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1 **Morphological and molecular diversity of monothalamids (Rhizaria,**  
2 **Foraminifera), including two new species and a new genus, from SW Greenland**

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## 29 Abstract

30

31 Single-chambered (monothalamous) foraminifera are poorly known compared to their  
32 multichambered relatives. In this first study of monothalamids from Greenland, we  
33 describe one new genus and two new species belonging to different clades from the  
34 Nuuk fjord system. *Nujappikia idaliae* Gooday & Holzmann gen. nov. sp. nov. (Clade  
35 Y) has a bottle-shaped test terminating in a single aperture located on a short neck.  
36 The flexible wall is basically organic but with a very fine agglutinated veneer.  
37 *Bathyallogromia kalaallita* Gooday & Holzmann sp. nov. (Clade C) has a broadly  
38 ovate test with an organic wall and a mound-like apertural structure. It is larger and  
39 genetically distinct from the two other *Bathyallogromia* species, both from the  
40 Southern Ocean. A survey of the morphological diversity of monothalamids in our  
41 samples revealed 49 morphospecies, of which 19, including the two new species,  
42 yielded DNA sequences. Five were assigned to the genera *Bathysiphon*, (Clade BM),  
43 *Micrometula*. (Clade BM), *Psammophaga*. (Clade E), *Hippocrepinella* (Clade D) and  
44 *Crithionina* (Clade J). The remaining twelve represented unknown taxa branching in  
45 clades A, C, F, and Y and one new clade. Our results add to growing evidence that  
46 monothalamids are common and diverse in fjords and other high-latitude settings.

47

48 **Keywords:** meiofauna, benthos, soft-walled saccamminids, molecular phylogeny,  
49 subarctic, biogeography

50

51

52

## 53 Introduction

54

55 Monothalamids form a paraphyletic group of single-chambered foraminifera at the  
56 base of the foraminiferal evolutionary tree (Pawlowski et al., 2003, 2013). They were  
57 well-known to 19<sup>th</sup>-century scientists and are widespread in the oceans as well as  
58 being the only foraminiferal group represented in freshwater and damp terrestrial  
59 habitats (Holzmann et al., 2021). Some marine monothalamids, for example, species  
60 of *Astrorhiza*, *Bathysiphon*, *Hyperammia*, *Rhabdammina* and *Saccorhiza*, have  
61 large, fairly robust tests and were described well over a century ago. These  
62 conspicuous foraminifera are sometimes very abundant, particularly at upper bathyal  
63 depths (Table 2 in Gooday et al., 1997) and in Arctic settings (e.g., Thorson, 1934).  
64 However, it is clear from recent studies that the majority of monothalamids, at least in  
65 coastal waters, are small, delicate, relatively inconspicuous and to a large extent  
66 undescribed. These ‘soft-walled’ forms have organic or finely agglutinated test walls  
67 and are often overlooked or destroyed when sieve residues are dried for picking.  
68 Having little fossilization potential, they may also be simply ignored, particularly in  
69 geologically-oriented studies. However, the fact that monothalamids often represent a  
70 largely undocumented component of foraminiferal diversity in coastal sediments  
71 makes them worthy of attention (Pawlowski et al. 2002a, Habura et al. 2008).

72

73 Here, we focus on monothalamids, the majority of them small and delicate,  
74 from fjords in the area around Nuuk in the SW of Greenland. We describe two new  
75 species, one of them representing a new genus, together with a survey of the diversity  
of monothalamids based on morphological and genetic data. Previous studies of

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76 Arctic and Scandinavian foraminifera included a few of the larger and more robust  
77 representatives of this group (e.g., Brady, 1881; Goës, 1894; Loeblich and Tappan,  
78 1953), while Höglund's classic 1947 study of foraminifera from the Gullmar Fjord  
79 and Skagarak included species (e.g., *Hippocrepinella* spp., *Pilulina argentea*) with  
80 tests that are somewhat soft-walled, but still fairly large and coherent. The first really  
81 delicate soft-walled monothalamous foraminifera from Scandinavia were described by  
82 Nyholm (1952, 1953, 1954, 1955, 1974) from the Gullmar Fjord on the Swedish west  
83 coast. This important series of papers established a number of organic-walled genera,  
84 namely *Cylindrogullmia*, *Gloiogullmia*, *Micrometula*, *Nemogullmia*, and *Tinogullmia*,  
85 that are widely distributed in mainly coastal waters. More recent surveys from fjords  
86 on the west coast of Spitzbergen (Svalbard archipelago) and the Håkon-Mosby Mud  
87 Volcano in the Barents Sea have yielded a rich variety of small monothalamids,  
88 including both organic-walled and agglutinated forms (Gooday et al, 2005, 2013).  
89 Combined molecular and morphological studies carried out in Antarctica and the sub-  
90 Antarctic island of South Georgia have also revealed a high diversity of mainly small  
91 monothalamids (Pawlowski et al. 2002a, 2005, 2008, Majewski et al. 2015, Holzmann  
92 et al.,2022).

93 Spärck (1933) and Thorson (1934) described a macrofaunal community  
94 characterized by the relatively large monothalamid *Rhabdammina cornuta* Brady,  
95 1884 (up to 6 mm long according to the original description) and the miliolid  
96 *Planispirinoides bucculentus* (Brady, 1884) in Franz Joseph Fjord and Scoresby  
97 Sound on the east coast, but otherwise all previous studies of modern foraminifera in  
98 Greenland fjords (Lloyd et al., 2006; Holtegaard Nielsen et al., 2010; Jennings et al.,  
99 2020a, 2020b) have had a geological focus and included only one or two  
100 monothalamids with rigid tests, such as *Lagenammia* and *Hyperammia* species. The  
101 only foraminiferal study in the Nuuk fjord system (Ameralik Fjord) focused on Late  
102 Holocene assemblages (Møller et al., 2006). This is therefore the first study dedicated  
103 to soft-walled monothalamids in Greenland fjords. In a previous publication (Gooday  
104 et al., 2021), we described new species of the rhizarian genus *Gromia* from the same  
105 region.

106

## 107 **Methods**

108

### 109 **Sample collection, processing and morphological methods**

110

111 Samples were collected in the Nuuk fjord (formerly Godthåbsfjord) system in July  
112 2018. The sampling and processing methods were the same as those described for the  
113 gromiids collected during the same expedition (Gooday et al., 2021). Briefly, samples  
114 were taken at 13 sites in different branches of the fjord system (Table 1) from a small  
115 boat using a Van Veen grab, and the surficial sediment removed with a spoon. The  
116 sediment was immediately washed onboard through a series of sieves with mesh sizes  
117 of 500, 250, 125 µm and placed in plastic bottles. As soon as possible after collection,  
118 the residues were sorted in seawater for monothalamids by project participants using  
119 stereo-microscopes in a laboratory of the Greenland Institute of Natural Resources in  
120 Nuuk. Where possible (mainly the finer residues), photographs of freshly-picked  
121 monothalamids were taken before preservation in either RNA later for genetic  
122 analyses or 10% buffered formalin for morphological study. Other photographs were

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123 taken in Geneva using a Leica M205 C microscope fitted with a Leica DFC 450 C  
124 camera, and in Southampton using an Olympus SZX7 stereo-microscope and an  
125 Olympus BH2 compound microscope, both equipped with a Canon 60D SRL digital  
126 camera.

127

#### 128 **DNA extraction, PCR amplification and sequencing**

129

130 Forty-nine foraminiferal specimens were extracted individually using guanidine lysis  
131 buffer (Pawlowski, 2000). Semi-nested PCR amplification was carried out for the  
132 SSU rDNA barcoding fragment of foraminifera (Pawlowski and Holzmann, 2014)  
133 using primers s14F3 (acgcamgtgtgaaacttg)-s20r (gacgggcggtgtgtacaa) for the first and  
134 primers s14F1 (aagggcaccacaagaacgc)-s20r for the second amplification. Thirty-five  
135 and 25 cycles were performed for the first and the second PCR, with an annealing  
136 temperature of 50°C and 52°C, respectively. The amplified PCR products were  
137 purified using the High Pure PCR Cleanup Micro Kit (Roche Diagnostics).  
138 Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle  
139 Sequencing Kit (Applied Biosystems) and analyzed on a 3130XL Genetic Analyzer  
140 (Applied Biosystems). The resulting sequences were deposited in the NCBI/GenBank  
141 database. Isolate and Accession numbers are summarised in Table 2.

142

143

#### 144 **Phylogenetic analysis**

145

146 The sequences obtained were added to 107 sequences that are part of the publicly  
147 available 18S database of monothalamous foraminifera (NCBI/Nucleotide;  
148 [www.ncbi.nlm.nih.gov/nucleotide/](http://www.ncbi.nlm.nih.gov/nucleotide/)). All sequences were aligned using the Muscle  
149 automatic alignment option, as implemented in SeaView vs. 4.3.3 (Gouy et al. 2010),  
150 Based on the preliminary alignment, the new sequences were assigned to established  
151 monothalamous clades (Pawlowski et al. 2002b). Three partial alignments were  
152 generated subsequently, including the representatives of selected clades and new  
153 sequences. Because of the high genetic variability between clades (Pawlowski et  
154 al.2002b), separate alignments allow a better resolution of tree topology. The  
155 alignment of clades A, BM, C (Fig. 1) contains 68 sequences with 1611 sites used for  
156 analysis. The alignment of clades D, E, F (Fig. 2) contains 50 sequences with 1379  
157 sites used for analysis. The alignment of clades J, Y, New Clade (Fig. 3) contains 42  
158 sequences with 1392 sites used for analysis.

159

160 The phylogenetic trees were constructed using maximum likelihood  
161 phylogeny (PhyML 3.0) as implemented in ATGC: PhyML (Guindon et al. 2010). An  
162 automatic model selection by SMS (Lefort et al. 2017) based on Akaike Information  
163 Criterion (AIC) was used, resulting in a HKY85+G+I substitution model being  
164 selected for the first analysis (Fig.1) and a GTR+G+I substitution model being  
165 selected for the remaining analyses (Figs. 2, 3). The initial trees are based on BioNJ.  
166 Bootstrap values (BV's) are based on 100 replicates.

166

167 Pairwise genetic distances were calculated using MEGA7, with a Maximum  
168 Composite Likelihood method and uniform rates among sites applied to the analysis  
(Kumar et al. 2016).

169

□

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170 **Results**

171

172 **Systematic descriptions**

173 Rhizaria Cavalier-Smith, 2002

174 Retaria Cavalier-Smith, 1999

175 Foraminifera D'Orbigny, 1826

176 Monothalamids Pawlowski, Holzmann and Tyszka, 2013

177

178 Given the uncertain status of the monothalamids, we use the informal name rather  
179 than the formal Monothalamea for this paraphyletic group (Pawlowski et al., 2013).  
180 The type material is deposited in the Natural History Museum, London, registration  
181 numbers NHMUK PM ZF 9946–9957.

182

183 *Nujappikia* Gooday & Holzmann gen. nov.

184

185 **Etymology.** The name is derived from that of a hunter from East Greenland named  
186 Nujappik, who's image, based on a photograph taken on 1906, is painted on the outer  
187 wall of an apartment block in Nuuk, the capital of Greenland.

188

189 **Diagnosis.** Monothalamid with more or less cylindrical test and single terminal  
190 aperture at end of short neck. Test wall translucent, composed of organic material  
191 with very finely agglutinated veneer. Cytoplasm pale, often containing some large  
192 ingested particles.

193

194 **ZooBank registration:** urn:lsid:zoobank.org:act:B5B8EB8C-528B-4108-A476-  
195 DBB0B29D00EF

196

197 *Nujappikia idaliae* Gooday & Holzmann gen. & sp. nov.

198

199 Figs 4–7

200

201 **Etymology.** In honour of Idalia (Alina) Pawlowska, who played a large role in  
202 organising our expedition to Greenland in 2018.

203

204 **Diagnosis.** Test 387 – 895  $\mu\text{m}$  (mean 590  $\mu\text{m}$ ) long, 165 – 285  $\mu\text{m}$  (mean 222  $\mu\text{m}$ )  
205 wide, L/W ratio 1.7 – 4.0 (mean 2.65). Other characteristics as for genus.

206

207 **ZooBank registration:** urn:lsid:zoobank.org:act:7F5A6C13-293E-4696-AD4E-  
208 638A27C0DF69

209

210 **Type material.** Station 16: inner part of Lysefjord off the sandur field; 64°12.656'  
211 N, 050°15.751' W; water depth 61 m. The holotype (reg. no. NHMUK PM ZF  
212 9946) and seven paratypes (reg. nos NHMUK PM ZF 9947–9953) are preserved in  
213 10% formalin.

214

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215 **Other material.** Station 16: six sequenced specimens (isolates 19842–44,  
216 19847, 19848, 19850); 13 specimens for morphology.

217 Station 15: inner part of Lysefjord off the sandur field; water depth 95 m;  
218 64°12.639' N, 050°16.074' W; eight specimens for morphology.

