

Calcareous sponges of the genera *Clathrina* and *Guancha* (Calcinea, Calcarea, Porifera) of Norway (north-east Atlantic) with the description of five new species

HANS TORE RAPP*

University of Bergen, Department of Biology, Bergen High Technology Centre, N-5020 Bergen, Norway

Received September 2004; accepted for publication October 2005

The taxonomy and distribution of 11 species of calcareous sponges of the subclass Calcinea from the Norwegian coast are reviewed. The Norwegian Calcinea represents a mixture of southern boreal/boreal and boreoarctic species, and the calcinean sponge fauna of northern Norway has strong similarities to the Greenlandic and the White Sea/Barents Sea sponge faunas. Most Norwegian Calcinea have their main distribution between 20 and 100 m depth, although some species are found only in the shallow sublittoral or from sublittoral to abyssal depths. Six species were previously reported in the area: *Clathrina coriacea* (Montagu, 1818), *Clathrina cribrata* Rapp *et al.*, 2001, *Clathrina nanseni* (Breitfuss, 1896), *Clathrina septentrionalis* Rapp *et al.*, 2001, *Guancha blanca* Miklucho-Maclay, 1868 and *Guancha lacunosa* (Johnston, 1842). Five species are new to science: *Clathrina corallicola*, *Clathrina jorunnae*, *Guancha arnesenae*, *Guancha camura*, and *Guancha pellucida* spp. nov. A key to the known Norwegian Calcinea is provided. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 147, 331–365.

ADDITIONAL KEYWORDS: depth distribution – dispersal – morphology – North Atlantic – reproduction – taxonomy – zoogeography.

INTRODUCTION

The fauna of Porifera along the Norwegian coast is rich, representing about 260 species (Tendal, Brattegard & Rapp, 2001). However, despite the great number of species, very few taxonomic works based on Norwegian sponges have been published.

The study of Calcarea from the Norwegian coast started with collections made by Haeckel in 1869 on the Norwegian west coast, and later he reported 14 species from Norway (Haeckel, 1872). During the following 30 years Norwegian Calcarea were mentioned in several reports (Haeckel, 1874; Hansen, 1885; Brunchorst, 1891; Herdman, 1892; Breitfuss, 1896). However, the first comprehensive work was that by Arnesen (1901a). She re-evaluated all the previous records and included new material from the southern, western and northern coasts. In total she reported 33

species of Calcarea, including five varieties, and provided at that time a highly useful key for their identification. In the early 20th century Breitfuss published several reports on calcareous sponges from the North Atlantic and Arctic oceans, in which also species from the Norwegian coast were included (Breitfuss, 1911, 1927, 1933, 1936). Some further records were provided by Arndt (1913), Burton (1931) and Gulliksen (1978). A summary of the known Norwegian species was given by Burton (1930b) in his work on the Norman collection, also with some minor additions of new data. Finally, about 70 years later, the next taxonomic paper on calcareous sponges from the Norwegian coast was published, describing two new species of *Clathrina* Gray, 1867 (Rapp, Klautau & Valentine, 2001).

The Calcarea Bowerbank, 1864 comprises the two subclasses Calcinea Bidder, 1898 and Calcaronea Bidder, 1898. Calcinea includes species with mainly regular (equiangular and equiradiate) triactines and tetractines, and basinuclate choanocytes with spher-

*E-mail: hans.rapp@bio.uib.no

ical nuclei, while the Calcaronea includes species with diactines, sagittal triactines and tetractines, and with apinucleate choanocytes (Borojevic, Boury-Esnault & Vacelet 1990, 2000). Sponges of the subclass Calcinea have a great variability of forms, but their general organization and the basic characteristics of their cytology and embryology show that they represent a monophyletic group (Borojevic *et al.*, 1990; Manuel *et al.*, 2002, 2003, 2004). Two orders may be separated among the Calcinea, the Clathrinida Hartman, 1958 emend., and the Murrayonida Vacelet, 1981. Clathrinida includes sponges with only free spicules. It is a highly variable group, representing all developmental stages, from simple olynthus-like sponges to complex forms with an elaborate aquiferous system (Borojevic *et al.*, 1990). The second order Murrayonida comprises only a few recent sponges in which the skeleton is composed of spicule tracts and/or supplemented with a non-spicular calcareous skeleton. All known Norwegian species of Calcinea belong to the order Clathrinida.

The Calcarea (and especially the Calcinea) has a reputation of being obscure and taxonomically difficult. This is because these animals offer very few morphological characters for reliable phylogenetic reconstructions. Furthermore, calcarean morphological characters appear to be highly susceptible to convergence (Manuel *et al.*, 2002). However, the use of numerical analyses of shape, size and distribution of spicules, and detailed histology have thrown new light on the classification of Calcarea, revealing that the species diversity in calcareous sponges is much higher than was previously expected (Wörheide & Hooper, 1999, 2002; Borojevic & Klautau, 2000; Rapp *et al.*, 2001; Rapp, 2004a, b). Together with detailed histology, molecular data appear to be essential to provide corroboratory evidence for previous phylogenetic hypotheses based on traditional morphological methods (Manuel *et al.*, 2002, 2003, 2004; Wörheide, Hooper & Degnan, 2003). During the last century there have been several contrasting trends in how to deal with morphological variation within the Calcarea. Haeckel (1872) was thrilled by the high variation in outer shape of the calcareous sponges, and ended up by splitting each species into several named 'varieties'. By contrast, Topsent (1936), Sará (1953) and Burton (1963) reduced the number of 'valid species' drastically based on lumping together species with more or less the same types of spicules, paying little or no attention to distribution of spicule types and organization of the aquiferous system. However, this extensive lumping was soon heavily criticized (Hartman, 1964), and has not been followed since.

The present study is the first comprehensive work dedicated to the study of Norwegian calcareous sponges for over 100 years (Arnesen, 1901a, b). As

many of the species studied are new to science and the number of species is high, only the subclass Calcinea will be treated here. The subclass Calcaronea comprises approximately 35 species (my unpubl. data) that will be published separately. Many of the species of Calcinea previously reported from Norwegian waters have been subject to misidentification, and a thorough re-examination of the older museum material combined with examination of newly retrieved material has been necessary to revise the species of this group. A re-description and a key to all the species within the subclass Calcinea occurring along the Norwegian coast are presented. Eleven species have been identified: *Clathrina corallicola* sp. nov., *C. coriacea* (Montagu, 1818), *C. cribrata* Rapp *et al.*, 2001, *C. jorunnæ* sp. nov., *C. nanseni* (Breitfuss, 1896), *C. septentrionalis* Rapp *et al.*, 2001, *Guancha arnesenæ* sp. nov.; *G. blanca* Miklucho-Maclay, 1868, *G. camura* sp. nov., *G. lacunosa* (Johnston, 1842) and *G. pellucida* sp. nov.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London, UK; IB, Department of Biology, University of Bergen, Norway; TMU, Tromsø Museum, University of Tromsø, Norway; VM, Museum of Natural History and Archaeology, The Norwegian University of Science and Technology (NTNU), Trondheim, Norway; ZIL, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; ZMO, Zoological Museum, University of Oslo, Norway; ZMUB, Zoological Museum, University of Bergen, Norway; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

MATERIAL AND METHODS

The present study is based on sponge specimens from the collections in the Norwegian natural history museums, The Natural History Museum, London, The Zoological Institute of the Russian Academy of Sciences, St. Petersburg, and the Zoological Museum of Copenhagen. The collections of the author, mainly specimens acquired during a recent benthic survey in the Trondheimsfjord in the years 1995–96 (Rapp, 1999), and specimens collected by diving in the years 1995–2001, are also included. Specimens from the inter-Nordic projects BIOFAR (benthic invertebrates around the Faroe Islands) and BIOICE (benthic invertebrates from Icelandic waters) have been studied for comparison of particular species. A total of 438 specimens from the Norwegian coast were studied. The present study area comprises the entire Norwegian coast, extending from the southern tip of Norway (57°57.55'N) near Mandal, to the northernmost point, Knivskjellodden (71°11.13'N) on Magerøy.

SPICULE PREPARATIONS

Descriptions of spicules were based on examination of different regions of the sponge. For permanent spicule preparations small pieces of sponge tissue were dissolved in sodium hypochlorite. After digestion of the soft tissue, the solution was drained, and the spicules washed three times in distilled water, once in 75% ethanol and once in absolute ethanol. Spicules were spread out on preheated microscopic slides, allowed to dry, embedded in Euparal and covered by a cover slip. The slides were kept at 50 °C for 48 h to allow the Euparal to polymerize. Measurements of 30 spicules of each type were taken using a micrometric ocular.

HISTOLOGICAL SECTIONS

Small pieces of sponge tissue were stained in a saturated solution of acid Fuchsin in 70% ethanol for 60 min, washed in 75% ethanol (2 × 30 min), transferred to 90% ethanol (30 min), and to two changes of absolute ethanol (2 × 30 min). For clearing the sponge tissue was transferred into xylene (2 × 30 min). For infiltration tissue was transferred to a 1 : 1 mixture of xylene and melted paraffin wax in an oven (60 °C) for 60 min, followed by two changes of paraffin wax at 60 °C (60 min each). The sponge tissue was embedded in paraffin, and when partly set, the blocks were put into the refrigerator to avoid crystallization of the wax. The blocks were cut by hand at various thickness (c. 30–100 µm) under a dissection microscope. The sections were placed on preheated microscopic slides to allow the paraffin to melt and to flatten out the section. Excess paraffin was soaked up by porous paper. The slides were allowed to re-harden, and were deparaffinized in xylene (3 × 15 min). The sections were mounted using Euparal and cover-slipped, and slides were kept at 50 °C for 48 h to allow the Euparal to polymerize (method modified from Wörheide & Hooper, 1999; Rapp, 2004a).

DESCRIPTION OF SPECIES

For each species the following information is given: synonyms and citations, including original allocation and other names used in the north-east Atlantic and Arctic region. Type locality and deposition of type material (when known). Previous records from the Norwegian coast. Overview of material examined, including locality data and where the material is deposited. Etymology (for new species). General description. Geographical and depth distribution along the Norwegian coast, with comments on the total distribution range. Further information and discussion is presented in a remarks section for each species.

SYSTEMATICS

The higher classification follows the schemes presented by Borojevic *et al.* (1990, 2002). Definitions and technical terms used in this study can be found in Boury-Esnault & Rützler (1997) and Manuel *et al.* (2002).

SYSTEMATIC INDEX

CLASS CALCAREA BOWERBANK, 1864
 SUBCLASS CALCINEA BIDDER, 1898
 ORDER CLATHRINIDA HARTMAN, 1958 *EMEND.*
 FAMILY CLATHRINIDAE MINCHIN, 1900
CLATHRINA GRAY, 1867
***C. corallicola* sp. nov.**
C. coriacea (Montagu, 1818)
C. cribrata Rapp *et al.*, 2001
***C. jorunnae* sp. nov.**
C. nansenii (Breitfuss, 1896)
C. septentrionalis Rapp *et al.*, 2001
GUANCHA MIKLUCHO-MACLAY, 1868
***G. arnesenae* sp. nov.**
G. blanca Miklucho-Maclay, 1868
***G. camura* sp. nov.**
G. lacunosa (Johnston, 1842)
***G. pellucida* sp. nov.**

CLASS CALCAREA BOWERBANK, 1864

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

Calcarea with regular (equiangular and equiradial), or exceptionally parasagittal or sagittal triactines, and/or a basal system of tetractines. In addition to the free spicules, there may be a non-spicular basal calcareous skeleton. In terms of ontogeny, triactines are the first spicules to be secreted. Choanocytes are basinucleate with spherical nuclei. The basal body of the flagellum is not adjacent to the nucleus. Calcinea incubate coeloblastula larvae.

ORDER CLATHRINIDA HARTMAN, 1958 *EMEND.*

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

FAMILY CLATHRINIDAE MINCHIN, 1900

Clathrinida with an essentially tubular organization. The skeleton is formed by tangential triactines, to which tripods, tetractines and diactines may be added.

The continuous choanoderm lines all the internal cavities. The water crosses the wall through pores, delimited by porocytes. The young sponges have an olynthus form that grows through longitudinal median division, budding and anastomosis of individual tubes to form the large units, called the cormus. There is neither a common cortex nor a well-defined inhalant or exhalant aquiferous system.

GENUS *CLATHRINA* GRAY, 1867

Type species: Clathrina clathrus (Schmidt, 1864).

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

Remarks on Clathrina

The genus *Clathrina* is represented by more than 40 described species in all seas (Klautau & Valentine, 2003). The classification is difficult due to the existence of only few, easily recognizable morphological criteria that can be used as descriptors, especially in species whose skeleton is composed only of triactines (Borojevic & Boury-Esnault, 1987). The paucity of morphological characters, combined with lack of information concerning growth, ecological distribution and reproductive cycle, has frequently misled to give the impression of a cosmopolitan distribution of species. 'Cosmopolitanism' of some sponge species seems to be mainly a result from the systematic difficulty and not from adaptability. Moreover, sympatric populations, which are morphologically almost identical, supported by genetic evidence sometimes seemed to represent sibling species, and shows the importance of use of slight morphological differences (e.g. spicule size or spicule arrangement) to distinguish species of *Clathrina* (Klautau, Solé-Cava & Borojevic, 1994). The use of statistical analyses of shape, size and distribution of spicules has thrown new light on the classification of the group, and previous numbers of species in any given geographical area are expected to be underestimated (Wörheide & Hooper, 1999; Borojevic & Klautau, 2000; Klautau & Borojevic, 2001; Rapp *et al.*, 2001; Klautau & Valentine, 2003; Rapp, 2004b).

***CLATHRINA CORALLICOLA* SP. NOV.**

(FIGS 1A–D, 2, TABLE 1)

Type locality: Trondheimsfjord, stn. T-96061704 (63°28.3'N, 10°00.2'E), 200–275 m, 17.06.1996.

Holotype: VM-001. Museum of Natural History and Archaeology, NTNU.

Paratype: ZMUB-68273, Røberg, Trondheimsfjord, Norway (63°28.6'N, 09°59'E), 250–300 m, 21.02.1996, one specimen.

Etymology: From Latin, 'on coral' referring to the sole occurrence on dead parts of the scleractinian corals *Lophelia pertusa* (L. 1758) (Norway and Shetland) and *Solenosmilia variabilis* Duncan, 1873 (Iceland).

Previous records: None.

Additional material examined: 23 specimens.

IB. Korsfjord, 60°09.1'N, 05°08.5'E, 500 m, 17.01.2002, 2 specimens. Røberg, Trondheimsfjord, Norway, stn. T-96052002 (63°55.6'N, 09°53.5'E), 200–530 m, 3 specimens. Røberg, Trondheimsfjord, Norway, stn. T-96061704 (63°28.3'N, 10°00.2'E), 200–275 m, 2 specimens. TMU. TM-141, Vågsfjord by Trondenes, 68°00'N, 16°39.8'E, 90–150 m, 28.08.1954, 2 specimens. TM-142, Gildeskål, 67°1.48'N, 14°1.3'E, 100–200 m, 21.08.1954, 1 specimen. VM. VM-16831, Medfjordgrunnen by Garten, 63°38'N, 09°31'E, 140–200 m, 06.07.1923, 1 specimen. VM-16832, Fedje, 60°46'N, 04°26'E, 315 m, 09.03.1998, 1 specimen. VM-16833, Røberg, Trondheimsfjord, stn. HM 001, 250–350 m, 21.02.1996, 4 specimens. VM-16834, Steinavær, 69°10'N, 16°38'E, 300–320 m, 26.07.1934, 7 specimens (fragmentary).

Description

Cormus composed of large tubes, irregular and very loosely anastomosed. Some of the tubes end in a cul-de-sac whereas others have the function of oscular tubes. In the apical region there is no anastomosis. The size is up to 4 cm. No water-collecting tubes are present. Surface is smooth and the walls are 30–40 µm thick and highly translucent. Colour is greyish white when alive and in ethanol. The walls are perforated by evenly distributed ostia. The skeleton comprises regular to subregular triactines of two size groups and regular to subregular tetractines of two size groups. Scattered sagittal tetractines are found in the apical region of the oscular tubes. All spicules with conical and sharp-pointed actines. Large tetractines with a short, cone-shaped and irregular apical actine. The small tetractines have a short, slender and irregularly curved apical actine. The spicules have no special orientation except that the small triactines and tetractines are found on the outer surface, and most of the large tetractines are lining the atrium. The apical actine of the tetractines is orientated towards the interior of the tubes. Triactines of the smallest size group and the large tetractines are the most numerous spicules, whereas large triactines and small tetractines are quite rare.

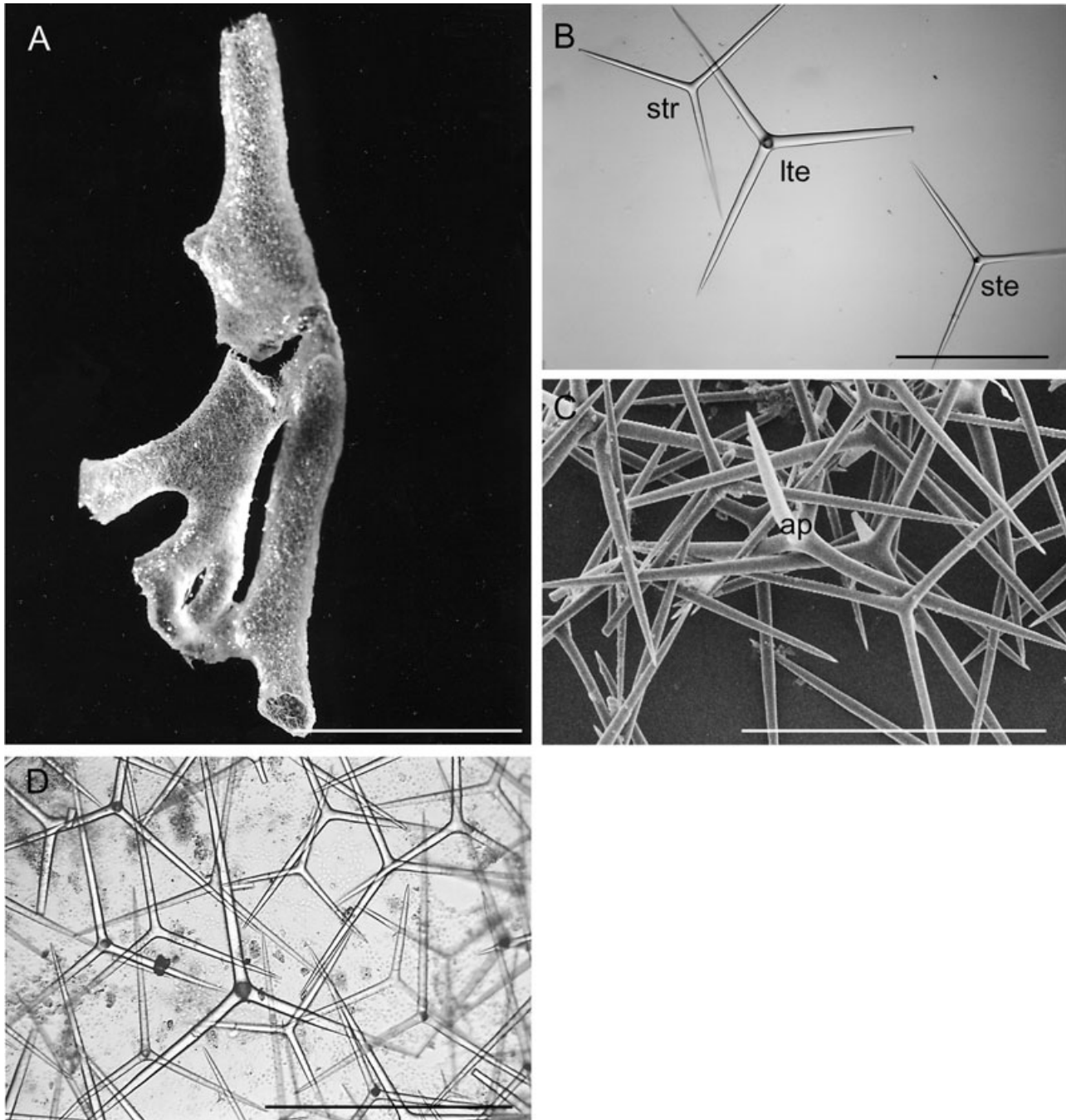


Figure 1. A, holotype of *Clathrina corallicola* sp. nov. Scale bar = 1 cm. B, spicules of *C. corallicola*. lte = large tetractines, ste = small tetractines and str = small triactines. Scale bar = 200 µm. C, SEM photo of spicules of *C. corallicola*. ap = apical actine of sagittal tetractine. Scale bar = 200 µm. D, distribution of spicules seen from the atrial side of the tube wall. Note that the apical actines of the tetractines are orientated towards the interior of the tube. Scale bar = 200 µm.

