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Arctic cheilostome bryozoan species of the genus *Escharoides*

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Abstract
This investigation focuses on the diversity and identity of species of *Escharoides* found north of the Arctic Circle. Study of type and other material from this region using SEM shows that only two Arctic species can be recognized, *Escharoides bidenkapi* (Kluge) and *E. jacksoni* (Waters). The first of these is characterized by the distolateral orientation of the avicularia located beside the orifice, and by the suboral shelf on the distal border of the autozooidal orifice which is crenulated. *Escharoides jacksoni* differs in having slightly larger avicularia that are directed laterally, and a smooth suboral shelf.

Keywords: *Arctic, Bryozoa,* Escharoides, *taxonomy*

Introduction

The ascophoran cheilostome bryozoan genus *Escharoides* contains approximately 45 species, fossil and living (Bock 2006). It is one of the longest ranging of all ascophoran genera, with recorded occurrences stretching back to the Late Cretaceous (e.g. Guha and Nathan 1996), although some putative species from the Cretaceous are better assigned to other genera (Taylor and McKinney 2006). Recent species are distributed worldwide across all climatic zones, from the poles to the tropics. There are no obvious diversity hot spots, although species richness does seem to be greatest in temperate seas. To date 15 species have been described from the northern hemisphere (Bock 2006). The present paper focuses on species of *Escharoides* from the Arctic (i.e. north of the Arctic Circle).

Kluge's (1962, 1975) comprehensive taxonomic study of Arctic bryozoans listed four species and one variety of *Escharoides*. These are *Escharoides coccinea* (Abildgaard, 1806), *E. bidenkapi* (Kluge, 1946), *E. jacksoni* (Waters, 1900), *E. monstruosa* (Kluge, 1946), and *E. jacksoni* var. *rostrata* Kluge, 1946. However, *E. coccinea* is Atlantic boreal in distribution and has never been recorded in the Arctic (Kluge 1975; Hayward and Ryland 1999).

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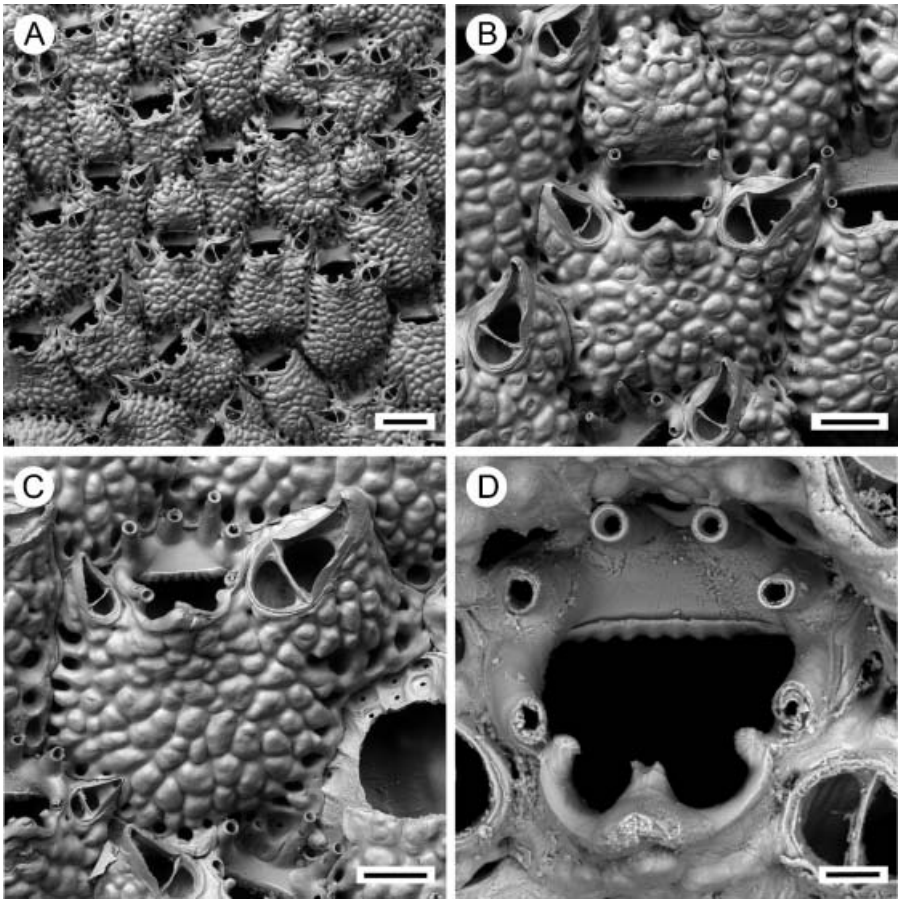