219

## 220 **Description**

221 *Test.* In lateral view the test is approximately cylindrical to somewhat ovate in outline  
222 (Figs 4–6) and circular in cross-section. Preserved specimens are sometimes more or  
223 less flattened, although this is probably an artefact. The sides are approximately  
224 parallel, slightly convex, or in a few elongate specimens slightly concave (Fig. 7A).  
225 The abapertural end is usually evenly rounded while the apertural end is more or less  
226 tapered. The length ranges from 387 to 895  $\mu\text{m}$  (mean  $590\pm 106\ \mu\text{m}$ ), the maximum  
227 width from 165 to 285  $\mu\text{m}$  (mean  $222\pm 27\ \mu\text{m}$ ), and the length/width ratio from 1.7 to  
228 4.0 (mean  $2.65\pm 0.44$ ) ( $n=45$  in each case). A rather more elongate specimen (one of  
229 several in Fig. 4B), which was not available for measurement, had a length/width ratio  
230 of 4.26.

231 *Apertural structures.* The single terminal aperture is typically located at the  
232 end of a short neck, 30 – 95  $\mu\text{m}$  long and 50 – 110  $\mu\text{m}$  wide. A well-developed  
233 peduncle (pseudopodial trunk) sometimes extends along the axis of the apertural neck.  
234 It is variably developed but sometimes forms a prominent feature, 45 to 58  $\mu\text{m}$  wide  
235 (Figs. 6F, H; 7A, B, D). The peduncle appears to develop directly from the cell body  
236 and there is no evidence for a peduncular sheath (invagination of the cell body) in any  
237 of the specimens that were examined in detail.

238 *Test wall and contents.* The wall is flexible, translucent, particularly in freshly  
239 collected specimens, with a slight reflective sheen resulting from a veneer of very  
240 fine, agglutinated particles overlying an organic layer. The surface is smooth,  
241 sometimes with weak transverse undulations (Fig. 4C). After prolonged preservation  
242 in formalin, however, the surface tends attract particles of detritus. The cytoplasm  
243 forms a pale, well-defined, brownish mass when fresh, and is visible through the test  
244 wall. It fills most of the test interior, but often with a narrow gap that is usually widest  
245 at the abapertural end. In preserved specimens, the cytoplasm is less clearly defined.  
246 When viewed in transmitted light in a compound microscope, it appears more or less  
247 heterogeneous, with numerous small particles and in some cases a few large  
248 inclusions. The latter include unknown spherical structures (Figs 5E, H; 7E, F),  
249 probable mineral grains (Fig. 7A, E, F), a single diatom frustule (Fig. 5D), and an  
250 apparently intact copepod exoskeleton or moult (Figs. 5E; 7E). An obvious nucleus  
251 was not observed, possibly because it was obscured by these particles.

252

## 253 Remarks

254 The cylindrical test of *Nujappikia idaliae* is similar in shape to that of *Gloiogullmia*  
255 *eurystoma*, as illustrated by Nyholm (1974), but the wall is translucent with a milky  
256 appearance, suggesting that it has a surface layer of very fine agglutinated particles. In  
257 addition, although some debris adheres to the wall in preserved specimens, the new  
258 species lacks the sticky outer test layer that is typical of *Gloiogullmia*. Among the  
259 many undescribed ‘saccamminids’ (a group in which the wall includes an  
260 agglutinated component), illustrated in the literature, Saccamminid sp. 11 from the  
261 Adriatic Sea [Pl. 2, fig. 8 in Sabbatini et al. (2010); Pl. 4, fig. 14 in Sabbatini et al.  
262 (2014)] resembles the more ovate specimens of the *N. idaliae* most closely.

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263

264 **Molecular characteristics.** The partial SSU rDNA sequences of *N. idaliae* contain  
265 799 nucleotides and the GC content ranges from 48.9% to 49.1%.

266

267

268

*Bathyallogromia kalaallita* Gooday & Holzmann sp. nov.

269

270

Figs 8–11

271

272 **Etymology.** From the Inuit word *Kalaallit*, the name of the main group of indigenous  
273 inhabitants of Western Greenland.

274

275 **Diagnosis:** Test ranging from almost spherical to ovoid, 338 – 571  $\mu\text{m}$  (mean 470  
276  $\mu\text{m}$ ) long, 282 – 498  $\mu\text{m}$  (mean 393  $\mu\text{m}$ ) wide, L/W ratio 0.98 – 1.44 (mean 1.20).

277

278 **ZooBank registration:** urn:lsid:zoobank.org:pub:658496E9-0DA1-42D5-9023-  
279 33E1F035156A

280

281 **Type material.** Station 3: Qôrgut fjord, 64°14.957' N; 052.196' W; water depth 58  
282 m, sandy mud. The holotype (reg. no. NHMUK PM ZF 9954) and three paratypes (reg.  
283 nos NHMUK PM ZF 9955–9957) preserved in 10% formalin for morphology.

284

285 **Other material.** Station 3: three sequenced specimens (isolates 19861-63); 9  
286 specimens for morphology.

287

### 288 **Description.**

289 *Test.* The test is broadly oval to almost spherical in side view (Fig. 8) with a circular  
290 cross section. Most specimens are more or less symmetrical about a longitudinal axis  
291 passing through the aperture, but some of the more spherical specimens are somewhat  
292 asymmetrical (Fig. 10A, E). The test ranges from 338 to 571  $\mu\text{m}$  (mean 470  $\mu\text{m}$ ) in  
293 length, 282 to 498  $\mu\text{m}$  (mean 393  $\mu\text{m}$ ) in width, with a L/W ratio of 0.98 – 1.44 (mean  
294 1.20) (n = 23).

295

296 *Apertural structures.* The apertural end of the test is produced into a low,  
297 sometimes truncated mound, in five specimens measuring 83–101  $\mu\text{m}$  wide and 11–  
298 28  $\mu\text{m}$  high. A well-developed peduncle extends through the mound (Fig. 10A–D).  
299 This feature is clearly visible in the specimens photographed in May 2022 where the  
300 cell body had shrunk (Fig. 11). Here, the peduncle is often somewhat narrower in the  
301 middle (width 20 – 30  $\mu\text{m}$ ) than in the lower part (21 – 33  $\mu\text{m}$ ), widening again into a  
302 funnel-shaped feature (width 44 – 56  $\mu\text{m}$ ) towards the top. In several specimens, the  
303 peduncle seems to be a tubular structure with a central thread of cytoplasm (Fig. 11D,  
304 H). The thread of cytoplasm (pseudopodial trunk) descends into the cell body within a  
305 peduncular sheath. In two glycerol-mounted specimens where it can be seen most  
306 clearly (Fig. 10A–D), the sheath is 65  $\mu\text{m}$  and 75  $\mu\text{m}$  wide and extends for at least 50  
307  $\mu\text{m}$  into the cell.

307

308 *Test wall and contents.* The wall is transparent, flexible, and entirely organic  
309 with reflective highlights (Fig. 9A, C, E). It is between 7.3 and 16.4  $\mu\text{m}$  thick, with  
some differences between individuals (for example, 7.3 – 9.1  $\mu\text{m}$  compared to 12.7 –

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310 16.4  $\mu\text{m}$  in two cases) and is often rather thinner at the abapertural end of the test  
311 compared to near the aperture. In freshly collected specimens the cytoplasm is  
312 typically brownish orange (Fig. 8A, B), sometimes tinged with grey or in a few cases  
313 almost completely grey, but after storage in formalin for 6 months it lost much of its  
314 colour and appeared whitish or greyish in reflected light (Figs. 8C,D; 9). The cell  
315 body fills most or all of the test (Figs 9, 10). By May 2022, after almost four years in  
316 formalin, however, it had shrunk and was separated from the test wall by a clear space  
317 (Figs. 8D; 11). When viewed in water using a compound microscope with transmitted  
318 light, the cytoplasm appears fine-grained with some small, scattered, mainly dark  
319 particles, which become more obvious with the test immersed in glycerol (Fig. 10A–  
320 C, F). These are presumably mineral grains. In two specimens a single large circular  
321 structure measuring 51 and 93  $\mu\text{m}$  in diameter is visible (Fig. 10A, B). This may be a  
322 nucleus, although the absence of any obvious internal structure, such as nucleolus,  
323 makes this somewhat doubtful.

324  
325

#### 326 Remarks

327 *Bathyallogromia kalaallita* closely resembles the two previously described species of  
328 the genus, but is larger than both. The mean lengths of *B. weddellensis* from the deep  
329 Weddell Sea (1000 – 6000 m depth) and *B. olivacea* from South Georgia are 251  $\mu\text{m}$   
330 and 314  $\mu\text{m}$ , respectively (Gooday et al., 2004; Holzmann et al., submitted),  
331 compared to 470  $\mu\text{m}$  for *B. kalaallita*. There are also differences in shape.

332 *Bathyallogromia weddellensis* is the most nearly spherical of the three species with a  
333 mean length/width ratio of 1.09 and *B. olivacea* is the most ovate, with a mean  
334 length/width ratio of 1.45. The new species has a shape that is intermediate between  
335 these extremes (mean length/width ratio 1.20).

336 When freshly collected, the three species also displayed differences in the  
337 colour of the cell body, light grey or greenish in *B. weddellensis*, olive-green in *B.*  
338 *olivacea*, and brownish orange to greyish in *B. kalaalita*. However, it is not certain  
339 that these colours have any value as taxonomic characters. It is more likely that they  
340 reflect the consumption of different food material, as in other foraminifera (e.g.,  
341 Jepps, 1942; Moodley et al., 2000). In any case, the colours disappear in preserved  
342 specimens, in which the cytoplasm is generally whitish.

343 Two almost spherical *Bathyallogromia*-like organic-walled monothalamids  
344 from ~1300 m depth on the Håkon-Mosby Mud Volcano (Fig. 2a,b in Gooday et al.,  
345 2013) measure about 122 and 233  $\mu\text{m}$  in length (including the apertural structure),  
346 and are therefore more similar in size and shape to the Weddell Sea species than to *B.*  
347 *kalaallita*.

348

349 **Molecular characteristics.** The partial SSU rDNA sequences of *B. kalaallita* contain  
350 1009 nucleotides (isolate 19863) and 1015 nucleotides (isolates 19861, 19862)  
351 respectively and the GC content amounts to 41.1%.

352

#### 353 **Morphological and molecular diversity**

354 Including the two species described above, our samples from the Nuuk fjord system  
355 yielded a total of 49 morphologically distinct types for which we have photographic



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356 documentation. The majority are from the 125 – 500 µm size fraction. For thirty of  
357 these (illustrated in Supplementary Figs S1–3) no molecular data are available. They  
358 include a mixture of organic-walled monothalamids (Supplementary Fig. S1A,E,I,K)  
359 and agglutinated forms, including flask-shaped ‘saccamminids’ (Supplementary Figs  
360 S1B–D, F–H, L–N; S2A, B, D), many of which cannot be assigned to a genus, as  
361 well as *Pelosina*, *Pelosina*-like and *Crithionina*-like morphotypes (Supplementary  
362 Fig. S3). It should be noted that organic-walled monothalamids, agglutinated  
363 ‘saccamminids’ and *Crithionina*-like morphotypes are distributed in different clades.  
364 Without genetic data, these terms can only be used in an informal sense to indicate  
365 morphology-based groupings; they have no phylogenetic or taxonomic meaning. In  
366 addition, some monothalamids, including *Pelosina* species, can have quite variable  
367 test shapes, which further complicates the recognition of species. In many cases,  
368 therefore, the taxonomic assignment of monothalamid morphotypes belonging to  
369 these groups should be avoided in the absence of genetic data.

370 Sequences were obtained from the remaining 19 morphotypes. In addition to  
371 the two new species (*Bathyallogromia kalaallita* and *Nujappikia idaliae*), these  
372 included single undescribed representatives of five genera (*Bathysiphon*,  
373 *Micrometula*, *Psammophaga*, *Hippocrepinella*, *Crithionina*), and twelve undescribed  
374 monothalamids that cannot be assigned to known genera. Together, these 19  
375 morphotypes represent the following nine monothalamid clades, eight of them  
376 established by Pawlowski et al. (2002b): Clade A (two indeterminate forms illustrated  
377 in Fig. 12A,C), Clade BM (*Bathysiphon* sp. and *Micrometula* sp.; Figs 12B,  
378 Supplementary Fig. S1R, respectively), Clade C (*Bathyallogromia kalaallita* and four  
379 indeterminate forms, Fig. 12D–F; isolate 20304 is not illustrated), Clade D  
380 (*Hippocrepinella* sp., Fig. 13), Clade E (*Psammophaga* sp., Fig. 12G), Clade F  
381 (indeterminate form, Fig. 12H), Clade J (*Crithionina* sp., Fig. 12I), Clade Y  
382 (*Nujappikia idaliae*; four indeterminate forms, Fig. 12J–M), New Clade  
383 (indeterminate attached forms, Fig. 12N,O).

384

## 385 **Molecular phylogeny**

386

387 Clade A (Fig. 1) comprises a large number of undetermined monothalamids including  
388 three Greenland isolates. Two of these form a well-supported group (97% BV) with  
389 an undetermined monothalamid from Antarctica while the third branches separately.  
390 *Limaxia alba*, the first morphologically described species belonging to Clade A  
391 (Holzmann et al., 2022), branches with undetermined monothalamids from Antarctica  
392 (93% BV). Clade A is well supported (91% BV) and branches as sister to Clade BM  
393 (100% BV), which includes two closely related genera, *Bathysiphon* and  
394 *Micrometula*. The specimens from Greenland branch with other undescribed species  
395 of these genera, with strong support; 93% for *Bathysiphon* sp. and 100% for  
396 *Micrometula* sp.. *Bathysiphon flexilis* and *B. argentea* branch at the base of the two  
397 groups, but the branching is not supported.