Distribution

The species is found along the entire Norwegian coast except in the southernmost part, 90–500 m. The species is also known from 1300 m depth at the

Reykjanes Ridge, Iceland (on *Solenosmilia variabilis*), and west of the Shetland Islands on dead *Lophelia pertusa* at 140–530 m depth (my pers. observ.).

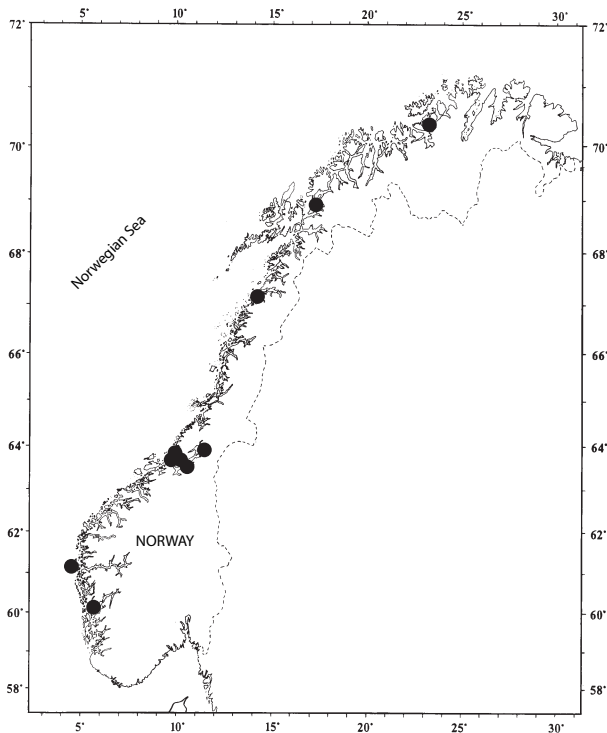


Figure 2. Distribution of *Clathrina corallicola* sp. nov. along the Norwegian coast.

Table 1. Spicule measurements of *Clathrina corallicola* sp. nov.

| Spicule | Length (μm) | | | | Width (μm) | | N |
|-----------------------------|--------------------------|------|----------|------|-------------------------|----------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Holotype VM-001 | | | | | | | |
| Small triactines | 98 | 157 | ± 33 | 220 | 10 | ± 1 | 30 |
| Large triactines | 178 | 234 | ± 26 | 293 | 19 | ± 1 | 5 |
| Small tetractines | 181 | 193 | ± 17 | 205 | 10 | ± 1 | 15 |
| Apical actine | – | – | – | 37 | 5 | ± 2 | 10 |
| Large tetractines | 163 | 245 | ± 50 | 342 | 21 | ± 5 | 30 |
| Apical actine | – | – | – | 25 | 20 | ± 5 | 30 |
| Sagittal tetractines | 163 | 197 | ± 30 | 220 | 16 | ± 4 | 10 |
| Paired actine | 85 | 140 | ± 22 | 195 | 18 | ± 2 | 10 |
| Unpaired actine | – | – | – | 56 | 12 | ± 3 | 6 |
| Apical actine | | | | | | | |
| Paratype | | | | | | | |
| ZMUB-68273 | | | | | | | |
| Small triactines | 116 | 158 | ± 20 | 194 | 10 | ± 1 | 30 |
| Large triactines | 170 | 241 | ± 23 | 289 | 22 | ± 1 | 7 |
| Small tetractines | 136 | 155 | ± 18 | 184 | 10 | ± 1 | 15 |
| Apical actine | – | – | – | 97 | 5 | ± 2 | 10 |
| Large tetractines | 184 | 223 | ± 36 | 330 | 20 | ± 5 | 30 |
| Apical actine | – | – | – | 21 | 19 | ± 3 | 30 |
| Sagittal tetractines | 155 | 178 | ± 15 | 194 | 15 | ± 2 | 10 |
| Paired actine | 126 | 146 | ± 14 | 165 | 17 | ± 1 | 10 |
| Unpaired actine | 49 | 89 | ± 29 | 126 | 12 | ± 2 | 5 |
| Apical actine | | | | | | | |

Remarks

The species is closely associated with the dead parts of *Lophelia pertusa*. The irregularly anastomosing tubes are attached to the coral at any part of the corium that is close to the coral branches. Although the shape of the different types of spicules is very constant, the length of the actines within the different groups of spicules is variable. However, there are no difficulties in delimiting the different groups of spicules. The species resembles most *Clathrina ascandroides* Borojevic, 1971. However, the growth-form of *C. ascandroides* is almost always small solitary tubes or tubes anastomosing near the base (1–1.5 mm wide). All the specimens of *C. corallicola* sp. nov. have irregular corium composed of 2- to 5-mm-wide tubes that are slightly anastomosed at the base and free in the apical region. Both species have two types of regular to subregular tetractines. However, *C. corallicola* also has two types of regular to subregular triactines, whereas *C. ascandroides* has only one. The larger tetractines have the same length of actines in both species, but they are about twice as thick in *C. ascandroides* than in *C. corallicola* (Borojevic, 1971; Klautau & Borojevic, 2001; Klautau & Valentine, 2003). In addition, *C. corallicola* has sagittal tetractines.

CLATHRINA CORIACEA (MONTAGU, 1818)
(FIGS 3A–C, 4, TABLE 2)

Original description: *Spongia coriacea* Montagu, 1818: 116.

Synonyms and citations

Ascetta coriacea (Arnesen, 1901a: 10–11, 1901b: 67–68).

Clathrina coriacea (Rapp, 1999: 45–50; van Soest, 2001: 101; Klautau & Valentine, 2003: 22–23).

Leucosolenia coriacea (Alander in Jägerskiöld, 1971: 60).

Type locality: Budleigh Salterton, South Devon, England.

Neotype: BMNH 1882.3.6.7 (Dry). Budleigh Salterton, South Devon, England. H.J. Carter Collection (Klautau & Valentine, 2003). Type specimen not examined.

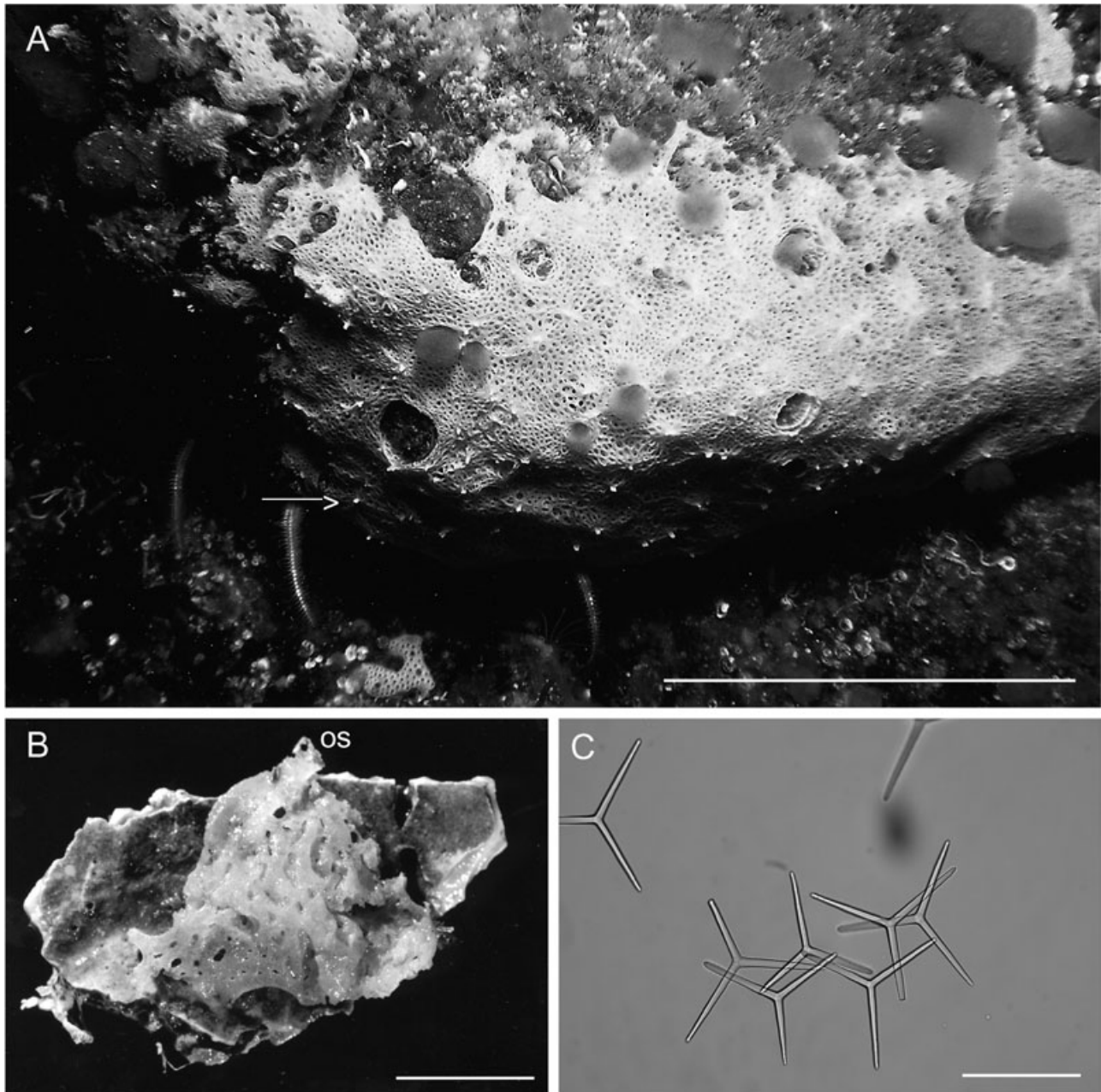


Figure 3. A, *Clathrina coriacea* at 10 m depth. Scale bar = 5 cm. Note the many chimney-like oscula (arrow). B, habitus of a smaller fixed specimen. os = osculum. Scale bar = 1 cm. C, regular triactines from *C. coriacea*. Scale bar = 100 μ m.

Previous records: The only true records are from the Bergen area by Arnesen (1901a, b) and from the Trondheimsfjord (Rapp, 1999).

Material examined: 47 specimens.

IB. Aursøy, Mausundvær, 63°53'N, 08°38'E, 1 m, 17.04.2000, 4 specimens. Fofafoten, Trondheimsfjorden, 63°27.3'N, 10°44.0'E, 14–35 m, 08.01.1996, 1 specimen. Saltvikhamna, Trondheimsfjorden, 63°46.5'N, 11°00.2'E, 25–150 m, 10.11.1995, 1 specimen. Ærholmen, Stora Kalsøy, 60°08'N, 05°02'E, 15–45 m, 06.08.2001, 6 specimens. Sæbuøya, Hitra, 63°29'N, 08°14'E, 10–15 m, 27.04.2001, 2 specimens. Blåskykøya, Hitra, 63°34'N, 08°18'E, 3–7 m,

29.04.2001, 3 specimens. Horgo, Austevoll, 60°08'N, 05°06'E, 10 m, 13.03.2001, 1 specimen. Vatlestraumen, 60°20'N, 05°11'E, 20 m, 15.05.2001, 1 specimen. Værøy, 67°40'N, 12°40'E, littoral, 04.06.1928, 1 specimen. TMU. TM-143, Tromsø, 69°40'N, 19°00'E, 40–60 m, 1 specimen. TM-144, Vannøy, 70°14'N, 19°29.2'E, 100 m, 10.06.1924, 2 specimens. VM. VM-16835, Finnsnes, 69°14'N, 17°58'E, 25–40 m, 18.06.1914, 1 specimen. VM-16836, Rystrømmen, 69°33'N, 18°44'E, 35 m, 15.05.1925, 1 specimen. VM-16837, Kristiansund, 63°10'N, 07°40'E, littoral, 22.04.1937, 1 specimen. VM-16838, Bjarkøy, 68°58'N, 16°42'E, 30–60 m, 06.09.1912, 1 specimen (fragmentary). VM-16839, Helløy, Støtt, 66°54'N, 14°24'E, littoral, 29.07.1934, 1 specimen (fragmentary). VM-16840, Storhallaren, Frøya, 63°41'N, 08°37'E, littoral, 17.07.1935, 1 specimen. VM-16841, Meltefjord, Sørøya, 70°30'N, 22°23'E, 1 specimen. VM-16842/16843, Knarlagsundet, 63°40'N, 09°05'E, littoral, 13.08.1938, 3 specimens. VM-16844/16845, Breivik, Herdlevær, 60°34'N, 04°52'E, littoral, 16.09.1936, 4 specimens. VM-16846, Titran, 63°40'N, 08°18'E, littoral, 17.04.1931, 2 specimens. VM-16847, Blåskykøya, Hitra, 63°34'N, 08°18'E, 3–7 m, 28.04.2001, 2 specimens. VM-16848, Vallersund, 63°52'N, 09°44'E, littoral, 10.08.1926, 1 specimen. VM-16849, Bjørøya, 64°34'N, 10°50'E, littoral, 09.08.1927, 1 specimen. VM-16850, Titran, 63°40'N, 08°18'E, 19–23.04.1928, littoral, 1 specimen. VM-16851, Ålesundsaksla, 62°28'N, 06°08'E, littoral, 09.08.1930, 1 specimen. VM-16852, Storfjellet, Røst, 67°27'N, 11°57'E, littoral, 15.07.1930, 1 specimen. ZMUB. ZMUB-114, Bergen, 1 specimen (fragmentary). ZMUB-10882, Bergen, 55–65 m, 1 specimen (fragmentary).

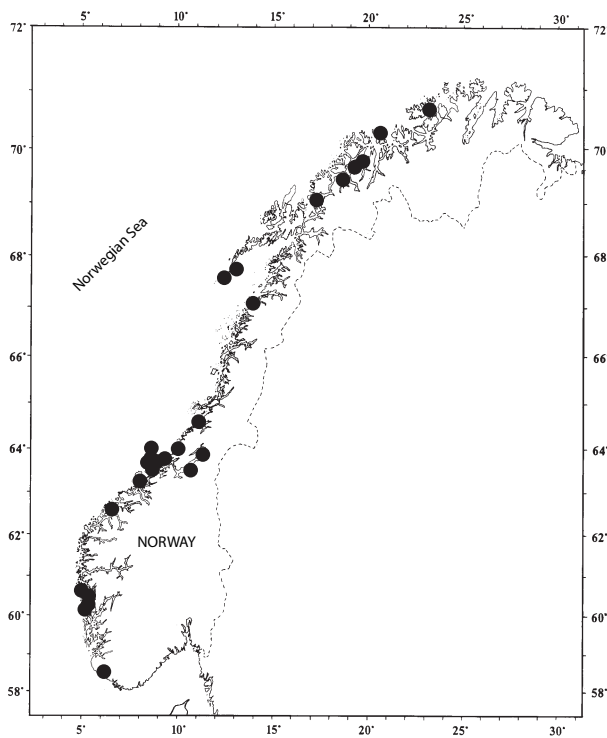


Figure 4. Distribution of *Clathrina coriacea* along the Norwegian coast.

Description

Cornus somewhat flattened or cushion-shaped, made of small, thin and loosely anastomosing tubes. Water-collecting tubes are present, and osculi are scattered over most parts of the cornus. Surface is smooth, and

Table 2. Spicule measurements of *Clathrina coriacea* (Montagu, 1818)

| Spicule | Length (µm) | | | | Width (µm) | | N |
|-------------------------|-------------|------|----|-------|------------|------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Neotype BMNH 1882.3.6.7 | | | | | | | |
| Triactines | 62.5 | 88 | ±7 | 102.5 | 9 | ±0.8 | 30 |
| VM-16846 | | | | | | | |
| Triactines | 61 | 87 | ±9 | 110 | 9 | ±2 | 30 |
| VM-16847 | | | | | | | |
| Triactines | 66 | 83 | ±8 | 102 | 9 | ±2 | 30 |

the texture is soft and somewhat elastic. Colour usually bright white, greyish white, light beige or yellow when alive, and greyish white to brown in alcohol. The cormus is normally up to 30 cm in diameter. The wall of the single tubes is composed of several layers of spicules and is about 40 µm thick. The skeleton has no special organization, and is composed of equiangular and equiradiate triactines. Actines are conical or slightly conical, undulated at the distal part, and have a constriction near the end, which is rounded or blunt.

Distribution

The species is known from the entire Norwegian coast except from the southernmost part, littoral to 150 m. The species is most frequent in the littoral and shallow sublittoral. The species is common in shallow water in the north-east Atlantic.

Remarks

The species is often found at exposed and moderately exposed localities on the outer coasts, but is also common in slightly more sheltered areas in the outer parts of the fjords. At some localities it may cover areas up to 1 m in diameter or form horizontal bands 20–30 cm wide and several metres long immediately beneath the kelp zone (*Laminaria hyperborea* (Gunnerus) Foslie, 1884). The very irregular outline of 'specimens' of this size may indicate that they represent several fused specimens of different size and age as previously reported in a *Clathrina* from California (Johnson, 1979).

Recently, several new species of yellow *Clathrina* have been described from Australia, Brazil and New Caledonia, species that are only slightly different from other related species in respect of spicule characteristics (Wörheide & Hooper, 1999; Borojevic & Klautau, 2000; Klautau & Borojevic, 2001). However, several

yellow specimens of *Clathrina coriacea* from the Norwegian coast have been investigated. No significant differences in the spicules or morphology of the cormus when compared with the white specimens were observed. It is concluded that at least in *C. coriacea* the colour of the live sponge is variable, and there is no reason to regard the yellow variety as a distinct species.

Re-examination of museum material revealed that the published records from the Norwegian coast by Haeckel (1872) and Burton (1930b) were *Clathrina cribrata* and *C. nanseni*, respectively, and that most of the records by Arnesen (1901a, b) were actually specimens belonging to *Guantha arnesenae* sp. nov., *G. blanca* and *Clathrina nanseni*. The report on *Leucosolenia coriacea* by Breitfuss (1897, 1898c) only refers to Haeckel's misidentified specimen of *C. cribrata*. Size of spicules and organization of the cormus in the examined specimens agree very well with the type material. Spicule measurements of the neotype are from Klautau & Valentine (2003).

CLATHRINA CRIBRATA RAPP ET AL., 2001

(FIGS 5A–D, 6, TABLE 3)

Original description: *Clathrina cribrata* Rapp et al., 2001: 70–71, figure 1A–C.

Synonyms and citations

Clathrina cribrata (Klautau & Valentine, 2003: 23–24).

Clathrina coriacea (Haeckel, 1872 pars.).

Clathrina primordialis (Burton, 1930b: 488, 1963).

Type locality: Kristiansund, western Norway. No coordinates indicated on the original label. Approximate location, 63°10'N, 07°40'E.

Holotype: BMNH 1931.10.28.2.

Previous records: The species was reported from Bergen by Haeckel (1872) as *C. coriacea*, and from Kristiansund and Trondheimsfjord by Rapp et al. (2001).

