

# Revision of the genus *Clathrina* (Porifera, Calcarea)

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The genus *Clathrina* has one of the most difficult systematic arrangements in the Porifera, Class Calcarea. Few morphological characters can be used to describe its species, and the systematics and the geographical distribution of its species have changed several times, according to the point of view of the systematists. ‘Lumpers’ consider that clathrinas are morphologically plastic, while ‘splitters’ believe that even slight morphological differences should be considered sufficient to distinguish between species. The morphology of several specimens/species of *Clathrina*, including the type species, when possible, was studied and used to produce the first revision of this genus. Using results obtained from previous morphological and molecular studies, the morphological characters were chosen and analysed in all studied specimens. In total, 43 species were found, nine of which are new to science. These results agree with the viewpoint that morphological characters such as type and distribution of spicules, size of actines, spines, anastomosis of the cormus, organization of the osculum and presence of granules in cells, are useful when establishing the taxonomy of the genus. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 139, 1–62.

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## INTRODUCTION

The genus *Clathrina* is defined almost exclusively by negative characters (Borojevic & Boury-Esnault, 1987). It has the simplest organization among the sponges – the asconoid aquiferous system – which means that all the cavities are lined by choanocytes. Moreover, its skeleton is also simple, comprising a few spicule types: diactine, triactine and/or tetractine. The absence of many morphological characters produces the difficult systematics of the genus, particularly when the skeleton contains only triactines (Borojevic & Boury-Esnault, 1987).

The first *Clathrina* described was *C. coriacea*, originally named *Spongia coriacea* Montagu, 1818, from the British Isles. Schmidt (1862) created a

new genus, *Nardoa*, and described another, *Clathrina*, which he named *Nardoa reticulum*. However, the name *Nardoa* had already been used by Gray in 1840 for a genus of Asteroidea and had to be rejected. The genus *Leucosolenia*, with *L. botryoides* (Ellis & Solander, 1786) as the type species, was created by Bowerbank (1864). In the same year, however, Schmidt (1864) described a new species of *Clathrina* as *Grantia clathrus*. Two years later, Bowerbank (1866) defined four species in his genus *Leucosolenia*, including *Clathrina contorta* sp. nov. and *Clathrina coriacea*. Schmidt (1866) criticized Bowerbank’s genera and species, retaining *Leucosolenia* for *Grantia botryoides* and *pulchra*, and maintaining his genus *Nardoa* for the ‘massive Grantien’, i.e. *lacunosa*, *spongiosa* and *reticulum*. Gray (1867) classified Ascons as *Leucosolenia*: *L. botryoides* (‘arborescent’), *L. contorta* and *L. lacunosa* (‘massive *Nardoa*’), and *L. coriacea* (‘incrusting’), and he created the genus *Clathrina*, with *C. sulphurea* (= *Grantia clathrus* Schmidt, 1864) as the type species.

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Haeckel (1872) proposed seven genera of asconoid Calcarea, 'based upon the permutations and combinations of triradiate, quadriradiate, and oxeote spicules'. De Poléjaeff (1883) 'placed the whole of the species in the genus *Leucosolenia* of Bowerbank'. Von Lendenfeld (1891) modified Haeckel's system, retaining only two genera: *Ascetta* (without oxea) and *Ascandra* (with oxea). In the same year, Dendy (1891) proposed the subdivision of the genus *Leucosolenia* into 'sections and subsections', according to the type of colony formation and canal system (*Simplicia*, *Reticulata* (*Indivisa* and *Subdivisa*) and *Radiata*). Only *Radiata* still has some value, being transferred to the genus *Dendya* by Bidder (1898).

Minchin (1896) outlined the distinction between three genera of Homocoela: *Leucosolenia*, *Ascandra* and *Clathrina*. His diagnosis of *Clathrina* Gray (1867) was as follows:

'The full-grown colony forms a system or systems of reticulate and anastomosing tubes, each system terminating in a cloaca-like osculum; incrusting, massive or stalked. The principal spicules of the skeleton are equiangular triradiate systems, to which may be added sagittal triradiates in certain parts of the sponge, and monaxons. Collar cells with nucleus at the base. Larva parenchymella. First spicules to appear triradiate systems'.

Minchin (1900) recognized two distinct families – Clathrinidae and Leucosoleniidae – considering *Clathrina* to be a synonym of *Ascetta*, *Ascaltis* and *Leucascus*.

According to Dendy & Row (1913) 'the genus *Clathrina* Gray (1867) was originally based on the reticulate form of the sponge colony, and this is still almost the only character which could be made use of in practice as a distinction from *Leucosolenia*, but here again we know that no sharp separation can be drawn between the two types of external form, for one and the same colony may be reticulate in its lower, and nonreticulate in its upper portion'. Dendy & Row (1913) did not accept the subdivision made by Minchin into Clathrinidae and Leucosoleniidae and instead proposed four genera in the family Homocoelidae: *Leucosolenia*, *Ascute*, *Ascysa* and *Dendya*. In their article they also stated that *Ascute*, *Ascysa* and *Dendya* were definable, but that *Leucosolenia* 'is distinguished almost entirely by negative characters, and contains a very large number of species, presenting a very great diversity amongst themselves, both in colony-form and spiculation'. The diagnosis of *Leucosolenia* in that article was 'Diverticula of the gastral cavity, if any, never radially arranged around a central tube. Skeleton composed of triradiate or quadriradiate spicules, to which oscula may be added. No uteoid dermal skeleton. Nucleus of collared cells basal or apical.'

Topsent (1936) continued using the genus *Leucosolenia* for clathrinas and considered that all specimens with regular triactines only, should be identified as *coriacea*. He considered a high morphological variability in asconoid sponges and reduced the number of species of *Clathrina*.

Divergent interpretations in relation to the plasticity of morphological characters in *Clathrina* created two mainstream classification strategies, which further complicated the systematics. Authors that follow one or other of these are called either 'lumpers' or 'splitters' (Solé-Cava *et al.*, 1991). Lumpers consider that morphological variation in specimens of *Clathrina* has resulted from the plasticity of these characters. They have reduced the number of accepted species, creating several synonyms, and widening the geographical distribution of these few accepted species. Splitters believe that even a few morphological differences correspond to real genetic differences. They recognize a large number of species with restricted geographical distribution.

Recently, to address this question of the morphological variability and distribution of species of *Clathrina*, sympatric and allopatric populations were studied using genetic and morphological approaches (Solé-Cava *et al.*, 1991; Klautau, Solé-Cava & Borojevic, 1994). It was observed that some species previously considered cosmopolitan have in fact more restricted distributions. These results suggested the use of even slight morphological differences to recognize species, which agreed with the splitters' point of view. Ecological distribution and the reproductive cycle can also provide important information about the recognition of species in a particular habitat (Borojevic, 1967; Johnson, 1978) and numerical analysis of spicules is also helping with classification (Borojevic *et al.*, 1990; Wörheide & Hooper, 1999).

The present work is the first revision of *Clathrina*. Specimens collected in Brazil or deposited in The Natural History Museum, London, together with type material deposited in other museums around the world were studied. Only morphological characters were analysed. In total, 43 species were recognized, nine of them considered new to science. The only species not included in this revision were those where the type or a specimen from the type locality could not be examined: *Leucosolenia darwinii* Haeckel, 1870 (which is probably a complex of species, as it is very plastic according to the description); *Ascaltis cerebrum* var. *decipiens* Haeckel, 1872; *Clathrina latitubulata* Carter, 1886; *Leucosolenia nanseni* Breitung, 1896; *Ascetta primordialis* var. *dictyoides* Haeckel, 1872; *Clathrina coriacea* var. *rubra* Sarà, 1958 (as the slide was not well preserved); and *Clathrina sulphurea*

Gray, 1867 (currently considered as synonymous with *Clathrina clathrus*).

Other species not included here are those that were considered to belong to *Clathrina* at one time, but which should now be assigned to other genera: *Clathrina cavata* Carter, 1886 (which should be assigned to *Ascaltis*); *Clathrina osculum* Carter, 1886 (which is probably synonymous with *Leucetia clathrata* Carter, 1883); *Leucosolenia intermedia* Kirk, 1896, *Leucosolenia proxima* Dendy, 1891, and *Leucosolenia wilsoni* Dendy, 1891 (all of which should be assigned to *Ascaltis*); *Clathrina poterium* (Haeckel, 1872) (which was originally described by Haeckel as a variety of *Clathrina primordialis* but was elevated to the rank of species by Ridley (1881), and which should be assigned to *Ascaltis*); *Clathrina ventricosa* Carter, 1886 (which belongs to *Leucascus*).

#### LIST OF SPECIES ASSIGNED TO *CLATHRINA* GRAY, 1867

- C. adusta* Wörheide & Hooper, 1999  
*C. ascandroides* Borojevic, 1971  
*C. aspina* Klautau, Solé-Cava & Borojevic, 1994  
*C. atlantica* (Thacker, 1908)  
*C. aurea* Solé-Cava, Klautau, Boury-Esnault, Borojevic & Thorpe, 1991  
*C. biscayae* Borojevic & Boury-Esnault, 1987  
*C. brasiliensis* Solé-Cava, Klautau, Boury-Esnault, Borojevic & Thorpe, 1991  
*C. canariensis* (Miklucho-Maclay, 1868)  
*C. cerebrum* (Haeckel, 1872)  
*C. ceylonensis* (Dendy, 1905)  
*C. chrysea* Borojevic & Klautau, 2000  
*C. clathrus* (Schmidt, 1864)  
*C. conifera* Klautau & Borojevic, 2001  
*C. contorta* Minchin, 1905  
*C. coriacea* (Montagu, 1818)  
*C. cribrata* Rapp, Klautau & Valentine, 2001  
*C. cylindractina* Klautau, Solé-Cava & Borojevic, 1994  
*C. dubia* (Dendy, 1891)  
*C. gardineri* (Dendy, 1913)  
*C. helveola* Wörheide & Hooper, 1999  
*C. heronensis* Wörheide & Hooper, 1999  
*C. laminoclathrata* Carter, 1886  
*C. luteoculcitella* Wörheide & Hooper, 1999  
*C. panis* (Haeckel, 1872)  
*C. parva* Wörheide & Hooper, 1999  
*C. primordialis* (Haeckel, 1872)  
*C. procumbens* (von Lendenfeld, 1885)  
*C. quadriradiata* Klautau & Borojevic, 2001  
*C. reticulum* (Schmidt, 1862)  
*C. sagamiana* (Hôzawa, 1929)  
*C. septentrionalis* Rapp, Klautau & Valentine, 2001  
*C. tenuipilosa* (Dendy, 1905)  
*C. tetractina* Klautau & Borojevic, 2001  
*C. wistariensis* Wörheide & Hooper, 1999

- C. sueziana* sp. nov.  
*C. hispanica* sp. nov.  
*C. sinusarabica* sp. nov.  
*C. hondurensis* sp. nov.  
*C. clara* sp. nov.  
*C. africana* sp. nov.  
*C. hirsuta* sp. nov.  
*C. rotunda* sp. nov.  
*C. tetrapodifera* sp. nov.

#### Institutional abbreviations

- BMNH The Natural History Museum, London, UK  
 CUMZ Cambridge University Museum of Zoology, UK  
 LBIM-C Laboratoire de Biologie des Invertébrés Marins-Calcaires (MNHN)  
 MNHN Muséum national d'Histoire Naturelle, Paris, France  
 MNRJ Museu Nacional do Rio de Janeiro, Brazil  
 PMJ Phyletisches Museum, Jena, Germany  
 QM Queensland Museum, Brisbane, Australia  
 ZMB Museum für Naturkunde an der Universität Humboldt zu Berlin, Germany  
 ZMUC Zoological Museum, Copenhagen, Denmark

#### MATERIAL AND METHODS

All the specimens identified as *Clathrina*, *Leucosolenia*, *Ascetta*, *Ascandra*, *Ascaltis* or *Leucascus* deposited at BMNH were studied. Several *Clathrina* species were wrongly identified or retained old systematic names. Type specimens deposited in other museums worldwide were loaned.

Each studied specimen was first observed under a stereomicroscope in order to analyse the anastomosis pattern of the cormus, distribution of oscula and the presence or absence of water-collecting tubes (i.e. tubes that collect the excurrent water and conduct it to a few apical oscula).

For the spicule analysis, small pieces of the cormus were transferred to test tubes and dissolved in sodium hypochlorite. After digestion, the spicules were washed five times in distilled water and twice in absolute ethanol. Several drops of ethanol containing the spicules were transferred to slides and the ethanol was heat-evaporated. The mounting medium used was Canada Balsam.

Sections were prepared in order to analyse the organization of the skeleton and establish the presence or absence of cells with granules. A small piece of the cormus was stained with an alcoholic solution of acid Fuchsin for 20 min. The excess of Fuchsin was removed by rinsing the fragment in absolute ethanol. The fragment was clarified in HistoClear at 50°C for 1 h and transferred to molten paraffin wax also for 1 h

at 60°C. It was then embedded in paraffin wax and sectioned with a microtome at various thicknesses. Sections were transferred to a microscope slide and the wax removed with HistoClear at 50°C. The mounting media was Canada Balsam.

All photomicrographs of specimens were taken with a Zeiss medium format camera fitted to a Carl Zeiss Universal Microscope. Photographs of the spicules and sections were taken with an Olympus microscope. For the micrometry analyses we measured the length and the width of the base of one of the facial actines and, in the case of the tetractines, also the length and the width of the base of the apical actine. For the thickness of the diactines, we measured the thickest portion of the spicule. Measurements were made using an ocular micrometer. The results are presented in tabular form, featuring length (minimum, mean, maximum and SD [ $\sigma$ ]) and width (mean and SD) and number analysed ( $n$ ). In each case measurements were taken of 30 spicules of each type. Sometimes, however, the specimens analysed were either very small or had many broken spicules; in these cases fewer spicules could be measured. A summary of the main characteristics is presented in the Appendix.

## RESULTS

### CLASS CALCAREA BOWERBANK, 1864

*Diagnosis:* Exclusively marine Porifera in which the mineral skeleton is composed entirely of calcium carbonate. Spicules are diactines, triactines and tetractines. Calcarea are always viviparous.

### SUBCLASS CALCINEA BIDDER, 1898

*Diagnosis:* Calcarea with regular (equiangular and equiradiate) or exceptionally parasagittal or sagittal triactines and a basal system of tetractines. In terms of ontogeny, triactines are the first spicules to be secreted. Choanocytes are basinnucleate with spherical nuclei. The basal body of the flagellum is not adjacent to the nucleus. Calcinea incubate coeloblastula larvae.

### ORDER CLATHRINIDA HARTMAN, 1958

*Diagnosis:* Calcinea with skeleton composed exclusively of free spicules, without hypercalcified nonspicular reinforcements, spicule tracts, calcareous scales or plates.

### FAMILY CLATHRINIDAE MINCHIN, 1900

*Diagnosis:* Clathrinida with an essentially tubular organization. A continuous choanoderm lines all the

internal cavities. Growth is by longitudinal median division and anastomosis of tubes to form large units called the cormus. There is neither a common cortex nor a well-defined inhalant and exhalant aquiferous system.

### GENUS CLATHRINA GRAY, 1867

*Diagnosis:* Clathrinidae in which the choanoderm is flat or rarely raised up into conuli by the apical rays of the tetractines, but never forms true folds, at least when the sponge is in the extended state. The cormus comprises anastomosed tubes. Regular, equiangular and equiradiate triactines and/or tetractines, to which diactines, tripods or tetrapods may be added.

Type-Species: *Clathrina clathrus* (Schmidt, 1864).

### CLATHRINA ADUSTA WÖRHEIDE & HOOPER, 1999

*Type locality:* South side of Wistari Reef, Great Barrier Reef, Australia (18 m depth).

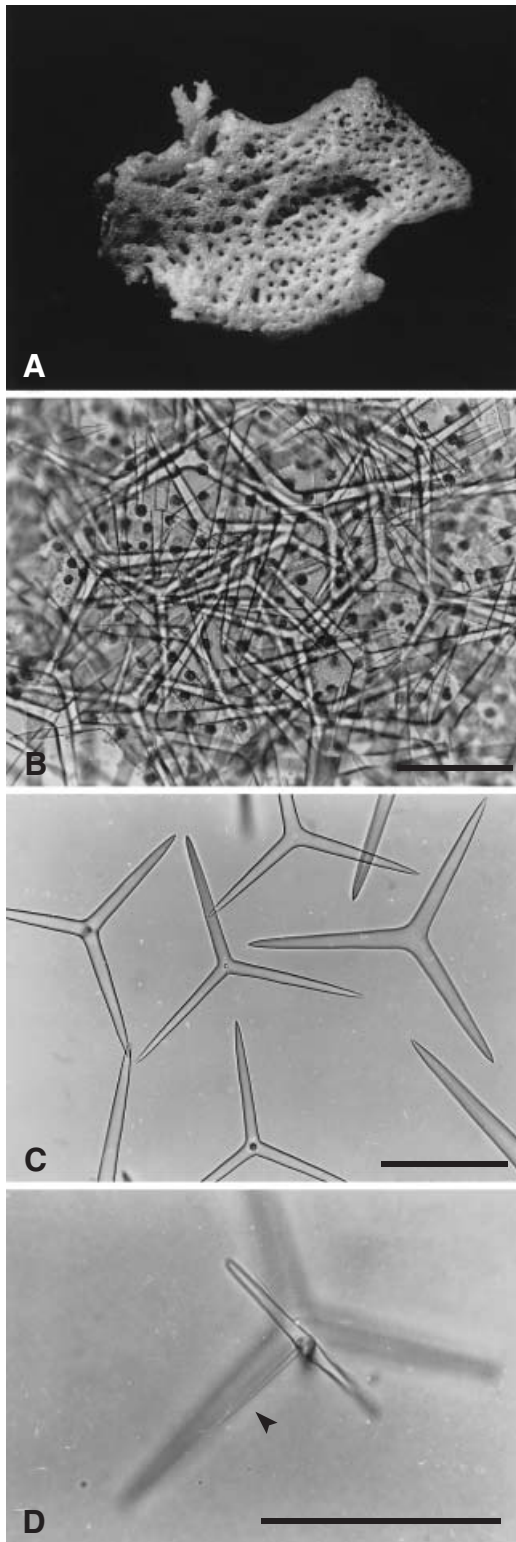
*Type:* QMG 313665 (holotype/alcohol). South side of Wistari Reef, Great Barrier Reef, Australia, 23°29.4'S, 151°52.8'E, 18 m depth. Collected by: G. Wörheide, 7 July 1998.

*Colour:* The colour of the holotype has changed from white to dark brown while preserved in alcohol (Wörheide & Hooper, 1999).

*Description:* The cormus comprises thin, regular and tightly anastomosed tubes which seem bright because of the spicules (Fig. 1A). At the apical region, the tubes become larger and have terminal oscula. They are typical water-collecting tubes. In some parts of the cormus, a structure resembling a cortex appears to be present and small cavities can sometimes be found below it. The brownish colour results from the presence of cells with brown granules (Fig. 1B).

The skeleton has no special organization, comprising equiangular and equiradiate triactines and tetractines (Fig. 1C), the former slightly more abundant. Actines are conical with sharp tips and slightly undulated. The apical actine of the tetractines (Fig. 1D) is shorter and thinner than the facial ones, cylindrical, sharp, smooth and straight.

Spicule	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			$n$
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	64.8	109.9	$\pm 20.9$	156.0	12.7	$\pm 2.9$	30
Tetractines	62.4	110.9	$\pm 29.5$	192.0	12.0	$\pm 3.4$	30
Apical actine	24.0	60.7	$\pm 16.8$	84.0	3.8	$\pm 0.7$	15



**Figure 1.** *Clathrina adusta*. A, photograph of the holotype ( $\times 4$ ). B, Cells with brown granules. C, triactines and tetractines. D, apical actine of a tetractine (arrow). Scale bar = 100  $\mu\text{m}$ .

*Remarks:* This agrees with the original description of *C. adusta*, if one considers the presence of one size class of triactines. However, this population is very variable and, perhaps, there are in fact two populations of triactines, differing in their sizes. In relation to the shape of the actines, it is considered as conical and not 'more-or-less cylindrical'. In the original description (Wörheide & Hooper, 1999), the micrometry of the triactines was:

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	$n$
Triactines	90	108.1	$\pm 14.3$	142	14.1	$\pm 2.0$	30

The organization of the cormus, together with the cells with granules, is the best character to recognize this species

*CLATHRINA ASCANDROIDES* BOROJEVIC, 1971

*Type locality:* Cabo de São Tomé, Rio de Janeiro, Brazil.

*Type:* MNRJ 2096 (holotype/alcohol); MNHN-LBIM-C-1971-1 (paratype/alcohol). Cabo de São Tomé, Rio de Janeiro, Brazil; attached to *Laminaria brasiliensis*. Collected by H. de Souza Lima.

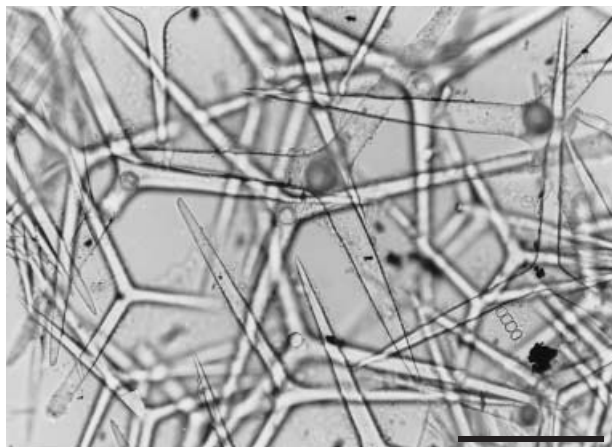
*Citations:* Borojevic & Peixinho (1976); Borojevic & Boury-Esnault (1987); Klautau & Borojevic (2001).

*Colour:* The specimen deposited in MNHN was not found; the MNRJ specimen was examined. It is small and fragmented and was collected attached to *Laminaria brasiliensis*. It is preserved in alcohol. The colour is still white, although other specimens collected in Brazil became brown when preserved in alcohol or when frozen.

*Description:* The cormus is formed of large tubes, irregular and loosely anastomosed. In the apical region there is no anastomosis. Oscula are distributed through all the tubes. No water-collecting tubes are present. As the type is very fragmented, the organization of the cormus could not be recognized; several other specimens were analysed.

The skeleton comprises tetractines of two different size classes, and triactines of only one size class (Fig. 2A). Triactines are the most abundant spicules. Spicules are equiradiate and equiangular.

The triactines and the smaller tetractines are the same size. Their actines are slightly conical and very sharp. Both triactines and tetractines are located outside the tubes, giving them a smooth surface. The api-



**Figure 2.** *Clathrina ascandroides*. A, triactines and the two populations of tetractines. Scale bar = 100 µm.

cal actine of the smaller tetractines is conical, sharp, smooth, shorter and curved. It is thinner than the facial ones and projected into the tubes.

The large tetractines surround the interior of the tubes, and also project their apical actines into them. Actines are conical and sharp. The apical actine is curved, conical, sharp, smooth, shorter and a little thinner than the facial ones.

	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	<i>n</i>
Triactines	90.0	130.0	±20.0	163.0	13.0	±2.0	30
Tetractines	107.5	164.5	±35.0	260.0	16.5	±2.8	30
Apical actine	26.4	40.6	±17.0	79.2	8.2	±1.2	08
Large tetractines	193.8	313.1	±63.2	418.2	39.8	±8.2	26
Apical actine		84.0			21.6		01

**Remarks:** *Clathrina ascandroides* was first described by Borojevic (1971), who collected specimens from the Cape of São Tomé in Rio de Janeiro. It is very similar to *C. atlantica* (Thacker, 1908) from the Cape Verde Islands, although it differs from the latter by the absence of diactines.

The original description refers to only one kind of triactine and tetractine, measuring, respectively, 60–110 µm/8–12 µm and 300 µm/40 µm. Borojevic considered the cormus of this species to be very characteristic, with tubes anastomosing near the base, and not anastomosed in the distal part, as in *Ascandra falcata*. Another species similar to *C. ascandroides*, according to Borojevic, is *Ascaltis gegenbauri* Haeckel, 1872. Topsent (1936) considered

*A. gegenbauri* to be a synonym of *A. falcata*, the former being a variety with rare or absent diactines. Borojevic confirmed this after analysing a specimen of *A. gegenbauri* deposited in MNHN (Borojevic, 1966). He found some of the rare diactines and the characteristic internal folds of the choanoderm. He suggested that the specimens from the Azores, identified by Topsent (1892) as *A. gegenbauri* might, in fact, be *C. ascandroides*. He also suggested that *C. ascandroides* could be related to *A. falcata*, but was clearly distinct from it and from *A. falcata* f. *gegenbauri*, which has well-developed internal folds.

Borojevic & Peixinho (1976) and Borojevic & Boury-Esnault (1987) identified specimens from, respectively, north-east Brazil (75 m) and the Bay of Biscay (Azores, 340–560 m) as *C. ascandroides*, which suggested that the distribution of this species was probably amphiatlantic. When describing the specimens from Brazil, they noted the presence of one kind of triactine and two kinds of tetractines.

The size of the spicules of both populations is very similar; the species awaits genetic studies to confirm or refute the hypothesized distribution.

	CS Tomé	NE Brazil	B Biscay	A do Cabo	CS Tomé (present article)
Triactines					
Length (µm)	60–110	30–200	142–164	83–168	90.0–163.0
Width (µm)	8–12	10–20	13	11	13
Tetractines					
L		80–270	161–200	123–173	107.8–260
W		10–20	11.7–13	13	16.5
Apical actine					
L		45	52	64	26.4–79.2
W			5.2	12	8.2
Large tetractines					
L	300	270–400	299–364	183–225	193.8–418.2
W	40	20–45	26.6–31.2	23	39.8
Apical actine					
L		160	62.4–114.4	95	84
W			15.6–20.8	34	21.6

*CLATHRINA ASPINA* KLAUTAU, SOLÉ-CAVA & BOROJEVIC, 1994

**Type locality:** Arraial do Cabo (Gruta Azul), Rio de Janeiro, Brazil.

**Type:** BMNH 1999.9.16.3 (holotype/alcohol). Arraial do Cabo (Gruta Azul), Rio de Janeiro, Brazil. Collected by G. Muricy (13 June 1987), MNRJ 4053 (paratype/alcohol). Arraial do Cabo (Gruta Azul), Rio de Janeiro, Brazil. Collected by N. Boury-Esnault (13 June 1987).

*Citations:* Klautau & Borojevic (2001).

*Colour:* White in life and when preserved.

*Description:* Massive cormus formed of thin, regular and tightly anastomosed tubes (Fig. 3A) similar to those of *C. brasiliensis* and *C. cerebrum*. Oscula are simple apertures surrounded by a thin membrane. They are located on the top of conical projections distributed throughout the cormus and receive the excurrent water from water-collecting tubes. In preserved specimens, it is difficult to recognize the oscula.

The skeleton has no special organization, and it comprises triactines, tetractines and tripods (Fig. 3B). Triactines and tetractines are equiangular and equiradiate; their actines are slightly conical, with blunt tips. Triactines are the most abundant spicules; the apical actine (Fig. 3C) is shorter and thinner than the facial ones. It is also straight, conical, sharp and, unlike that of *C. brasiliensis* and *C. cerebrum*, smooth. Occasionally, it is possible to find apical actines with vestigial spines. Tripods are typical, with a raised centre and conical actines but sometimes are only similar to large conical triactines. They are distributed in a monolayer on the external tubes, delimiting the cormus. *C. aspina* has a sciaphile habitat.

	Length (µm)			Width (µm)			<i>n</i>
	min	mean	σ	max	mean	σ	
Triactines	55.0	70.0	± 7.5	80.0	6.0	± 1.0	30
Tetractines	52.5	68.8	± 7.8	82.5	6.0	± 1.0	30
Apical actine	40.0	50.3	± 6.3	62.5	5.0	0	30
Tripods	62.5	78.8	± 8.8	92.5	9.5	± 0.8	30

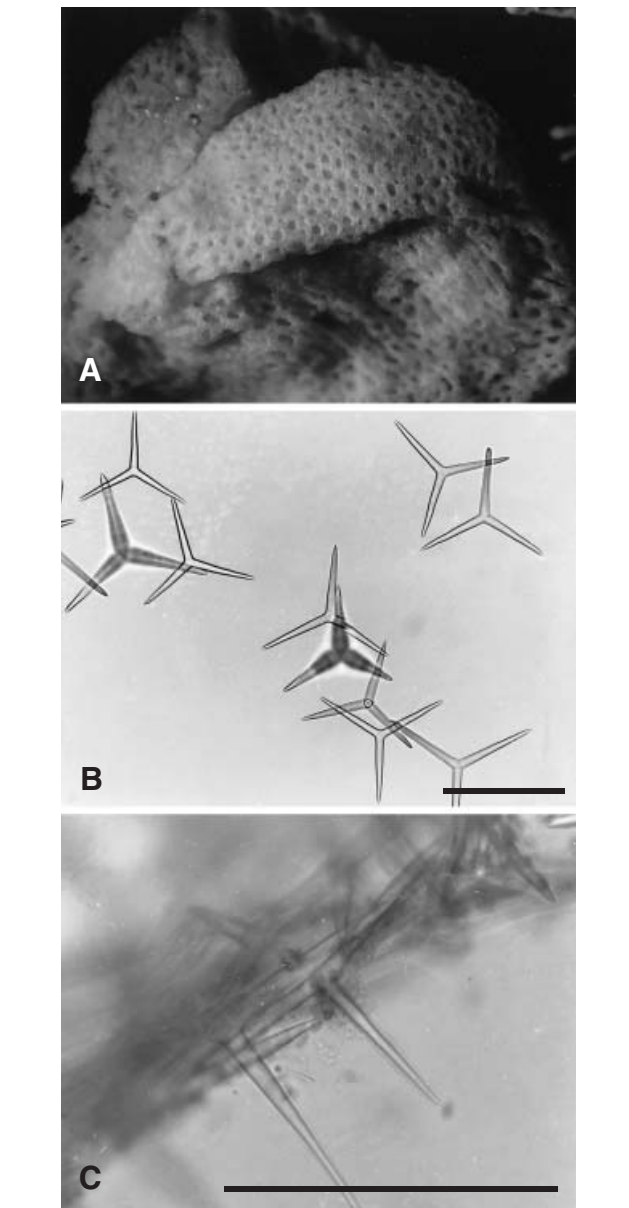
*Remarks:* Although there are morphological similarities to *C. brasiliensis* and *C. cerebrum*, *C. aspina* is easily distinguished from those species by the absence of spines on the apical actine of the tetractines. Allozyme variation studies of the populations of *C. aspina* and *C. brasiliensis* from Arraial do Cabo have been undertaken (Klautau *et al.*, 1994) and results show that, although living in sympatry, there is no gene flow between them.

***CLATHRINA ATLANTICA* (THACKER, 1908) COMB. NOV.**

*Original name:* *Leucosolenia atlantica* Thacker, 1908

*Type locality:* Boa Vista Island, Cape Verde Islands.

*Type:* CUMZ-R.N.5 (holotype/alcohol) and CUMZ-R.N.4 (paratype/alcohol); slides BMNH 1924.7.2.6 (from the holotype) and BMNH 1924.7.2.5 (from the



**Figure 3.** *Clathrina aspina*. A, photograph of the holotype ( $\times 10$ ). B, triactines, tetractines and tripods. C, apical actine of the tetractines. Scale bar = 100 µm.

paratype). Cape Verde Islands, 37 m depth, North Point, Boa Vista Island.

*Citations:* Dendy & Row (1913); Tanita (1942, 1943); Burton (1963); Borojevic & Peixinho (1976).

*Colour:* White when preserved.

*Description:* Cormus formed of a few isolated white tubes (Fig. 4A), the largest measuring  $0.6 \times 0.2 \times 0.1$  cm, with a diameter of 0.1 cm. Consequently, there is no true anastomosis, although there

is fusion at some points. Oscula are present at the end of the tubes, and there are no water-collecting tubes. The surface of the tubes is a little hispid because of the presence of diactines, which are particularly more abundant near the base.