398 In Clade C (98 % BV, Fig. 1), our new species *Bathyallogromia kalaallita*  
399 (100% BV) branches next to *B. olivacea* from South Georgia fjords. The two species  
400 build a sister clade to *B. weddellensis* from the deep Weddell Sea and  
401 *Bathyallogromia* sp. from the east Greenland shelf. The genus *Bathyallogromia* is  
402 supported by 90% BV. In addition to *Bathyallogromia*, six monothalamids from

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403 Greenland branch within Clade C. Four cluster as sister to *Hippocrepinella alba* from  
404 South Georgia, their branching being strongly supported (99% BV). Two others  
405 cluster with specimens from Antarctica and Patagonia (100% BV).

406 Eleven monothalamids from Greenland identified as *Hippocrepinella* sp.  
407 branch together with other representatives of this genus from Svalbard and Antarctica,  
408 within Clade D (Fig.2). Bootstrap support for this group is weak (74%) and it  
409 branches as sister to two *Hippocrepinella* sp. from Tjärnö, Sweden, and Svalbard  
410 (93% BV). *Hippocrepinella hirudinea* from South Georgia and Antarctica branch at  
411 the base of Clade D, as sister to *Hippocrepinella* sp. The relations between these  
412 different *Hippocrepinella* species are strongly supported (100% BV).

413 The Greenland *Psammophaga* sp. clusters in Clade E (Fig. 2) and builds a  
414 group with *Psammophaga* specimens from Svalbard and western Canada. The group  
415 branches next to the Adriatic species *P. zirconia*, but the branching is not supported.  
416 Two other monothalamids from Greenland branch as sister to *Hemisphaerammina*  
417 *bradyi*, but bootstrap support for this branching is weak (73% BV). All of them form  
418 a strongly supported (96% BV) clade F, which also contains the deep-sea genus  
419 *Vanhoeffenella* and the Antarctic genus *Notodendrodes*.

420 The *Crithionina* sp. sequence from Greenland branches in Clade J (Fig. 3)  
421 next to *C. granum* from Sweden and *C. delacai* from Antarctica and South Georgia  
422 (89% BV). The group is a sister to *Crithionina* sp. from South Georgia and a deep-sea  
423 species, *Capsamina patelliformis*. Clade J is strongly supported (100% BV) and  
424 branches next to Clade Y (86% BV), which includes our new species *Nujappikia*  
425 *idaliae* (89% BV) from Greenland. The closest relative of *N. idaliae* is an  
426 environmental sequence from Sapelo Island, USA. Clade Y also contains *Hilla*  
427 *argentea* from South Georgia as well as nine monothalamid isolates from Greenland,  
428 eight of them divided between three groups and one branching with an environmental  
429 clone from the Japan Sea. Finally, three of the Greenland monothalamid isolates form  
430 a new clade (Fig.3) composed of a sequence obtained from *Astrorhiza limicola* and  
431 several environmental sequences from Antarctica and the Florida Keys, USA. The  
432 new clade is strongly supported (100% BV).

433

## 434 Discussion

435

### 436 Monothalamid biodiversity

437

438 The Nuuk fjords join similar high latitude fjords in Svalbard (Gooday et al., 2005;  
439 Majewski et al., 2005; Sabbatini et al., 2007) and South Georgia (Holzmann et al.,  
440 2022), and the shallow New Harbor area of Antarctica (Gooday et al, 1996;  
441 Pawlowski et al., 2002a), in hosting diverse assemblages of monothalamids. ‘Soft-  
442 walled saccamminids’ with finely agglutinated tests, and to a lesser extent  
443 agglutinated spheres (‘psammophaerids’) and organic-walled morphotypes, represent  
444 the majority of species in the finer fractions (Table 3). Representatives of the mud-  
445 walled genus *Pelosina* are often present in the coarser residues as well as in some  
446 Norwegian fjords (Cedhagen, 1993). Some shallow temperate habitats are inhabited  
447 by similar taxa (Habura et al., 2008; Gooday et al., 2010; Sergeeva et al., 2010). For  
448 example, Sabbatini et al. (2013) illustrated 38 organic-walled, 27 ‘saccamminid’ and  
449 7 ‘psammophaerid’ morphotypes (72 in total) from depths of <50 m in the Adriatic

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450 Sea. *Pelosina* species are sometimes common at upper bathyal depths in lower-  
451 latitude settings (e.g., Levin et al., 1991; Gooday et al., 2009; Cedhagen et al., 2013).  
452 Monothalamid assemblages comparable to those in fjords are also recorded at greater  
453 water depths (~1300 m) around the Håkon Mosby Mud Volcano in the Barents Sea  
454 (Gooday et al., 2013).

455 The monothalamids in our samples have tests with organic, finely agglutinated  
456 or coarsely agglutinated walls and span a wide morphological range. They include  
457 tubular, elongate ovate, and approximately spherical morphotypes, as well as several  
458 low, finely agglutinated domes attached to mineral grains (Fig. 12, 13). Among those  
459 that were sequenced, organic-walled and agglutinated forms are often found in the  
460 same clades. Only a few clades comprise species with similar morphologies. Among  
461 those represented in the present study, Clade BM includes forms with elongate,  
462 basically tubular tests (Fig. 12B, Supplementary Fig. S1R), Clade E includes  
463 *Psammophaga* species and Clade D includes *Hippocrepinella* species. Other clades  
464 encompass contrasting morphotypes; for example, an attached, coarsely agglutinated  
465 dome, an elongate ovate ‘silver saccamminid’, two organic-walled tubes, and the  
466 bottle-shaped *N. idaliae* (Fig. 12 J–M) are all assigned to Clade Y. Similarly, clade C  
467 contains spherical to ovate morphotypes from Greenland in addition to the giant deep-  
468 sea xenophyophores, which are morphologically very different.

469 Our Greenland *Hippocrepinella* species branches as a sister group to the type  
470 species *H. hirudinea* from its type area, South Georgia (Fig. 2). However, the  
471 Greenland specimens display considerable morphological variation. Those that were  
472 sequenced range from a long, tubular specimen (isolate 20332, length = 2.9 mm; Fig.  
473 13A) to a much smaller, barrel-shaped specimen (isolate 20333, length = 0.50 mm;  
474 Fig. 13E). Some have a finely agglutinated, smooth test surface (isolates 20333,  
475 20264) and resemble *H. hirudinea* of Höglund (1947) from Gullmar Fjord. The  
476 barrel-shaped isolate 20333, which also has a smooth surface, is more similar to *H.*  
477 *acuta* of Höglund (1947, Pl. 1, Figs. 17-23) while others are more coarsely  
478 agglutinated (isolates 20332, 20334, 20366). In most of our Greenland specimens, the  
479 test ends bluntly, but in isolate 20264 (length = 2.35 mm; Fig. 13D) one end is  
480 somewhat produced into a poorly defined neck, a feature also seen in *H. acuta* (Pl. 1,  
481 figs 17, 18 in Höglund, 1947). Nevertheless, the eleven sequenced specimens of  
482 *Hippocrepinella* sp. group together in the tree, albeit with a relatively low BV value  
483 of 74% and a pairwise genetic distance between them ranging from 0 to 0.003.

484

## 485 **Biogeography**

486

487 Because monothalamids have relatively few taxonomic characters, phylogenetic data  
488 are particularly important for establishing reliable biogeographic patterns, as well as  
489 for defining species. The present study adds to a growing body of genetic information  
490 for this poorly-documented group of foraminifera. In the first study to address  
491 distributions from mainly shallow-water (depths <100 m) higher latitude sites,  
492 Pawlowski et al. (2008) showed that morphologically similar populations of  
493 monothalamids assigned to *Hippocrepinella hirudinea* and the genera *Gloiogullmia*,  
494 *Micrometula*, and *Psammophaga* were genetically distinct. Our recent study of  
495 monothalamids from South Georgia fjords (Holzmann et al., 2022) established  
496 distributions at a regional scale across parts of the Southern Ocean for  
497 *Psammosphaera* sp., *Micrometula* sp., and a *Crithionina* species. However,

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498 Holzmann et al. (2022) found no evidence for the occurrence outside South Georgia  
499 of two other species they described, *Bathyallogromia olivacea* and *Hilla argentea*.  
500 The current investigation reveals similar regional-scale distributions for a  
501 number of monothalamid species at high northern latitudes. In Clade BM,  
502 *Bathysiphon* sp. is represented in the Nuuk Fjord system and Storfjord in Norway  
503 (pairwise genetic distance 0.002). It is genetically distinct from *B. argenteus* and *B.*  
504 *flexilis* of Höglund (1947) from the Gullmar Fjord, and its relatively short, wide test is  
505 different from the long, thin test of *B. minutus*, another species found by Höglund, for  
506 which no molecular data are available. The Nuuk species of *Micrometula* sp., also  
507 located in Clade BM, clusters with sequenced specimens from Svalbard (0.004 –  
508 0.007) and near Vancouver in western Canada (0.003 – 0.013). In Clade E, isolates of  
509 the widely-distributed genus *Psammophaga* sp. are close to specimens from Svalbard  
510 (0.001 – 0.002) and eastern Canada (0.001 – 0.003). On the other hand, the Nuuk  
511 *Bathysiphon* sp. clusters (BV 93%) with Antarctic isolates from McMurdo Sound,  
512 Adelaide Island off the Peninsula, and King George Island in the South Shetlands  
513 group, in addition to sequences from Svalbard (pairwise distance 0.001 – 0.003). The  
514 *Bathysiphon* species from Nuuk is represented by a single sequenced specimen with  
515 one transition in the variable region 49/e (Pawlowski and Lecroq 2010) that  
516 distinguish it from its Antarctic counterparts. Based on this single Greenland  
517 specimen and our single gene analysis it is difficult to decide whether these Northern  
518 and Southern Hemisphere *Bathysiphon* populations represent the same species or  
519 different species. A multi-gene analysis will be necessary in order to resolve this  
520 problem. Similarly, the Nuuk *Hippocrepinella* sp. (Clade D) clusters with two  
521 sequences from New Harbor in McMurdo Sound, Antarctica (pairwise distance 0.001  
522 – 0.004), as well as with one sequence from Svalbard (0 – 0.001). The sequences of  
523 the Antarctic *Hippocrepinella* sp. are distinguished by a transition in the variable  
524 region 43/e (Pawlowski and Lecroq 2010) from the Northern hemisphere  
525 *Hippocrepinella*.

526 Our two newly described species are currently known only from the Nuuk  
527 fjord system. In Clade C, *Bathyallogromia kalaallita* is closely related to *B. olivacea*  
528 from comparable settings in South Georgia fjords (Holzmann et al., 2022), and more  
529 distantly to the type species *B. weddellensis*, from much deeper water in the Weddell  
530 Sea (Gooday et al. 2004). The pairwise distance ranges from 0.001 – 0.002 and 0.021  
531 – 0.022, respectively. A single sequence of an undescribed *Bathyallogromia* from the  
532 East Greenland Shelf is closely related to *B. weddellensis* (0.003 – 0.004). In Clade Y,  
533 the sequence of an environmental clone (Sap 10) from Sapelo Island, USA is the  
534 closest relative to *Nujappikia* with a pairwise genetic distance ranging from 0.047 to  
535 0.048, compared to between 0 and 0.003 within *N. idaliae*. In Clade J, the loosely  
536 agglutinated *Crithionina* species from Nuuk is morphologically similar to the  
537 Northern hemisphere species *C. granum* (Goës, 1894) and also to the Southern  
538 hemisphere species *C. delacai* (Gooday et al., 1995). It is closely related genetically  
539 to both species but is not identical (pairwise distance ranging from 0.155 to 0.178).

540  
541

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548

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556 Editing, Resources, Funding acquisition.

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#### 558 **Author contributions**

559 Author contributions AJG, MH, TC, and JP collected and picked foraminifera from  
560 the Greenland samples. MH and ES were responsible for DNA extraction,  
561 amplification and sequencing; MH carried out the phylogenetic analysis, and wrote  
562 the genetic parts of the text, with contributions from JP. The remainder of the text was  
563 written by AJG, with edits from MH, JP and TC. AJG was responsible for the  
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570 **Data availability.** All data generated and analysed during this study are included in  
571 this published article. Type specimens are deposited in the Natural History Museum,  
572 London.

573

574

575

#### 575 **Figure captions**

576

577 **Fig.1.** PhyML phylogenetic tree based on the 3'end fragment of the SSU rRNA gene,  
578 showing the evolutionary relationships of 68 monothalamid foraminiferal sequences  
579 belonging to Clades A, BM, C. Taxa marked in bold indicate those for which  
580 sequences were acquired for the present study. The tree is unrooted. Specimens are  
581 identified by their isolate numbers (1st) and accession numbers (2nd). Numbers in  
582 brackets refer to clones. Numbers at nodes indicate bootstrap values (BV). Only  
583 BV>70% are shown.

584

585 **Fig.2.** PhyML phylogenetic tree based on the 3'end fragment of the SSU rRNA gene,  
586 showing the evolutionary relationships of 50 monothalamid foraminiferal sequences  
587 belonging to Clades D, E, F. Taxa marked in bold indicate those for which sequences  
588 were acquired for the present study. The tree is unrooted. Specimens are identified by  
589 their isolate numbers (1st) and accession numbers (2nd). Numbers at nodes indicate  
590 bootstrap values (BV). Only BV>70% are shown.