Figure 1. *Escharoides coccinea* (Abildgaard, 1806), NHM 1911.10.1.1034, Guernsey, bleached. (A) Colony showing autozooids and ovicellate zooids; (B) ovicellate zooid with two lateral avicularia; (C) autozooid with two lateral avicularia of strikingly unequal sizes; (D) orifice of autozooid. Scale bars: 200 μm (A); 100 μm (B, C); 30 μm (D).

Furthermore, *Escharoides monstruosa* lacks the lateral avicularia characteristic of *Escharoides* (see Figure 1) and is considered to belong elsewhere.

Species of *Escharoides* possess complex calcified skeletons, which should facilitate determination of species and allow taxonomic resolution within this genus. However, the lack of scanning electron microscopy (SEM) of the genus has hindered progress, and the number of species inhabiting the Arctic has remained uncertain. For example, Bille-Hansen (1962) synonymized *E. jacksoni* and *E. bidenkapi*, an opinion followed by Hayward and Ryland (1999). There is also uncertainty whether a variety of *E. jacksoni* (Waters, 1900), *E. jacksoni* var. *rostrata* Kluge, 1946, should be regarded as a distinct species. Here we use SEM to study type and other Arctic material of *Escharoides* in order to evaluate the species diversity of this genus in the Arctic and to provide up-to-date descriptions and illustrations.

Material and methods

Material studied is lodged in the Natural History Museum, London (NHM); University of Manchester Museum (MM); Canadian Museum of Nature, Ottawa (CMN); and

Zoological Institute of the Russian Academy of Sciences, St Petersburg (ZI). Both historical and new collections were employed for this study.

Scanning electron microscopy was undertaken with a low-vacuum instrument (LEO 1455-VP) capable of imaging uncoated specimens using back-scattered electrons.

Systematics

Order CHEILOSTOMATA Busk, 1852
Suborder ASCOPHORINA Levinsen, 1909
Superfamily LEPRALIELLOIDEA Vigneaux, 1949
Family EXOCHELLIDAE Bassler, 1935
Genus *Escharoides* Milne-Edwards, 1836

Type species. *Cellepora coccinea* (Abildgaard, 1806).

Diagnosis

Frontal shield with marginal areolae, lacking pseudopores; umbonuloid, with ring scar on underside. Oral spines present on distal border of orifice; secondary orifice generally peristomate and/or with denticles. Avicularia well developed, single or paired, lateral to orifice, pointed. Ovicell prominent, hyperstomial.

Remarks

Although *Escharoides coccinea* has never been recorded from the Arctic (Kluge 1975), it is the type species of *Escharoides* and we therefore present SEM images of this species to illustrate the key characteristics of the genus (Figure 1). Hayward and Ryland (1999) provided a detailed description of this species. The frontal shield is more coarsely tuberculate in *E. coccinea* than in either of the two Arctic species of *Escharoides*; there are six rather than four oral spines; and the paired avicularia are often of different sizes (Figure 1C), a feature not seen in either *E. bidenkapi* or *E. jacksoni*.