Table 3. Spicule measurements of *Clathrina cribrata* Rapp et al., 2001

| Spicule | Length (µm) | | | | Width (µm) | | N |
|----------------------------|-------------|------|----|------|------------|----|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Holotype BMNH 1931.10.28.2 | | | | | | | |
| Triactines | 48 | 69 | ±7 | 75 | 6 | ±1 | 30 |
| VM-16863 | | | | | | | |
| Triactines | 51 | 67 | ±6 | 78 | 6 | ±1 | 30 |
| VM-16866 | | | | | | | |
| Triactines | 49 | 65 | ±6 | 73 | 6 | ±1 | 30 |
| ZMO B-1278 | | | | | | | |
| Triactines | 39 | 53 | ±5 | 63 | 6 | ±1 | 30 |

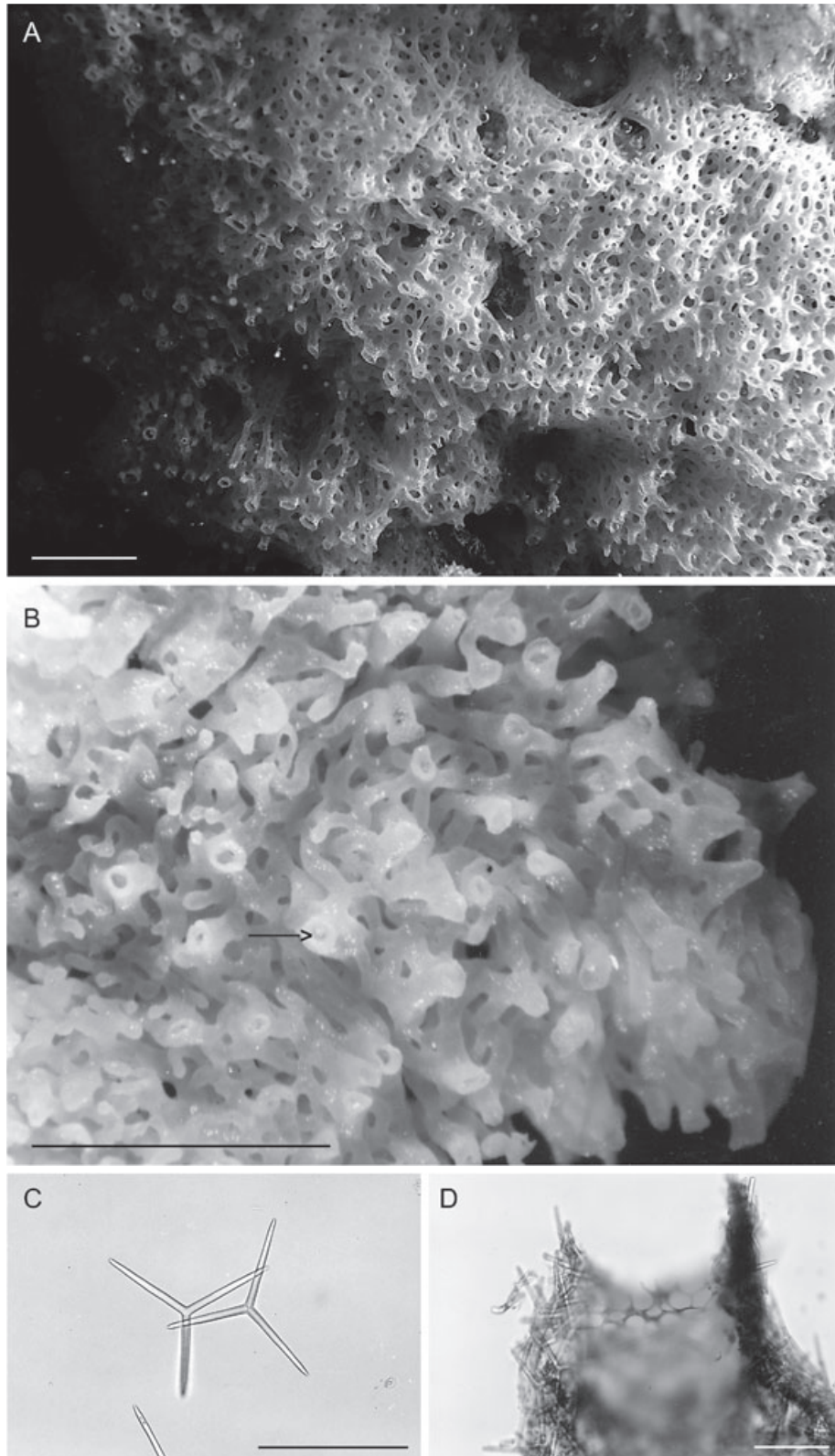


Figure 5. A, *Clathrina cribrata* at 5 m depth. Scale bar = 1 cm. B, holotype of *Clathrina cribrata*. Note the many erect oscular tubes (arrow). Scale bar = 1 cm. C, regular triactines. Scale bar = 100 μ m. D, transverse section of the osculum, showing the sieve of cells (cribrum). Scale bar = 100 μ m.

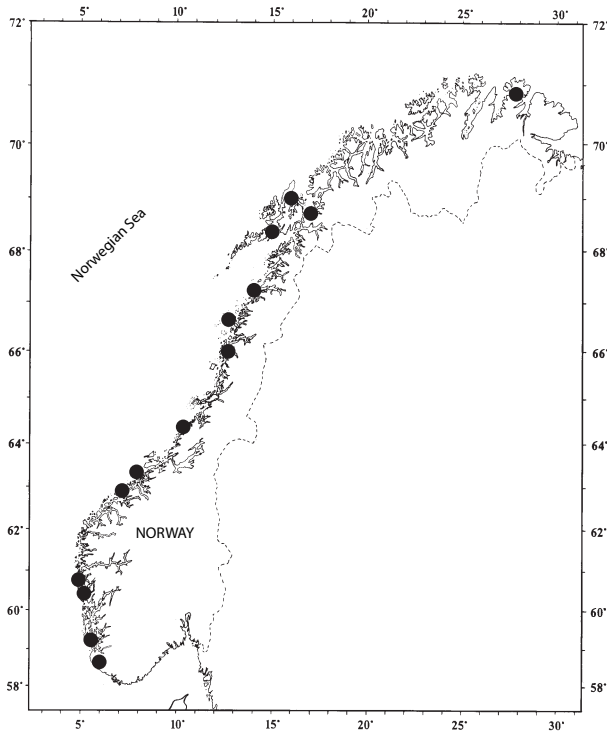


Figure 6. Distribution of *Clathrina cribrata* along the Norwegian coast.

Additional material examined: 23 specimens.

VM. VM-16855, Vestrefjord, Romsdalsfjord, 62°40'N, 07°00'E, littoral, 20.07.1932, 1 specimen (fragmentary). VM-16856, Breivik, Herdlevær, 60°34'N, 04°52'E, littoral, 15.09.1936, 2 specimens (fragmentary). VM-16857, Langholm, Kvitsøy, 59°04'N, 05°25'E, littoral, 02.10.1937, 6 specimens (fragmentary). VM-16858, Marøy, Vikna, 64°51'N, 11°15'E, littoral, 11.07.1938, 3 specimens. VM-16859, Rogsøy, 68°49'N, 15°32'E, littoral, 26.03.1934, 1 specimen (fragmentary). VM-16860, Sørkråkøy, 64°09'N, 10°09'E, littoral, 29.04.1933, 1 specimen (fragmentary). VM-16861, Gausvik, 68°39.5'N, 16°31'E, littoral, 23.07.1933, 1 specimen. VM-16862, Helløy, Støtt, 66°54'N, 14°24'E, littoral, 25.07.1933, 1 specimen (fragmentary). VM-16863, Torskefjord, Laksefjord, 70°42'N, 27°05'E, littoral, 07.09.1932, 1 specimen (fragmentary). VM-16864, Kvaløy, 66°29'N, 12°02'E, littoral, 01.07.1937, 1 specimen. VM-16865, Vågan, 68°13'N, 14°29'E, littoral, 07.07.1937, 1 specimen (fragmentary). VM-16866, Rosøya, Tjøtta, 65°50'N, 12°20'E, littoral, 26.07.1933, 1 specimen (fragmentary). VM-16867, Gibostad, 69°21'N, 18°05'E, 50 m, 27.07.1917, 1 specimen (dry). ZMO. B-1278, Bergen, Haeckel-material, no other information on the label, 1 specimen (dry). B-1279, Balsnes, 69°34.1'N, 18°52'E, 40–60 m, 1 specimen.

Description

The cormus is massive and composed of large, irregular and loosely anastomosed tubes. On the surface of the cormus, tubes are no longer anastomosed, but distally ramified, similar to what is found in the genus *Soleneiscus*. Some of these tubes end in a cul-de-sac, whereas others are opened at the end, and function as oscula. Water-collecting tubes are absent. Immediately below the oscula, which are simple apertures, there is always a sieve formed by spread cells arranged in a mono-layer, with oval apertures measuring 17–27 µm. No spicules are found in this sieve. The colour is white to greyish-white when alive, and beige in alcohol. Surface is smooth. The wall of the tubes is thin (25 µm), and its skeleton has no special organization. Spicules are only triactines, of a homogeneous size. They are equiangular and equiradiate, but parasagittal spicules are also common. Actines are cylindrical, slightly undulated, with a blunt end.

Distribution

The species is found along the entire Norwegian coast except from the southernmost part, littoral to 60 m. No records outside the Norwegian coast.

Remarks

Clathrina cribrata is different from all other described species of the genus *Clathrina* because of the sieve of cells below the osculum and the peculiar anastomosis of the tubes. Such a sieve has previously been described in '*Clathrina coriacea*' from the littoral zone in Plymouth (Minchin, 1892). Several specimens of *C. coriacea* from the type locality have been examined, and no sieve has been observed in the oscular tubes. It is therefore concluded that no sieve is present in *C. coriacea*, and that Minchin's specimen was not *C. coriacea*, but another *Clathrina* closely related to *C. cribrata* (Rapp *et al.*, 2001). The peculiar anastomosis of the tubes is not typical of *Clathrina*, but in many ways is similar to the organization of the cormus of *Soleneiscus* (Borojevic *et al.*, 1990) or perhaps something between these two genera. In *C. cribrata*, tubes are anastomosed as in *Clathrina*, but superficially they become ramified as in *Soleneiscus*. Because of the dominance of anastomosing tubes and the small size of the individual tubes when compared with species of *Soleneiscus*, the species is considered most closely related to the genus *Clathrina* (Rapp *et al.*, 2001; Klautau & Valentine, 2003). The specimen from Norway (Kristiansund) examined by Burton (1963), and identified as *C. primordialis*, was re-examined and described as *Clathrina cribrata* by Rapp *et al.* (2001). In his work on the Norwegian sponges from the Norman collection, Burton (1930b) also reported *C. primordialis* from Stavanger. Owing to Burton's

misconception of '*primordialis*' there is reason to believe that the specimen from Stavanger was not *primordialis* but *C. cribrata* or another *Clathrina*.

***CLATHRINA JORUNNAE* SP. NOV.**

(FIGS 7A, B, 8, TABLE 4)

Type locality: Ørdalsneset, Trondheimsfjord, Norway.

Holotype: VM-396, Ørdalsneset, Trondheimsfjord, Norway (63°51.5'N, 11°03.7'E), 25–200 m, 09.11.1995.

Etymology: In the memory of my grandmother Jorunn Lovise Berg who with impressive patience taught me the very first names of marine organisms.

Previous records: None.

Additional material examined: None.

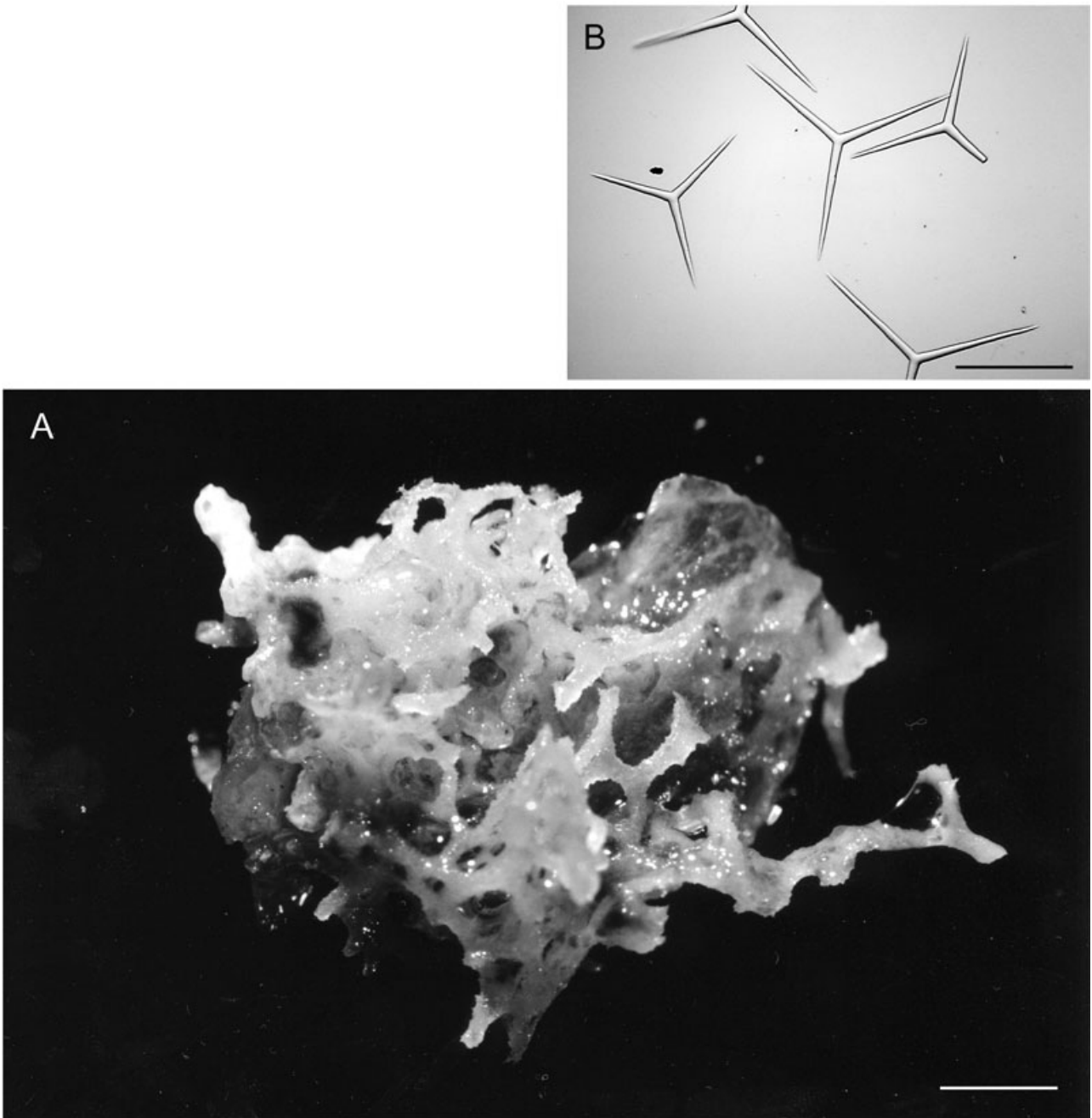


Figure 7. A, holotype of *Clathrina jorunnae* sp. nov. Scale bar = 1 mm. B, regular triactines of *C. jorunnae*. Scale bar = 100 µm.

Description

Cormus composed of very thin and highly irregularly and loosely anastomosing tubes. No oscula are visible on the surface. Water-collecting tubes are absent. Colour light beige when alive and white in alcohol. The surface of the tubes minutely hispid due to single actines of the triactines irregularly protruding through the outer surface. The texture is fragile but compressible. Cormus 8 mm in diameter. Skeleton composed of one group of equiangular and equiradiate triactines. The actines are straight, conical and sharply pointed.

Distribution

Only known from the type locality, dredged at 25–250 m depth. The specimen was attached to a bryozoan of the genus *Reteporella*.

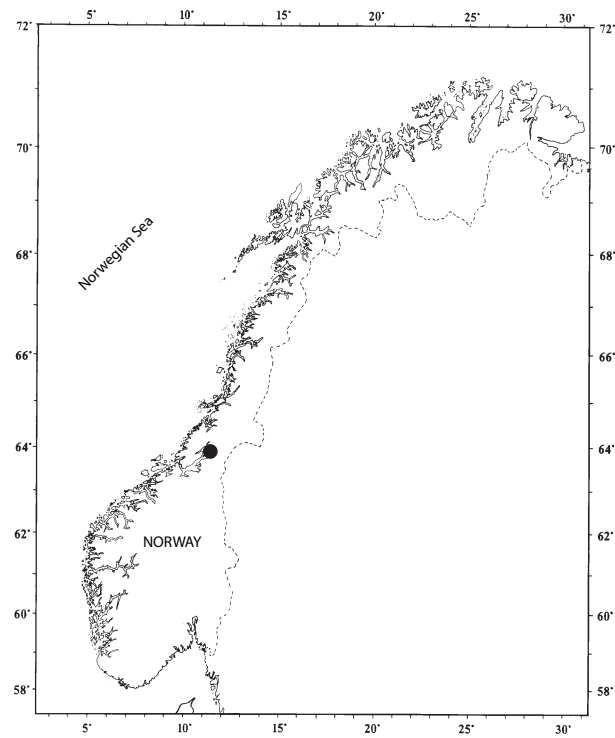


Figure 8. Distribution of *Clathrina jorunnae* sp. nov. along the Norwegian coast.

Remarks

The triactines of this species are large compared with those in *C. coriacea* and *C. cribrata*, and the actines are sharply pointed instead of rounded or blunt, respectively. The anastomosis of the cormus is very loose and irregular, and combined with the large triactines the species is not similar to any other Atlantic *Clathrina* species with only one population of triactines. The shape of the triactines, conical with sharp tips, and the loose and irregular anastomosis of the cormus resembles those in *Clathrina helveola* Wörheide & Hooper, 1999, *C. procumbens* (Von Lendenfeld, 1885), *C. sinusarabica* Klautau & Valentine, 2003 and *C. hondurensis* Klautau & Valentine, 2003. However, there are some important differences. *C. procumbens* and *C. hondurensis* differ from the other species by having a smooth tube surface. In addition, *C. procumbens* possess water-collecting tubes. The cormus in *C. helveola* is massive, partly covered by a thin cortex, whereas no such cortex is present in *C. jorunnae* sp. nov. *C. jorunnae* and *C. sinusarabica* are both composed of a very open meshwork of irregularly anastomosing tubes, and *C. sinusarabica* is the species considered most similar to *C. jorunnae*. There are two major differences between the two species. First, there is a large oscular tube in *C. sinusarabica* whereas no prominent oscula could be found in *C. jorunnae*. Secondly, the spicules are much bigger in *C. jorunnae* than in *C. sinusarabica* ($117 \times 10 \mu\text{m}$ and $91.9 \times 8.4 \mu\text{m}$, respectively).

CLATHRINA NANSENI (BREITFUSS, 1896)
(FIGS 9A–F, 10, TABLE 5)

Original description: *Leucosolenia nanseni* Breitfuss, 1896: 427–428.

Synonyms and citations

Ascetta coriacea (Arnesen, 1901a: 10–11).

Clathrina nanseni (Rapp *et al.*, 2001: 72–73; van Soest, 2001: 101).

Leucosolenia canariensis (Breitfuss, 1933: 240, pars).

Leucosolenia nanseni (Breitfuss, 1898a: 106–108, 1898b: 13, 1911: 224, 1933: 242).

Table 4. Spicule measurements of *Clathrina jorunnae* sp. nov.

| Spicule | Length (μm) | | | | Width (μm) | | N |
|-----------------|--------------------------|------|----------|------|-------------------------|----------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Holotype VM-396 | | | | | | | |
| Triactines | 92 | 117 | ± 10 | 136 | 10 | ± 2 | 30 |

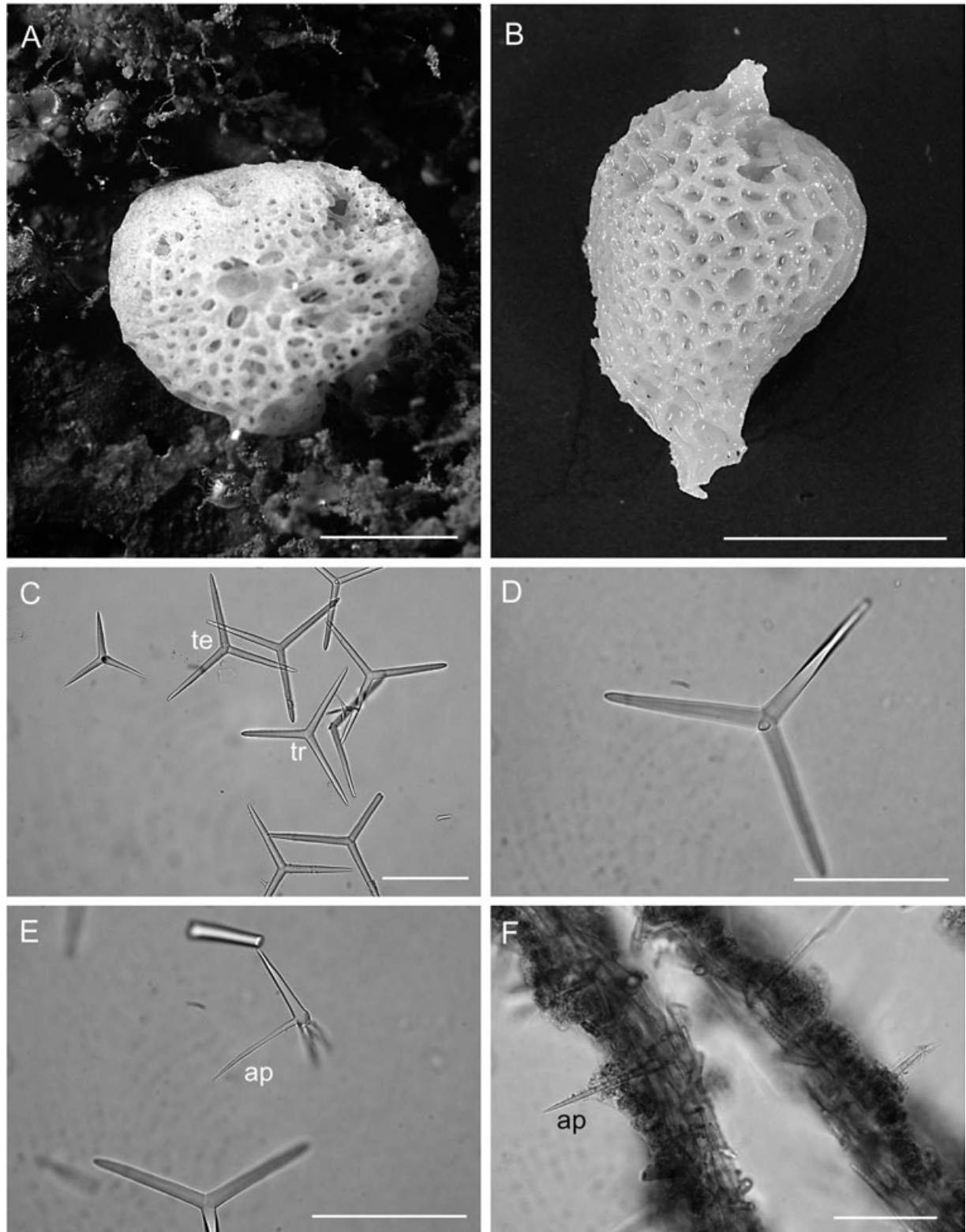


Figure 9. A, *Clathrina nanseni* at 5 m depth. Scale bar = 1 cm. B, habitus of a fixed specimen. Scale bar = 1 cm. C, spicules of *C. nanseni*. tr = regular triactine. te = regular tetractine. Scale bar = 100 μ m. D, tetractine with rudimentary and rounded apical actine. Scale bar = 100 μ m. E, sharply pointed apical actine of a normal tetractine (ap). Scale bar = 100 μ m. F, section of ascon tubes with the apical actines (ap) projecting into the interior of the tube. Scale bar = 100 μ m.

