

# 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

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## Steenstrupia



Rapp, H. T. The first record of the genus *Leucascus* Dendy, 1892 (Porifera, Calcarea, Calcinea) from the Atlantic Ocean, with description of *Leucascus lobatus* sp. nov. from Greenland. – *Steenstrupia* 28 (2): 119–127. Copenhagen, Denmark. December 2004 (for 2002). ISSN 0375-2909.

Representatives of the genus *Leucascus* Dendy, 1892 are previously known only from the Indo-Pacific region and Japan. The description of *Leucascus lobatus* sp. nov. is given, based on material from Greenland. The species bears strongest resemblance to *L. neocaledonicus* Borojevic & Klautau, 2000, from New Caledonia, and *L. soyo* (Hozawa, 1933), from Japan. *Leucascus lobatus* sp. nov. differs from *L. neocaledonicus* by having much bigger spicules, and from *L. soyo* by having an atrial skeleton composed of triactines and tetractines of the same types as those of the choanosome, and not of special atrial tri- and tetractines as in *L. soyo*. The present reports of *Leucascus lobatus* sp. nov. are the first records of the genus from the Atlantic Ocean.

Keywords: Porifera, Calcarea, Calcinea, Leucascidae, *Leucascus lobatus* sp. nov., *Ascaltis*, Greenland, Atlantic Ocean

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## INTRODUCTION

Research on calcareous sponges of Greenland dates back to the 18<sup>th</sup> century, the first specimens being described by Fabricius (1780). Until the first part of the 20<sup>th</sup> century several papers on the Calcarea of Greenland were published, and about thirty species are at present known from Greenlandic waters (Schmidt 1869; Haeckel 1870, 1872, 1874; Fristedt 1887; Vanhöffen 1897; Breitfuss 1897, 1898, 1933; Lundbeck 1909; Brøndsted 1914, 1916, 1933; Burton 1934; Koltun 1964; Tendal 1970).

The family Leucascidae Dendy, 1892 comprises two genera, *Ascaltis* Haeckel, 1872 and *Leucascus* Dendy, 1892. Species of *Ascaltis* are known from most oceans, and are represented by *A. lamarcki* Haeckel, 1872 in the North Atlantic and the Arctic (Haeckel 1872; Breitfuss 1898, 1933; Borojevic & Boury-Esnault 1987).

There are no previous records of any *Leucascus* from the Atlantic Ocean, and the present

study concerns the record of a new species of the genus from Greenland.

## MATERIALS AND METHODS

The sponge specimens are from the collections of the Zoological Museum, University of Copenhagen (ZMUC).

The material comprises 25 specimens from five different Danish expeditions. These are the “Tjalfe” expedition in 1909, the “Godthaab” expedition in 1928, the “Thule” expedition in 1968 to western and north-western Greenland, the Danish Three-Year Expedition to East Greenland 1931–34, and the “Kap Farvel” expedition in 1970 to the southernmost part of Greenland.

Descriptions of spicules are based on examination of different regions of the sponge. For permanent spicule preparations, small pieces from different regions of the sponge were dissolved in sodium hypochlorite. After dissolution of the

soft tissue, the solution was drained, and the spicules washed four times in distilled water and twice in absolute ethanol. The solution of ethanol and spicules was spread on microscope slides and allowed to dry. The mounting medium used was Euparal. Each set of measurements is based on 30 spicules.

Histological sections were made from small pieces of sponge. They were stained with acid Fuchsin for 20 minutes and the excess was removed, followed by rinsing in absolute ethanol. The fragment was cleared in xylene for 1 hour, transferred to a mixture of xylene and molten paraffin wax (1:1) for 30 min at 60 °C, and transferred to molten paraffin wax for another 1 hour at 60 °C. The fragment was then embedded in paraffin wax and sectioned by hand at various thicknesses using a microtome knife. Sections were transferred to a microscope slide and de-paraffinised by xylene. Euparal was used as mounting medium.

## TAXONOMY

The classification used here follows the schemes presented by Borojevic et al. (1990, 2002).

Class CALCAREA Bowerbank, 1864  
Subclass CALCINEA Bidder, 1898  
Order CLATHRINIDA Hartman, 1958, emend.

Family LEUCASCIDAE Dendy, 1892

Clathrinida with the body differentiated into a cortex and a choanosome whose organisation is reminiscent of a clathroid body composed of anastomosed tubes. The cortex contains a specific skeleton composed of large triactines and/or tetractines. Choanocyte chambers are tubular, often highly ramified and anastomosing. The choanoskeleton is restricted to the walls of the choanocyte chambers, maintaining a distinctly tubular organisation (Borojevic et al. 1990, 2002).