591

592 **Fig.3.** PhyML phylogenetic tree based on the 3'end fragment of the SSU rRNA gene,  
593 showing the evolutionary relationships of 42 monothalamid foraminiferal sequences

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594 belonging to Clades J, Y and a new Clade. Taxa marked in bold indicate those for  
595 which sequences were acquired for the present study. The tree is unrooted. Specimens  
596 are identified by their isolate numbers (1st) and accession numbers (2nd). Numbers in  
597 brackets refer to clones. Numbers at nodes indicate bootstrap values (BV). Only  
598 BV>70% are shown.  
599

600 **Figure 4.** *Nujappikia idaliae* gen. & sp. nov. A–D. Unfixed specimens photographed  
601 in July 2018, soon after collection. E, F. Specimens fixed in formalin, photographed  
602 in April 2019. Scale bars in E and F = 0.50 mm.  
603

604 **Figure 5.** *Nujappikia idaliae* gen. & sp. nov.; type specimens, photographed in  
605 glycerol in April 2019. A. Holotype, NHMUK PM ZF 9946. B. Paratype 1, NHMUK  
606 PM ZF 9947. C. Paratype 2, NHMUK PM ZF 9948. D. Paratype 3, NHMUK PM ZF  
607 9949. E. Paratype 4, NHMUK PM ZF 9950. F. Paratype 5, NHMUK PM ZF 9951.  
608 G. Paratype 6, NHMUK PM ZF 9952. H. Paratype 7, NHMUK PM ZF 9953. Scale  
609 bars = 250 µm.  
610

611 **Figure 6.** *Nujappikia idaliae* gen. & sp. nov.; (A, C, E, G, I) Dark field views of  
612 specimens photographed in LifeGuard in February 2019. (B, D, F, H, J) Light field  
613 views of the same specimens. Scale bars = 250 µm.  
614

615 **Figure 7.** *Nujappikia idaliae* gen. & sp. nov. (A). Unusually shaped specimen. (B–D).  
616 Apertural structures. (B) Paratype 5, NHMUK PM ZF 9951. (C) Paratype 2, NHMUK  
617 PM ZF 9948. (D). Paratype 6, NHMUK PM ZF 9952. (E) Abapertural end of  
618 Paratype 4, NHMUK PM ZF 9950. (F). Abapertural end of Paratype 7, NHMUK PM  
619 ZF 9953. Scale bars = 250 µm (A), 100 µm (B–F)  
620

621 **Figure 8.** *Bathyallogromia kalaallita* sp. nov. (A, B) Unfixed specimens  
622 photographed in July 2018, soon after collection. (C) Specimens fixed in formalin,  
623 photographed in April 2019. (D) Specimens photographed in May 2022, by which  
624 time the cell body had shrunk, leaving a clear space between it and the cell wall. Scale  
625 bars = 1.0 mm  
626

627 **Figure 9.** *Bathyallogromia kalaallita* sp. nov. Corresponding views of three  
628 specimens photographed in LifeGuard in February 2019 under different lighting  
629 conditions. Scale bars = 250 µm.  
630

631 **Figure 10.** *Bathyallogromia kalaallita* sp. nov. Specimens photographed in April  
632 2019 using transmitted light and either with (A – E) or without (F – H) Nomarski  
633 interference optics. (A) Small specimen with well-developed peduncle, peduncular  
634 sheath and large nucleus. (B) Detail of apertural region and nucleus. (C) Ovate  
635 specimen. (D) Detail of apertural region. (E) Large almost spherical specimen. (F)  
636 Ovate specimen. (G) More elongate ovate specimen. (H) Detail of apertural region.  
637 Scale bars = 250 µm.  
638

639 **Figure 11.** *Bathyallogromia kalaallita* sp. nov. Type specimens, photographed in  
640 May 2022 when the cell body had shrunk, revealing good views of the peduncle. (A)  
641 Holotype NHMUK PM ZF 9954. (B) Holotype, detail of apertural region. (C)

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642 Paratype 1 NHMUK PM ZF xxxx. (D) Paratype 1, detail of apertural region. (E)  
643 Paratype 2 NHMUK PM ZF 9956; the test wall has been distorted in the preservative.  
644 (F) Paratype 2, detail of apertural region. (G) Paratype 3 NHMUK PM ZF 9957. (H)  
645 Paratype 3, detail of apertural region. Scale bars = 250  $\mu\text{m}$  (A, C, E, G), 100  $\mu\text{m}$  (B,  
646 D, E, G).

647

648 **Figure 12.** Sequenced specimens that can only be identified to genus level or are  
649 indeterminate. (A) Indeterminate, finely agglutinated monothalamid, St. 2B; isolate  
650 20261, Clade A. (B) *Bathysiphon* sp., St. 12; isolate 20435, Clade BM. (C)  
651 indetermined monothalamid, St. 13; isolate 20296 – 96, Clade A. (D) Ovate  
652 saccamminid, St. 2B; isolate 20256, Clade C. (E) Small saccamminid with apertural  
653 neck, St. 2B; isolate 20246, Clade C. (F) Ovate, organic-walled test with brownish  
654 contents, St. 12; isolate 20403, Clade C. (G) *Psammophaga* sp., St. 15; isolate 20371,  
655 Clade E. (H) Small organic-walled allogomiid, St. 16; isolate 20351, Clade F. (I)  
656 *Crithionina* sp., St. 11; isolate 20399, Clade J. (J) Coarsely agglutinated attached test,  
657 St. 13; isolate 20290, Clade Y. (K) Silver saccamminid, St. 5; isolate 20321, Clade Y.  
658 (L) *Nemogullmia* sp., St. 5; isolate 19859; Clade Y. (M) Elongate organic-walled test  
659 with what appear to be terminal apertures, St. 16; isolate 20350, Clade Y. (N) Whitish  
660 dome attached to mineral grain, St. 13; isolate 20285, New Clade. (O) Similar dome,  
661 St. 13; isolate 20286, New Clade. Scale bars = 250  $\mu\text{m}$  except where indicated  
662 otherwise.

663

664 **Figure 13.** *Hippocrepinella* sp. (A–E) Sequenced specimens, photographed in  
665 RNAlater in Geneva. Note that C and particularly E are much smaller than other  
666 specimens. (A) Isolate 20332, St. 8. (B) Isolate 20334, St. 7. (C) Isolate 20366, St.  
667 15. (D) Isolate 20264, St. 13. (E) Isolate 20333, St. 7. (F, G) Specimens fixed in  
668 formalin that were not sequenced, photographed in Southampton. Scale bars = 0.50  
669 mm.

670

671

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**Table 1.** Sampling sites for the new species in Greenland, with corresponding DNA isolate numbers and species names. Undescribed isolates from Greenland that are included in the trees are also listed.

Sampling location	Latitude (N)	Longitude (W)	Depth (m)	DNA Isolates
St 2, Itissoq embayment of Qôrnup Suvdlua branch	64°15.347'	51°14.532'	111	Indeterminate Clade A: 20261, Indeterminate Clade C: 20246, 20256
St. 3. Qôrgut fjord	64°14.957'	50° 52.196'	58	<i>Bathyallogromia kalaallita</i> Unsequenced silver saccamminid, Fig. S2D
St 4, Oorgut embayment of Ûmánap Suvdlua branch	64°15.039'	50°53.467'	118	<i>Hippocrepinella indivisa</i> unsequenced: Fig. S1H <i>Micrometula</i> sp.: 20326 Unsequenced specimens: Fig. S1G,L,P Unsequenced silver saccamminid, Fig. S2B
St 5, South of Uumanaq island	64°27.600'	50°48.856'	240	Indeterminate Clade Y: 19859 Indeterminate Clade C: 20304
St. 6, Qôrnup assua channel	64°43.916'	50°26.189'	521	Unsequenced spindle: Fig. S1J Unsequenced organic-walled form: Fig. S1E
St. 7 Qôrnup assua channel	64°43.784'	50°23.356'	274	<i>Hippocrepinella</i> sp., 20333, 20334
St. 8 Qôrnup assua channel	64°43.750'	50°24.634'	195	<i>Hippocrepinella</i> sp., 20332
St. 11 Kobbefjord	64°09.680'	51°25.849'	150	<i>Crithonina</i> sp. Clade J: 20399
St 12, Kobbefjord	64°08.733'	51°23.658'	43	<i>Bathysiphon</i> sp. Clade BM: 20435 Indeterminate Clade C: 20403
St 13, Kobbefjord	64°08.580'	51°23.377'	22	<i>Hippocrepinella</i> sp., Clade D 20264 Indeterminate Clade A: 20296 Indeterminate Clade D: 20264 Indeterminate Clade Y: 20290 Indeterminate Clade Y: 20403 Indeterminate New Clade: 20285, 20286
St 14, Inner part of Lysefjord	64°12.040'	50°20.948'	212	<i>Pelosina</i> sp.: Fig. S3B
St. 15, Inner part of Lysefjord	64°12.639'	50°16.074'	95	<i>Nujappikia idaliae</i> <i>Hippocrepinella</i> sp. Clade D: 20366 <i>Psammophaga</i> sp. Clade E: 20371
St. 16, Inner part of Lysefjord	64°12.656'	050°15.751'	61	<i>Nujappikia idaliae</i> Indeterminate Clade F: 20351 Indeterminate Clade Y: 20350

**Table 2.** Isolate and GenBank accession numbers, and locality data for sequenced monothalamid specimens. Taxa shown in bold indicate those analysed for the current paper.

