection from invading organisms, in the Achramorphidae the subatrial tetractines have apparently taken over this function, forming a long apical actine bent towards the atrial cavity. Achramorphidae is thus characterised simultaneously by the absence of the atrial tangential skeleton and the presence of subatrial tetractines that are chiacines. All known species of Achramorphidae have a relatively thin wall with either an inarticulated skeleton, or only a few scattered spicules in the choanoskeleton.

### ACHRAMORPHA JENKIN, 1908

#### Synonymy

*Achramorpha* Jenkin, 1908a: 30; Dendy & Row, 1913: 765; Hooper & Wiedenmayer, 1994: 495; Borojevic *et al.*, 2000: 241.

#### Type species

*Achramorpha nivalis* Jenkin, 1908a (by subsequent designation; Dendy & Row, 1913).

#### Diagnosis

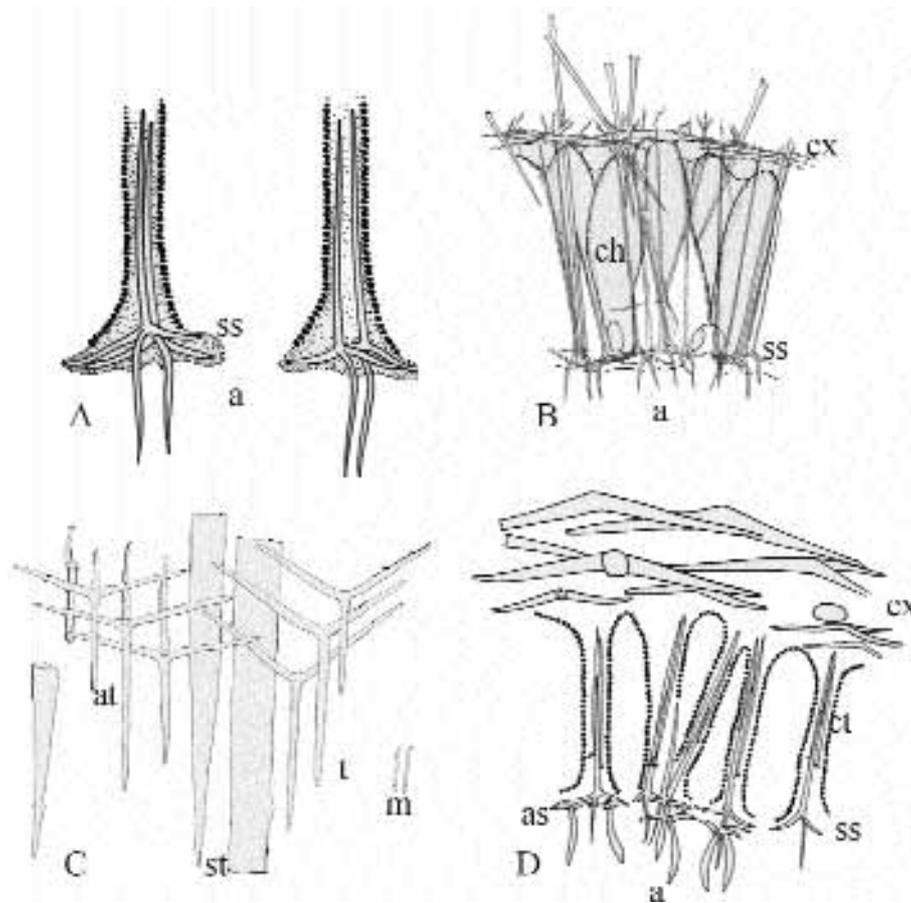
Achramorphidae with syconoid organization.

#### Material examined

Holotype. BMNH 1907.8.6.122 (and fragment MNHN LBIM C1968.23).

#### Scope

Three species have been allocated by Jenkin (1908a) to *Achramorpha*: *A. nivalis*, *A. glacialis* and *A. grandinis*, all with a circumantarctic distribution.



**Fig. 11.** A, Achramorphidae fam. nov., diagram of the subatrial skeleton (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). B, *Achramorpha nivalis* Jenkin, 1908, diagram of a transverse section through the wall (after Jenkin) (abbreviations: a, atrium; ch, choanoderm; cx, cortex; ss, subatrial spicules). C, *Megapogon cruciferus* (Poléjaeff, 1893) (spicule types after Jenkin, 1908) (abbreviations: at, atrial tetractines; m, minute spined oxea; st, stout acerate diactines; t, triactines). D, *Grantiopsis*, diagram of a transverse section through the wall (abbreviations: a, atrium; as, atrial skeleton; ct, choanosomal spicules tracts composed of nail-like triactines; cx, cortex; ss, subatrial spicules).

### MEGAPOGON JENKIN, 1908

#### Synonymy

*Megapogon* Jenkin, 1908a: 35; Dendy & Row, 1913: 767; Hooper & Wiedenmayer, 1994: 496; Borojevic *et al.*, 2000: 241; Poléjaeff, 1883: 60 [as *Leuconia crucifera*].