Escharoides bidenkapi (Kluge, 1946)
(Figure 2)

Peristomella bidenkapi Kluge 1946, p 200, Plate 2, Figure 6.
Escharoides bidenkapi: Kluge 1962, p 566, Figure 400; Kluge 1975, p 690, Figure 400; Hayward and Ryland 1978, p 150, Figure 5A, B.
Escharoides jacksoni (Waters, 1900): Hayward and Ryland 1999, p 116, Figure 33.

Type material examined

Lectotype: ZI 30/2945, Kara Sea, "Sadko" Stn 58/98, 12 September 1935, det. Kluge from Gorbunov material, Kluge Collection. This specimen from the Kluge Collection is here chosen as the lectotype based on the match between the locality information and that given in the original description (Kluge 1946).

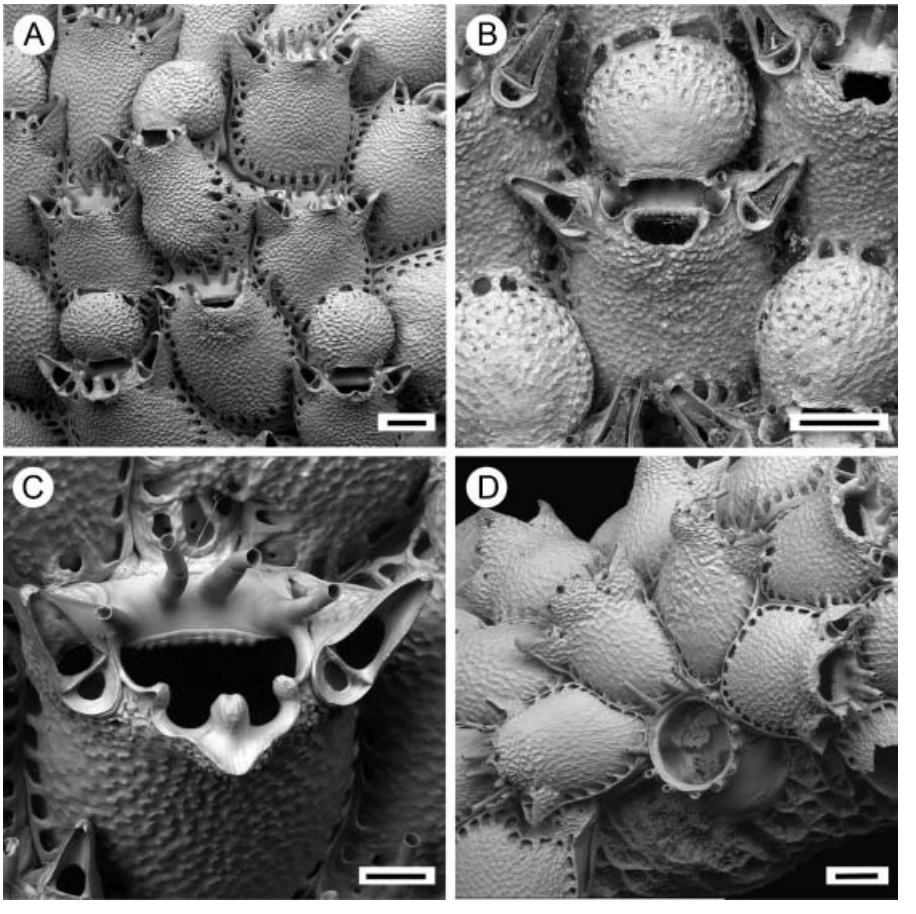

Figure 2. *Escharoides bidenkapi* (Kluge, 1946), bleached. (A) Colony showing autozooids and ovicellate zooids (lectotype: ZI 30/2945); (B) ovicellate zooid with two lateral avicularia (ZI 36/5223); (C) orifice of autozooid with two lateral avicularia and characteristic suboral shelf with distal crenulation (ZI 38/5468); (D) ancestrula and surrounding zooids (ZI 38/5468). Scale bars: 100 μm (A, C); 200 μm (B, D).