Type locality: The original description refers to Deeviebai, Tjuvfjorden, eastern Spitsbergen, at approximately 77°20'N, 20°E, 30 m depth, and north of Ryke Yseøyene, at approximately 77°40'N, 25°E,

130 m depth as the type locality. No further information is given on the label. Breitfuss (1896) never indicated which specimen should be regarded as the type specimen. I have elected the only complete specimen to be the lectotype and the remaining specimen to be the paralectotype.

Lectotype: ZIL, Breitfuss collection no. 1.

Paralectotype: ZIL, Breitfuss collection no. 2.

Previous records: From Tromsø as *C. canariensis* (Breitfuss, 1933) (see remarks), and from Balsnes and Tromsø as *Ascetta coriacea* (Arnesen, 1901a).

Additional material examined: 158 specimens.

TMU. TM-145, Korsfjord, Sør-Varanger, 69°45'N, 29°46.4'E, 25–30 m, 12.07.1937, 4 specimens. TM-146, Evenskjer, 68°35'N, 16°35'E, 60–85 m, 12.08.1913, 1 specimen. TM-147, Grindøya, Tromsø, 69°37'N, 18°54'E, 25.07. 1891, 1 specimen. TM-148, Hamnbukt, Porsanger, 70°05'N, 25°05'E, 0–20 m, 09.08.1956, 2 specimens. TM-149, Lysbotngrunnen, Porsanger, 70°36.2'N, 25°42'E, 16–20 m, 15.08.1956, 1 specimen. TM-151, indre Porsanger, Rodnessjøen, 70°13'N, 25°20'E, 30–38 m, 11.09.1959, 6 specimens. TM-152, Kjøfjord, 69°45.3'N, 29°38.5'E, 15–20 m, 14.07.1937, 2 specimens. TM-153, Brusund, 100 m, 14.09.1959, 2 specimens. TM-156, Porsangerfjord, 70°17.2'N, 25°22.8'E, 60–65 m, 07.07.1939, 1 specimen. TM-157, Tromsø, 69°40'N, 19°00'E, 40–60 m, 1 specimen. TM-158, Aldesfjord, 30–40 m, 12.09.1959, 1 specimen. TM-159, Hamnbukt, Porsanger, 70°05'N, 25°05'E, 20 m, 09.08.1956, 3 specimens. TM-160, Jekkigrunnen, indre Porsanger, 70°10'N, 25°10'E, 40–60 m,

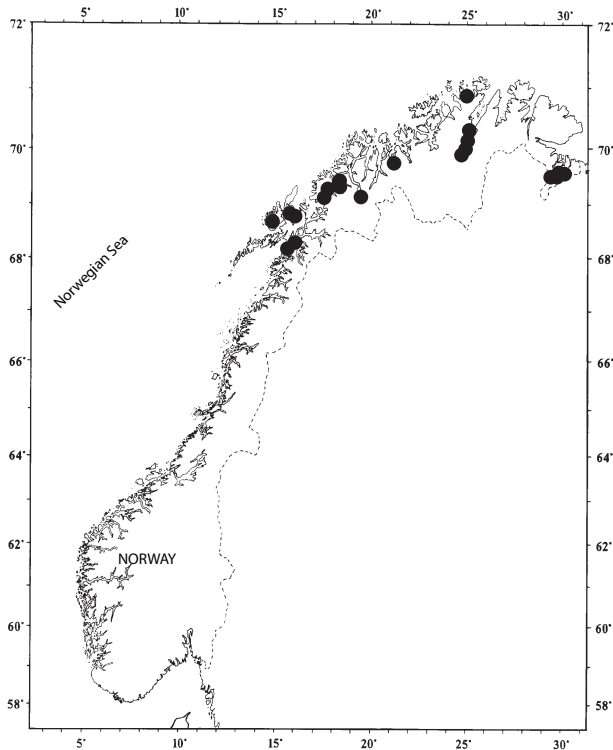


Figure 10. Distribution of *Clathrina nanseni* along the Norwegian coast.

Table 5. Spicule measurements of *Clathrina nanseni* (Breitfuss, 1896)

| Spicule | Length (µm) | | | | Width (µm) | | N |
|--|-------------|------|-------|------|------------|------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Lectotype ZIL Breitfuss coll. no. 1 | | | | | | | |
| Triactines | 85 | 104 | ±8.3 | 125 | 11 | ±1.1 | 30 |
| Tetractines | 78 | 99 | ±9.4 | 124 | 10 | ±0.9 | 30 |
| Apical actine | 24 | 56 | ±13.4 | 76 | 4.2 | ±0.8 | 30 |
| VM-16869 | | | | | | | |
| Triactines | 94 | 104 | ±8 | 128 | 11 | ±1 | 30 |
| Tetractines | 90 | 107 | ±9 | 124 | 11 | ±1 | 30 |
| Apical actine | 42 | 64 | ±11 | 80 | 4 | ±1 | 30 |
| VM-16868 | | | | | | | |
| Triactines | 73 | 91 | ±7 | 107 | 10 | ±1 | 30 |
| Tetractines | 83 | 90 | ±5 | 102 | 10 | ±1 | 30 |
| Apical actine | 32 | 57 | ±12 | 76 | 4 | ±1 | 30 |
| VM-16870 | | | | | | | |
| Triactines | 90 | 108 | ±9 | 122 | 11 | ±1 | 30 |
| Tetractines | 92 | 109 | ±7 | 116 | 10 | ±1 | 30 |
| Apical actine | 21 | 61 | ±13 | 73 | 4 | ±1 | 30 |

11.09.1959, 1 specimen. TM-161, Balsnes, 69°34'N, 18°52'E, 10–30 m, 06.07.1955, 1 specimen. TM-163, Brusund, 100 m, 14.09.1959, 1 specimen. TM-164, Bøkfjord, 69°52.2'N, 29°58.1'E, 5–13 m, 26.06.1937, 2 specimens. TM-165, Kvænangen, 69°47'N, 21°45.7'E, 50–52 m, 25.06.1938, 1 specimen. TM-166, Jarfjord, 69°40.7'N, 30°24.7'E, 30–45 m, 03.07.1937, 1 specimen. TM-167, Kjølford, 69°45.3'N, 29°38.5'E, 15–20 m, 14.07.1937, 1 specimen. TM-168, Porsangerfjord, 70°17.2'N, 25°22.8'E, 60–65 m, 07.07.1939, 1 specimen. VM-16868, Finnsnes, 69°14'N, 17°58'E, 25–35 m, 06.06.1914, 7 specimens. VM-16869, Lødingen, 68°24'N, 15°58'E, 25–45 m, 06.08.1912, 2 specimens. VM-16870, Ramfjorden, 69°33'N, 10°10'E, 20–49 m, 11.07.1921, 2 specimens. VM-16871, Flatøysund, Bjarkøy, 69°05'N, 16°30'E, 90–100 m, 13.07.1933, 3 specimens. VM-16872/18673, Rystrømmen, 69°33'N, 18°44'E, 35 m, 15.05.1921, 10 specimens. VM-16874, Ramfjorden, 69°33'N 10°10'E, 28.07.1921, 2 specimens. VM-16875, Lødingen, 68°24'N, 15°58'E, 25–45 m, 06.08.1912, 1 specimen. VM-16876, Evenskjer, 68°35'N, 16°35'E, 45–50 m, 23.07.1912, 3 specimens. VM-16877, Gibostad, 69°21'N, 18°05'E, 25 m, 15.07.1910, 3 specimens. VM-16878, Evenskjer, 68°35'N, 16°35'E, 33–39 m, 19.08.1919, 1 specimen. VM-16879, Ramfjorden, 69°33'N, 10°10'E, 20–35 m, 11.07.1921, 1 specimen. VM-16880, Gibostad, 69°21'N, 18°05'E, 40 m, 24.01.1912, 1 specimen. VM-16881, Ramfjorden, 69°33'N 10°10'E, 10–20 m, 14.07.1921, 1 specimen. VM-16882, Bjarkøy, 68°58'N, 16°42'E, 60–90 m, 07.09.1912, 1 specimen. VM-16883, Evenskjer, 68°35'N, 16°35'E, 60–85 m, 12.08.1913, 3 specimens. VM-16884, Gibostad, 69°21'N, 18°05'E, 15–25 m, 25.05.1912, 2 specimens. VM-16885, Evenskjer, 68°35'N, 16°35'E, 25–65 m, 03.08.1911, 2 specimens. VM-16886, Gibostad, 69°21'N, 18°05'E, 50 m, 23.05.1912, 1 specimen (dry). VM-16887, Evenskjer, 68°35'N, 16°35'E, 35–40 m, 09.08.1919, 1 specimen (dry). VM-16888, Evenskjer, 68°35'N, 16°35'E, 50–70 m, 11.08.1919, 2 specimens (dry). VM-16889, Finnsnes, 69°14'N, 17°58'E, 25–40 m, 18.06.1914, 7 specimens (dry). VM-16890, Evenskjer, 68°35'N, 16°35'E, 50 m, 19.08.1919, 2 specimens (dry). ZMO. B-1280, Horsnes, Lyngen, 69°19'N, 20°02'E, 60 m, 1 specimen. B-1281, south of Tromsøya, 69°35'N, 18°55'E, 6–8 m, 04.06.1946, 1 specimen. B-1282, Gjesvær, 71°06'N, 25°22'E, 07. 1894, 1 specimen. B-1283, Tromsø, 69°40'N, 19°00'E, 1 specimen. B-1284, Tromsø, 69°40'N, 19°00'E, 1900, 37 specimens. B-1285, Balsnes, 69°34'N, 18°52'E, 60 m, 11 specimens. ZMUC. Haugneset, Ramfjord, 15 m, 2 specimens.

Description

The cormus of this species is composed of regularly and tightly anastomosing tubes forming a massive

and more or less globular or pear-shaped cormus. Up to 5 cm in diameter. The cormus is often wider at the top than at the base, and some specimens have a poorly developed stalk composed of normal tubes with choanoderm. Water-collecting tubes converge at the centre of the sponge, ending in one or several large oscula. Texture is soft. White to greyish white in life and greyish white to light brown in alcohol.

The skeleton has no special organization, and it is composed of regular and equiangular triactines of one type, and two types of tetractines. Slightly parasagittal triactines are sometimes present in the base of the sponge. The apical actine of the tetractines is projected into the interior of the tubes. Actines are cylindrical to slightly conical with short points. In the first type of tetractines the apical actine is thinner than the facial ones, cylindrical, slightly curved and sharply pointed. In the other type of tetractines the apical actine is very short or rudimentary. Breitfuss (1896) named these spicules as 'triactines with a flat knob in the middle' but in my opinion they should be regarded as tetractines with a poorly developed apical actine. Both types of tetractines are of equal size.

Distribution

Northern Norway, shallow sublittoral to 100 m. The species is widely distributed in the Arctic (north-east Canada, Greenland, Iceland, Spitsbergen, Bear Island and the Murman coast), shallow sublittoral to 650 m.

Remarks

Clathrina nanseni is very similar to *C. septentrionalis* (Rapp *et al.*, 2001), but can be distinguished from *C. septentrionalis* by the presence of tetractines with a rudimentary apical actine, slightly parasagittal triactines in the basal part of the sponge, and by absence of special cells with brown inclusions (Rapp *et al.*, 2001; Klautau & Valentine, 2003). A quite large variation in spicule size between individuals is observed, with mean values of triactines and tetractines ranging from 90 to 108 µm on the Norwegian coast (reported here), about 110 µm close to Bear Island, and 115 µm in Duvefjord, northern Spitsbergen (my pers. observ.). Spicules from the specimens from Spitsbergen and Bear Island described by Breitfuss (1896, 1898a) are of the same size as the largest found in Norway, and are very close to what was found in the new material from the same areas. Breitfuss separated *C. nanseni* from the closely related *C. canariensis* (Miklucho-Maclay, 1868) by the presence or absence of the apical actine of the tetractines in the interior of the tubes. He stated that the apical actines in *C. nanseni* were covered by a layer of cells, forming small and flattened papillae on the

atrial side of the tubes, while in *C. canariensis* the apical actines protrude into the atrium. However, re-examination of the type material revealed free apical actines also in *C. nanseni*. Breitfuss (1933) reported a specimen of *Leucosolenia canariensis* from Tromsø, but the specimen has not been found. According to the recent revision of the genus *Clathrina* (Klautau & Valentine, 2003) true *canariensis* is only found in the Mediterranean and around the Canary Islands. The spicules are considerably smaller in *C. canariensis* than in *C. nanseni*, but as shown here the size of the spicules in this species is variable. In addition, Breitfuss was aware of the close relationship between *canariensis* and *nanseni*; given that no other specimens of *C. canariensis* have been found in this investigation, the large variation in spicule size reported here and the presence of apical actines in the atrium also in *C. nanseni* it is most likely that Breitfuss' specimen was actually a specimen of *C. nanseni*. The presence of a peduncle in some specimens of *C. nanseni* have raised the question of whether the species should be allocated to the genus *Guancha* instead of *Clathrina* (Rapp *et al.*, 2001; Klautau & Valentine, 2003). However, re-examination of the type specimens revealed no consistent presence of parasagittal spicules, even in the peduncle. Some spicules were slightly parasagittal, which is also common among several species of *Clathrina*. It is therefore concluded that the species should remain in the genus *Clathrina*.

CLATHRINA SEPTENTRIONALIS RAPP *ET AL.*, 2001
(FIGS 11A–D, 12, TABLE 6)

Original description: *Clathrina septentrionalis* Rapp *et al.*, 2001: 72–73, figure 2A–C.

Synonyms and citations

Clathrina septentrionalis (Klautau & Valentine, 2003: 39–40).

Type locality: Langfjorden, Norway. Stn. 76. 10 m. No coordinates are indicated on the original label. Approximate location, 70°05'N, 22°40'E.

Holotype: BMNH 1910.1.1.790. From the Norman Collection.

Paratype: BMNH 1910.1.1.789. Langfjorden, Norway. Collected in 1890. 30–50 m. Approximate location, 70°05'N, 22°40'E.

Previous records: Langfjorden (type locality) and VM-16892, Fagernes, Ramfjord, Norway. No coordinates are indicated on the original label. Approximate location, 69°33'N 10°10'E, 1 specimen (Rapp *et al.*, 2001).

Additional material examined: 1 specimen. ZMO. B-1286, south of Tromsøya, 69°35'N, 18°55'E, 6–8 m, 04.06.1946, 1 specimen.

Description

The cormus of the holotype is well delimited, massive or cushion shaped, composed of thin, irregular and tightly anastomosed tubes. Water-collecting tubes converge at the centre of the sponge, ending in large central oscula, which are localized at the top of conical projections. The species is creamy white when alive, and light beige to dark brown in alcohol. Cells with brown inclusions are scattered in the mesohyl. The skeleton is composed of equiangular and equiradiate triactines and tetractines. Triactines are slightly more abundant than tetractines. Actines are cylindrical, with a blunt end. The apical actine of the tetractines is projected into the interior of the tubes. It is thinner than the facial ones, cylindrical, sharp, smooth and slightly curved at the end.

Distribution

The species is known from two localities on the northernmost coast of Norway and one on the south-west

Table 6. Spicule measurements of *Clathrina septentrionalis* Rapp *et al.*, 2001

| Spicule | Length (µm) | | | | Width (µm) | | N |
|----------------------------|-------------|------|-----|------|------------|----|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Holotype BMNH 1910.1.1.790 | | | | | | | |
| Triactines | 95 | 113 | ±10 | 135 | 10 | ±1 | 30 |
| Tetractines | 98 | 111 | ±10 | 125 | 9 | ±1 | 30 |
| Apical actine | 53 | 72 | ±11 | 88 | 5 | ±1 | 30 |
| ZMO B-1286 | | | | | | | |
| Triactines | 94 | 112 | ±11 | 137 | 10 | ±1 | 30 |
| Tetractines | 97 | 110 | ±9 | 131 | 9 | ±1 | 30 |
| Apical actine | 40 | 70 | ±15 | 82 | 5 | ±1 | 30 |

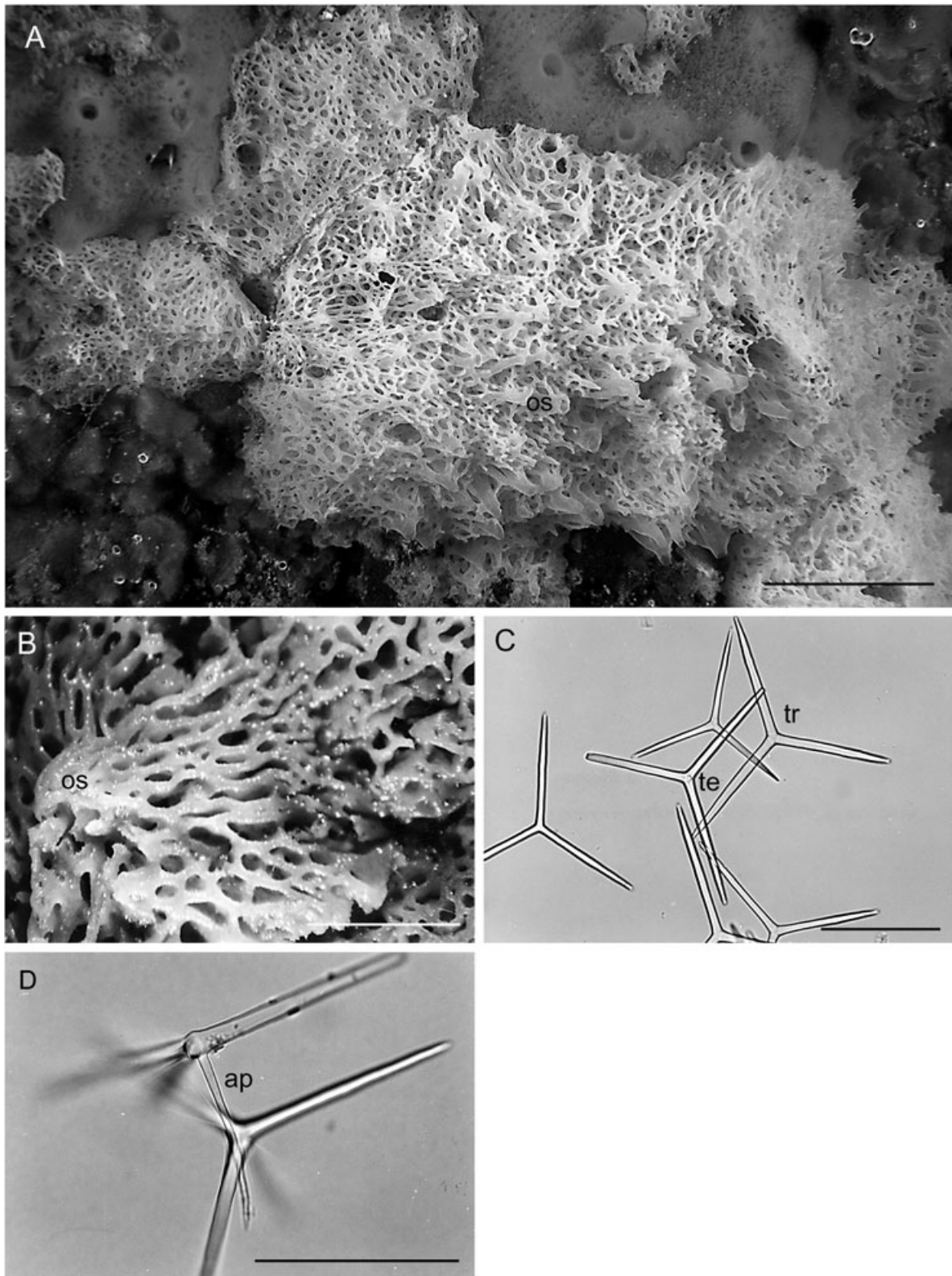


Figure 11. A, large specimen of *Clathrina septentrionalis* at 3 m depth. Note the large oscular tubes (os). Scale bar = 1 cm. B, holotype of *Clathrina septentrionalis*. os = osculum. Scale bar = 1 cm. C, spicules of *C. septentrionalis*. tr = regular triactines and te = regular tetractines. Scale bar = 100 μ m. D, apical actine of a tetractine (ap). Scale bar = 100 μ m.