### Remarks

The family Leucascidae is characterised by a common cortex composed of the pinacoderm, or the cortical membrane, and the skeletogenous

layer (Borojevic et al. 1990). In *Ascaltis* only the inhalant aquiferous system leads the water from the cortex to the innermost choanocyte tubes. In the morphologically more complex *Leucascus*, a central exhalant atrium is also differentiated, and delimited by a wall with no choanoderm (Borojevic et al. 1990). However, examination of a large specimen of *Leucascus ventricosa* (Carter, 1886) from ZMUC revealed that the cortical membrane was more or less absent, and it appears that presence of a cortical membrane in fixed museum material is highly dependent on proper fixation and storage. The same problem has been observed in *Clathrina cribrata* Rapp, Klautau & Valentine, 2001, which have a cribrum, or sieve of cells below the osculum, a structure that is morphologically very similar to the cortical membrane in the Leucascidae (Rapp et al. 2001). In old museum collections the cribrum is often partly or completely destroyed. In cases where also the skeleton showed the first signs of corrosion, the sieve of cells was usually absent (personal observation).

The status of the genus name *Ascaltis* Haeckel, 1872, was questioned by Hooper & Wiedenmayer (1994). They reintroduced the name *Aulorrhiza* Haeckel, 1870, and due to their quite wide definition of the genus they included in *Aulorrhiza* several species that actually belong to the genus *Leucascus*. However, Haeckel's diagnosis of *Aulorrhiza* is very incomplete, and he did not even give a description of the type species *A. intestinalis* Haeckel, 1870 (Haeckel 1870). In his monograph he described the genus *Ascaltis*, with the type species *Ascaltis lamarcki*, and here he regarded *Aulorrhiza* as a synonym of *Ascaltis*, and *Aulorrhiza intestinalis* as a synonym and variety of *Ascaltis lamarcki* (Haeckel 1872). A short description of the variety *A. intestinalis* was also given. The type material of *A. intestinalis* has never been found (Hooper & Wiedenmayer 1994). The name *Ascaltis* is in current usage, and because no proper description or type material of *Aulorrhiza* exists, the commonly used name is used here. In general the generic and subgeneric names published by Haeckel (1870) have not been in use for well over 50 years, and they fall into the category of *nomina oblita* as defined by the International Code of Zoological Nomenclature (ICZN 1999). A

detailed review of the difficulties with the names proposed by Haeckel was recently given by Manuel et al. (2002).

### Genus *Leucascus* Dendy, 1892

Type species: *Leucascus simplex* Dendy, 1892

Leucascidae with copiously branched and anastomosing choanocyte tubes. The exhalant aquiferous system is represented by a well-developed atrium delimited by a specific wall with no choanoderm, supported by a specific skeleton (Borojevic et al. 1990, 2002).

### *Leucascus lobatus* sp. nov.

Figs 1–3, Table 1.

*Leucosolenia primordialis*. – Brøndsted 1933: 4 (not Haeckel, 1872).

Material examined:

**Type material:** **Holotype:** Kap Farvel, S Greenland, “Kap Farvel” expedition, sta. 83, 60°07.7'N, 44°17.0'W, 230–250 m, 08.Aug.1970, substratum of large stones (ZMUC POR-245, alcohol and slide). **Paratypes:** Same data as holotype (ZMUC POR-246, 3 spec., alcohol; Bergen Museum no. 67217, 2 spec., alcohol; and no. 67218, slide).

**Additional material** (all in ZMUC POR): “Tjalfe”, 65°06'N, 54°19'W, 85 m, 07 Jun 1909 (3 spec.). – “Godthaab” sta. 188, 60°22'N, 47°27'W, 120 m, 10 Oct 1928 (7 spec., fragmentary). – The Danish Three-Year Expedition to East Greenland 1931–34, sta. 295, 70°40'N, 22°W, 14 Aug 1933, 17–31 m (1 spec.). – “Thule” sta. 20, 76°34.5'N, 69°24.5'W, 14 Aug 1968, 35 m (1 spec.). – “Kap Farvel” sta. 83, 60°07.7'N, 44°17.0'W, 230–250 m, 08 Aug 1970 (5 spec., fragmentary); “Kap Farvel” sta. 102, 60°15'N, 44°17'W, 250–400 m, 17 Aug 1970 (1 spec.); “Kap Farvel” sta. 136, 60°04.5'N, 43°02.7'W, 240 m, 25 Aug 1970 (1 spec.).

### Previous records

W Greenland: Julianehåb Bank, “Godthaab” sta. 188 (identified as *Leucosolenia primordialis* (Haeckel, 1872) by Brøndsted 1933: 4).

