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Order Clathrinida Hartman, 1958

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Clathrinida (Calcarea, Calcinea) includes six families and 16 genera. In this order four parallel and continuous evolutionary lines are recognized, starting from simple sponges similar to representatives of the Recent genera, *Soleneiscus* and *Clathrina*.
Keywords: Calcarea; Calcinea; Clathrinida; Clathrinidae; Soleneiscidae; Levinellidae; Leucaltidae; Leucascidae; Leucettidae; *Ascaltis*; *Ascandra*; *Burtonulla*; *Clathrina*; *Dendya*; *Guancha*; *Leucaltis*; *Leucascus*; *Leucetta*; *Leucettusa*; *Leuclathrina*; *Leucomalthe*; *Levinella*; *Pericharax*; *Soleneiscus*; *Sycettaga*.

DIAGNOSIS & SCOPE

Synonymy

Clathrinida Hartman, 1958a: 108; Hartman, 1980b: 31; Borojevic *et al*., 1990: 349; Hooper & Wiedenmayer, 1994: 447; Wörheide & Hooper, 1999: 863.

Type family

Clathrinidae Minchin, 1900 (by original designation).

Diagnosis

Calcinea with the skeleton composed exclusively of free spicules, without hypercalcified non-spicular reinforcements, spicule tracts, calcareous scales or plates.

Scope

Clathrinida is a very rich and variable group. All developmental stages are present, from olynthus-like sponges to complex ones with an elaborate aquiferous system. Different parallel evolutionary lines may be distinguished, in each of which can be observed a complete series from simple asconoid organization to elaborate leuconoid systems. Three evolutionary lines have been recognized (Borojevic *et al*., 1990) all of which originate from sponges organized as a simple olynthus. In all lines there is a progressive evolution from a homocoel to a heterocoel grade of organization. All may represent a monophyletic homogenous clade and together they cannot be divided into two orders, the Clathrinida and the Leucettida, by their homocoel or heterocoel grade of organization, respectively, as proposed by Hartman (1958a). Borojevic *et al*. (1990) thus proposed a single order, Clathrinida for all Calcinea without a hypercalcified skeleton.

KEY TO GENERA

(1) Sponge body composed of individual, anastomosed or ramified tubes, choanocytes line all internal cavities of the sponge 2
Choanocytes do not line all internal cavities of the sponge 9
(2) No differentiated diverticuli on external part of the tubes; when a large cormus is formed there is no common cortex covering the whole body 4
Differentiated diverticuli on the external part of the tubes with a particular skeleton 3
(3) Central tube ornamented with short, external, regularly distributed, radial diverticuli ..... ***Sycettaga***
Central tube ornamented with external groups of ovoid diverticuli, which communicate with the central tube through a shallow cavity ..... ***Levinella***
(4) Choanoderm flat, or exceptionally elevated in the form of cones around apical rays of tetractines, but never forming true folds 5
Choanoderm forming folds inside the choanocoel, delimiting shallow or deep radial spaces or tubes, supported by apical rays or tetractines from the external skeletal layer ..... ***Ascandra***
(5) Sponge body in form of solitary, sometimes distally ramified tubes, or composed of anastomosed tubes forming a large cormus 6
Sponge in the form of a large central tube bearing long radially arranged tubes, amply ramified in their distal part, but only occasionally anastomosed in their proximal part ..... ***Dendya***
(6) Sponge in the form of solitary tubes, sometimes terminally ramified, or groups of erect tubes, growing from creeping stolon-like tubes ..... ***Soleneiscus***
Sponge in the form of anastomosed tubes 7
(7) Sponge cormus with distinct peduncle, solid or formed of normally organized, partially or fully coalescent tubes. Skeleton composed of parasagittal spicules, or of regular spicules to which parasagittal spicules are added, at least in the peduncle ..... ***Guancha***
Sponge cormus without a distinct peduncle 8

(8) Sponge body formed of anastomosed tubes, without a common cortex surrounding the whole cormus ..... ***Clathrina***
Sponge body composed of amply anastomosed tubes covered by a distinct cortex surrounding the whole body. No exhalant aquiferous system; a pseudoatrium may be exceptionally formed through the calyciform growth of the sponge ..... ***Ascaltis***
(9) Sponge composed of central, occasionally ramified tubes, ornamented with distinct external diverticuli having their own skeleton, different from that of the central tube ..... ***Burtonulla***
Sponge with a compact body without external diverticuli 10
(10) Sponge body composed of a network of anastomosed and ramified tubes with a proper skeleton and covered by a thin cortex. Central atrial cavity surrounded by a thin wall, with a proper skeleton ..... ***Leucascus***
Sponge body solid; when the choanocyte chambers are elongated they do not have a proper skeleton, but are embedded in the choanosomal skeleton 11
(11) Sponge with a clear distinction between a solid cortex and the choanosome. Choanoskeleton and/or atrial skeleton absent, or when present, composed of diffuse triactines and/or tetractines much smaller than spicules of the cortical skeleton 12
Sponge without a clear distinction between the solid cortex and the choanosome supported by a reduced choanoskeleton 14
(12) Sponge composed of an external wall sustained by large radiate spicules; aquiferous system leuconoid, choanosome devoid of a skeleton ..... ***Leuclathrina***
Sponge with elongate and/or spherical choanocyte chambers; in addition to the strong cortical skeleton, smaller spicules present in atrial and/or choanosomal skeleton 13
(13) Sponge body composed of large anastomosed tubes; the wall of each tube consists of a distinct cortex, a choanosome containing elongated choanocyte chambers and a large central atrium ..... ***Leucaltis***
Sponge body solid, occasionally ramified but not in the form of anastomosed tubes; aquiferous system containing elongated and/or spherical chambers. Large central atrium always present ..... ***Leucettusa***
(14) Sponge body solid; atrium often reduced to exhalant channels opening directly into osculum. Leuconoid organization with choanosome supported by a regular network of triactines to which tetractines may be added; no distinct subcortical layer of inhalant chambers ..... ***Leucetta***
Sponge body solid with large atrium. Leuconoid organization with subcortical system of inhalant cavities supported by a skeleton in part composed of centripetal rays of cortical triactines ..... ***Pericharax***

FAMILY CLATHRINIDAE MINCHIN, 1900

Synonymy

Clathrinidae Minchin, 1900: 110; Borojevic, 1968: 204; Borojevic *et al*., 1990: 249; Hooper & Wiedenmayer, 1994: 454; Wörheide & Hooper, 1999: 863.

Diagnosis

Clathrinida with an essentially tubular organisation. The skeleton is formed by tangential triactines, to which tripods, tetractines and diactines may be added. A continuous choanoderm lines all the internal cavities. The water crosses the wall through pores, delimited by porocytes. The young sponges have an olynthus form that grows through longitudinal median division, budding and anastomosis of individual tubes, forming large units called the 'cormus'. There is neither a common cortex nor a well-defined inhalant or exhalant aquiferous system.