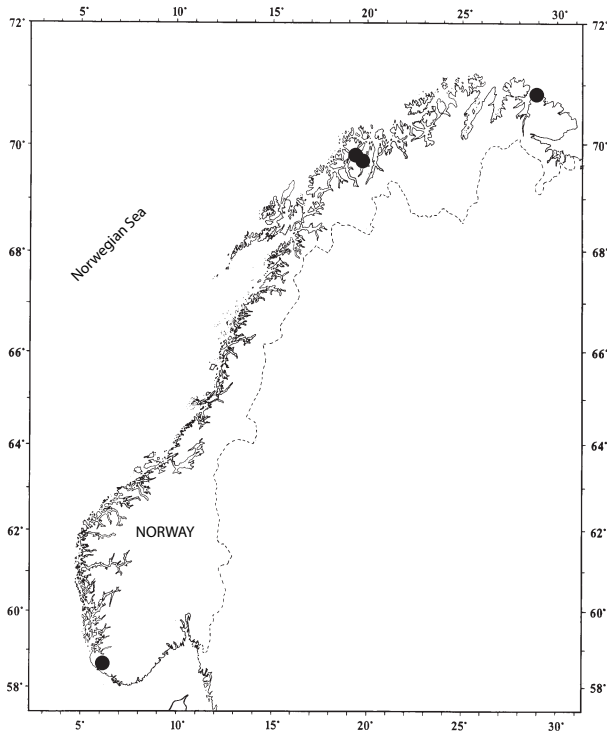


Figure 12. Distribution of *Clathrina septentrionalis* along the Norwegian coast.

coast, at a depth of 3–50 m. The species is also known from south-west Ireland (Rapp *et al.*, 2001; Klautau & Valentine, 2003).

Remarks

See remarks under '*Clathrina nanseni*'. Detailed information can be found in Rapp *et al.* (2001) and Klautau & Valentine (2003).

GUANCHA MIKLUCHO-MACLAY, 1868

Type species: Guancha blanca Miklucho-Maclay, 1868. Clathrinidae with a cormus composed of a peduncle and a clathroid body. The peduncle may be formed by true tubes with a normal choanoderm, or may be solid with a special skeleton. The skeleton is composed of regular (equiangular and equiradiate) spicules to which parasagittal spicules may be added, at least in the peduncle. In some species, only parasagittal spicules are present. The unpaired actine of parasagittal spicules is always basipetally orientated.

Remarks on *Guancha*

Prior to this work, the genus was represented by 'about six' species (Borojevic *et al.*, 2002). Species within the genus *Guancha* display a progressive dif-

ferentiation into a clathroid body and a peduncle. In the more simple species, such as *G. arnesenae* sp. nov., *G. blanca* Miklucho-Maclay, 1868 and *G. sagittaria* (Haeckel, 1872), the peduncle is composed of normal tubes with a complete choanoderm. *G. blanca* is only slightly different from a typical *Clathrina*, and only the fact that it represents the starting point for an evolutionary line makes it possible to separate it into a distinct genus (Borojevic & Peixinho, 1976). In more morphologically complex species such as *Guancha challengerii* (Poléjaeff, 1883), *G. lacunosa* (Johnston, 1842) and *G. pulcherrima* (Dendy, 1891) the peduncle acquires a solid form, consequently with no choanoderm, and with a particular skeleton. *Guancha* is also characterized by possessing parasagittal triactines organized in a parallel manner with the unpaired actine basipetally orientated. In *G. blanca* the parasagittal spicules are found in the peduncle only, whereas in species such as *G. arnesenae* sp. nov., *G. tetela* Borojevic & Peixinho, 1976 and *G. sagittaria* all the spicules are parasagittal.

The classification of *Guancha* is especially difficult when the skeleton is composed of more-or-less uniform spicules with only slightly longer unpaired actine in the peduncular triactines. *G. blanca* has been reported from most oceans, from the littoral zone to the abyssal plains (Barthel & Tendal, 1993; Janussen, Rapp & Tendal, 2003). Cosmopolitanism is very rare among sponges (Klautau *et al.*, 1999), and in the closely related *Clathrina* the use of statistical analyses of shape, size and distribution of spicules, combined with molecular methods, have shed new light on the classification of the genus, and have revealed that geographical distribution of the different species is more restricted (Klautau *et al.*, 1994; Wörheide & Hooper, 1999; Rapp *et al.*, 2001; Klautau & Valentine, 2003). In agreement with Borojevic *et al.* (2002), I consider that *G. 'blanca'* represents a complex of species, and that the ongoing work revising the genus, including analysing specimens of *G. 'blanca'* from different geographical regions and from shallow to abyssal depths with a morphological and molecular approach, will reveal a number of new species.

GUANCHA ARNESENAE SP. NOV.

(FIGS 13A, B, 14, TABLE 7)

Type locality: Evenskjer, 68°35'N, 16°35'E, 25 m.

Holotype: VM-398, Evenskjer, 68°35'N, 16°35'E, 25 m, 18.08.1919, 1 specimen.

Paratype: TM-183, Ramfjorden, 10–20 m, 14.07.1921, 1 specimen.

Etymology: Named in memory of the Norwegian spongiologist Emily Arnesen (1867–1928).

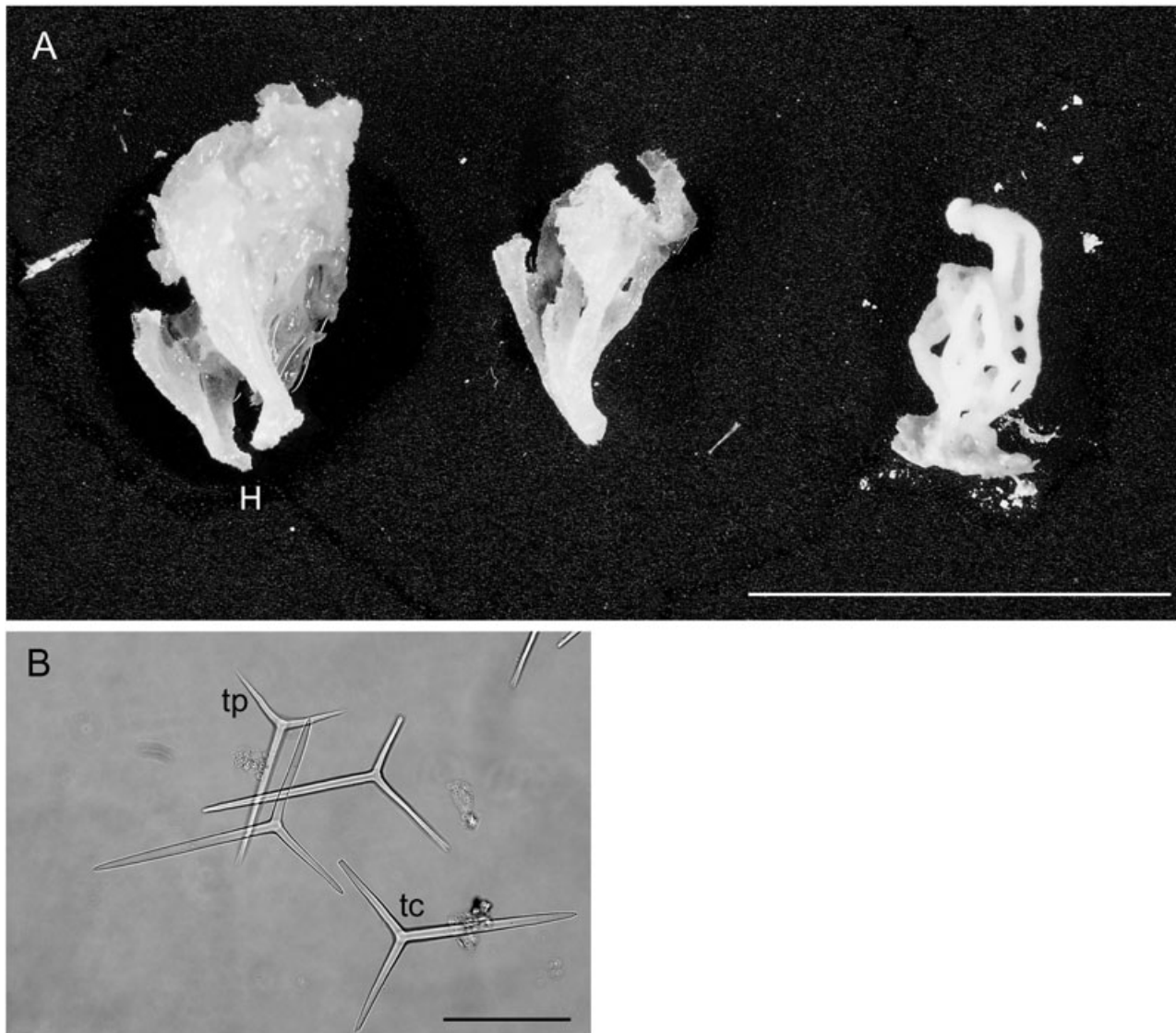


Figure 13. A, fixed specimens of *Guancha arnesenae* sp. nov. H = holotype. Scale bar = 1 cm. B, parasagittal triactines from the cormus (tc) and from the peduncle (tp). Scale bar = 100 µm.

Previous records: None.

Additional material examined: 28 specimens.

IB. Evenskjer, 68°35'N, 16°35'E, 25 m, 18.08.1919, 2 specimens. TMU. TM-150, Ramfjorden, 69°33'N, 10°10'E, 10–20 m, 14.07.1921, c. 10 specimens (small and fragmentary). VM. VM-16904, Tromsø, 69°40'N, 19°00'E, 30–35 m, 28.10.1916, 1 specimen. VM-16905, Tromsø, 69°40'N, 19°00'E, 30 m, 21.09.1917, 1 specimen. VM-16906, Gibostad, 69°21'N, 18°05'E, 50 m, 23.05.1912, 4 specimens (dry). VM-16907, Lødingen, 68°24'N, 15°58'E, 70–90 m, 22.08.1913, 1 specimen (dry). ZMO. B-1289, Balsnes, 69°34'N, 18°52'E, 40–60 m, 9 specimens.

Description

Clathrinidae with a cormus normally composed of a clathroid cormus of irregularly and loosely anastomosing tubes and a peduncle. Size ranging from 4 to 10 mm in height. Several true tubes with a normal choanoderm form the peduncle. The peduncular tubes run in parallel, sometimes free, or slightly anastomosed. In specimens without a proper peduncle the cormus is narrower at the base than in the apical region. Water-collecting tubes converge at the centre of the sponge, ending in one or several apical oscula. The single tubes are about 0.5 mm in diameter. Colour is light beige in alcohol and when dried. Texture soft. The skeleton of the cormus is solely

composed of tripodic, parasagittal triactines. The spicules are irregularly orientated in several layers in the walls of the tubes, resulting in a wall thickness of about 30–50 µm. In the peduncle the skeleton

consists of tripodic parasagittal triactines, generally similar to those in the cormus, but with shorter paired actines. In addition, there are very characteristic parasagittal triactines where the paired actines are bent, forming a concave ‘U’. Spicules in the peduncle with their unpaired actine basipetally orientated. All the actines are straight, cylindrical and with blunt tips.

Distribution

The species is found in the northern part of Norway at 10–90 m depth.

The species is also known from Greenland at 30–54 m depth (my unpubl. data).

Remarks

The species is very similar to *Guancha sagittaria* Haeckel, 1872. However, there are some differences. Haeckel (1872) made his original description based on three very small olynthus tubes, dredged from Storebælt (Denmark) during the Pommerania-Expedition in 1871, probably representing very young specimens. All the specimens examined here have clathroid cormi, and a more-or-less developed peduncle. Both species have the typical shape of the parasagittal triactines from the peduncle, but whereas all spicules are cylindrical in *G. arnesenae* they are conical in *G. sagittaria* (Haeckel, 1872). The presence of only parasagittal triactines in *G. arnesenae* differentiates it from all other species of *Guancha* except *Guancha tetela* Borojevic &

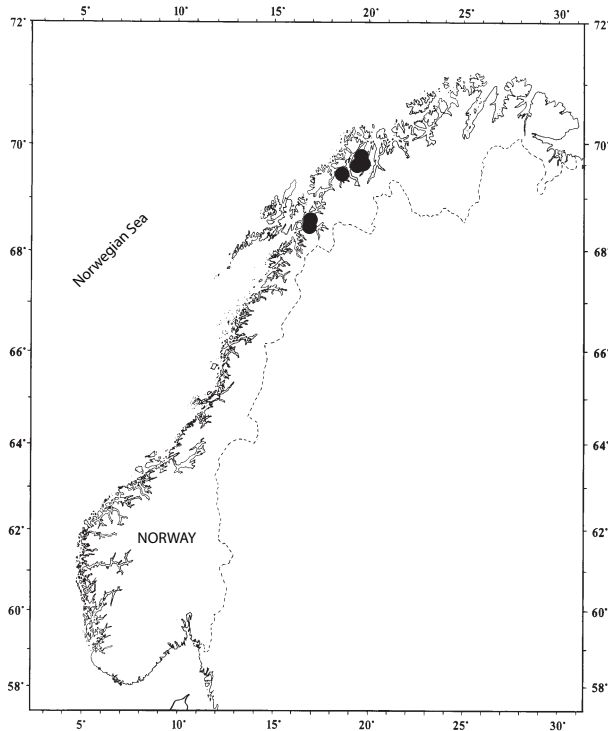


Figure 14. Distribution of *Guancha arnesenae* sp. nov. along the Norwegian coast.

Table 7. Spicule measurements of *Guancha arnesenae* sp. nov.

| Spicule | Length (µm) | | | | Width (µm) | | N |
|--------------------------|-------------|------|-----|------|------------|------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Holotype VM-398 | | | | | | | |
| Triactines from body | | | | | | | |
| Paired actines | 55 | 78 | ±13 | 120 | 8.4 | ±1.1 | 30 |
| Unpaired actine | 95 | 131 | ±18 | 160 | 9.8 | ±1.2 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 50 | 63 | ±5 | 75 | 9.5 | ±1.1 | 30 |
| Unpaired actine | 115 | 135 | ±12 | 160 | 10.8 | ±1.2 | 30 |
| Paratype TM-183 | | | | | | | |
| Triactines from body | | | | | | | |
| Paired actines | 45 | 75 | ±15 | 125 | 8.3 | ±1.1 | 30 |
| Unpaired actine | 95 | 128 | ±16 | 155 | 9.7 | ±1.0 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 40 | 61 | ±7 | 70 | 9.4 | ±1.2 | 30 |
| Unpaired actine | 110 | 132 | ±11 | 160 | 10.6 | ±1.4 | 30 |

Peixinho, 1976 from Brazil. However, *G. arnesenae* and *G. tetela* are easily distinguished by the shape of the paired actines of the parasagittal triactines from the peduncle, forming a concave 'U' in *arnesenae* and close to a 'T' in *tetela*.

GUANCHA BLANCA MIKLUCHO-MACLAY, 1868
(FIGS 15A–D, 16, TABLE 8)

Original description: *Guancha blanca* Miklucho-Maclay, 1868: 221–232, plates 4 and 5.

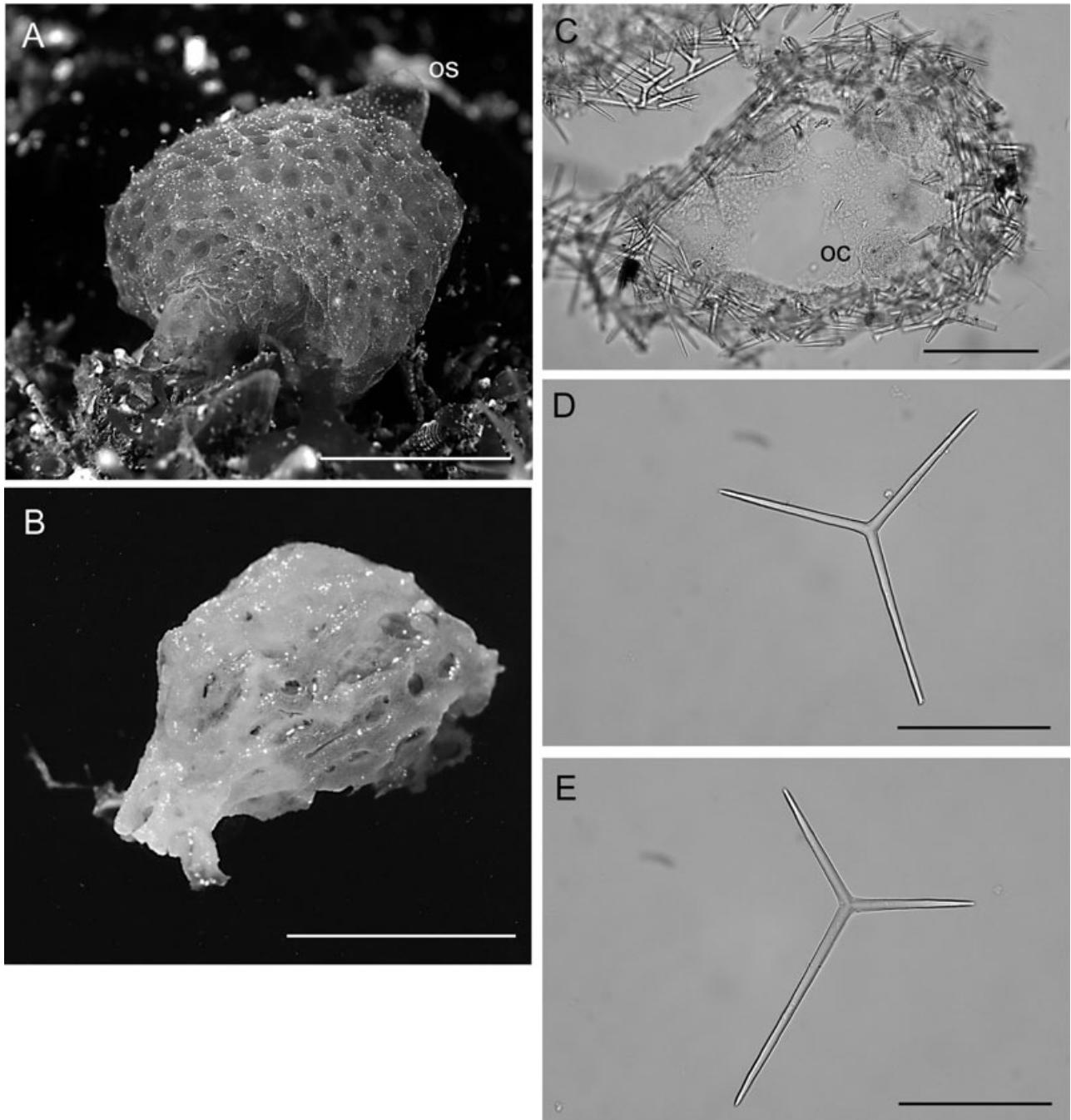


Figure 15. A, *Guancha blanca* at 10 m depth. os = osculum. Scale bar = 1 cm. B, habitus of a fixed specimen. Scale bar = 1 cm. C, section through an ascon tube with mature oocytes (oc). Scale bar = 100 μ m. D, slightly parasagittal triactine from the cormus. Scale bar = 100 μ m. E, parasagittal triactines from the peduncle. Scale bar = 100 μ m.

Synonyms and citations

Ascetta blanca (Hansen, 1885: 20; Arnesen, 1901a: 9–10).

Clathrina blanca (Ereskowsky, 1995: 730).

Guancha blanca (Borojevic & Boury-Esnault, 1987: 14–15; Borojevic *et al.*, 1990: 252; Barthel & Tendal, 1993: 84; Rapp, 1999: 65–71; van Soest, 2001: 101; Borojevic *et al.*, 2002: 1143–1144; Janussen *et al.*, 2003: 17–19).

Leucosolenia blanca (Levinsen, 1886; Breitfuss, 1898a: 105–106, 1898b: 13–14, 1898c: 295–296, 1911: 224; Derjugin, 1915: 289; Breitfuss, 1927: 27, 1933: 240, 1936: 5; Alander *in* Jägerskiöld, 1971: 60).

Leucosolenia lacunosa (Burton, 1930b: 488).

Leucosolenia macleayi (Burton, 1930a: 14–17, 1930b: 487; Arndt, 1935: 8–9).