Other material examined

NHM 1911.10.1.1037, Greenland, 72°10′N, 20°37′E, depth 364–546 m, Norman Collection; NHM 1911.10.1.1045, Kvenanger Fjord, Finmark, Norway, April 1899, 100 m depth; NHM 1985.1.2.67, 51°10′N, 11°47′W, 1390–1582 m, 26 June 1960, Sarsia Stn 21/2; NHM 2006.07.31.1, Belgica Bank, East Greenland, ''Polarstern'' Expedition, coll. Bader; ZI 36/5223, Barents Sea, Kolski Bay, 13 August 1908, Trawl, det. Kluge, coll. Avrucev; ZI 38/5468, Polar Basin, Stn 12, ''Litke'', 14 September 1955, det. Gostilovskaya, coll. Koltun; ZI 12, Shokalski Strait (located north of Wilkitzki Strait), 77°56′N, 103°33′E, Stn 26, 6–7 September 1932, ''Rusanov'', trawl, det. Kluge, coll. Vagin; ZI 1, Kara Sea, Dickson Island–Cape Cheluskin, Stn 26, ''Sibiriakov'', trawl, 28 August 1933, det. Kluge, coll. Gorbunov.

Description

Colony forming a thick unilaminar crust (Figure 2A). Ancestrula (Figure 2D) tatiform, oval, with narrow cryptocyst, broad proximal gymnocyst, and 14 spines.

Autozooids large, irregular in shape, separated by deep grooves, 0.61–1.03 mm long (mean 0.84 mm, $n=20$) by 0.50–0.76 mm wide (mean 0.62 mm, $n=20$). Frontal shield usually granular with polygonal surface patterning, bordered by a single or double row of round areolae. Orifice suborbicular; distal border with a broad, crenulated suboral shelf (Figure 2C); proximal edge developed as a thick, projecting peristome with usually three (one median and paired lateral) thickened denticles around proximal inner margin, and with a median notch on the rim. Denticles and notch sometimes missing. Denticles when present striated. Oral spines usually numbering four, short, thick, the outer two fused with the peristome. Ovicellate zooids have only two visible oral spines. Avicularia typically paired at distolateral corners of autozooids, sometimes single, very rarely lacking, large, 0.17–0.28 mm long (mean 0.23 mm, $n=20$) by 0.09–0.13 mm wide (mean 0.11 mm, $n=20$), directed distolaterally, rostrum narrowly triangular, hooked at tip, avicularian chamber often with pores at the base and rarely on the chamber itself; mandible elongate-triangular, crossbar calcified.

Ovicell (Figure 2B) hyperstomial, globular, finely granular, slightly longer than broad, large, 0.33–0.52 mm long (mean 0.42 mm, $n=20$) by 0.39–0.56 mm wide (mean 0.47 mm, $n=20$); pesudopores scattered over distal part, bordered by a series of round areolae.

Distribution

This Arctic and deep-water temperate species has been most frequently recorded from the Atlantic part of the Arctic. There are some records from the East Siberian Sea but none so far from the Canadian Arctic, which means that *E. bidenkapi* is probably not circumpolar in distribution. The species has been recorded as far south as the Bay of Biscay, at depths of 1390–1582 m in the temperate Atlantic (Hayward and Ryland 1978).

Escharoides jacksoni (Waters, 1900)
(Figures 3, 4)

Smittina jacksoni Waters 1900, p 87, Plate 12, Figure 18.

Mucronella coccinea (Abildgaard, 1806): Bidenkap 1897, p 624, Plate 25, Figures 5, 6.

Escharoides jacksoni var. *rostrata* Kluge 1946, p 201, Figure 6; Kluge 1962, p 569, Figure 402; Kluge 1975, p 693, Figure 402.

Escharoides jacksoni: Kluge 1962, p 568, Figure 401; Kluge 1975, p 692, Figure 401; Powell 1968, p 2294, Plate 5, Figure B; Bille-Hansen 1962, p 33.

