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Three new species of *Gromia* (Protista, Rhizaria) from western Greenland fjords

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Abstract.

Species of large, testate, rhizarian protists in the genus *Gromia* are often common in high-latitude coastal environments, including fjords, but are frequently overlooked and almost all are undescribed. Here, we describe three new gromiid species from the Nuuk fjord system on the west coast of southern Greenland. Morphologically, the new species differ in the size and shape of the test. *Gromia cucumiformis* sp. nov. is elongate, up to 5.5 mm long, with a length:width (L/W) ratio of 4.3–5.5; *Gromia botelliformis* sp. nov. is up to 2.1 mm long, with a L/W ratio of 3.0–4.8; *Gromia brevis* is typically less than 1.0 mm long, with a L/W ratio around 2.0. Genetically, they are well-characterised and split between two clades. *Gromia cucumiformis* and *G. brevis* branch with several species of deep-water gromiids from the Arabian Sea and the Weddell Sea, while *G. botelliformis* branches with deep Weddell Sea species and several unnamed and morphologically uncharacterised gromiids from different parts of the world. *Gromia botelliformis* and *G. brevis* are currently known only from the Nuuk fjords, but sequences of *G. cucumiformis* from Greenland group together with sequences from Svalbard and the White Sea. Our genetic data reveal four additional clades of undescribed *Gromia* species. Two contain sequences from Greenland, Svalbard and the White Sea, one comprises sequences from Greenland and the White Sea and one is limited to sequences from Greenland. These results demonstrate the high genetic diversity of gromiids and their widespread distribution in Arctic as well as in deep-sea environments.

Keywords Arctic, Svalbard, White Sea, gromiids, biogeography, SSU RNA gene sequences

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Introduction

Gromiids are protists with single-chambered (monothalamous), predominantly organic-walled tests, presently accommodated within a single genus, *Gromia,* type species *G. oviformis* Dujardin, 1835. There has been considerable uncertainty regarding the phylogenetic position of the genus. In the second edition of the Illustrated Guide to the Protozoa, Patterson et al. (2000) placed *Gromia* among the 'Amoebae of Uncertain Affinity'. The first detailed genetic study, based on complete SSU RNA gene sequences, suggested that *G. oviformis* belonged to the phylum Cercozoa (Burki et al. 2002), a group of amoeboid protists that was later included in the supergroup Rhizaria (Nikolaev et al. 2004). Subsequent studies have confirmed that *Gromia* belongs in the Rhizaria, but have not confirmed its placement in the Cercozoa, leaving the relationship between gromiids and other rhizarian groups, including the Cercozoa and the phylum Foraminifera, still not fully resolved (e.g., Longet et al. 2004; Pawlowski and Burki 2009; Burki et al. 2010; Hess et al. 2012; Sierra et al. 2013; Ward et al. 2018). The most recent classification of eukaryotes places gromiids within the Endomyxa, a group of rhizarian protists that is either sister to or encompasses the Retaria, which includes the Foraminifera (Adl et al. 2019).

Some early studies assigned various species of monothalamous foraminifera from fresh-water (Penard 1902) and marine (e.g., Gruber 1884) habitats to the genus *Gromia.* These mistakes were corrected by Rhumbler (1904), who recognised that *Gromia* lacked the characteristic granuloreticulate pseudopodial system of foraminifera, although the confusion persisted for another 50 or so years (Hedley 1958). For many years, the only genuine gromiids were *G. oviformis* and a species from Norwegian fjords described as *Gromia* sp. by Schulze (1875) and named *G. schulzei* by Norman (1892). Further species were not added until the beginning of the 21st Century, when the first deep-sea gromiids, *G. sphaerica* Gooday, Bowser, Bett, Smith, 2000 and *G. pyriformis* Gooday and Bowser, 2005, were described from the Pakistan margin of the Arabian Sea (Gooday et al. 2000; Gooday and Bowser 2005; Aranda da Silva and Gooday 2009). The total number of gromiid species that are scientifically described currently stands at six. In addition, *Allogromia marina* Nyholm and Gertz, 1973 from Swedish waters, described as a monothalamous foraminifera ('allogromiid') by Nyholm and Gertz (1973), displays all the morphological characteristics of a gromiid.

With only six formally described species (seven including *Allogromia marina*), *g*romiids remain a poorly-known group taxonomically. However, these relatively large and conspicuous protists have now been recognised at increasing numbers of marine sites around the world, from intertidal to extreme hadal depths (Arnold 1972; Matz et al. 2008; Rothe et al. 2009; Goldstein et al. 2011; Sergeeva et al. 2012; LeDuc and Rowden 2017; Gooday and Goineau 2019; Pavel et al. 2021) and they clearly encompass many undescribed species (Aranda da Silva et al. 2006; Aranda da Silva and Gooday 2009; Rothe et al. 2011). The present study adds to our knowledge of gromiid diversity by describing three new species from fjords around Nuuk in SW Greenland. The species are well characterised genetically and morphologically. DNA sequences from one of them, and from several undescribed Greenland gromiids, are identical to those obtained from gromiids collected at Arctic and sub-Arctic sites in Svalbard and the White Sea (Fig. 1).

Methods

Study areas, sampling, and morphological methods

Greenland. Samples were collected during July 2018 from sub-Arctic fjords in southeast Greenland (Fig. 1B; Table 1). Four sites were located in the Nuuk fjord (formerly Godthåbsfjord) system to the

east and northeast of Nuuk, three of them in sheltered embayments, two in the inner parts of Itissoq (an embayment of the central Qôrnup Suvdlua branch of the fjord system) and one in Qôrqut (an embayment of the eastern Ũmánap Suvdlua branch) at depths around 100 m. The fourth sample was taken at a more open site in deeper water (>200 m) to the south of Ũmánaq Island in the upper reaches of the Ũmánap Suvdlua branch. Three additional samples were taken to the south of the Nuuk fjord system, two near the end of the relatively narrow Kobbefjord immediately east of Nuuk at depths of less than 50 m, and the other in the Ameragdla branch of the Ameralik fjord at 212 m depth.

Sediments were sandy mud in the Itissoq and Qôrqut embayments (Stations 1, 2, 4) and clay near Ũmánaq Island (Station 5). The two sites in Kobbefjord (Stations 12, 13) were characterised by grey-brown sediments that became anoxic in deeper layer. The sediment in the Ameragdla branch contained much less of organic matter and was generally not anoxic. Environmental data are not available for any of these sampling sites but a detailed account of the hydrography observed along the axis of the main (western) branch (Nûp Kangerdlua) of the Nuuk fjord system is given by Mortensen et al. (2014). Extrapolating these data suggests that the bottom-water temperatures at our four sampling sites in the central and eastern branches were in the range 0° to 2.5° C and salinity 33.3 to 33.6. At a 100-m deep site near the centre of Kobbefjord, Middelboe et al. (2012) report that temperatures measured with a CTD in the water column in May 2008 were 0° C at depths below 20 m, compared with ~5° C between 20 and 50 m in September 2007. Salinity was 33 below 20 m in May dropping to ~30 at 20 m and ~31 at 40 m in September. Our 212-m-deep sampling site in the Ameragdla branch are likely to experience a bottom-water temperature of 1.1° C and a salinity of 33.3.

The samples were obtained using a Van Veen grab (Table 1). Surface sediment was removed using a spoon and immediately washed through a series of sieves with mesh sizes of 500, 250, and 125 microns. The residues were placed in plastic jars with seawater and stored in a laboratory refrigerator at the Greenland Institute of Natural Resources in Nuuk. As soon as possible after collection, the different residues were sorted in seawater in a Petri dish for gromiids and foraminifera, while being kept chilled using a freezer pack. Specimens for genetic analyses were preserved in RNAlater; samples for morphological analysis were preserved in 4% formalin buffered with borax. Following the expedition, the gromiids were returned to Geneva, where they were photographed using a Leica M205 C microscope fitted with a Leica DFC 450 C camera. Further photographs taken subsequently in Southampton using an Olympus SZX7 microscope and Canon 60D SRL digital camera

Svalbard. In western Svalbard, samples for the study of foraminifera and gromiids were collected in August 2001 in Tempelfjord, Kongsfjord and Van Meijenfjord during a cruise of the *R/V Jan Mayen* (Gooday et al. 2005). The sequence data reported here are for gromiids from Kongsfjord (Fig. 1C). Sample collection and processing methods are described in Gooday et al. (2005). Briefly, the samples from Station 7 in Kongsfjord (= Station 0777 of Gooday et al. 2005) were obtained using an USNEL-type box corer and the upper few centimetres of sediment sieved on deck on sieves with a mesh size of 1000, 500, 250 and 125 µm. The >1000 µm and 500–1000 µm fractions were sorted as soon as possible on the ship, the finer fractions (250–500 µm and 150–250 µm) were sorted later in the University Courses in Svalbard laboratory in Longyearbyen. Specimens for genetic analyses were frozen in liquid nitrogen and returned to the University of Geneva laboratory, where genetic analyses were conducted.

White Sea. Sampling sites were located in the outer reaches of the fjord-like Chupa inlet on the western side of Kandalaksha Bay, near the White Sea Biological Station ‘Kartesh’ (Fig. 1D). See Howland et al. (1999) for a general description of the morphology and hydrography of the Chupa inlet. Samples were collected during the summer of 2007 using a Van Veen grab at four sites in water

depths ranging from 70 to 117 m. The sediment was mud at Stations 21 and 22, and sandy mud at Stations 23 and 24. There are no other environmental data relating directly to these sites, but it can be expected that summer bottom-water temperatures were about 0° C at Station 21, and around 2° C at the other sites, with bottom salinities ~28 at all stations (Howland et al. 1999). The bottom water in this region is always highly oxygenated with concentrations of 8 mL/L.

DNA extraction, PCR amplification and sequencing

Forty specimens of *Gromia* (21 from Greenland, 13 from the White Sea, 5 from Svalbard, 1 from Naples Bay) were extracted individually using Guanidin lysis buffer (Pawlowski 2000). Isolate numbers are given in the supplementary table (Online Resource 1). Semi-nested PCR amplification was carried out for the 3' end fragment of the Small Subunit Ribosomal DNA (SSU rDNA) using eukaryotic SSU forward primer s12.2 (GATYAGATACCGTCG) at the first amplification step, the gromiid SSU forward primers 13.3 (CGTTGGATAGGACTC) for the reamplification and the 20r eukaryotic SSU reverse primer (5′GACGGGCGGTGTGTACAA) for both amplification steps. These primers amplify a fragment of the SSU rDNA situated at the 3' end and were used by Aranda da Silva et al. (2006) to delimitate species in *Gromia.* This fragment can be regarded as a molecular barcode for gromiids generally. The obtained PCR products were cloned for 14 isolates (supplementary table; Online Resource 1). Cloning was performed using the TOPO TA Cloning Kit (Invitrogen) following the manufacturer's instructions and transforming amplified PCR products into competent *Escherichia coli*.

The amplified PCR products were purified using the High Pure PCR Cleanup Micro Kit (Roche Diagnostics). Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and analyzed on a 3130XL Genetic Analyzer (Applied Biosystems). The newly acquired sequences were deposited in the EMBL/GenBank database (accession numbers MG519738, MT906517-21, MT906528-32, MT906536-40, MT906607-08, MT906544-46, MT906549-51, MT906560-63, MT906575-76, MT906584-89, MT906590-613; supplementary table, Online Resource 1).