#### Type species

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

#### Diagnosis

Achramorphidae with sylleibid or leuconoid organization.

#### Scope

Five species have been allocated by Jenkin (1908a) to *Megapogon*: *M. crucifera*, *M. crispatus* Jenkin, 1908a, *M. pollicaris*

Jenkin, 1908a, *M. raripilus* Jenkin, 1908a, and *M. villosus* Jenkin, 1908a.

#### Distribution

The type locality of the type species is Azores (NE Atlantic), however this species was found also in Antarctica by Jenkin. All others species have a circumantarctic distribution.

### FAMILY LELAPIIDAE DENDY & ROW, 1913

#### Synonymy

Lelapiidae Dendy & Row, 1913: 784; Hôzawa, 1929: 379; de Laubenfels, 1936a: 197; Borojevic *et al.*, 2000: 241.

#### Diagnosis

Leucosolenida with 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.

### Scope

Lelapiidae is characterised by spicular tracts that are not found in other Leucosolenida. 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 fossil Calcarea. Two lines of evolution can be distinguished in this family. In the *Grantiopsis* – *Kebira* line the tracts 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 skeleton 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 *Guancha* (Calcinea, Clathrinida) 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, the Lelapiidae belong to the Leucosolenida, where they represent a rather specialized and well-delimited family, but 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. Four genera have been allocated to Lelapiidae by Borojevic *et al.* (2000): *Grantiopsis*, *Kebira*, *Lelapia* and *Paralelapia*

### GRANTIOPSIS DENDY, 1892

#### Synonymy

*Grantiopsis* Dendy, 1892a: 73; Jenkin, 1908a: 35; Dendy & Row, 1913: 762; Hooper & Wiedenmayer, 1994: 463; Borojevic *et al.*, 2000: 242.

#### Type species

*Grantiopsis cylindrica* Dendy, 1892 (by monotypy).

#### Diagnosis

Lelapiidae with syconoid or syllebid 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.

### Material examined

BMNH 1925.11.1.100 – specimen from the Dendy collection, Abrolhos Island (fragment MNHN LBIM C.1968.30).

### Scope

*Grantiopsis* has a particular skeleton that is characterised by triactines with reduced paired actines in the wall of the tubes. As 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. 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 articulated 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 suggesting to the origin of the Lelapiidae from sponges like the Grantiidae, in which *Grantiopsis* had previously been classified.

### Distribution

Three species can be presently allocated to *Grantiopsis*, all from SW Pacific (Australian coasts).

### KEBIRA ROW, 1909

#### Synonymy

*Kebira* Row, 1909: 210; Dendy & Row, 1913: 785; Borojevic *et al.*, 2000: 242.

#### Type species

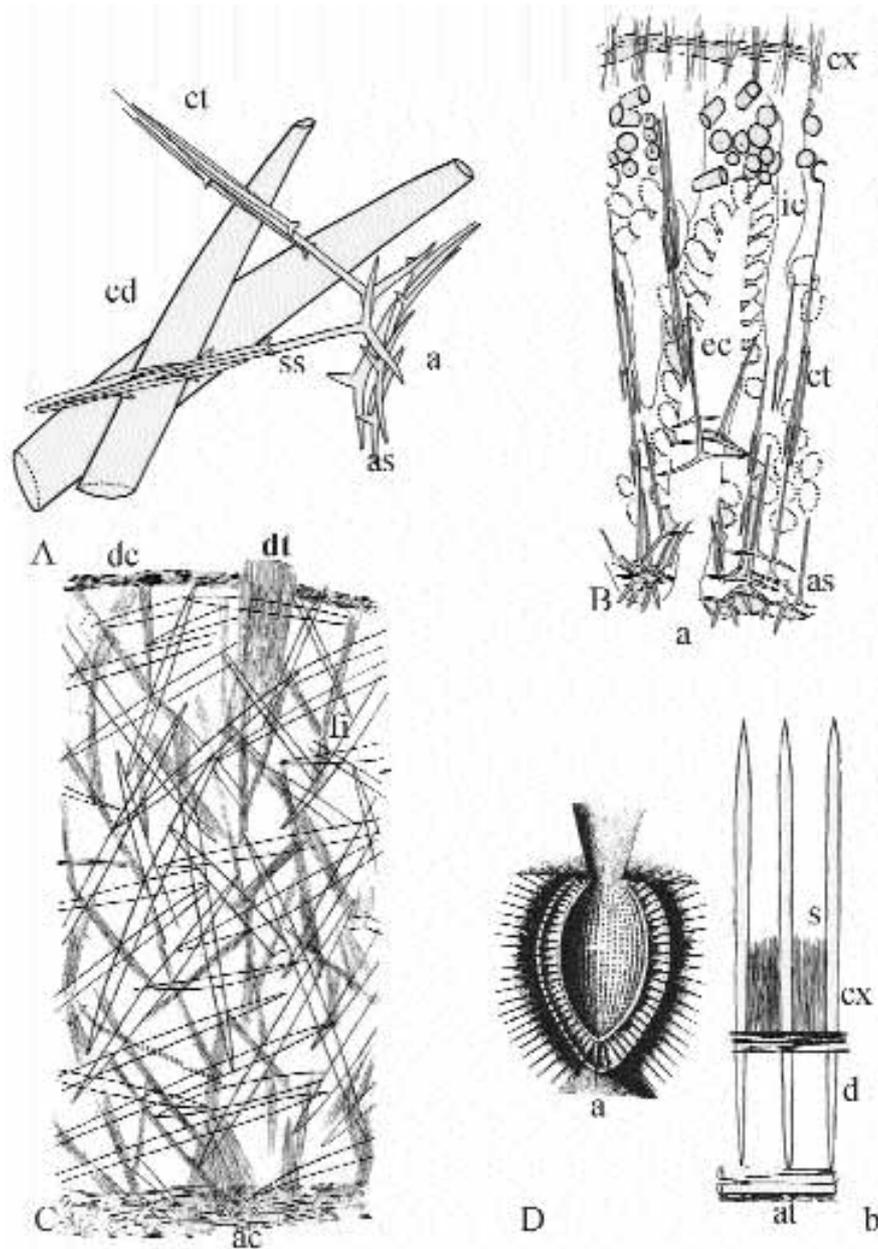
*Kebira uteoides* Row, 1909 (by monotypy).