Type material examined

Holotype: MM 4307, 77°55′N, 55°10′E, collected during Jackson-Harmsworth Expedition, 7 October 1897, Waters Collection.

Other material examined

NHM 2006.07.31.2, Laptev Sea, 74°30.0′N, 137°05.0′E, Transdrift 1 project, Stn 48, 18 August 1993, 22 m depth, dredge, coll. Schmid; ZI 30/2945, East Siberian Sea, Stn 25, 23 August 1937, ''Sadko'', det. Kluge, coll. Gorbunov; ZI 50/354, NE Polar Basin, Stn 73, 1948, det. Petrovskaya; ZI 7, Fram Straight, Stn 43, 1901, ''Zaria'', det. Kluge, coll. R.P.E.; ZI 10, Laptev Sea, in front of Pronchischev Bay, Stn 34, ''Sibiriakov'', trawl, 14 September 1933, det. Kluge, coll. Gorbunov; ZI 15, Kara Sea, O-b Ruskij–Dickson Bay,

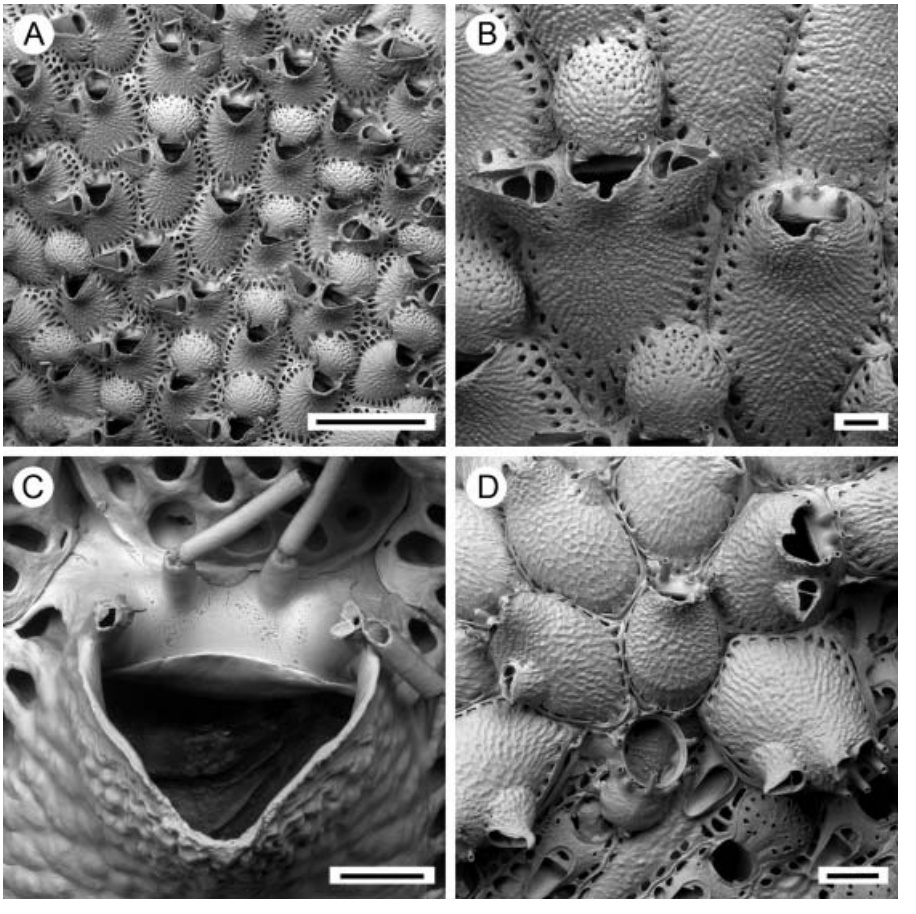

Figure 3. *Escharoides jacksoni* (Waters, 1900), bleached. (A) Colony showing autozooids and ovicellate zooids (NHM 2006.07.31.2); (B) autozooid lacking avicularia and ovicellate zooid with paired lateral avicularia (ZI 50/354); (C) orifice of autozooid with characteristic plain suboral shelf (NHM 2006.07.31.2); (D) ancestrula and surrounding zooids (ZI 50/354). Scale bars: 1 mm (A); 100 μm (B, C); 200 μm (D).