Phylogenetic analysis

A total of 67 *Gromia* sequences was used for the phylogenetic analysis; 44 sequences were obtained during the current study and 23 were published previously by Gooday et al. (2000), Burki et al. (2002) and Aranda da Silva et al. (2006). The sequences were aligned using the Muscle automatic alignment option as implemented in SeaView vs. 4.3.3. (Gouy et al. 2010). The alignment contains 758 sites, of which 225 were used for the phylogenetic analysis. These 225 sites correspond to those in the alignment that display polymorphism. Nucleotide frequencies are 0.20 (A), 0.24 (C), 0.27 (G) and 0.29 (T).

The phylogenetic tree was constructed using maximum likelihood phylogeny (PhyML 3.0) as implemented in ATGC: PhyML (Guindon et al. 2010). An automatic model selection by SMS (Lefort et al. 2017) based on Akaike Information Criterion (AIC) was used, resulting in a GTR substitution model being selected for the analysis. The initial tree is based on BioNJ. Bootstrap values (BV) are based on 100 replicates.

Results

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Systematic descriptions

The type material is deposited in the Natural History Museum, London (Protist Collection). Specimens are stored in 10% formalin in 1.25 ml cryovials.

RHIZARIA Cavalier-Smith, 2002
ENDOMYXA Cavalier-Smith, 2002
Class GROMIIDEA Cavalier-Smith, 2003
Order GROMIIDA Claparède and Lachmann, 1856
Family GROMIIDAE Reuss, 1862
Gromia Dujardin, 1835

Remarks. A later description by Dujardin (1841) of the type species, *Gromia oviformis*, reads as follows. 'Coque globuleuse, lisse, avec une ouverture entourée d'un goulot court, expansions rameuses, peu anastomées. Largeur de la coque 1 à 2 mm, longueur des expansions, 2 à 4 mm'. (Translated as: 'Globular test, with an aperture surrounded by a short neck, branched pseudopods with few anastomoses. Size of the test: 1 to 2 mm, Length of pseudopods: 2 to 4mm'). He goes on to add the following remarks. 'I have found them in Toulon, Marseille, Sète and on the coast of Calvados between tufts of marine plants and I conserved them alive in bottles with sea water for several months. Their pseudopods are thick at the base (0.066 mm) Their movement (...) is quite pronounced under the microscope, but the general movement is so slow (...) that within an hour they move not more than 2 mm along the bottom of the flask.'

The brief description given by Dujardin (1835) includes the fact that the branched pseudopodia include few anastomoses, a defining morphological characteristic of gromiids. The 'aperture surrounded by a short neck' refers to what was later termed the 'oral apparatus' (Arnold 1952) or 'oral capsule' (Hedley 1960, 1962), another typical gromiid feature that, unlike the pseudopodia, can be seen in preserved specimens.

Gromia cucumiformis Gooday and Holzmann sp. nov.

Figs 2-5

Diagnosis: Species of *Gromia* with elongate, cucumber-shaped test, sometimes slightly curved and with a single terminal oral capsule. Length 2.5 to 5.5 mm, length:width ratio 4.3 to 5.5. Wall transparent and devoid of obvious features.

ZooBank registration: urn:lsid:zoobank.org:act:90198C30-9431-4672-8AA4-8FA7CE7C8716.

Type material: Station 12, Kobbefjord (Fig. 1B, Table 1): Van Veen grab sample; water depth 43 m; 64° 08.733' N, 051° 23.658' W. The holotype (reg. no. NHMUK 2021.3.5.1) and 3 paratypes (NHMUK 2021.3.5.2–4) are preserved in 10% formalin for morphology.

Other material:
1) Nuuk area of southwestern Greenland.
- Station 12 (as above): 3 specimens used for genetics (isolates 19995, 19997, 19998); 7 additional specimens preserved in 10% formalin for morphology.
- Station 2, Itissoq embayment of the Qôrnup Suvdlua branch of the Nuuk fjord system: Van Veen grab sample B; sandy mud; water depth 111 m; 64°15.347' N, 051°14.532' W: 1 specimen used for genetics (isolate 20000).

- Station 4, Qorgut embayment of the Ũmánap Suvdlua branch of the Nuuk fjord system: sandy mud; water depth; 118 m; 64°15.039' N, 050°53.467' W: 1 specimen used for genetics (isolate 20019).

2) Svalbard.

- Station 7, Kongsfjord: water depth 106 m; 78° 55.19' N, 12° 15.03' E; 3 specimens used for genetics (isolates 4685–4687).

3) Chupa inlet, White Sea.

- Station 23: water depth 117 m; 66° 18.461' N, 33° 54.431' E; 1 specimen used for genetics (isolate 9769).
- Station 21: 66° 18.163' N, 33° 37.578' E; 1 specimen used for genetics (isolate 9782).
- Station 22: water depth 70 m; 66° 18.009' N' 33° 39.422' E; 70 m; 2 specimens for genetics (isolates 9907, 9908).
- Station 23: water depth 117 m; 66° 18.461' N, 33° 54.431' E; 1 specimen used for genetics (isolate 9769).
- Station 24: water depth 80 m; 66° 18.262' N, 33° 57.386' E; 3 specimens for genetics (9923, 9924, 9928).

Etymology: Latin *cucumis*, cucumber

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Description. In specimens from the type locality, the test is fairly large and approximately cylindrical (Figs 2, 3, 4a–c): length 2.62–5.39 mm, mean 3.62 ± 0.84 mm; width 0.52–1.05 mm, mean 0.67 ± 0.17 mm; length/width ratio 4.28–6.58, mean 5.44 ± 0.60 (n = 27 in all cases). It follows a more or less straight or slightly curved course with a rounded adapertural (posterior) end. A single specimen (DNA isolate 20019; Fig. 4d) from Station 1 is rather smaller, 2.33 mm long without the oral capsule, 2.65 mm long including the oral capsule, and 0.68 mm wide; length/width ratios 3.72 and 3.87, respectively. The oral capsule is relatively large, 115–200 µm long, 125–215 µm wide. The test wall appears to extend for some distance up the side of the capsule, appearing in optical cross-sections as an irregularly tapered feature on either side of the capsule (indicated by arrows in Fig. 5b). The capsule may expand into a more or less distinct collar-like feature associated with irregular excrescences and filaments that appear whitish in reflected light. A central canal is usually clearly developed; in one specimen with complex terminal excrescences, the canal appears to branch several separate channels (Fig. 5d).

The test maintains its shape in LifeGuard and RNAlater solution (Figs. 2, 4), although it collapses after prolonged preservation in formalin (Fig. 3). The wall is thin and transparent with a reflective, slightly iridescent surface. In preserved specimens the test contents are a pale greyish brown, although larger specimens tend to be more grey in colour than smaller ones. The contents comprise mainly small round stercomata, 8–15 µm diameter, with a variable proportion of small, darker, usually brownish, particles scattered amongst them. Some fairly large mineral grains (up to 100 or more µm in size), dark greenish (possibly hornblende) or transparent (quartz), may be present. These are usually located towards the apertural end of the test and concentrated on one side, possibly as a result of density settling (Fig. 5e). The stercomata and other particles appear to be embedded in cytoplasm. In places, notably immediately below the oral capsule, they merge into white cytoplasm devoid of stercomata. Larger quantities of this ‘pure’ cytoplasm accumulate at the adapertural end in two specimens (Figs. 1a, 4a).

Molecular characteristics. Although *Gromia cucumiformis* is not supported by bootstrap value (i.e., <70% BV), it forms a consistent clade that branches as sister to 3 deep sea species (*G. sphaerica*, *Gromia* sp. 5, *Gromia* sp. 6) and the newly described *G. brevis* (Fig. 6). The partial SSU rDNA

sequences of *G. cucumiformis* contain between 612 and 615 nucleotides and the GC content ranges from 47.6 to 48.3. Pairwise distances range from 0 to 0.007.

Remarks. We base the description of *G. cucumiformis* on a collection of well-documented specimens from near Nuuk in southwest Greenland. Assignment of specimens from other Arctic and sub-Arctic sites (Svalbard and the White Sea) is based on sequence data. However, they are recorded as being 'elongated' or 'sausage-like', which is consistent with their placement in this species.

Elongate, sausage-shaped gromiids similar in shape to *G. cucumiformis* are reported from sublittoral and bathyal settings in different parts of the world, although none is formally described. Two morphotypes from Svalbard fjords, neither of which has been sequenced, are considerably smaller than the new species (0.2–0.4 mm long according to Fig. 2B, D in Gooday et al. 2005). Morphospecies 297, 1B, and 2 from the bathyal (1140–2108 m depth) Weddell Sea, also not sequenced, are comparable in length or only slightly smaller (1.5–3.6 mm) than *G. cucumiformis* and have similar test proportions (Figs 4e, g, i, respectively, in Rothe et al. 2009). However, all exhibit differences: sp. 297 has a thin wall that wraps around the test contents like cling-film; sp. 1B has a smaller, neater oral capsule; sp. 2 has a patterned test surface. Sausage-shaped gromiids (Gromiid sp. 3 of Aranda da Silva et al. 2006; Aranda da Silva and Gooday 2009) are common on the bathyal Oman and Pakistan margins but reach considerably greater lengths than *G. cucumiformis* (11 mm according to Gooday et al. 2000). Genetic data indicate that the Arabian Sea Gromiid sp. 3 is not closely related to the new species (Fig. 6).

Distribution. Currently known from the Nuuk fjord system (SW Greenland), Kongsfjord (Svalbard), and the Chupa inlet of Kandalaksha Bay (White Sea, Russian sub-Arctic).

Gromia botelliformis Gooday and Holzmann sp. nov.

Figs 7–9

Diagnosis: Species of *Gromia* with fairly elongate, sausage-shaped test and single terminal oral capsule. Length 1.1 to 2.1 mm, length:width ratio 3.0 to 4.8. Wall transparent with fine reticulated ornamentation.

ZooBank registration: urn:lsid:zoobank.org:act:D3014685-C8A4-47BC-A6A1-E032DFCECCD7.

Type material: Station 2, Itissoq embayment of the Qôrnup Suvdlua branch of the Nuuk fjord system (Fig. 1B, Table 1): Van Veen grab sample B: sandy mud; water depth 111 m; 64°15.347' N, 051°14.532' W. Holotype (reg. no. NHMUK 2021.3.5.5) and 3 paratypes (reg. nos NHMUK 2021.3.5.6–9) preserved in 10% formalin for morphology.

Other material:
Station 2, Itissoq embayment (as above): 2 specimens used for genetics (isolates 20001, 20002).
Station 1, Itissoq embayment: sandy mud; water depth 98 m; 64°15.748' N, 051°15.466' W: 2 specimens used for genetics (isolates 20008, 20010); 2 specimens preserved in 10% formalin for morphology.
Station 4, Qorgut embayment of the Ũmánap Suvdlua branch of the Nuuk fjord system: sandy mud; water depth; 118 m; 64°15.039' N, 050°53.467' W: 1 specimen used for genetics (isolate 20018), 1 specimen preserved in 10% formalin for morphology.