Type locality: Lanzarote, Canary Islands.

Holotype: The type is probably lost (A. Plotkin, ZIL, pers. comm.).

Previous records: Bergen and Stavanger (Burton, 1930b; as *L. macleayi*); Singlefjord (Breitfuss, 1936).

Additional material examined: 147 specimens.

IB. Skarnsundet, 63°53'N, 11°04'E, 200 m, 09.10.1968, 3 specimens. Trondheimsfjord, c. 63°30'N, 10°30'E, 35 different localities, 14–500 m, 1995–96, 126 specimens. Nord-Leksa, 63°35.9'N, 09°26.3'E, 150–200 m, 21.03.1996, 2 specimens. Korsfjord, 60°09.12'N, 05°08.52'E, 300 m, 12.02.2003, 1 specimen. Balsnes, 69°34.1'N, 18°52'E, 40–60 m, 1 specimen. TMU. TM-180, Beiarn, 67°04'N, 14°35'E, 35–45 m, 02.08.1955, 2 specimens. TM-181, Trondenes, Vågsfjord, 68°50'N, 16°35'E, 90–150 m, 28.08.1954, 2 specimens. VM. VM-16893, Bjarkøy, 68°58'N, 16°42'E, 60–90 m, 07.09.1912, 2 specimens. VM-16894, Bjarkøy, 68°58'N, 16°42'E, 30–60 m, 06.09.1912, 1 specimen. VM-16895, Varanger, 70°05'N, 29°30'E, 160–170 m, 18.07.1937, 1 specimen. VM-16896, Trænfjorden, 66°25'N, 12°15'E, 40 m, 18.07.1939, 1 specimen. VM-16897, Mefjæra, Vågsfjord, 68°55'N, 16°55'E, 150–200 m, 06.07.1933, 2 specimens. VM-16898, Gibostad, 69°21'N, 18°05'E, 40 m, 20.07.1917, 1 specimen (dry). VM-16899, Værøy, 67°40'N, 12°40'E, littoral, 03.06.1929, 1 specimen. ZMO. B-1287, Håka, Oslofjord, 16.09.1953, 1 specimen. B-1288, Tromsø, 69°40'N, 19°00'E, 2 specimens.

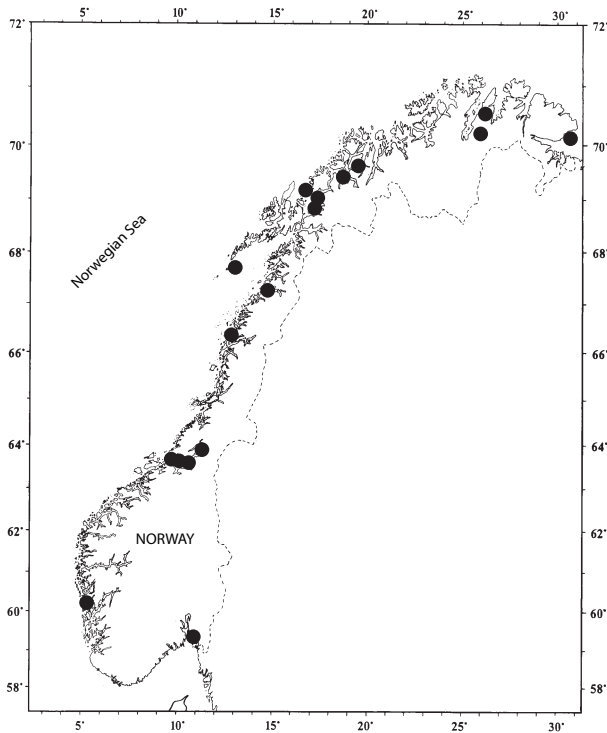


Figure 16. Distribution of *Guancha blanca* along the Norwegian coast.

Table 8. Spicule measurements of *Guancha blanca* Miklucho-Maclay, 1868

| Spicule | Length (µm) | | | | Width (µm) | | N |
|----------------------------------|-------------|------|-----|------|------------|------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| ZMO B-1288 | | | | | | | |
| Triactines from body | 105 | 126 | ±11 | 150 | 9.4 | ±1.2 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 65 | 110 | ±23 | 145 | 9.6 | ±1.1 | 30 |
| Unpaired actine | 140 | 184 | ±32 | 255 | 11.9 | ±2.7 | 30 |
| IB Skarnsundet 09.10.1968 | | | | | | | |
| Triactines from body | 100 | 130 | ±12 | 145 | 9.8 | ±1.4 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 70 | 114 | ±19 | 140 | 10.1 | ±1.2 | 30 |
| Unpaired actine | 145 | 189 | ±27 | 270 | 11.9 | ±2.4 | 30 |

Description

Clathrinidae with a cormus normally composed of a clathroid cormus of regularly and tightly anastomosing tubes and a peduncle. Up to 2 cm in height and 2 cm in diameter. One or several true tubes with a normal choanoderm form the peduncle. Sometimes the peduncle is very short or absent. In specimens without a peduncle the cormus is often narrower at the base than in the apical region. Water-collecting tubes converge at the centre of the sponge, ending in one or sometimes several apical oscula. The single tubes are about 0.3–0.7 mm in diameter. Surface is smooth. Colour white, greyish white or beige when alive, and with almost the same colours in alcohol. Dried specimens usually light beige. The skeleton of the cormus is composed of regular (equiangular and equiradiate) triactines to which parasagittal spicules may be added. The spicules are irregularly orientated in several layers in the walls of the tubes, resulting in a wall thickness of about 80 µm. In the peduncle the skeleton consists of only parasagittal triactines, with the unpaired actine basipetally orientated. All the actines are straight, cylindrical and with blunt tips.

Distribution

The species is found along the entire Norwegian coast from littoral to 500 m depth. *G. blanca* is the only species among the Norwegian Calcinea that is reported to be common in abyssal depths in the North Atlantic (Barthel & Tendal, 1993; Janussen *et al.*, 2003). However, recent examination of material from the abyssal Norwegian Sea revealed that these deep records probably represent another new species of *Guancha* (H. T. Rapp & O. S. Tendal, unpubl. data).

Remarks

In the reticulate/cushion-shaped form the parasagittal spicules are not as numerous, and the unpaired actine is usually shorter than in the pedunculated form. However, parasagittal triactines are always present, also in the young olynthus. The high degree of morphological variation figured by Miklucho-Maclay has previously been questioned (Burton, 1930a, b). However, material from Trondheimsfjord support some of Miklucho-Maclay's observations, and the variation is assumed to be mainly due to different life stages of the sponges.

The species has previously been reported from Trondheim and Stavanger (Burton, 1930b). In his work on the calcareous sponges from the Siboga-Expedition, Burton (1930a) decided to include all species of *Guancha* (*Leucosolenia*) with a clathroid cormus (except *G. lacunosa*) in *Guancha macleayi* (Von Lendenfeld, 1885), a species originally described

from Australia. He retained only Miklucho-Maclay's olynthus-form as the true *Guancha blanca*, and the consequence was a cosmopolitan distribution of *G. macleayi*, a conclusion that has never been supported by later authors. Re-examination of Burton's specimens from the Norwegian coast revealed that they should be identified as *G. blanca*.

GUANCHA CAMURA SP. NOV.

(FIGS 17A–C, 18, TABLE 9)

Type locality: Østerbotn, Porsanger, north-east Norway at 70°15.1'N, 25°21.1'E.

Holotype: TMU-185, Østerbotn, Porsanger, 70°15.1'N, 25°21.1'E, 27–33 m, 14.08.1956.

Paratype: TMU-184, Bøkfjord, 69°52.2'N, 29°38.5'E, 50–90 m, 25.06.1937, 1 specimen.

Etymology: From 'camur' (Latin), meaning tortuous or bent, referring to the horn-shaped paired actines of the parasagittal triactines from the peduncle.

Additional material examined: 5 specimens.

TMU. TM-186, Jarfjord, 69°40.7'N, 30°24.7'E, 30–45 m, 03.07.1937, 1 specimen. VM. VM-16900, Evenskjer, 68°35'N, 16°35'E, 60–85 m, 12.08.1913, 2 specimens (dry). VM-16901, Gibostad, 69°21'N, 18°05'E, 50 m, 27.07.1917, 1 specimen (dry). VM-16902, Lødingen, 68°24'N, 15°58'E, 35–40 m, 18.08.1913, 1 specimen (dry).

Description

Clathrinidae with a cormus normally composed of a clathroid body of irregularly and loosely anastomosing tubes and a peduncle. Up to 3 cm in height and 2 cm wide. Consistency soft because of the very thin walls of the tubes (about 20 µm). Surface smooth. Several true tubes with a normal choanoderm form the peduncle. The skeleton of the cormus is composed of regular (equiangular and equiradiate) triactines to which parasagittal spicules are frequently added. In the peduncle the skeleton consists of only parasagittal triactines. The unpaired actine of peduncular parasagittal triactines is always basipetally orientated. The paired actines are bent in a manner making them 'horn'-shaped, whereas the unpaired actine is straight. All actines are cylindrical with slightly blunt tips.

Distribution

The species is found in the northern part of Norway at 27–90 m depth.

The species is also known from Greenland at 125–200 m depth (my pers. observ.).

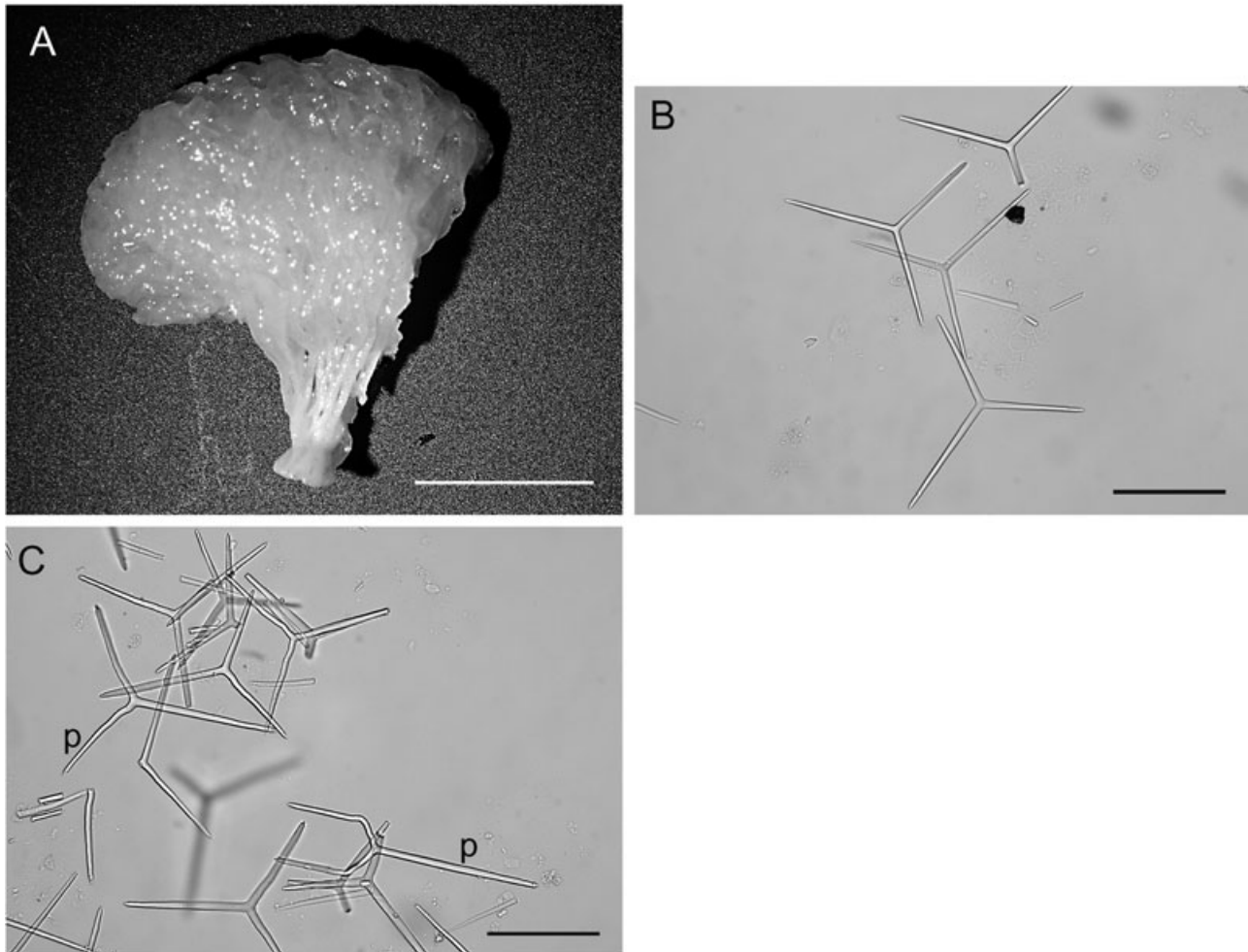


Figure 17. A, holotype of *Guancha camura* sp. nov. Scale bar = 1 cm. B, triactines from the cormus. Scale bar = 100 μm . C, parasagittal triactines from the peduncle (p). Scale bar = 100 μm .

Table 9. Spicule measurements of *Guancha camura* sp. nov.

| Spicule | Length (μm) | | | | Width (μm) | | N |
|--------------------------|--------------------------|------|----------|------|-------------------------|-----------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Holotype TMU-186 | | | | | | | |
| Triactines from body | 95 | 114 | ± 12 | 145 | 9.6 | ± 1.2 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 75 | 94 | ± 7 | 105 | 9.3 | ± 1.2 | 30 |
| Unpaired actine | 115 | 135 | ± 12 | 170 | 10.6 | ± 1.3 | 30 |
| Holotype TMU-185 | | | | | | | |
| Triactines from body | 90 | 116 | ± 10 | 150 | 9.7 | ± 1.0 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 70 | 96 | ± 8 | 115 | 9.5 | ± 1.1 | 30 |
| Unpaired actine | 115 | 141 | ± 9 | 185 | 10.7 | ± 1.5 | 30 |

Remarks

G. camura sp. nov. differs from other species mainly because of the horn-shaped parasagittal triactines in the peduncle. Such spicules have been found in the olynthus-form of *G. 'blanca'* from Neapel (Metschnikoff, 1879). None of his specimens has been available for examination, but from the distribution of *G. camura* it is reasonable to believe that they represent two different species. These spicules also bear similarities to sagittal tripods found in *G. challengerii*

(Polejaeff, 1883) from Australia and New Zealand, but in *G. challengerii* they are found together with tripods, forming conules on the outer surface. *G. challengerii* also possesses a solid peduncle (Polejaeff, 1883), whereas the peduncle is composed of true tubes in *G. camura*. The species also bears similarities to *G. pellucida* sp. nov. However, the spicules in *G. camura* are considerably shorter and thicker than the long and slender spicules in *G. pellucida*.

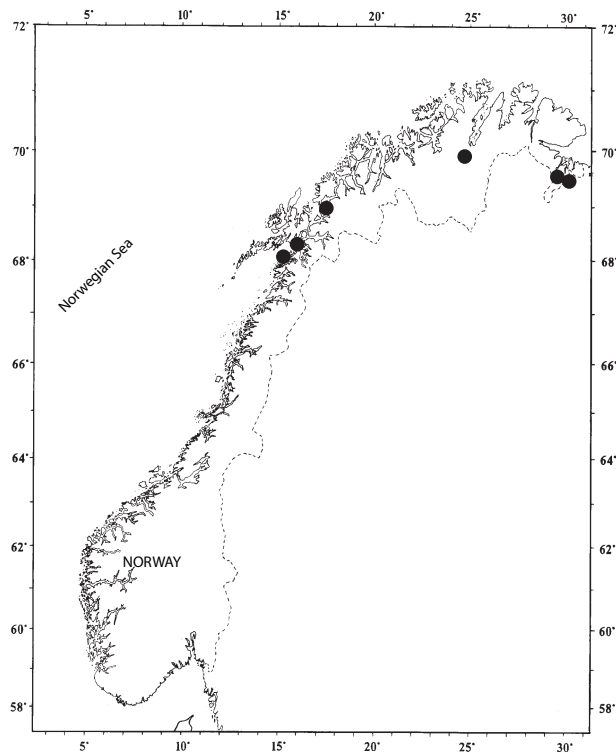


Figure 18. Distribution of *Guancha camura* sp. nov. along the Norwegian coast.

GUANCHA LACUNOSA (JOHNSTON, 1842)
(FIGS 19A–C, 20, TABLE 10)

Original description: *Grantia lacunosa* Bean in Johnston, 1842: 176.

Synonyms and citations

Ascandra angulata Von Lendenfeld, 1891.
Ascandra angulata (Arnesen, 1901a: 13; 1901b: 68).
Ascortis lacunosa (Haeckel, 1872: 70–71).
Guancha lacunosa (Borojevic & Boury-Esnault, 1987: 15–16; Rapp, 1999: 72).
Leucosolenia angulata (Breitfuss, 1927: 27).
Leucosolenia lacunosa (Breitfuss, 1933: 241).

Type locality: Scarborough, UK.

Holotype: According to Burton (1930a) the type is lost.

Previous records: Hjeltefjorden, Bergen (Arnesen, 1901a).

Material examined: 2 specimens.

VM. VM-16903, Finnsnes, 69°14'N, 17°58'E, 25–40 m, 18.06.1914, 1 specimen (dry, peduncle broken off and missing). ZMUB. ZMUB-9678, Hjeltefjorden, Bergen, 60°35'N, 04°55'E, 55–200 m, 1 specimen.

Description

Sponge composed of an ovoid body of thin, tightly and regularly anastomosing tubes, and a solid peduncle

Table 10. Spicule measurements of *Guancha lacunosa* (Johnston, 1842)

| Spicule | Length (µm) | | | | Width (µm) | | N |
|--------------------------|-------------|------|-------|------|------------|------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| Zmub-9678 | | | | | | | |
| Triactines from body | | | | | | | |
| Paired actines | 54 | 65 | ±9.1 | 80 | 6.6 | ±0.8 | 30 |
| Unpaired actine | 62 | 90 | ±20.7 | 155 | 6.6 | ±0.7 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 20 | 37 | ±10.3 | 52 | 7.6 | ±1.2 | 30 |
| Unpaired actine | 130 | 205 | ±24.6 | 280 | 11.8 | ±1.6 | 30 |
| Diactines | 215 | 411 | ±94 | 550 | 12.7 | ±1.6 | 30 |
| Irregular diactines | 69 | 113 | ±29 | 160 | 4.2 | ±1.1 | 12 |

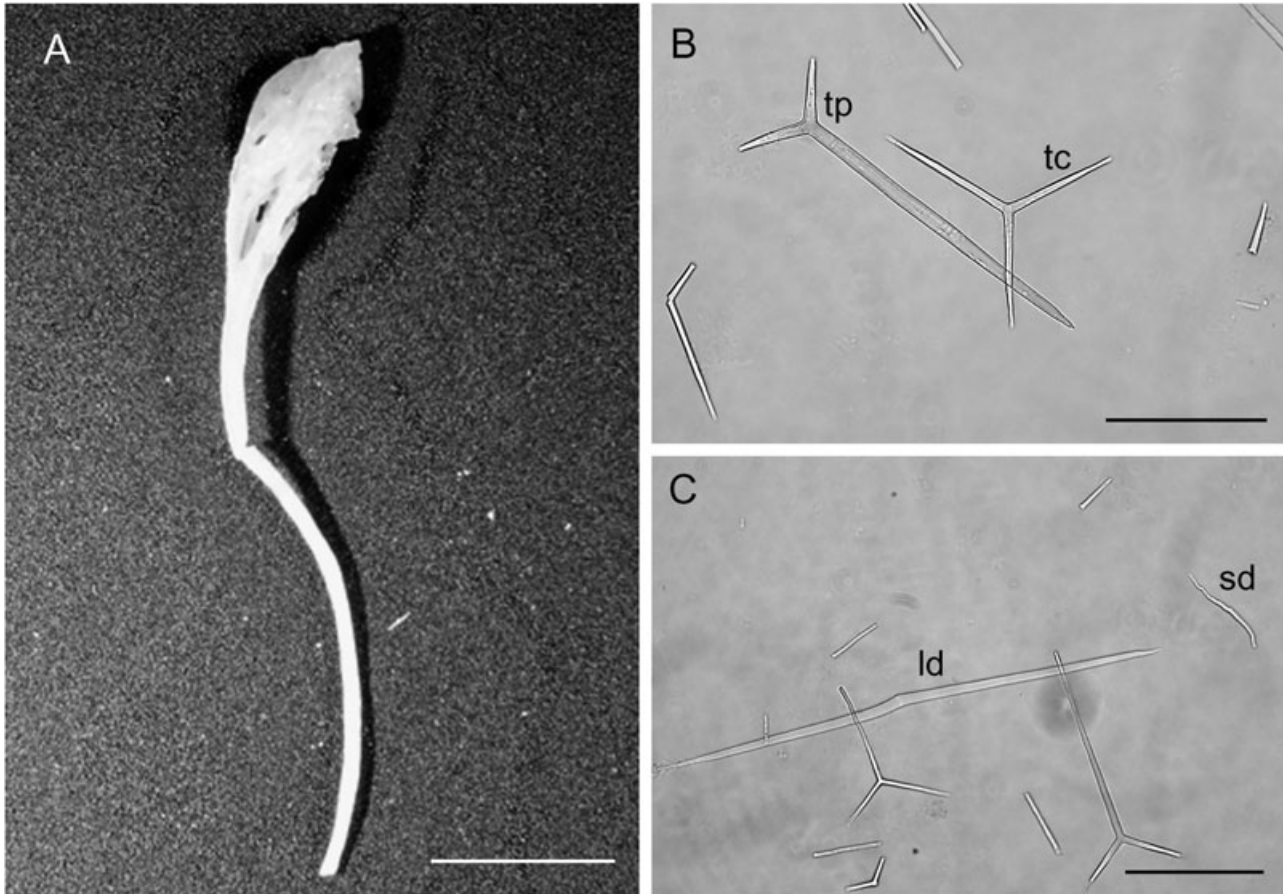


Figure 19. A, habitus of a fixed specimen of *Guancha lacunosa*. Scale bar = 1 mm. B, regular to parasagittal triactines from the cornus (tc) and parasagittal triactines from the peduncle (tp). Scale bar = 100 μ m. C, large diactines with an angle in the middle region (ld) and small distorted diactines (sd), all from the peduncle. Scale bar = 100 μ m.

without any choanoderm. Water-collecting tubes converge into one apical osculum. Colour white in ethanol and light beige when dried.