### Description

The collection contains several large specimens up to 6 cm in diameter. The cormus of this species is white to light beige in alcohol, and is composed of very regularly and tightly anastomosing tubes forming a massive, laterally compressed, and more or less elongated to folded lobate mass. Large oscula (up to 5 mm in diameter) are located

along the upper margin of the cormus (Fig. 1A–B). Remnants of a cortical membrane are found in open spaces between tangential cortical spicules. The surface is smooth, pierced by the openings of the elongated incurrent canals or chambers (Fig. 2A). The walls of the incurrent canals are smooth and have no choanocytes (Fig. 2D). The body wall is 2–5 mm thick, and surrounds the flattened central atrium, whose surface is pierced by circular to elongated openings of the exhalant cavities (Fig. 2A). The choanosome is composed of more or less radially arranged choanosomal tubes that open into exhalant canals (Fig. 2A). One to several layers of scattered large regular triactines measuring  $181 \pm 21 \mu\text{m}$  long and  $11 \pm 1.3 \mu\text{m}$  wide, and several layers of smaller regular to

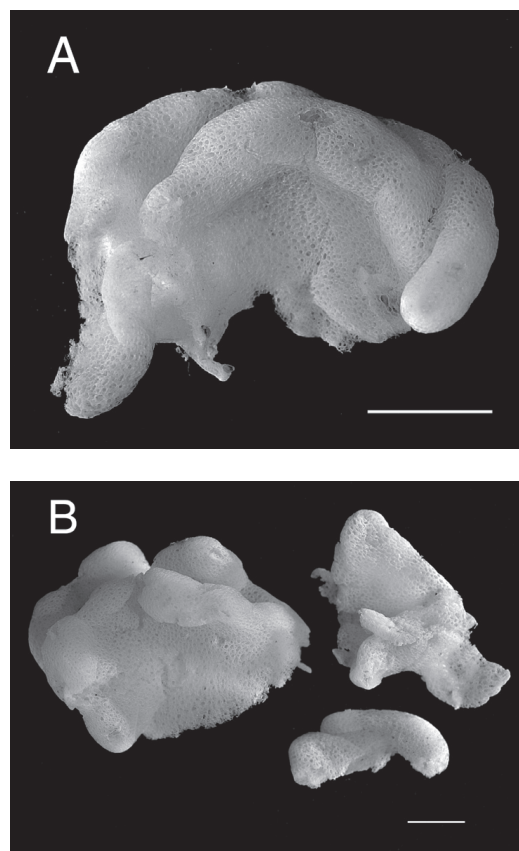


Fig. 1. Type specimens of *Leucascus lobatus* sp. nov. A. Holotype (ZMUC POR-245). B. Paratypes (ZMUC POR-246). – Scale = 1 cm (photo Geert Brovad).