The skeleton comprises triactines, tetractines of two different sizes (Fig. 4B), diactines (Fig. 4C) and trichoxeas. The triactines and tetractines are equiradial and equiangular, and triactines are the most abundant spicules. The actines are straight, cylindrical or conical, with a sharp tip. Both triactines and tetractines are approximately the same size. The apical actine of the tetractines protrudes into the interior of the tubes, and it is smooth, conical, sharp and thinner and shorter than the facial ones.

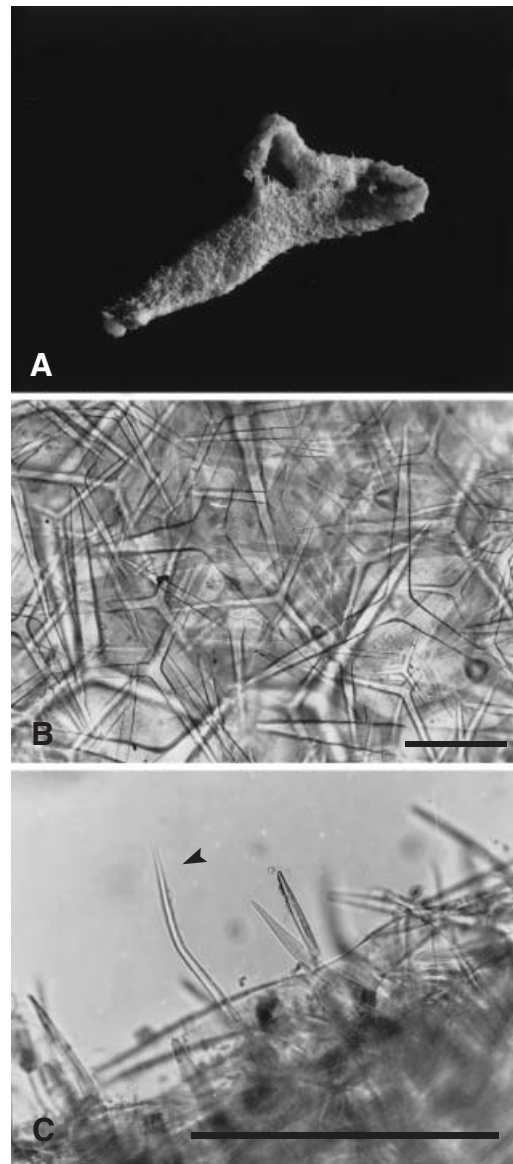
Large tetractines are only found on the surface of the tubes. Their actines are conical and stout, with a sharp tip. Their apical actine projects inside the tubes. It is conical, smooth, straight and sharp, and always shorter than the facial ones.

Diactines are not evenly distributed. They are found mainly in the basal tubes, where they are located perpendicular to the wall. They are slightly curved at one tip or, sometimes, at both tips. In the latter case, they are curved in opposite directions (sigmoid). Very occasionally they are straight. Both tips are sharp, and the proximal tip is a little thicker, while the distal tip is curved.

Trichoxeas are also present. Thacker had observed these, but considered them to be a character with no taxonomic value. We believe by contrast that they are important in the description of *C. atlantica* and should be considered as a distinctive taxonomic character to distinguish it from other species.

Spicule	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )		
	min	mean $\sigma$	max	mean $\sigma$	$n$	
Triactines	75.0	108.3 $\pm$ 16.5	140.0	10.0	$\pm$ 1.5	30
Tetractines	85.0	106.0 $\pm$ 13.5	145.0	9.8	$\pm$ 1.5	30
Apical actine	10.2	35.0 $\pm$ 13.4	51.0	7.8	$\pm$ 2.8	14
Large tetractines	87.5	165.0 $\pm$ 30.5	225.0	23.0	$\pm$ 4.0	30
Apical actine	40.8	69.1 $\pm$ 23.8	102.0	18.9	$\pm$ 7.0	13
Diactines	125.0	201.8 $\pm$ 37.5	250.0	7.5	$\pm$ 0.8	19

**Remarks:** *Clathrina atlantica* was first described by Thacker (1908) as *Leucosolenia atlantica*, when he analysed two specimens from the Cape Verde Islands (Crossland Coll.). Many years would pass before another specimen was identified as *atlantica*. Tanita (1943) described this species from Japan. Borojevic &



**Figure 4.** *Clathrina atlantica*. A, photograph of the holotype ( $\times 40$ ). B, triactines and tetractines. C, diactines at the surface (arrow). Scale bar =  $100 \mu\text{m}$ .

Peixinho (1976) described it from Brazil, calling it *Clathrina* for the first time.

Although the specimens collected in these three localities have the same kind of spicules – triactines, tetractines of two different sizes and diactines – they are not identical. There are important differences involving the organization of the cormus and the size and shape of the spicules.

The specimens from Japan and from Brazil have a clathrate cormus while those from the Cape Verde Islands have nonanastomosed tubes, which are sometimes fused, as in *C. ascandroides*. The shape of the diactines is different. The types have cylindrical diac-



tines, with sharp tips, while in the specimens from Japan and from Brazil, the diactines are more fusiform and, in the Brazilian specimens, one of the tips resembles an arrow. The size of the spicules in the specimens from these three localities is also different (see below).

Considering these morphological differences, we believe that specimens from these three localities are in fact distinct species and that the distribution of *C. atlantica* is restricted at the moment to the Cape Verde Islands. The specimens from Japan and Brazil should be considered as distinct species, new to science. However, as they were unavailable to us, they could not be studied, and were not included in this revision.

	Cape Verde (Thacker, 1908)	Cape Verde (this work)	Japan	Brazil
<b>Triactines</b>				
L (µm)	120	108 (± 17)	90–130	80–300
W (µm)	10	10 (± 2)	8–13	8–25
<b>Tetractines</b>				
L	120	106 (± 14)	90–130	80–300
W	10	10 (± 2)	8–13	8–25
<b>Apical actine</b>				
L	30		70–160	10–30
W	7		6–10	
<b>Large tetractines</b>				
L	200	165 (± 31)	200–230	300–500
W	35	23 (± 4)	30–45	30–45
<b>Apical actine</b>				
L	100		150–210	20–140
W	25		22–36	
<b>Diactines</b>				
L	300	202 (± 38)	300–450	100–500
W	9	8 (± 1)	10–15	10–50

*CLATHRINA AUREA* SOLÉ-CAVA, KLAUTAU, BOURY-ESNAULT, BOROJEVIC & THORPE, 1991

*Type locality:* Arraial do Cabo, Rio de Janeiro, Brazil.

*Type:* MNHN-LBIM.C. 1989.1 (holotype/alcohol). Arraial do Cabo (Anjos Beach), Rio de Janeiro, Brazil. Collected by E. Hajdu (15 November 1987), BMNH 1999.9.19.6 (paratype/alcohol). Arraial do Cabo (Forno Beach), Rio de Janeiro, Brazil. Collected by G. Muricy (19 April 1987), 5-m depth.

*Citations:* Borojevic & Klautau (2000); Klautau & Borojevic (2001).

*Colour:* Living specimens have a clathrate gold yellow cormus, which becomes beige when preserved.

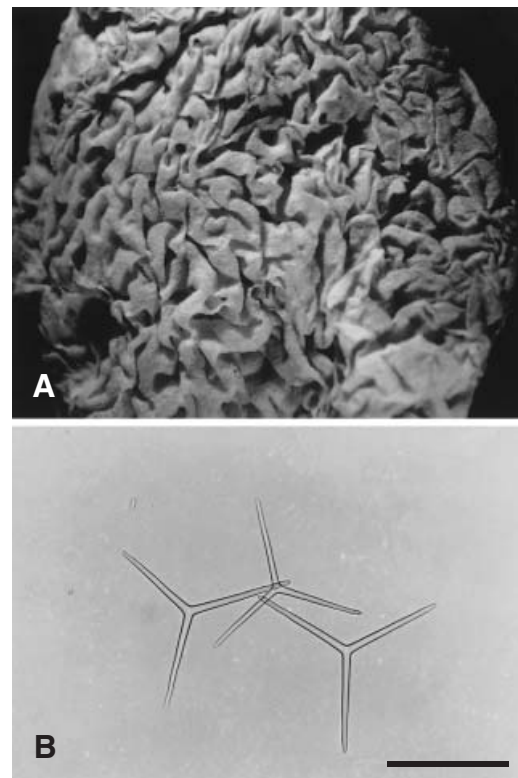
*Description:* Cormus formed of large, irregular and loosely anastomosed tubes, with several oscula. No water-collecting tubes are present (Fig. 5A).

The skeleton has no special organization, comprising equiangular and equiradiate triactines only (Fig. 5B). Actines are cylindrical and characteristically undulated at the distal part. Their tips are always rounded.

This species has a sciaphilous habitat and lives in areas protected from the action of waves. It is frequently found on the roofs of small caves or inside crevices.

	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	n
Triactines	65.0	73.8	± 4.8	82.5	5.5	± 0.9	30

*Remarks:* *Clathrina aurea* is very similar to its sibling *C. clathrus* from the Mediterranean. Both species are yellow and have only triactines with undulated actines and rounded tips. Studying the allozyme variation of both populations (Solé-Cava *et al.*, 1991),



**Figure 5.** *Clathrina aurea*. A, photograph of the holotype (× 10). B, triactines. Scale bar = 100 µm.

very low levels of genetic identity were found between them, indicating the absence of gene flow. Consequently, both populations are considered distinct species. Although morphologically similar, some differences could be recognized between specimens of each population after the genetic study. The spicules of *C. aurea* are always shorter than those of *C. clathrus* ( $92\ \mu\text{m}$  ( $\pm 7\ \mu\text{m}$ )/ $6\ \mu\text{m}$  ( $\pm 1\ \mu\text{m}$ )). Moreover, the organization of the cormus in both species is different. While *C. aurea* has several oscula spread through the tubes, *C. clathrus* has water-collecting tubes. They also differ in another less evident characteristic: in *C. clathrus* the tip of the actines is more rounded than it is in *C. aurea*. However, in order to use this character to distinguish between the two species, it is necessary to simultaneously compare examples of both.

*CLATHRINA BISCAYAE* BOROJEVIC &  
BOURY-ESNAULT, 1987

*Type locality*: Bay of Biscay.

*Type*: MNHN-LBIM.C. 1985.3 (holotype/alcohol). Bay of Biscay (Station U 842:  $44^{\circ}11' 3\text{N}$ ,  $8^{\circ}41' 2\text{W}$  at 500–520 m depth). Collected by the N.O. *Thalassa*.

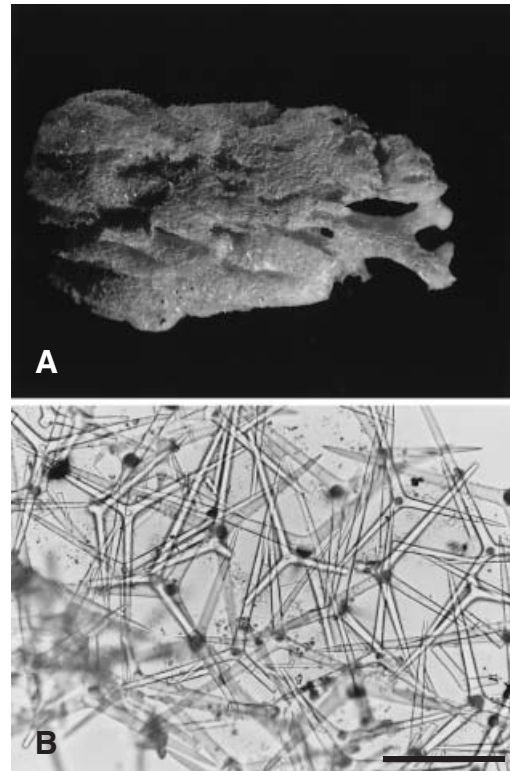
*Clathrina biscayae* was first described by Borojevic & Boury-Esnault in 1987. Several specimens of this species were collected in the Bay of Biscay at depths of 322–645 m, according to the authors. The holotype is deposited at MNHN under the registration number LBIM.C. 1985.3.

*Colour*: White when preserved.

*Description*: Holotype is very small ( $0.5 \times 0.4 \times 0.2\ \text{cm}$ ). Cormus formed of large and irregular tubes (Fig. 6A). In the basal area the tubes are free, while in the apical area they are anastomosed and, sometimes, virtually fused. The skeleton comprises triactines and tetractines (Fig. 6B).

On the surface of the tubes, there are more triactines than tetractines. Some of the triactines are equiradial and equiangular, but they are mainly pseudosagittal spicules. Actines of these external spicules are strongly conical, with sharp tips.

Inside the tubes, the tetractines are the most abundant spicules. Again, it is possible to find equiangular and equiradial spicules, but they are very rare and the pseudosagittal spicules are the most abundant.



**Figure 6.** *Clathrina biscayae*. A, photograph of the holotype ( $\times 10$ ). B, triactines and tetractines. Scale bar =  $100\ \mu\text{m}$ .

Two size classes of internal tetractines can be recognized according to the shape of the actines, which are slightly conical and sharp in one and more conical and sharp in the other.

The size of the unpaired actines is variable. Therefore, measurements were taken of the paired actines.

The apical actine of the tetractines is always shorter and thinner than the facial ones. Nevertheless, its size is very variable. The apical actine is very thin and sharp. It is smooth and straight or bent, normally in the direction of the paired actines.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
External triactines	77.5	111.5	$\pm 22.0$	167.5	9.8	$\pm 1.0$	20
External triactines	120.0	157.5	$\pm 21.3$	197.5	16.3	$\pm 2.0$	25
Internal tetractines	112.5	145.3	$\pm 14.8$	177.5	9.0	$\pm 1.5$	30
Apical actine	19.2	60.7	$\pm 23.5$	96.0	6.0	$\pm 1.2$	08
Internal tetractines	97.5	155.5	$\pm 20.3$	187.5	14.3	$\pm 1.5$	20
Apical actine	36	53.5	$\pm 15.6$	81.6	10.1	$\pm 1.0$	06

**Remarks:** In the original description, the skeleton was described as comprising triactines and that 'tetractines are occasionally added', but that 'in some specimens they can be present in relatively large numbers'. This is the case for the holotype of this species. Tetractines are the most abundant spicules, triactines being more abundant only in the external part of the tubes.

Borojevic and Boury-Esnault described three kinds of spicules: regular triactines, pseudosagittal triactines, and tetractines. We consider that there is a further spicule type, a second population of internal tetractines, characterized by a different size.

We also found thin trichoxeas on the surface of the tubes. These spicules were not mentioned in the original description; while they are not very abundant, we believe that they should be mentioned.

*CLATHRINA BRASILIENSIS* SOLÉ-CAVA, KLAUTAU,  
BOURY-ESNAULT, BOROJEVIC & THORPE, 1991

**Type locality:** Arraial do Cabo, Rio de Janeiro, Brazil.

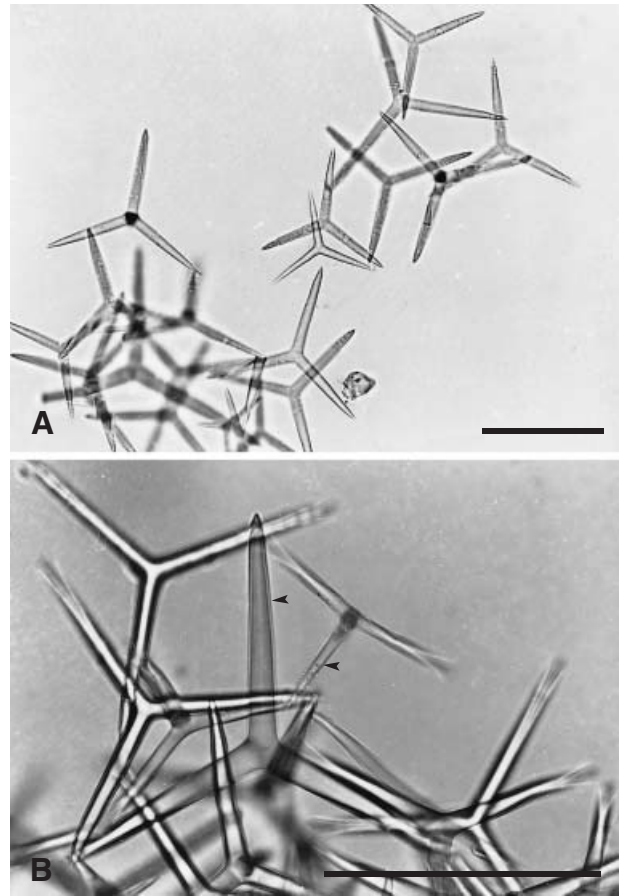
**Type:** MNHN-LBIM.C. 1989.2 (holotype/alcohol). Arraial do Cabo (Enseada), Rio de Janeiro, Brazil. Collected by G. Muricy (16 December 1986).

**Citations:** Klautau *et al.* (1994); Klautau & Borojevic (2001).

**Colour:** White in life and when preserved.

**Description:** Cormus massive, formed of thin, regular and tightly anastomosed tubes. Oscula are simple openings, surrounded by a thin membrane, and located on the top of short conical projections. They receive water from large water-collecting tubes.

The skeleton comprises three kinds of spicule: triactines, tetractines (Fig. 7A) and tripods (Fig. 7B). The triactines and tetractines are equiradiate and equiangular, with conical actines and blunt tips. The apical actine (Fig. 7B) of the tetractines is shorter and thinner than the facial ones, and it is conical, sharp and covered with short spines. This actine is always projected towards the inside of the tubes. Tripods are more irregular than the triactines and tetractines, and frequently they are sagittal. They normally have their centre raised but sometimes look like large conical triactines. However, it is possible to distinguish them from large triactines because of the strong conical shape of their actines and because of their location. They are distributed on the surface of the external tubes in a monolayer, delimiting the cormus. Habitat is sciaphile.



**Figure 7.** *Clathrina brasiliensis*. A, triactines and tetractines. B, tripods (large arrow) and the apical actine of a tetractine full of spines (short arrow). Scale bar = 100 µm.

	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	n
Triactines	60.9	78.2	± 10.6	102.2	10.8	± 1.5	20
Tetractines	56.5	75.3	± 10.0	91.3	10.4	± 1.3	20
Apical actine	17.4	36.4	± 9.1	50.0	8.0	± 2.2	20
Tripods	67	81	± 8.2	95.7	11	± 1.7	20

**Remarks:** Specimens are morphologically very similar to those of *C. cerebrum* from the Mediterranean Sea. However, they were recognized as a distinct species after genetic studies (Solé-Cava *et al.*, 1991) showed that there was no gene flow between the two populations, resulting in a very low level of genetic identity. The only morphological differences found here were in the size of the spicules, which are a little longer and thinner in the Mediterranean population (triactines: 85 µm (±7 µm)/7 µm (±1 µm); tetractines: 83 µm (±9 µm)/7 µm (±1 µm); tripods: 89 µm (±15 µm)/11 µm

( $\pm 2 \mu\text{m}$ )), and in the spines of the apical actine, which are also longer in *C. cerebrum* and very short in *C. brasiliensis*.

*CLATHRINA CANARIENSIS* (MIKLUCHO-MACLAY, 1868)

*Original name: Nardoa canariensis* Miklucho-Maclay, 1868

*Type locality:* Lanzarote Beach, Canary Islands.

*Type:* PMJ-Inv. Nr. Porif. 103 (syntype/alcohol). Lanzarote Beach, Canary Islands, Haeckel u. Miklucho-Maclay.

*Citations:* Haeckel (1872); Lackschewitsch (1886); Thacker (1908); Dendy & Row (1913); Hôzawa (1918, 1933, 1940); Breiffuss (1932); Tanita (1941, 1942, 1943).

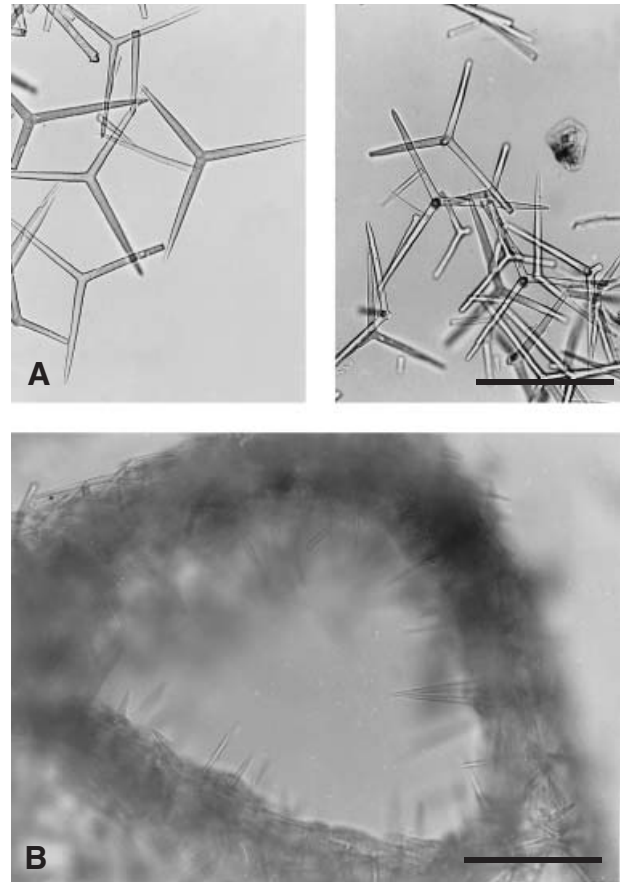
A syntype of *C. canariensis*, which is deposited in PMJ under the registration number Porif.103 Calcarea was examined. Our description for this species is closer to Haeckel's than Miklucho-Maclay's. There are three fragments, all well preserved in alcohol, the largest measuring approximately  $2.2 \times 1.5 \times 0.8 \text{ cm}$ .

*Colour:* Varies from white to light yellow.

*Description:* Cormus formed of thin, irregular and tightly anastomosed tubes, which are variable in diameter. Large water-collecting tubes converge, forming oscula that are projected above the surface.

The skeleton of the tubes is thin (its wall has 4–5 layers of spicules), and it comprises an irregular meshwork containing triactines and tetractines (Fig. 8A). The apical actine of the tetractines is always found inside the tubes. The length of the apical actine is never longer than the diameter of the tubes.

Regular triactines are the most abundant spicules. The size of the triactines and tetractines is very uniform. Actines are almost cylindrical and straight, with a blunt tip. The distal part of the actines is frequently slightly undulated. The apical actine of the tetractines (Fig. 8B) is straight, smooth and sharp at the tip, and it has the same diameter as the facial actines. Frequently, it is shorter, but its length is variable. The shape of the triactines resembles that of *C. clathrus*.



**Figure 8.** *Clathrina canariensis*. A, triactines and tetractines. B, apical actines of the tetractines projected into a tube. Scale bar = 100  $\mu\text{m}$ .

*Remarks:* *Clathrina canariensis* was described by Miklucho-Maclay (1868) under the name *Nardoa canariensis*. As in other clathrinids, some confusion is associated with *C. canariensis*, and several species have been subsumed to become its synonyms. The following species, at some point in time, have been considered synonyms of *C. canariensis*:

*Nardoa rubra* Miklucho-Maclay, 1868  
*Nardoa sulphurea* Miklucho-Maclay, 1868  
*Ascaltis compacta* Schuffner, 1877  
*Leucosolenia nanseni* Breiffuss, 1896  
*Leucosolenia tenuipilosa* Dendy, 1905  
*Clathrina canariensis* var. *compacta* Row, 1909

*Nardoa rubra* and *N. sulphurea* were described by Miklucho-Maclay (1868) in the same article in which he described *N. canariensis* and he gave them the status of distinct species. He said that the distinction between them was based only on their different colours (*N. canariensis* was white, *N. rubra* was red and *N. sulphurea*, yellow). He gave no further information.

	Length ( $\mu\text{m}$ )				Width ( $\mu\text{m}$ )		
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	67.5	77.8	$\pm 4.6$	87.5	5.0	0	30
Tetractines	62.5	74.3	$\pm 5.8$	87.5	5.0	0	30
Apical actine	35.0	43.8	$\pm 5.6$	55.0	5.0	0	15

Haeckel (1872) again described *C. canariensis* as *Ascaltis canariensis*; his description, more complete than that of Miklucho-Maclay, became the accepted one. He analysed specimens collected by both of them in the Canary Islands (Lanzarote Beach). He questioned the validity of *N. rubra* and *N. sulphurea* as true species, saying that the colour of other ascones was very changeable, and that the three forms did not show any differences in relation to their spicules. He also criticized the description made by Miklucho-Maclay, which had not mentioned the presence of tetractines and papillae in the inner surface of the tubes of *C. canariensis*. Indeed, Miklucho-Maclay said only that 'Spicula sind dreistrahlig' ('Spicules are triactines'), and he did not mention the tetractines. Therefore, Haeckel described *C. canariensis* as a species with changeable colours, and equiangular and equiradiate triactines and tetractines with similar dimensions. The apical actine of the tetractines was described as straight, sharp, smooth and as thick as the facial actines. This became the accepted description of *C. canariensis*.

Thacker (1908) considered *A. compacta* Schuffner, 1877, *L. nanseni* Breitfuss, 1896 and *L. tenuipilosa* Dendy, 1905 to be synonyms of *C. canariensis*, as well as agreeing with Haeckel's opinion on, *N. rubra* and *N. sulphurea*. He considered *L. nanseni* to be a synonym because he did not feel that the size of the spicules, the shape of the apical actine, and the presence of papillae were satisfactory for the purpose of identification, as he had already found intermediary forms of sponges that possessed them. Thacker also commented that he thought *L. nanseni* resembled *A. compacta*, which has regular triactines and tetractines and was found off Mauritius. Schuffner, however, had separated *A. compacta* from *C. canariensis* 'because (1) it had no papillae on the inner surfaces of 'the Ascon-tubes' and 'because' (2) of the different shape of the apical rays of the quadriradiates'. Nonetheless, Thacker said that he had found great variability in the apical actines of his specimens. As he considered the use of papillae a poor character to distinguish species due to its variability, he decided to include *A. compacta* in *C. canariensis*, and said that *C. canariensis* also did not differ from *L. nanseni*.

Thacker deemed *L. tenuipilosa* to be only a variety of *C. canariensis*, with 'the same relationship to typical specimens of *L. canariensis* as *L. coriacea ceylonensis*'. He said that he had found hair-like oxea (trichoxea) in several of the specimens from the Cape Verde Islands, and that in some specimens, these spicules were numerous, but in others, very scarce, and that the latter specimens 'form connecting links between the typical form of the species and the variety *L. canariensis tenuipilosa*.' However, the subsequent year, Row (1909) rejected the synonymy of

*L. tenuipilosa* with *C. canariensis*, saying that 'the presence of oxea of such unusual and constant form, being very long and extremely slender, should undoubtedly separate it specifically from forms where oxea are entirely absent, even though the number and frequency of the oxea may show very considerable variation as they do in Thacker's specimens.'

In this same article, however, Row described a specimen that he said was identical to *A. compacta*, but that he could not separate from *C. canariensis*, because 'all intermediate forms have been described by Thacker from the Cape Verde Islands'. However, as the specimen he was analysing was so different from the typical *C. canariensis* described by Haeckel (he did not mention Miklucho-Maclay's description), he decided to consider it as a distinct variety: *C. canariensis compacta* from the shore at Suez.

With respect to the previously considered synonyms or varieties, there was only the opportunity to analyse the type specimen of *C. canariensis* var. *compacta*, but it could be compared with *A. compacta* and *L. nanseni*, from the original descriptions in the literature. In relation to *N. rubra* and *N. sulphurea*, no comments can be made, as there were no specimens available to analyse, and their description in the literature is very incomplete.

Although from the description the external shape of *C. canariensis* and *C. canariensis* var. *compacta* could seem similar, they are not. As in many other clathrininas, both have an aquiferous system consisting of large water-collecting tubes, which terminate in a larger tube projected above the surface, functioning as an osculum. However, the cormus of *C. canariensis* is tight, while that of *C. canariensis* var. *compacta* is loose, which apparently is not due to the state of its preservation.

Nevertheless, the most important differences between them are in the skeleton: the presence of trichoxeas in *C. canariensis* var. *compacta*, the shape and the size of the actines, and the proportion of the triactines and tetractines. The trichoxeas could be enough to separate them as distinct species. However, the differences in the shape, size and proportion of triactines and tetractines seem to be more important. The spicules of *C. canariensis* are shorter and have cylindrical actines, while those of *C. canariensis* var. *compacta* are larger and very conical. Moreover, *C. canariensis* has almost the same number of triactines and tetractines, while *C. canariensis* var. *compacta* has more triactines than tetractines.

The holotype of *C. compacta* was not found. However, comparing the description given by Schuffner with the holotype of *C. canariensis*, it is possible to distinguish between these species due to the differences in the size of the actines. The spicules of *C. compacta*

are much longer and thicker than those of *C. canariensis* (120 µm/12 µm).

The syntype of *C. canariensis* was shown to be very different from other specimens deposited in BMNH under that name. This observation suggests that the distribution of this species is much narrower than previously imagined (Arctic; Atlantic coasts of Europe; Mediterranean; Cape Verde and the Canary Islands; Mexico; Mauritius; Red Sea; NW Pacific (Commandor-ski Islands); Japan *sensu* Burton (1963). Observations during this study suggest that the distribution of *C. canariensis* is possibly restricted to the Atlantic coasts of Europe and, perhaps, the Mediterranean Sea.

We therefore suggest that the specimen PMJ-Inv.Nr.Porif. 103 be treated as a lectotype of *C. canariensis*.

*CLATHRINA CEREBRUM* (HAECKEL, 1872)

*Original name:* *Ascaltis cerebrum* Haeckel, 1872

*Type locality:* Adriatic Sea (Lesina).

*Type:* PMJ-Inv. Nr. Porif. 156. (Syntype/alc. alcohol). Adriatic Sea (Lesina). Haeckel Collection.

*Citations:* Bianco (1888); von Lendenfeld (1891); Bidder (1891); Kirk (1896); Minchin (1896); Breitfuss (1896, 1898, 1935); Dendy & Row (1913); Burton (1933, 1963); Topsent (1934, 1936); Borojevic (1967, 1971); Borojevic & Peixinho (1976); Solé-Cava *et al.* (1991).

A syntype of *C. cerebrum*, which is deposited in PMJ, under the registration number Porif 156 Calcareous was examined. Our description matches that given by Haeckel. It is fragmented, mixed with algae.

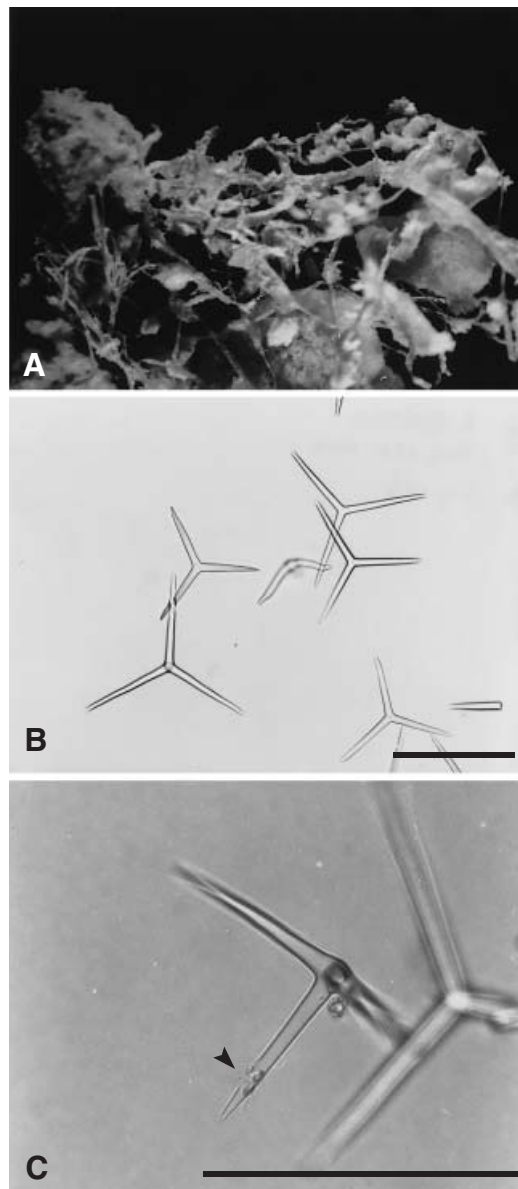
*Colour:* Light yellow.