History and biology

Clathrinidae, used within the scope defined by Borojevic *et al*. (1990), comprises most of the typical homocoel Calcinea. It corresponds closely to the concept proposed by Minchin (1896, 1900), revised by Hartman (1958a). Clathrinidae are simple Calcinean sponges whose organisation corresponds to simple tubes, identified in general as the 'ascon' or the 'asconoid grade of organisation'. They are formed by a pinacoderm-covered external layer containing spicules and an internal layer of choanocytes. Both layers are pierced by pores, each surrounded by a porocyte. This simple tube, called the 'olynthus', is found in early development of Clathrinidae but each segment of the complex adult body still corresponds to an olynthus. Clathrinidae grow from the olynthus grade of organisation through division, ramification and anastomosis of tubes to form a larger functional unit called the 'cormus' (Borojevic, 1968) (Fig. 1A). In the large cormus of the Clathrinidae, a certain degree of differentiation may be observed in tube-size and spiculation. A radial organisation of the cormus may be very noticeable, with the central tube taking on the function of an atrium. This tube becomes larger, but it is still covered by a normal choanoderm and has the typical ascon organisation. On the other hand, special spicule types such as tripods in *Clathrina cerebrum* (Haeckel, 1872), or diactines in *Clathrina contorta* (Bowerbank, 1864), may be found only in external tubes of the cormus, where they reinforce the external skeleton. However, these spicules are never a part of a continuous cortex. In the genus *Guancha* a solid peduncle may be formed by coalescent tubes which have lost the choanoderm.

Distribution

Clathrinidae are widely distributed in all seas, generally in shallow waters. They are particularly frequent in shaded and cryptic habitats, such as the coralligenous zone and submarine caves. In temperate and subtropical regions they are larger and more abundant during summer when sexual reproductive.

CLATHRINA GRAY, 1867

Synonymy

[*Nardoa*] Schmidt, 1862: 18 (preoccupied for a genus of Asteroidea). *Clathrina* Gray, 1867a: 557; Minchin, 1896: 350; Borojevic, 1968: 204; Borojevic & Boury-Esnault, 1987a: 2; Borojevic *et al*., 1990: 250; Hooper & Wiedenmayer, 1994: 455; Wörheide & Hooper, 1999: 863.

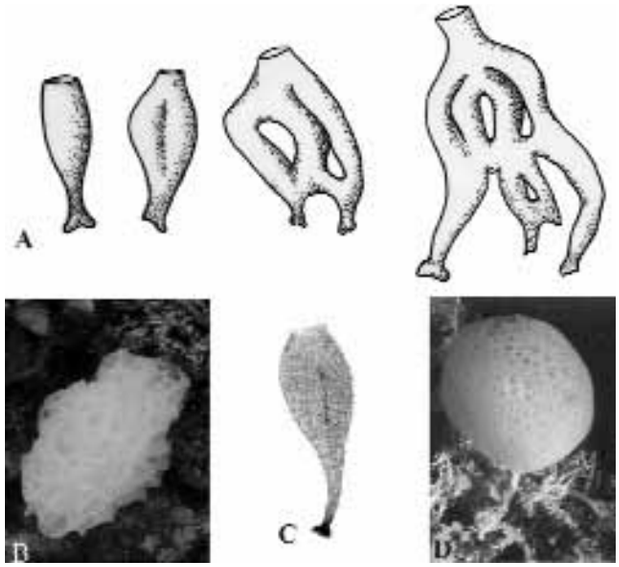

Fig. 1. Family Clathrinidae. A, cormogenesis of the family Clathrinidae through longitudinal median divisions of tubes (after Hadzi, 1917). B, underwater photograph of *Clathrina clathrus* (3.6 cm) from the Mediterranean (photo J. Vacelet). C, *Guancha blanca*, young specimen (2.5 mm) from the Bay of Biscay. D, underwater photograph of *Guancha lacunosa* (9 cm) from the Mediterranean (photo J. Vacelet).

Type species

Grantia clathrus Schmidt, 1864 (by original designation) (Fig. 1B).

Diagnosis

Clathrinidae in which the choanoderm is flat or rarely raised up into conules by the apical actines of the tetractines, but never forms true folds (at least when the sponge is in the normal physiological extended state). The full-grown cormus is composed of anastomosed tubes. The skeleton is composed of regular equiangular and equiradiate triactines and/or tetractines, to which diactines or tripods may be added.

Scope

The genus *Clathrina* is very large and represented by numerous species in all seas. The classification of *Clathrina* is difficult, especially when the skeleton is composed only of triactines (Borojevic & Boury-Esnault, 1987a). Detailed knowledge of their growth, ecological distribution and reproductive cycle may provide useful information to recognise species from defined habitats (Borojevic, 1967d; Johnson, 1980). Detailed genetic studies of sibling sympatric and allopatric species of *Clathrina* have shown that even very small morphological differences can characterise sponge populations which are genetically isolated, apparently without any gene flow, thus corresponding to biologically well-defined species (Solé-Cava *et al*., 1991, Klautau *et al*., 1994). This indicates that the traditional identification of species, solely on the bases of morphological data, probably underestimates the number of species in any given area. According to the literature many species of *Clathrina* with only a few spicule categories have a cosmopolitan distribution. It is probable, however, that these observations are due to the lack of recognition of differences between specimens collected by occasional sampling. The use of numerical analysis of shape, size and distribution of the spicules, or a biochemical approach by studying isoenzymes, may shed new light on the classification of this difficult group of the Calcarea.

Distribution

Worldwide.

GUANCHA MIKLUCHO-MACLAY, 1868

Synonymy

Guancha Miklucho-Maclay, 1868: 221; Borojevic & Peixinho, 1976: 997; Borojevic *et al*., 1990: 252; Hooper & Wiedenmayer, 1994: 457.

Type species

Guancha blanca Miklucho-Maclay, 1868 (by monotypy) (Fig. 1C).

Diagnosis

Clathrinidae with a cormus composed of a peduncle and a clathroid body. The peduncle may be formed by true tubes with a normal choanoderm, or may be solid with a special skeleton. The skeleton is composed of regular (equiangular and equiradiate) spicules to which parasagittal spicules are added, at least in the peduncle. In some species only parasagittal spicules are present. Their unpaired actine of parasagittal spicules is always basipetally oriented.

Scope

Among the Clathrinidae massive sponges composed of anastomosed tubes frequently display a progressive differentiation of particular parts of their cormus. In *Guancha* this differentiation involves a progressive distinction between a peduncle and a massive clathroid body. In the simplest species, such as *G. blanca*, the peduncle is still formed of normal tubes with a complete choanoderm. *Guancha blanca* is only slightly different from a typical *Clathrina* (Borojevic & Peixinho, 1976). The peduncle can also acquire a solid form with a special skeleton as in *G. pulcherrima* (Dendy, 1891) or *G. lacunosa* (Johnston, 1842) (Fig. 1D), which is certainly the most typical and differentiated of *Guancha* known. It has always a long peduncle supported by a special and elaborate skeleton. In parallel, with the differentiation of the pedunculate cormus, *Guancha* species are characterised by parasagittal spicules. In *G. blanca* these are localised in the peduncle and are always arranged parallel with their unpaired actine oriented basipetally. This tendency is more noticeable in other *Guancha*, such as *G. tetela* Borojevic & Peixinho, 1976, in which all the spicules are parasagittal. In *G. lacunosa* similar spicules can be observed with vestigial paired actines. These spicules take on the function of large diactines, in addition to smaller contorted true diactines that are present in the skeleton of the peduncle. There are about six species of *Guancha* although *G. blanca*, in particular, which has been collected throughout the

Atlanto-Mediterranean region and certain regions within the Indo-Pacific is very likely a complex of species – and this possibly also applies to other species.