Triactines from the clathroid body range from almost regular to parasagittal with straight actines. Close to the peduncle there are parasagittal spicules with the longest unpaired actine pointing towards the peduncle. The skeleton of the peduncle is composed of large diactines with a break on the middle, and parasagittal triactines with a very long unpaired actine and short paired actines. Irregular diactines of variable sizes are present at low numbers in the peduncle. All actines are cylindrical with slightly blunt to sharp points.

Distribution

From the Norwegian coast, *G. lacunosa* is only known from Hjeltefjorden in the Bergen area and at Finnsnes in northern Norway, 25–200 m depth.

The species is also reported from the Mediterranean (Von Lendenfeld, 1891), the Bay of Biscay down to 550 m depth (Borojevic & Boury-Esnault, 1987), Great Britain (Ackers *et al.*, 1985) and the Arctic (Breitfuss, 1911, 1927, 1933; Derjugin, 1915).

Remarks

In his work on the Norwegian sponges from the Norman collection, Burton (1930b) reported *Guancha lacunosa* from Bergen and Stavanger. Re-examination of these specimens revealed that they should be identified as *Guancha blanca* and *Clathrina nanseni*.

GUANCHA PELLUCIDA SP. NOV. (FIGS 21A–D, 22, TABLE 11)

Type locality: Porsangerfjord, northern Norway, at approximately 70°15'N, 25°21'E.

Holotype: TMU-179, Porsangerfjord, approximately 70°15'N, 25°21'E, 140–155 m, 03.08.1931.

Paratype: VM-397, Senja, 190 m, 08.07.1933, 1 specimen. No more information given on the original label.

Etymology: Named 'pellucida' from Latin 'pellucidus', meaning translucent, referring to the very thin-walled and translucent tubes of the cormus.

Additional material examined: 4 specimens.

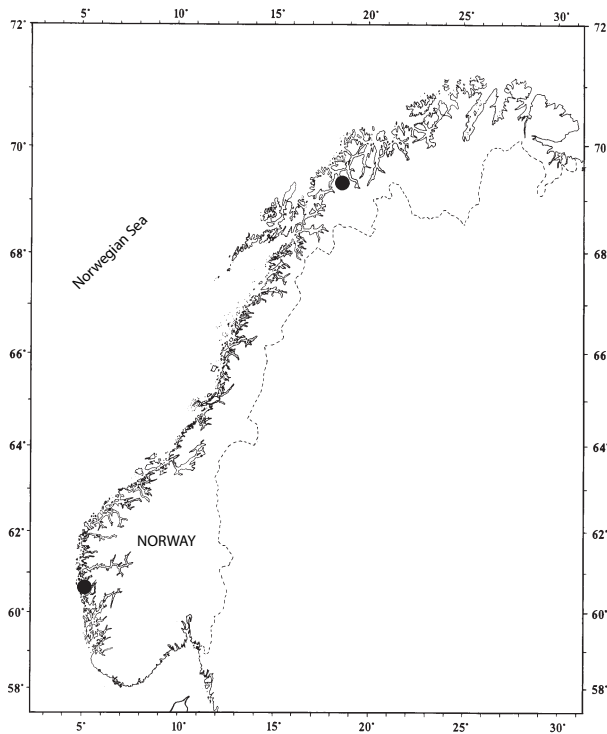


Figure 20. Distribution of *Guancha lacunosa* along the Norwegian coast.

IB. Trondheimsfjord, approximately 63°30'N, 10°30'E, 3 different localities, 100–275 m, 1996, 4 small specimens.

Description

Clathrinidae normally composed of a globular and highly compressible clathroid cormus of irregularly but tightly anastomosing tubes, and a very short peduncle. Up to 3 cm in height and 2.5 cm in diameter. Several anastomosing true tubes with a normal choanoderm form the peduncle. In full-grown specimens water-collecting tubes converge into one large apical osculum. Texture soft and fragile. Surface smooth. Colour greyish white and highly translucent when alive, and yellowish white in alcohol. The skeleton of the cormus is composed of 1–3 layers of very slender regular to subregular triactines, to which parasagittal spicules may be added. The walls of the tubes are only 10–15 µm thick. In the peduncle the skeleton consists of parasagittal triactines with unpaired actine of highly variable length. The unpaired actine of peduncular parasagittal triactines is always basipetally orientated. All actines are undulated, especially close to the centre of the spicule, cylindrical or slightly conical with blunt tips.

Distribution: The species is found in the northern part of Norway at 100–275 m depth.

The species is also known from Greenland at 20–190 m depth and close to Jan Mayen at 890 m depth (my pers. observ.).

Remarks

The species bears some similarities to *G. camura* sp. nov., but is clearly separated by the long, slender and slightly undulated actines.

Table 11. Spicule measurements of *Guancha pellucida* sp. nov.

| Spicule | Length (µm) | | | | Width (µm) | | N |
|--------------------------|-------------|------|-----|------|------------|------|----|
| | Min. | Mean | σ | Max. | Mean | σ | |
| <i>Holotype</i> TMU-179 | | | | | | | |
| Triactines from body | 115 | 143 | ±12 | 175 | 8.1 | ±1.2 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 40 | 131 | ±30 | 185 | 8.2 | ±1.1 | 30 |
| Unpaired actine | 120 | 173 | ±18 | 195 | 8.5 | ±1.6 | 30 |
| <i>Paratype</i> VM-397 | | | | | | | |
| Triactines from body | 112 | 131 | ±11 | 149 | 8.0 | ±1 | 30 |
| Triactines from peduncle | | | | | | | |
| Paired actines | 105 | 129 | ±18 | 175 | 8.2 | ±1.6 | 30 |
| Unpaired actine | 149 | 201 | ±23 | 245 | 8.3 | ±1.5 | 30 |

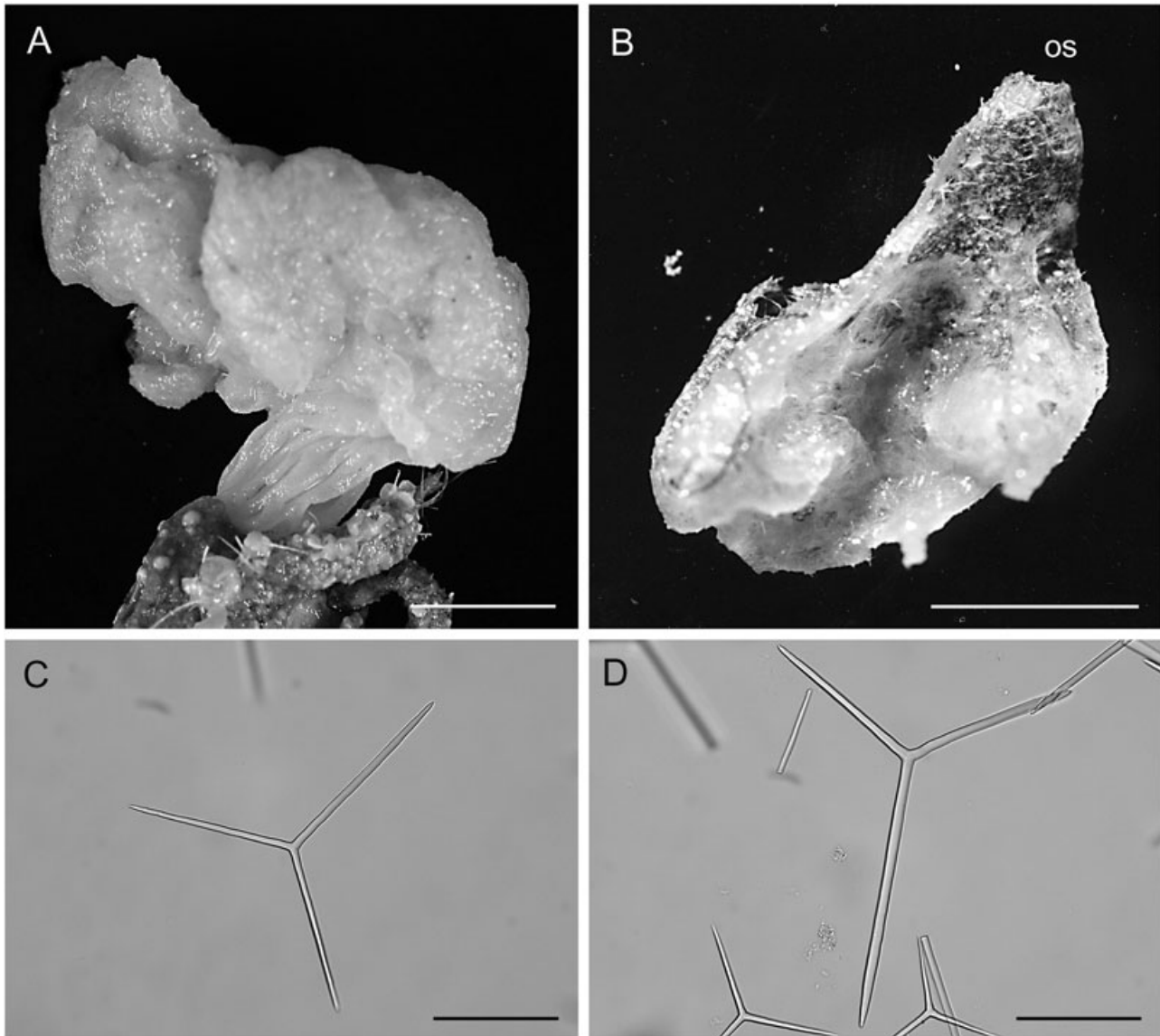


Figure 21. A, holotype of *Guancha pellucida* sp. nov. Scale bar = 1 cm. B, habitus of a young specimen without a peduncle. os = osculum. Scale bar = 1 mm. C, triactine from the cormus. Scale bar = 100 µm. D, parasagittal triactine from the peduncle. Scale bar = 100 µm.

EXCLUDED SPECIES

It is obvious that some previous authors working on Norwegian Calcarea have identified their specimens from outer morphology only, missing the information that would have been provided by composition of spicules and spicule size. This work revealed that quite a substantial part of the specimens of Calcarea previously reported from the Norwegian coast have been erroneously identified, or following modern standards, should be allocated to other taxa. These misidentifications have also resulted in several species no longer being considered as a part of the Norwegian Calcanean

sponge fauna: *Clathrina canariensis* reported from Tromsø (Breitfuss, 1933) should be identified as *Clathrina nansenii*; *Clathrina primordialis* reported from Kristiansund and Stavanger (Burton, 1930b, 1963) should be identified as *Clathrina cribrata*, and *Guancha macleayi* reported from Trondheim and Stavanger (Burton, 1930b) should be named *Guancha blanca*. *Asclatis lamarcki* Haeckel, 1872 has been reported once from the Vardø area (Breitfuss, 1898b). As his specimen has not been found, and no other material from the Norwegian coast has been available, the record cannot be verified. *Pericharax polejaevi* Breitfuss, 1896 was reported from the Tromsø area by

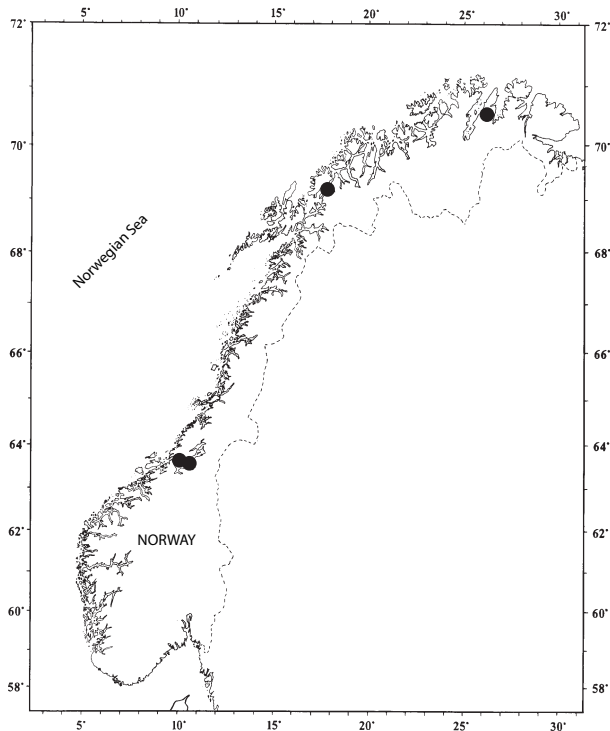


Figure 22. Distribution of *Guancha pellucida* sp. nov. along the Norwegian coast.

Breitfuss (1933). However, Dendy & Row (1913) excluded *polejaevi* from the genus *Pericharax* based on the fact that there is no specific skeleton supporting the subcortical inhalant chambers, and moved it to the calcarean genus *Leucandra*. Examination of several specimens from Greenland revealed that there are subcortical inhalant chambers in *polejaevi*, supported by bundles of subcortical diactines. However, spicule types and arrangement of the skeleton resemble a typical *Leucandra*. The presence of such chambers is obviously not unique for *Pericharax* within the Calcarea. Re-examination of a fragment of the type of *Leucandra cumberlandensis* Lambe, 1900 from Kingawa Fjord (eastern Canada) showed that this species has subcortical inhalant chambers also (my unpubl. data).

REPRODUCTION AND DISPERSAL

Although asexual dispersal by fragmentation may play an important role in sponge reproduction (Johnson, 1978a; Battershill & Bergquist, 1990; Maldonado & Uriz, 1999), the apparent restricted capabilities of sponge larvae for dispersal appears to be responsible for the high genetic divergence of populations and the frequent occurrence of cryptic speciation in sponges (Klautau *et al.*, 1999; Solé-Cava *et al.*, 1991; Borchellini *et al.*, 2000; Wörheide, Hooper & Degnan, 2003).

KEY TO THE KNOWN NORWEGIAN CALCINEA

- Sponge cornus with distinct peduncle, solid or formed of normally organized, partly or fully coalescent tubes. Skeleton composed of parasagittal spicules, or of regular spicules to which parasagittal spicules are added, at least in the peduncle *Guancha* 1
- Sponge cornus without a distinct peduncle *Clathrina* 5
- 1. Peduncle solid and without any choanosome *G. lacunosa*
- Peduncle made of true tubes with choanosome 2
- 2. Spicules are all parasagittal triactines *G. arnesenae* sp. nov.
- Spicules are regular triactines, with additional parasagittal spicules, at least in the peduncle 3
- 3. All spicules have straight actines *G. blanca*
- Spicules are undulated or 'horn-shaped' 4
- 4. All spicules are slender with undulated actines *G. pellucida* sp. nov.
- Peduncular parasagittal triactines have horn-shaped paired actines *G. camura* sp. nov.
- 5. Spicules are only triactines 6
- Spicules are triactines and tetractines 8
- 6. Oscular tubes with a sieve of cells (cribrum) beneath the opening *C. cribrata*
- Oscular tubes without a sieve of cells 7
- 7. Actines rounded or blunt with a constriction near the end *C. coriacea*
- Actines sharply pointed, without constriction *C. jorunnæ* sp. nov.
- 8. Sponge as single or loosely anastomosing/ramifying tubes *C. corallicola* sp. nov.
- Cornus massive or cushion-shaped 9
- 9. Tetractines of one type only, with a long apical actine *C. septentrionalis*
- Tetractines of two types, with long or only rudimentary apical actine *C. nanseni*

High production of larvae, a short free-living stage and the restricted ability of active locomotion of the sponge larvae over a longer distance result in very large local populations of some species of Calcarea. Along the Norwegian coast, calcinean species such as *Clathrina coriacea* and *Clathrina nanseni*, and the calcaronean species *Sycon quadrangulatum* (Schmidt, 1868) and *Sycandra utriculus* (Schmidt, 1869) are, when present, very numerous within certain areas (my pers. observ.). These are species with a rapid growth, numerous offspring and a short lifespan (annual life cycle). Similar observations have been reported in shallow water '*Guancha blanca*' and '*Clathrina coriacea*' from California (Johnson, 1978b), who reported a high sexual and asexual reproduction potential in both species, and an annual life cycle. Species such as *Clathrina corallicola* sp. nov. and *Ute gladiata* Borojevic, 1966 are found in very low numbers in very specialized habitats, and have a very low rate of larvae production. *Clathrina corallicola* sp. nov. was collected monthly through one year at a *Lophelia*-bank in Trondheimsfjord, and mature oocytes were found only in two specimens collected in June. Contrasting with *C. coriacea* and *S. quadrangulatum* in which the entire sponge may be more or less filled with oocytes and/or larvae, only 2–3 mature oocytes (and no immature ones) were found in each of the two specimens of *C. corallicola*. Specimens of the calcaronean *Ute gladiata* were collected in the same habitat as *C. corallicola*, and maintained in an aquarium for three years. This species also has a low rate of larvae production. These species probably have a comparably longer lifespan than *C. coriacea* and *S. quadrangulatum*. Thus, it is obvious that reproduction strategy and lifespan in Calcarea are highly variable. All these species have a comparably wide distribution in the north-east Atlantic, and number of larvae produced by each specimen, or population size, appear to have no direct effect on the distribution range of the species.

ZOOGEOGRAPHY

The Norwegian coast extends through 13°23.58' of latitude, or a straight south–north difference of about 1470 km (Brattegard & Holthe, 1997). The coastline has many types of marine habitats, ranging from small and sheltered brackish lagoons, to fjords of more than 1000 m depth, and the highly exposed and topographically diverse outer coastline. Throughout the Norwegian coast and shelf there are distinct gradients in temperature, salinity, tidal amplitude and bottom type, resulting in a rich and varied marine fauna and flora. Thus, the marine fauna and flora, including the sponges, demonstrate gradients of change throughout the Norwegian coast. The main biogeographical gradients follow the change in latitude and partly in longi-

tude, from outer shelf to the inner parts of the fjords, and from the intertidal zone to the deep basins of the shelf or fjords (Brattegard & Holthe, 1997).

The Norwegian Calcinea represent a mixture of southern boreal/boreal and boreoarctic species. The southern element is mainly composed of *C. coriacea*, a species distributed north to mid-Norway. This species has previously been reported from the entire Atlantic/Arctic region (and more-or-less all seas). However, re-examination of specimens from the White Sea, Spitsbergen, Iceland and Greenland previously identified as *C. coriacea* (Lundbeck, 1909; Brøndsted, 1914; Burton, 1930b, 1934) has revealed that most of the specimens should be allocated to other species of *Clathrina* or *Guancha* as understood here. I believe that further analyses of material will indicate that *C. coriacea* is not a part of the Arctic sponge fauna. Also, Klautau & Valentine (2003) indicated a North Atlantic distribution of the species.

The boreoarctic element comprises *C. nanseni*, *Guancha arnesenae* sp. nov., *G. blanca*, *G. camura* sp. nov. and *G. pellucida* sp. nov.; this sponge fauna has strong similarities to the Greenlandic and the White Sea/Barents Sea sponge faunas (Merejkowsky, 1878; Levinsen, 1886; Breiffuss, 1898b, 1911; Derjugin, 1915, 1928; Rapp, 2004b). The distribution patterns of *Clathrina jorunnae* sp. nov. and *C. septentrionalis* are more difficult to judge as *C. jorunnae* is only known from the type locality and *C. septentrionalis* is known from only four localities on the Norwegian coast and one in Ireland. *Clathrina corallicola* sp. nov. and *Guancha lacunosa* seem to be parts of the boreal faunal element. None of the examined species has an exclusive arctic distribution, and to my knowledge there are no real arctic species of the subclass Calcinea. The calcinean sponge fauna of northern Norway bears strong similarities to that found along the coast of Greenland, where *G. camura* has been found on the southernmost coast, *G. arnesenae* on the western coast, and *G. pellucida* and *C. nanseni* over a wide distribution in Greenlandic waters (Rapp, 2004b).