Stn 40, ''Sibiriakov'', trawl, 27 August 1933, det. Kluge, coll. Gorbunov; ZI 65/50534, Chukchi Sea, depth 39 m, Stn 17, 13 August 2004, ''Prof. Khromov'', coll. Sirenko, Gagaev, Denisenko Collection; CMN 2006-0013, southwestern Baffin Island, 69°55.7′N, 80°19′W, Stn 820, depth 73 m, 28 August 1956, Powell Collection; CMN 2006-0014, Cornwallis Island, 72°44.1′N, 94°06′W, Stn 62-2014, depth 35 m, 25 July 1962, Powell Collection; CMN 2006-0015, Nunavut, Frozen Strait, 65°32′N, 84°52′W, Stn 61-39, depth 38–42 m, 27 August 1961, Powell Collection; CMN 2006-0016, Creswell Bay, 72°46.5′N, 94°15.5′W, Stn 62-2052, depth 59–62 m, 11 August 1962, Powell Collection.

Description

Colony forming a thick unilaminar crust (Figure 3A). Ancestrula (Figure 3D) tatiform, oval, with narrow cryptocyst, broad proximal gymnocyst, and 11 spines.

Autozooids irregular in shape, separated by deep grooves, large, 0.88–1.33 mm long (mean 1.02 mm, $n=20$) by 0.58–0.88 mm wide (mean 0.69 mm, $n=20$). Frontal shield