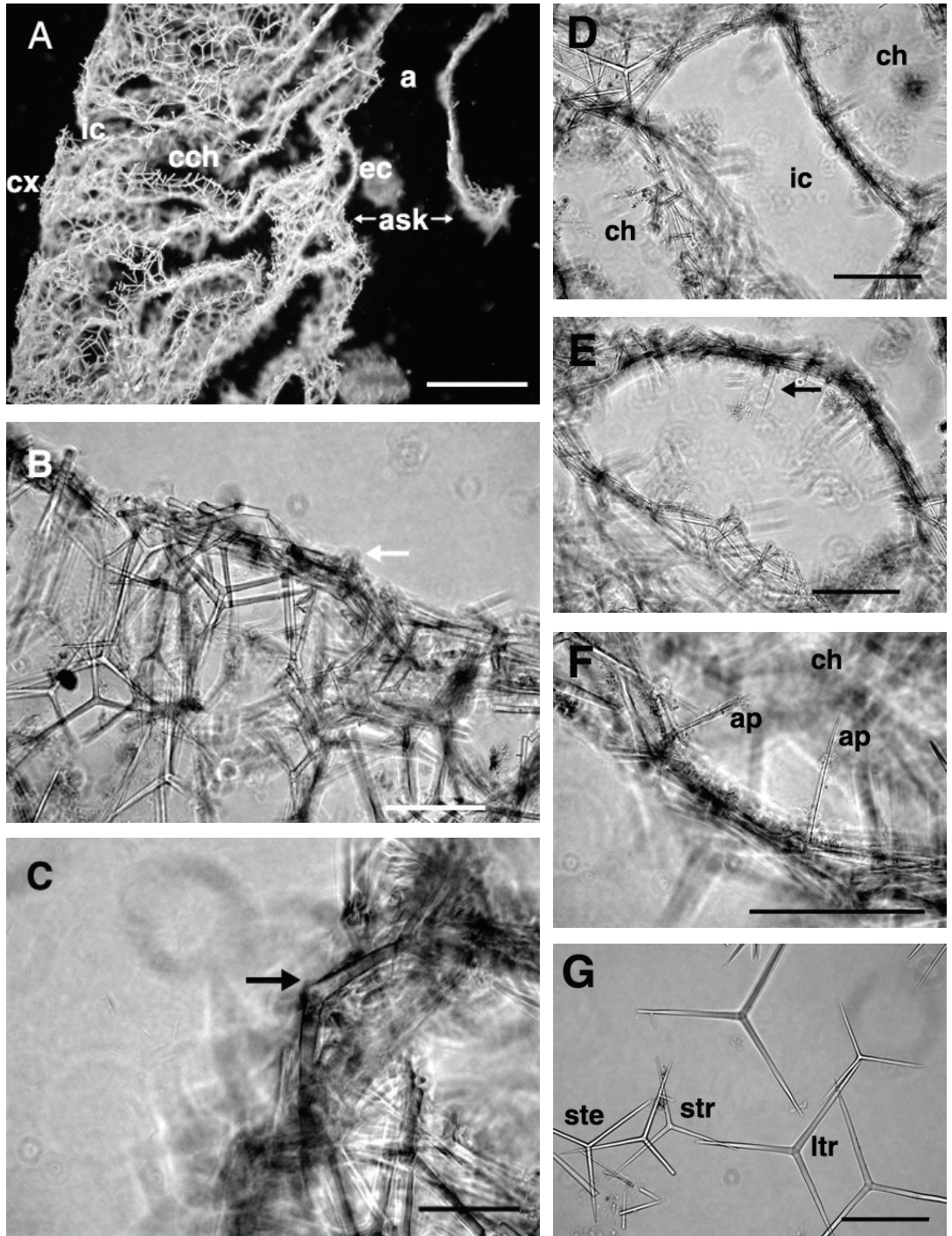


Fig. 2. Skeletal features and spicules of *Leucascus lobatus* sp. nov. A. Cross-section of body wall showing arrangement

sub-regular triactines measuring  $126 \pm 13 \mu\text{m}$  long and  $7 \pm 1 \mu\text{m}$  wide, and tetractines measuring  $129 \pm 13 \mu\text{m}$  long by  $7 \pm 1 \mu\text{m}$  wide represent a weakly developed cortical skeleton (about  $50 \mu\text{m}$  thick) (Fig 2B and G; Table 1). The large triactines are slightly tripodite (Fig. 2C). The choanosomal skeleton is composed of irregularly arranged small tri- and tetractines, and scattered large triactines, of the same types as those in the cortex. The apical actines of the tetractines are directed inwards into the interior of the choanosomal tubes (Figs 2E–F). The sponge has a well-developed atrium delimited by an atrial skeleton composed of small, regular to sub-regular triactines and tetractines of the same shape and size as the small spicules in the cortex and the choanosome. The atrial skeleton is smooth as the apical actine of the atrial tetractines is directed towards the choanosome. The atrial wall is devoid of choanocytes.

### Etymology

Named from the shape of the cornus.

Table 1. Spicule dimensions of *Leucascus lobatus* sp. nov. N = 30 for all measurements, SD = standard deviation.

Spicule type	Length ( $\mu\text{m}$ )				Width ( $\mu\text{m}$ )	
	Min.	Max.	Mean	SD	Mean	SD
<b>HOLOTYPE</b>						
Large triactines	148	230	181	$\pm 21.1$	10.9	$\pm 1.3$
Small triactines	100	148	126	$\pm 13.2$	6.9	$\pm 0.9$
Tetractines	98	152	129	$\pm 13.4$	7.1	$\pm 1.0$
Apical actine	1	70	16	$\pm 18.1$	4.5	$\pm 1.0$
<b>PARATYPE</b>						
Large triactines	149	240	187	$\pm 24.9$	10.3	$\pm 1.0$
Small triactines	98	139	125	$\pm 14.0$	7.1	$\pm 0.8$
Tetractines	100	155	130	$\pm 13.9$	7.5	$\pm 0.8$
Apical actine	1	80	20	$\pm 21.9$	4.5	$\pm 1.0$

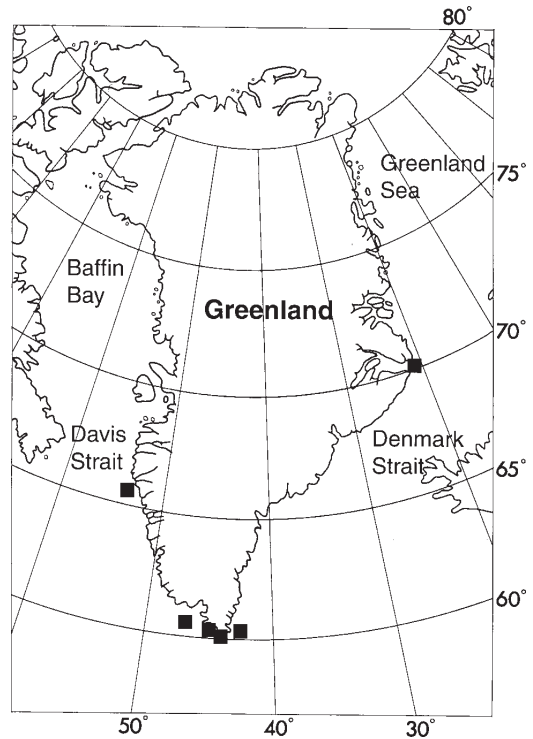


Fig. 3. Distribution of *Leucascus lobatus* sp. nov. along the coast of Greenland.

### Distribution

The species is only known from western, southern and eastern Greenland at depths of 17–400 m (Fig. 3).