Etymology. Latin *botellus*, a small sausage, referring to the somewhat elongate test shape.

Description. The test is elongate, approximately cylindrical (Figs 7, 8); length 1.11–2.09 mm, mean 1.52 ± 0.22 mm; width 0.35–0.57 mm, mean 0.44 ± 0.08 mm; length/width ratio 2.98–4.81, mean 3.54 ± 0.44 (n=18 in all cases). It is more or less straight to gently curved with sides that are approximately parallel or slightly curved and a rounded posterior end. The oral capsule generally forms a truncated cone, 70–100 µm long and tapering from 80–130 µm wide at the base to 60–90 µm wide at the top, where it sometimes expands into a collar-like feature (Fig. 9). A central canal is typically clearly developed and irregular masses of fine-grained material that appear whitish in reflected light are often developed at the end of the oral capsule, occasionally giving rise to longer filaments. Extensions of the test wall that rapidly thin to create wedge-shaped features on either side of the capsule are often visible in optical sections of the oral capsules (arrowed in Fig. 9b).

The transparent wall is thin but fairly distinct, with a slightly iridescent reflective surface. It is sufficiently resistant to retain the shape of the test in LifeGuard and RNAlater preservative solutions (Fig. 8), although the test sometimes loses its shape after prolonged preservation in formalin (Fig. 7a,b). A fine ornamentation, which appears to consist of tiny surface dimples forming a reticulated pattern, is sometimes visible when the wall is observed in transmitted light in a compound microscope (Fig. 9e). The test contents are pale, greyish brown in preserved specimens; clear whitish cytoplasm is sometimes visible just behind the oral capsule (Fig. 8c) or in the adapertural part of the test (Fig. 8b). Variable quantities of small, brownish grains are often present, and clusters of larger mineral particles, including quartz, mica and a green mineral, possibly hornblende, are sometimes visible on one side of the test. In the holotype and one of the paratypes, these occur towards the posterior end (Fig. 7c,d).

Molecular characteristics. *Gromia botelliformis* is supported by 79% BV and branches next to *Gromia* sp. 2 and *G. marmorea*, their branching being supported by 88% BV. The partial SSU rDNA sequences contain between 623 and 624 nucleotides, the GC content ranges from 46.2 to 47.0. Pairwise distances range from 0 to 0.13.

Remarks. In terms of overall test shape, *G. botelliformis* is shorter and relatively wider than *G. cucumiformis.* The new species resembles more closely the life-sized illustrations given by Schultze (1875; Pl. II, fig. 11a-c therein) of *Gromia* sp. (= *G. schulzei* Norman, 1892) from 183–668 m depth in Norwegian fjords, although Schulze's species is much larger (length 8–9 mm). *Gromia botelliformis* strongly resembles *Gromia* sp. 1A (Fig. 3a,b in Rothe et al. 2009) from 1584 m depth in the Powell Basin off the tip of the Antarctic Peninsula. Both species also have very similar oral capsules, although the test is larger in the Antarctic species (3.5–8.5 mm compared to 1.1–2.1 mm in *G. botelliformis*).

Distribution. Currently known only from the Nuuk fjord system (SW Greenland)

Gromia brevis Gooday and Holzmann sp. nov.

Figs. 10–12

Diagnosis: Species of *Gromia* with a relatively small, somewhat oval test (length <1.0 mm), usually widest behind the mid-point and with a length:width ratio of approximately 2.0.

ZooBank registration: urn:lsid:zoobank.org:act:7DF6C1E4-C6DE-44D0-A5A7-442FCECF846C.

Type material: Station 1, Itissoq embayment of the Qôrnup Suvdlua branch of the Nuuk fjord system (Fig. 1B, Table 1): Van Veen grab sample B; sandy mud; water depth 111 m; 64°15.347' N, 051°14.532' W. Holotype (reg. no. NHMUK 2021.3.5.10) and 5 paratypes (reg. nos NHMUK 2021.3.5.11–15) preserved in 10% formalin for morphology.

Other material from the Nuuk fjords.
Station 1, Itissoq embayment (as above): 3 specimens used for genetics (isolates 20004-20006); 24 specimens preserved in 10% formalin for morphology.
Station 13, Kobbefjord: 1 specimen used for genetics (isolate 20021); water depth; 22 m; 64°08.580' N, 051°23.377' W.

Etymology: Latin *brevis* meaning short.

Description. The test is relatively small (Table 2), ranging in length from 299 to 667 µm (mean 458±89 µm) without the oral capsule, 317 to 696 µm (mean 482±92 µm) with the oral capsule, and in width from 164 to 358 µm (mean 236±50 µm). The shape is asymmetrically oval and usually widest behind the mid-point, from which it tapers towards the oral capsule at the apertural end (Fig. 10). The length/width ratio ranges from 1.80 to 2.29 (mean 1.95 ± 0.13) if the oral capsule is excluded, and from 1.91 to 2.41 (mean 2.04 ± 0.14) if the oral capsule is included.

The oral capsule is relatively small, typically forming a rounded, dome-like structure (Fig. 11). The test wall is rather thin, in some cases collapsing onto the test contents in RNAlater, but more commonly maintaining its shape. The surface is smooth with no obvious ornamentation. The test contents are pale whitish with a yellowish tinge. A few small brownish inclusions are sometimes present, but mineral grains have not been observed.

Molecular characteristics. *Gromia brevis* is highly supported (100% BV). A single sequence (*Gromia* sp. 20017) branches at its base (95% BV). The species branches in a group of deep water gromiids (*G. sphaerica*, *Gromia* sp. 6, *Gromia* sp. 5). The partial SSU rDNA sequences contain 638 nucleotides, the GC content is 47. No pairwise distances are observed.

Variation. The holotype and paratypes were taken from a larger collection of gromiids from Station 1. The types are all oval to somewhat droplet-shaped with L/W ratios of approximately 2.0 and were selected because of their morphological similarity to specimens that had already been sequenced. The group photographs in Fig. 12a–c, which were taken using different lighting at an early stage of the study before types had been chosen, show a morphologically rather variable assemblage. The largest specimen, which has a rather more cylindrical shape than the others (Fig. 13b), was sequenced (isolate 20007) and proved to be unrelated to *G. brevis* (Fig. 6). The remaining specimens include at least one that was sequenced (isolate 20004) and several of the specimens subsequently chosen as paratypes (P2, P4, P5). The entire group displays a rather wide range of test sizes and morphologies, with some being more elongated than others. A selection of more elongate forms (some of them also present in Figs. 12a–c) are shown in Fig. 12d. They range in length from 618 µm to 912 µm with length:width ratios between 2.23 and 3.53. Unfortunately, we have no genetic data for any of these more elongate specimens. Nevertheless, Fig. 12a–c show that those with shorter tests and those with more elongate tests form a continuum, rather than being distinct morphotypes, and we therefore consider them to represent a single species.

Remarks. *Gromia brevis* is closely related genetically to a single specimen (isolate 20017) from Station 13 in Kobbefjord (Fig. 6), which has a larger and relatively longer test (length 1865 µm with,

and 1790 µm without, the fairly prominent oral capsule), and a length:width ratio of 2.55 (Fig. 13a). *Gromia pyriformis,* described morphologically from around 1000 m depth on the Pakistan margin (Gooday and Bowser 2005), is quite similar to some of the more elongate specimens of *G. brevis,* particularly those in which the posterior part of the test is somewhat inflated. In the absence of genetic data for *G. pyriformis,* is not possible to determine whether this species is related to *G. brevis.* The only other morphologically similar gromiid, *G. oviformis,* usually has a more regularly oval test (Burki et al. 2002). However, the *oviformis*-like morphotypes for which we have genetic data are found in different clades (Fig. 6).

Distribution. Currently known only from the Nuuk fjord system (SW Greenland)

Molecular Characterization

The tree (Fig. 6) contains two major groups, one consisting of the newly described species *G. cucumiformis* and *G. brevis* (100% BV), together with the deep-water clades *Gromia* sp. 7 (100% BV), *Gromia* sp. 3 (99% BV), *Gromia* sp. 5 (99% BV), *Gromia* sp. 6 (100% BV) and *G. sphaerica* (100% BV). The other group contains two undescribed clades, one comprising *Gromia* sp. 4482, *Gromia* sp. 9926, *Gromia* sp. 9930, and *Gromia* sp. 20015 (Fig. 13c) (99% BV), the other comprising *Gromia* sp. 9931, and *Gromia* sp. 20016 (Fig. 13d) (100% BV). The two clades branch at the base of *G. oviformis, G. marmorea, Gromia* sp. 2 and *G. botelliformis* (79% BV). Several deep-water species branch at the base of these two major groups. They include *Gromia* sp. 4, *Gromia* sp. 8, *G. melinus, Gromia* sp. 1 (100% BV), *G. winnetoui* as well as two undescribed clades, supported by 99% and 100% BV.

Discussion

In terms of size, the new gromiids span an order of magnitude from lengths of <500 µm to >5 mm. The two larger species, *Gromia cucumiformis* and *G. botelliformis,* were picked from sediment residues retained on a sieve with a mesh size of 500 µm. Because freshly-collected samples had to be sorted quickly in the Nuuk laboratory before new samples arrived from the field for processing, the finer fractions passing though the 500-µm mesh were not always examined. As a result, smaller ('juvenile') specimens belonging to these two species may have been lost. The finer fractions (125–250 µm or 250–500 µm) of some samples were sorted, however, and these yielded specimens of the smaller species, *G. brevis*.

In a few specimens of our two larger Greenland species, *G. cucumiformis* and *G. botelliformis,* the adapertural part of the test is occupied by whitish cytoplasm, which stands out in contrast to the remaining much darker, stercomata-dominated test contents. This phenomenon is well-known in *G. oviformis* from coastal environments and indicates that the individual is undergoing gametogenesis. Arnold (1972, p. 95 therein) remarks that gamete-filled specimens 'are relatively easy to find, even without a hand lens, in intertidal areas…' It also appears to be common in laboratory cultures of *G. oviformis* (Hedley 1962). For example, Jepps (1926) describes how 'a whitish film appears on the surface of the brown protoplasmic body' and develops further until 'the Gromia becomes milky white in its upper half'. This whitish cytoplasm is full of flagellate gametes. The occurrence of whitish cytoplasm in *G. cucumiformis* and *G. botelliformis* provides the first evidence for gametogenesis in a gromiid species other than *G. oviformis.* The small amount of similar material

below the aperture in one specimen of *G. cucumiformis* (Fig. 4b) may also be indicative of gametogenesis, or it could be comparable to the 'mass of clear protoplasm just within the mouth' observed by Jepps (1926) in *G. oviformis.*

Gromiids are widely reported from coastal waters (Hedley 1962; Arnold 1972; Goldstein et al. 2011) and the deep sea (Gooday et al. 2000; Aranda da Silva et al. 2006; Aranda da Silva and Gooday 2009; Rothe et al. 2009, 2011). They are sometimes conspicuous members of faunal assemblages, particularly in shallow and deeper coastal settings (e.g. fjords). Very high densities (500 to 89,000 individuals per m^2) of a species identified as *G. oviformis* occurred on rocky surfaces (15 m water depth) near McMurdo Station, Antarctica, reflecting the relatively eutrophic conditions on the eastern side of McMurdo Sound (Bowser et al. 1996). Large populations of '*Allogromia*' *marina*, an organism 3-4 mm in size that is clearly a gromiid, occurred between 10 and 100 m depth in the Gullmar Fjord on the west coast of Sweden, and down to 500 m in the Skagerrak (Nyholm and Hertz 1973). The large (8–9 mm) *Gromia* sp. of Schulze (1875) (= *G. schulzei* Norman, 1892) was moderately abundant ('mässig häufig') at two Norwegian localities, one near Sölsvig (183 m depth) and the other in deeper water (688 m) in 'Bukenfjord' (Boknafjorden). We have recently observed numerous large gromiids in fjords on the north coast of South Georgia (Pawlowski, Holzmann, Gooday unpublished). Gromiids therefore seem to flourish where there is an adequate supply of detrital food material, including in high-latitude fjords. Their tests often stand upright on the sediment surface with the aperture downwards and the pseudopodia deployed into the detritus-rich sediment (Fig. 9 in Nyholm and Gertz 1973).