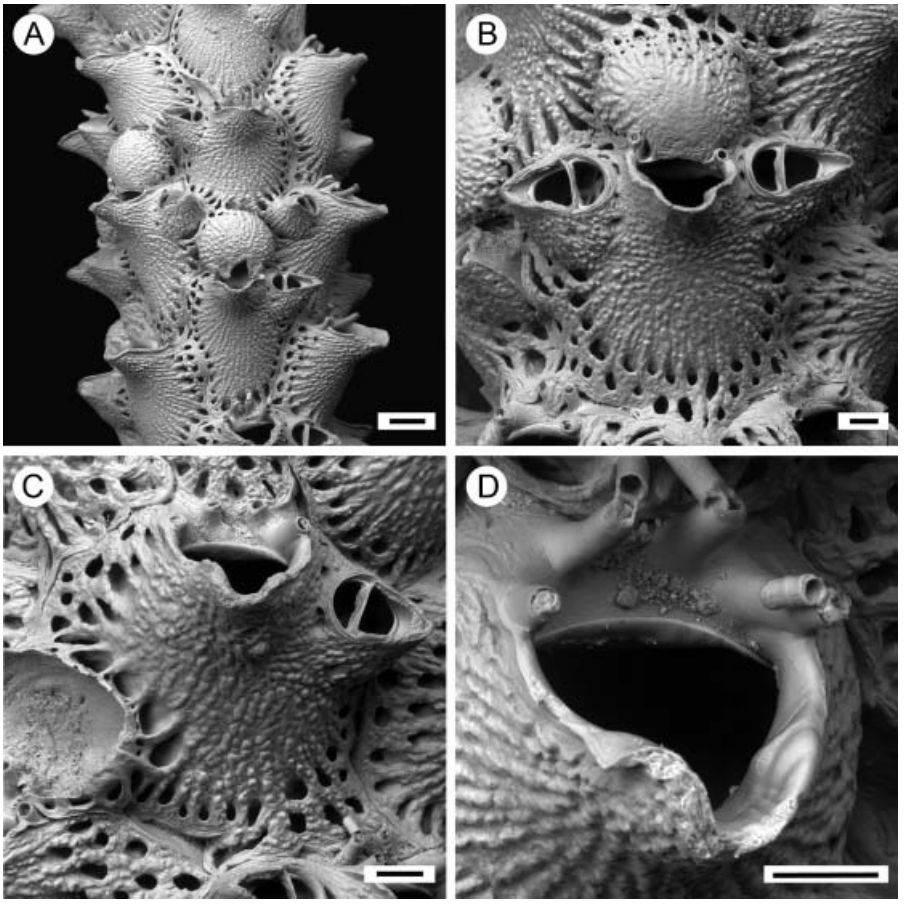

Figure 4. *Escharoides jacksoni* (Waters, 1900), material formerly placed in *Escharoides jacksoni* var. *rostrata* (Kluge, 1946) (ZI 1/2364), bleached. (A) Colony encrusting a stem showing autozooids and ovicellate zooids; (B) ovicellate zooid with paired lateral avicularium; (C) autozooid with one lateral avicularia; (D) orifice of autozooid with characteristic plain suboral shelf. Scale bars: 200 µm (A); 100 µm (B, C, D).

finely granular, bordered by a single or double row of small, round areolae. Orifice suborbicular; distal border with a broad, smooth, suboral shelf; proximal edge developed as a thick, projecting peristome, sometimes with one or two thickened lateral denticles around proximal inner margin (Figures 3B, 4B), and often with a median notch on the rim. Denticles striated when present. Oral spines short, usually numbering four, the outer two fused with the peristome, only two visible in ovicellate zooids. Avicularia typically paired at distolateral corners of autozooids, sometimes single or absent, large, 0.22–0.32 mm long (mean 0.27 mm, $n=20$) by 0.13–0.20 mm wide (mean 0.15 mm, $n=20$), directed laterally, rostrum long, tapering distally, rarely hooked at tip; avicularian chamber well developed, pores often present at the base and rarely on chamber itself; mandible elongate-triangular, crossbar calcified.

Ovicell (Figures 3B, 4B) hyperstomial, globular, finely granular, slightly longer than broad, large, 0.35–0.46 mm long (mean 0.40 mm, $n=20$) by 0.37–0.44 mm wide (mean 0.41 mm, $n=20$); pseudopores scattered over distal part, bordered by a single or double series of small, round areolae.

Distribution

An Arctic, circumpolar species recorded from the Greenland, Barents, Kara, Laptev, East Siberian, and Chukchi Seas; and the Canadian Arctic (Kluge 1975; current account).

Remarks

Bille-Hansen (1962) and Hayward and Ryland (1999) synonymized *Escharoides bidenkapi* (Kluge, 1946) with *E. jacksoni* (Waters, 1900). However, their analyses were based on small sample sizes, and the synonymy is not supported by a more detailed comparison. Our broader investigation using SEM permits us to distinguish *E. bidenkapi* (Figure 2) and *E. jacksoni* (Figures 3, 4) as separate species. Both species have a similar peristome shape, but there is large variation both among colonies and within colonies of *Escharoides* in this character. However, a few skeletal morphological characters do allow us to distinguish these two species with confidence. In general, the peristome of *E. bidnekapi* is much more complex than that of *E. jacksoni.* In *E. jacksoni* the peristome is never produced into three prominent denticles (cf. Figure 2C). On average, autozooids of *E. bidenkapi* are smaller than those of *E. jacksoni*, as are the avicularia. Also, in the majority of cases, avicularia of *E. bidenkapi* are directed distolaterally, whereas those of *E. jacksoni* are typically directed laterally. The frontal shield texture of *E. bidenkapi* is polygonal, whereas that of *E. jacksoni* is finely granulated, although in early astogeny *E. jacksoni* also has frontal shields with a polygonal texture (see Figures 2D, 3D). A very stable character of skeletal morphology among the specimens studied is the structure of the distal edge of the suboral shelf. In *E. bidenkapi* this is crenulated, whereas in *E. jacksoni* it is always smooth. *Escharoides jacksoni* has more bulbous avicularian chambers, which are better demarcated from the autozooidal frontal shield than in *E. bidenkapi*.