Taxa	Isolate	Accession number	Sampling site	Additional remarks
<b>Clade A</b>				
<i>Limaxia alba</i>	21252	OM422947	UK, South Georgia, Fortuna Bay	
<i>Limaxia alba</i>	21300	OM422948	UK, South Georgia, Cumberland Bay	
undet. monothalamid	1212	AJ307744	Antarctica, New Harbor	<i>Cylindrogullmia</i> -like
undet. monothalamid	2226	AJ514858	Antarctica, New Harbor	elongate
undet. monothalamid <sup>o</sup>	3022	OM422851, ON053330	Antarctica, New Harbor	<i>Cylindrogullmia</i> -like
undet. monothalamid	3132	HE998678	Antarctica, McMurdo	coarsely agglutinated, attached
undet. monothalamid	3133	OM422938	Antarctica, McMurdo	coarsely agglutinated, attached
undet. monothalamid	3523	OM422939	Weddell Sea, abyssal	Allogromia like
undet. monothalamid	3552	OL772090	Weddell Sea, abyssal	Allogromia like
<b>undet. monothalamid*</b>	20261		Greenland, Nuuk Fjord, St.2B	elongate, finely agglutinated
<b>undet. monothalamid*</b>	20295		Greenland, Nuuk Fjord, St.13	elongate, sticky, soft walled
<b>undet. monothalamid*</b>	20296		Greenland, Nuuk Fjord, St.13	elongate, sticky, soft walled
<b>Clade BM</b>				
<i>Bathysiphon argenteus</i>	1780	AJ514836	Sweden, Gullmar Fjord	
<i>Bathysiphon flexilis</i>	1784	AJ514837	Sweden, Gullmar Fjord	
<i>Bathysiphon</i> sp. <sup>o</sup>	5324	ON053431, ON053432	Norway, Storfjord	
<i>Bathysiphon</i> sp. <sup>o</sup>	7517	ON053433	Antarctica, McMurdo	
<i>Bathysiphon</i> sp.	8029	ON053440	Antarctica, King George Island	
<i>Bathysiphon</i> sp.	8157	ON053441	Antarctica, King George Island	
<i>Bathysiphon</i> sp. <sup>o</sup>	17432	ON053434, ON053435	Antarctica, Adelaide Island	
<b><i>Bathysiphon</i> sp.</b>	20435	ON053442	Greenland, Nuuk Fjord, St.12	
<i>Micrometula</i> sp.	2880	ON053443	Norway, Svalbard	
<i>Micrometula</i> sp.	4518	ON053444	Norway, Svalbard, Kongsfjorden	
<i>Micrometula</i> sp.	4683	ON053445	Norway, Svalbard, Kongsfjorden	
<i>Micrometula</i> sp. <sup>o</sup>	4684	ON053436	Norway, Svalbard, Kongsfjorden	
<i>Micrometula</i> sp. <sup>o</sup>	4747	ON053437	Norway, Svalbard, Adventfjorden	
<i>Micrometula</i> sp.	4888	ON053446	Norway, Svalbard, Adventfjorden	
<i>Micrometula</i> sp. <sup>o</sup>	5053	ON053438	Canada, Vancouver, Howe Sound	
<i>Micrometula</i> sp. <sup>o</sup>	5082	ON053439	Canada, Vancouver, Howe Sound	
<b><i>Micrometula</i> sp.</b>	20326	ON053447	Greenland, Nuuk Fjord, St.4	
<b>Clade C</b>				
<b><i>Bathyallogromia kalaallita</i></b>	19861	ON053401	Greenland, Nuuk Fjord, St.3	
<b><i>Bathyallogromia kalaallita</i></b>	19862	ON053402	Greenland, Nuuk Fjord, St.3	
<b><i>Bathyallogromia kalaallita</i></b>	19863	ON053403	Greenland, Nuuk Fjord, St.3	
<i>Bathyallogromia olivacea</i>	21323	OM422961	UK, South Georgia, Stromness Bay	
<i>Bathyallogromia olivacea</i>	21324	OM422962	UK, South Georgia, Stromness Bay	
<i>Bathyallogromia olivacea</i>	21325	OM422963	UK, South Georgia, Stromness Bay	
<i>Bathyallogromia olivacea</i>	21326	OM422964	UK, South Georgia, Stromness Bay	
<i>Bathyallogromia</i> sp. <sup>o</sup>	5396	OM422905	Denmark, East Greenland Shelf	
<i>Bathyallogromia weddellensis</i> <sup>o</sup>	3334	OM422904	Weddell Sea, abyssal	
<i>Bathyallogromia weddellensis</i> <sup>o</sup>	3338	FR875101	Weddell Sea, abyssal	
<i>Bathyallogromia weddellensis</i> <sup>o</sup>	3339	FR875100	Weddell Sea, abyssal	
<i>Bathyallogromia weddellensis</i> <sup>o</sup>	3553	FR875102	Weddell Sea, abyssal	
<i>Gloioigullmia eurystoma</i>	526	AJ317981	Sweden, Tjaerno	
<i>Gloioigullmia eurystoma</i> <sup>o</sup>	2882	LT796823	Norway, Svalbard	
<i>Hippocrepina indivisa</i> <sup>o</sup>	17534	OM422906	Chile, Patagonia, Beagle Channel	
<i>Hippocrepinella alba</i>	20870	OM422966	UK, South Georgia, Fortuna Bay	
<i>Hippocrepinella alba</i>	20873	OM422968	UK, South Georgia, Fortuna Bay	
<i>Leptamma grisea</i> <sup>o</sup>	8352	FM209503	Weddell Sea, abyssal	
<i>Leptamma grisea</i> <sup>o</sup>	8353	FM209505	Weddell Sea, abyssal	
<i>Marsipella</i> sp.	4074	FR875147	France, Mediterranean Sea	
<i>Marsipella</i> sp.	4076	FR875148	France, Mediterranean Sea	
<i>Pilulina argentea</i>	2837	OL873224	Norway, Svalbard	
<i>Pilulina argentea</i>	2841	OL873225	Norway, Svalbard	
<i>Techinitella</i> sp.	R5	FR754396	Norway, Oslo Fjord	
<i>Toxisarcon alba</i>	WC18H	AJ307750	UK, Scotland, Loch Linnhe	
<i>Toxisarcon synsuicida</i>	1370	AJ315955	Sweden, Tjaerno	
<i>Toxisarcon taimyr</i>	14533	KF931124	Russia, Kara Sea	
undet.monothalamid	7702	ON053411	Chile, Patagonia, Beagle Channel	<i>Phainogullmia</i> -like
undet.monothalamid <sup>o</sup>	14322	ON053398	Antarctica, New Harbor	
undet.monothalamid <sup>o</sup>	14323	ON053399	Antarctica, New Harbor	
<b>undet. monothalamid*</b>	20246		Greenland, Nuuk Fjord, St.2B	oval, apertural neck, finely agglutinated
<b>undet. monothalamid*</b>	20256		Greenland, Nuuk Fjord, St.2B	elongate, agglutinated
<b>undet. monothalamid*</b>	20304		Greenland, Nuuk Fjord, St.5	elongate
<b>undet. monothalamid*</b>	20341		Greenland, Nuuk Fjord, St.7	oval, finely agglutinated
<b>undet. monothalamid*</b>	20393		Greenland, Nuuk Fjord, St.13	oval, finely agglutinated
<b>undet. monothalamid*</b>	20403		Greenland, Nuuk Fjord, St.12	oval, brownish, soft walled
<b>Clade D</b>				
<i>Hippocrepinella hirudinea</i>	7863	LN873692	Antarctica, King George Island	
<i>Hippocrepinella hirudinea</i>	14310	LN873683	Antarctica, New Harbor	
<i>Hippocrepinella hirudinea</i>	21241	OM422932	UK, South Georgia, Stromness Bay	
<i>Hippocrepinella hirudinea</i>	21241	OM422931	UK, South Georgia, Stromness Bay	
<i>Hippocrepinella</i> sp.	530	AJ307765	Sweden, Tjaerno	
<i>Hippocrepinella</i> sp.	2857	OM422929	Norway, Svalbard	

<i>Hippocrepinella</i> sp.	4821	OM422893	Norway, Svalbard	
<i>Hippocrepinella</i> sp.	14308	LN873677	Antarctica, New Harbor	
<i>Hippocrepinella</i> sp.	14309	LN873680	Antarctica, New Harbor	
<b>Hippocrepinella</b> sp.	20264	ON053393	Greenland, Nuuk Fjord, St.13	
<b>Hippocrepinella</b> sp.	20266	ON053394	Greenland, Nuuk Fjord, St.13	
<b>Hippocrepinella</b> sp.	20267	ON053395	Greenland, Nuuk Fjord, St.13	
<b>Hippocrepinella</b> sp.	20332	ON053396	Greenland, Nuuk Fjord, St.8	
<b>Hippocrepinella</b> sp.	20333	ON053387	Greenland, Nuuk Fjord, St.7	
<b>Hippocrepinella</b> sp.	20334	ON053397	Greenland, Nuuk Fjord, St.7	
<b>Hippocrepinella</b> sp.	20335	ON053388	Greenland, Nuuk Fjord, St.7	
<b>Hippocrepinella</b> sp.	20336	ON053389	Greenland, Nuuk Fjord, St.7	
<b>Hippocrepinella</b> sp.	20366	ON053390	Greenland, Nuuk Fjord, St.15	
<b>Hippocrepinella</b> sp.	20367	ON053391	Greenland, Nuuk Fjord, St.15	
<b>Hippocrepinella</b> sp.	20368	ON053392	Greenland, Nuuk Fjord, St.15	
<b>Clade E</b>				
<i>Nellya rugosa</i>	10150	FN995336	Ukraine, Sevastopol Shelf, Balaklava Bay	
<i>Nellya rugosa</i>	10151	FN995333	Ukraine, Sevastopol Shelf, Balaklava Bay	
<i>Psammophaga crystallifera</i>	1786	FN995294	Sweden, Gullmar Fjord	
<i>Psammophaga crystallifera</i>	2361	FN995293	Sweden, Tjaerno	
<i>Psammophaga fuegia</i>	17381	KU313688	Chile, Patagonia, Beagle Channel	
<i>Psammophaga fuegia</i>	17510	KU313694	Chile, Patagonia, Beagle Channel	
<i>Psammophaga magnetica</i>	2976	FN995274	Antarctica, Mc Murdo	
<i>Psammophaga magnetica</i>	3184	FN995272	Antarctica, Mc Murdo, Gneiss Point	
<i>Psammophaga sapela</i>	c2	JX645726	USA, Sapelo Island	
<i>Psammophaga sapela</i>	c5	JX645725	USA, Sapelo Island	
<i>Psammophaga</i> sp.	10285	ON053376	Canada, Halifax, Chezzetcook Inlet	
<i>Psammophaga</i> sp.	19260	ON053377	Norway, Svalbard	
<i>Psammophaga</i> sp.	19261	ON053378	Norway, Svalbard	
<i>Psammophaga</i> sp.	19262	ON053379	Norway, Svalbard	
<i>Psammophaga</i> sp.	19263	ON053380	Norway, Svalbard	
<b>Psammophaga</b> sp.	20369	ON053327	Greenland, Nuuk Fjord, St.15	
<b>Psammophaga</b> sp.	20370	ON053328	Greenland, Nuuk Fjord, St.15	
<b>Psammophaga</b> sp.	20371	ON053329	Greenland, Nuuk Fjord, St.15	
<i>Psammophaga zirconia</i>	9495	LN886765	Ukraine, Sevastopol Shelf, Omega Bay	
<i>Psammophaga zirconia</i>	18412	LN886768	Italy, Adriatic Sea	
<i>Vellaria zucchelli</i>	3792	FN995311	Antarctica, Terranova Bay	
<i>Vellaria zucchelli</i>	3804	FN995310	Antarctica, Terranova Bay	
<b>Clade F</b>				
<i>Hemisphaerammina bradyi</i>	1439	AJ311216	France, Mediterranean Sea, Banyuls	
<i>Notodendrodes antarcticos</i>	1082	AJ311213	Antarctica, New Harbor	
<i>Notodendrodes hyalinosphaira</i>	1225	AJ311214	Antarctica, New Harbor	
<i>Notodendrodes hyalinosphaira</i>	1921	AJ514860	Antarctica, New Harbor	
<b>undet. monothalamid*</b>	20351		Greenland, Nuuk Fjord, St.16	rounded, soft walled
<b>undet. monothalamid*</b>	20352		Greenland, Nuuk Fjord, St.16	rounded, soft walled
<i>Vanhoeffenella dilatata</i>	3256	MF457695	Weddell Sea, abyssal	
<i>Vanhoeffenella dilatata</i>	3291	MF457696	Weddell Sea, abyssal	
<b>Clade J</b>				
<i>Capsamina patelliformis</i> <sup>o</sup>	10069	FJ646885	Portugal, NE Atlantic, Nazare Canyon	
<i>Capsamina patelliformis</i> <sup>o</sup>	10070	FJ646888	Portugal, NE Atlantic, Nazare Canyon	
<i>Crithionina delacai</i>	189	AJ317988	Antarctica, Mc Murdo	
<i>Crithionina delacai</i>	21390	OM422882	UK, South Georgia, Stromness Bay	
<i>Crithionina granum</i>	156	AJ317987	Sweden, Kosterfjord	
<b>Crithionina</b> sp.	20399	ON053450	Greenland, Nuuk Fjord, St.11	
<i>Crithionina</i> sp.	21354	OM422880	UK, South Georgia, Cumberland Bay	
<i>Crithionina</i> sp.	21355	OM422881	UK, South Georgia, Cumberland Bay	
<b>Clade Y</b>				
environmental clone	808-34	JN003669	Japan, Sagami Bay, 1453m depth	
environmental clone	Sap10	EU213230	USA, Sapelo Island	
<i>Hilla argentea</i>	21333	OM422871	UK, South Georgia, Cumberland Bay	
<i>Hilla argentea</i>	21334	OM422872	UK, South Georgia, Cumberland Bay	
<b>Nujappikia idaliensis</b>	19842	ON053404	Greenland, Nuuk Fjord, St.16	
<b>Nujappikia idaliensis</b>	19843	ON053405	Greenland, Nuuk Fjord, St.16	
<b>Nujappikia idaliensis</b>	19844	ON053406	Greenland, Nuuk Fjord, St.16	
<b>Nujappikia idaliensis</b>	19847	ON053407	Greenland, Nuuk Fjord, St.16	
<b>Nujappikia idaliensis</b>	19848	ON053408	Greenland, Nuuk Fjord, St.16	
<b>Nujappikia idaliensis</b>	19850	ON053409	Greenland, Nuuk Fjord, St.16	
undet. monothalamid	2091	OM422864	Antarctica	finely agglutinated, flask like
undet. monothalamid	2861	ON053400	Norway, Svalbard	<i>Cylindrogullmia</i> -like
undet. monothalamid <sup>o</sup>	9296	OM422884	Japan, Yokosuka	yellow-green colour
undet. monothalamid <sup>o</sup>	9300	OM422885	Japan, Yokosuka	yellow-green colour
undet. monothalamid <sup>o</sup>	9323	OM422886	Japan, Yokosuka	yellow-green colour
<b>undet. monothalamid*</b>	19857		Greenland, Nuuk Fjord, St.5	<i>Nemogullmia</i> -like, yellow
<b>undet. monothalamid*</b>	19859		Greenland, Nuuk Fjord, St.5	<i>Nemogullmia</i> -like, yellow
<b>undet. monothalamid*</b>	20257		Greenland, Nuuk Fjord, St.2B	finely agglutinated
<b>undet. monothalamid*</b>	20290		Greenland, Nuuk Fjord, St.13	coarsely agglutinated, attached
<b>undet. monothalamid*</b>	20302		Greenland, Nuuk Fjord, St.3	finely agglutinated
<b>undet. monothalamid*</b>	20320		Greenland, Nuuk Fjord, St.5	finely agglutinated, silvery

<b>undet. monothalamid*</b>	20321		Greenland, Nuuk Fjord, St.5	finely agglutinated, silvery
<b>undet. monothalamid*</b>	20348		Greenland, Nuuk Fjord, St.16	elongate, finely gglutinated
<b>undet. monothalamid*</b>	20350		Greenland, Nuuk Fjord, St.16	elongate, finely gglutinated
undet. monothalamid	20868	OM422869	UK, South Georgia, Cumberland Bay	finely agglutinated, flask like
<b><u>New Clade</u></b>				
<i>Astrorhiza limicola</i>	n.a.	AF411217	Antarctica	
environmental clone	IC28	AY452798	Antarctica	
environmental clone	IC36	AY452797	Antarctica	
environmental clone	Keys16	EU213206	USA, Florida Keys	
environmental clone	Keys37	EU213205	USA, Florida Keys	
environmental clone	Keys60	EU213204	USA, Florida Keys	
<b>undet. monothalamid*</b>	20285		Greenland, Nuuk Fjord, St.13	white, agglutinated, hemisphaerical, attached
<b>undet. monothalamid*</b>	20286		Greenland, Nuuk Fjord, St.13	white, agglutinated, hemisphaerical, attached
<b>undet. monothalamid*</b>	20423		Greenland, Nuuk Fjord, St.13	white, agglutinated, hemisphaerical, attached