Little is known about the biogeography of gromiids. The type species, *G. oviformis,* is reported from shallow-water settings around the world (e.g., Hedley 1962; Arnold 1972), but genetic data suggest that it is a species complex (Burki et al. 2002). A large gromiid from 750–780 m depth near the Bahamas, was identified as *G. sphaerica* by Matz et al. (2008) based on its size (up to 30 mm in diameter), multiple apertures, and a single SSU rDNA gene sequences that placed it close to a specimen of this species collected 6,660 km away on the Pakistan margin (Gooday et al. 2000; Aranda da Silva et al. 2006, 2009). There were some differences, however. The Bahamian specimens had generally pear-shaped rather than spherical tests and were covered in a thin layer of sediment, probably collected during their movement across the seafloor. Additional sequences would help to test whether these Bahamian gromiids represent the same species as the Arabian Sea *G. sphaerica*.

Two of the gromiid species described here (*G. botelliformis* and *G. brevis*) are currently unknown outside the Nuuk area. An undescribed species, represented by three Greenland DNA isolates (20009, 20012, 20013; illustrated in Fig. 13e–g), also has a restricted distribution. On the other hand, sequences of *G. cucumiformis* are identical to gromiid sequences from Svalbard and the White Sea. Our genetic data also reveal three undescribed species that occur at more than one Arctic locality (Fig. 13b–d). One comprises isolates (20015, 4482, 9926, 9930) originating from Nuuk, Svalbard, and the White Sea, the other two comprise isolates (9918, 9932, 9933, 20007 and 2016, 9931) originating from Nuuk and the White Sea. In the case of *G. cucumiformis,* the direct distances between the localities in Nuuk and Svalbard and between Nuuk and the White Sea are 2560 km and 3674 km, respectively. Thus, it appears that some gromiid species have ranges spanning thousands of kilometers across this part of the Arctic.

As a group, gromiids are morphologically rather conservative, displaying little of the extraordinary range of test shapes found in foraminifera. Recurrent test morphologies include spherical, oval, grape-shaped, and elongate, sausage-shaped or sometimes carrot-shaped forms that range from fairly short to very long (Gooday et al. 2005; Aranda da Silva et al. 2006; Aranda da Silva and Gooday 2009; Rothe et al. 2009, 2011). Some species, such as *G. sphaerica* (spherical test with multiple apertures) and *G. winnetoui* (test enclosed in an agglutinated case), have distinctive morphological characteristics. However, our collection of gromiids from the Nuuk fjords helps to illustrate the fact that

DNA sequences, as well as test morphology, are often necessary in order to define species. For example, isolates 20007 and 20016 (Fig. 13b,d) are rather similar to typical specimens of *G. brevis* in terms of test morphology, indeed, isolate 20007 was initially included in *G. brevis* (Fig. 11a–c), but are both unrelated to the new species, as well as to each other (Fig. 6). As already noted, *G. botelliformis* closely resembles *G.* sp. 1A of Rothe et al. (2011) from the Southern Ocean, but whether they represent the same species cannot be determined in the absence of genetic data for the Antarctic species. We suspect that the conservative morphology of gromiids conceals a considerable degree of cryptic diversity. Further genetic studies in different environments will be required in order to reveal the true scale of diversity within this successful, widely distributed, but frequently overlooked group of protists.

Conclusions

Despite increasing evidence for their abundance and wide occurrence in marine habitats, few species of *Gromia* (excluding those transferred to the Foraminifera) have been described. Our description of three new species from fjords near Nuuk in SW Greenland increases the number of formally described species from six to nine. The new species are morphologically and also genetically distinct. The genetic data reveal that one of them, *G. cucumiformis,* and several undescribed species in our Greenland material, also occur thousands of miles away in Svalbard and the White Sea, suggesting that some gromiid species are widely distributed across the Arctic. However, the two other new species, *G. botelliformis* and *G. brevis,* are currently known only from Greenland. Gromiids probably play an important role as consumers of sedimentary detritus in benthic food webs in coastal to deep-sea habitats around the world. They appear to be particularly important at high latitudes in fjords and other coastal settings.

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Author contributions AJG, MH, TC, and JP collected and picked gromiids from the Greenland samples. AJG, TC, SK and JP collected Svalbard gromiids. SK collected the White Sea gromiids and prepared Fig. 1. MH and EG were responsible for DNA extraction, amplification and sequencing; MH carried out the phylogenetic analysis, prepared Fig. 6, and wrote the genetic parts of the text. The remainder of the text was written by AJG, with edits from SK, MH, JP and TC. AJG was responsible for the photography and all figures, except for Figs 1 and 6.

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Data availability All data generated and analysed during this study are included in this published article. Type specimens are deposited in the Natural History Museum, London, under registration numbers NHMUK 2021.3.5.1–15

Ethics declarations

Gooday et al. (2021). Three new species of *Gromia* (Protista, Rhizaria) from western Greenland fjords. Polar Biology. https://doi.org/10.1007/s00300-021-02858-9

Conflict of interest: The authors declare that they have no conflicts of interest.

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Figure captions

Fig. 1. Study areas and sampling sites. **a**. Overview map showing the three study areas. **b.** Nuuk fjord system in West Greenland. **c.** Kongs Fjord in Svalbard. **d.** Chupa Inlet in White Sea.

Fig. 2. ***Gromia cucumiformis*** Gooday and Holzmann sp. nov.; Station 12, Kobbefjord. **a**. Group of relatively large specimens; the two indicated by arrows are DNA isolates 19997 (left) and 19995 (right). **b.** Group of smaller specimens; the specimen indicated by an arrow is isolate number 19998. Scales 2.5 mm.

Fig. 3. ***Gromia cucumiformis*** Gooday and Holzmann sp. nov. Group photograph; Station 12, Kobbefjord. Holotype (*), reg. no NHMUK 2021.3.5.1, and three paratypes, numbered 1, 2, 3, reg nos NHMUK 2021.3.5.2–4, respectively. Scale 1.0 mm.

Fig. 4. ***Gromia cucumiformis*** Gooday and Holzmann sp. nov. Sequenced specimens. **a–c.** Station 12, Kobbefjord. **a.** DNA isolate 19997. **b.** Isolate 19995. **c.** Isolate 19998. **d.** Station 1, Itissoq embayment, isolate 20019. Scales 1.0 mm.

Fig. 5. ***Gromia cucumiformis*** Gooday and Holzmann sp. nov. **a–d.** Oral capsules, Station 12, Kobbefjord. **a.** Paratype, reg. no. NHMUK 2021.3.5.2. **b.** Paratype, reg. no. NHMUK 2021.3.5.3; the arrows indicate what appear to be optical cross-sections of a tapered extension of the wall that borders the lower part of the oral capsule. **c.** Holotype, reg. no. NHMUK 2021.3.5.1. **d.** Paratype, reg. no. NHMUK 2021.3.5.4. **e.** Apertural end of holotype showing mineral particles within the test. Scales 100 µm (a-d); 1mm (e).

Fig. 6. PhyML phylogenetic tree based on the 3' fragment of the SSU rRNA gene, showing evolutionary relationships of 60 gromiid taxa. The tree is unrooted. Numbers at nodes indicate bootstrap values (BV's) >70%.

Fig. 7. ***Gromia botelliformis*** Gooday and Holzmann sp. nov.; Station 2, Itissoq embayment. **a**. Six specimens, including the holotype (reg. no. NHMUK 2021.3.5.5, indicated by asterisk). **b.** Six specimens, the four paratypes numbered 1–4 (reg. nos. NHMUK 2021.3.5.6–9, respectively). **c.** Holotype. **d.** Paratype NHMUK 2021.3.5.9. Scales 0.5 mm.

Fig. 8. ***Gromia botelliformis*** Gooday and Holzmann sp. nov.; sequenced specimens. **a.** Station 2, Itissoq embayment, DNA isolate 20010. **b.** Station 4, Qorgut embayment, isolate 20018. **c.** Station 2, Itissoq embayment, isolate 20002. **d.** Station 2, Itissoq embayment, isolate 20001. Scales 0.5 mm.

Fig. 9. ***Gromia botelliformis*** Gooday and Holzmann sp. nov.; Station 2, Itissoq embayment. **a-d.** Oral capsules. The arrows in b indicate wedge-shaped features, interpreted as optical cross-sections of tapered extensions of the wall bordering the lower part of the oral capsule. **e.** Test wall ornamentation (Paratype NHMUK 2021.3.5.8). Scales 50 µm.

Fig. 10. ***Gromia brevis*** Gooday and Holzmann sp. nov.; Station 1, Itissoq embayment. **a.** Holotype (NHMUK 2021.3.5.10, indicated by the asterisk) and paratypes, numbered 1–5 (reg. nos NHMUK 2021.3.5.11–15, respectively). **b.** Holotype. **c–g.** Paratypes in same order (#1–5) as in Figure a. **h–j**.

Sequenced specimens. **h.** DNA isolate 20004. **i.** Isolate 20005. **j.** Isolate 20006. Scales 0.5 mm (a), 250 µm (b-j).

Fig. 11. ***Gromia brevis*** Gooday and Holzmann sp. nov.; Station 1, Itissoq embayment. **a, b.** Oral capsules of unregistered specimens. Scales 50 µm.

Fig. 12. ***Gromia brevis*** Gooday and Holzmann sp. nov.; Station 1, Itissoq embayment. **a – c.** Collection of specimens photographed in Geneva in May 2019 under different lighting showing range of variation in test morphology. Note that the arrangement of specimens is slightly different in the different images, and a few are present in only one or two images. DNA isolates 20004 and 20007 were sequenced; 20004 (also illustrated in Figure 10h) is included in *G. brevis*, but 20007 is unrelated (Figure 5) although morphologically similar. All other specimens are assigned to *G. brevis* based on morphology. The three labelled P2, P4, P5 were later selected as paratypes (Figure 10d, f, g); the two other paratypes could not be recognised. **d.** Five elongate specimens photographed in Southampton in November 2020. From left to right the length/width ratios are 3.53, 3.19, 2.70, 2.43, 2.23 (length including oral capsule). The two indicated by asterisks are also recognisable in Figures a-c. Scales 1 mm.