*Description:* As the cormus is fragmented, it was not possible to determine its organization, or establish the presence of water-collecting tubes. In some parts, the tubes have even collapsed, and it is impossible to distinguish them (Fig. 9A).

The wall of the tubes is thin, comprising an irregular meshwork of triactines, tetractines and a few tripods (Fig. 9B), which are located only on external tubes. Projecting into the interior of the tubes are the apical actines of the tetractines.

Spicules are equiangular and equiradiate triactines, tetractines, and tripods. Triactines are the most abundant spicules.

The size of the triactines and tetractines is uniform. The actines of the triactines are conical or cylindrical, while the tetractines are always conical. They are straight, with a blunt tip. The apical actine of the tetractines (Fig. 9C) is conical, sharp, straight and thin-



**Figure 9.** *Clathrina cerebrum*. A, photograph of the syntype ( $\times 10$ ). B, triactines, tetractines and tripods. C, apical actine of a tetractine with spines (arrow). Scale bar = 100 µm.

ner and shorter than the facial ones. In the distal part, before the tip of the actine, there are sharp spines arranged in 3–4 rows. These spines are directed toward the tip of the actine. Some apical actines, particularly those of young spicules, have only vestigial spines.

Tripods are not abundant, as they are located only on the surface of external tubes. They are approximately the same length as the other spicules, but their actines are much more conical and stout. The

centre of these spicules is frequently raised, and their tips are sharp. When the centre is not raised, they are similar to large triactines, but it is still possible to recognize them by the shape of the stout conical actines.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	57.5	71.8	$\pm 6.0$	85.0	6.5	$\pm 1.3$	30
Tetractines	52.5	71.8	$\pm 7.3$	90.0	7.3	$\pm 0.5$	30
Apical actine	47.5	57.5	$\pm 7.0$	70.0	5.8	$\pm 1.3$	09
Tripods	40.0	60.0	$\pm 9.5$	82.5	9.5	$\pm 1.5$	18

*Remarks:* *Clathrina cerebrum* was described by Haeckel (1872) as *Ascaltis cerebrum*, a species from Lesina, in the Adriatic Sea. Haeckel also identified two varieties of this species in Lesina: *gyrosa* and *decipiens*. He described *gyrosa* as having triactines with the same shape and size, while *decipiens* was described as having tripods on the external tubes. After Haeckel, however, nobody found specimens corresponding to *gyrosa*, only to *decipiens* (von Lendenfeld, 1891; Kirk, 1896; Breitfuss, 1897; Ferrer-Hernandez, 1918, according to Topsent, 1936).

Dendy & Row (1913) elevated *decipiens* to the status of species, *Leucosolenia decipiens*, saying that 'certain of Haeckel's so-called Specific Varieties, to which he has already given distinctive names appear to us, after careful consideration of his descriptions, to deserve to rank as separate species'. Topsent (1936) suggested that Haeckel had probably made insufficient observations about some specimens or worked with incomplete material when he described *gyrosa*, which was then completely abandoned. Topsent said that *decipiens* was probably the normal state of *C. cerebrum* (i.e. a sponge with triactines, tetractines with spines in the apical actine and tripods or large triactines on the external tubes), and placed the two species in synonymy.

Unfortunately, Haeckel did not produce a drawing of either the cormus or the spicules of this variety.

As in other clathrinans, the biggest problem we found in the systematics of *C. cerebrum* was its possible morphological plasticity. We analysed several specimens from the Adriatic and the Mediterranean Seas, including the syntype, which we described above. At the end of our morphological observations, we were astonished by the apparent variability in the cormus organization and in the shape and size of spicules. Even now, we are not sure whether this morphological variability is real or if *C. cerebrum* is in fact a complex of morphologically similar species.

Previous genetic studies have shown that there are both allopatric (Solé-Cava *et al.*, 1991) and sympatric (Klautau *et al.*, 1994) populations, which were previously identified as *C. cerebrum*. It was observed that these populations were genetically isolated, therefore constituting distinct species, although they were morphologically very similar. Considering these results, we believe that *C. cerebrum* can probably be split into several new species, but as we observed such morphological variability, we have decided not to split it until a detailed genetic study has been undertaken.

In 1936, Topsent had already observed this phenomenon in the skeleton of *C. cerebrum* and had even suggested a possible synonymy with *L. intermedia* and *L. proxima*, considering that the absence of tetractines in those species was no indication of their specificities. We do not share the same opinion as Topsent in relation to the synonym of *C. cerebrum* with *L. intermedia* and *L. proxima*, principally because these two species are actually from a different genus, *Ascaltis*. However, we cannot ignore the morphological variability in *C. cerebrum*, because some of the characters considered important for the identification of this species are variable even among specimens of the same population. The shape of tripods, for example, is very variable. Some specimens have abundant true tripods, while others have only large triactines; a third category has both large triactines and true tripods. Borojevic (1967) has already pointed out the variability in the shape of tripods in *C. cerebrum*, and shown that the different shapes have probably resulted from different exposures of the specimens to waves. In other words, specimens exposed to strong waves would have more true tripods while less exposed specimens would have a higher proportion of large triactines.

Another very variable character is the presence of spines on the apical actine of the tetractines. In a single specimen, the apical actine can have spines, vestigial spines or even be smooth. A further variable morphological character was in relation to the shape of actines, which can vary from cylindrical to conical in the same individual. Also the size of spicules is very variable.

Although these observations point to high morphological variability, we cannot discount the different proportions of these characters in some specimens. Some individuals have the apical actine predominantly spined or smooth, or abundant true tripods or large triactines; or else more cylindrical or conical actines. We still do not know whether these different proportions have a systematic basis or not. At the moment, however, as we have already said, we will not split *C. cerebrum*, but we do not consider its previous, cosmopolitan, distribution (Adriatic, Mediterranean, Ternate, Roscoff, South Africa, Brazil and New Zealand) as valid. We think it is better to restrict the

distribution of this species to the Adriatic and the Mediterranean Seas, considering our earlier observations that sponges (and particularly clathrinins) do not have a high capacity for dispersal (Solé-Cava *et al.*, 1991).

We also propose that the specimen PMJ-Inv.Nr.Porif. 156 become a lectotype of *C. cerebrum*.

**CLATHRINA CEYLONENSIS** (DENDY, 1905) COMB. NOV.

*Original name:* *Leucosolenia coriacea* var. *ceylonensis* Dendy, 1905

*Type locality:* Sri Lanka.

*Type:* BMNH 1907.2.1.101 (holotype/alcohol). Cheval Paar, Ceylon (Sri Lanka). W.A. Herdman's Ceylon Pearl Oyster Collection, 1902.

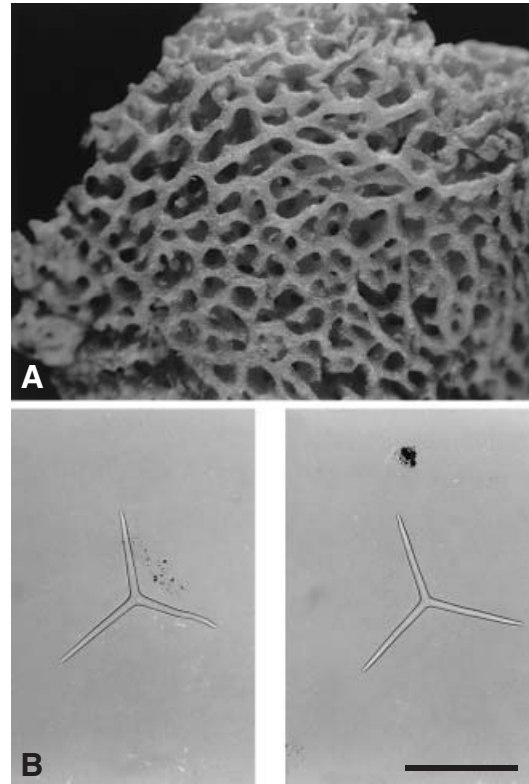
*Colour:* Light yellow when preserved.

*Description:* Cormus massive, formed of thin, irregular and tightly anastomosed tubes, with a reticulated surface (Fig. 10A). According to the original description, water-collecting tubes were present.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	67.2	78.5	$\pm 7.9$	96.0	7.4	$\pm 0.5$	30

The skeleton has no special organization, comprising equiangular and equiradiate triactines (Fig. 10B). Actines are conical, with blunt tips, never rounded.

Dendy described this species as a variety of *C. coriacea*. He noted the presence of water-collecting tubes as 'small but prominent true oscula formed each by the coalescence of several tubes in a projection from the general surface'. He also found triactines measuring about  $88 \mu\text{m}/8 \mu\text{m}$ , and 'few very slender oxea', which were probably trichoxeas. We studied the holotype. No trichoxeas were found, but these spicules are sometimes difficult to find. We therefore decided not to consider the presence of trichoxeas in our description. We are elevating this variety to the status of a species because *C. ceylonensis* is very distinct from *C. coriacea*. Despite morphological similarities, such as the presence of water-collecting tubes and the size of the triactines, they can easily be distinguished. *C. coriacea* has undulated actines with a constriction near the tip, which is rounded or blunt, while *C. ceylonensis* has straight actines with blunt, unrounded tips. The distribution of *C. coriacea* seems to be restricted to northern Europe, while *C. ceylonensis* occurs only in the Indian Ocean.



**Figure 10.** *Clathrina ceylonensis*. A, photograph of the holotype ( $\times 10$ ). B, triactines. Scale bar =  $100 \mu\text{m}$ .

**CLATHRINA CHRYSSEA** BOROJEVIC & KLAUTAU, 2000

*Type locality:* Canal Woodin, New Caledonia.

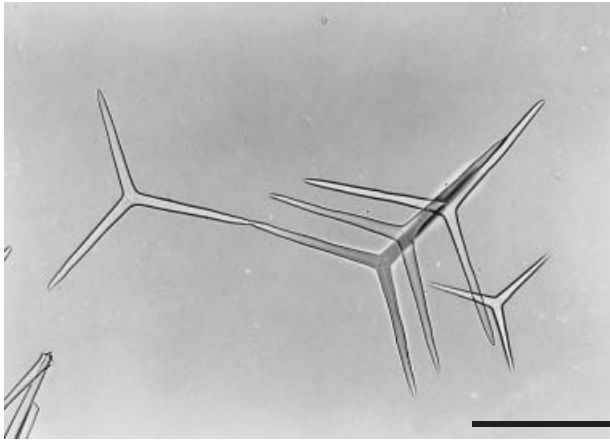
*Type:* MNHN-LBIM-C-1999-01 (holotype/alcohol). South coast, Canal Woodin, New Caledonia (28 m depth). R-1360.

*Colour:* Cormus of holotype bright yellow, white when preserved in alcohol.

*Description:* Cormus formed of thin, regularly anastomosed tubes. There are no water-collecting tubes. The skeleton of the tubes has no special organization, comprising a thin meshwork of equiangular and equiradiate triactines (Fig. 11A). Actines are straight and conical, with a sharp distal tip. They are slightly undulated at the tip.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	67.2	101.8	$\pm 11.8$	112.8	9.8	$\pm 1.4$	30





**Figure 11.** *Clathrina chrysea*. Triactines. Scale bar = 100  $\mu\text{m}$ .

Biochemical studies separated *C. clathrus* from another yellow clathrina we earlier named *C. aurea* (Solé-Cava *et al.*, 1991), suggesting that *C. clathrus* is not widespread. Based on this result, Borojevic & Klautau (2000) recognized the specimen from New Caledonia as a new species. The main difference between this and other yellow clathrinas relates to the tip of the actines of the triactines, which is sharp in *C. chrysea* and rounded in *C. clathrus* and *C. aurea*. The yellow colour of the cormus and the skeleton composed only of triactines with cylindrical and undulated actines suggest that these clathrinas constitute a group of closely related species.

Breitfuss (1897) reported a yellow clathrina he called *C. clathrus* in the Indo-Pacific region (Ternate). Borojevic & Klautau (2000) commented that he was probably referring to *C. chrysea*.

In the original description of *C. chrysea*, the micrometry of the triactines was 105  $\mu\text{m}$  ( $\pm 9 \mu\text{m}$ )/10  $\mu\text{m}$  ( $\pm 1 \mu\text{m}$ ).

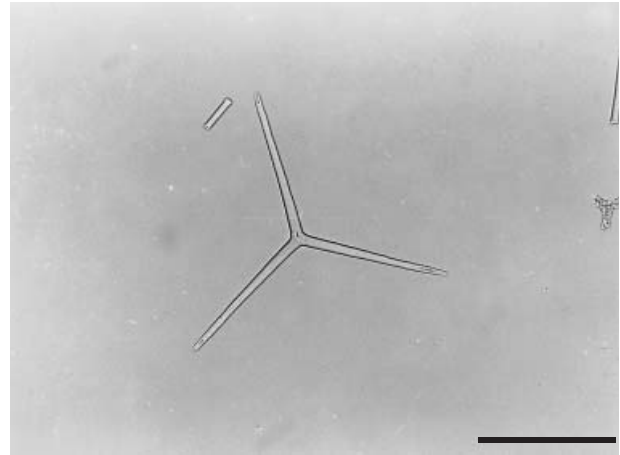
#### *CLATHRINA CLATHRUS* (SCHMIDT, 1864)

*Original name:* *Grantia clathrus* Schmidt, 1864

*Type locality:* Lesina, Adriatic Sea.

*Type:* Unregistered (syntype/alcohol), Schmidt specimen, ZMUC.

*Citations:* Gray (1867); Haeckel (1870, 1872); Vosmaer (1881); Lackschewitsch (1886); Priest (1887); Bianco (1888); von Lendenfeld (1891); Bidder (1891); Topsent (1894, 1934, 1936); Kirk (1896); Minchin (1896); Breitfuss (1896, 1898, 1935); Dendy & Row (1913); Ferrer-Hernandez (1916, 1918, 1922); Burton (1935, 1963); Borojevic (1968); Solé-Cava *et al.* (1991); Borojevic & Klautau (2000).



**Figure 12.** *Clathrina clathrus*. Triactines. Scale bar = 100  $\mu\text{m}$ .

The specimen we received from ZMUC is a syntype of *Ascetta (Clathrina) clathrus* Schmidt, 1864, collected in Lesina, Adriatic Sea. There are three large fragments of the specimen, preserved in alcohol. The largest is 2.5  $\times$  2.0  $\times$  0.5 cm.

*Colour:* Cormus of preserved specimen is brownish-yellow.

*Description:* Cormus formed of large, irregular and loosely anastomosed tubes. It was not possible to recognize water-collecting tubes in the syntype. However, we analysed several other specimens from the Mediterranean Sea and the water-collecting tubes were always found.

The wall of the tubes is 102  $\mu\text{m}$  thick. The skeleton has no organization, comprising equiradiate and equiangular triactines only (Fig. 12B). Actines are cylindrical, with rounded tips and they are undulated at their distal part.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	85.0	92.0	$\pm 4.3$	100.0	7.3	$\pm 0.5$	20

*Remarks:* *Clathrina clathrus* (Schmidt, 1864) is the type-species of the genus *Clathrina* Gray, 1867. In his original description, Schmidt discussed the 'beautiful sulphur yellow colour' of specimens of this species, and said that if the colour was a constant character in *C. clathrus*, it would be easy to recognize it. As this species has only one type of spicule, it would be very useful to be able to use the colour

as an effective character. Unfortunately, the colour is not an exclusive character, although it helps in identification.

Once authors began to report a high variation of colour (including white and red as well as yellow), its distribution, initially described from the Adriatic Sea (Lesina), started to increase. Burton (1963) listed occurrence of *C. clathrus* in the following localities: Mediterranean (Adriatic to Minorca); British Isles; Spain (Asturias); Ternate; New Zealand (Cook Strait), in depths varying from 0 to 50 m.

It is not difficult to see that many of the specimens described for localities other than the Adriatic and the Mediterranean Seas were not in fact *C. clathrus*. The yellow colour of this species seems to be very constant, and because of this, some authors began, erroneously, to identify all yellow clathrinids as *C. clathrus*.

Allozyme analysis of specimens previously identified as *C. clathrus* from the Atlantic (Rio de Janeiro, Brazil) and the Mediterranean (Marseille, France) established that both populations were reproductively isolated and constituted distinct species. We have retained the name *C. clathrus* for the Mediterranean population. In addition to the molecular results, we also found differences in the size of the spicules, which are longer in the Mediterranean populations. Also, studying the morphology of some specimens of a yellow *Clathrina* from New Caledonia which has only triactines in its skeleton, we found differences in the thickness and tip of these actines, which was not rounded as in *C. clathrus*, but sharp. It was named *C. chrysea* Borojevic & Klautau, 2000.

It is clear that the yellow clathrinids constitute a group of species which only have triactines in their skeleton. These triactines have cylindrical actines, undulated at the distal part, and are blunt or rounded at the tip.

Analysing all the specimens deposited at BMNH previously identified as *C. clathrus*, we again found some distinct species. We have already mentioned the importance of the shape of the actines in the genus *Clathrina*, and using this character to differentiate between species, we could distinguish three species in the collection. We considered those specimens with water-collecting tubes, yellow colour in life, and triactines with cylindrical actines, undulated at the distal part, and rounded at the tip as the true *clathrus*. Using these morphological characters, the distribution of *C. clathrus* is restricted to the Adriatic and the Mediterranean Seas.

We suggest that the specimen from ZMUC be considered the lectotype of *C. clathrus*.

	Length ( $\mu\text{m}$ )				Width ( $\mu\text{m}$ )	
	min	mean	$\sigma$	max	mean	$\sigma$
<i>C. aurea</i>	65	74	$\pm 5$	83	6	$\pm 1$
<i>C. chrysea</i>	60	97	$\pm 16$	120	10	$\pm 1$
<i>C. clathrus</i>	85	92	$\pm 4$	100	7	$\pm 1$

#### *CLATHRINA CONIFERA* KLAUTAU & BOROJEVIC, 2001

*Type locality*: Arraial do Cabo, Rio de Janeiro, Brazil.

*Type*: BMNH 1999.9.16.19 (holotype/alcohol). Arraial do Cabo (Anjos Beach), Rio de Janeiro, Brazil. Collected by G. Muricy (15 November 1987).

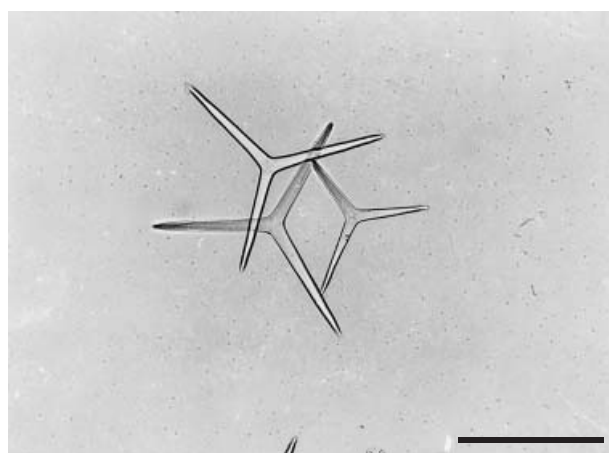
*Citations*: Klautau *et al.* (1994) (as *C. primordialis*).

*Colour*: Cormus of preserved specimen is white.

*Description*: Specimens of this species are very similar to those of *C. cylindractina*, and can easily be mistaken for them. The massive, yet delicate, cormus is formed of large, irregular and loosely anastomosed tubes and oscula are spread throughout. No water-collecting tubes are present. The cormus comprises a few tubes spread on rocks when the sponge is still very young.

The skeleton has no special organization and comprises only one kind of spicule, the triactine. Triactines are equiangular and equiradiate and their actines are straight and conical, with blunt tips (Fig. 13B).

*C. conifera* is sciaphilous, being frequently found under rocks or other animals, such as other sponges, tunicates and soft corals.



**Figure 13.** *Clathrina conifera*. Triactines. Scale bar = 100  $\mu\text{m}$ .

	Length (µm)			Width (µm)			<i>n</i>
	min	mean	σ	max	mean	σ	
Triactines	62.5	77.3	±9.3	97.5	9.0	±1.0	30

*Remarks:* This species, which we now call *C. conifera*, was first described in a previous article (Klautau *et al.*, 1994) as *C. primordialis* (Haeckel, 1872). In his description, Haeckel did not give the type locality of this species, but mentioned several places at which it was found, including Rio de Janeiro. As he had not elected a holotype, and as the syntypes seemed to have disappeared, we have selected the specimen from Arraial do Cabo matching his description as the neotype of *C. primordialis*, and suggest that Rio de Janeiro should become the *locus typicus* of this species.

However, for the current work, we did manage to locate a syntype of *C. primordialis* in PMJ. It was collected from Lesina (Adriatic), which means that the type locality of this species should be considered as Lesina and not Rio de Janeiro. Although there are similarities between the description given by Haeckel and the specimens from Arraial do Cabo, we decided not to consider our specimens as *C. primordialis*. These morphologically simple species of *Clathrina* seem to be a complex of species that should be split into new species.

Considering our previous results with *Clathrina* populations from the Mediterranean and from the Atlantic, we name the specimens from Arraial do Cabo with conical actines as *C. conifera*, to distinguish the species from its sibling *C. primordialis* from the Adriatic Sea.

Besides similarities with *C. primordialis*, *C. conifera* is also morphologically similar to *C. cylindractina*, another species from Arraial do Cabo. However, they can be distinguished by the size and shape of their actines: *C. cylindractina* has larger spicules than *C. conifera*. However, the most important morphological difference between them relates to the shape of their actines. In *C. cylindractina*, the actines are cylindrical or only slightly conical, while in *C. conifera* they are markedly conical.

Both populations have already been subjected to allozyme analysis (Klautau *et al.*, 1994) and, although living in sympatry, it was confirmed that no gene flow occurs between them, indicating that they are distinct species.

*CLATHRINA CONTORTA* MINCHIN, 1905

*Original name:* *Leucosolenia contorta* Bowerbank, 1866

*Type locality:* Guernsey, Channel Islands (changed to the Mediterranean Sea).

*Type:* BMNH 1896.9.15.1 (suggested neotype/alcohol). As *Nardoia contorta*. Banyuls-sur-Mer, Pyrenees, France. E. A. Minchin Collection.

*Leucosolenia contorta* (syntype/dry) BMNH 1950.10.12.6. Guernsey, Bowerbank Coll.

*Ascandra contorta* (specimen/dry) BMNH 1910.1.1.434B. Guernsey, Norman Coll.

*Citations:* Bowerbank (1866, 1874); Gray (1867); Haeckel (1870, 1872); Hanitsch (1890); Topsent (1891, 1892, 1894, 1936); Breitfuss (1898, 1927, 1932); Jenkin (1908); Dendy & Row (1913); Arndt (1935, 1941); Tanita (1942); Burton (1963); Borojevic & Boury-Esnault (1987).

*Colour:* Neotype (BMNH 1896.9.15.1) light yellow.

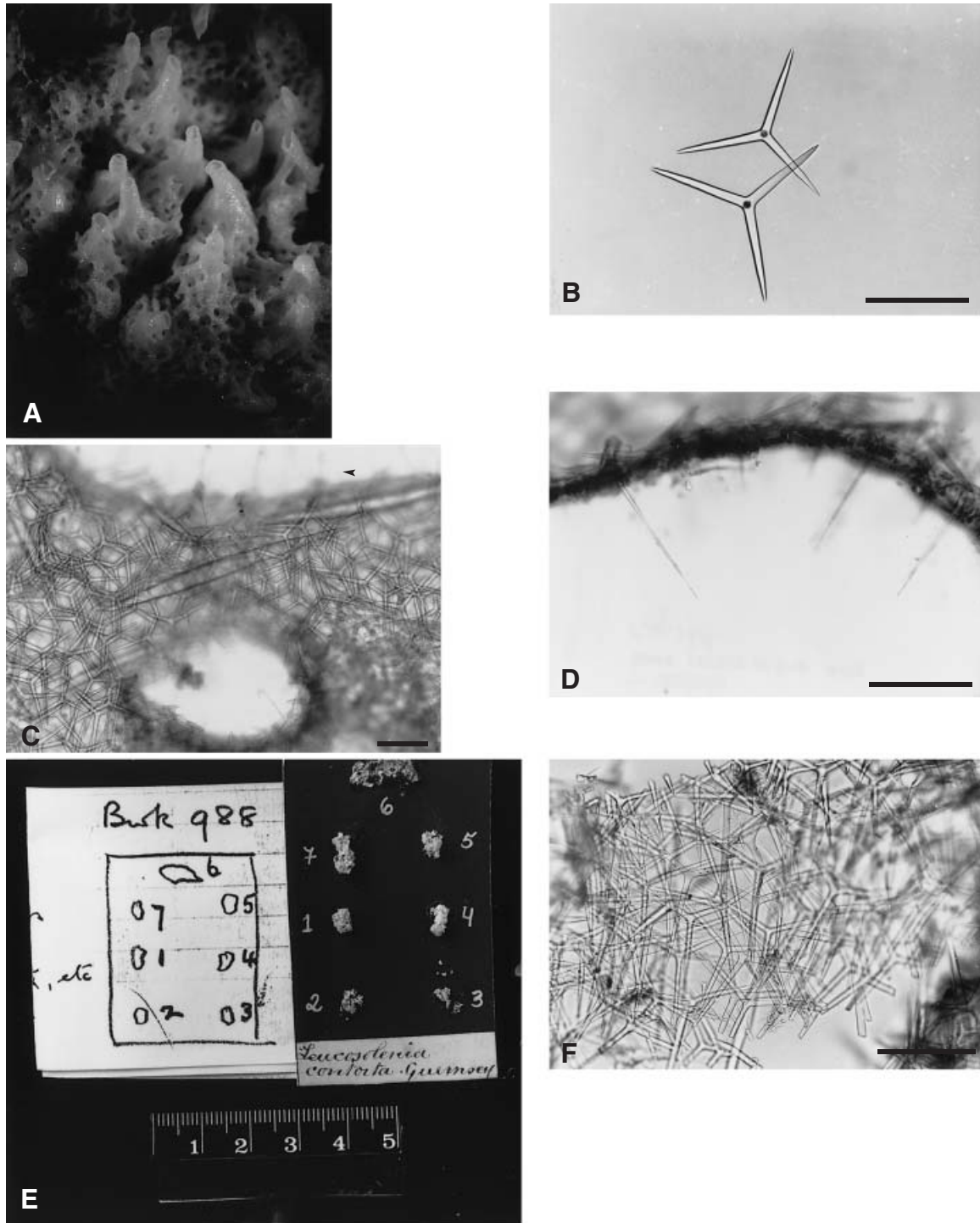
*Description:* Cormus formed of irregular and tightly anastomosed tubes. Water-collecting tubes converge to the oscula, which are projected above the surface (Fig. 14A). Sediment, as well as polychaetes, can be seen inside and among the tubes. The surface of the cormus is smooth. The specimen is full of embryos (*c.* 120/63 µm) embedded in the wall of the tubes.

The skeleton comprises triactines, tetractines (Fig. 14B), diactines and trichoxeas (Fig. 14C). Tetractines are more abundant than (although very similar to) triactines. They are equiangular and equiradiate. Actines are conical, sharp and slightly undulated. The apical actine (Fig. 14D) of the tetractines is very characteristic, being much thinner than the facial ones even at its base. It is cylindrical, sharp, straight, smooth and variable in size, sometimes being longer than the facial actines. The apical actines are projected inside the canals.

Diactines are not abundant and can be found parallel to the surface. They are fusiform, slightly curved and have sharp tips. Their size is very variable. Trichoxea (Fig. 14C) can also be found.

	Length (µm)			Width (µm)			<i>n</i>
	min	mean	σ	max	mean	σ	
Triactines	67.5	87.3	±9.5	102.5	10.0	±0.5	25
Tetractines	72.5	94.5	±9.8	115.0	9.8	±1.0	30
Apical actine	32.5	81.8	±39.5	155.0	5.0	±1.3	30
Diactines	173.4	503.9	±145.9	816.0	31.6	±8.2	30

*Remarks:* Twenty-eight specimens of *Leucosolenia contorta* were analysed by Bowerbank, but none of



**Figure 14.** *Clathrina contorta*. A, photograph of the neotype ( $\times 10$ ). B, tetractines. C, diactines on the surface and trichoxea (arrow). D, apical actines of the tetractines projected into a tube. E, syntypes of *C. contorta* ( $\times 4$ ). F, skeleton of a syn-type of *C. contorta*. Scale bar = 100  $\mu\text{m}$ .

them was designated as the holotype. Analysing some of these syntypes, we concluded that Bowerbank was working with more than one species when he described *L. contorta*. Some of these specimens are deposited in BMNH as syntypes of *L. contorta*:

BMNH 1950.10.12.6 (from Guernsey, Bowerbank Coll., as *Leucosolenia contorta*) (Fig. 14E);

BMNH 1910.1.1.434B (from Guernsey, Norman Coll., identified by Haeckel as *Ascandra contorta*) (Fig. 14F).

Sample BMNH 1950.10.12.6 is a study series containing seven dried specimens only one of which is a real *Clathrina* (number 6), the others being leucosolenias of several different species. Under the registration number BMNH 1910.1.1.434, there are two specimens, and both are also leucosolenias, again of a different species. This variety of species in the syntypes clearly illustrates the confusion related to *C. contorta*.

The only specimen that is a clathrina is quite different from Bowerbank's description of *L. contorta*, although his description does match the *Leucosolenia* specimens well, which made us suspect that he was in fact describing a *Leucosolenia*. The specimens of *Leucosolenia* under the registration number BMNH 1950.10.12.6 have a cormus formed by irregular and loosely anastomosed tubes and a skeleton of triactines, tetractines and diactines. The triactines and tetractines are sometimes almost equiangular and equiradiate, but we could clearly see that the majority are in fact sagittal. Actines are cylindrical and have a sharp tip. The apical actine of the tetractines is short, smooth and curved in the opposite direction to the unpaired actine. Diactines are present on the surface of the tubes, and they are slightly curved, smooth and have both tips sharp or sometimes one lance tip. They are typical spicules of *Calcaronea*.

On the other hand, if we examine BMNH 1910.1.1.434 A, we see a slightly different morphology. This specimen is not formed by anastomosed tubes, but rather by ramified tubes that are larger near the ends where there are oscula. The skeleton comprises triactines, tetractines and diactines. Triactines and tetractines are sagittal. Actines are cylindrical, slightly undulated and have a sharp tip. Sometimes, pseudosagittal spicules can also be seen. The apical actine of the tetractines is shorter and thinner than the facial ones, and it is smooth and curved in the direction of the unpaired actine. Diactines are slightly curved, and one of the tips is clearly lance-shaped.

Therefore, we have at least two different leucosolenias considered as *L. (Clathrina) contorta*. In our opinion, the syntype (BMNH 1950.10.12.6) is most similar to the description given by Bowerbank, while the morphology of the second specimen (BMNH 1910.1.1.434B) matches Haeckel's description better.

Bowerbank described his *L. contorta* as having 'equiangular triradiate' but he had already used this term to describe the sagittal spicules of *L. botryoides*, as noticed by Minchin (1905). And, as we observed, the spicules of some specimens of the study series BMNH 1950.10.12.6, actually resemble those of *Calcinea*. Bowerbank remarked that the actines have 'nearly the same diameter or are attenuated very gradually until near the apices, and are then more suddenly acuminate'. We interpreted this as the cylindrical actine with sharp tips that we saw in the (*Leucosolenia*) specimens of the syntype. Bowerbank also said that 'the spicule rays of the internal defensive spicules are much shorter in proportion to those of *L. botryoides*, rarely exceeding one fourth or one fifth of the interior diameter'. In fact, the apical actine of the tetractines from the specimens of *Leucosolenia* of the study series is shorter than the other actines (and not longer as in specimen number six of the type series, which is a *Clathrina*). Finally, he described the presence on the external surface of 'acerate spicula, mostly disposed in a longitudinal direction'. Diactines are present in the leucosolenias of the study series, but not in the *Clathrina* specimen, as has already been discussed.