#### Diagnosis

Lelapiidae with 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.

### Scope

*Kebira* appears to be 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 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. 12.** A, *Kebira*, diagram of the subatrial region of the skeleton (abbreviations: a, atrium; as, atrial skeleton; ct, choanosomal spicules tracts composed of nail-like triactines; cd, choanosomal diactines; ss, subatrial spicules). B, *Paralelapia nipponica* Hara, 1894, diagram of a cross-section through the wall (1 mm thick) (after Hôzawa, 1923) (abbreviations: a, atrium; as, atrial skeleton; ct, choanosomal spicules tracts composed of tuning-fork-shaped triactines; cx, cortex; ec, exhalant canal; ic, inhalant canal). C, *Lelapia australis* Gray, 1867a, skeletal arrangement in a longitudinal section (5 mm thick) (after Dendy, 1894) (abbreviations: ac, atrium; dc, dermal cortex; dt, dermal tuft of triactines and slender diactines; fi, spicular fibres formed of tuning-fork-shaped triactines; ac, atrial cortex). D, *Sycyssa huxleyi* Haeckel, 1872. a, section through holotype. b, section at right angle to the surface (after Haeckel) (abbreviations: at, atrium; cx, cortex; d, diactines; s, surface).

Although Row (1909) and Ilan & Vacelet (1993) do not specifically mention subatrial spicules, examination of specimens studied by the latter authors 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*. Both *Grantiopsis* and *Kebira* lack the classical articulated 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.

#### Distribution

Red Sea.

#### PARALELAPIA HÔZAWA, 1923

#### Synonymy

*Paralelapia* Hôzawa, 1923: 185; Borojevic *et al.*, 2000: 243.

1184

Porifera • Calcarea • Calcaronea • Leucosolenida

**Type species***Lelapia nipponica* Hara, 1894 (by monotypy).**Diagnosis**

Lelapiidae with 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.

**Scope**

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 Grantiidae. The loose spicular tracts are associated proximally with the subatrial spicules, and the cortical skeleton is well separated from the choanoskeleton.

**Distribution**

Sagami Bay (Japan, NW Pacific).

**LELAPIA GRAY, 1867****Synonymy**

*Lelapia* Gray, 1867a: 557; Dendy, 1892a: 105; Dendy & Row, 1913: 785; Hôzawa, 1929: 379; Burton, 1963: 148; Borojevic *et al.*, 2000: 244.

**Type species***Lelapia australis* Gray, 1867a (by monotypy).**Diagnosis**

Lelapiidae with 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.

**Scope**

*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.

**Distribution**

SW Pacific (Australian coasts).

**SYCYSSA HAECKEL, 1872 (INCERTAE SEDIS)****Synonymy**

*Sycyssa* Haeckel, 1872: 260; Dendy & Row, 1913: 767; Burton, 1963: 570; Borojevic *et al.*, 2000: 244.

**Type species***Sycyssa huxleyi* Haeckel, 1872 (by monotypy).**Diagnosis**

Leucosolenida (?) with syconoid organization. The skeleton consists only of diactines.

**Scope**

This species was described from two specimens collected by Haeckel from the Adriatic, and not recorded since. The absence of all the radiate spicules is quite remarkable. This condition is similar to that seen in the family Trichogypsiidae in the order Baerida. However, no other characteristics of the Baerida 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 is the relationship of this sponge to other Calcaronea. However, it seems to be closer to the Leucosolenida than to the Baerida.