### Remarks

No species of *Leucascus* has previously been reported from the Atlantic Ocean. The only other representative of the family Leucascidae is *Ascaltis lamarcki* Haeckel, 1872, a species with a very wide distribution in the Atlantic. The two

of body parts from external side (left) to atrium (right). B. Enlargement of cortex containing several layers of tangential triactines of two size classes and tetractines of one size class. C. Detail of cortex showing slightly tripodite shape of large triactines (arrow). D. Longitudinal section of body wall showing smooth incurrent canal between choanocyte chambers. E. Cross-section of a choanocyte chamber/canal. Note that the apical actines of the tetractines are directed towards the interior of the tube (arrow). F. Detail of skeleton in wall of choanocyte chamber. G. Spicule categories. – Abbreviations: a = atrium; ap = apical actine of tetractines; ask = atrial skeleton; cch = choanocyte chamber/canal; ch = interior of choanocyte chamber; cx = cortex; ec = atrial opening of exhalant canal; ic = incurrent canal; ltr = large triactine; ste = small tetractine; str = small triactine. – Scales: A = 500  $\mu\text{m}$ ; B–C, F–G = 100  $\mu\text{m}$ ; D = 150  $\mu\text{m}$ ; E = 75  $\mu\text{m}$ .

genera *Ascaltis* and *Leucascus* both have a distinct cortex, and *Leucascus* is separated from *Ascaltis* by the presence of a distinct and well developed atrium lined with pinacocytes in *Leucascus*, and a less distinct atrium or several exhalant canals lined with choanocytes in *Ascaltis*. In *Leucascus* the atrial skeleton is clearly separated from the skeleton of the choanosome, while in *Ascaltis* it is not. The quite loosely arranged choanosome of *Leucascus lobatus* sp. nov. results in the species resembling *Ascaltis grisea* (Dendy & Frederick, 1924) and other complex species of *Ascaltis*. However, the presence of an atrial wall devoid of choanocytes clearly distinguishes this species the genus *Ascaltis*.

The cortical membrane characteristic for the Leucascidae is indeed not prominent in *L. lobatus*, and is only seen as scattered remnants between cortical spicules. The cortical membrane in the Leucascidae is in general easily destroyed, and the presence of a cortical membrane in old museum specimens is highly dependent on proper fixation and storage. The remnants of a cortical membrane in *L. lobatus* might therefore be an artefact due to the conditions of fixation and storage. This is supported by the fact that some individual spicules show signs of corrosion. Unfortunately no fresh material has been available for examination, so no proper description of the membrane in living specimens can be given.

However, hypothetically, if a proper cortical membrane covering the entire cormus proved to be absent in living specimens, this would be a new combination of characters, and would require the creation of a new genus. As long as no fresh material is available to answer that question, the species is retained in the genus *Leucascus*.

According to Dendy & Row (1913), there are only three species of *Leucascus*: *L. clavatus* Dendy, 1892, *L. insignis* (Row & Hozawa, 1931), and *L. simplex* Dendy, 1892, all from Australian waters. Dendy & Row (1913) included *L. insignis* in *Leucascus* based on an unpublished manuscript of Row, and the final description was published many years later (Row & Hozawa 1931). Borojevic (1968) pointed out that several species previously described as *Leucosolenia* should be included in the Leucascidae, without making any final statements. However, recently Borojevic & Klautau

(2000) described *Leucascus neocaledonicus* from New Caledonia. At the same time they argued that several other species from the Indo-Pacific region, previously described under the name *Leucosolenia*, probably should be included in the genus *Leucascus*. These species are *L. ventricosa* Carter, 1886, *L. wilsoni* Dendy, 1891, *L. pelliculata* Dendy, 1891, and *L. protogenes* Haeckel, 1872, but Borojevic & Klautau (2000) state this explicitly only for *Ascoleugetta compressa* Dendy & Frederick, 1924. One specimen of *L. ventricosa* deposited in ZMUC has been examined, and it clearly belongs to the genus *Leucascus*.

However, it is here indicated that also two species of "*Leucosolenia*" from Japan should be included in *Leucascus*. These are *L. amitsbo* Hozawa, 1929 and *L. soyo* Hozawa, 1933. *L. amitsbo* and *L. soyo* are described as having a canal system of "Dendy's reticulate type D" (Dendy 1891) with distinct cortical and atrial skeletons, a choanosome of ascon tubes, and an atrium devoid of choanocytes (Hozawa 1929, 1933).

Species previously described under the genus *Leucettusa* Haeckel, 1872 should also be taken into consideration. Re-examination of the type specimen of *L. mariae* Brøndsted, 1926, deposited in ZMUC, revealed that also this species should be included in *Leucascus*.

*Leucascus lobatus* sp. nov. is in many ways similar to *L. compressa*, *L. insignis*, *L. neocaledonicus* and *L. pelliculata* in having two distinct size classes of triactines and one size class of tetractines. However, there are some important differences. *L. compressa* and *L. pelliculata* both have a thicker and more developed cortex, and the cortical triactines have rays that are longer (about 250 µm compared to 180 µm) and about three times as thick as those found in *Leucascus lobatus* sp. nov. (Dendy & Frederick 1924). In *L. insignis* the cortical triactines are mainly tripods with very stout actines with blunt points, whereas the actines in *L. lobatus* sp. nov. are straight with sharp to slightly blunt points.