\* undetermined monothalamid sequences obtained for this study will be submitted to GenBank if they can be assigned to genera or species

° PCR products have been cloned prior to sequencing

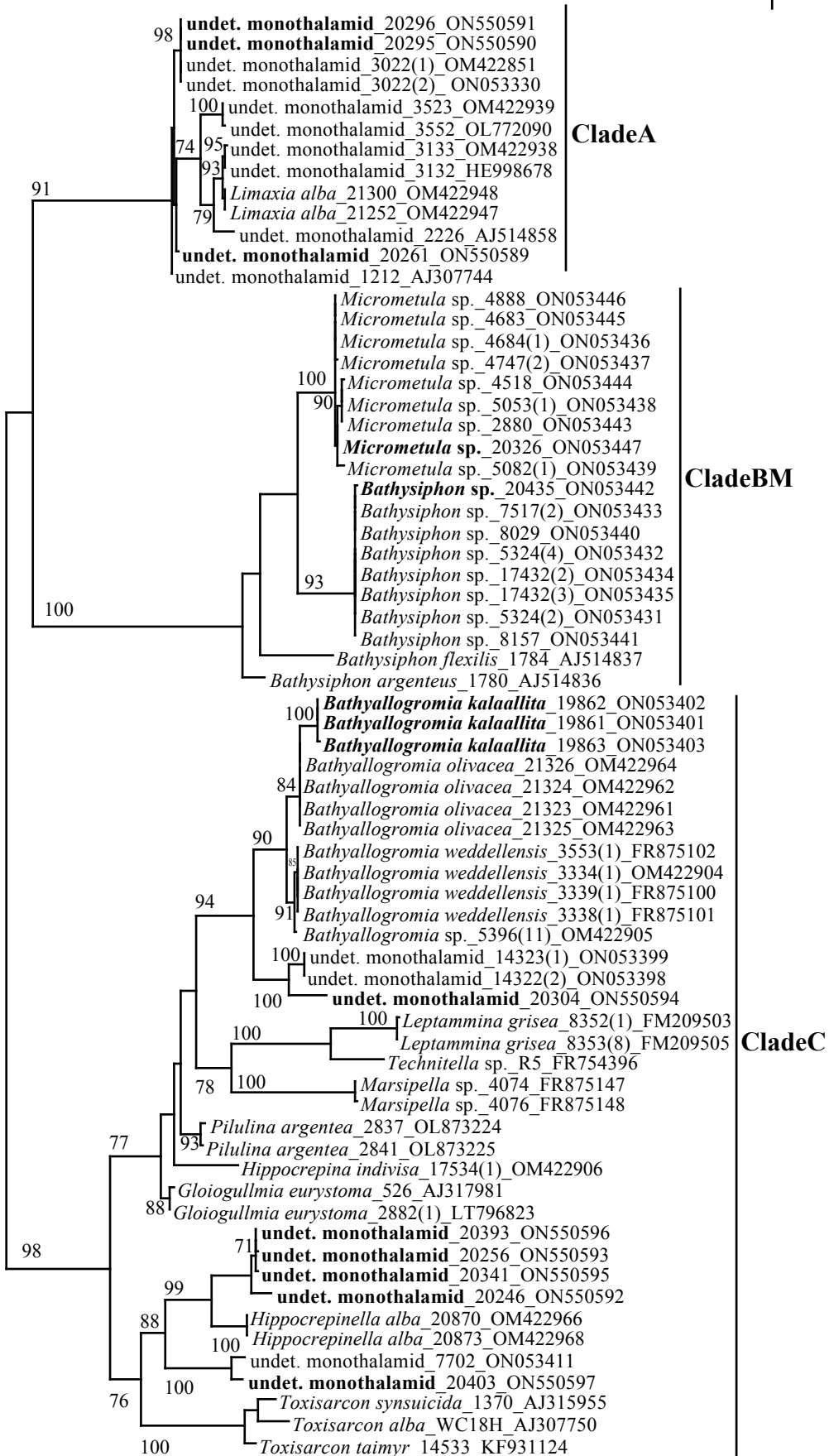
**Table 3.** Taxonomic composition of monothalamid assemblages in Nuuk and Svalbard Fjords and the New Harbor area of McMurdo Sound, Antarctica.

	Nuuk	Svalbard	Svalbard: Kongsfjord, Isfjord Adventfjord	Svalbard Tempelfjord	New Harbor
<b>Depth (m)</b>	22–521	26–313 <sup>2</sup>	6–345	26–104	<30 m
<b>Size fractions (µm)</b>	125–250, 250–500, >500	125–250, 250–500 >500	125–500 >500	63–125, 125–300, >500	125–400, 400–1000 >1000
<b>Methods</b>	Morphology & Genetics	Morphology	Morphology	Morphology	Genetics
<b>Reference</b>	This study	Gooday et al. (2005)	Majewski et al. (2005)	Sabbatini et al. (2007)	Pawłowski et al. (2002)
Organic walled 'Saccamminids'	14 17	13 23	10 12	23 34	6 8
Spheres and domes	5	10	3	7	6
<i>Pelosina</i> sp.	8	6	1	-	2
Tubes <sup>1</sup>	3	3	3	-	2
<i>Hippocrepina</i>	-	1	5	-	-
<i>Hyperammina</i>	1	3	2	-	-
<i>Astrorhiza</i>	-	1	-	-	-
Others	1	-	-	-	5
<b>TOTAL</b>	<b>49</b>	<b>60</b>	<b>36</b>	<b>64</b>	<b>27</b>

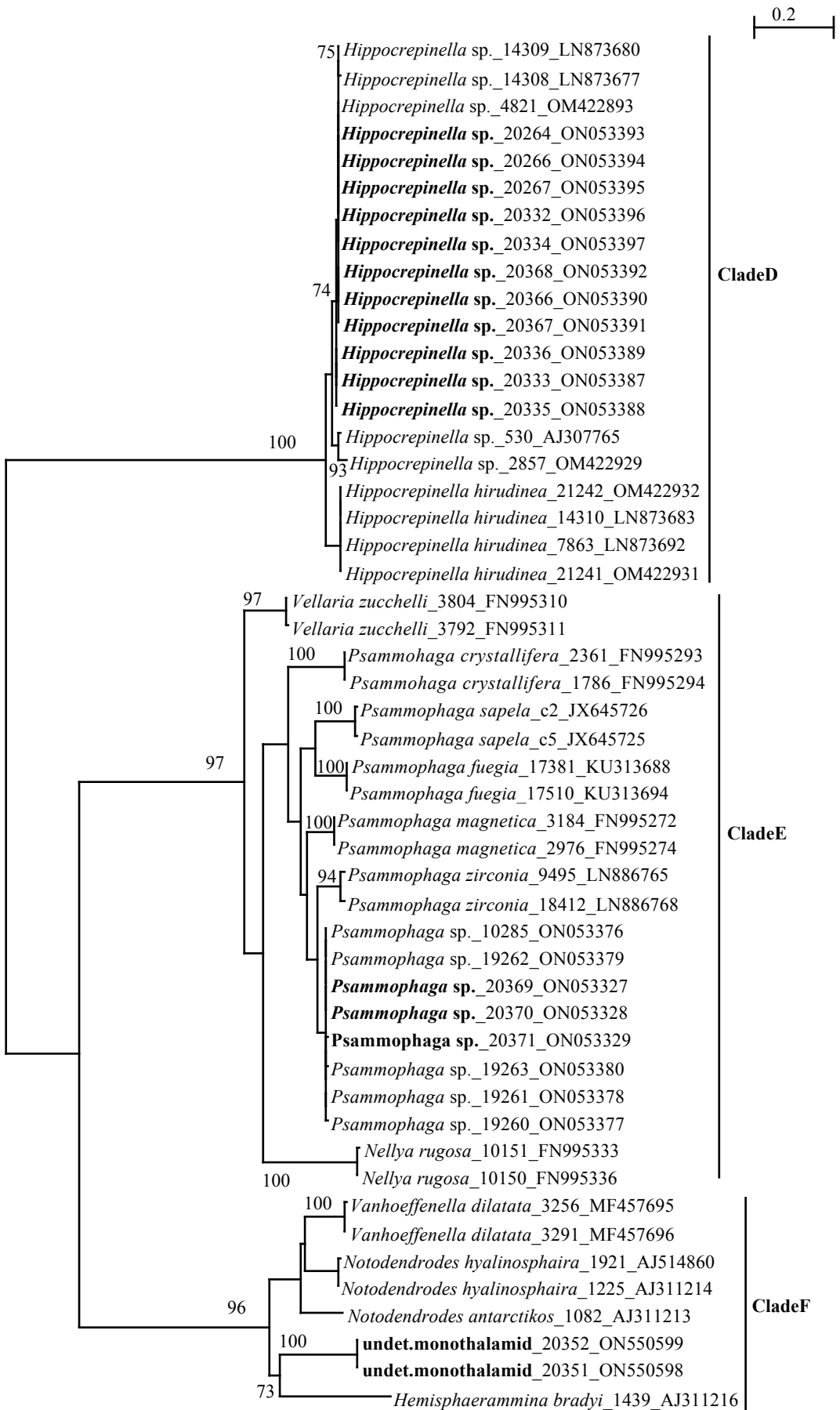
<sup>1</sup>Including *Hippocrepinella hirudinea*

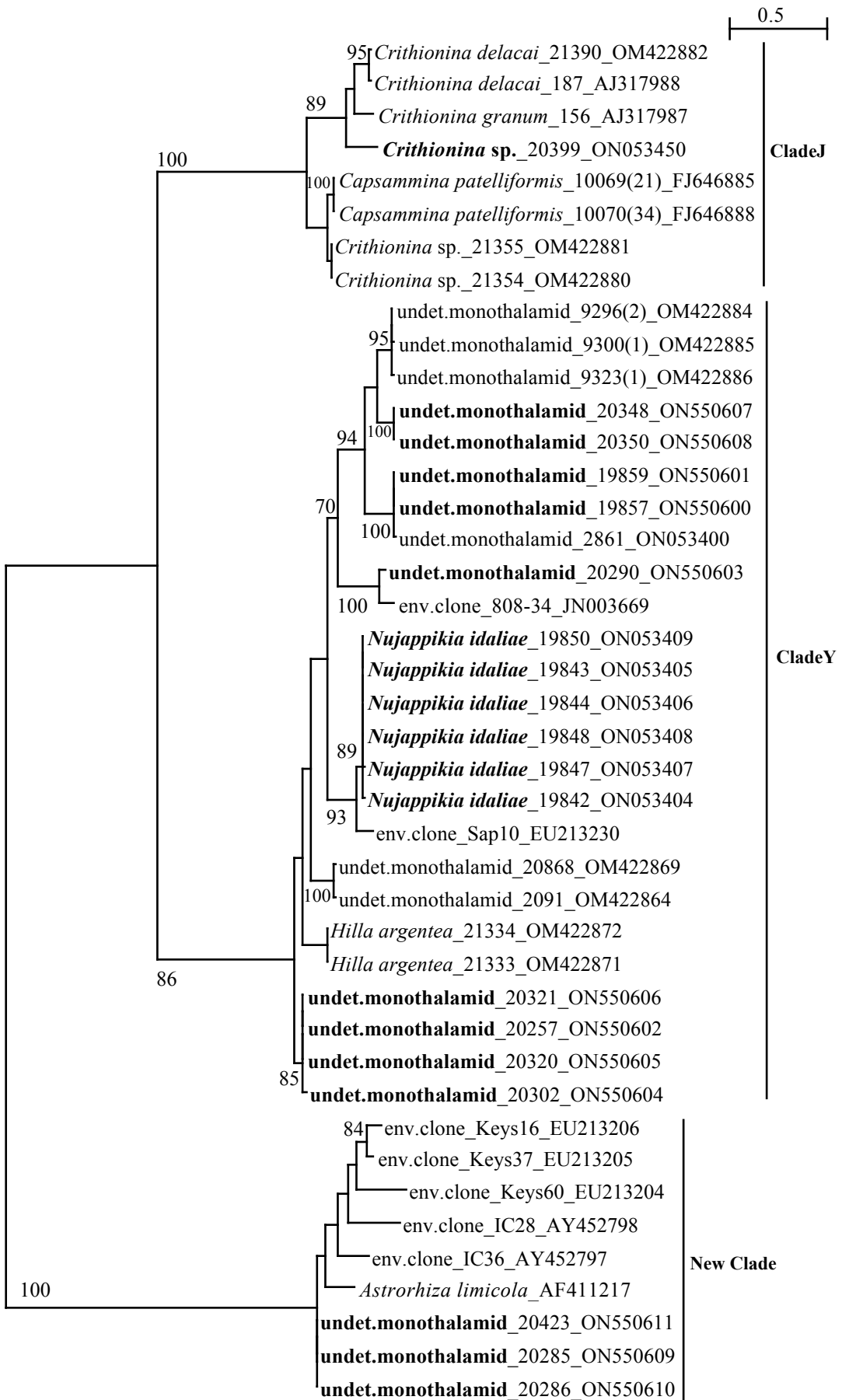
<sup>2</sup>Isford trough and slope sites (313–2472 m depth) are disregarded