Escharoides bidenkapi and *E. jacksoni* overlap in geographical distribution but whereas *E. jacksoni* is circumpolar in distribution, *E. bidenkapi* does not occur in some parts of the Arctic (e.g. Canadian Arctic, Chukchi Sea). In our study material, we found one instance of the two species growing together on the same substratum (Figure 5). The adjacent colonies show the distinctive characters mentioned above for the two species, which cannot be ecophenotypic as the colonies are juxtaposed. This specimen therefore supports the assertion that *E. bidenkapi* and *E. jacksoni* are two separate species.

According to Kluge (1946), *E. jacksoni* var. *rostrata* (Figure 4) exhibits an atypical peristome shape ("strongly raised forward and narrows toward the end"). However, the majority of skeletal characters (frontal shield, avicularian size and shape, smooth-edged suboral shelf) allow us to subsume this taxon into *E. jacksoni* (Waters).

Discussion

The complexity of the skeleton found in *Escharoides* makes recognition of the genus relatively straightforward. However, despite possessing numerous skeletal characters, species determination is challenging, as reflected by errors in the taxonomic literature. Small samples may be misleading in not allowing within species variability to be taken into account when identifying species of *Escharoides*. Kluge (1962, 1975) believed the Arctic biodiversity of *Escharoides* to comprise four species and one variety (see Introduction). Comparative scanning electron microscopy of type and other material has confirmed the distinctiveness of two species, *E. bidenkapi* (Kluge) and *E. jacksoni* (Waters), which have in the past been incorrectly synonymized under the name *E. jacksoni* (e.g. Bille-Hansen 1962;

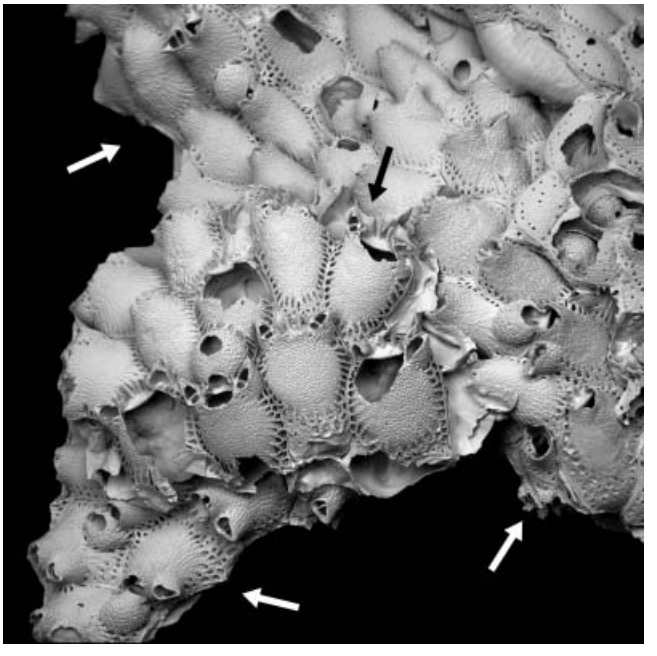

Figure 5. *Escharoides bidenkapi* (Kluge, 1946) (black arrow) growing on a colony of *Escharoides jacksoni* (Waters, 1900) (white arrows) (ZI 1), bleached.

Hayward and Ryland 1999). The third species (*E. coccinea*) listed by Kluge (1962, 1975) seems not to occur in the Arctic, and the fourth species (*E. monstruosa*) does not belong to *Escharoides*. As with the majority of bryozoans, genetic studies of *Escharoides* are needed to test species distinctions made using skeletal morphology.

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