DEPTH DISTRIBUTION

Within the Norwegian Calcinea, *C. coriacea* and *C. cribrata* (with their main distribution from 0 to 15 m depth) are the most common species in the lower littoral and the shallow sublittoral zones (Table 12). Most Norwegian Calcinea have their main distribution between 20 and 100 m depth (*C. nanseni*, *C. septentrionalis*, *G. arnesenae*, *G. camura* and *G. lacunosa*). *G. pellucida* was found at 100–127 m depth, and is known from 890 m close to Jan Mayen, while *C. corallicola* was found at 90–500 m, and has been recorded from 1000 m depth at the Reykjanes Ridge, Iceland (my pers. observ.). *C. jorunnae* is only

Table 12. Depth distribution of calcinean calcareous sponges in Norwegian waters. Records are given as number of localities (and specimens) of each species found in the different depth intervals. A dash indicates no record

| Species | Depth | | | | |
|----------------------------------|--------|--------|--------|---------|----------|
| | 0–5 m | 6–50 m | 51–200 | 201–400 | 401–1000 |
| <i>Clathrina cribrata</i> | 13(20) | 1(1) | 1(1) | – | – |
| <i>Clathrina coriacea</i> | 13(19) | 8(15) | 5(6) | – | – |
| <i>Clathrina septentrionalis</i> | – | 3(3) | – | – | – |
| <i>Clathrina nanseni</i> | – | 29(72) | 15(32) | – | – |
| <i>Guancha camura</i> | – | 4(4) | 2(3) | – | – |
| <i>Guancha lacunosa</i> | – | 1(1) | 1(1) | – | – |
| <i>Guancha arnesenae</i> | – | 6(19) | 2(11) | – | – |
| <i>Clathrina jorunnae</i> | – | – | 1(1) | – | – |
| <i>Guancha pellucida</i> | – | – | 2(2) | 3(4) | – |
| <i>Clathrina corallicola</i> | – | – | 3(4) | 4(14) | 2(5) |
| <i>Guancha blanca</i> | 1(1) | 10(57) | 32(92) | 3(8) | 2(3) |

known from one dredge haul from 25–250 m depth. *G. blanca* is found from the shallow sublittoral zone down to at least 1500 m depth in the Norwegian Sea (my pers. observ.).

ACKNOWLEDGEMENTS

This study has been heavily dependent upon access to a number of museum collections. I wish to express my gratitude to the following people for providing access to their respective collections: Wim Vader (Tromsø Museum, University of Tromsø, Norway), Torkild Bakken (Museum of Natural History and Archaeology, NTNU, Trondheim, Norway), Alexander Plotkin (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia), Dag Gammelsæter and Marit E. Christiansen (Zoological Museum, University of Oslo, Norway), Jon A. Kongsrud (Zoological Museum, University of Bergen, Norway), Ole S. Tendal (Zoological Museum, University of Copenhagen, Denmark), Gudmundur Gudmundsson (Icelandic Institute and Museum of Natural History, Iceland, the BIOICE collection) and Jan Sørensen (Kaldbak Marine Biological Laboratory, Faroe Islands, the BIOFAR collection). The underwater photographs were provided by Torkild Bakken (Fig. 3A), Bjørn Gulliksen (Fig. 9A) and Erling Svensen (Figs 5A, 11A, 13A), to whom I am very grateful. Turid Solbakken is thanked for putting equipment at my disposal and for assistance with photography of spicules. Dag Altin made a great job with the layout of figures, and his effort is highly appreciated. I owe a great debt to Ole Tendal for his hospitality during several visits in Copenhagen, and for helpful discussions and critical reading of the manuscript. Two anonymous reviewers are thanked for

suggestions on the manuscript. This project was supported by the Norwegian Research Council, project number 28630, and the European Community – Access to Research Infrastructure action of the Improving Human Potential Programme, through Copenhagen Biosystematics Centre (COBICE), project numbers 232 and 638.

REFERENCES

- Ackers RG, Moss D, Picton B, Stone SMK. 1985.** *Sponges of the British Isles, Sponge IV*. Herefordshire UK: Marine Conservation Society.
- Arndt W. 1913.** Zoologische Ergebnisse der ersten Lehr-Expedition der Dr. P. Schott-länderschen Jubiläums-Stiftung. *Schlesischer Gesellschaft für Vaterland und Kultur, Jahresbericht* **90** (1): 110–119.
- Arndt W. 1935.** Porifera. *Tierwelt Nord und Ostsee* **3a**: 1–140.
- Arnesen E. 1901a.** Spongier fra den norske kyst. I. Calcarea. Systematisk katalog med bemerkninger og bestemmelsestabell. *Bergens Museums Årbok* **1900** (5): 1–44.
- Arnesen E. 1901b.** Calcarea. In: *Meeresfauna von Bergen*, 1. Bergen: Bergen Museum, 65–72.
- Barthel D, Tendal OS. 1993.** The sponge association of the abyssal Norwegian–Greenland Sea: species composition, substrate relationships and distribution. *Sarsia* **78**: 83–93.
- Battershill C, Bergquist PR. 1990.** The influence of storms on asexual reproduction, recruitment, and survivorship of sponges. In: Rützler K, ed. *New perspectives in sponge biology*. Washington, DC: Smithsonian Institution Press, 397–403.
- Borchiellini C, Chombard C, Lafay B, Boury-Esnault N. 2000.** Molecular systematics of sponges (Porifera). *Hydrobiologia* **420**: 15–27.
- Borojevic R. 1971.** Éponges calcaires des côtes du sud-est Brésil, épibiontes sur *Laminaria brasiliensis* et *Sargassum cymorum*. *Revista Brasileira de Biologia* **31**: 525–530.

- Borojevic R, Boury-Esnault N. 1987.** Calcareous sponges collected by N.O. Thalassa on the continental margin of the Bay of Biscay. I. Calcinea. In: Vacelet J, Boury-Esnault N, eds. *Taxonomy of Porifera from the NE Atlantic and Mediterranean Sea*. NATO Asi Series, G13. Berlin: Springer-Verlag, 1–27.
- Borojevic R, Boury-Esnault N, Manuel M, Vacelet J. 2002.** Order Clathrinida Hartman, 1958. In: Hooper JNA, van Soest RWM, eds. *Systema Porifera. A guide to the classification of sponges*. New York: Kluwer Academic/Plenum Publishers, 1141–1152.
- Borojevic R, Boury-Esnault N, Vacelet J. 1990.** A revision of the supraspecific classification of the subclass Calcinea (Porifera, class Calcarea). *Bulletin du Museum National d'Histoire Naturelle, Paris 4, Series, 12, Section A 2*: 243–276.
- Borojevic R, Boury-Esnault N, Vacelet J. 2000.** A revision of the supraspecific classification of the subclass Calcaronea (Porifera, class Calcarea). *Zoosystema 22*: 203–263.
- Borojevic R, Klautau M. 2000.** Calcareous sponges from New Caledonia. *Zoosystema 22*: 187–201.
- Borojevic R, Peixinho S. 1976.** Éponges calcaires du nord-nord-est do Bresil. *Bulletin du Museum National d'Histoire Naturelle. Paris 402 (Zoologie) 279*: 987–1036.
- Boury-Esnault N, Rützler K, eds. 1997.** Thesaurus of sponge biology. *Smithsonian Contributions to Zoology 596*: 1–55.
- Brattegard T, Holthe T, eds. 1997.** Distribution of marine benthic macroorganisms in Norway. A tabulated catalogue. Preliminary edition. *Research Report for DN 1997-1*. Directorate for Nature Management.
- Breitfuss LL. 1896.** Kalkschwämme der Bremer-Expedition nach Ost-Spitsbergen. *Zoologischer Anzeiger 514*: 426–432.
- Breitfuss LL. 1897.** Catalog der Calcarea der zoologischen Sammlung des königlichen Museums für Naturkunde zu Berlin. *Archiv für Naturgeschichte 63*: 205–226.
- Breitfuss LL. 1898a.** Die Kalkschwammfauna von Spitzbergen. Nach den Sammlung der Bremer Expedition nach Ost-Spitzbergen im Jahre 1889. (Prof. W. Kükenenthal und dr. A. Walther). *Zoologische Jahresbericht (Abteilung Systematik) 11*: 103–120.
- Breitfuss LL. 1898b.** Kalkschwammfauna des Weissen Meeres und der Eismeerküsten des europäischen Russlands. *Mémoires de l'Académie Imperiale des Sciences de St. Pétersbourg Ser. 8 6 (2)*: 1–41.
- Breitfuss LL. 1898c.** Die arctische Kalkschwamm-fauna. *Archiv für Naturgeschichte 1 (3)*: 277–316.
- Breitfuss LL. 1911.** Zur Kenntnis der Spongio-Fauna des Kola-Fjords. *Travaux de la Société Impériale des Naturalistes de St Pétersbourg 4*: 223–226.
- Breitfuss LL. 1927.** Die Kalkschwämme der Nord und Ostsee. *Zoologischer Anzeiger 70*: 26–36.
- Breitfuss LL. 1933.** Die Kalkschwammfauna des arctischen Gebietes. *Fauna Arctica 6*: 235–252.
- Breitfuss LL. 1936.** Kalkschwämme von Skagerrak und Kattegat. *Göteborgs Kungliga Vetenskaps- och Vitterhets Samhälles Handlingar 5 följd. Ser. B 4 (15)*: 1–16.
- Brøndsted HV. 1914.** Conspectus Fauna Groenlandicae. Porifera. *Meddelelser om Grønland 23*: 459–544.
- Brunchorst J. 1891.** Die Biologische Meeresstation im Bergen. *Bergen Museums Aarsberetning Part 5*: 1–31, Pl. I–V.
- Burton M. 1930a.** The Porifera of the Siboga Expedition III. Calcarea. *Siboga-Expeditie, Leiden 6a*: 1–7.
- Burton M. 1930b.** Norwegian sponges from the Norman collection. *Proceedings of the Zoological Society of London 487–546*.
- Burton M. 1931.** The Folden Fjord. Report on the sponges collected by Mr. Soot-Ryen in the Folden Fiord in the year 1923. *Tromsø Museums Skrifter 1 (13)*: 1–8.
- Burton M. 1934.** Zoological results of the Norwegian Scientific Expedition to East Greenland III. Report on the sponges of the Norwegian Expeditions to East Greenland (1930, 1931 and 1932). *Skrifter om Svalbard og Ishavet 61*: 3–34.
- Burton M. 1963.** A revision of the classification of the calcareous sponges. With a catalogue of all the specimens in the British Museum (Natural History). London: British Museum of Natural History.
- Dendy A, Row RWH. 1913.** The classification and phylogeny of the calcareous sponges with a reference list of all the described species. *Proceedings of the Zoological Society of London 704–813*.
- Derjugin KM. 1915.** La faune du golfe de Kola et les conditions de son existence. *Mémoires de l'Académie Imperiale des Sciences de Petrograd Ser. 8 34 (1)*: 1–929 [in Russian].
- Derjugin KM. 1928.** Fauna des Weissen Meeres und ihre existenzbedingungen. Extract from *Explorations des Mers d'URRS 7-8*: 1928. Leningrad. [In Russian].
- Ereskowsky AV. 1995.** Materials to the Faunistic Study of the White and Barents seas sponges. 6. The origin of the White and Barents seas sponge faunas. *Berliner Geowissenschaftliche Abhandlungen 16*: 715–730.
- Gulliksen B. 1978.** Rocky bottom fauna in a submarine gully at Loppakalven, Finnmark, northern Norway. *Estuarine and Coastal Marine Science 7*: 361–372.
- Haeckel E. 1872.** *Die Kalkschwämme. Eine Monographie*, Volumes 1–3. Berlin: Georg Reimer.
- Haeckel E. 1874.** Kalk und Gallertspongien. *Die Zweite Deutsche Nordpolarfahrt II*. Leipzig: Brockhaus, 434–436.
- Hansen A. 1885.** Spongidae. *Den Norske Nordhavs-Expedisjon 1876–1878 (3)*: 1–25.
- Hartman WD. 1964.** Taxonomy of Calcareous sponges. *Science 144*: 711–712.
- Herdman WA. 1892.** Notes on the collections made during the cruise of the S.Y. 'Argo' up the west coast of Norway in July 1891. *Proceedings and Transactions of the Liverpool Biological Society 6*: 70–93.
- Jägerskiöld LA. 1971.** A survey of the marine benthonic macro-fauna along the Swedish West coast 1921–1938. *Acta Regiae Societatis Scientiarum Gothoburgensia, Zoologica 6*: 1–146.
- Janussen D, Rapp HT, Tendal OS. 2003.** A myth vanished: calcareous sponges are alive and well at abyssal depths. *Deep-Sea Newsletter 32*: 17–19.
- Johnson MF. 1978a.** Studies on the reproduction cycles of the calcareous sponges *Clathrina coriacea* and *C. blanca*. *Marine Biology 50*: 73–79.

- Johnson MF. 1978b.** Significance of life history studies of calcareous sponges for species determination. *Bulletin of Marine Science* **28** (3): 570–574.
- Johnson MF. 1979.** Recruitment, growth, mortality and seasonal variations in the calcareous sponges *Clathrina coriacea* (Montagu) and *C. blanca* (Micluch-Maclay) from Santa Catalina Island, California. In: Levi C, Boury-Esnault N, eds. *Biologie des Spongiaires*. Paris: Colloques internationaux du CNRS, 325–334.
- Johnston G. 1842.** *A history of British Sponges and Lithophytes*. Edinburgh.
- Klautau M, Borojevic R. 2001.** Sponges of the genus *Clathrina* Gray, 1867 from Arraial do Cabo, Brazil. *Zoosystema* **23** (3): 395–410.
- Klautau M, Russo CAM, Lazoski C, Boury-Esnault N, Thorpe JP, Solé-Cava AM. 1999.** Does cosmopolitanism result from overconservative systematics? A case study using the marine sponge *Chondrilla nucula*. *Evolution* **53** (5): 1414–1422.
- Klautau M, Solé-Cava AM, Borojevic R. 1994.** Biochemical systematics of sibling sympatric species of *Clathrina* (Porifera: Calcarea). *Biochemical Systematics and Ecology* **22**: 367–375.
- Klautau M, Valentine C. 2003.** Revision of the genus *Clathrina* (Porifera, Calcarea). *Zoological Journal of the Linnean Society* **139**: 1–62.
- Lambe LM. 1900.** Sponges from the coasts of north-eastern Canada and Greenland. *Transactions of the Royal Society of Canada, Second Series* **6**: 19–38.
- Levinsen GMR. 1886.** Kara-Havets Svampe (Porifera). Lütken C 1887. *Dijmphna-Togtets zoologisk-botaniske Udbytte*. Kjøbenhavn, 341–372. [In Danish].
- Lundbeck W. 1909.** The Porifera of East Greenland. *Meddelelser om Grønland* **24**: 423–464.
- Maldonado M, Uriz MJ. 1999.** Sexual propagation by sponge fragments. *Nature* **398**: 476.
- Manuel M, Borchellini C, Alvion E, Boury-Esnault N. 2004.** Molecular phylogeny of calcareous sponges using 18S rRNA and 28S rRNA sequences. *Bollettino dei Musei e Degli Istituti Biologici dell'Università di Genova* **68**: 449–461.
- Manuel M, Borchellini C, Alvion E, Le Parco Y, Vacelet J, Boury-Esnault N. 2003.** Phylogeny and evolution of calcareous sponges: monophyly of Calcinea and Calcaronea, high level of morphological homoplasy, and the primitive nature of axial symmetry. *Systematic Biology* **52**: 311–333.
- Manuel M, Borojevic R, Boury-Esnault N, Vacelet J. 2002.** Class Calcarea Bowerbank, 1864. In: Hooper JNA, van Soest RWM, eds. *Systema Porifera. A guide to the classification of sponges*. New York: Kluwer Academic/Plenum Publishers, 1157–1184.
- Merejkowsky C. 1878.** Études sur Les Éponges de la Mer Blanche. *Mémoires de l'Académie Impériale des Sciences de St-Petersbourg VII Série XXVI* (7): 1–50.
- Metschnikoff E. 1879.** Spongiologische Studien. *Zeitschrift für Wissenschaftliche Zoologie* **3**: 277–316.
- Miklucho-Maclay N. 1868.** Beiträge zur Kenntnis der Spongien. I. Über *Guancha blanca* einen neuen Kalkschwamm. *Jenaische Zeitung* **4**: 221–240.
- Minchin EA. 1892.** Note on a sieve-like membrane across the oscula of a species of *Leucosolenia*. *Quarterly Journal of Microscopical Science* 251–272, pls x: xi.
- Montagu G. 1818.** An essay on Sponges, with descriptions of all the species that have been discovered on the coasts of Great Britain (1812). *Memoires of the Wernerian Society of Edinburgh* **2**: 67–122.
- Polejaeff N. 1883.** Report on the Calcarea dredged by the HMS Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage Challenger (Zoology)* **8**: 1–73.
- Rapp HT. 1999.** *Kalksvamper (Porifera, Calcarea) i Trondheimsfjorden – Taksonomi, forekomst og generell biologi. Hovedfagsoppgave i marin biologi til graden Candidatus Scientiarum, NTNU*. Unpublished thesis, Norwegian University of Science and Technology. [In Norwegian].
- Rapp HT. 2004a.** The first record of the genus *Leucascus* Dendy, 1892 from the Atlantic Ocean, with description of *Leucascus lobatus* sp. nov. (Porifera, Calcarea, Calcinea) from Greenland. *Steenstrupia* **28** (2): 1–9.
- Rapp HT. 2004b.** *A revision of calcareous sponges (Porifera, Calcarea) in coast and shelf areas of Norway and Greenland*. Dr scient Thesis, Department of Biology, University of Bergen.
- Rapp HT, Klautau M, Valentine C. 2001.** Two new species of *Clathrina* (Porifera, Calcarea) from the Norwegian coast. *Sarsia* **86**: 69–74.
- Sará M. 1953.** Variabilità delle *Leucosolenia* del Golfo di Napoli e nuove vedute sulla sistemica del gruppo. *Annuario dell'Istituto e Museo di Zoologia della Università di Napoli* **5**: 1–110.
- van Soest R. 2001.** Porifera. In: Costello MJ, Emblow CS, White Royal, eds. *European Register of Marine Species. A checklist of the marine species in Europe and a bibliography of guides to their identification*. *Patrimoines Naturels* **50**: 85–103.
- Solé-Cava AM, Klautau M, Boury-Esnault N, Borojevic R, Thorpe JP. 1991.** Genetic evidence for cryptic speciation in allopatric populations of two cosmopolitan species of the calcareous sponge *Clathrina*. *Marine Biology* **111**: 381–386.
- Tendal OS, Brattegard T, Rapp HT. 2001.** Phylum Porifera. In: Brattegard T, Holthe T, eds. *Distribution of marine benthic macroorganisms in Norway. A tabulated catalogue. Preliminary edition. Research Report for DN 2001-3*. Directorate for Nature Management, 36–51. <http://www.naturforvaltning.no/wbch3.exe?ce=11547>.
- Topsent E. 1936.** Étude sur les *Leucosolenia*. *Bulletin de l'Institut Océanographique, Monaco* **711**: 1–47.
- Von Lendenfeld R. 1885.** A monograph on the Australian sponges. III. The Calcispongiae. *Proceedings of the Linnean Society of New South Wales* **4**: 1083–1150.
- Von Lendenfeld R. 1891.** Die spongien der Adria. I. Die Kalkschwämme. *Zeitschrift für Wissenschaftliche Zoologie* **53** (2): 185–321.
- Wörheide G, Hooper JNA. 1999.** Calcarea from the Great Barrier Reef. I: Cryptic Calcinea from Heron Island and

- Wistari Reef (Capricorn-Bunker group). *Memoirs of the Queensland Museum* **43**: 859–891.
- Wörheide G, Hooper JNA. 2002.** New species of Calcaronea (Porifera: Calcarea) from cryptic habitats of the southern Great Barrier Reef (Heron Island and Wistari Reef, Capricorn-Bunker Group, Australia). *Journal of Natural History* **37**: 1–47.
- Wörheide G, Hooper JNA, Degnan BM. 2003.** Phyleogeography of western Pacific *Leucetta* 'chagosensis' (Porifera, Calcarea) from ribosomal DNA sequences: implications for population history and conservation of the Great Barrier Reef World Heritage Area (Australia). *Molecular Ecology* **11**: 1753–1768.