Distribution

Indo-Pacific, N and S Atlantic, Mediterranean.

FAMILY SOLENEISCIDAE NOM. NOV.

Synonymy

[Soleniscidae] Borojevic *et al*., 1990: 252 (preocc.); Hooper & Wiedenmayer, 1994: 494; Wörheide & Hooper, 1999: 871.

Diagnosis

Clathrinida with an essentially tubular organisation, forming an individual ascon tube (olynthus) with several tubes growing from the basal stolon-like tubes, or forming distally ramified but not anastomosed tubes radially arranged around a central olynthus without any special skeletal differentiation. A continuous choanoderm lines all the internal cavities. Spicules are regular triactines and/or tetractines, to which tripods or diactines may be added.

Scope

A new name is designated here to replace [Soleniscidae] Borojevic *et al*., 1990, as the type genus [*Soleniscus*] Borojevic *et al*., 1990 is a junior homonym and following Art. 39 of the IZCN, the family name is invalid. [Soleniscidae] Borojevic *et al*., 1990 was erected to separate the genera *Soleneiscus* (ex. *Soleniscus*) and *Dendya* from the Clathrinidae. These sponges correspond, in their adult stage, to a simple olynthus or to several olynthus-like tubes, either linked at their base in the former, or distally ramified in the latter genus (Fig. 2B). Clathrinidae form the olynthus grade of organisation early after the larvae settle. They grow by longitudinal median division of their tubes to form directly anastomosed clathrate bodies. Conversely, Soleneiscidae either maintain an olynthus form of organisation throughout their life, or their tubes divide terminally, forming cormus composed of distally branched tubes. This form of growth is typical of *Leucosolenia* (within the Calcaronea), but it is quite rare among the Calcinea.

SOLENEISCUS NOM. NOV.

Synonymy

[*Soleniscus*] Borojevic *et al*., 1990: 253 (preoccupied by a mollusc); Wörheide & Hooper, 1999: 871.

Type-species

Leucosolenia stolonifer Dendy, 1891 (by original designation).

Diagnosis

Soleneiscidae that grow in form of an individual ascon tube, with several ascon tubes growing upright from basal stolon-like tubes, or in the form of creeping, distally-ramified but only rarely anastomosing tubes.

Scope

Soleniscus was described by Haeckel (1870a,b) in his '*Prodromus*' to include asconoid sponges with individual tubes bearing terminal oscules. Although the taxon was subsequently used as a 'generic variety' for sponges displaying the described type of growth it has not been attributed to any particular species, and Wörheide & Hooper (1999), following the ICZN (1999) attributed authorship to Borojevic *et al*. (1990). Unfortunately, this name appears to be a junior homonym for *Soleniscus* Meek & Worthen, 1860 (Mollusca). Therefore, we attribute a new name *Soleneiscus*. Seven species have been allocated to *Soleneiscus*: *S. stolonifer*, *S. japonica* (Haeckel, 1872), *S. irregularis* (Jenkin, 1908b), *S. hispida* (Brøndsted, 1931), *S. apicalis* (Brøndsted, 1931), *S. olynthus* (Borojevic & Boury-Esnault, 1987a) and *S. radovani* Wörheide & Hooper, 1999.

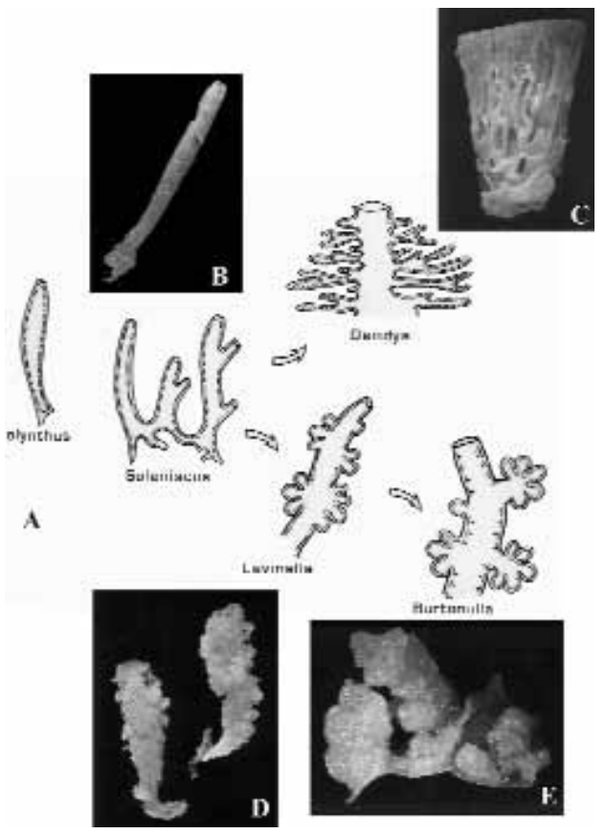

Fig. 2. Families Soleneiscidae and Levinellidae. A, the formation of the cormus in Soleneiscidae is through terminal division and ramification of the olynthus tube whereas for Levinellidae it is through formation of external diverticuli. B, type specimen of *Soleneiscus olynthus* (from Borojevic & Boury-Esnault, 1987a) (7.5 cm long). C, longitudinal section through the type-specimen of *Dendya tripodifera* (from Borojevic & Boury-Esnault, 1986) (2.6 cm high). D, type specimens of *Levinella thalassae* (from Borojevic & Boury-Esnault, 1986). Natural size, 2–2.5 cm. E, portion of the type specimen of *Burtonulla sibogae* (from Borojevic & Boury-Esnault, 1986) (2 cm maximum height).

Distribution

Only *S. olynthus* has been described from the NE Atlantic (Bay of Biscay), whereas all other species are recorded from the N and S Pacific Ocean (Fig. 2A).

DENDYA BIDDER, 1898

Synonymy

Dendya Bidder, 1898: 74; Dendy & Row, 1913: 728; Tanita, 1942: 110; Burton, 1963: 229; Borojevic *et al*., 1990: 254; Hooper & Wiedenmayer, 1994: 494.

Type species

Clathrina tripodifera Carter, 1886b (by monotypy) (Fig. 2B).

Diagnosis

Soleneiscidae where the cormus consists of a large central tube from which smaller radially arranged tubes branch off.