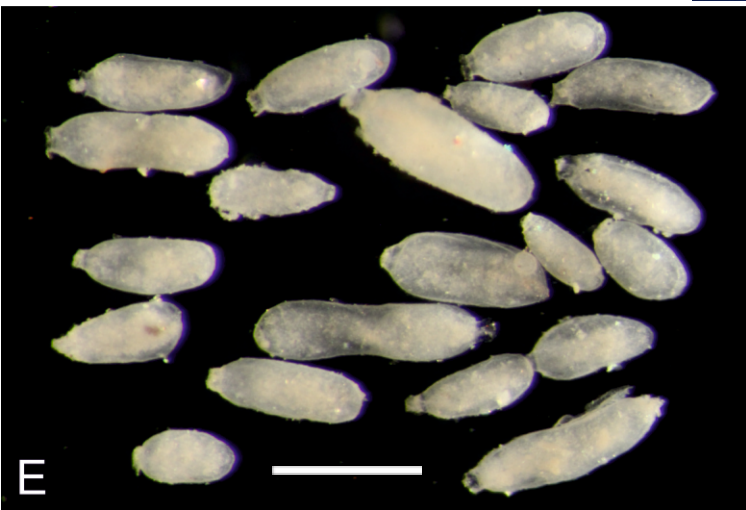
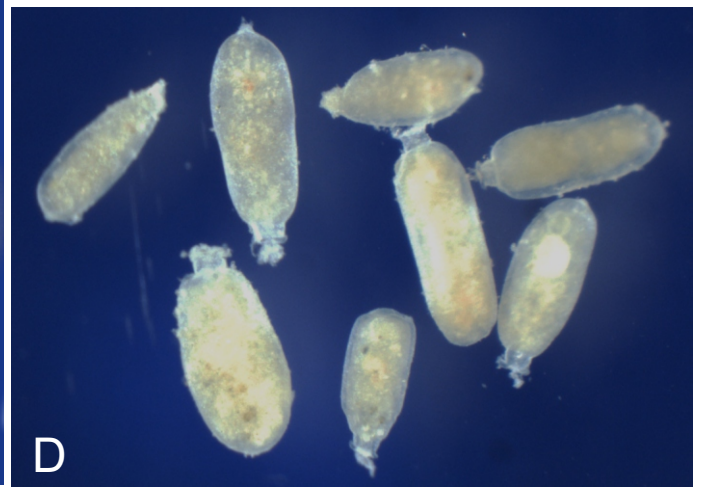
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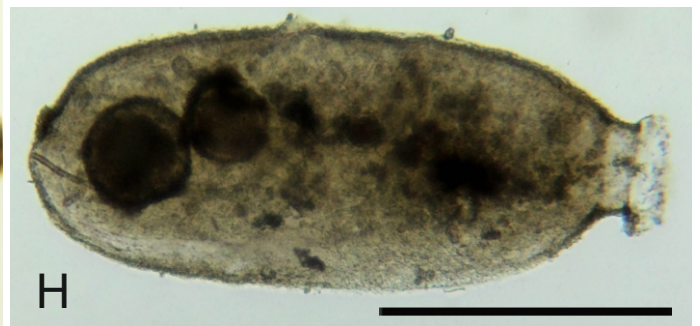
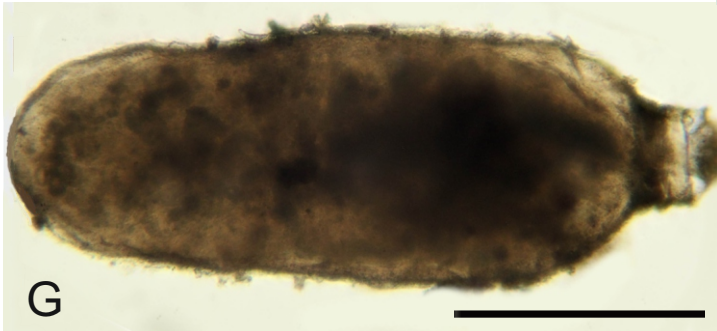
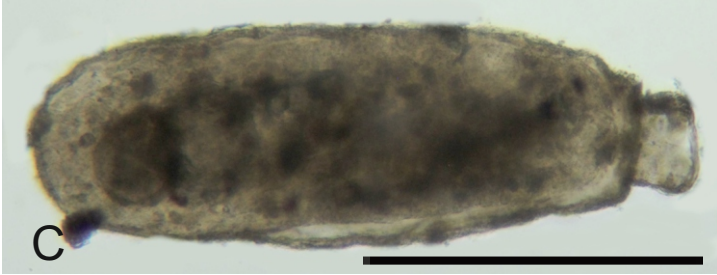
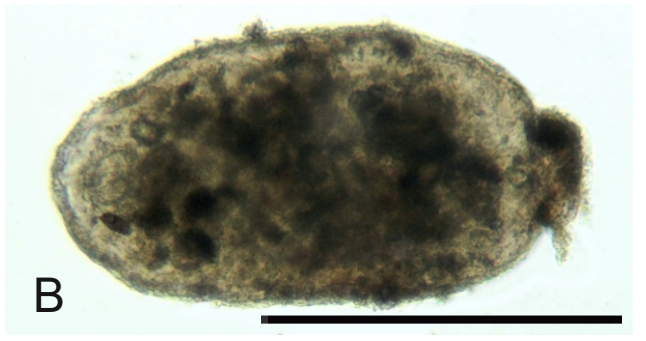


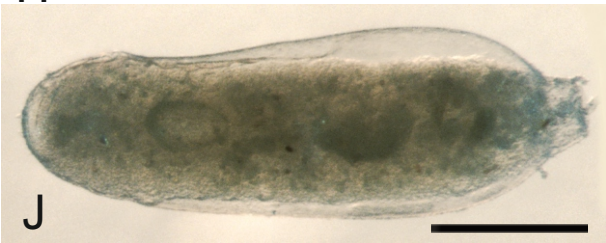
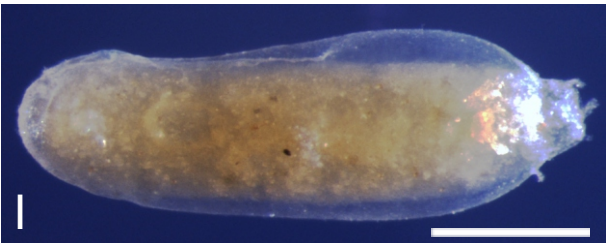
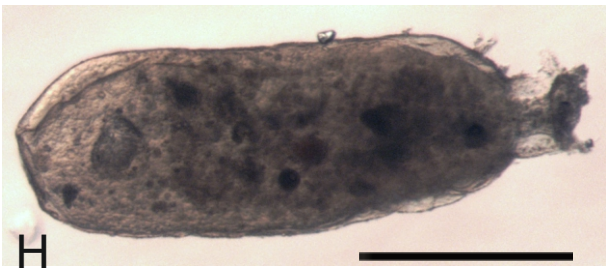
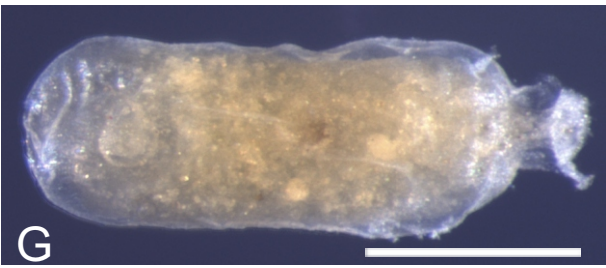
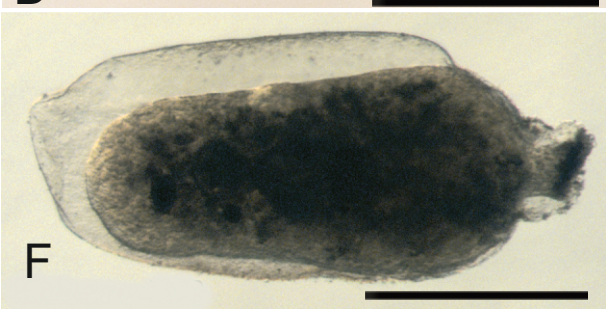
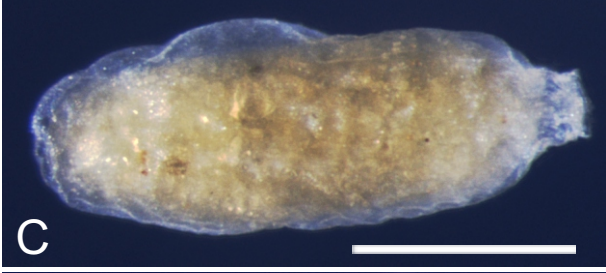
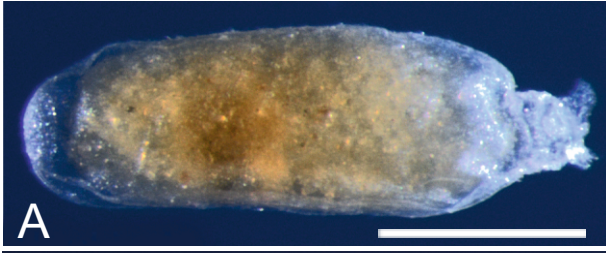


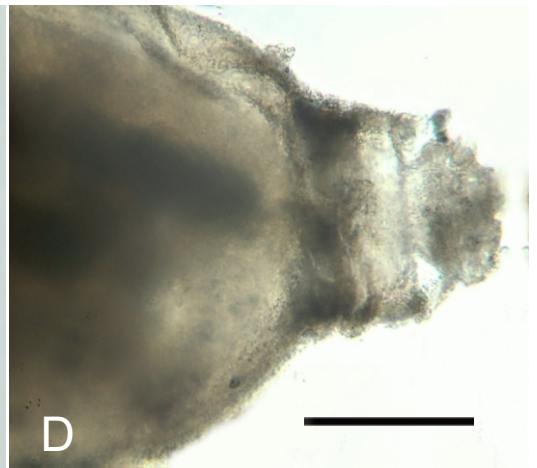
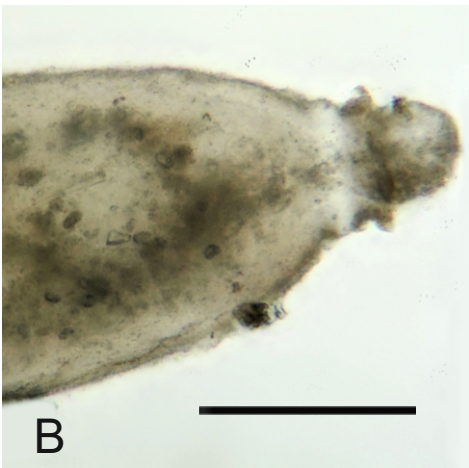
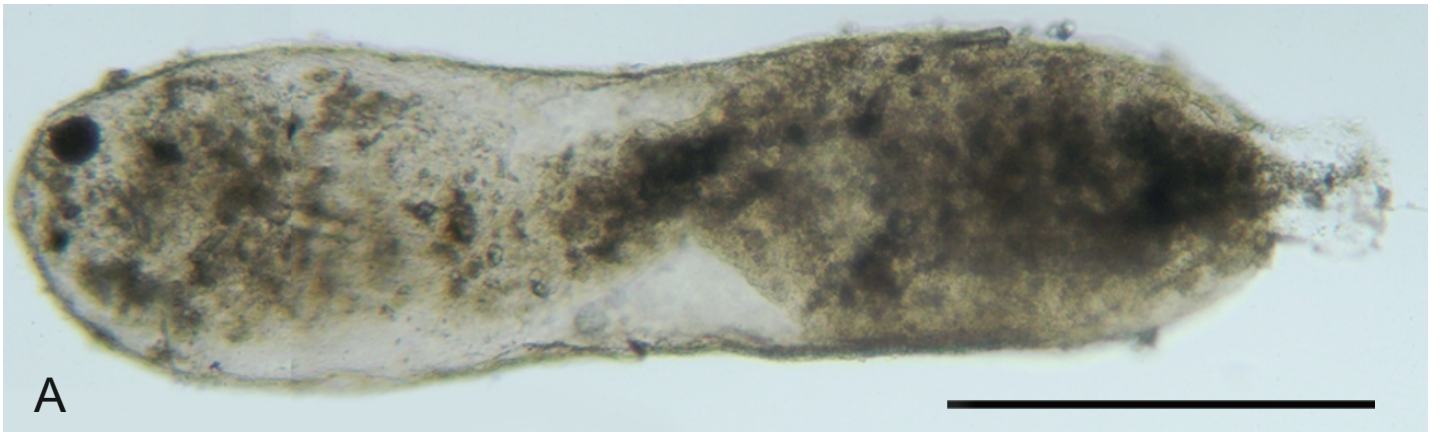