Haeckel (1872) re-diagnosed *L. contorta* under the name of *Ascandra contorta*. However, Minchin (1905) considered that 'the diagnosis given is incorrect in two points, namely, in stating that the monaxons possess a lance-head at their distal extremity, and that the gastral rays of the quadriradiates are curved oral wards'. Haeckel was probably analysing BMNH 1910.1.1.434, which has a label in his handwriting and matches his description perfectly, including the lance-head diactine and the apical actine 'curved oral wards' that Minchin criticized. It appears that both Bowerbank and Haeckel used the name *Leucosolenia (Ascandra) contorta* to represent a true *Leucosolenia*, very similar (or identical) to *L. complicata* (Montagu).

It was Minchin (1905) who, in his re-description, first applied the name *C. contorta* that is still used today. He considered that the true type of *C. contorta* (Bowerbank) was the sole specimen of *Clathrina* from the type series BMNH 1950.10.12.6. However, he based his re-description on a specimen from Banyuls-sur-Mer, France, and not on the specimen from the study series. The former possessed diactines (as well as triactines, and tetractines with very long and thin apical actines), while the latter did not. Assuming cospecificity of the two specimens, he placed *Ascetta spinosa* Lendenfeld (1891) in synonymy with *Clathrina contorta* (Bowerbank). He considered that only the adults of *C. contorta* had diactines and that the specimen of the study series was probably a young form of this species. In doing so, he considered that there really was a clathrina among the series, which was cospecific with the specimen from Banyuls-sur-

Mer. We will not discuss his proposed synonymy; however, the specimen of the study series is not conspecific with the French specimen, not only due to the absence of diactines, but also in the shape of the actines and in the proportion between triactines and tetractines, a characteristic that Topsent (1936) said was very important to differentiate *C. contorta* from *C. reticulum*.

The dried clathrina from the study series is very small ( $0.6 \times 0.4$  cm) and its colour is white. The cormus is massive but delicate, formed by irregular and loosely anastomosed tubes. Oscula cannot be distinguished.

The skeleton comprises triactines and tetractines, with the former more abundant. Actines are cylindrical, slightly undulated, and blunt at the tip. A second triactine type is also present, larger and with conical actines, also blunt at the tip, frequently found on the surface of the tubes. Actines are equiangular and equiradiate, although spicules with different actine sizes or sagittal spicules are also found. The apical actine of the tetractines varies in size, but it is frequently longer than the other actines. It is always much thinner, even at the base, where it is straight and smooth. Tetractines with a very long apical actine are commonly sagittal; the apical actine is sometimes undulated at the tip and penetrates the canals.

When comparing the descriptions of the clathrina from the study series and the specimen from Banyuls-sur-Mer, we can see that there are in fact many morphological differences between them. However, in view of the confusion relating to the noncospecificity of the syntypes of *C. contorta* and its validity as a species (the species described by Bowerbank as *L. contorta* was probably a specimen of *L. complicata*), the species *L. contorta sensu* Bowerbank becomes invalid. ICZN (2000) recommends the maintenance of names which have been used consistently; in accordance with this we recommend that the name *C. contorta* continue to be valid, and that it continue to designate specimens conspecific to that from Banyuls-sur-Mer, as described by Minchin (1905). Since it differs from the one described originally by Bowerbank, it should be regarded as a new species and its author should be Minchin. We suggest that BMNH 1896.9.15.1 be considered the neotype.

*CLATHRINA CORIACEA* (MONTAGU, 1818)

*Original name:* *Spongia coriacea* Montagu, 1818

*Type locality:* Budleigh Salterton, S. Devon, England.

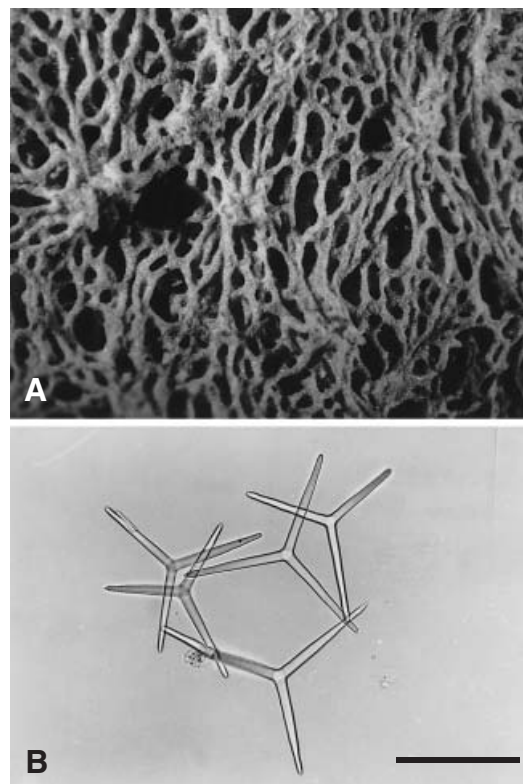
*Type:* BMNH 1882.3.6.7 (suggested neotype/dry). Budleigh Salterton, S. Devon, England. H.J. Carter Collection.

*Citations:* Gray (1821, 1867); Fleming (1828); Johnston (1842); Bowerbank (1866, 1874, 1882); Haeckel (1872); Carter (1877); Vosmaer (1881); Ridley (1881); Fristedt (1885, 1887); Vosmaer (1887); Hanitsch (1890, 1895); Topsent (1891, 1892, 1894, 1936); Grentzenberg (1891); Knipowitsch (1893); Minchin (1896); Breitfuss (1898, 1927, 1932, 1935, 1936); Arnesen (1901); Jenkin (1908); Lundbeck (1909); Row (1909); Dendy & Row (1913); Ferrer-Hernandez (1918); Prenant (1925); Burton (1926, 1929, 1933, 1963); Arndt (1928, 1935, 1941); Row & Hôzawa (1931); Burton & Srinivasa Rao (1932); Renouf (1936, 1937); Tanita (1942, 1943); Borojevic & Grua (1964); Borojevic (1967); Johnson (1978).

The type locality of *C. coriacea* is Budleigh Salterton, S. Devon, England. However, Montagu elected no holotype. The lack of a holotype and the poor original description caused *C. coriacea* to be considered morphologically variable and widespread. We are electing a dried specimen collected by Carter in Budleigh Salterton (BMNH 1882.3.6.7), as the neotype of *C. coriacea*.

*Colour:* Dried specimen is light brown.

*Description:* Cormus formed of thin, irregular and loosely anastomosed tubes. Water-collecting tubes are



**Figure 15.** *Clathrina coriacea*. A, photograph of the neotype ( $\times 10$ ). B, triactines. Scale bar = 100  $\mu\text{m}$ .

present (Fig. 15A). The skeleton has no special organization, comprising equiangular and equireadial triactines (Fig. 15B). Actines are conical or slightly conical, undulated at the distal part and with a constriction near the tip, which is rounded or blunt. The spicules resemble those of *C. clathrus* and *C. aurea*. However, in these species, actines are cylindrical.

	Length (µm)			Width (µm)			<i>n</i>
	min	mean	σ	max	mean	σ	
Triactines	62.5	88.0	± 7.0	102.5	9.0	± 0.8	30

*Remarks:* Montagu first described *C. coriacea* in 1818 under the name *Spongia coriacea*. This description, however, is very incomplete, as it only discusses the external form of this sponge. Johnston (1842) gave a better description and provided an illustration of the spicules. The specimens he studied, however, were from Scarborough (Berwick Bay) and Dublin Bay, and not from the type locality. In his *Monograph of the British Spongiadae*, Bowerbank (1866) again described *C. coriacea*. In this work, he widened the distribution to other places in Britain, although, curiously, he did not mention the type locality. Interestingly, although Bowerbank uses the name *coriacea*, he commented that 'Montagu's description of his *Spongia coriacea* applies very much more correctly to a small specimen of *Raphyrus griffithsii* (a siliceous sponge) of this work than to the calcareous species described above'.

In his monograph, Haeckel (1872) distinguished *C. coriacea*, *C. clathrus* and *C. primordialis* on the basis of differences in the shape of the actines of the triactines and geographical distribution. According to Haeckel, *C. clathrus* could be distinguished from the others by the characteristic shape of its spicules (triactines with undulated actines and a rounded tip) and its restricted distribution in the Adriatic Sea. *C. coriacea*, on the other hand, he considered to be more widespread, found 'on the Atlantic coasts and islands of Europe (Norway, Britain, Ireland, France) and appear[ing] to take the place of *A. primordialis*'. He used the actines to distinguish the species: cylindrical in *C. primordialis* and conical in *C. coriacea*. He also studied specimens from the type locality (Lesina, Adriatic Sea) and then described a species with undulated actines and rounded tips as *Ascetta clathrus*.

Carter (1884) studied specimens from Budleigh Salterton, South Devon, to try to clarify the problem. He either overlooked or ignored the morphological differences pointed out by Haeckel. He considered *C. clathrus* to be a synonym of *C. coriacea*, and con-

cluded that the confusion surrounding the latter 'has arisen from Haeckel having made a separate species of Schmidt's *Grantia clathrus* under the name of *Ascetta clathrus*, with a different form of spicule from that which Schmidt has given as characteristic of it.' The problem is that Schmidt (1864) did not make a good drawing of *C. clathrus* and did not describe the shape of the actines of his *G. clathrus*. As already mentioned, we have had the opportunity to examine Schmidt's specimen and the description made by Haeckel matches it perfectly. Consequently, Carter seems to have created the confusion, by considering *C. coriacea* and *C. clathrus* synonymous.

Minchin (1900) described what he considered to be morphotypes of *C. coriacea*, and stated that this species was very plastic, although characteristic of the North Atlantic. Despite this, *C. coriacea* continued being described as being found from localities worldwide.

Topsent (1936) analysed several specimens from the Mediterranean Sea (identifying them as *C. coriacea*), and said that he had found great morphological variability in this species. He placed several species in synonymy with *C. coriacea*, including *C. primordialis*, and concluded that *C. coriacea* was a cosmopolitan species. After that time, several authors began to identify as *C. coriacea* clathrinids whose skeletons only comprised triactines.

As initially proposed by Haeckel (1872), Borojevic & Peixinho (1976) and Borojevic & Boury-Esnault (1987) distinguished *C. coriacea* (English Channel) and *C. primordialis* (tropical Atlantic, although probably erroneously) on the basis of actine shape.

We therefore conclude that *C. coriacea* is a distinct species with characteristic morphological features that can be easily used to recognize it. Furthermore, it does not seem to be cosmopolitan, but a geographically well-defined species from the North Atlantic.

#### *CLATHRINA CRIBRATA* RAPP, KLAUTAU & VALENTINE, 2001

*Type locality:* Kristiansund, Norway.

*Type:* BMNH 1931.10.28.2 (holotype/alcohol). Kristiansund, Norway. Trondheim Museum Exchange (Collection number T.28).

*Colour:* Preserved specimen is beige.

*Description:* Massive size. The cormus is formed of large, irregular and loosely anastomosed tubes (Fig. 16A). However, the anastomosis is not typical of *Clathrina* in the apical region, but similar to that of *Soleneiscus*. On the surface of the cormus, tubes are no longer anastomosed, but distally ramified. Some of them end in a cul-de-sac, while others are open-ended

and work as oscula. Inside these oscula, which are simple apertures, there is always a sieve formed by spread cells (Fig. 16B), with oval apertures measuring 17–27  $\mu\text{m}$ . Here they lie in a monolayer, probably to protect the sponge against the invasion of foreign organisms.

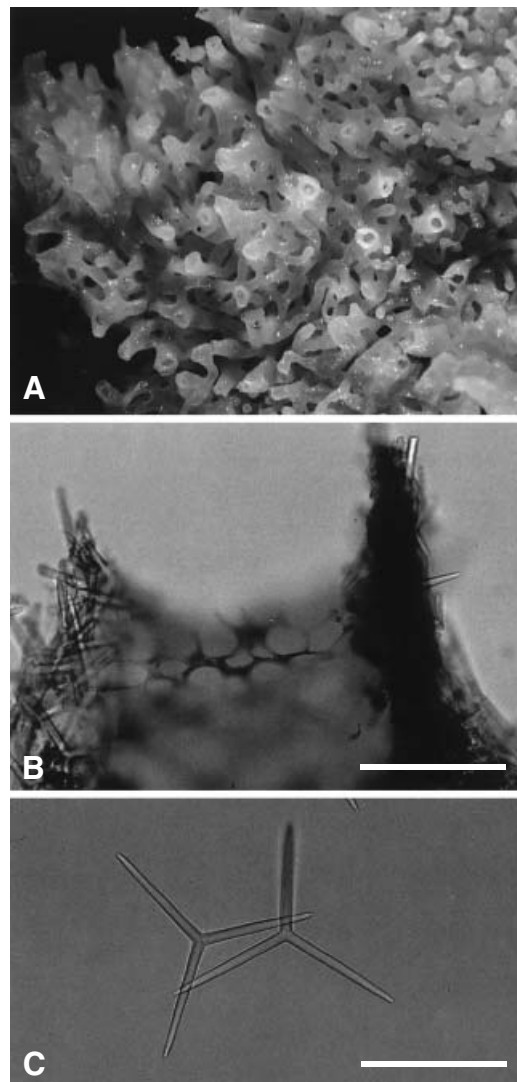
The wall of the tubes is thin (25  $\mu\text{m}$ ), and its skeleton has no organization. Spicules are only triactines, of homogeneous size (Fig. 16C). They are equiangular and equiradiate. Actines are cylindrical, slightly undulated, with a blunt tip.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	47.5	68.5	$\pm 6.8$	75.0	5.8	$\pm 0.6$	30

*Remarks:* *C. cribrata* is very different from all the other species of *Clathrina* we have seen. The organization of the cormus is the character that makes it so unusual. When we first described this species, we were doubtful if it was a true *Clathrina* or a *Soleneiscus*. However, as the anastomosis of the tubes is characteristic of *Clathrina*, becoming similar to *Soleneiscus* only at the apical region, we decided to describe it as such. Another peculiar characteristic is the large number of open or closed terminal tubes at the surface and the existence of the mesh of cells (cribriform membrane) below the opened tubes (oscula). This structure was first described by Minchin (1892) when he was studying some sponges from Plymouth, England which he identified as *C. coriacea*. Eight years later he published an article about the morphological plasticity of *C. coriacea* (Minchin, 1900) in which he discussed the formation of oscula, saying that the most common way was by ‘perforation à l’extrémité du cul-de-sac’ (perforation of the end of the cul-de-sac). He also mentioned that in one of the morphological types he had described, there was a ‘membrane cribriform’. We did not find structures like this in other specimens, and we question whether it is common among the *Clathrina*. Perhaps Minchin was describing as *C. coriacea* a specimen of *C. cribrata* or a related species. Further studies on these morphological characters (cul-de-sac and cribriform membrane) are required. Minchin suggested that the presence of a mesh below the oscula could have the function of a sphincter, permitting the sponge to close oscula at low tide.

*CLATHRINA CYLINDRACTINA* KLAUTAU, SOLÉ-CAVA & BOROJEVIC, 1994

*Type locality:* Arraial do Cabo, Rio de Janeiro, Brazil.



**Figure 16.** *Clathrina cribrata*. A, photograph of the holotype ( $\times 10$ ). B, sieve in the osculum. C, triactines. Scale bar = 100  $\mu\text{m}$ .

*Type:* BMNH 1999.9.16.21 (holotype/alcohol). Arraial do Cabo (Anjos Beach), Rio de Janeiro, Brazil. Collected by G. Muricy (20 August 1987).

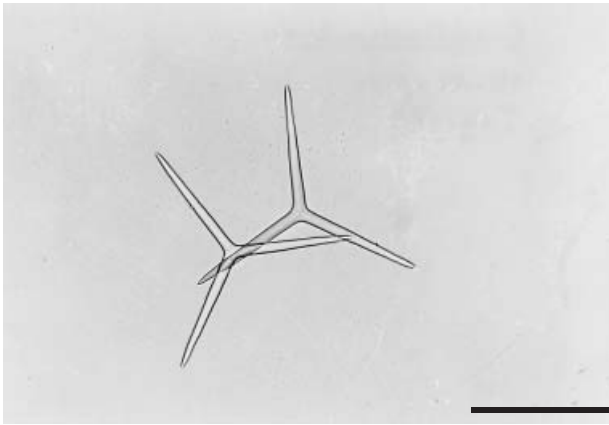
*Citations:* Klautau & Borojevic (2001).

*Colour:* White both when alive and preserved.

*Description:* Cormus very delicate, formed of large, irregular and loosely anastomosed tubes. No water-collecting tubes are present, and oscula are present throughout all the cormus as simple openings on the tubes.

The wall of the tubes is thin (25  $\mu\text{m}$ ). Its skeleton has no special organization, comprising only equiangular and equiradiate triactines (Fig. 17A). Sometimes, it is possible to find a few tetractines. Actines





**Figure 17.** *Clathrina cylindractina*. Triactines. Scale bar = 100  $\mu$ m.

are straight and cylindrical or slightly conical, with blunt tips.

Found in cryptic habitats, such as under rocks or even on other organisms, protected against light and wave action.

	Length ( $\mu$ m)			Width ( $\mu$ m)			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	47.5	83.8	$\pm 12.3$	100.0	8.3	$\pm 1.3$	30

**Remarks:** Morphologically similar to another sympatric species, *C. conifera*. However, the size of the spicules and the shape of the actines (cylindrical in *C. cylindractina* and conical in *C. conifera*) serves to distinguish them. These morphological differences were confirmed genetically by electrophoretic analysis, which showed that no gene flow occurred between them (Klautau *et al.*, 1994).

#### *CLATHRINA DUBIA* (DENDY, 1891)

**Original name:** *Leucosolenia dubia* Dendy, 1891

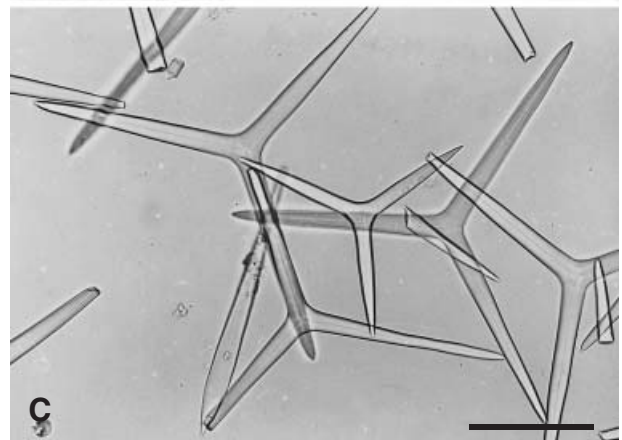
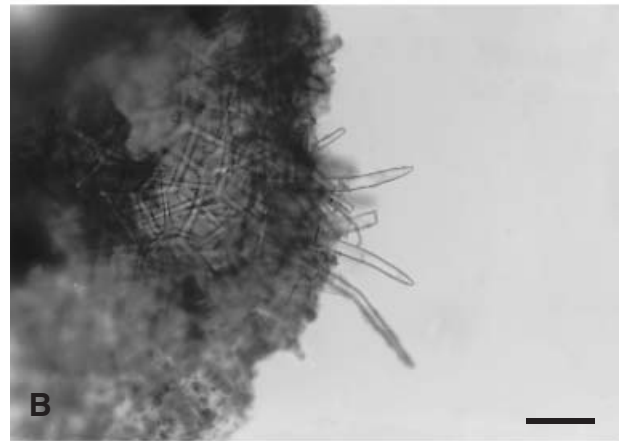
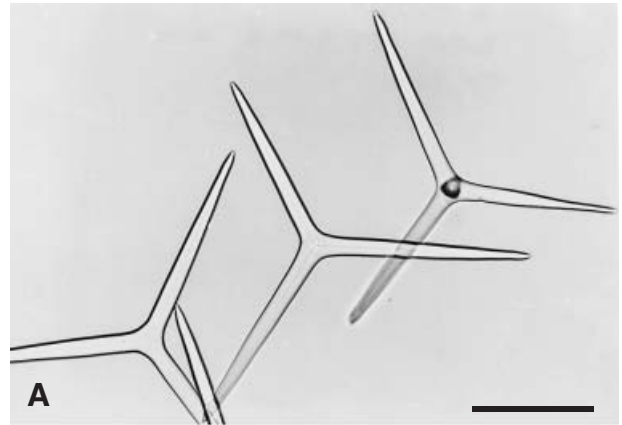
**Type locality:** Near Port Phillip Heads, Australia.

**Type:** BMNH 1891.9.19.2 (lectotype/alcohol), BMNH 1891.9.19.3 (paralectotype/alcohol). Near Port Phillip Heads, Australia. Collected by J. B. Wilson. Dendy Collection.

**Citations:** Dendy & Row (1913); Burton (1963).

**Colour:** Preserved specimen is light yellow.

**Description:** Cormus formed of irregular and loosely anastomosed tubes. There is no cortex but sometimes it appears that some of the tubes could be forming one.



**Figure 18.** *Clathrina dubia*. A, triactines and tetractines. B, Diactines on the surface. C, triactines and a club-shaped diactine. Scale bar = 100  $\mu$ m.

The wall of the tubes is thick (100  $\mu$ m). In some areas the tubes are hispid.

Cells with yellow granules are present in the mesohyl, as are embryos (138/75  $\mu$ m), which are always found near choanocytes. The cells with yellow granules are distributed homogeneously throughout the mesohyl.

The skeleton comprises equiangular and equiradiate triactines (Fig. 18A). Tetractines are also present, but they are rare (Fig. 18A). Actines are conical or cylindrical, but they always have sharp tips. Sometimes, they are slightly undulated. Diactines are abundant on the external tubes (Fig. 18B); they are curved or straight, vary in size and have sharp tips, one of which is club-shaped (Fig. 18C). The largest diactines are curved at the tip. They project through the surface in some parts of the corium only, and the club-shaped portion of the spicule lies inside the tube.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	92.5	151.5	$\pm 14.0$	170.0	15.5	$\pm 1.8$	30
Tetractines	120.0	140.3	$\pm 9.5$	155.0	16.0	$\pm 1.0$	09
Apical actine	100.0	110.0	$\pm 6.8$	117.5	9.8	$\pm 0.5$	04
Diactines	77.5	256.0	$\pm 97.0$	418.2	13.7	$\pm 5.0$	30

*Remarks:* We did not find oscula in the lectotype, although Dendy (1891) described 'very small, round apertures, situated on the apices of small papillae formed by the anastomosis of several Ascon-tubes', which we understand to be water-collecting tubes.

Dendy drew attention to the similarity between *C. dubia* and *C. cavata* Carter, 1886, in relation to the presence of 'great numbers of 'yellow granules' embedded in the mesoderm'. He even supposed that *C. dubia* could be a young form of *C. cavata*. We do not agree, since *C. cavata* is not even a *Clathrina*, but an *Ascaltis*. The curious point about this subject is that Wörheide & Hooper (1999) described some cells for *C. adusta* (another Australian species) that we consider very similar to those found in *C. dubia* and *Ascaltis cavata*.

#### CLATHRINA GARDINERI (DENDY, 1913)

*Original name:* *Leucosolenia gardineri* Dendy, 1913

*Type locality:* Salomon (Chagos Archipelago).

*Type:* BMNH 1920.12.9.47 (lectotype/alcohol), BMNH 1920.12.9.48 (paratype/alcohol). Salomon (Chagos Archipelago), 10–14 fathoms (18–25 m), 'Sealark' Expedition. Dendy Collection (Collection numbers CXX 7 and CXX 11, respectively).

*Citations:* Dendy & Row (1913); Tanita (1942, 1943); Hôzawa, 1941; Burton (1963).

*Colour:* Preserved specimen is light yellow.

*Description:* Formed of regularly and tightly anastomosed, very thin, delicate tubes (Fig. 19A). In shape it is lobose, and full of folds. Each fold is flat, thin and delicate. We did not see any oscula.

In the centre of each fold there is a large tube (pseudoatrium) (Fig. 19B), with choanocytes, surrounded by thinner tubes. Covering the external tubes, there are some large triactines (Fig. 19C). The wall of the tubes is very thin. The tubes are perpendicular to the surface, and converge at a large central tube. Above the central tube, it is possible to see some lacunes.

The skeleton is formed of two types of triactines, of different sizes, and tetractines of the same size as the shorter triactines (Fig. 19D, E). The spicules are equiradiate and equiangular. Actines are conical with sharp tips.

The large triactines are present only in the outside of the external tubes, where they lie side by side. The other triactines are spread along the tubes.

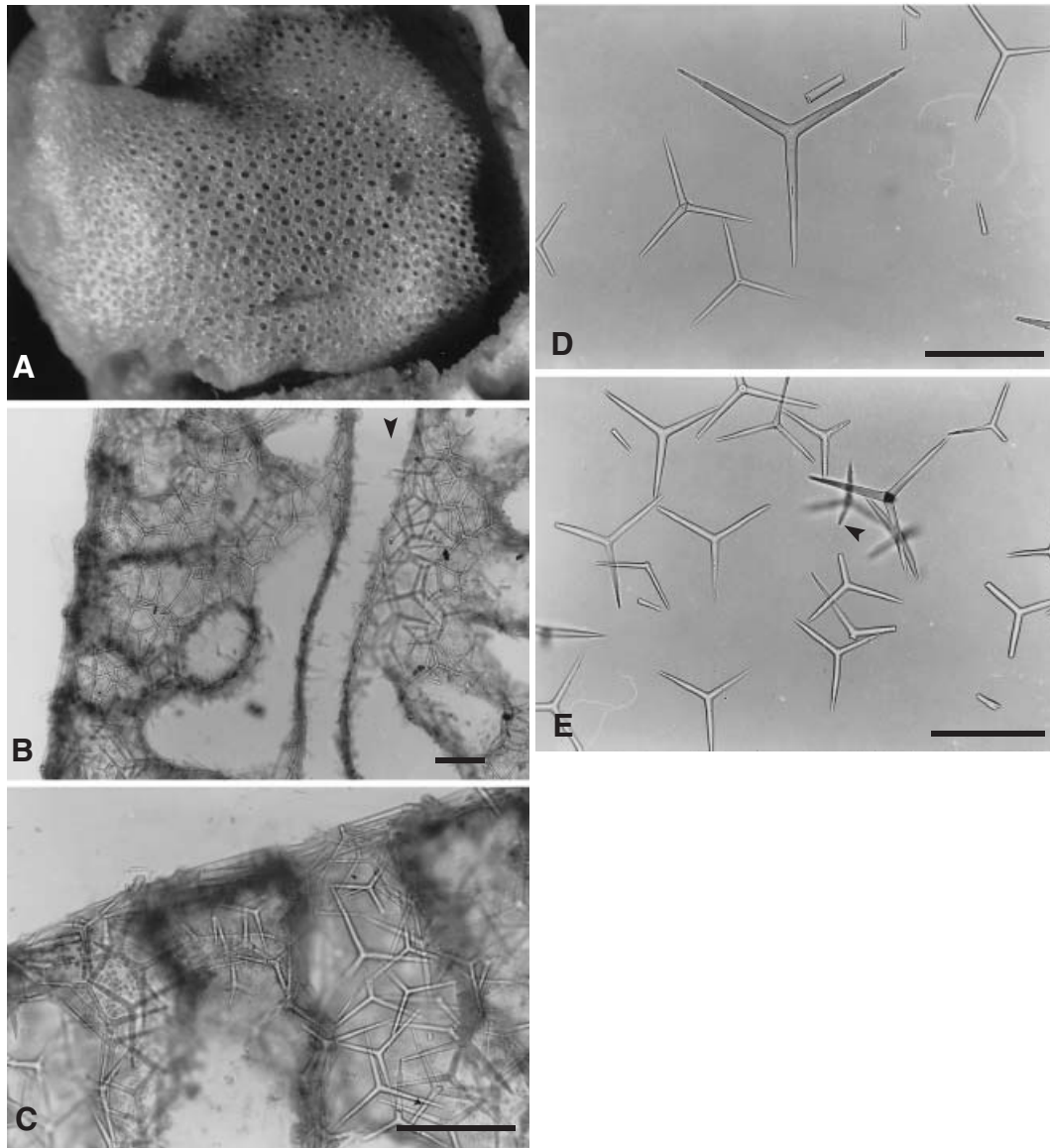
Tetractines are less abundant than triactines. Their apical actine is almost the same thickness as the other actines. It is conical, sharp, shorter, straight and smooth and projected inside the tubes.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	45.0	60.0	$\pm 5.0$	67.5	6.3	$\pm 1.0$	30
Large triactines	87.5	110.0	$\pm 11.8$	137.5	10.8	$\pm 1.3$	30
Tetractines	55.0	65.5	$\pm 9.8$	107.5	6.8	$\pm 1.5$	30
Apical actine	32.5	39.8	$\pm 7.5$	65.0	5.0	$\pm 0.8$	30

*Remarks:* Dendy (1913) used BMNH 1920.12.9.47 and BMNH 1920.12.9.48 to describe his species *L. gardineri*, and named them as lectotype and syntype, respectively.

He discussed morphological differences between them which he thought were either a result of the reproductive state of the syntype, or because they were in different states of contraction when collected. We were very suspicious about this because even the size of the spicules is different. Spicule sizes of the syntype (BMNH 1920.12.9.48) are given in the next table.

However, we believe that other specimens from the type locality collected at different times of year should be analysed before further conclusions are made.



**Figure 19.** *Clathrina gardineri*. A, photograph of the lectotype ( $\times 4$ ). B, pseudoatrium (arrow). C, external tubes with large triactines. D, triactines, tetractine and large triactine. E, triactines, tetractines and an apical actine of a tetractine (arrow). Scale bar = 100  $\mu\text{m}$ .

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	70.0	85.0	$\pm 7.0$	100.0	9.0	$\pm 1.0$	30
Large triactines	95.0	108.0	$\pm 10.0$	125.0	13.0	$\pm 1.0$	10
Tetractines	73.0	84.0	$\pm 6.0$	100.0	9.0	$\pm 1.0$	30
Apical actine	43.0	67.0	$\pm 18.0$	105.0	6.0	$\pm 1.0$	30

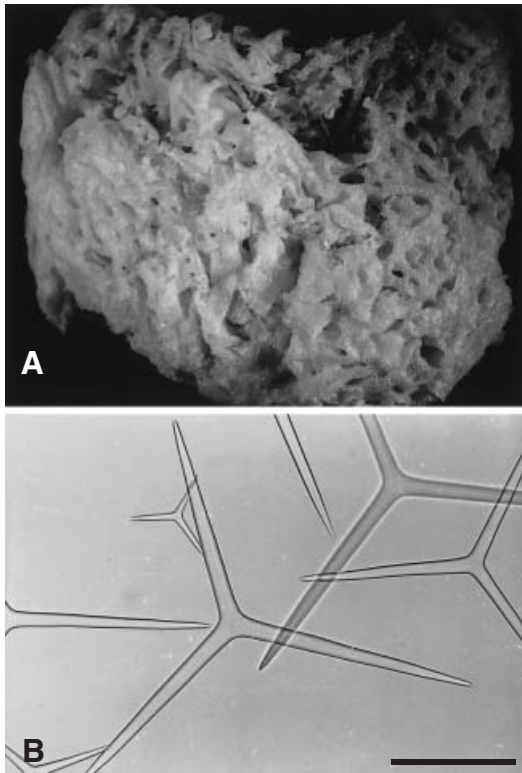
*CLATHRINA HELVEOLA* WÖRHEIDE & HOOPER, 1999

*Type locality:* Great Barrier Reef.

*Type:* QMG 313680 (holotype/alcohol). South side of Heron Island, Great Barrier Reef, 23°28.2'S, 151°56.7'E, 17 m depth. Collected by G. Wörheide (8 July 1998).

*Colour:* Preserved holotype is light yellow.