Fig. 13. Sequenced specimens of undescribed *Gromia* species from Greenland. **a.** DNA isolate 20017, Stn 14, branching close to *G. brevis*. **b.** Isolate 20007, Stn 1, branching with three sequences from the White Sea. **c.** Isolate 20015, Stn 13, branching with two sequences from the White Sea and one from Svalbard. **d.** Isolate 20016, Stn 13, branching with a sequence from the White Sea. **e, f, g.** Three isolates that branch together. **e.** Isolate 20009, Stn 1. **f, g.** Isolate 20012, 20013, Stn 5.

Gooday et al. (2021). Three new species of *Gromia* (Protista, Rhizaria) from western Greenland fjords. Polar Biology. https://doi.org/10.1007/s00300-021-02858-9

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757 Table 1. Sampling sites for the new species in Greenland, Svalbard, and the Chupa inlet in the White Sea, with corresponding DNA isolate
758 numbers and species names.

Sampling location	Latitude °N	Longitude °E	Depth (m)	Isolates
Nuuk fjord system, Greenland				
Stn 1, Itissoq embayment of Qôrnup Suvdlua branch	64°15.748'	51°15.466'	98	20004–20006 (*G. brevis*) 20008, 20010 (*G. botelliformis*) 20007 (undescribed species) 20009 (undescribed species)
Stn 2, Itissoq embayment of Qôrnup Suvdlua branch	64°15.347'	051°14.532'	111	20000 (*G. cucumiformis*) 20001-20002 (*G. botelliformis*)
Stn 4, Oorgut embayment of Ũmánap Suvdlua branch	64°15.039'	050°53.467'	118	20018 (*G. botelliformis*) 20019 (*G. cucumiformis*)
Stn 5, south of Ũmanaq Island	64°27.600'	050°48.856'	240	20012, 20013 (undescribed species)
Stn 12, Kobbefjord	64°08.733'	051°23.658'	43	19995, 19997, 19998 (*G. cucumiformis*) 20015 (undescribed species) 20016 (undescribed species)
Stn 13, Kobbefjord	64°08.580'	051°23.377'	22	20017 (undescribed species)
Stn 14, Ameragdla branch of Ameralik (Lysefjord)	64°12.040'	050°20.948'	212	20021 (*G. brevis*)
Svalbard				
Stn 7, Kongsfjord	78° 55.19'	12° 15.03'	106	4685–4687 (*G. cucumiformis*)
Chupa inlet, White Sea				
Stn 21	66° 18.163'	33° 37.578'		9782 (*G. cucumiformis*)
Stn 22	66° 18.009'	33° 39.422'	70	9907 (*G. cucumiformis*)
Stn 23	66° 18.461'	33° 54.431'	117	9769 (*G. cucumiformis*)
Stn 24	66° 18.262'	33° 57.386'	80	9923 (*G. cucumiformis*)

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Gooday et al. (2021). Three new species of *Gromia* (Protista, Rhizaria) from western Greenland fjords. Polar Biology. https://doi.org/10.1007/s00300-021-02858-9

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761 Table 2. *Gromia brevis* sp. nov. Test dimensions of type specimens, sequenced specimens, and unregistered specimens that have dimensions
762 similar dimensions and considered to represent the same species. L1 = test length not including oral capsule; L2 = test length including oral
763 capsule; W = test width.

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Specimen	Registration/isolate	L1	L2	W	L1/W	L2/W
Holotype		560	590	299	1.87	1.97
Paratype 1		522	552	295	1.77	1.83
Paratype 2		511	541	243	2.11	2.23
Paratype 3		485	511	235	2.06	2.17
Paratype 4		407	425	220	1.85	1.93
Paratype 5		418	440	224	1.87	1.97
Sequenced 1	20004	667	696	358	186	194
Sequenced 2	20005	510	532	258	1.98	2.06
Sequenced 3	20006	522	547	266	1.96	2.06
Specimen 1		416	435	213	1.95	2.04
Specimen 2		371	394	206	1.80	1.91
Specimen 3		454	476	222	2.05	214
Specimen 4		299	317	164	1.82	1.93
Specimen 5		410	429	205	2.00	2.09
Specimen 6		369	396	194	1.90	2.04
Specimen 7		410	433	179	2.29	2.41
Mean		458.2	482.1	236.3	1.95	2.04
S.D.		89.4	92.5	49.6	0.13	0.14

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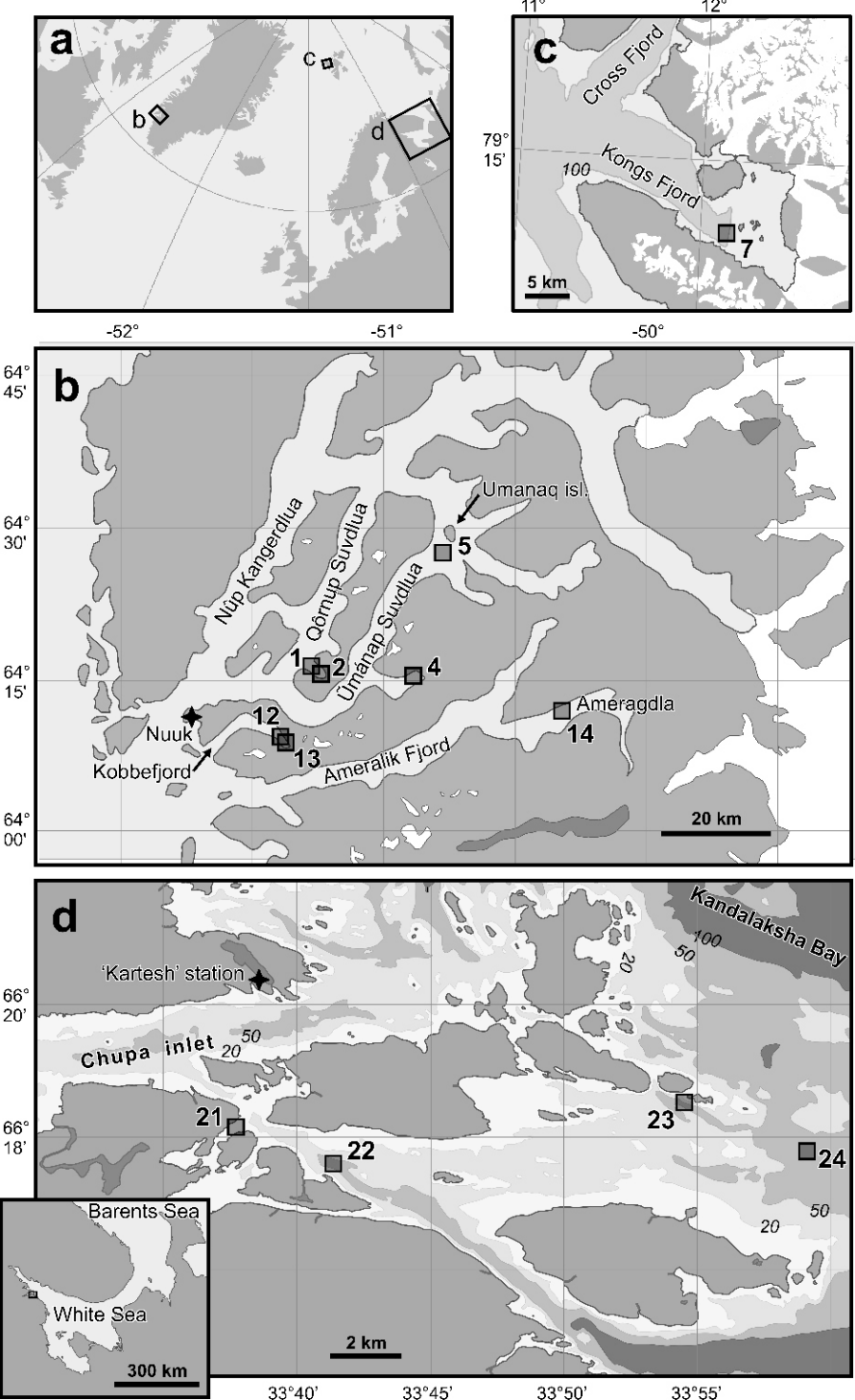

a
b
c
d
-52°
-51°
11°
12°
c
Cross Fjord
79°
15'
100
Kongs Fjord
7
5 km
-50°
b
64°
45'
64°
30'
64°
15'
64°
00'
Umanaq isl.
5
Nûp Kangerdlua
Qôrnup Suvdlua
Ûmánap Suvdlua
1
2
4
Nuuk
12
13
Kobbefjord
Ameralik Fjord
Ameragdla
14
20 km
d
66°
20'
66°
18'
'Kartesh' station
Chupa inlet
50
20
Kandalaksha Bay
100
50
20
21
22
23
24
50
20
Barents Sea
White Sea
300 km
2 km
33°40'
33°45'
33°50'
33°55'