Scope

Dendya is characterised by a rigorously radiate organisation. However, the whole cormus is composed of tubes that have the typical organisation of the olynthus without a differentiation of the skeleton, and thus belongs to Soleneiscidae.

Distribution

S Pacific and Subantarctic region.

FAMILY LEVINELLIDAE BOROJEVIC & BOURY-ESNAULT, 1986

Synonymy

Levinellidae Borojevic & Boury-Esnault, 1986: 444; Borojevic & Boury-Esnault, 1987a: 22; Borojevic *et al*., 1990: 255; Wörheide & Hooper, 1999: 875.

Diagnosis

Clathrinida with a cormus composed of a central tube, simple or ramified, and external diverticuli isolated or grouped in clusters. The skeleton of the central and radial tubes is composed of regular (equiradiate and equiangular) spicules. The skeleton of the diverticuli is composed of regular and/or parasagittal spicules, distinct from the spicules which compose the skeleton of the central tube. The choanoderm can either line all the internal cavities of the sponge, or is restricted to the diverticuli.

Scope

Levinellidae was proposed for a small group of Calcinea with a very particular organisation (Borojevic & Boury-Esnault, 1986). Three genera have been allocated to the family: *Levinella, Sycettaga* Haeckel, 1872 and *Burtonulla* Borojevic & Boury-Esnault, 1986. They have a large central, somewhat vesicular tubes provided with external diverticuli. These ovoid or spherical outgrowths can be individual and irregularly dispersed over the central tube, or arranged in clusters. Each cluster is centred around a small central cavity which communicates directly with the main cavity. In the simplest Levinellidae, such as *Sycettaga primitiva* Haeckel, 1872 (Borojevic *et al*., 2000), the central tube is ornamented only by small, simple, isolated outgrowths (Fig. 3). In *Levinella* the central tubular cavity is still unique and lined by the choanoderm, but the outgrowths can be grouped around common exhalant openings. In *Burtonulla*, the cormus is ramified and the choanoderm is restricted to external diverticuli. The central tube of *Burtonulla* thus represents an atrium. The thin sponge wall is supported by a tangential skeleton, composed of different spicules in the central tube and the diverticuli (Borojevic & Boury-Esnault, 1986).

LEVINELLA BOROJEVIC & BOURY-ESNAULT, 1986

Synonymy

Levinella Borojevic & Boury-Esnault, 1986: 444; Borojevic & Boury-Esnault, 1987a: 22; Borojevic *et al*., 1990: 255; Wörheide & Hooper, 1999: 874.

Type species

Levinella thalassae Borojevic & Boury-Esnault, 1986 (by original designation) (Fig. 2C).

Diagnosis

Levinellidae with a cormus divided into a central tube ornamented by external groups of ovoid diverticuli, which communicate with the central tube through a shallow cavity. The central tube is not ramified. A choanoderm lines all the internal cavities.

Material examined

Holotype. MNHN LBIM C1985-2, Bay of Biscay, 44°00′7N, 7°06′9W. Paratypes. SME-T476, SME-U842, SME-T503.

Scope

Young specimens of *Levinella* have a typically olynthus organisation. Since they can grow quite large before forming external diverticuli young specimens may be confused with typical *Soleneiscus* species. With an increase in size diverticuli are formed, and give to the sponge an alveolated appearance. Diverticuli are original structures, distinct from the initial central asconoid tube, with a specific skeleton clearly different from that supporting the central olynthus. Two species have been allocated to *Levinella*: *L. thalassae* and *L. prolifera* (Dendy, 1913).

Distribution

The type species has been found in the NE Atlantic (Bay of Biscay), 490–620 m depth, and *L. prolifera* (Dendy, 1913) is an Indo-Pacific species from the littoral zone (to about 20 m depth).

SYCETTAGA HAECKEL, 1872

Synonymy

Sycettaga Haeckel, 1872: 236; Hooper & Wiedenmayer, 1994: 499; Borojevic *et al*., 2000: 218.

Type species

Sycetta primitiva Haeckel, 1872 (by original designation) (Fig. 3).

Diagnosis

Levinellidae with a simple central tube, ornamented with short radiate, simple, diverticuli.

Scope

Sycetta primitiva was described by Haeckel (1872) and included by Dendy & Row (1913) within the family Sycettidae, assigned to the Calcaronea. In contrast to other species of *Sycetta*, Haeckel (1872) characterised this species by the presence of regular, equiangular and equiradiate spicules, which are clearly described and illustrated in the original description. Haeckel (1872, Pl. 41) (Fig. 3C) also showed that choanocytes were apparently closer to the basinucleate type than to the apinucleate type. Although Haeckel's descriptions must be assessed cautiously, and moreover *S. primitiva* has not been observed since this original description, he indicated quite clearly that this was a calcinean sponge, quite different from other *Sycetta*, and consequently it must be classified as a typical member of Levinellidae. *Sycetta primitiva* Haeckel, 1872, was also assigned to a subgenus *Sycettaga*, and Borojevic *et al*. (2000) transferred this genus to Levinellidae, containing a single species – *Sycettaga* (ex. *Sycetta*) *primitiva* Haeckel, 1872.

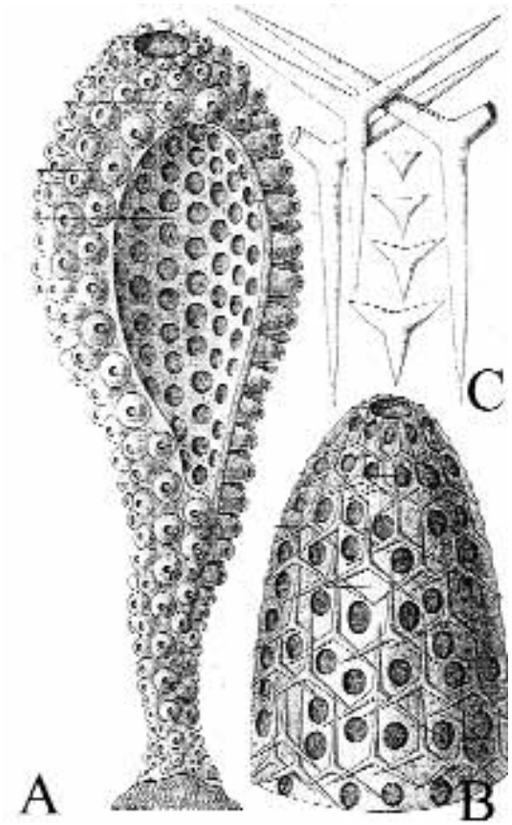

Fig. 3. *Sycettaga* (after Haeckel, 1872). A, drawing of a specimen, which is a simple central tube, ornated with short radiate simple diverticuli. Natural size, 4.5 cm. B, detail of a single radial simple diverticulum. C, spicule types.

Distribution

Southern Australia, Bass Strait and Gulf of St Vincent.

BURTONULLA BOROJEVIC & BOURY-ESNAULT, 1986

Synonymy

Burtonulla Borojevic & Boury-Esnault, 1986: 447; Borojevic *et al*., 1990: 255; *Dendya prolifera, sensu* Burton 1930a: 2.