*Description:* The corumus in this massive holotype is delicate, formed of large, irregular and loosely anastomosed tubes (Fig. 20A). In some parts of the corumus, a



**Figure 20.** *Clathrina helveola*. A, photograph of the holotype (× 4). B, triactines. Scale bar = 100 μm.

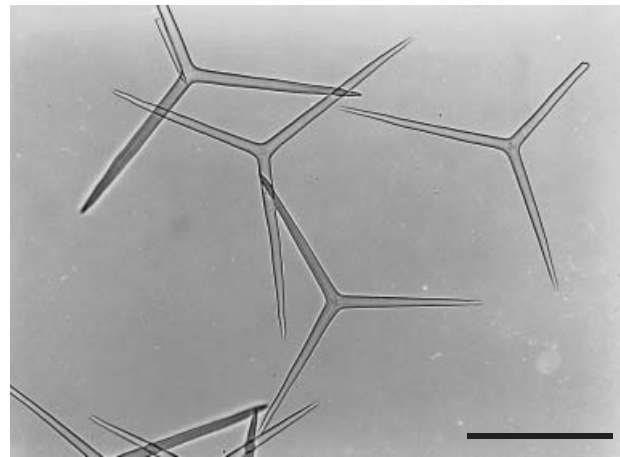
thin cortex can be seen. Cells with granules are present.

The skeleton has no special organization. It comprises equiangular and equiradiate triactines (Fig. 20B). Actines are conical and sharp, and slightly undulated at the tip.

	Length (μm)			Width (μm)			
	min	mean	σ	max	mean	σ	n
Triactines	64.8	154.1	± 25.0	182.4	13.2	± 1.7	25

According to the original description the micrometry is:

	Length (μm)			Width (μm)			
	min	mean	σ	max	mean	σ	n
Triactines	114.0	159.6	± 20.9	200.0	16.3	± 1.8	30



**Figure 21.** *Clathrina heronensis*. Triactines. Scale bar = 100 μm.

*CLATHRINA HERONENSIS* WÖRHEIDE & HOOPER, 1999

*Type locality:* Great Barrier Reef.

*Type:* QMG 313647 (holotype/alcohol). Heron Island, at Wistari Channel, Great Barrier Reef, 23°26.9'S, 151°54.6'E, opposite Research Station, 300 m south of shipping channel, at reef crest. Collected by G. Wörheide (21 June 1998).

*Colour:* The preserved holotype is light brown.

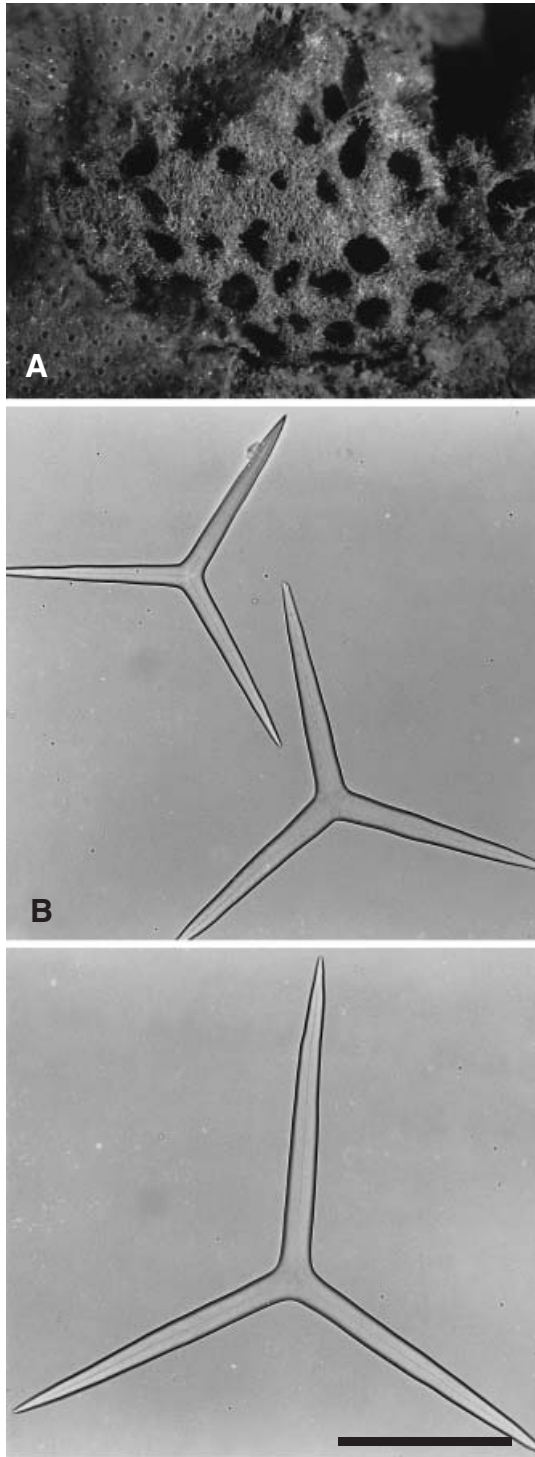
*Description:* Large, irregular and loosely anastomosed tubes form the cormus. The spicules are very bright and can easily be seen. The mesohyl is full of porocytes with brown granules.

The skeleton has no special organization, comprising equiangular and equiradiate triactines (Fig. 21). Actines are cylindrical, undulated and sharp at the tip.

	Length (μm)			Width (μm)			
	min	mean	σ	max	mean	σ	n
Triactines	80.0	128.5	± 21.8	170.0	10.0	± 0.6	25

According to the original description the micrometry is:

	Length (μm)			Width (μm)			
	min	mean	σ	max	mean	σ	n
Triactines	84.0	107.0	± 12.1	126.0	10.0	± 1.39	30



**Figure 22.** *Clathrina laminoclathrata*. A, photograph of the lectotype ( $\times 10$ ). B, the three categories of triactine. Scale bar = 100  $\mu\text{m}$ .

*CLATHRINA LAMINOCATHRATA* CARTER, 1886

*Type locality:* Port Phillip Heads, VIC. (Australia).

*Type:* BMNH 1887.7.12.42 (lectotype/dry). There is a label on which is written: *Grantia laminoreticulata* n.sp. Ott n°18 (12.2.86).

BMNH 1887.7.12.43 (syntype/dry).

Both from Port Phillip Heads, VIC. (Australia), J. Bracebridge Wilson Collection.

*Citations:* Dendy (1891); Dendy & Row (1913); Burton (1963).

*Colour:* There are two dried sponges attached to a stone. One of them is light yellow and has a continuous and hispid surface, with large external spicules. The specimen in question is on the other side of the stone. It is light grey and is formed by regular and tightly anastomosed tubes (Fig. 22A).

*Description:* This specimen is a little different from the other *Clathrina* species examined. Under the tubes, directly in contact with the substrate, there is a continuous membrane, a basal lamina, and above it the anastomosed tubes characteristic of *Clathrina*. It is possible that this basal lamina is only an artefact created by the dried state of the specimen as Dendy (1891) supposed, but the skeleton in this region of the sponge is different from the skeleton in the tubes.

The skeleton is formed by triactines only (Fig. 22B), as stated by Carter (1886) in the original description, although there are in fact three different categories of triactines, based on size. All have conical actines and sharp tips. The largest are generally found on the external tubes of the sponge, i.e. on the surface of the cormus. They can also be found in the basal lamina, although this is rare. The other two sizes of triactines are more abundant in the basal lamina, and can also be seen on the surface of the tubes, but are less abundant.

There is no specialization of the tubes and the organization of the cormus is typical of *Clathrina*.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	50.0	72.0	$\pm 15.0$	113.0	8.0	$\pm 2.0$	30
Triactines	88.0	132.0	$\pm 16.0$	168.0	13.0	$\pm 2.0$	30
Triactines	125.0	188.0	$\pm 31.0$	235.0	18.0	$\pm 3.0$	30

*Remarks:* In 1886, Carter described this species from Port Phillip Heads from a dried specimen. He described the cormus as sub-circular, steel-grey, clathrous, reticulated at the surface and with a basal lam-

ina, and the skeleton as formed of equiangular and equiradiate triactines which vary in size.

Dendy (1891) suggested that Carter could have been mistaken when he described the basal lamina, adding that as he had examined a small, dried specimen, the lamina was probably the result of collapsed tubes. He concluded that the species should be abandoned. He later (Dendy & Row, 1913) put it on his *Leucosolenia* list, but as a species of doubtful value, and supported this opinion with the observation that this species was 'too imperfectly described to be recognisable'.

We examined two specimens deposited at BMNH. Both are very similar and were collected on the South Coast of Australia, one of them from the type locality. J. Bracebridge Wilson collected them and were both dried. One (BMNH 1887.7.12.42) is labelled as a lectotype, and the other (BMNH 1887.7.12.43) as a syntype (cotype). They match the description given by Carter (1886) perfectly, although this description is really very incomplete. We believe that *C. laminoclathrata* is a valid species. Even if we consider that the basal lamina is an artefact of desiccation, there are three different categories of triactines in these specimens, which justifies the specific level. Furthermore, the distribution of these categories is different in the distinct body parts of this species, while the 'basal lamina' has a specific skeleton, which suggests that it is a genuine structure. As there is no well-preserved specimen, we decided to redescribe the species, based principally on the three different categories of triactines and their distribution, and consider the presence of a basal lamina only as a possibility.

*CLATHRINA LUTEOCULCITELLA* WÖRHEIDE & HOOPER, 1999

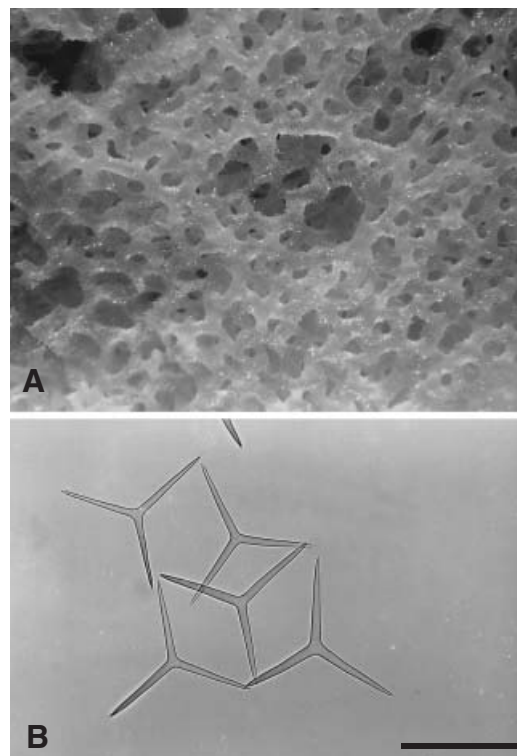
*Type locality*: Great Barrier Reef.

*Type*: QMG 313684 (holotype/alcohol). 'The Patch', at the N end of the channel between Heron Island and Wistari Reef, Great Barrier Reef, 23°26.6'S, 151°53.4'E, 25 m depth. QMG 313806 (paratype/alcohol), same locality. Collected by G. Wörheide (9 July 1998).

*Colour*: The preserved holotype is light yellow.

*Description*: Holotype massive yet delicate. The corrus has folds and is formed of thin, irregular and tightly anastomosed tubes (Fig. 23A). However, in the interior, tubes are loosely anastomosed. Oscula are simple apertures surrounded by a thin membrane. There are no water-collecting tubes.

The skeleton comprises equiangular and equiradiate triactines (Fig. 23B) and diactines. The actines of the triactines are conical, slightly undulated and



**Figure 23.** *Clathrina luteoculcitella*. A, photograph of the holotype ( $\times 40$ ). B, triactines. Scale bar = 100  $\mu\text{m}$ .

sharp. Diactines are straight and one of the tips is thicker than the other one. They are found perpendicular to the surface of all tubes (not just the external tubes) and the largest tip penetrates the corrus. The mesohyl is full of bacteria.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	64.8	75.8	$\pm 5.0$	91.2	7.7	$\pm 1.0$	25
Diactines	91.2	125.3	$\pm 24.5$	168.0	3.8	$\pm 0.7$	10

The photograph we have is of the paratype (QMG 313806). According to the original description, the micrometry of the spicules of the holotype is:

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	68.0	77.7	$\pm 4.5$	84.0	9.4	$\pm 1.2$	30
Diactines	90.0	164.4		220.0	3.12		30

*CLATHRINA PANIS* (HAECKEL, 1872)

*Original name:* *Ascandra panis* Haeckel, 1872

*Type locality:* Atlantic coast of North America (Florida, Agassiz).

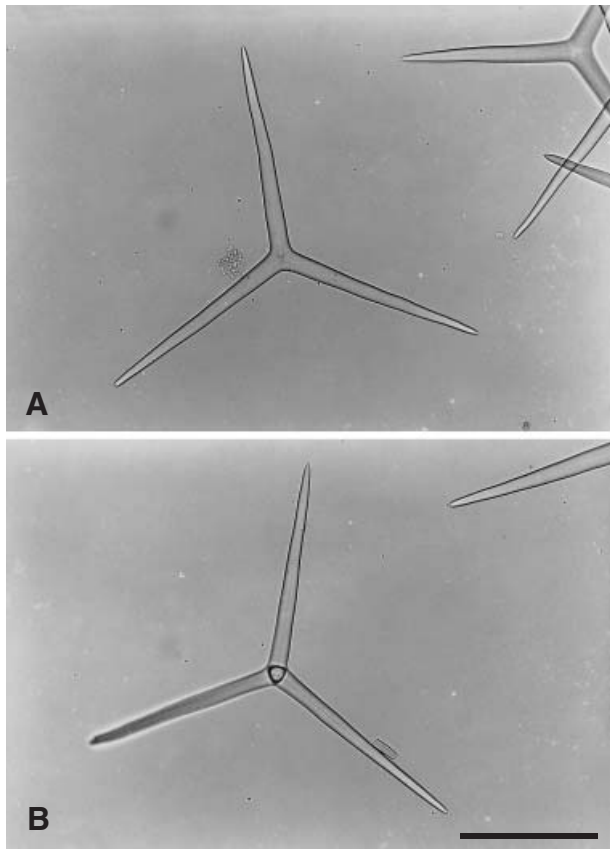
*Type:* PMJ. Inv. Nr. Porif. 152 (syntype/alcohol). Florida, North America.

*Citations:* Thacker (1908); Dendy & Row (1913); Tanita (1942).

*Colour:* Preserved specimen is white.

*Description:* Almost spherical, formed of irregular and loosely anastomosed tubes. Sediment is present inside the corium. A large tube (pseudoatrium) can also be found inside the corium.

Triactines (Fig. 24A), tetractines (Fig. 24B) and a few diactines form the skeleton. Triactines and tetractines are equiangular and equiradiate and their actines are conical and a little undulated, with sharp tips. The apical actine of the tetractines is a little shorter, thinner, conical, smooth and straight, and it is projected to the interior of the tubes. Tetractines are



**Figure 24.** *Clathrina panis*. A, triactines. B, tetractines. Scale bar = 100  $\mu\text{m}$ .

less abundant than triactines. There are very few diactines. They are fusiform and penetrate the surface of the sponge.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	137.5	162.0	$\pm 11.3$	180.0	15.5	$\pm 1.5$	30
Tetractines	135.0	159.8	$\pm 11.5$	180.0	14.5	$\pm 1.3$	30
Apical actine	105.0	156.8	$\pm 22.8$	187.5	9.5	$\pm 1.8$	17
Diactines	285.6	474.3	$\pm 184.6$	1122.0	29.6	$\pm 19.4$	20

*Remarks:* We received a syntype from Haeckel's collection deposited at PMJ. Haeckel (1872) said that he based his description on one specimen, which appears to be very similar to the one we examined. Our description matches his. The specimen sent by PMJ is probably the holotype.

*CLATHRINA PARVA* WÖRHEIDE & HOOPER, 1999

*Type locality:* Great Barrier Reef.

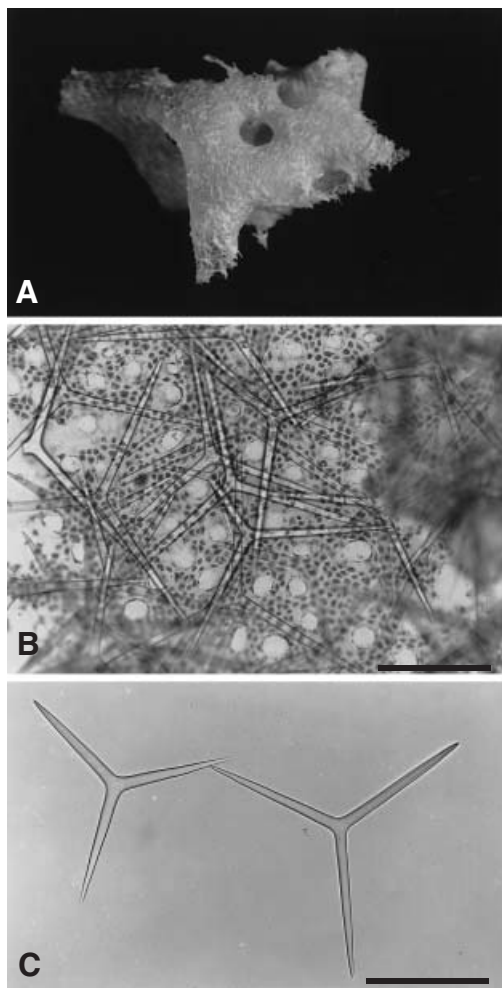
*Type:* QMG 313666 (holotype/alcohol). South side of Wistari Reef, Great Barrier Reef, 23°29.4'S, 151°52.8'E, 18 m depth. Collected by G. Wörheide (7 July 1998).

*Colour:* Preserved holotype is white.

*Description:* The corium is delicate, small and transparent, formed by large, irregular and loosely anastomosed tubes (Fig. 25A). Water-collecting tubes arrive at large oscula projected above the surface. In the osculum, spicules are arranged in parallel. The mesohyl is full of porocytes with brown granules and large vacuoles (Fig. 25B). The skeleton has no special organization, comprising equiangular and equiradiate triactines (Fig. 25C), but sagittal spicules can also be found. Actines are cylindrical, sharp and undulated at the tip.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	90.0	129.3	$\pm 16.7$	160.0	9.7	$\pm 1.1$	15

According to the original description the micrometry is:



**Figure 25.** *Clathrina parva*. A, photograph of the holotype ( $\times 10$ ). B, mesohyl full of porocytes with brown granules and large vacuoles. C, triactines. Scale bar = 100  $\mu\text{m}$ .

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	80.0	143.0	$\pm 21.0$	185.0	13.7	$\pm 2.23$	30

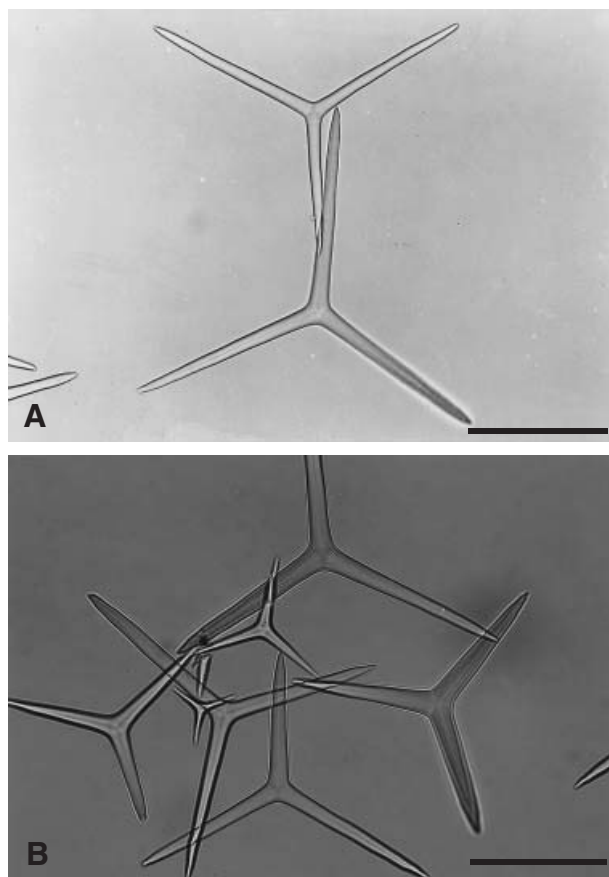
*CLATHRINA PRIMORDIALIS* (HAECKEL, 1872)

*Original name:* *Proscymum primordiale nomen nudum* Haeckel, 1870, *Ascetta primordialis* Haeckel, 1872

*Type locality:* Lesina, Adriatic Sea.

*Type:* ZMB 1306 (suggested lectotype/alcohol). Naples, PMJ. Inv.Nr.Porif. 154 (type/alcohol). Lesina, Adriatic Sea.

*Citations:* Haeckel (1870); von Lendenfeld (1885, 1891); Carter (1886); Lackschewitsch (1886);



**Figure 26.** *Clathrina primordialis*. A, two categories of triactines. B, triactines of ZMB 1306. Scale bar = 100  $\mu\text{m}$ .

Minchin (1896); Breiffuss (1898, 1932, 1935); Arnesen (1901); Jenkin (1908); Row (1909); Dendy & Row (1913); Ferrer-Hernandez (1918); Burton (1926, 1963); Bronsted (1931); Row & Hôzawa (1931); Arndt (1941); Tanita (1942, 1943); Borojevic (1971); Borojevic & Peixinho (1976); Klautau *et al.* (1994).

We received from PMJ (Inv.Nr.Porif. 154) a syntype collected from Lesina. Mixed with this specimen, which has only triactines, was a specimen of *C. cerebrum*.

*Colour:* The preserved specimen of *A. (Clathrina) primordialis* is white.

*Description:* Cormus formed of large, irregular and loosely anastomosed tubes. Skeleton comprises two kinds of equiangular and equiradiate triactines (Fig. 26A); some actines conical, others cylindrical. In both kinds, the tip of the actines is sharp.



	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	n
Triactines (con)	97.5	134.5	±17.0	157.5	14.8	±2.0	23
Triactines (cyl)	107.5	134.5	±11.3	157.5	11.5	±1.0	24

*Remarks:* Haeckel (1870) introduced the species for the first time under the name *Prosyncum primordiale*, from Naples, Italy. He did not give a description, simply presenting a systematic list of calcareous sponges. It was a *nomen nudum*. In his famous monograph of 1872 he provided a detailed morphological description of several calcareous species, including those he had previously cited in 1870, which were described as new. Consequently, the accepted date of many of these species, including *C. primordialis*, became 1872.

The ‘Natural System’ of classification proposed by Haeckel distinguished the genera of calcareous sponges by their spiculation. Therefore, as *P. primordiale* was formed only of triactines, he changed its genus to *Ascetta* and called it *A. primordialis*. In 1870 Haeckel designated Naples as the type locality. In 1872, he did not elect one type locality but instead listed several where *A. primordialis* could be found, concluding that this species was cosmopolitan. Nevertheless, he listed where he had found it for the first time and, strangely, he said that it was in Nizza in 1856 and then in Naples (1859) and several other localities, Lesina (Adriatic Sea) being the last one (1871).

Haeckel probably described *A. primordialis* as a series of different species and even genera. We can see this looking at some of his drawings and analysing some specimens identified by him. Consequently, his description was a generalization, based only on the presence of anastomosed tubes composing the cornus, and triactines with slightly conical or cylindrical actines near the centre and semifusiform at the distal part, always with a sharp tip (or tips). He elected four varieties of *A. primordialis*, all from Australia: var. *dictyoides*, var. *loculosa*, var. *poterium* and var. *protogenes*. Later, von Lendenfeld (1885) elevated two of those varieties to the rank of species (*A. loculosa* and *A. poterium*), and returned var. *dictyoides* (*Leucosolenia dictyoides* Haeckel, 1870) to the specific level, as *A. dictyoides*. He did not mention *protogenes*, although Tanita (1942) considered a new species described by von Lendenfeld, 1885 (*A. procumbens*) to be a synonym of it. Dendy and Row (1913) again reinforced the position of these varieties as distinct species, putting all of them in the genus *Leucosolenia*. We had access to

the holotype of only one of these varieties – *poterium* – and it is clearly an *Ascaltis* (based on the organization of the cornus, which is surrounded by a cortical membrane and missing a true atrium). In relation to the other ‘varieties’, we only had access to some of the specimens from Australia, and they are, indeed, distinct species.

In the original description of *C. primordialis*, Haeckel said that the actines of the triactines were slightly conical or cylindrical near the centre and semifusiform at the distal part, but always with sharp tips.

We also received another syntype under the name *Prosyncum primordiale*. This came from Berlin (ZMB 1306) and was collected in Naples. As the first mention of *C. primordialis* was under the name *P. primordiale* and the specimen was from Naples, the coincidence proved interesting. This sponge is beige when preserved and its cornus is formed of thin, irregular and loosely anastomosed tubes. Larger tubes project above the surface, their openings then functioning as oscula; they are water-collecting. The skeleton comprises equiangular and equiradiate triactines (Fig. 26B). Actines are conical or slightly conical, and we can separate two populations of spicules based on this difference, the spicules with conical actines being the most abundant. The tip of the actines is always sharp and the size of the spicules matches the size given by Haeckel:

	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	n
ZMB 1306							
Triactines (con.)	84.0	91.9	±5.8	103.2	9.6	±0.5	20
Triactines (slightly con.)	64.8	86.6	±13.0	117.6	11.3	±0.7	20
<i>C. primordialis</i> (orig. description)							
Triactines	100			150	8–12		

We also found two other specimens in BMNH that matched this one exactly. One (BMNH 1897.3.25.3) is from Lesina, while the other (BMNH 1898.5.7.3) is from Naples. We did not find any specimens which we considered as morphologically similar to PMJ.Inv.Nr.Porif.154.

Considering that originally Haeckel (1870) had given Naples as the type locality of *C. primordialis*, we suggest that ZMB 1306 should become the lectotype. Contrary to his concept of the species’ great morphological variability, we think that it is very well defined morphologically, being recognized by the shape of the actines of both triactine populations, by the sharp tip and even by the size of the actines, which seems to be

quite consistent (conical triactines: 91.9 ( $\pm 5.8$ )/9.6 ( $\pm 0.5$ ); slightly conical triactines: 86.6 ( $\pm 13.0$ )/11.3 ( $\pm 0.7$ )). The specimen sent from Jena as a syntype of *primordialis* (Porif. 154) is probably a new species, as the size of the spicules and the presence of cylindrical actines in one of the populations of triactines are very distinctive. However, we decided not to describe it as a new species in the present article, since we only had one very old specimen to study.

The systematics of sponges with only one kind of spicule is always very difficult. Species of *Clathrina* whose skeletons are composed only of triactines are considered to be the most morphologically plastic and geographically widespread. Topsent (1936) considered that this high level of plasticity in clathrinins only involved triactines, and subsequently placed *C. primordialis* in synonymy with *C. coriacea*. Since then, except for *C. clathrus*, all other clathrinins with a skeleton composed only of triactines became *C. coriacea*. In the 1970s the name *C. primordialis* started being used again (Borojevic, 1971; Borojevic & Peixinho, 1976). The synonymy of *C. primordialis* with *C. coriacea* was questioned when the authors compared specimens with triactines from Brazil with specimens of *C. coriacea* from the British Isles (*locus typicus*). The shape and size of the spicules were so different that they decided to call the Brazilian specimens *C. primordialis*. The main difference related to the tip of the actines, which had already been used by Haeckel in 1872 to distinguish specimens of *C. primordialis* (sharp) from *C. coriacea* (blunt). Klautau *et al.* (1994) also considered the shape of the actines to be a useful character to distinguish specimens from two sympatric populations of *Clathrina* from Arraial do Cabo (Rio de Janeiro). Allozyme analysis of specimens from both populations found that there was no gene flow between them, that they are reproductively isolated and thus constitute distinct species.

As the type specimens of Haeckel's species, including *C. primordialis*, seemed at that time to be lost, the population with triactines with conical actines and a sharp tip was called *C. primordialis*. Therefore Klautau *et al.* (1994) suggested that the *locus typicus* of this species should be considered as Rio de Janeiro. Recently, however, we have been able to work with specimens originally identified by Haeckel. We believe that it is more appropriate to consider Naples as the *locus typicus*, which implies that the Brazilian population should be considered as a new species (*C. conifera*). The distribution of *C. primordialis* is thus restricted to the Mediterranean and the Adriatic Seas.

#### CLATHRINA PROCUMBENS (VON LENDENFELD, 1885)

*Original type: Ascetta procumbens* von Lendenfeld, 1885

*Type locality:* East coast (Port Jackson) and South coast (Port Phillip, VIC) of Australia.

*Type:* BMNH 1886.6.7.3 (lectotype/alcohol). South coast of Australia (Port Phillip, VIC), BMNH 1886.6.7.1–2 (syntypes/alcohol). East Coast of Australia (Port Jackson). Both from the Dr von Lendenfeld Collection.

*Citations:* Dendy (1891); Burton (1963).

The specimens named as the syntypes are typical clathrinins. One of them is attached to a *Mytilus* shell.

*Colour:* Preserved specimens white to light yellow.

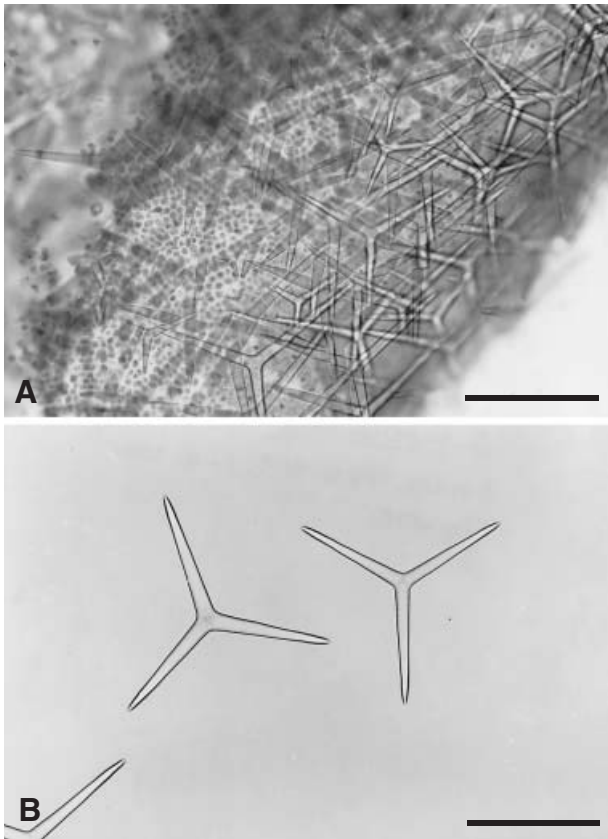
*Description:* Cormus formed of irregular and loosely anastomosed tubes with variable diameters. The surface of these tubes is smooth. In some places, tubes attach to the substrate to anchor the sponge. At the apical region there are water-collecting tubes converging into the oscula. The skeleton has no special organization (Fig. 27A), comprising equiangular and equiradial triactines (Fig. 27B). Actines are conical with sharp tips. The size of spicules is quite uniform, but there are also some small young spicules.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	62.5	87.3	$\pm 8.5$	100.0	11.3	$\pm 1.3$	30

*Remarks:* *Ascetta (Clathrina) procumbens* was considered a synonym of *Leucosolenia protogenes* (*Ascetta primordialis* var. *protogenes* Haeckel, 1872) by Dendy (1891). This synonymy was confirmed by Burton (1963), and no one has resurrected this species since.

Three types of this species are deposited in BMNH: two syntypes and a lectotype. When we examined these specimens, we finally understood the problem involving *C. procumbens*.

As Dendy wrote: 'one of his (Lendenfeld) figures (Pl. LXI, Fig. 1a) agrees with this description (the original description of *C. procumbens*), but three others, said to be of the same species (Pl. LXI, Figs 1b, c, d), represent a massive, lobose sponge of very different appearance. The fragment also, sent to me from the British Museum, is evidently a portion of a massive sponge'. Dendy was right about this, but not about the synonymy of *C. procumbens* and *L. protogenes*. The specimen he agreed matched the description made by von Lendenfeld is the one



**Figure 27.** *Clathrina procumbens*. A, skeleton. B, triactines. Scale bar = 100 µm.

attached to a *Mytilus* shell (the syntype), which we analysed. Together with the syntype, we also analysed the lectotype, which is indeed very different from the syntype (Dendy mentioned that he received a specimen of *C. procumbens*, but he did not say that it was a type). The lectotype is probably a specimen of *L. protogenes*, and thus not a clathrina. On the other hand, the syntype evidently corresponds to the specimen described by von Lendenfeld as *Ascetta (Clathrina) procumbens*.