*Leucascus neocaledonicus* and *L. soyo* are the species most similar to *L. lobatus* sp. nov. *L. lobatus* sp. nov. differs from *L. neocaledonicus* by the larger size of the cortical (181 ± 21 µm compared to 130 ± 27 µm) and choanosomal



spicules ( $126 \pm 13 \mu\text{m}$  compared to  $100 \pm 14 \mu\text{m}$ ). Borojevic & Klautau (2000) have not distinguished between choanosomal and atrial spicules, so no comparison is possible at this stage. The cortical and choanosomal spicules of *L. lobatus* sp. nov. and *L. soyo* are very similar, but the two species differ clearly by *L. soyo* having a distinct set of atrial tri- and tetractines, while in *L. lobatus* sp. nov. these are similar to choanosomal spicules. *Leucascus lobatus* sp. nov. clearly differs from the other species in the genus by the fact that *L. protogenes* and *L. wilsoni* have triactines of two types and no tetractines, *L. clavatus* and *L. simplex* have only one type of triactines and only occasionally have tetractines, and *L. clavatus* and *L. ventricosa* have additional diactines (Carter 1886; Haeckel 1872; Dendy 1891, 1892). *L. mariae* is the only species having two types of triactines and two types of tetractines. *L. amitsbo* has very large spicules, and like *L. soyo* it has an extra set of atrial triactines and tetractines differing from the cortical and choanosomal spicules.

Except for the material examined of *L. mariae* (holotype) and *L. ventricosa* (one specimen), the comparisons are based on the original descriptions of the different species.

The specimens of *L. lobatus* sp. nov. from "Godthaab" sta. 188 were previously (mis)identified and published by Brøndsted (1933) as *Leucosolenia primordialis* (Haeckel, 1872). However, in his publication on the sponges from New Zealand (Brøndsted 1926) it is clear that like many other spongiologists at that time (Burton 1930, Topsent 1936), he had a very wide definition of *L. primordialis*, or more correctly *Clathrina primordialis*.

## ZOOGEOGRAPHICAL REMARKS

*Leucascus lobatus* sp. nov. is found in two quite different water masses around Greenland. At the localities on the eastern and western coast are water masses are characterized by cold ( $-1.3$  to  $0.8 \text{ }^\circ\text{C}$ ) and low salinity (32.52–33.9 S) arctic water from the East Greenland Current, the West Greenland Current, and the Labrador Sea (Thorson & Ussing 1934, Dinter 2001). The lo-

calities along the southern coast are more influenced by Atlantic water with higher temperature (about  $5.5 \text{ }^\circ\text{C}$ ) and higher salinity (about 34.3 S) (Fig. 3).

No specimens of *Leucascus lobatus* sp. nov. have been found during examination of large collections of calcareous sponges from the Norwegian coast, Bear Island (Barents Sea), Spitsbergen, and Iceland (Rapp, unpublished data). Given the size of the species, it is unlikely that it has been overlooked in earlier investigations, and it is probably not present in the eastern part of the North Atlantic.

However, it is possible that the species occurs in the arctic-influenced cold water of the deeper water layers along the north-eastern coast of North America and Canada, where investigations on calcareous sponges are very scarce (Verrill 1874; Lambe 1896, 1900c; Laubenfels 1942). The presence of *Leucascus lobatus* sp. nov. along the north-western and eastern Greenlandic coast might indicate that it is a real arctic species only occasionally found in Atlantic water, and a more plausible explanation would then be that the species is distributed further west in the northernmost part of Canada, Alaska, and the Bering Sea.

Low sampling effort taken into consideration, it is not surprising that no species of *Leucascus* have been reported from these areas, or from the west coast of Canada and North America (Lambe 1892, 1893, 1894, 1900a, 1900b). However, Hozawa (1919) reported a specimen from Comandorski Islands (NW Pacific) that he identified as *Leucosolenia canariensis* (Miklucho-Maclay, 1868) where "The entire outer surface of the sponge seems to be covered with a finely folded continuous membrane", indicating that it really might have been a specimen of a Leucascidae. New records of *Leucascus* from arctic Canada or the Bering Sea would indicate a continuous distribution of the genus from the high arctic Greenland, through Canada and the Bering Sea, along the eastern Russian coast to Japan, and further on to the tropical and subtropical Indo-Pacific region.

The tropical and subtropical species of *Leucascus* mainly comprise shallow-water forms, exceptionally found down to 140 m (*L. ventricosa*), while *L. amitsbo* and *L. soyo* from the northern temperate Japanese waters are found down to 700

m and 170 m, respectively, and the arctic *L. lobatus* sp. nov. is found down to 400 m depth.