Type species

Burtonulla sibogae Borojevic & Boury-Esnault, 1986 (by original designation) (Fig. 2D).

Diagnosis

Levinellidae whose central tube is ramified. The choanoderm is limited to the external diverticuli.

Material examined

Holotype. ZMA POR 146, Siboga Exped. stat. 301 (SE 538), E coast Roti Island, Indonesia, 10°38′S, 123°25.2′E, 22 m (fragment MNHN-LBIM.1968.90). Paratype. ZMA POR 145, Siboga Exped. stat. 164 (SE 373), 1°42.5′S, 130°47.5′E, 32 m.

Scope

Burtonulla has an organisation of the body and the skeleton quite similar to that of *Levinella*, with the central tube which can be extensively ramified. However, the choanoderm is limited to the diverticuli and the central tube lacks choanocytes. Functionally, this organisation is quite similar to that of *Sycetta*. *Burtonulla* has apparently acquired a heterocoel organisation through an entirely independent evolutionary pathway.

Distribution

Indonesia.

FAMILY LEUCALTIDAE DENDY & ROW, 1913

Synonymy

Leucaltidae Dendy & Row, 1913: 736; Borojevic, 1968: 207; Borojevic & Boury-Esnault, 1987a: 18; Borojevic *et al*., 1990: 255; Hooper & Wiedenmayer, 1994: 479; Wörheide & Hooper, 1999: 876; Borojevic & Klautau, 2000: 190.

Diagnosis

Clathrinida with a tubular, ramified or even anastomosed cormus with many oscula, or individualised with a large central atrium and a single osculum. The sponge wall is composed of a distinct cortex sustained by a well developed skeleton, and a choanosome. The skeleton of the choanosome and the atrial wall may be absent or composed of small and dispersed triactines and tetractines.

Scope

In Leucaltidae the sponge wall is clearly divided into a cortex supported by a strong skeleton, and a choanosome which can have no skeleton or can be provided with a dispersed choanoskeleton composed of small spicules only. Dendy & Row (1913) proposed that the family was derived from *Dendya* by a secondary corticalization, whereas Borojevic *et al*. (1990) suggested that the external skeletogenous layer is more likely to be a primary structure. The more complex genera of this family are derived from *Ascandra* by internal folding of the choanoderm (Fig. 4A). Thus, the choanoskeleton is clearly a secondary structure, composed of small and scattered spicules with unusual forms (Borojevic, 1968; Borojevic *et al.*, 1990). In *Ascandra*, the most simple species *A. falcata* (Fig. 4B) has an organisation similar to that of *Clathrina* with a basal region of the cormus composed of anastomosed tubes, and with larger solitary vertical tubes, which display the typical organisation of Leucaltidae with internal folds of the choanoderm. In *A. minchini* Borojevic, 1966a, and in other Leucaltidae such as *Leucaltis* and *Leucettusa*, the choanosome is formed by extensive folding of the choanoderm. Large apical actines of the external tetractines support the whole choanosome and in *A. minchini* and *Leucettusa simplicissima* Burton, 1932b (Fig. 4C) no other spicules are present in the choanoskeleton. In species where additional spicules are present in the choanosome, the choanoskeleton is composed of small and scattered spicules having no distinct relationship with the arrangement of the choanocyte tubes. Simultaneously, the development of a distinct atrial cavity is followed by the formation of a secondary skeleton for the atrial wall.

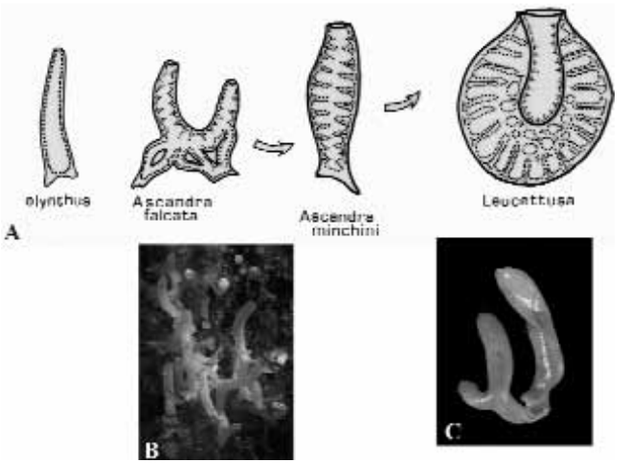

Fig. 4. Family Leucaltidae. A, proposed evolution of Leucaltidae from olynthus through formation of internal choanodermal folds. B, underwater photograph of *Ascandra falcata* (2 cm) from Mediterranean (photo J. Vacelet). C, type specimen of *Leucettusa simplicissima* (1 cm high).

ASCANDRA HAECKEL, 1872

Synonymy

Ascandra Haeckel, 1872: 83; Minchin, 1896: 352; Minchin, 1897: 49; Borojevic, 1966a: 363; Borojevic *et al*., 1990: 257. [*Homandra*] Lendenfeld, 1891.

Type species

Ascandra falcata Haeckel, 1872 (by monotypy) (Fig. 4B).

Diagnosis

Leucaltidae with single or anastomosed tubes in which the choanoderm forms folds inside the choanocoel, isolating radially arranged shallow cavities or true radial tubes. The choanosomal folds are supported by apical actines of the external tetractines only.

Material examined

Holotype (fragment). MNHN LBIM C1968.628, Haeckel's slide deposited in the MNHN, Lesina, Adriatic Sea.

Scope

The genus *Ascandra* may represent a starting-point of an independent evolutionary line among Clathrinida, in which the increase in the choanodermal surface is obtained by the formation of folds inside the choanocoel. These folds delimit only shallow cavities in *A. falcata*, but in *A. minchini* they delimit deep radial tubes. Consequently, *A. minchini* can grow in the form of large individual tubes, with the external surface covered by a continuous pinacoderm and supported by a specific skeleton corresponding to a cortex. The distance between the external surface and the internal parts of the choanoderm makes the constitution of a complex system of inhalant aquiferous cavities necessary. The central choanocoel opens directly into the osculum, and there is no differentiated exhalant aquiferous system. About six species have been recognized in *Ascandra*.

Distribution

The type locality is Adriatic and Mediterranean. The genus is distributed worldwide.

LEUCALTIS HAECKEL, 1872

Synonymy

Leucaltis Haeckel, 1872: 159; Dendy & Row, 1913: 737; Borojevic & Peixinho, 1976: 1002; Borojevic *et al*., 1990: 258; Borojevic, 1998: 75; Wörheide & Hooper, 1999: 877; Borojevic & Klautau, 2000: 190.

Type species

Leucaltis clathria Haeckel, 1872 (by subsequent designation, Dendy & Row, 1913) (Fig. 5A).

Diagnosis

Leucaltidae with a body composed of large, ramified and anastomosed tubes. Each tube has a distinct cortex, a choanoderm composed of elongated and ramified choanocyte chambers, and a central atrium. The choanoderm and the atrial wall have a secondary skeleton composed of small triactines and tetractines.