The specimens BMNH 1886.6.7.1–2 (syntypes attached to the *Mytilus* shell) match the description and the drawing of the cormus made by von Lendenfeld. However, the description of the shape of the actines is not the same. He wrote that ‘The rays are pretty stout, conic and slightly rounded at the ends’, while we consider the same spicules to be conical, with sharp tips.

We consider *C. procumbens* to be a true species of *Clathrina*, the syntypes of which are BMNH 1886.6.7.1–2. The proposed lectotype of this species (BMNH 1886.6.7.3) does not correspond to even the same genus as the syntypes of *procumbens*, being probably a specimen of *L. (Ascallis) protogenes*.

*CLATHRINA QUADRIRADIATA* KLAUTAU & BOROJEVIC, 2001

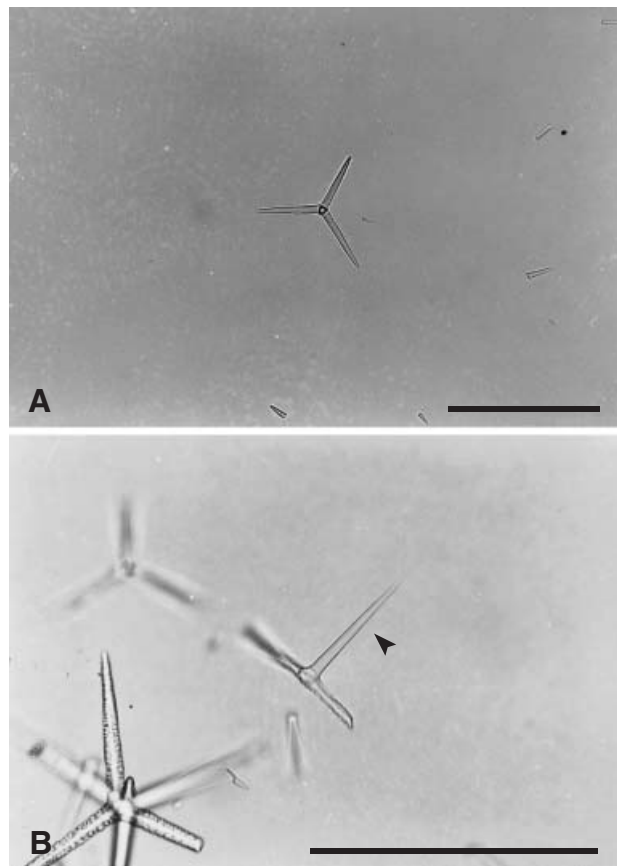
*Type locality:* Arraial do Cabo, Rio de Janeiro, Brazil.

*Type:* BMNH 1999.9.16.30 (holotype/alcohol). Arraial do Cabo, Rio de Janeiro, Brazil. Collected by G. Muricy (18 March 1990).

*Colour:* Cormus is white in life and when preserved.

*Description:* The specimen studied is very small. Formed of very thin, regular and tightly anastomosed tubes. Oscula are simple openings located on the top of conical projections, which receive the excurrent water from water-collecting tubes.

The skeleton comprises tetractines (Fig. 28A) and a few triactines. Actines are straight and conical, with blunt tips. The apical actine of the tetractines (Fig. 28B) is only a little thinner than the facial ones at the base. It is also shorter, conical, sharp and smooth. Only one specimen of this species was collected.



**Figure 28.** *Clathrina quadriradiata*. A, tetractine. B, apical actine of a tetractine (arrow). Scale bar = 100 µm.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	47.5	56.3	$\pm 4.8$	67.5	6.3	$\pm 0.8$	30
Tetractines	42.5	54.3	$\pm 4.8$	62.5	6.0	$\pm 0.8$	30
Apical actine	20.0	34.8	$\pm 8.3$	55.0	4.3	$\pm 0.8$	30

Although the tetractines are more abundant in relation to the triactines, this species is very different from *C. tetractina*. Triactines, although few, can still be found, while the spicules are shorter.

*Remarks:* This species is also very similar to *C. aspina* and *C. brasiliensis*. However, it has no tripods and tetractines are more abundant than triactines, while in *C. aspina* and *C. brasiliensis*, triactines are the main spicule. A less evident characteristic concerns the cormus, which is less regularly anastomosed in this species than in the other two.

#### *CLATHRINA RETICULUM* (SCHMIDT, 1862)

*Original name:* *Nardoa reticulum* Schmidt 1862

*Type locality:* Zara and Sebenico (Adriatic Sea).

*Type:* BMNH 1896.9.15.13 (proposed neotype/ alcohol). Banyuls-sur-Mer, Pyrenees, France. E.A. Minchin Collection.

*Citations:* Haeckel (1870, 1872); Vosmaer (1881); von Lendenfeld (1891); Minchin (1896); Breitfuss (1898, 1930, 1932, 1935); Dendy & Row (1913); Brondsted (1914); Topsent (1934, 1936); Hôzawa (1940); Arndt (1940, 1941); Tanita (1942, 1943); Burton (1963); Borojevic & Boury-Esnault (1987).

*Colour:* This preserved specimen is light yellow.

*Description:* Cormus spherical and formed of regular and tightly anastomosed tubes. Oscula can be seen on the surface and a delicate membrane (Fig. 29A) always surrounds them. Below each osculum there is a large tube resembling an atrium (pseudoatrium). The anastomosed tubes are more abundant near the surface of the sponge. Near the pseudoatrium the cormus is less ramified and there are fewer, wider tubes.

The skeleton comprises triactines, tetractines (Fig. 29B) and diactines (Fig. 29C). Triactines are the most abundant spicule type.

Triactines and tetractines have cylindrical actines with sharp tips. The apical actine of the tetractines (Fig. 29D) is much thinner than the others (resembling that of *C. contorta*); it is cylindrical, straight and smooth, and frequently shorter. Tetractines can be seen primarily near the pseudoatrium.

The diactines are present only on the surface and, unlike those of *C. contorta*, perpendicular to it (Fig. 29E). These spicules are not uniformly distributed (Fig. 29F), but appear patchily distributed like tufts, principally in the intersection points of the anastomosed tubes. They vary in size and both tips are different. One of them is similar to an arrowhead and always located inside the cormus. Sometimes, there are also more fusiform diactines.

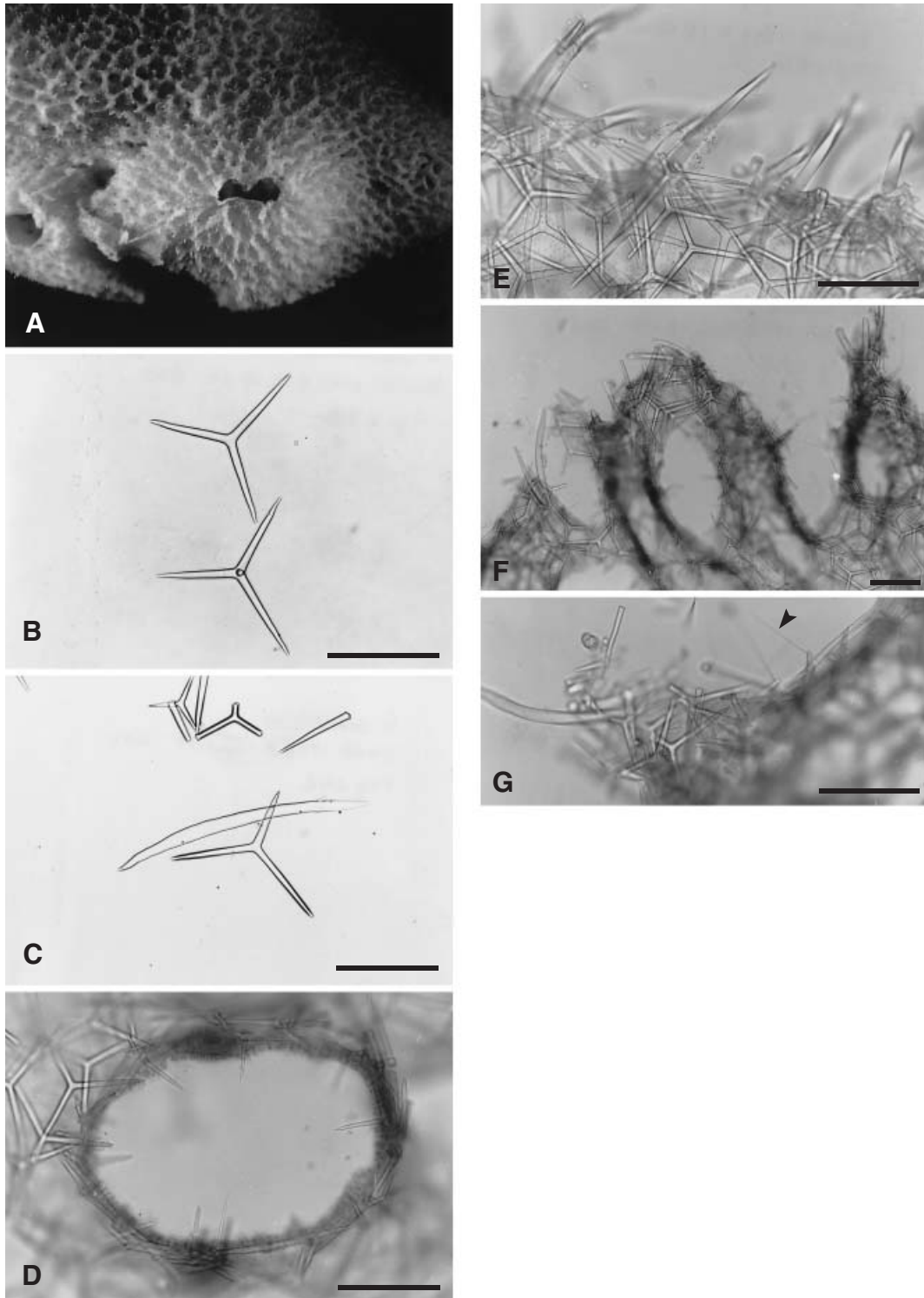
There is also another kind of spicule in this specimen that was not described by Schmidt, the trichoxea (Fig. 29G). These spicules are very thin, similar to filaments and they are present among the tubes.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	72.5	87.8	$\pm 7.5$	100.0	7.5	$\pm 1.0$	30
Tetractines	57.5	89.5	$\pm 11.0$	115.0	7.3	$\pm 0.5$	30
Apical actine	45.0	53.3	$\pm 13.5$	120.0	5.0	$\pm 0.3$	30
Diactines	102.0	212.2	$\pm 54.1$	306.0	14.3	$\pm 5.1$	25

*Remarks:* Schmidt first described this species in 1862 as *Nardoa reticulum* after analysing a specimen collected in the Adriatic Sea (near Zara and Sebenico at a depth of 27–36 m). It was spherical, with a prominent osculum and three kinds of spicules: triactines, tetractines and diactines ‘fusiformia, paulum curvata e superficie prominentia’ (fusiform, a little curved, prominent from the surface). His description is not quite complete, and the only drawing he made was of the cormus. No holotype was elected.

Haeckel (1872) re-described it as *Ascandra reticulum* while analysing other specimens from the Adriatic Sea collected by him and by Schmidt. The morphological description was more complete than that given by Schmidt. He also described triactines and tetractines with cylindrical actines and sharp tips, and the apical actine of the tetractines as much thinner than the others and as either shorter or longer (*C. ret* (H) in mini-table below). The diactines were described as more or less curved and fusiform. The micrometry is also similar to that which we found in the proposed neotype (triactines and tetractines: 90–120  $\mu\text{m}$ /7–8  $\mu\text{m}$ ; width of the apical actine: 3  $\mu\text{m}$ ; diactines: 160–300  $\mu\text{m}$ /12–16  $\mu\text{m}$ ).

Topsent (1936) re-described the species as *Leucosolenia reticulum*, and said that the specimens from the Adriatic (described by Haeckel, 1872 and von Lendenfeld, 1891) and from Portugal (described by Breitfuss,



**Figure 29.** *Clathrina reticulum*. A, photograph of the neotype ( $\times 10$ ). B, triactine and tetractine. C, diactine and triactine. D, apical actines of the tetractines projecting into a tube. E, diactines perpendicular to the surface. F, distribution of the diactines at the surface. G, trichoxea (arrow). Scale bar = 100  $\mu\text{m}$ .

1898), were different from the specimens he and Minchin had both found in the Mediterranean. According to Topsent, the diactines described by the previous authors were fusiform, spiral (sigmoid) or curved, and that both tips were similar (as described by Haeckel). After analysing specimens from the Mediterranean, first Minchin (1896) and later Topsent assumed that the diactines of *C. reticulum* were curved and possessed different tips, one of them being arrow-shaped (as we also found).

Kirk (1896), Hôzawa (1929) and Topsent (1936) all used the difference in the shape of the diactines to differentiate species from *reticulum*. Kirk (1896) described another new species, *L. laxa*, from the Pacific, in which one of the tips has a different thickness; Hôzawa described *L. sagamiana*. According to Topsent, the only difference between these species and *L. reticulum* is the size of the diactines, which are shorter in *L. reticulum*; Breitung (1935) had already placed them in synonymy. *C. reticulum* is also similar to *C. contorta* in the composition of the skeleton. The organization of the skeleton, however, is very different. First, in *C. reticulum* the triactines are more abundant than the tetractines. The diactines in *C. reticulum* are perpendicular to the external tubes, while in *C. contorta* they are parallel to these tubes. Moreover, the diactines in *C. reticulum* are arrow-shaped and patchily distributed, whereas in *C. contorta* they are randomly distributed and fusiform.

Among the specimens we analysed from the Mediterranean, we found great variety in the shape and size of the diactines. In a single specimen, the size can vary from 102 µm to 306 µm, and the shape can either be fusiform or have one arrow-shaped tip. This could mean that all the authors working on Mediterranean specimens were indeed observing the same species, but had described the various diactine shapes differently. The problem is that Schmidt gave a poor description and did not elect the holotype. Therefore, we need to accept the description given by Haeckel and by subsequent authors such as Minchin (1896) and Topsent (1936).

There was a problem in the alteration of the number of the syntype of *C. reticulum* of the Bowerbank collection, sent to him by Schmidt. The entry in the Register for specimen registration number BMNH 1955.11.2.27 reads: '*Leucosolenia reticulum* O.S. dry, from O. Schmidt. Bowerbank Coll. BK.345 (part), Now 67.3.11.87a'.

However, when we checked the specimen and the slide number BMNH 1967.3.11.87a, we found that they were different. Perhaps the slide is from a syntype. The specimen, however, is completely different from the slide. A mistake was probably

made when the number of the specimen was changed.

In the BMNH collections there is a specimen from Minchin's collection that corresponds to the currently accepted description for *C. reticulum*. This has the registration number BMNH 1896.9.15.13 and it is from the Mediterranean (Banyuls-sur-Mer, Pyrenees, France). We propose electing it as the neotype.

	<i>C. ret.</i> <i>C. ret.</i> (H)	<i>C. ret.</i> (this work)	<i>C. cont.</i>	<i>C. laxa</i>	<i>C. sagamiana</i>
<b>Triactines</b>					
L (µm)	90–120	73–100	68–103	110–170	118
W (µm)	7–8	8	10	10–16	10
<b>Tetractines</b>					
L	90–120	58–115	68–103	110–170	40–80
W	7–8	7	10	10–16	5
<b>Apical actine</b>					
L	90–120	45–120	33–155	130	33–68
W	3	5	5	8	4
<b>Diactines</b>					
L	160–300	102–306	173–816	250–320	275–347
W	12–16	14	32	16–20	13
<b>Large tetractines</b>					
L	–	–	–	–	98–143
W					10
<b>Diactines</b>					
shape	fus	arr	fus	fus	fus
distribution	perp	perp	parallel	perp	perp

Abbreviations. *C. ret.*, *C. reticulum*; H, Haeckel's description; *C. cont.*, *C. contorta*; fus, fusiform; arr, arrow-shaped; perp, perpendicular.

#### CLATHRINA SAGAMIANA (HÔZAWA, 1929)

*Original name:* *Leucosolenia sagamiana* Hôzawa, 1929

*Type locality:* Odawara, Sagami Sea, Japan.

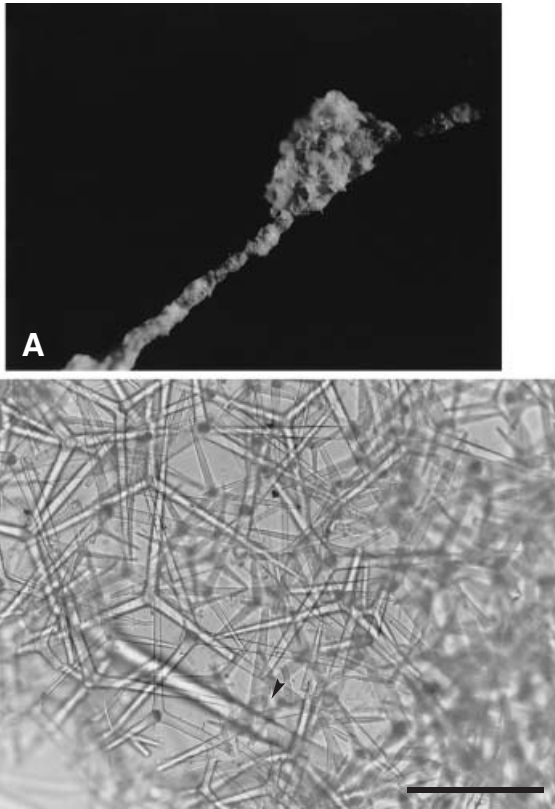
*Type:* Tokyo Sci. Fac. Spec. N°. 39. (holotype/alcohol). Front of Omeit water, Odawara, 120 Hine. Sagami Sea, Japan, 171 m depth. By hand with bamboo gear by Ijima (1 August 1895).

*Citations:* Tanita (1942, 1943); Burton (1963).

*Colour:* Preserved holotype is white.

*Description:* The holotype is completely fragmented, but some of the fragments are still attached to the *Alcyonaria* mentioned in the original description by Hôzawa. According to Hôzawa, the largest individual was provided with a terminal osculum. However, it is no longer possible to recognize the organization of the cormus (Fig. 30A).

The skeleton comprises two populations of equian-gular and equiradial tetractines (Fig. 30B), but there are also sagittal tetractines. Triactines are rare. Diactines are also present (Fig. 30B). Actines are conical,



**Figure 30.** *Clathrina sagamiana*. A, photograph of the holotype ( $\times 10$ ). B, skeleton comprising tetractines and diactines (arrow). Scale bar = 100  $\mu\text{m}$ .

straight and sharp. The apical actine of the tetractines is conical, smooth and has almost the same length as the facial actines. Diactines are fusiform and slightly curved. They are projected through the surface of the tubes.

	Length ( $\mu\text{m}$ )				Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$		
Tetractines	40.0	57.5	$\pm 11.8$	80.0	5.3	$\pm 1.0$	30	
Apical actine	32.5	52.5	$\pm 10.5$	67.5	4.0	$\pm 0.8$	06	
Large tetractines	97.5	116.3	$\pm 10.8$	142.5	10.0	$\pm 1.8$	30	
Apical actine		100			6		01	
Diactines	275.4	316.2	$\pm 23.5$	346.8	13.3	$\pm 3.1$	06	

**Remarks:** According to the original description, the holotype was attached to a branch of *Alcyonaria*, as we confirmed. The size of the spicules in the original description was:

	Length ( $\mu\text{m}$ )		Width ( $\mu\text{m}$ )	
	min	max	min	max
Triactines	80	140	6	8
Tetractines	80	150	6	12
Apical actine	120	380	4	8
Diactines	310	600	10	24

Although Hôzawa had not discriminated between the two populations of tetractines, he mentioned in his original description that the ‘dermal (tetractines) are usually slightly larger than the deep ones’.

*C. sagamiana* differs from *C. reticulum* in the size of its spicules (which are shorter in *C. reticulum*), in the shape of the diactines, which are not arrow-shaped in *C. sagamiana*, and in the shape of the actines of the triactines and tetractines, which is cylindrical in *C. reticulum* and conical in *C. sagamiana*, and also by the presence of a second population of tetractines in *C. sagamiana*.

The differences between *C. sagamiana* and *C. contorta* are mainly in the shape of the apical actine of the tetractines, which is conical in *C. sagamiana* and cylindrical in *C. contorta*, as well as in *C. reticulum*. In relation to *C. laxa*, the absence of the large tetractines, the diameter of the apical actine and of the tetractines, and the length of the actines of the tetractines are enough to differentiate it from *C. sagamiana*.

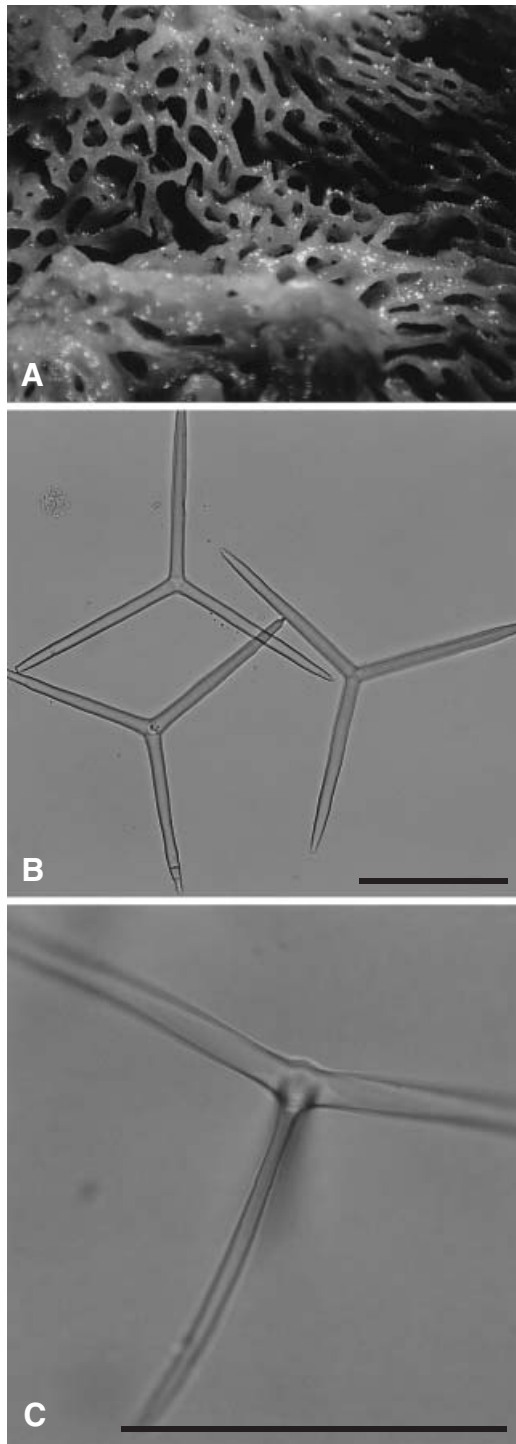
*CLATHRINA SEPTENTRIONALIS* RAPP, KLAUTAU & VALENTINE, 2001

*Type locality:* Langfjorden, Norway.

*Type:* BMNH 1910.1.1.790 (holotype/alcohol). Langfjorden, Norway. Stn. 76.5 fms. Canon A.M. Norman Collection; BMNH 1910.1.1.789 (paratype/alcohol). Langfjorden, Norway. 15–25 fms. Norman Collection.

*Colour:* Dark brown when preserved.

*Description:* Cormus of this massive sponge formed of thin, irregular and tightly anastomosed tubes. Water-collecting tubes converge at conical elevations with a terminal osculum (Fig. 31A). Cells with brown granules are scattered in the mesohyl. The skeleton has no special organization, comprising equiangular and equiradial triactines and tetractines (Fig. 31B). Actines are cylindrical, slightly undulated, with a blunt tip. The apical actine (Fig. 31C) of the tetractines is shorter than the facial ones, cylindrical, smooth, sharp and curved at the tip.



**Figure 31.** *Clathrina septentrionalis*. A, photograph of the holotype ( $\times 10$ ). B, triactines and a tetractine. C, apical actine of a tetractine. Scale bar = 100  $\mu\text{m}$ .

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	95.0	112.5	$\pm 10.3$	135.0	9.8	$\pm 1.0$	30
Tetractines	97.5	110.8	$\pm 10.0$	125.0	9.3	$\pm 0.8$	30
Apical actine	52.5	71.8	$\pm 10.8$	87.5	4.5	$\pm 0.5$	30

*Remarks:* In many characteristics, the morphology of *C. septentrionalis* matches that of *Leucosolenia nanseni* Breitfuss, 1896, a sponge from East Spitzbergen. The size of the actines of the triactines and tetractines of *L. nanseni*, for example, is 113–145  $\mu\text{m}/8$ –14  $\mu\text{m}$  according to Breitfuss (1896). The shape of the actines is cylindrical and the apical actine is sharp and a little curved. The colour is grey-brown to dark-grey, and the cormus is tightly anastomosed (Breitfuss, 1897).

However, Breitfuss also mentioned the appearance of spherical or pear-shaped cushions, the presence of a stalk varying in length, and the presence of one terminal osculum in the centre of the surface. Moreover, he mentioned a second category of spicule with a flat knob in the middle.

As we did not find the holotype or a paratype of this species, we could use only the written information given in Breitfuss' description and plates, which created difficulties in deciding if *C. septentrionalis* should be a synonym of *L. nanseni* or not. Nevertheless, based on the morphological differences we were able to recognize the difference between them, so we decided to distinguish *C. septentrionalis* from *L. nanseni*, although they are probably related species.

#### *CLATHRINA TENUIPILOSA* (DENDY, 1905)

*Original name:* *Leucosolenia tenuipilosa* Dendy, 1905

*Type locality:* Sri Lanka.

*Type:* BMNH 1907.2.1.102 (paratype/alcohol). Ceylon (Sri Lanka) (Stat. LXIV, 9 m, south-east of Modragam, March 17, 1902). Herdman Collection.

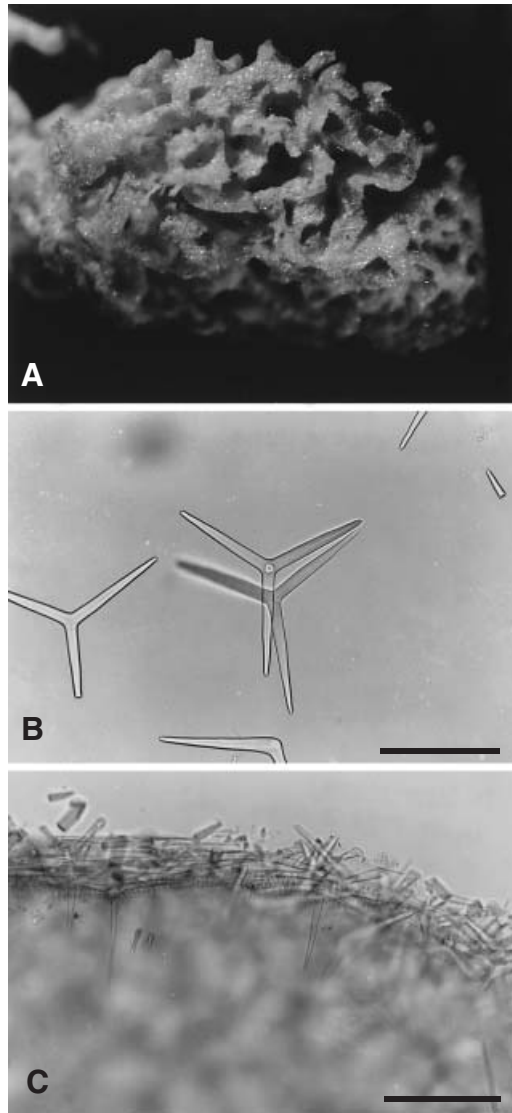
*Citations:* Row (1909); Dendy & Row (1913); Tanita (1942); Burton (1952, 1963).

*Colour:* Preserved specimen is light yellow.

*Description:* Cormus formed of large irregular and loosely anastomosed tubes of equal size (Fig. 32A). No large superficial water-collecting tubes are present. Many oscula open independently at the external surface. Special cells were not found.

The wall of the tubes is thick (approximately 48  $\mu\text{m}$ ), composed of an irregular meshwork of spicules, containing triactines, tetractines (Fig. 32B)





**Figure 32.** *Clathrina tenuipilosa*. A, photograph of the paratype ( $\times 40$ ). B, triactines and a tetractine. C, some apical actines of tetractines projecting into a tube. Scale bar = 100  $\mu\text{m}$ .

and trichoxeas. Triactines are the most abundant spicules, while tetractines are located surrounding the tubes and projecting their apical actines inside them (Fig. 32C). The apical actines do not cross the entire diameter of the tubes and the number of tetractines varies in each tube. Trichoxeas are distributed patchily on the surface of some tubes, where they are projected perpendicularly. They are present in the external as well as in the internal tubes.

Amongst equiangular and equiradiate triactines and tetractines, triactines are the most abundant spicules. Their size is uniform if we compare triactines

with tetractines, but triactines alone have variable sizes as a consequence of the presence of very small, young, triactines. Actines are a little undulated in their distal part, where there is sometimes also a slight constriction. They are conical or cylindrical, but conical spicules are more abundant, with a blunt tip. The apical actine of the tetractines has a variable length and its diameter at the base is almost the same as the facial actines. It is smooth and frequently straight, while the longest apical actines are curved in their distal part.

Trichoxeas are not very abundant and their quantity varies in each tube. They are very thin, long, smooth and straight.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	50.0	84.6	$\pm 14.7$	102.5	11.0	$\pm 1.5$	30
Tetractines	50.0	88.1	$\pm 13.8$	107.5	11.5	$\pm 1.2$	30
Apical actine	50.0	92.0	$\pm 24.5$	137.5	7	$\pm 1.0$	10
Trichoxeas		> 250.0			< 0.3		

*Remarks:* *C. tenuipilosa* was described by Dendy in 1905 from Ceylon (now Sri Lanka), and was considered by Thacker (1908) to be a synonym of *C. canariensis*. Thacker suggested that the presence of trichoxeas was a very variable characteristic, and therefore not a good one for systematics. One year later, Row (1909) rejected this synonym saying that 'the presence of oxea of such unusual and constant form, being very long and extremely slender, should undoubtedly separate it specifically from forms where oxea are entirely absent, even though the number and frequency of the oxea may show very considerable variation as they do in Thacker's specimens'.

Our opinion agrees with Row's in relation to the validity of this species. However, *C. tenuipilosa* should not be distinguished from other clathrinids only by the presence of trichoxeas. We analysed specimens with triactines, tetractines and trichoxeas from other localities, and also from the type locality, Ceylon, which showed important differences in the organization of the cormus and in the shape of the spicules. We consider that the presence of trichoxeas is not sufficient to identify this species. *C. tenuipilosa* should be distinguished from other species by characteristics such as the presence of trichoxeas, the shape of triactines and tetractines, and the organization of the cormus.

*C. tenuipilosa* has conical and cylindrical actines, with sharp tips. They are slightly undulated in the dis-

tal part and have a constriction near the tip. Triactines are present in two different sizes, one of them very small. The apical actine of the tetractines is smooth. The cormus has several oscula, and no water-collecting tubes.

The distribution of this species, as with other clathrininas, seems to be restricted to the Indian Ocean. Furthermore, we have analysed some specimens from Sri Lanka, which although similar to *C. tenuipilosa* in relation to their kinds of spicules, differ in the organization of their cormus and the shape of their spicules. These specimens are probably a distinct species, new to science.