## ACKNOWLEDGEMENTS

I thank Dr. Ole Secher Tendal (Zoological Museum, University of Copenhagen) for helpful discussions and critical reading of the manuscript. Two anonymous referees are also thanked for valuable comments on the manuscript.

This project was supported by the *European Community – Access to Research Infrastructure Action of the Improving Human Potential Programme*, through the Copenhagen Biosystematics Centre (COBICE), project number 232.

## REFERENCES

- Borojevic, R. 1968. Eponges calcaires des côtes de France IV. Le genre *Ascaltis* Haeckel emend. – Archives de Zoologie expérimentale et générale 109: 193–210.
- Borojevic, R. & N. Boury-Esnault. 1987. Calcareous sponges collected by N. O. Thalassa on the continental margin of the Bay of Biscaye: I. Calcinea. – Pp. 1–27 in J. Vacelet & N. Boury-Esnault (eds): *Taxonomy of Porifera from the NE Atlantic and Mediterranean Sea*. – NATO Asi Series G13: 321 pp.
- Borojevic, R., N. Boury-Esnault & J. Vacelet. 1990. A revision of the supraspecific classification of the subclass Calcinea (Porifera, class Calcarea). – Bulletin du Muséum National d'Histoire Naturelle, Paris (4, A) 12 (2): 243–276.
- Borojevic, R., N. Boury-Esnault, M. Manuel & J. Vacelet. 2002. Order Clathrinida Hartman, 1958. – Pp. 1141–1152 in J. N. A. Hooper & R. W. M. Van Soest (eds): *Systema Porifera. A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York, 1708 pp.
- Borojevic, R. & M. Klautau. 2000. Calcareous sponges from New Caledonia. – Zoosystema 22: 187–201.
- Breitfuss, L. 1897. Catalog der Calcarea der zoologischen Sammlung des königlichen Museums für Naturkunde zu Berlin. – Archiv für Naturgeschichte 63: 205–226.
- Breitfuss, L. 1898. Die arctische Kalkschwammfauna. – Archiv für Naturgeschichte 1: 1–40.
- Breitfuss, L. 1933. Die Kalkschwammfauna des arctischen Gebietes. – Fauna Arctica 6: 235–252.
- Brøndsted, H. V. 1914. Conspectus Faunae Groenlandicae. Porifera. – Meddelelser om Grønland 23: 457–544.
- Brøndsted, H. V. 1916. The Porifera collected by the Danish Expedition at north-east Greenland. – Meddelelser om Grønland 43: 475–483.
- Brøndsted, H. V. 1926. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. XXXV. Sponges from New Zealand. Part II. – Meddelelser fra Dansk natur-historisk Forening 81: 295–331.
- Brøndsted, H. V. 1933. The Godthaab Expedition 1928. Porifera. – Meddelelser om Grønland 79 (5): 1–25.
- Burton, M. 1930. Norwegian sponges from the Norman collection. – Proceedings of the Zoological Society of London 1930 (1): 487–546, pls 1–2.
- Burton, M. 1934. Zoological results of the Norwegian scientific expedition to East-Greenland. III. Reports on the sponges of the Norwegian expeditions to East-Greenland (1930, 1931 and 1932). – Skrifter om Svalbard og Ishavet 61: 3–34.
- Carter, H. J. 1886. Descriptions of sponges from the neighbourhood of Port Philip Heads. – Annals and Magazine of Natural History 18: 34–55 + 126–149.
- Dendy, A. 1891. A monograph of the Victorian sponges. I. The organisation and classification of the Calcarea Homocoela, with descriptions of the Victorian species. – Transactions of the Royal Society of Victoria 3 (1): 1–82.
- Dendy, A. 1892. Synopsis of the Australian Calcarea Heterocoela, with proposed classification of the group, and descriptions of some new genera and species. – Proceedings of the Royal Society of Victoria (N.S.) 5: 69–116.
- Dendy, A. & L. M. Frederick. 1924. On a collection of sponges from the Abrolhos Islands, Western Australia. – Journal of the Linnean Society of London, Zoology 35: 477–518.
- Dendy, A. & R. W. H. Row. 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 1913: 704–813.
- Dinter, W. P. 2001. *Biogeography of the OSPAR Maritime Area. A Synopsis and Synthesis of Biogeographical Distribution Patterns described for the North-East Atlantic*. Federal Agency for Nature Conservation, Bonn, Germany. 167 pp.
- Fabricius, O. 1780. *Fauna Groenlandica*. Hafniae et Lipsiae [Copenhagen and Leipzig], xvi + 415 pp., 1 pl.
- Fristedt, K. 1887. Sponges from the Atlantic Ocean. – Vega-Expeditionens Vetenskapliga Iakttagelser 4: 401–471.
- Haeckel, E. 1870. Prodomus eines Systems der Kalkschwämme. – Jenaische Zeitschrift 5: 236–254.
- Haeckel, E. 1872. *Die Kalkschwämme. Eine Monographie in zwei Bänden Text und einem Atlas mit 60 Tafeln Abbildungen*. Georg Reimer, Berlin. Pp. 1–484 + 1–418, pls 1–60.
- Haeckel, E. 1874. Kalk and Gallertspongien. – Pp 434–436 in: *Die zweite deutsche Nordpolarfahrt*. II. Brockhaus, Leipzig.
- Hooper, J. N. A. & F. Wiedenmayer. 1994. Porifera. Pp 1–624 in A. Wells (ed.): *Zoological Catalogue of Australia* 12. CSIRO, Melbourne, Australia, xiii + 624 pp.
- Hozawa, S. 1919. Report on the calcareous sponges collected during 1906 by the United States fisheries steamer Albatross in the north-western Pacific. – Proceedings of the United States National Museum 54: 525–557.
- Hozawa, S. 1929. Studies on the calcareous sponges of Japan. – Journal of the Faculty of Science, Imperial University of Tokyo, Section IV, Zoology 1: 277–389.