Material examined

Holotype (fragment). MNHN LBIM C1968.667, Haeckel's slide deposited in the MNHN, made from material sent by Agassiz to Haeckel, from Florida.

Scope

Monotypic. The body of the single species, *Leucaltis clathria*, is composed of very large anastomosed tubes, each of which is reminiscent of an *Ascandra*. The large atrium is an original structure, developed after the formation of radial tubes, delimited by a continuous layer sustained by specific spicules. The general organisation of the *Ascaltis* wall is reminiscent of *Sycon*, and it is quite similar to *Leucettusa* with elongate choanocyte chambers, the major distinction being the particular pattern of growth of the *Leucaltis* cormus.

Distribution

Leucaltis clathria has been reported from all the tropical seas, and the described specimens are indeed morphologically quite homogenous. However, recent studies on genetic characteristics of sponge populations have questioned the taxonomy of the supposedly cosmopolitan species (Solé-Cava *et al*., 1991; Boury-Esnault *et al*., 1999). *Leucaltis clathria* is an other interesting model to address the question of cosmopolitanism through an extensive morphological and genetic analysis as already suggested by Wörheide & Hooper (1999) and Borojevic & Klautau (2000).

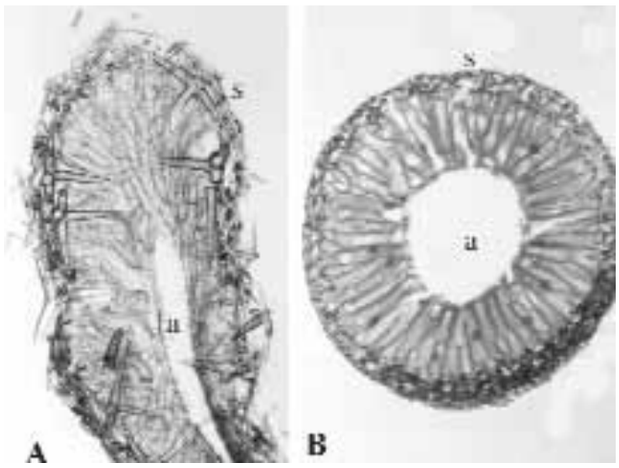

Fig. 5. Family Leucaltidae. A, transverse section through *Leucaltis clathria* (the thickest part is 3 cm). B, transverse section through a specimen of *Leucettusa simplicissima* (125 μm in diameter) (abbreviations: s, surface; a, atrium).

***LEUCETTUSA* HAECKEL, 1872**

Synonymy

Leucettusa Haeckel, 1872: 129; Dendy & Row, 1913: 738; Burton, 1963: 147; Borojevic *et al*., 1990: 258; Hooper & Wiedenmayer, 1994: 481.

Type species

Leucetta corticata Haeckel, 1872 (by subsequent designation, Dendy & Row, 1913).

Diagnosis

Leucaltidae with a simple tubular body, a large atrium, and choanocyte chambers which are either elongated, spherical or both.

Scope

Leucettusa seems clearly derived from a sponge similar to *Ascandra minchini*. The simplest representative of the genus, *L. simplicissima* (Fig. 4C), differs from *A. minchini* only in the formation of an atrium, whose thin wall bears delicate periatrial spicules (Fig. 5B). The whole choanosome is composed of radially arranged elongated chambers, supported exclusively by large apical actines of the cortical tetractines. Its organisation is thus analogous to the syconoid aquiferous system of Calcaronea. In *L. vera* (Poléjaeff, 1883), spherical chambers are added to the elongated ones and a new choanoskeleton composed of scattered spicules is progressively developed. In *L. corticata*, the whole aquiferous system is composed of spherical choanocyte chambers.

Distribution

The type locality is Cuba, Caribbean. The other species (about 12) are mostly been found in the Arctic and Antarctic regions, New Zealand and SW Australia.

***LEUCLATHRINA* BOROJEVIC & BOURY-ESNAULT, 1987**

Synonymy

Leuclathrina Borojevic & Boury-Esnault, 1987a: 18; Borojevic *et al*., 1990: 259.

Type species

Leuclathrina asconoides Borojevic & Boury-Esnault, 1987a (by original designation) (Fig. 6).

Diagnosis

Leucaltidae with a leuconoid organisation. The skeleton is restricted to the cortex sustained by triactines; the choanosome completely lacks spicules.

Material examined

Holotype. MNHN LBIM C1985.5, Bay of Biscay, 44°11.2′N, 8°41.3′W, 400 m depth.

Scope

Leuclathrina may be derived from an olynthus through a progressive folding of the choanoderm inside the primary olynthus tube. In *Ascandra*, in which the radially arranged apical actines of tetractines support the choanodermal folds, radial organisation of the choanoderm is well preserved. In *Leucettusa* the spherical choanocyte chambers are obtained through a progressive rounding of elongated choanocyte chambers, and in *Leucettusa vera* for example, both forms of choanocyte chambers still coexist in the same sponge. In *Leuclathrina*, in which the external skeleton is sustained only by triactines (Fig. 6B), no elements of primary olynthus support the choanoderm folds. No radial organisation can be recognised, and a lacunar leuconoid type of organisation has been apparently acquired directly without a passage through the elongate 'syconoid' choanocyte chambers. The choanosome of *L. asconoides* is located only in the central part of the sponge, and the oscula are situated at the end of chimneys with no choanoderm.

Distribution

NE Atlantic.

FAMILY LEUCASCIDAE DENDY, 1892

Synonymy

Leucascidae Dendy, 1892: 71; Dendy, 1893b: 228; Dendy & Row, 1913: 729; Borojevic, 1968: 207; Borojevic & Boury-Esnault, 1987a: 17; Borojevic *et al*., 1990: 259; Hooper & Wiedenmayer, 1994: 483; Borojevic & Klautau, 2000: 191.

Diagnosis

Clathrinida with a body differentiated into a cortex and a choanosome whose organisation is reminiscent of a clathroid cormus composed of anastomosed tubes. The cortex contains a specific skeleton, composed of large triactines and/or tetractines. Choanocyte chambers are tubular, often highly ramified and anastomosed. The choanoskeleton is restricted to the walls of the choanocyte chambers, maintaining a distinctly tubular organisation.

Scope

While the Leucaltidae are derived from large individual asconoid tubes through the inward folding of the choanoderm, the Leucascidae seem to be derived from species similar to massive *Clathrina* with a large cormus composed of densely anastomosed tubes (Fig. 7A). As pointed out previously by Dendy & Row (1913) and Borojevic (1968), the acquisition of a common cortex is a new grade of integration of the sponge cormus, and this makes it necessary to clearly separate the Leucascidae from the Clathrinidae. It should be emphasised that this cortex is not derived from the outermost tubes of the clathroid cormus, but is a new structure. In *Ascaltis*, only the inhalant aquiferous system has evolved in order to lead the water current from the cortex to the innermost choanocyte tubes. In *Leucascus* a central exhalant atrium is also differentiated. Similar to the cortex, it is surrounded by a wall composed of pinacocytes and a skeletal layer, with no choanoderm. The evolution from *Leucascus* to Leucettidae seems to go through the reorganisation of the choanosome and formation of a true leuconoid aquiferous system. The external common cortex, characteristic of *Ascaltis*, and the internal common leaflet which surrounds the atrium in *Leucascus*, are often thin and can be easily overlooked. The general aspect of the cormus in these cases is quite similar to that of *Clathrina*, and adequate attention should be given to the cortical and the atrial regions in a study of large cormi of the Clathrinidae, in order to avoid misinterpretations.