Figure 2

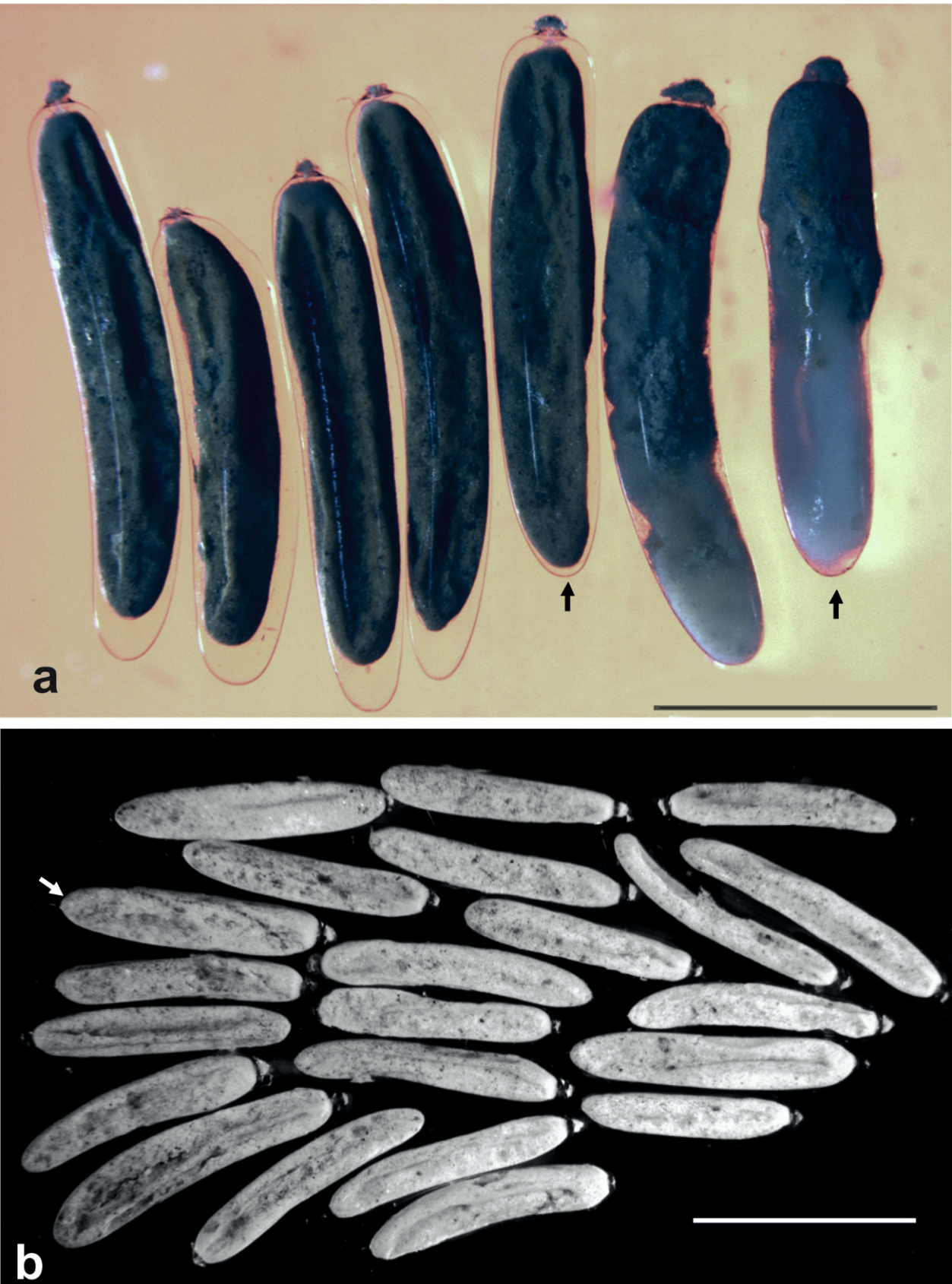
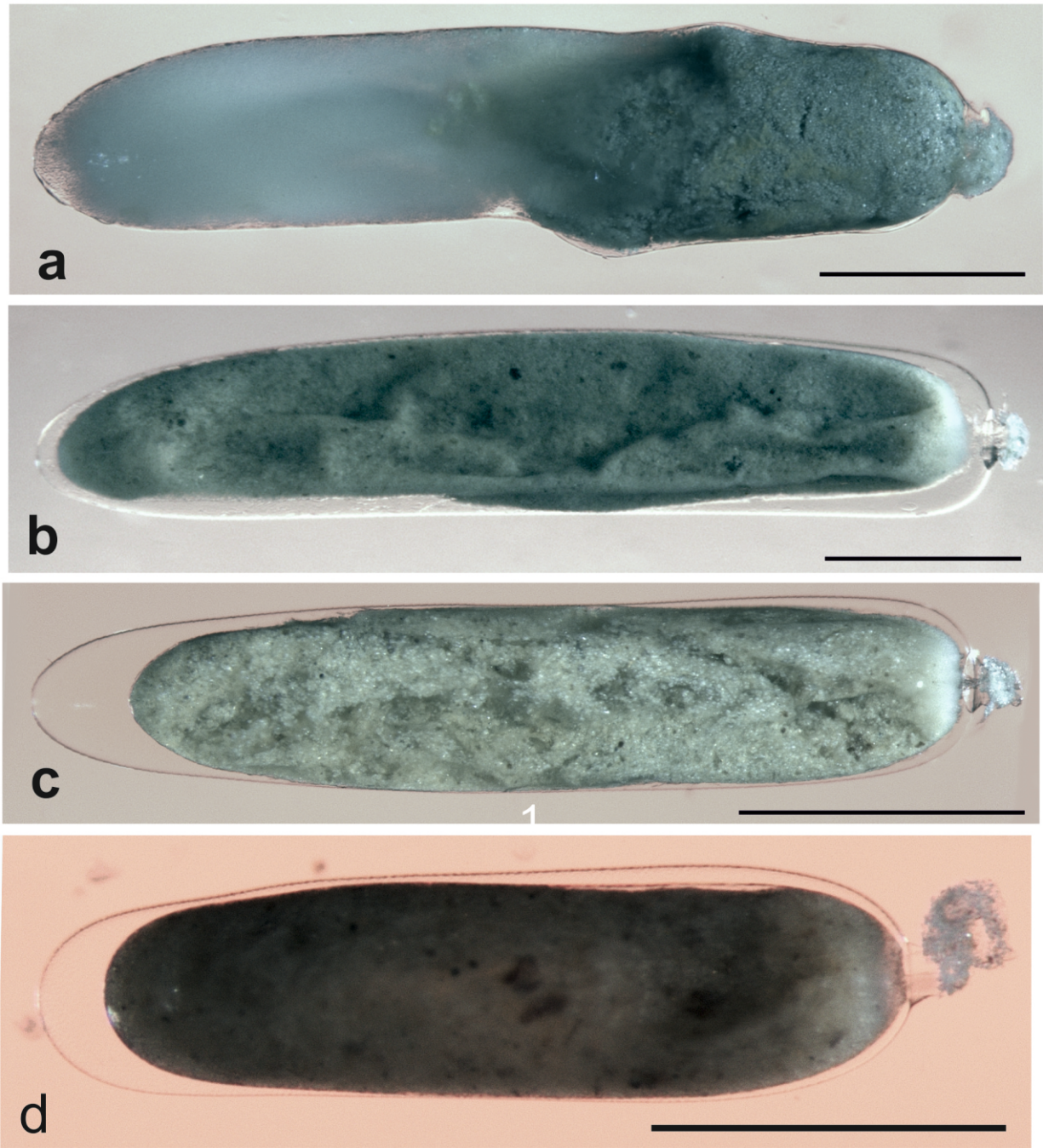


Figure 3

Figure 4



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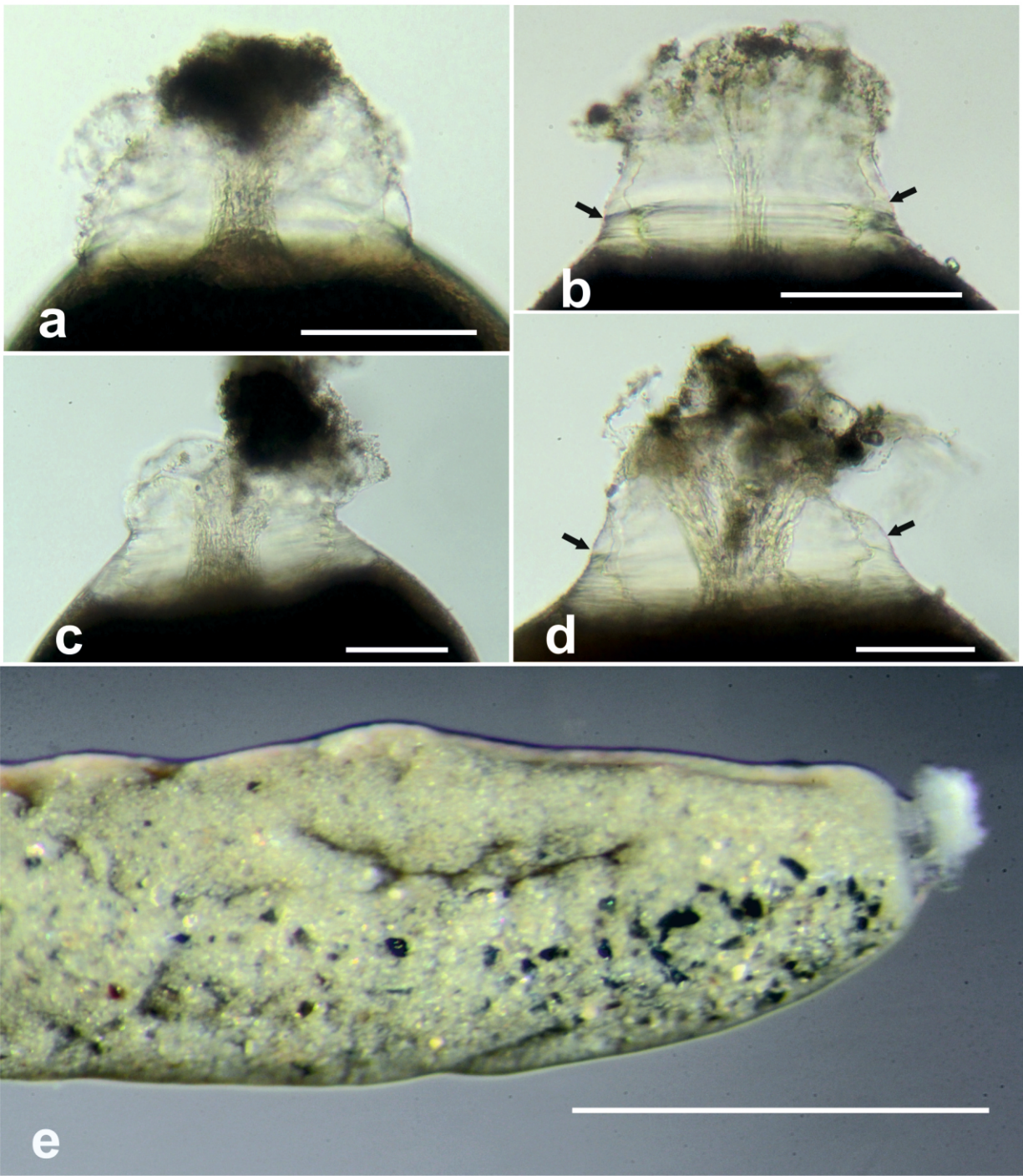