The specimen deposited at BMNH, considered to be the holotype of this species by Burton (1963) is, in fact, a paratype. In Dendy's (1905) description, he elected specimen R.N. 158 as the holotype. He also identified two other specimens (R.N. 380 and 381) from Sri Lanka (Cheval Paar) as *C. tenuipilosa*; these were deposited together in BMNH under the registration number BMNH 1907.2.1.102, and should be considered to be paratypes. However, they differ from the original description of the holotype with respect to their colour when preserved, which is light yellow and not pale grey as Dendy described. There are also no water-collecting tubes, as suggested by Dendy when he wrote 'the tubes converge to unite in small, prominent, true vents'.

*CLATHRINA TETRACTINA* KLAUTAU &  
BOROJEVIC, 2001

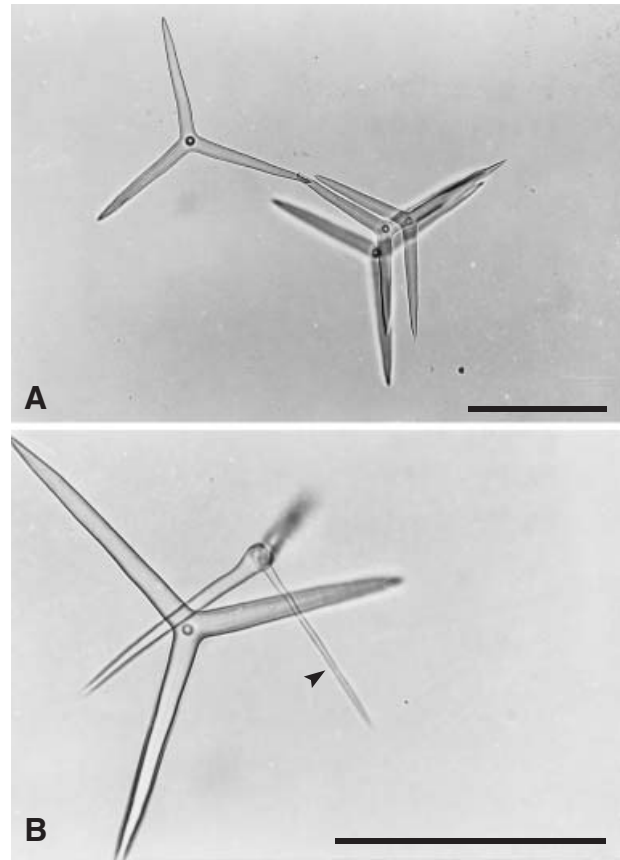
*Type locality:* Arraial do Cabo, Rio de Janeiro, Brazil.

*Type:* BMNH 1999.9.16.33 (holotype/alcohol). Arraial do Cabo (Pedra Vermelha), Rio de Janeiro, Brazil. Collected by G. Muricy (14 June 1987).

*Colour:* Cormus is white in life and when preserved.

*Description:* Cormus formed of large, irregular and loosely anastomosed tubes. Large superficial tubes collect the ex-current water, and then converge on a few apical oscula.

The wall of the tubes varies from 25 µm to 50 µm in thickness. The skeleton has no special organization, comprising mainly tetractines (Fig. 33A), although a few triactines can also be found. Spicules are equiradial and equiangular. Actines are conical, with sharp tips, and at the distal part they are slightly undulated. The apical actine (Fig. 33B) of the tetractines is very thin even at the base, and resembles the apical actine of the tetractines of *C. contorta* Minchin, 1905. It is straight, cylindrical, sharp, long and smooth and is projected into the tubes. Only one specimen of this species was found. Its habitat was sciaphilous.



**Figure 33.** *Clathrina tetractina*. A, tetractines. B, apical actine of a tetractine (arrow). Scale bar = 100 µm.

	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	n
Triactines	50.0	85.0	± 13.3	120.0	8.8	± 1.5	30
Tetractines	62.5	88.0	± 10.3	107.5	9.5	± 1.0	30
Apical actine	32.5	71.0	± 18.3	105.0	3.8	± 0.8	30

*Remarks:* Although there is a similarity to the tetractines of *C. contorta*, *C. tetractina* has no triactines or diactines. Moreover, *C. contorta* is a species from the Mediterranean Sea.

*CLATHRINA WISTARIENSIS* WÖRHEIDE & HOOPER,  
1999

*Type locality:* Great Barrier Reef.

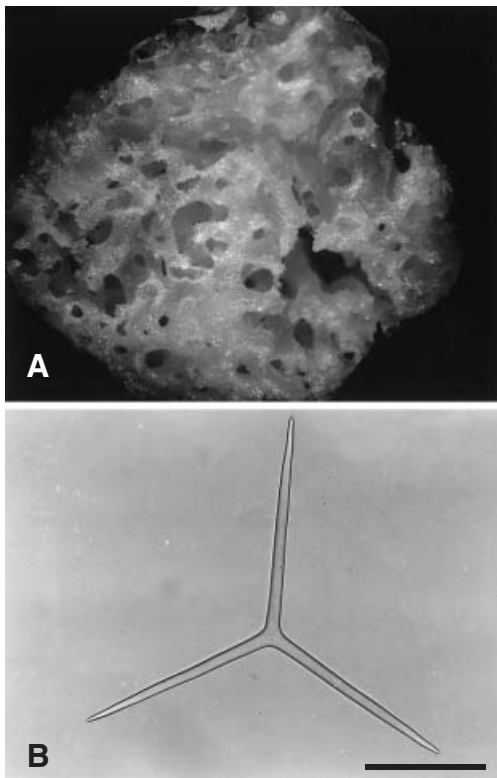
*Type:* QMG 313663 (holotype/alcohol). South side of Wistari Reef, 23°29.4'S, 151°52.8'E, 18 m depth. Collected by G. Wörheide (7 July 1998).

**Colour:** The colour of the holotype alive was white (Wörheide & Hooper, 1999), but it became light yellow when preserved.

**Description:** This sponge is delicate and the holotype is fragmented. It is difficult to recognize the organization of the cormus in this specimen now, but by observing the photograph of the holotype, it was possible to confirm that it comprises large, irregular and loosely anastomosed tubes. No water-collecting tubes were observed (Fig. 34A). The skeleton has no special organization, comprising equiangular and equiradiate triactines (Fig. 34B). Actines are cylindrical, with blunt tips. Young triactines can also be found and their actines are more conical. The mesohyl is full of porocytes with brown granules.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	132.5	167.3	$\pm 22.8$	220.0	12.5	$\pm 1.8$	20

In the original description, the micrometry of the spicules is:



**Figure 34.** *Clathrina wistariensis*. A, photograph of the holotype ( $\times 40$ ). B, triactine. Scale bar = 100  $\mu\text{m}$ .

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	150	175.16	$\pm 16.48$	230	13.7	$\pm 2.83$	30

#### *CLATHRINA SUEZIANA* SP. NOV.

**Original name:** *Clathrina canariensis* var. *compacta* Row, 1909

**Etymology:** From the type locality.

**Type locality:** Suez, Red Sea.

**Type:** BMNH 1912.2.1.3 (holotype/alcohol). Suez, Red Sea. C. Crossland Collection.

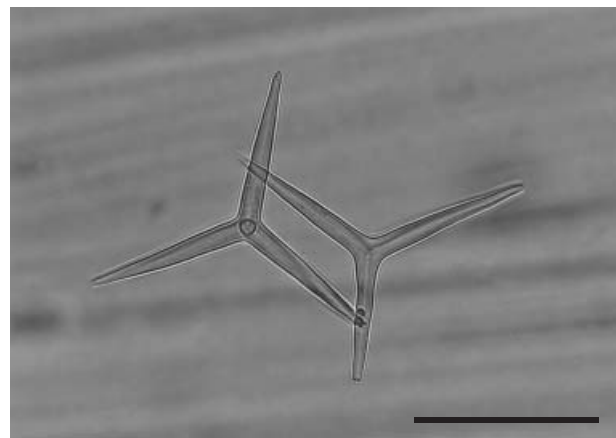
**Citation:** Burton (1963).

BMNH 1912.2.1.3 is the holotype of *C. canariensis* var. *compacta*.

**Colour:** The cormus of the holotype of *C. canariensis* var. *compacta*, now *C. sueziana* sp. nov., is white when preserved.

**Description:** Cormus of the holotype formed of thin, irregular and loosely anastomosed tubes. A large tube functioning as an osculum is physically connected to thinner water-connecting tubes, receiving the excurrent water from them.

The skeleton has no special organization, comprising equiangular and equiradiate triactines and tetractines (Fig. 35A) in roughly the same proportions. They are similar in size. Their actines are cylindrical or conical, with a blunt tip. Some of them are larger in the middle. The apical actine of the tetractines has almost the same diameter at the base as



**Figure 35.** *Clathrina sueziana* sp. nov. Triactine and tetractine. Scale bar = 100  $\mu\text{m}$ .

the facial actines. It is conical, shorter, straight, smooth and sharp. Trichoxeas are also present but there are very few.

	Length ( $\mu\text{m}$ )				Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	$n$	
Triactines	75.0	91.3	$\pm 10.9$	137.5	10.3	$\pm 1.5$	30	
Tetractines	70.0	86.0	$\pm 6.1$	97.5	9.4	$\pm 1.4$	30	
Apical actine	50.0	56.3	$\pm 4.5$	62.5	5.0	0	04	
Trichoxeas	> 250			< 0.3				

*Remarks:* Row (1909) said that this specimen was identical to *C. compacta* as described by Schuffner from the Mauritius Islands, and that he could not separate it from *C. canariensis* (Miklucho-Maclay, 1868) either. Furthermore, he said that Thacker (1908) had described many intermediate forms of *C. canariensis* from the Cape Verde Islands. Consequently, if *C. canariensis* was so plastic morphologically, var. *compacta* could be one of its forms rather than a distinct biological species.

Row (1909) therefore decided to designate this specimen from the Red Sea as a variety of *C. canariensis*, because it differed greatly from the *C. canariensis* described by Haeckel (1872) (Miklucho-Maclay's description was not complete). However, one important problem is that Row did not describe *C. canariensis* var. *compacta*. Fortunately, we were able to analyse the type specimen of this variety and compare it with that of *C. canariensis*. Although we did not have the holotype of *C. compacta*, we were able to compare this species with var. *compacta* through the literature; var. *compacta* differs from *C. canariensis* and *C. compacta* in its spicules and the organization of the cormus.

When we examined Schuffner's drawing of the cormus of *C. compacta*, we observed that this species has no water-collecting tubes, while *C. canariensis* and var. *compacta* do. The spicules of *C. compacta* (120/12  $\mu\text{m}$  according to Schuffner) are larger than those of var. *compacta*. Moreover, Schuffner only described conical actines, while var. *compacta* also has cylindrical ones. Nor did he mention the presence of spicules with actines wider at the middle, as we found in var. *compacta*.

In relation to *C. canariensis*, var. *compacta* has a similar cormus organization, with water-collecting tubes, but its spicules vary enormously. In *C. canariensis*, only cylindrical actines are present, all with blunt tips. The size of the spicules only differs slightly, *C. canariensis* having shorter spicules:

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	$n$
Triactines	67.5	77.8	$\pm 4.6$	87.5	5.0	0	30
Tetractines	62.5	74.3	$\pm 5.8$	87.5	5.0	0	30
Apical actine	35.0	43.8	$\pm 5.6$	55.0	5.0	0	15

Another species we consider to be close to *C. sueziana* sp. nov. is *C. tenuipilosa*, which has triactines and tetractines which are similar in shape and size. It also has trichoxeas, although in much more abundance than in *C. sueziana*. It does not, however, have water-collecting tubes. Moreover, the apical actine of the tetractines of *C. sueziana* is thinner at the base than we observe in *C. tenuipilosa*.

Considering all the morphological differences and the apparently low capacity of dispersion of clathrinins (Solé-Cava *et al.*, 1991; Klautau *et al.*, 1994), we decided to distinguish var. *compacta* from *C. canariensis*, *C. compacta* and *C. tenuipilosa*, and consider it as a valid distinct species.

#### CLATHRINA HISPANICA SP. NOV.

*Etymology:* From the type locality.

*Type locality:* Spain (Mediterranean coast).

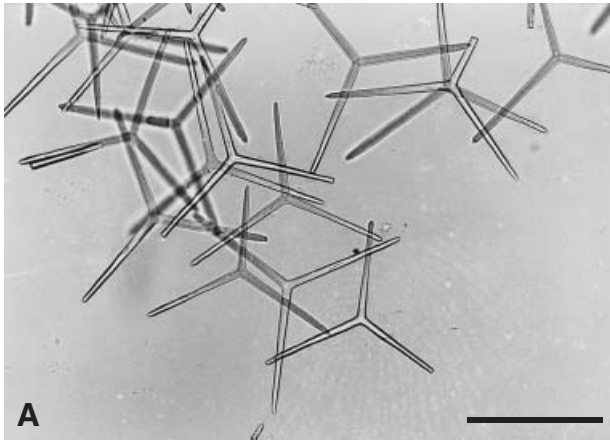
*Type:* BMNH 1999.9.16.20 (holotype/alcohol). Spain 9. Collected by N. Boury-Esnault (1997).

*Colour:* Holotype when preserved is white.

*Description:* Cormus of the holotype formed of large, irregular and loosely anastomosed tubes. Water-collecting tubes were not found. Cells with granules were also not found. The skeleton has no special organization, comprising equiangular and occasionally equiradial triactines (Fig. 36A). Actines are cylindrical, but they are slightly wider near the centre of the spicule. They are undulated at the distal part and their tip is blunt.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	$n$
Triactines	72.0	81.6	$\pm 6.2$	96.0	5.5	$\pm 0.7$	20

*Remarks:* *C. hispanica* sp. nov. is a common species in the Mediterranean Sea. At first sight its spicules can be mistaken for those of *C. clathrus*. However, *C. clathrus* has actines which are slightly thicker and their tips are strongly rounded, and not blunt as in



**Figure 36.** *Clathrina hispanica* sp. nov. Triactines. Scale bar = 100  $\mu$ m.

*C. hispanica*. Moreover, the colour of the cormus of *C. hispanica* is white and not the characteristic yellow of *C. clathrus*.

We did not include *C. rubra* Sarà, 1953 in our list of species, as we had only received a slide of spicules that were not well preserved. We took some measurements of these spicules so that we could compare them with those from *C. hispanica*. Despite some similarity in relation to the cylindrical shape of the actines, their thickness is different, being thinner in *C. hispanica* (*C. rubra* triactines: 71  $\mu$ m ( $\pm$ 9)/9  $\mu$ m ( $\pm$ 1)). *C. hispanica* could also be considered similar to *C. canariensis*, although the latter differs in having tetractines.

#### *CLATHRINA SINUSARABICA* SP. NOV.

*Original identification:* *Clathrina coriacea* (Montagu, 1818)

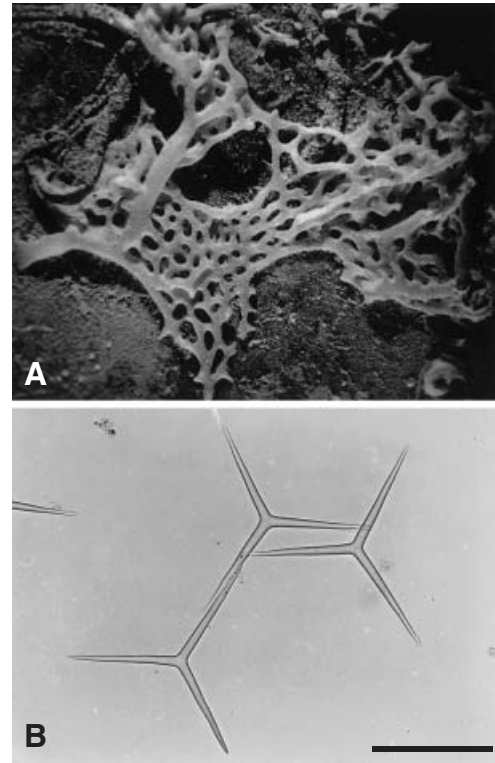
*Etymology:* From the type locality.

*Type locality:* Agig Harbour, Egypt, Red Sea.

*Type:* BMNH 1912.2.1.1 (holotype/alc. alcohol). Agig Harbour, Red Sea. C. Crossland Collection (8.1 m).

*Colour:* Holotype when preserved is beige.

*Description:* Cormus not massive, spread on a flat rock, formed of tubes of variable sizes, which are irregular and loosely anastomosed (Fig. 37A). There is one large, pre-eminent tube that forms the osculum. Cells with granules were not observed. The skeleton has no special organization, comprising equiangular and equiradiate triactines (Fig. 37B). Actines are conical, becoming very thin at the distal part. They are also undulated near the tip and very sharp.



**Figure 37.** *Clathrina sinusarabica* sp. nov. A, photograph of the holotype ( $\times$ 4). B, triactines. Scale bar = 100  $\mu$ m.

	Length ( $\mu$ m)				Width ( $\mu$ m)		
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	72.0	91.9	$\pm$ 9.1	103.2	8.4	$\pm$ 1.0	20

*Remarks:* *C. sinusarabica* sp. nov. is similar to many other clathrinas with triactines with regard to external features, such as the anastomosis of the cormus and the absence of water-collecting tubes. However, it can be distinguished by the shape and size of its spicules: it can be differentiated from *C. aurea*, *C. cribrata*, *C. cylindractina*, *C. heronensis*, *C. wistariensis* and *C. hispanica* sp. nov. by the conical shape of its actines. *C. conifera*, *C. helveola* and *C. hondurensis* sp. nov. have conical actines similar to those of *C. sinusarabica*. However, *C. conifera* has blunt tips, while *C. sinusarabica* has strong, sharp tips. *C. helveola* and *C. hondurensis* can be distinguished from *C. sinusarabica* by the size of the triactines, which are shorter and thinner in the latter.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )		
	min	mean	$\sigma$	max	mean	$\sigma$
<i>C. helveola</i>	64.8	154.1	$\pm 25.0$	182.4	13.2	$\pm 1.7$
<i>C. hondurensis</i>	105.6	133.4	$\pm 17.0$	156.0	15.6	$\pm 1.7$
<i>C. sinusarabica</i>	72.0	91.9	$\pm 9.1$	103.2	8.4	$\pm 1.0$

**CLATHRINA HONDURENSIS SP. NOV.**

*Original identification:* *Leucosolenia coriacea* (Montagu, 1818)

*Etymology:* From the type locality.

*Type locality:* Turneffe, British Honduras.

*Type:* BMNH 1938.3.28.4 (holotype/alcohol). Turneffe, British Honduras. Collected by J.H. Borley (20–22 March 1935).

*Colour:* Holotype when preserved is beige.

*Description:* Cormus formed of large, irregular and loosely anastomosed tubes. The diameter of the tubes is very variable, and the appearance of the cormus is reticulated (Fig. 38A). Its surface is very smooth and there are no water-collecting tubes. Cells with granules were not observed. The skeleton has no special organization, comprising large, equiangular and equiradiate triactines (Fig. 38B). Actines are conical, straight with sharp tips.

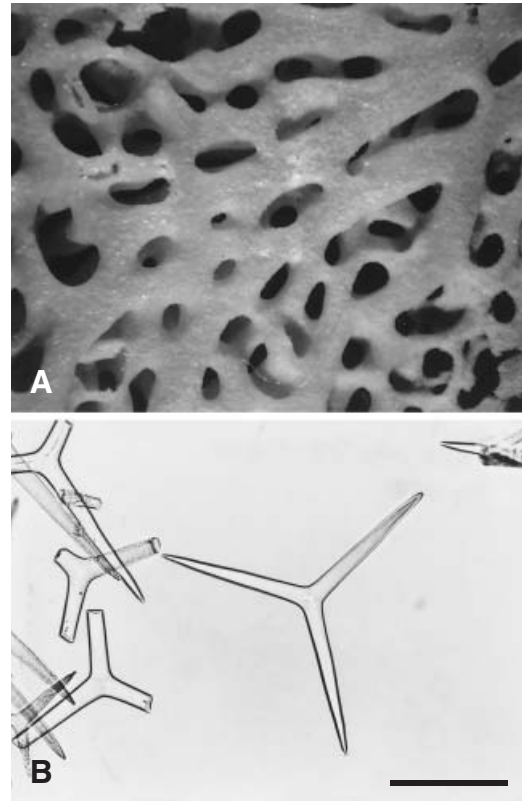
	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	105.6	133.4	$\pm 17.0$	156.0	15.6	$\pm 1.7$	20

*Remarks:* *C. hondurensis* sp. nov. is another clathrina with irregular and loosely anastomosed tubes and without water-collecting tubes. It can be differentiated from the other clathrinas by the shape of its actines, which are conical and sharp, and by their size. In this sense, the only species that could be mistaken for *C. hondurensis* is *C. helveola*. However, the actines of *C. helveola* are larger and thinner (154.1/13.2  $\mu\text{m}$ ) than those of *C. hondurensis* (133.4/15.6  $\mu\text{m}$ ).

**CLATHRINA CLARA SP. NOV.**

*Original identification:* *Clathrina coriacea* (Montagu, 1818)

*Etymology:* Latin *clarus* (= bright). Describing the bright surface.



**Figure 38.** *Clathrina hondurensis* sp. nov. A, photograph of the holotype ( $\times 10$ ). B, triactine. Scale bar = 100  $\mu\text{m}$ .

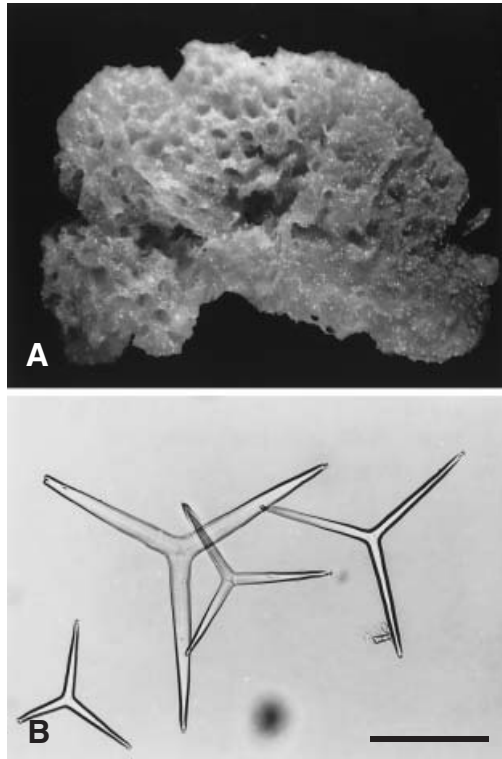
*Type locality:* Christmas Islands, Indian Ocean.

*Type:* BMNH 1927.2.14.152 (holotype/alcohol). Reef at low tide. Christmas Islands. R. Kirkpatrick Collection.

*Colour:* Holotype when preserved is light brown.

*Description:* Cormus massive, formed of thin, irregular and tightly anastomosed tubes and its surface is bright (Fig. 39A). Water-collecting tubes converge to the oscula. Cells with granules were not observed. The skeleton comprises two populations of equiangular and equiradiate triactines (Fig. 39B). Actines are conical and straight, with a sharp tip. The largest triactines are located only in the external tubes, delimiting the cormus, while the smaller triactines are found inside the cormus.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			<i>n</i>
	min	mean	$\sigma$	max	mean	$\sigma$	
Triactines	67.5	84.5	$\pm 8.8$	102.5	9.8	$\pm 0.8$	30
Large triactines	102.5	164.5	$\pm 34.3$	245.0	21.8	$\pm 3.5$	30



**Figure 39.** *Clathrina clara* sp. nov. A, photograph of the holotype ( $\times 10$ ). B, the two categories of triactines. Scale bar = 100  $\mu\text{m}$ .

*Remarks:* As *C. clara* has two populations of triactines of different sizes, it can be mistaken for *C. primordialis*. However, it is easy to differentiate the two species by the anastomosis of the tubes (tight in *C. clara* and loose in *C. primordialis*), and by the size of the spicules. The two populations of triactines of *C. primordialis* differ mainly in their thickness (91.9/9.6; 86.6/11.3  $\mu\text{m}$ ), while in *C. clara* the difference is also in the length (84.5/9.8; 164.5/21.8  $\mu\text{m}$ ). The large size of the triactines that remain on the surface of the tubes in *C. clara* is enough to differentiate it from the other clathrinas.

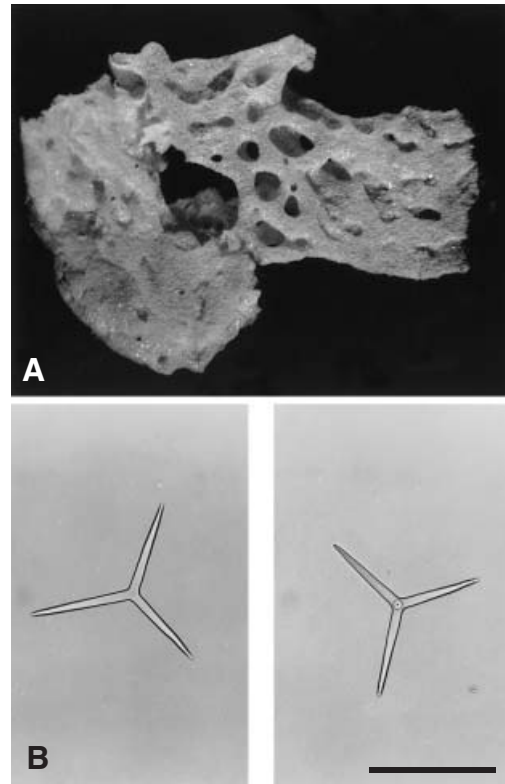
#### *CLATHRINA AFRICANA* SP. NOV.

*Original identification:* *Leucosolenia coriacea* (Montagu, 1818)

*Etymology:* From the type locality.

*Type locality:* St. James, Cape Town, South Africa.

*Type:* BMNH 1935.10.21.48 (holotype/alcohol). St. James, Cape Town, South Africa. Professor T.



**Figure 40.** *Clathrina africana* sp. nov. A, photograph of the holotype ( $\times 10$ ). B, triactine and tetractine. Scale bar = 100  $\mu\text{m}$ .

A. Stephenson Collection (11 February 1933) (Collection number F.184).

*Colour:* Holotype when preserved is white.

*Description:* Cormus formed of thin, irregular and loosely anastomosed tubes (Fig. 40A). No water-collecting tubes were observed. Cells with granules were also not observed. The skeleton has no special organization, comprising equiangular and equiradiate triactines and tetractines (Fig. 40B). Actines are conical, slightly undulated at the distal part, and with a sharp tip. The apical actine of the tetractines is shorter, smooth, conical, straight and sharp, and it is always projected into the tubes.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	60.0	77.3	$\pm 7.5$	90.0	8.5	$\pm 1.3$	30
Tetractines	7.58	75.8	$\pm 6.5$	90.0	8.3	$\pm 1.0$	30
Apical actine	35.0	51.0	$\pm 7.8$	62.5	6.5	$\pm 1.0$	14

*Remarks:* There are six clathrinins where the skeleton comprises a single population of triactines and tetractines: *C. adusta*, *C. canariensis*, *C. quadriradiata*, *C. septentrionalis*, *C. tetractina* and *C. africana* sp. nov. *C. africana* can be easily differentiated from *C. quadriradiata* and *C. tetractina* because the last two have tetractines as the main spicule type. To differentiate *C. africana* from the other three species, one can use the organization of the osculum and the anastomosis of the tubes. While *C. africana* has loosely anastomosed tubes and no water-collecting tubes, *C. adusta*, *C. canariensis* and *C. septentrionalis* have tightly anastomosed tubes and water-collecting tubes. Moreover, only *C. adusta* has conical actines, and these can be differentiated from those of *C. africana* by the size of their spicules and the shape of the apical actine of the tetractines (cylindrical in *C. adusta* and conical in *C. africana*).

	Triactines	Tetractines	Apical actine
<i>C. adusta</i>			
L (µm)	109.9	110.9	60.7
W (µm)	12.7	12.0	
<i>C. hondurensis</i> sp. nov.			
L	77.3	75.8	51.0
W	8.5	8.3	6.5

#### CLATHRINA HIRSUTA SP. NOV.

*Original identification:* *Leucosolenia cerebrum* (Haecckel, 1872)

*Etymology:* Latin *hirsutus* (= full of bristles). Describing the hispid surface.

*Type locality:* Stil Bay, Cape Town, South Africa.

*Type:* BMNH 1932.7.25.8 (holotype/alcohol). Stil Bay, Cape Town, South Africa. Professor T.A. Stephenson Collection (25 January 1932) (Collection number 183).

The holotype of *C. hirsuta* sp. nov. is a little fragmented and mixed with sediment.

*Colour:* Its colour when preserved is light yellow.

*Description:* The largest fragment is 1.0 × 0.8 × 0.4 cm. Cormus formed of large, irregular and loosely anastomosed tubes (Fig. 41A). Water-collecting tubes converge to form conical projections with an osculum. The surface of the tubes is hispid because of

the presence of diactines and trichoxea. Cells with granules were not observed. The skeleton comprises equiangular and equiradiate triactines (Fig. 41B) and very few tetractines. Actines are conical and straight, with a sharp tip. Diactines are fusiform and slightly curved (Fig. 41C). They are projected towards the exterior of the tubes. Trichoxeas are also present, perpendicular to the surface of the tubes.

	Length (µm)			Width (µm)			
	min	mean	σ	max	mean	σ	n
Triactines	107.5	122.5	± 8.0	135.0	13.3	± 0.8	20
Tetractines	100.0	122.3	± 12.8	155.0	12.5	± 1.3	20
Apical actine	57.6	80.9	± 17.8	100.8	6.5	± 1.2	03
Diactines	234.6	302.9	± 49.0	408.0	14.3	± 1.5	20

*Remarks:* Species with a single population of triactines, tetractines and diactines resembling that of *C. hirsuta* sp. nov. are *C. contorta*, *C. dubia*, *C. panis* and *C. reticulum*. *C. contorta* is easily distinguished from *C. hirsuta* by the presence of tetractines as the main spicule type, and also by the parallel disposition of the diactines in the tubes. *C. reticulum* and *C. dubia* have club or arrow-shaped diactines, while *C. hirsuta* and *C. panis* have fusiform diactines. *C. hirsuta* can be differentiated from *C. panis* by the presence trichoxeas, while spicules are larger in *C. panis*.

	Triactines	Tetractines	Apical actine	Diactines
<i>C. panis</i>				
L/W (µm)	162.0/15.5	159.8/14.5	156.8/9.5	474.3/29.6
<i>C. hirsuta</i> sp. nov.				
L/W (µm)	122.5/13.3	122.3/12.5	80.9/6.5	302.9/14.3

#### CLATHRINA ROTUNDA SP. NOV.

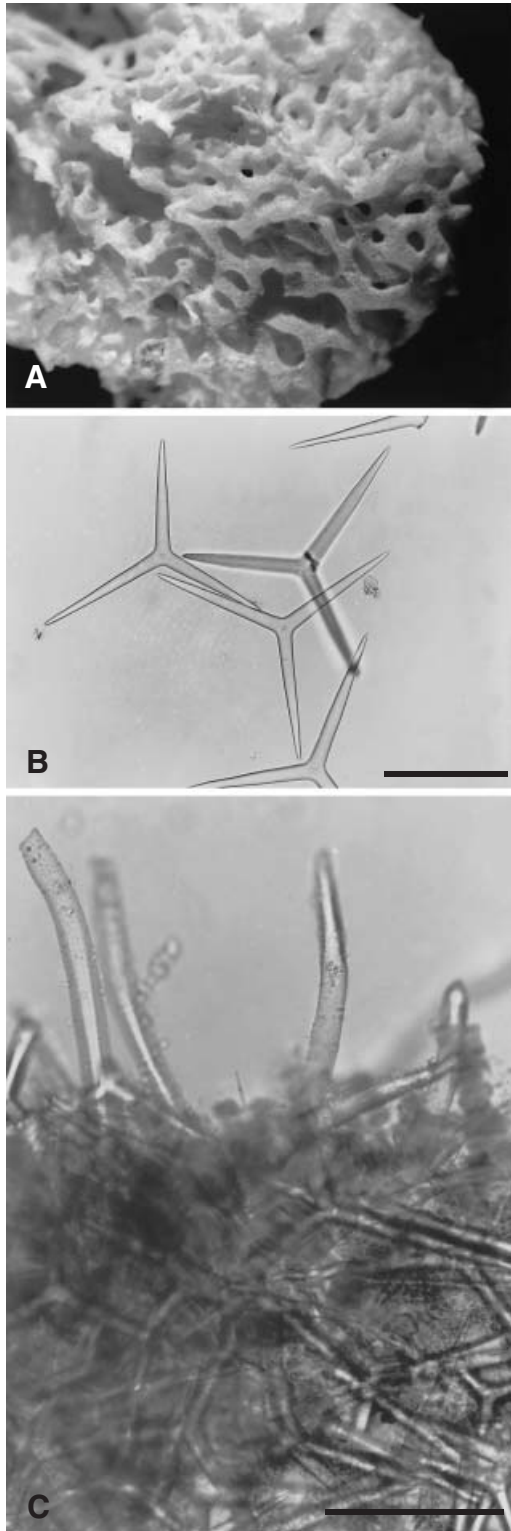
*Original identification:* *Leucosolenia canariensis* Miklucho-Maclay, 1868

*Etymology:* Latin *rotundus* (= spherical). Describing the shape of the cormus.