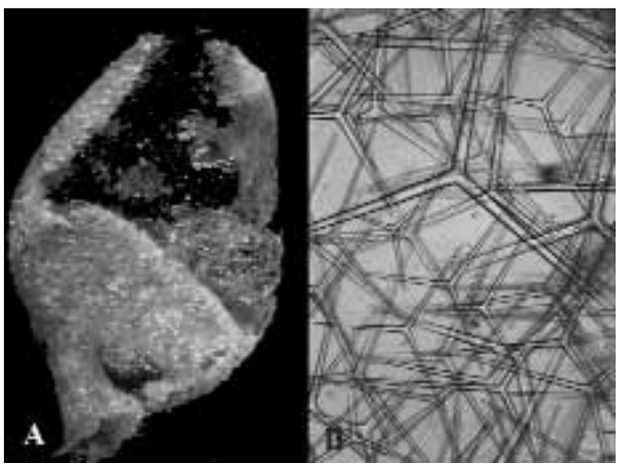

Fig. 6. *Leuclathrina*. A, type specimen of *Leuclathrina asconoides*; a piece of the wall has been cut and the central cavity is apparent (from Borojevic & Boury-Esnault, 1987a) (approx. 1 cm high). B, aspect of the skeleton of the external wall (1 cm = 150 μm).

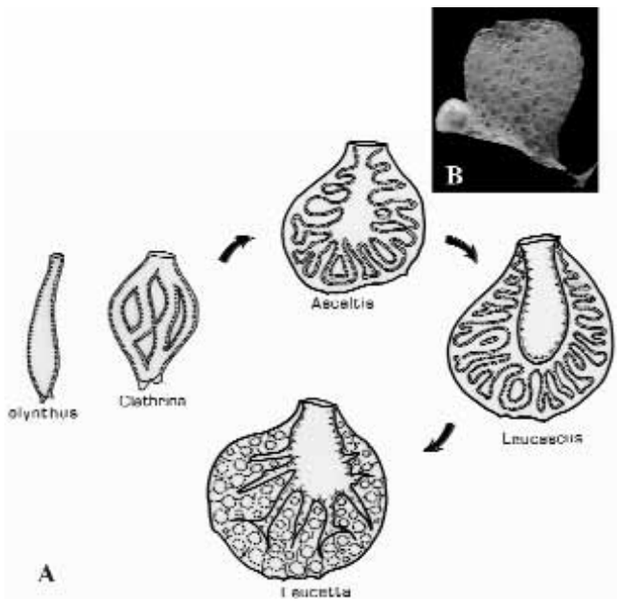

Fig. 7. Families Leucascidae and Leucettidae. A, evolution of these families from the clathroid body found in *Clathrina* through the formation of the external cortex in *Ascaltis* and atrial cavity in *Leucascus*. B, specimen of *Ascaltis lamarcki* from the Bay of Biscay. Natural size, 1 cm.

Many of the Leucascidae have originally been described as '*Clathrina*' or '*Leucosolenia*', and a thorough revision should be undertaken for many such species characterised by distinct spicules in the cortical or atrial region, in order to distinguish those in which such spicules ornate the outermost, otherwise typical tubes with choanocytes (e.g., *Clathrina cerebrum* Haeckel, 1872), from those which have a thin but true cortex devoid of choanocytes (e.g., *Ascaltis lamarcki* Haeckel, 1872).

ASCALTIS HAECKEL, 1872

Synonymy

Ascaltis Haeckel, 1872: 60; Borojevic, 1968: 204; Borojevic & Peixinho, 1976: 1000; Borojevic & Boury-Esnault, 1987a: 17; Borojevic *et al*., 1990: 261; Borojevic, 1998: 76; Borojevic & Klautau, 2000: 192. [*Ascoleucetta*] Dendy & Frederick, 1924: 481. [*Aulorhiza*] Haeckel, 1870a, b; Hooper & Wiedenmayer, 1994: 484.

Type species

Ascaltis lamarcki Haeckel, 1872 (by subsequent designation, Borojevic, 1968) (Fig. 7B).

Diagnosis

Leucascidae with a massive cormus composed of ramified and anastomosed tubes covered by a common cortex. The inhalant aquiferous system is represented by spaces delimited by the cortex and the walls of choanosomal tubes. The exhalant aquiferous system is reduced to the osculum or to a secondary atrial cavity formed by the calyciform growth of the cormus.

Material examined

Holotype (fragment). MNHN LBIM C1968.629, Haeckel's slide deposited in the MNHN. Specimen from Greenland.

Scope

The simplest species of *Ascaltis* are very similar to *Clathrina* with the cormus organised around a large central tube. The only distinction between *Clathrina reticulum* and *Ascaltis lamarcki*, for example, is the presence of a thin continuous cortex surrounding all the cormus and delimiting the inhalant spaces in the latter. In more differentiated species of *Ascaltis*, such as *A. compressa* (Dendy & Frederick, 1924), the cortex becomes well-structured and the sponge body acquires a solid and well-defined form. *Ascaltis*, as defined by Haeckel (1872), included seven species: *A. canariensis, A. cerebrum, A. darwini* which are in fact *Clathrina, A. goethei* and *A. botryoides* which are *Leucosolenia* and *A. lamarcki* and *A. gegenbauri*. Fortunately Haeckel (1872) did not designate a type species for the genus, leaving the concept intact despite many wrongly allocated species, and Borojevic (1968) subsequently designated *A. lamarcki* as the type species. As indicated in the Appendix for Calcarea (this work), all the names used by Haeckel (1870a, b) in his '*Prodromus*' have to be considered as invalid names, *Aulorhiza* which is a name that Haeckel used only in his '*Prodromus*' and never in his later works are here rejected, contrary to the actions of Wiedenmayer (in Hooper & Wiedenmayer, 1994).

Distribution

The type species is abundant in the NE Atlantic and Mediterranean, and the other species of the genus have been found mainly in the Indo-Pacific.

LEUCASCUS DENDY, 1892

Synonymy

Leucascus Dendy, 1892: 77; Dendy, 1893b: 228; Dendy, 1913: 9; Dendy & Row, 1913: 731; Row & Hôzawa, 1931: 742; Borojevic & Peixinho, 1976: 1001; Borojevic *et al*., 1990: 262; Hooper & Wiedenmayer, 1994: 486; Borojevic & Klautau, 2000: 191.