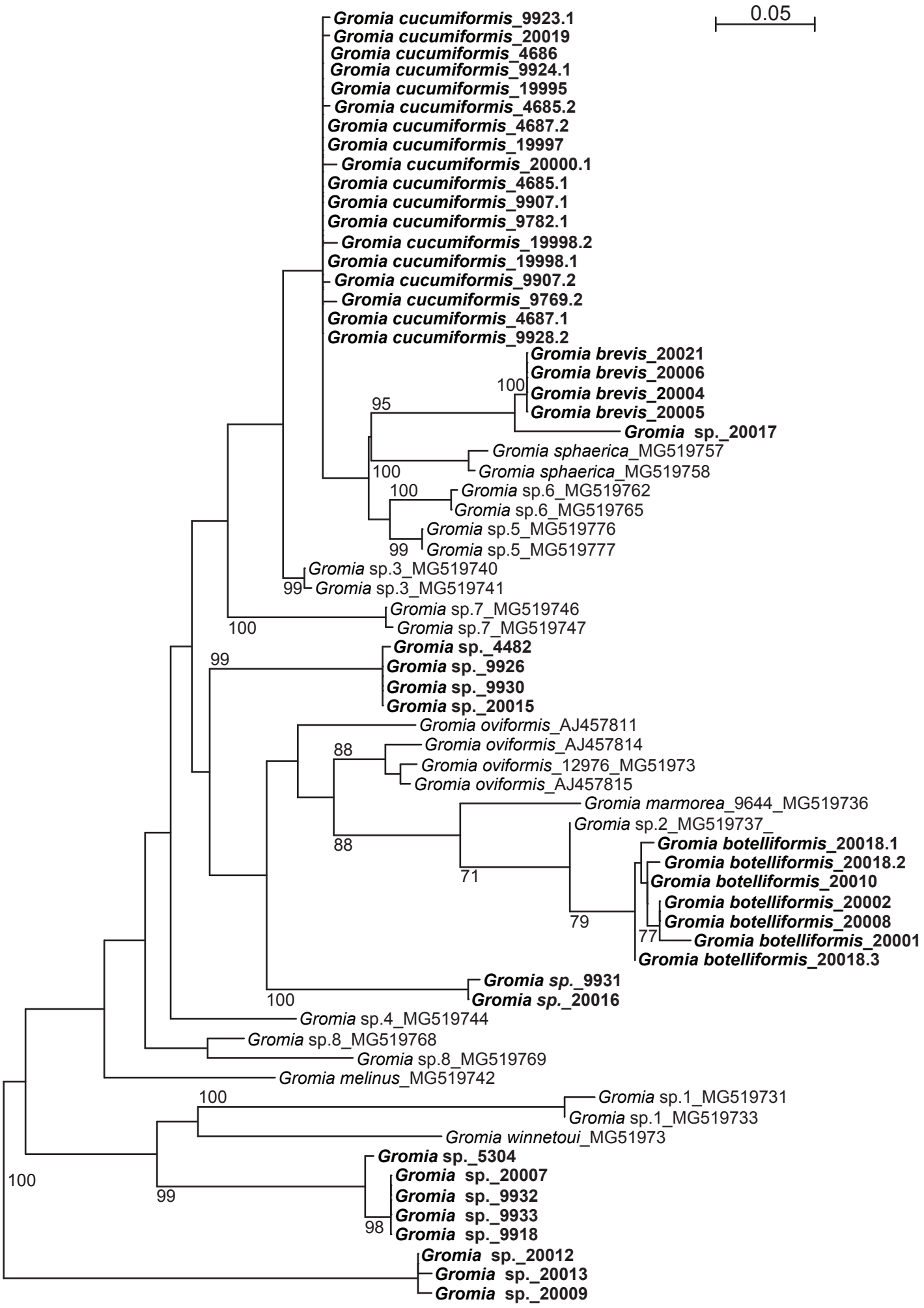
0.05
Gromia cucumiformis_9923.1
Gromia cucumiformis_20019
Gromia cucumiformis_4686
Gromia cucumiformis_9924.1
Gromia cucumiformis_19995
Gromia cucumiformis_4685.2
Gromia cucumiformis_4687.2
Gromia cucumiformis_19997
Gromia cucumiformis_20000.1
Gromia cucumiformis_4685.1
Gromia cucumiformis_9907.1
Gromia cucumiformis_9782.1
Gromia cucumiformis_19998.2
Gromia cucumiformis_19998.1
Gromia cucumiformis_9907.2
Gromia cucumiformis_9769.2
Gromia cucumiformis_4687.1
Gromia cucumiformis_9928.2
Gromia brevis_20021
Gromia brevis_20006
Gromia brevis_20004
Gromia brevis_20005
Gromia sp._20017
Gromia sphaerica_MG519757
Gromia sphaerica_MG519758
Gromia sp.6_MG519762
Gromia sp.6_MG519765
Gromia sp.5_MG519776
Gromia sp.5_MG519777
Gromia sp.3_MG519740
Gromia sp.3_MG519741
Gromia sp.7_MG519746
Gromia sp.7_MG519747
Gromia sp._4482
Gromia sp._9926
Gromia sp._9930
Gromia sp._20015
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Gromia oviformis_AJ457814
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Gromia oviformis_AJ457815
Gromia marmorea_9644_MG519736
Gromia sp.2_MG519737_
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Gromia botelliformis_20018.2
Gromia botelliformis_20010
Gromia botelliformis_20002
Gromia botelliformis_20008
Gromia botelliformis_20001
Gromia botelliformis_20018.3
Gromia sp._9931
Gromia sp._20016
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Gromia sp._20009
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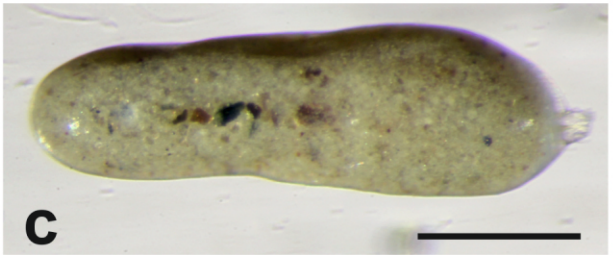
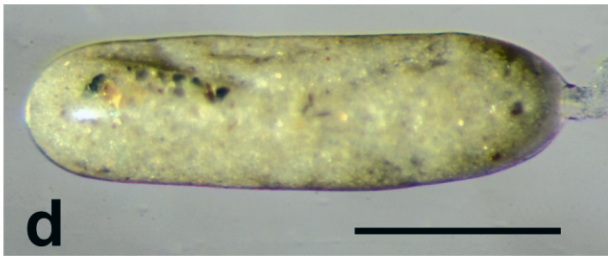
Figure 7





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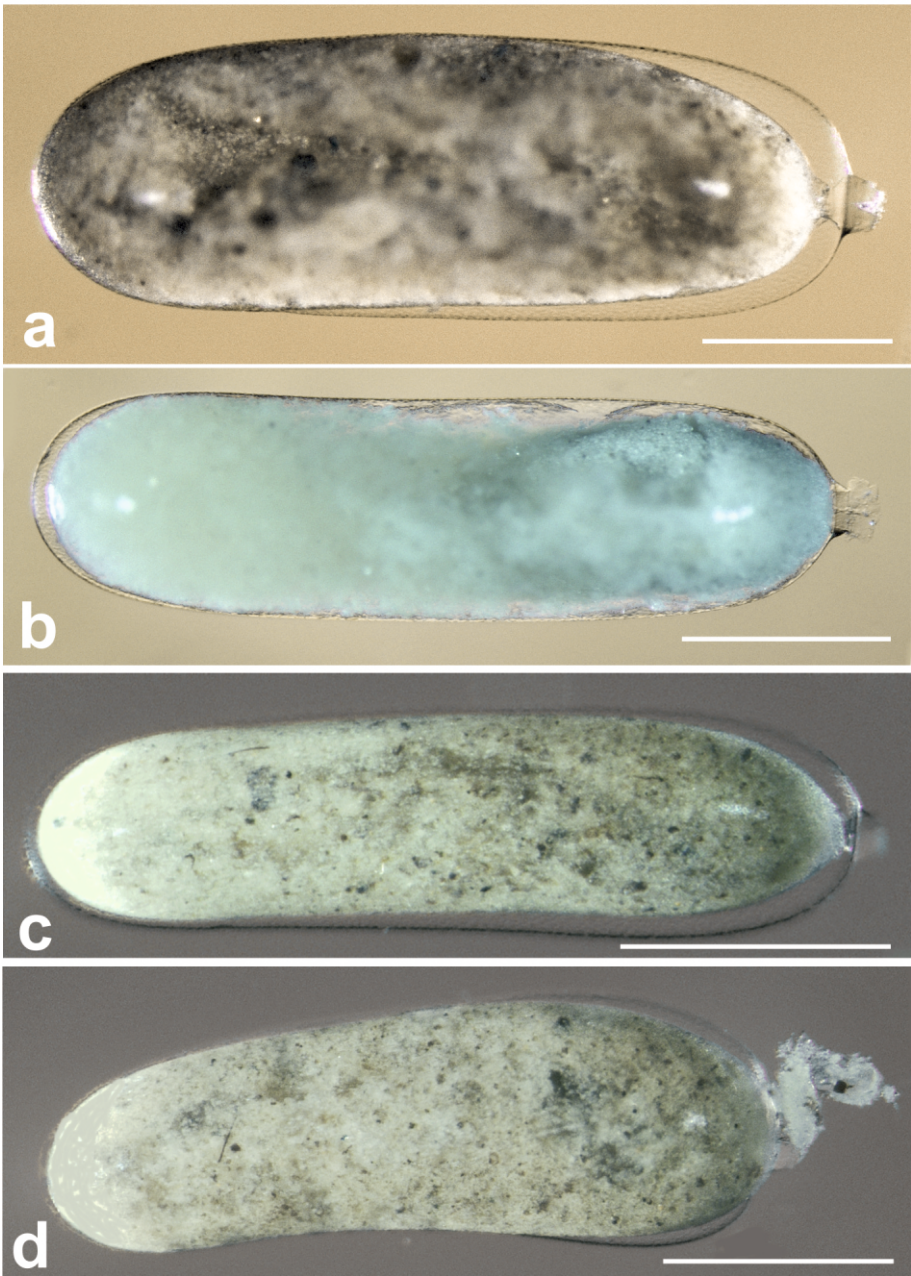