*Type locality:* St. James, Cape Town, South Africa.

*Type:* BMNH 1935.10.21.50 (holotype/alcohol) St. James, Cape Town, South Africa. Professor T. A.





**Figure 41.** *Clathrina hirsuta* sp. nov. A, photograph of the holotype ( $\times 10$ ). B, triactines. C, diactines at the surface. Scale bar = 100  $\mu\text{m}$ .

Stephenson Collection (5 September 1933) (Collection number F.232).

*Colour:* Light brown when preserved.

*Description:* Cormus spherical, formed of very thin tubes, irregular and tightly anastomosed. Many oscula can be seen, surrounded by a membrane, and only found in the apical region (Fig. 42A). Leading to these oscula, there are water-collecting tubes. Near the base, tubes are regularly anastomosed, and there are no oscula. The skeleton comprises triactines and tripods (Fig. 42B). The tripods are found in the external tubes, arranged side by side, forming a continuous layer, which delimits the cormus (Fig. 42C). Internally, there are only equiangular and equiradiate triactines. Their actines are conical, slightly undulated, with sharp tips.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	45.6	52.6	$\pm 3.6$	57.6	5.8	$\pm 0.7$	20
Tripods	45.6	59.0	$\pm 9.8$	79.2	9.6	$\pm 2.4$	20

*Remarks:* *C. rotunda* sp. nov. cannot be mistaken for any other of the described clathrinids because it is the only species in which the skeleton comprises triactines and tripods. Other species with tripods always have tetractines as well, such as *C. aspina*, *C. brasiliensis*, *C. cerebrum* and *C. tetrapodifera* sp. nov.

#### *CLATHRINA TETRAPODIFERA* SP. NOV.

*Original identification:* *Leucosolenia cerebrum* (Haeckel, 1872)

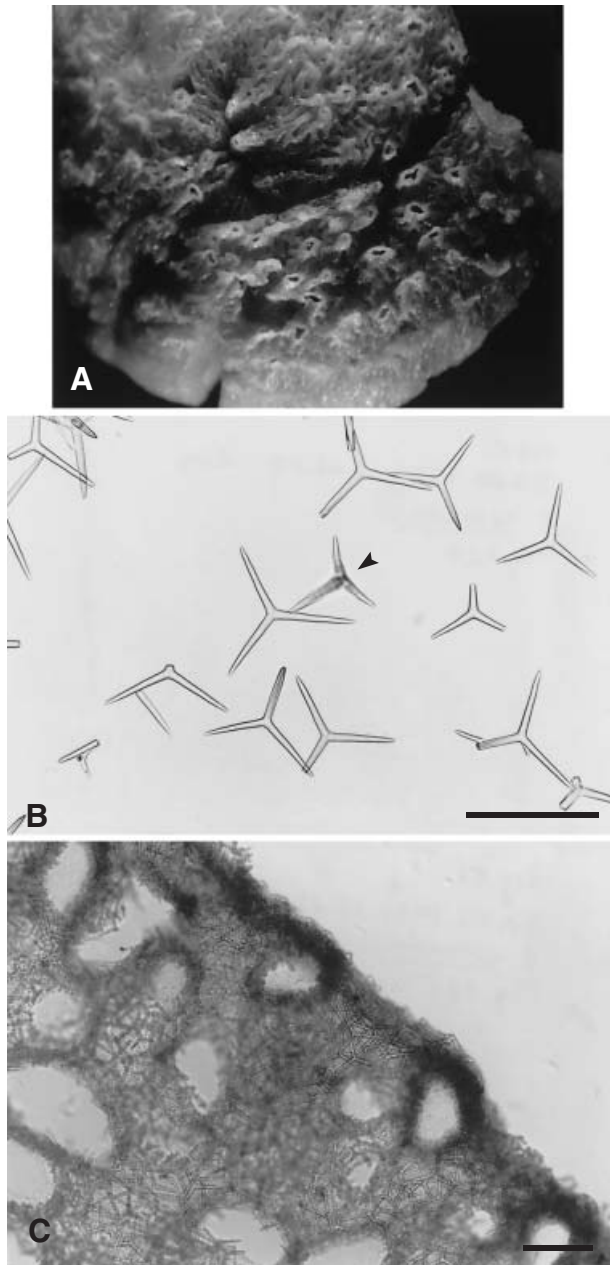
*Etymology:* Derived from the presence of tetrapods.

*Type locality:* New Zealand.

*Type:* BMNH 1938.8.24.53. (Holotype/dry) New Zealand. Miss L. B. Moore Collection (N.Z. 17).

*Colour:* Dried, fragmented holotype is white.

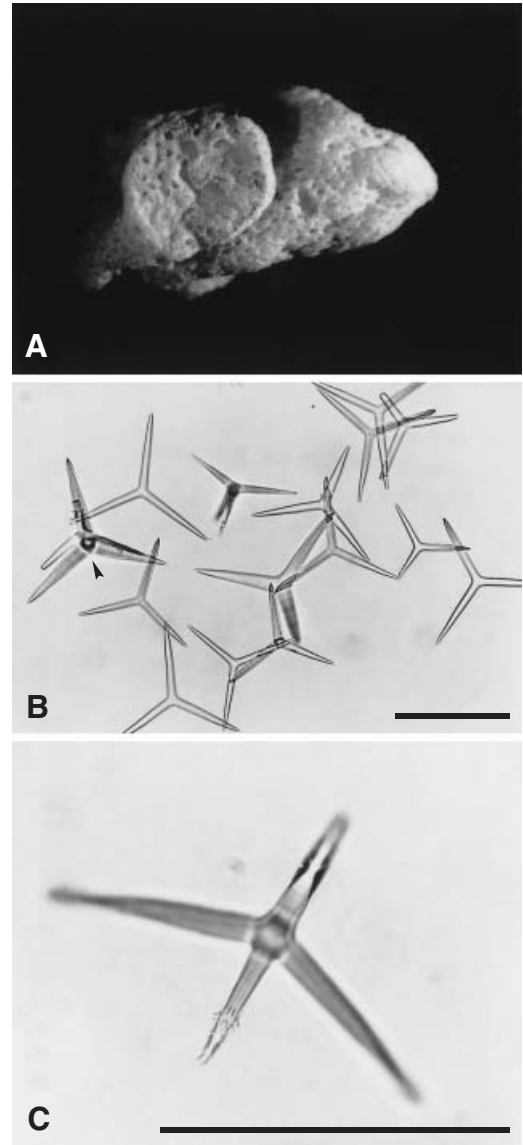
*Description:* The largest fragment (1.0  $\times$  0.6  $\times$  0.9 cm) is attached to algae. The cormus is formed of thin, regular and tightly anastomosed tubes (Fig. 43A). It is



**Figure 42.** *Clathrina rotunda* sp. nov. A, photograph of the holotype ( $\times 4$ ). B, triactines and a tripod (arrow). C, tripods side by side at the surface. Scale bar = 100  $\mu\text{m}$ .

attached to the substrate by a few tubes, which are not true stalks. There are no water-collecting tubes, but vents on the surface. We could not search for cells with granules because of the state of preservation of the specimen.

The skeleton comprises equiangular and equiradiate triactines and tetractines on the tubes' interior, and tripods and tetrapods on the exterior (Fig. 43B), delimiting the cormus. The actines of the triactines



**Figure 43.** *Clathrina tetrapodifera* sp. nov. A, photograph of the holotype ( $\times 4$ ). B, triactines, tetractines, tripods and tetrapods (arrow). C, apical actine of a tetractine covered with spines. Scale bar = 100  $\mu\text{m}$ .

and tetractines are conical, with sharp tips. The apical actine (Fig. 43C) of the tetractines is shorter than the facial ones, conical, sharp and straight. The spines are located at the tip. Tripods and tetrapods are very abundant. The tripods are true tripods. Tetrapods are similar to tripods in that they also possess stout actines and a raised centre. However, they have developed a fourth, apical, actine, which is shorter than the facial ones; it is conical and differs from the apical actine of the tetractines in that it is smooth.

	Length ( $\mu\text{m}$ )			Width ( $\mu\text{m}$ )			
	min	mean	$\sigma$	max	mean	$\sigma$	<i>n</i>
Triactines	50.0	63.3	$\pm 6.0$	75.0	7.3	$\pm 0.5$	20
Tetractines	55.0	64.5	$\pm 5.3$	80.0	8.0	$\pm 0.8$	20
Apical actine	14.4	37.0	$\pm 8.2$	48.0	5.5	$\pm 1.0$	16
Tripods	63.0	79.0	$\pm 8.0$	100.0	14.0	$\pm 3.0$	30
Tetrapods	65.0	77.0	$\pm 7.8$	95.0	14.8	$\pm 2.5$	16
Apical actine		36.0			9.6		01

*Remarks:* The most important characteristic of this species is the presence of the tetrapods. *C. tetrapodifera* sp. nov. is the only clathrina described with this type of spicule, which means that it can be easily separated from all other known species using this morphological character alone.

## DISCUSSION

One of the largest problems in the systematics of any group of organisms is establishing which morphological differences are related to actual genetic variability (Aron & Solé-Cava, 1991; Greenberg *et al.*, 1996; Knowlton *et al.*, 1997; Monteiro *et al.*, 1997) and which are the result of environmental pressures (Sarà, 1953; Burton, 1963). Consequently, it is fundamental to analyse them very carefully, in order to understand how each morphological character varies. Only then is it likely that the appropriate ones are used. Our group has been studying *Clathrina* systematics for several years using different approaches. Drawing on our previous morphological and molecular studies (Solé-Cava *et al.*, 1991; Klautau *et al.*, 1994; Borojevic & Klautau, 2000; Klautau & Borojevic, 2001), we have selected a number of characters that we now consider valid. We will discuss these characters next, as well as those that seem to us to be plastic and should consequently be avoided.

### ORGANIZATION OF THE CORMUS

#### *Anastomosis of the tubes*

Anastomosis of the tubes is considered to be a good character for the systematics of *Clathrina*. We found it to be distinctive when comparing specimens with tubes which were regularly or irregularly and tightly or loosely anastomosed. In some cases, the presence of regularly and tightly anastomosed tubes was related to the delimitation of the cormus, possibly indicative of a higher complexity in the species. Examples of species with a well-delimited cormus include *C. aspina*, *C. brasiliensis*, *C. cerebrum* and *C. tetrapodifera* sp. nov.

#### *Type of osculum*

We found that there are two types of osculum (aperture) in *Clathrina*: those that are located in the majority of the tubes of the cormus, and those, fewer in number, located in the apical region of the sponge and connected to a few tubes. While the former receive water from one tube (which we have termed 'water collecting'), the latter receive it from several. The type of osculum seems to be a consistent character of the species, indicating that it is good for systematics and possibly indicative of a higher evolutionary degree of the species. Examples of species with water-collecting tubes include *C. ceylonensis*, *C. clathrus*, *C. coriacea* and *C. parva*.

### ORGANIZATION OF THE SKELETON

#### *Spicule type*

After studying several specimens of *Clathrina*, including some species series, we considered skeletal structure (the range of different spicule types, and their distribution throughout the cormus) to be an important character. The distribution pattern of diactines is important, as well as their insertion (either parallel or perpendicular) in the tubes.

#### *Shape of actines of the triactines and tetractines*

The importance of this was established in our previous studies (Solé-Cava *et al.*, 1991; Klautau *et al.*, 1994) where morphologically similar, sympatric populations, whose sole difference was the shape of the actines (conical or cylindrical), were compared by allozymes. This technique evaluates whether breeding is occurring between the analysed specimens. Our results indicated that populations differing in the shape of the actines were reproductively isolated. Interestingly, Haeckel (1872) had already used this character to differentiate *C. coriacea* from *C. primordialis*. More recently, it was also used by Wörheide & Hooper (1999) to distinguish species of *Clathrina* from the Great Barrier Reef.

#### *Presence of spines*

Care needs to be taken when using ornament in apical actines as a taxonomic character. In some cases, we found, in the same specimen, apical actines with spines, without spines or with spines which were vestigial. This suggests that this character still requires to be thoroughly evaluated before it can be considered in systematics. Nonetheless, the presence (or absence) of spines at the apical actine has been shown to be a reliable character (Klautau *et al.*, 1994). In that work, sympatric populations of *Clathrina*, which differed in the presence or absence of spines in the apical actine of tetractines, were subjected to allozyme analysis,

which proved that the populations were reproductively isolated. The specimens without spines were separated from *C. brasiliensis* and named *C. aspina*.

#### Shape of tripods

Tripods can be defined as triactines with stout actines and a raised centre. However, we observed some variation in the shape of the tripods in many specimens. It is rather easy to find characteristic tripods, which we called true tripods, coexisting with tripods similar to large triactines. The latter do not have a raised centre; their actines are stout, though sometimes not as stout as those of true tripods. In spite of the fact that some intraindividual variation was observed, we considered the presence of tripods, always related to the individualization (delimitation) of the cormus, to be an important character. However, due to the variation, this character must be carefully analysed before species identification.

#### Diactines

In the literature, several authors (Dendy, 1905; Row, 1909) discussed the use of diactines, particularly trichoxeas. We believe that diactines are valid and important characters. Not only their presence or absence, but also their shape and distribution in the cormus should be used in systematics. The distinction between *C. contorta* and *C. reticulum*, for example, is easily made by establishing the presence of diactines parallel and perpendicular to the cormus respectively. The size of these spicules, however, sometimes varies within an individual. Consequently, we believe that size should only be considered when variation within individuals is small.

#### Size of the spicules

We have already reported putative environmental influences on spicule size in Demospongia (*Chond-*

*rilla*) (Solé-Cava *et al.*, 1991, Klautau *et al.*, 1999), and it appears to be a good character for systematics. Two allopatric populations (*C. cerebrum* and a morphologically similar Brazilian population) could be distinguished solely by the size of their spicules. When both populations were subjected to allozyme analysis, reproductive isolation was established. Spicule size was also used by Wörheide & Hooper (1999) to distinguish species of *Clathrina* from the Great Barrier Reef.

#### CELLS: PRESENCE OF GRANULES

The use of cells with granules in the systematics of Porifera is becoming more and more common (Boury-Esnault *et al.*, 1994; Muricy *et al.*, 1996; Boury-Esnault *et al.*, 1999). In *Clathrina* systematics, these cells have only recently begun to be used (Wörheide & Hooper, 1999). Unfortunately, we could not use this character for all the species due to the poor state of preservation of some specimens.

#### CONCLUSIONS

Many *Clathrina* species were formerly considered cosmopolitan. However, our results suggest that analysis based on morphological characters alone was sufficient to distinguish new, geographically restricted, species. Cosmopolitanism is only one aspect of a conservative systematics that has overlooked important morphological characters. Characters such as size and shape of spicules, their distribution, organization of the cormus, and oscula and cells with granules were shown to be consistent for the systematics of the group. We believe that even the slightest morphological difference between populations should be considered, to avoid artificial problems of cosmopolitanism.

#### KEY TO THE SPECIES OF *CLATHRINA*

- |                                                        |                         |
|--------------------------------------------------------|-------------------------|
| 1. Skeleton has tetractines .....                      | 22                      |
| – Skeleton does not have tetractines .....             | 2                       |
| 2. Skeleton composed of triactines and diactines ..... | <i>luteoculcitella</i>  |
| – Skeleton composed of triactines only .....           | 3                       |
| 3. Water-collecting tubes are present .....            | 4                       |
| – Water-collecting tubes are not present .....         | 11                      |
| 4. Tubes are tightly anastomosed .....                 | 5                       |
| – Tubes are loosely anastomosed .....                  | 7                       |
| 5. The tip of the actines is blunt .....               | <i>ceylonensis</i>      |
| – The tip of the actines is sharp .....                | 6                       |
| 6. There are two size populations of triactines .....  | <i>clara</i> sp. nov.   |
| – Triactines and tripods are present .....             | <i>rotunda</i> sp. nov. |

7. The tip of the actines is rounded.....	8
– The tip of the actines is sharp.....	9
8. Actines are cylindrical.....	<i>clathrus</i>
– Actines are conical.....	<i>coriacea</i>
9. There are two populations of triactines (conical and cylindrical).....	<i>primordialis</i>
– There is a single population of triactines.....	10
10. Actines are cylindrical.....	<i>parva</i>
– Actines are conical.....	<i>procumbens</i>
11. The tip of the actines is sharp.....	12
– The tip of the actines is not sharp.....	17
12. Actines are cylindrical.....	<i>heronensis</i>
– Actines are conical.....	13
13. There are three populations of triactines.....	<i>laminoclathrata</i>
– There is a single population of triactines.....	14
14. Cells with granules are present.....	<i>helveola</i>
– Cells with granules are absent.....	15
15. Actines are straight.....	<b><i>hondurensis</i> sp. nov.</b>
– Actines are not straight.....	16
16. Actines are undulated.....	<i>chrysea</i>
– Actines are very thin at the distal part.....	<b><i>sinusarabica</i> sp. nov.</b>
17. The tip of the actines is rounded.....	<i>aurea</i>
– The tip of the actines is blunt.....	18
18. Actines are cylindrical.....	19
– Actines are conical.....	<i>conifera</i>
19. Cells with granules are present.....	<i>wistariensis</i>
– Cells with granules are absent.....	20
20. A sieve can be found below the oscula.....	<i>cribrata</i>
– No sieve can be found below the oscula.....	21
21. Actines are straight.....	<i>cylindractina</i>
– Actines are undulated at the distal part and thicker near the centre.....	<b><i>hispanica</i> n. sp.</b>
22. Diactines are present.....	35
– Diactines are not present.....	23
23. Tripods are absent.....	27
– Tripods are present.....	24
24. Tetrapods are present.....	<b><i>tetrapodifera</i> sp. nov.</b>
– There are no tetrapods.....	25
25. Apical actine of the tetractines is smooth.....	<i>aspina</i>
– Apical actine of the tetractines has spines.....	26
26. Facial actines of the tri and tetractines are thicker than 9 µm.....	<i>brasiliensis</i>
– Facial actines of the tri and tetractines are thinner than 9 µm.....	<i>cerebrum</i>
27. There is a single population of triactines and tetractines.....	30
– There are more than a single population of tri and/or tetractines.....	28
28. Pseudosagittal spicules are abundant.....	<i>biscayae</i>
– Spicules are mainly regular.....	29
29. There are two populations of tetractines.....	<i>ascandroides</i>
– There is one population of tetractines.....	<i>gardineri</i>
30. Tetractines are the most abundant spicules.....	31
– Tetractines are not the most abundant spicules.....	32
31. The apical actine of the tetractines is conical.....	<i>quadriradiata</i>
– The apical actine of the tetractines is cylindrical.....	<i>tetractina</i>
32. Facial actines are conical.....	33
– Facial actines are cylindrical.....	34
33. Cells with granules are present.....	<i>adusta</i>
– Cells with granules are absent.....	<b><i>africana</i> sp. nov.</b>

34. Cells with granules are present.....	<i>septentrionalis</i>
– Cells with granules are absent .....	<i>canariensis</i>
35. There are two populations of tetractines .....	36
– There is a single population of tetractines.....	37
36. Diactines are fusiform .....	<i>sagamiana</i>
– Diactines have different tips .....	<i>atlantica</i>
37. Tubes are tightly anastomosed .....	38
– Tubes are loosely anastomosed .....	39
38. Diactines are disposed parallel to the surface.....	<i>contorta</i>
– Diactines are disposed perpendicular to the surface .....	<i>reticulum</i>
39. Diactines are only trichoxeas.....	40
– Diactines are not only trichoxeas .....	41
40. Water-collecting tubes are present .....	<i>sueziana n. sp.</i>
– Water-collecting tubes are absent .....	<i>tenuipilosa</i>
41. Diactines are club shaped .....	<i>dubia</i>
– Diactines are fusiform .....	42
42. Trichoxeas are present .....	<i>hirsuta sp. nov.</i>
– Trichoxeas are absent .....	<i>panis</i>

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APPENDIX  
SUMMARY

*Abbreviations.* \*Indicates species with tetractines as the most abundant spicules. Spicules: dia, diactines; tri, triactines; tet, tetractines; aa, apical actine; tric, tri-choeas; trip, tripods, tetra, tetrapods; (s), (surface); par, parallel, perp, perpendicular. L/W: length/width (µm). Shape: con, conical; cyl, cylindrical. Tip: s/c, sharp, curved. Und. (Undulation): n/s, no/smooth; c/s, curved/smooth; fus, fusiform; l/m, large in the middle. Anastomosis: reg, regular; irreg, irregular. WCT: water-collecting tubes

Species	Actine				Cormus				Cells/granules	Geog. distribution
	Spicules	L/W	Shape	Tip	Und.	Anastomosis	WCT			
<i>C. aurea</i>	tri	73.8/5.5	cyl	rounded	yes	irreg, loose	absent	absent		Rio de Janeiro, Brazil
<i>C. ceylonensis</i>	tri	78.5/7.4	con	blunt	no	irreg, tight	present	absent		Indian Ocean
<i>C. chrysea</i>	tri	101.8/9.8	con	sharp	yes	reg, loose	absent	absent		New Caledonia
<i>C. clathrus</i>	tri	92.0/7.3	cyl	rounded	yes	irreg, loose	present	absent		Mediterranean Sea
<i>C. conifera</i>	tri	77.3/9.0	con	blunt	no	irreg, loose	absent	absent		Rio de Janeiro, Brazil
<i>C. coriacea</i>	tri	88.0/9.0	con	rounded	yes	irreg, loose	present	absent		British Channel
<i>C. cribrata</i>	tri	68.5/5.8	cyl	blunt	yes	irreg, loose	absent	absent		Norway
<i>C. cylindractina</i>	tri	83.8/8.3	cyl	blunt	no	irreg, loose	absent	absent		Rio de Janeiro, Brazil
<i>C. helveola</i>	tri	154.1/13.2	con	sharp	yes	irreg, loose	absent	present		Great Barrier Reef
<i>C. heronensis</i>	tri	128.5/10.0	cyl	sharp	yes	irreg, loose	absent	present		Great Barrier Reef
<i>C. hispanica</i> sp. nov.	tri	81.6/5.5	cyl	blunt	yes	irreg, loose	absent	absent		Mediterranean Sea
<i>C. parva</i>	tri	129.3/9.7	cyl	sharp	yes	irreg, loose	present	present		Great Barrier Reef
<i>C. procumbens</i>	tri	87.3/11.3	con	sharp	no	irreg, loose	present	present		Australia
<i>C. wistariensis</i>	tri	167.3/12.5	cyl	blunt	no	irreg, loose	absent	present		Great Barrier Reef
<i>C. sinusarabica</i> sp. nov.	tri	91.9/8.4	con	sharp	yes	irreg, loose	absent	absent		Red Sea
<i>C. hondurensis</i> sp. nov.	tri	133.4/15.6	con	sharp	no	irreg, loose	absent	absent		Honduras

<i>C. clara</i> sp. nov.	tri	84.5/9.8	con	sharp	no	irreg, tight	present	absent	Christmas Islands
<i>C. primordialis</i>	tri (s)	164.5/21.8	con	sharp	no				
	tri	91.9/9.6	con	sharp	no	irreg, loose	present	absent	Mediterranean Sea
<i>C. laminoclathrata</i>	tri	86.6/11.3	con	sharp	no	reg, tight	absent	?	Australia
	tri	72.0/8.0	con	sharp	no				
	tri	132.0/13.0	con	sharp	no				
	tri	188.0/18.0	con	sharp	no	irreg, tight	present	absent	South Africa
<i>C. rotunda</i> sp. nov.	tri	52.6/5.8	con	sharp	yes				
	trip (s)	59.0/9.6	con	sharp	yes	reg, tight	present	present	Great Barrier Reef
<i>C. adusta</i>	tri	109.9/12.7	con	sharp	yes				
<i>C. canariensis</i>	tet	110.9/12.0	con	sharp	yes				
	aa	60.7/3.8	cyl	sharp	n/s				
	tri	77.8/5.0	cyl	blunt	yes	irreg, tight	present	absent	Canary Islands
	tet	74.3/5.0	cyl	blunt	yes				
	aa	43.8/5.0	con	sharp	n/s				
	tri	56.3/6.3	con	blunt	no	reg, tight	present	absent	Rio de Janeiro, Brazil
<i>C. septentrionalis</i>	tet	54.3/6.0	con	blunt	no				
	aa	34.8/4.3	con	sharp	n/s				
	tri	112.5/9.8	cyl	blunt	yes	irreg, tight	present	present	Norway
	tet	110.8/9.3	cyl	blunt	yes				
	aa	71.8/4.5	cyl	sharp	c/s				
<i>C. tetractina</i> *	tri	85.0/8.8	con	sharp	yes	irreg, loose	present	absent	Rio de Janeiro, Brazil
	tet	88.0/9.5	con	sharp	yes				
<i>C. africana</i> sp. nov.	aa	71.0/3.8	cyl	sharp	n/s				
	tri	77.3/8.5	con	sharp	yes	irreg, loose	absent	absent	South Africa
	tet	75.8/8.3	con	sharp	yes				
	aa	59.9/6.5	con	sharp	n/s				

Species	Actine				Cormus				WCT	Cells/granules	Geog. distribution
	Spicules	L/W	Shape	Tip	Und.	Anastomosis	WCT				
<i>C. ascandroides</i>	tri	130.0/13.0	con	sharp	no	irreg, loose	absent	absent	absent	Rio de Janeiro, Brazil	
	tet	164.5/16.5	con	sharp	no						
	aa	40.6/8.2	con	sharp	c/s						
	tet	313.1/39.8	con	sharp	no						
	aa	84.0/21.6	con	sharp	c/s						
<i>C. biscayae</i>	tri (s)	111.5/9.8	con	sharp	no	irreg, loose	absent (?)	absent	absent	Bay of Biscay	
	tri (s)	157.5/16.3	con	sharp	no						
	tet	145.3/9.0	con	sharp	no						
	aa	60.7/6.0	con	sharp	c/s						
	tet	155.5/14.3	con	sharp	no						
<i>C. gardineri</i>	aa	53.5/10.1	con	sharp	c/s						
	tri	60.0/6.3	con	sharp	no	reg, tight	pseudo-atrium	absent	absent	Chagos Archipelago	
	tri (s)	110.0/10.8	con	sharp	no						
	tet	65.5/6.8	con	sharp	no						
	aa	39.8/5.0	con	sharp	n/s						
<i>C. contorta*</i>	tri	87.3/10.0	con	sharp	yes	irreg, tight	present	present	absent	Mediterranean Sea	
	tet	94.5/9.8	con	sharp	yes						
	aa	81.8/5.0	cyl	sharp	n/s						
	dia (par)	503.9/31.6	fus	sharp	curved						
	tric										
<i>C. dubia</i>	tri	151.5/15.5	con/ cyl	sharp	yes	irreg, loose			present	Australia	
	tet	140.3/16.0	con/ cyl	sharp							
	aa	110.0/9.8									
	dia (perp)	256.0/13.7		club	curved or straight						
	tri	162.0/15.5	con	sharp	yes	irreg, loose	?	?	?	Atlantic Coast of North America	
<i>C. panis</i>	tet	159.8/14.5	con	sharp	yes						
	aa	156.8/9.5	con	sharp	n/s						
	dia (perp)	474.3/29.6	fus	sharp							

<i>C. reticulum</i>	tri	87.8/7.5	cyl	sharp	no	reg. tight	pseudo-atrium	absent	Mediterranean Sea
	tet	89.5/7.3	cyl	sharp	no				
	aa	53.3/5.0	cyl	sharp	n/s				
	dia (perp)	212.2/14.3	arrow						
	tric								
<i>C. hirsuta</i> sp. nov.	tri	122.5/13.3	con	sharp	no	irreg, loose	present	absent	South Africa
	tet	122.3/12.5	con	sharp	no				
	aa	80.9/6.5							
	dia (perp)	302.9/14.3	fus	sharp	curved				
	tric								
<i>C. tenuipilosa</i>	tri	84.6/11.0	con	blunt	yes	irreg, loose	absent	absent	Indian Ocean
	tet	88.1/11.5	con	blunt	yes				
	aa	92.0/7.0			no,	no,			
					sometimes	c/s			
	tric								
<i>C. sueziana</i> sp. nov.	tric	> 250.0/ < 0.3							
	tri	91.3/10.3	con/cyl	blunt	l/m	irreg, loose	present		Red Sea
	tet	86.0/9.4	con/cyl	blunt	l/m				
	aa	56.3/5.0	con	sharp	n/s				
	tric	> 250.0/ < 0.3							
<i>C. atlantica</i>	tri	108.3/10.0	con/cyl	sharp	no	few tubes	absent		Cape Verde Islands
	tet	106.0/9.8	con/cyl	sharp	no				
	aa	35.0/7.8	con	sharp	n/s				
	tet (s)	165.0/23.0	con (stout)	sharp	no				
	aa	69.1/18.9	con	sharp	n/s				
<i>C. aspina</i>	dia (perp)	201.8/7.5	s/c						
	tric								
	tri	70.0/6.0	con	blunt	no	reg. tight	present	absent	Rio de Janeiro, Brazil
	tet	68.8/6.0	con	blunt	no				
	aa	50.3/5.0	con	sharp	n/s				
	78.8/9.5	con	blunt	no					
		trip (s)							

Species	Actine			Cormus				WCT	Cells/granules	Geog. distribution
	Spicules	L/W	Shape	Tip	Und.	Anastomosis				
<i>C. brasiliensis</i>	tri	78.2/10.8	con	blunt	no	reg, tight	present	absent	Rio de Janeiro, Brazil	
	tet	75.3/10.4	con	blunt	no					
	aa	36.4/8.0	con	sharp	no/spines					
<i>C. cerebrum</i>	trip (s)	81.0/11.0	con	blunt	no					
	tri	71.8/6.5	con/cyl	blunt	no	reg, tight	present	absent	Mediterranean Sea	
	tet	71.8/7.3	con	blunt	no					
<i>C. tetrapodifera</i> sp. nov.	aa	57.5/5.8	con	sharp	no/spines					
	trip (s)	6.0/9.5	con	blunt	no					
	tri	63.3/7.3	con	sharp	no	reg, tight	absent	?	New Zealand	
	tet	64.5/8.0	con	sharp	no					
	aa	37.0/5.5	con	sharp	no/spines					
	trip (s)	79.0/14.0	con	sharp	no					
<i>C. luteoculcitella</i>	tetra (s)	77.0/14.8	con	sharp	no					
	aa	36.0/9.6	con	sharp	n/s					
	tri	75.8/7.7	con	sharp	yes	irreg, tight	absent	absent	Great Barrier Reef	
	dia (perp)	125.3/3.8	fus	one	no	(loose in interior)				
	tet	larger tip	con	sharp	no	?	?	?	Sagami Sea, Japan	
<i>C. sagamiana</i>	aa	52.5/4.0	con	sharp	n/s					
	tet	116.3/10.0	con	sharp	no					
	aa	100/6.0	con	sharp	n/s					
	dia (perp)	316.2/13.3	fus	sharp	curved					