Type species

Leucascus simplex Dendy, 1892 (by subsequent designation, Dendy & Row, 1913) (Fig. 8A).

Diagnosis

Leucascidae with copiously branched and anastomosed choanocyte tubes. The exhalant aquiferous system is represented by a well-developed atrium delimited by a wall with no choanoderm, supported by a specific skeleton.

Scope

The genus *Leucascus* is similar to *Ascaltis* and it is clearly reminiscent of the tubular organisation of the clathroid cormus. However, the constitution of a common atrium, distinct from both the inhalant and exhalant aquiferous systems, is a new character shared by all species of the genus which differentiates it from *Ascaltis*.

Distribution

The type species has an allegedly circumtropical distribution and clearly needs revision (as do all reported cosmopolitan species), whereas the other species have a S Pacific distribution.

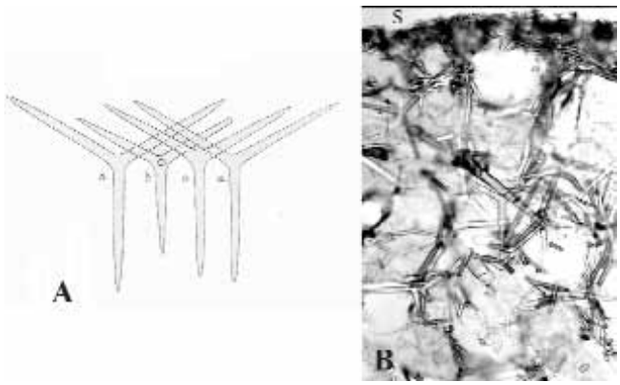

Fig. 8. Families Leucascidae and Leucettidae. A, spicules from *Leucascus simplex* from Dendy, 1892 (1cm = 80 μm) (abbreviations: a, triactines; b, tetractines). B, transverse section through the wall of a specimen of *Leucetta chagosensis* (1 cm = 200 μm) (abbreviation: S, surface).

FAMILY LEUCETTIDAE DE LAUBENFELS, 1936

Synonymy

Leucettidae de Laubenfels, 1936a; Borojevic, 1968: 207; Borojevic *et al*., 1990: 262; Hooper & Wiedenmayer, 1994: 487; Borojevic, 1998: 77; Wörheide & Hooper, 1999: 879. Borojevic & Klautau, 2000: 192.

Diagnosis

Clathrinida with a solid body. The aquiferous system is always leuconoid. The choanoskeleton is well-developed, in the form of a regular network composed of triactines and/or tetractines. The cortex is thin and composed of spicules similar to those of the choanoskeleton.

Scope

Leucettidae (*sensu* Borojevic, 1968) are apparently Clathrinida that have reached the highest degree of differentiation. They are probably derived from Leucascidae (Fig. 7A). Spherical choanocyte chambers are diffusely distributed throughout the choanosome supported by a regular network of the choanoskeleton. The choanosome of Leucettidae no longer recalls the tubular organisation of the clathroid cormus. While in Leucascidae the choanoskeleton is still a two-dimensional structure formed by the curved walls of the choanocyte tubes, in Leucettidae the choanoskeleton is a true three-dimensional structure.

LEUCETTA HAECKEL, 1872

Synonymy

Leucetta Haeckel, 1872: 118; Dendy & Row, 1913: 732; Borojevic *et al*., 1990: 262; Hooper & Wiedenmayer, 1994: 487; Wörheide & Hooper, 1999: 879; Borojevic & Klautau, 2000: 193.

Type species

Leucetta primigenia Haeckel, 1872 (by original designation).

Diagnosis

Leucettidae with a homogeneous organisation of the wall and a typical leuconoid aquiferous system. There is neither a clear distinction between the cortex and the choanoskeleton, nor the presence of a distinct layer of subcortical inhalant cavities. The atrium is frequently reduced to a system of exhalant canals that open directly into the osculum.

Material examined

Holotype (fragment). MNHN LBIM C1968.661, Haeckel's slide deposited in the MNHN. Specimen from the West Indies.

Scope

The definition of *Leucetta* is that of Dendy and Row (1913). These sponges have attained a high degree of functional organisation, similar to that of most Porifera, and in particular the Demospongiae, which are typically leuconoid (Fig. 8B).

Distribution

Leucetta are well-adapted to shallow water habitats, and are the most frequent Calcinea of tropical regions where they can reach a considerable size and occur in large populations. Some species, like *L. microraphis* (Haeckel, 1872), have been considered to be cosmopolitan, but as already suggested by Borojevic & Klautau (2000) we are faced with a complex of species. A comprehensive morphological and genetic study is necessary for most of the *Leucetta* species (Wörheide & Hooper, 1999).

PERICHARAX POLÉJAEFF, 1883

Synonymy

Pericharax Poléjaeff, 1883: 66; Dendy & Row, 1913: 735; Borojevic *et al*., 1990: 263; Hooper & Wiedenmayer, 1994: 489; Wörheide & Hooper, 1999: 886; Borojevic & Klautau, 2000: 195.

Type species

Pericharax carteri var. *heteroraphis* Poléjaeff, 1883 (by subsequent designation, Dendy & Row, 1913).

Diagnosis

Leucettidae with a large central atrium surrounded by a thick wall. The wall is divided into a choanoderm and a thin subcortical layer of inhalant cavities supported by a peculiar skeleton partially composed of centripetal actines of the special cortical triactines.

Scope

Pericharax has an organisation quite similar to that of *Leucetta*. However, the presence of a particular differentiation of the subcortical inhalant cavities with a specific skeleton easily indicates the difference between these genera.

Distribution

The type species is widely distributed and allegedly nearly cosmopolitan: Tristan da Cunha, Indian Ocean and tropical Pacific region. All these populations need to be carefully revised as to their alleged conspecificity.

CLATHRINIDA *INCERTAE SEDIS*

LEUCOMALTHE HAECKEL, 1872

Synonymy

Leucomalthe Haeckel, 1872: 172; Dendy & Row, 1913: 732; Borojevic *et al*., 1990: 263.

Type species

Leucomalthe bomba Haeckel, 1872 (by monotypy).

Diagnosis

Clathrinida with a solid body and a large central cavity. Choanocyte chambers greatly elongated, tubular and copiously branched. Skeleton consists of regular triactines and microdiactines in the cortex, regular triactines in the choanoskeleton, and sagittal tetractines both in the atrial skeleton and in the exhalant channels. Large longitudinal diactines present throughout the body.

Scope

This sponge, which was described by Haeckel from a single specimen, has never been found again. The special organization of its aquiferous system is reminiscent of *Dendya* and one may speculate that it originated from a *Dendya*-like sponge through progressive corticalization and formation of an atrium. However, as pointed out by Dendy & Row (1913), this sponge was assigned to the Calcinea on somewhat dubious grounds. In particular, sagittal spicules in the atrial skeleton are not normally found in Calcinea, and it is necessary to discover new material to identify the exact taxonomic position of this species and genus.

Distribution

Viti Levu Island, Fiji, Pacific Ocean.