Figure 9

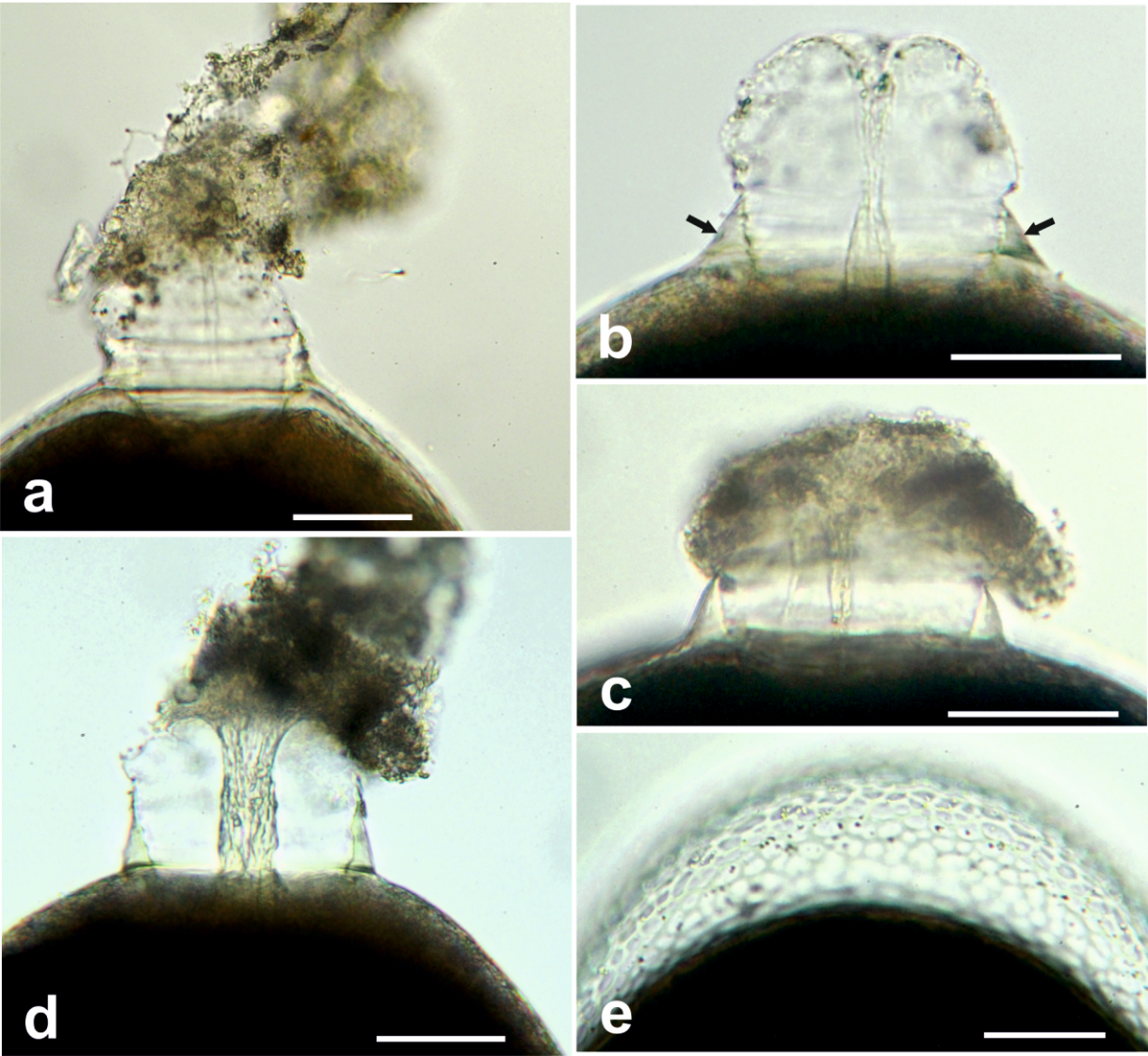

Figure 10

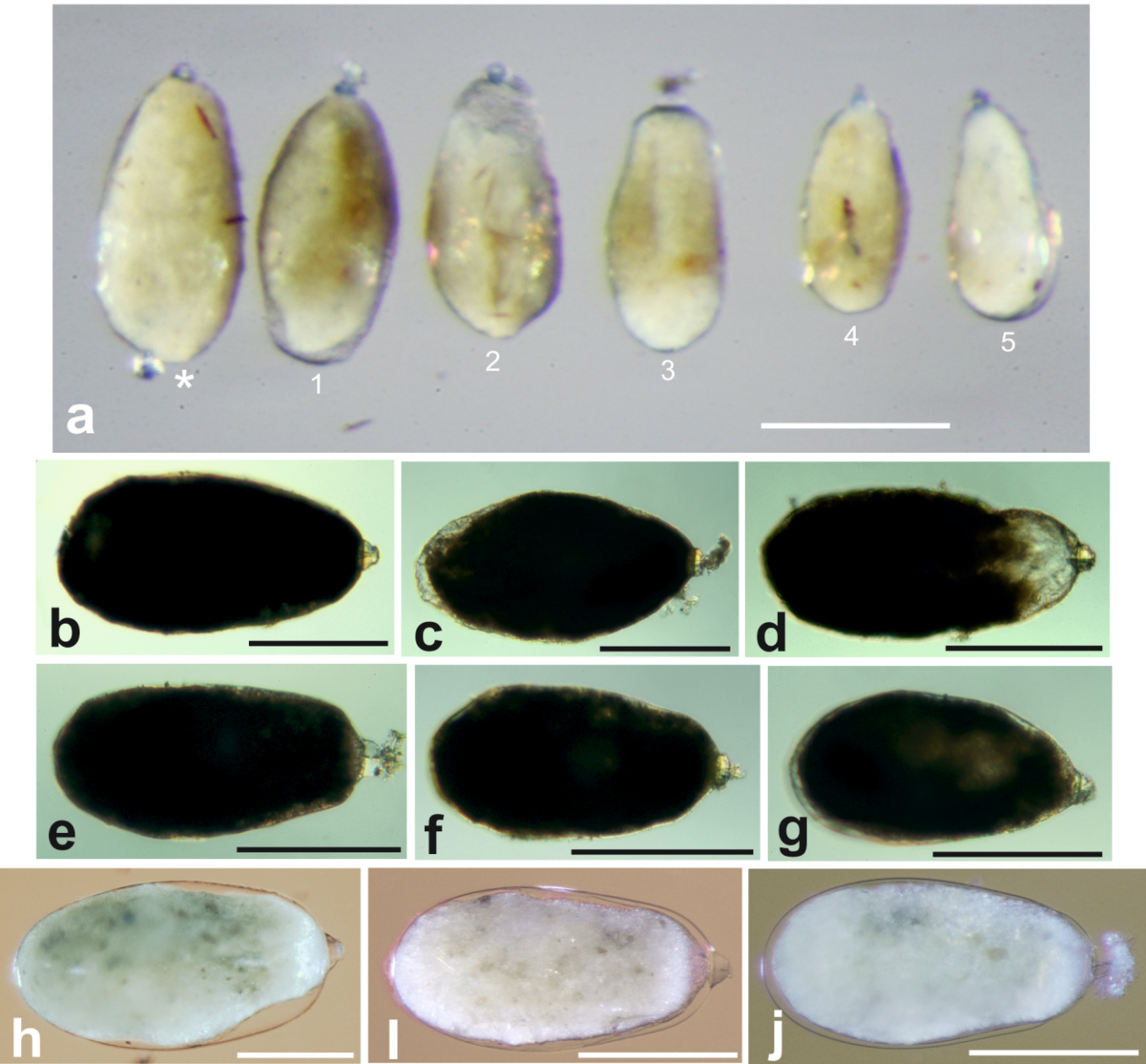

Figure 11

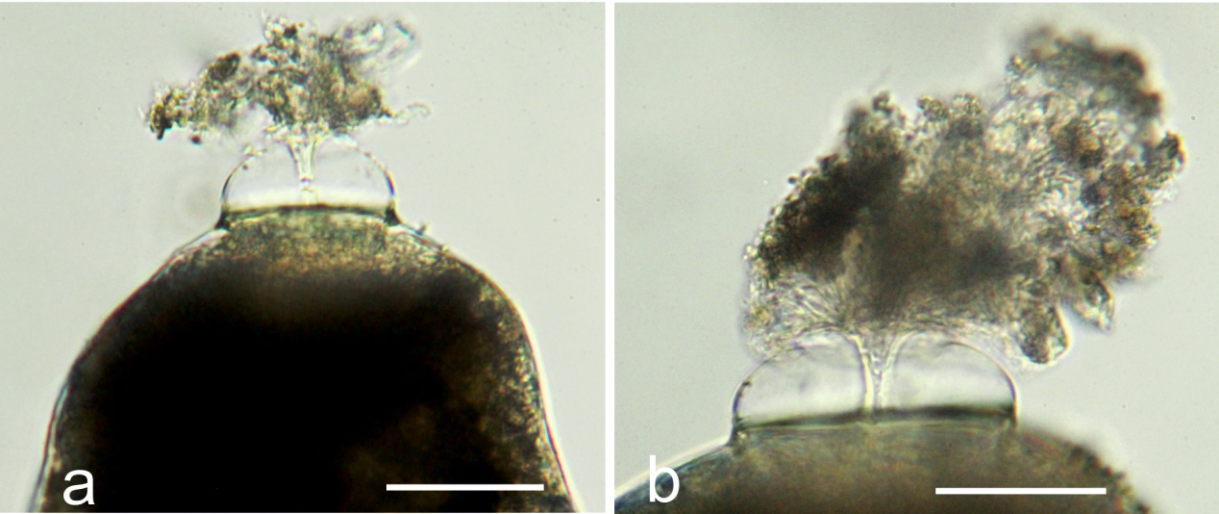

Figure 12

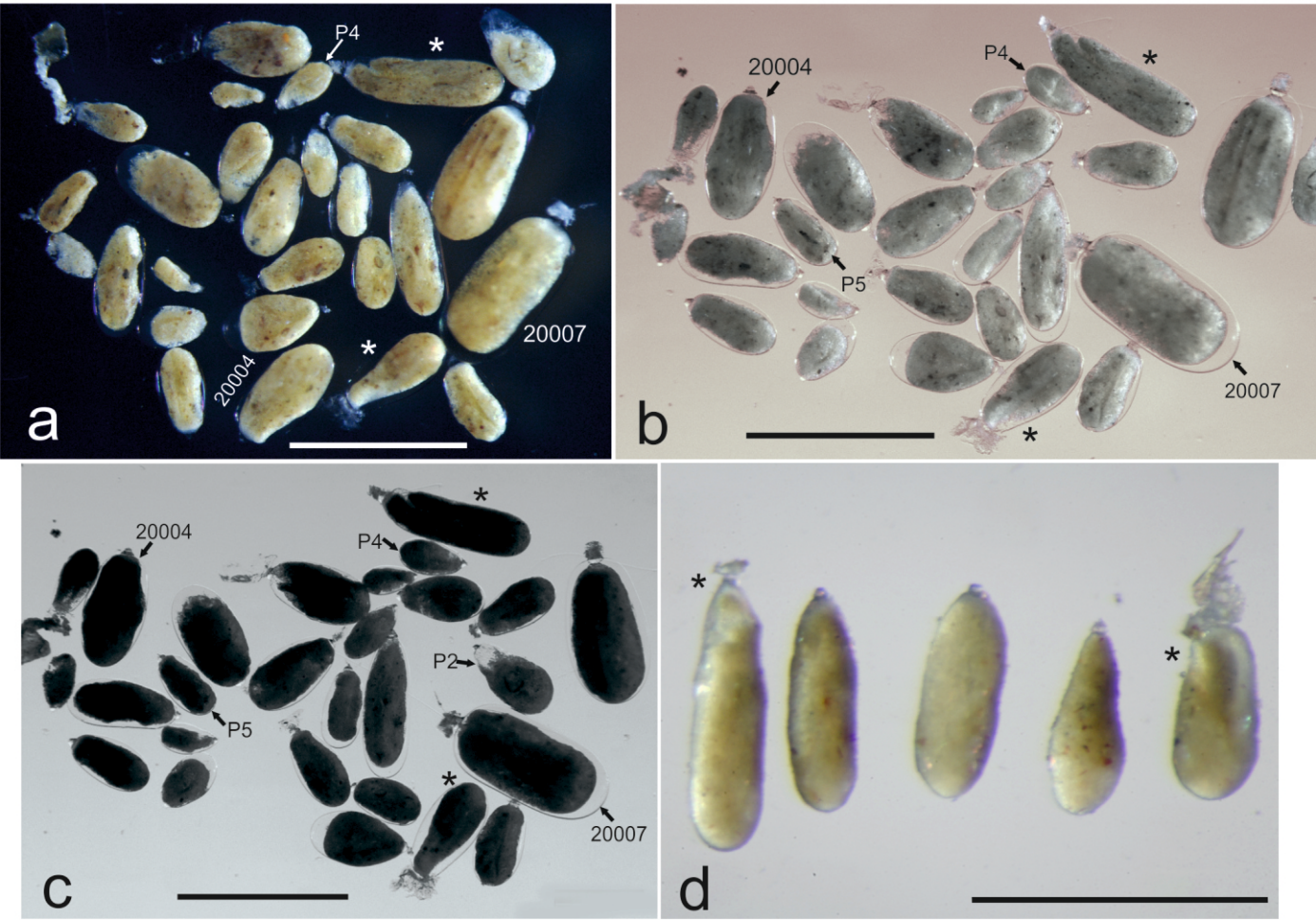

Figure 13