- Hozawa, S. 1933. Report on the calcareous sponges obtained by the survey of the continental shelf bordering on Japan. – Science Reports of the Tōhoku Imperial University, Fourth Series 8: 1–20.
- [ICZN] International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth edition. International Trust for Zoological Nomenclature, the Natural History Museum, London. Pp. 1–306.
- Koltun, V. M. 1964. Porifera. In: Scientific results in the higher latitudes. Oceanographic investigations in the northern part of the Greenland Sea and the adjacent Arctic basins [In Russian]. – Works from the Arctic and Ant-arctic Scientific Institute 259: 143–166.
- Lambe, L. M. 1892. On some sponges from the Pacific coast of Canada and Bering Sea. – Transactions of the Royal Society of Canada, Series 4, 10: 67–78.
- Lambe, L. M. 1893. Sponges from the Pacific coast of Canada. – Transactions of the Royal Society of Canada, Series 4, 11: 25–43.
- Lambe, L. M. 1894. Sponges from the western coast of North America. – Transactions of the Royal Society of Canada, Series 4, 12: 113–138.
- Lambe, L. M. 1896. Sponges from the Atlantic coast of Canada. – Transactions of the Royal Society of Canada, Series 2, 2: 181–211.
- Lambe, L. M. 1900a. Notes on Hudson Bay sponges. – The Ottawa Naturalist 13: 277.
- Lambe, L. M. 1900b. Description of a new species of calcareous sponge from Vancouver Island, B. C. – The Ottawa Naturalist 13: 261–262.
- Lambe, L. M. 1900c. Sponges from the coasts of north-eastern Canada and Greenland. – Transactions of the Royal Society of Canada, Series 2, 6: 19–38.
- Laubenfels, M. W. De. 1942. Porifera from Greenland and Baffinland collected by Capt. Robert A. Barlett. – Journal of the Washington Academy of Sciences 32: 263–269.
- Lundbeck, W. 1909. The Porifera of East-Greenland. – Meddelelser om Grønland 29: 423–464.
- Manuel, M., R. Borojevic, N. Boury-Esnault & J. Vacelet. 2002. Class Calcarea Bowerbank, 1864. – Pp. 1157–1184 in J. N. A. Hooper & R. W. M. Van Soest (eds): *Systema Porifera. A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York, 1708 pp.
- Rapp, H. T., M. Klautau & C. Valentine. 2001. Two new species of *Clathrina* (Porifera, Calcarea) from the Norwegian coast. – Sarsia 86: 69–74.
- Row, R. W. H. & S. Hozawa. 1931. Report on the Calcarea obtained by the Hamburg South-West Australian Expedition of 1905. – Science Reports of the Tōhoku Imperial University 6: 727–809.
- Schmidt, O. 1869. Vorläufige Mitteilungen über die Spongien der Grönländischen Küste. – Mitteilungen des Naturwissenschaftlichen Vereins für Steiermark 2 (1): 89–97.
- Tendal, O. S. 1970. Sponges from the Jørgen Brønlund Fjord, North Greenland. – Meddelelser om Grønland 184 (7): 1–14.
- Thorson, G. & H. Ussing. 1934. Contributions to the animal ecology of the Scoresby Sound Fjord complex (East Greenland). – Meddelelser om Grønland 100 (3): 1–67.
- Topsent, E. 1936. Étude sur les *Leucosolenia*. – Bulletin de l'Institut Océanographique, Monaco 711: 1–47.
- Vanhöffen, E. 1897. Die Fauna und Flora Grönlands. Die Schwämme. – Pp. 246–249 in: *Grönland-Expedition der Gesellschaft für Erdkunde zu Berlin 1891–1893*. Vol. II. W. H. Kuhl, Berlin.
- Verrill, E. A. 1874. Exploration of Casco Bay by the U. S. Fish Commission, in 1873. – Proceedings of the American Association for the Advancement of Science 22: 340–395.

Submitted 30.viii. 2002, accepted 3.vi.2003