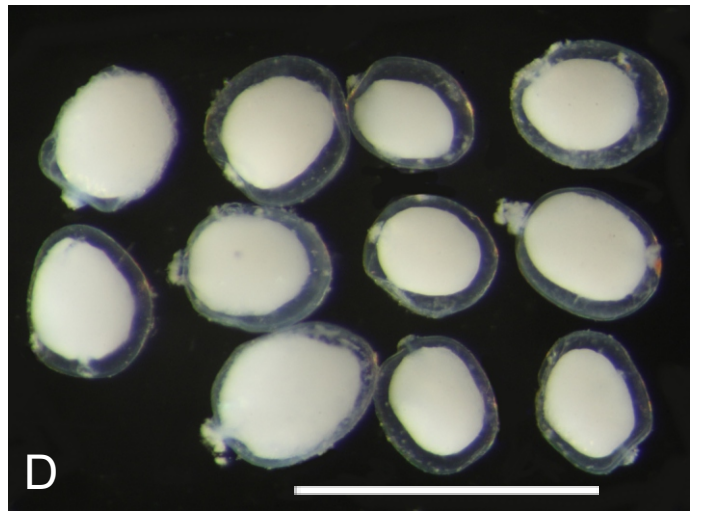
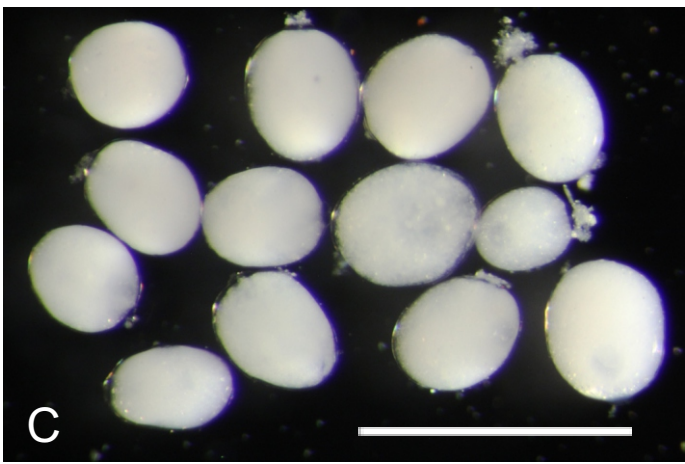
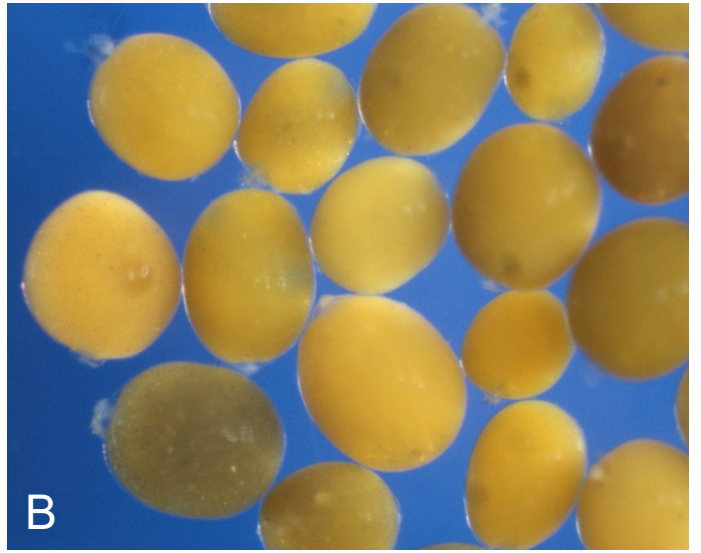
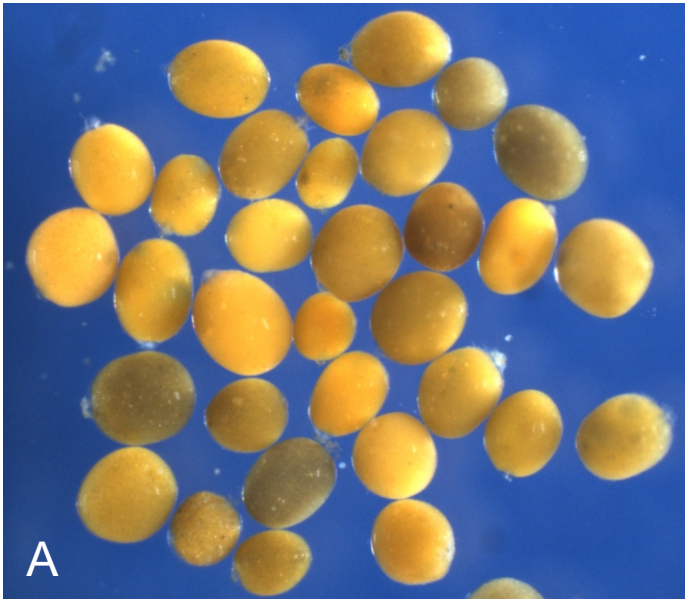


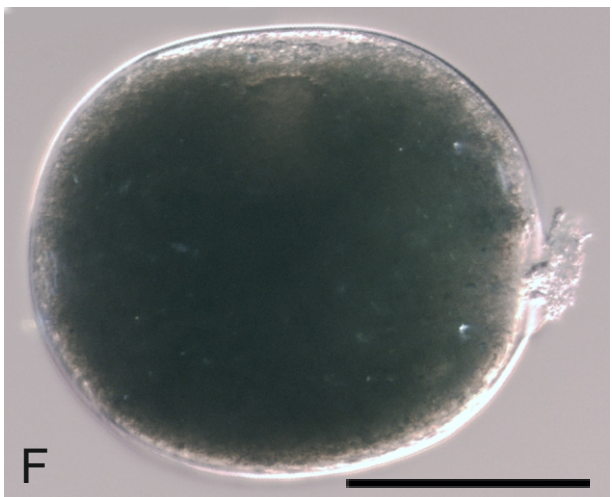
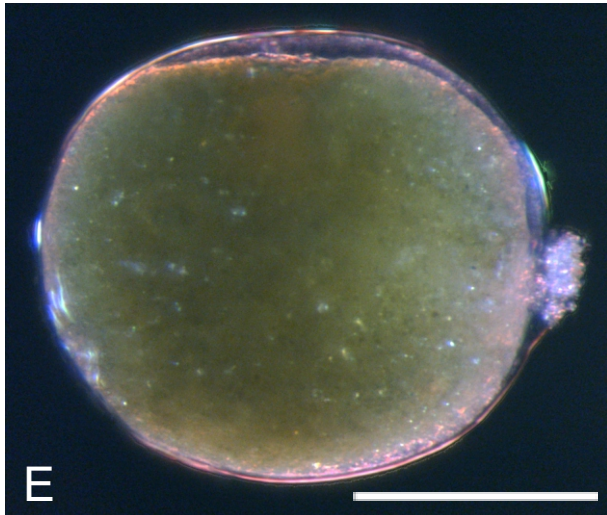
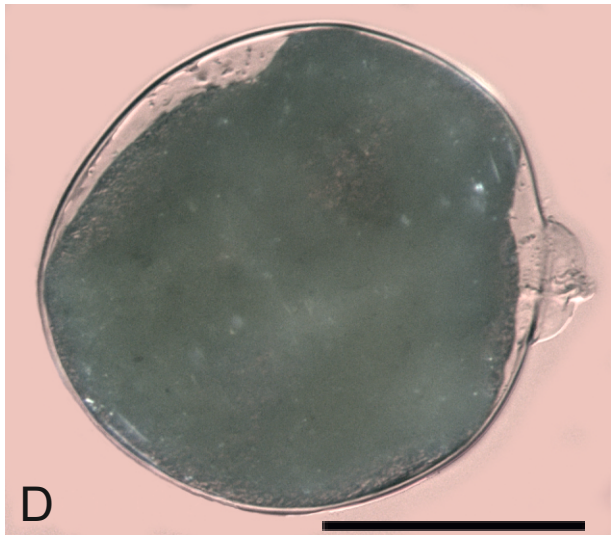
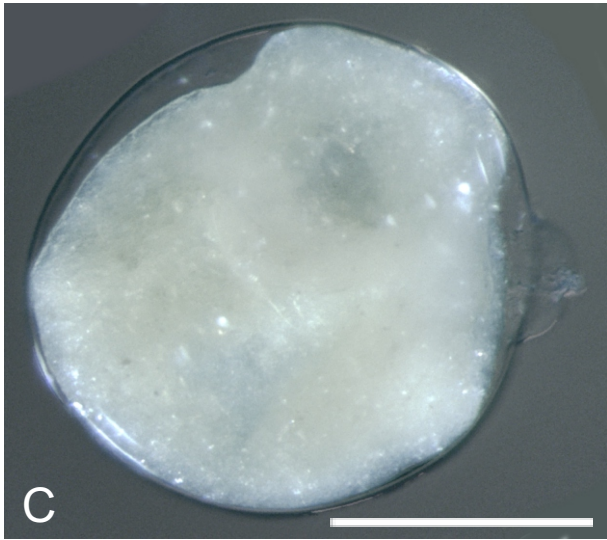
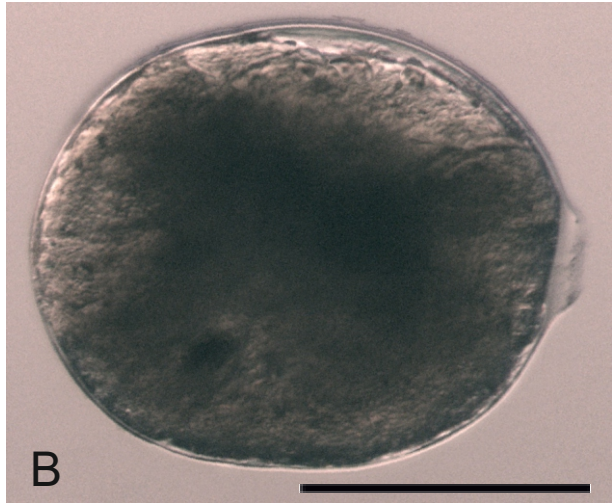
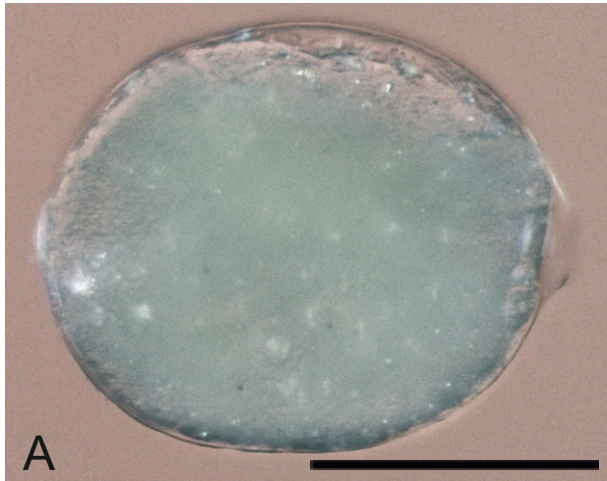




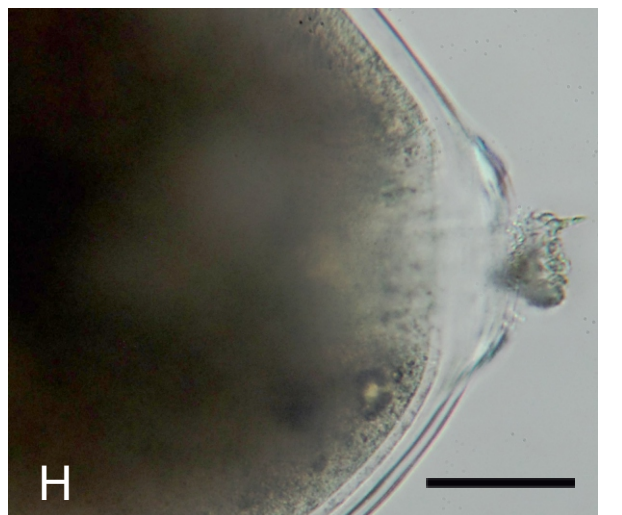
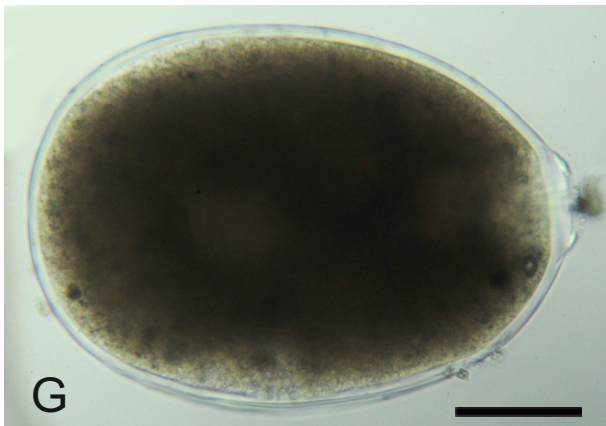
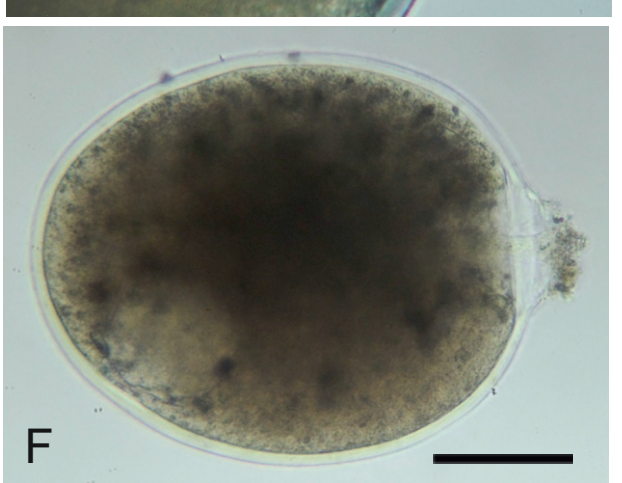
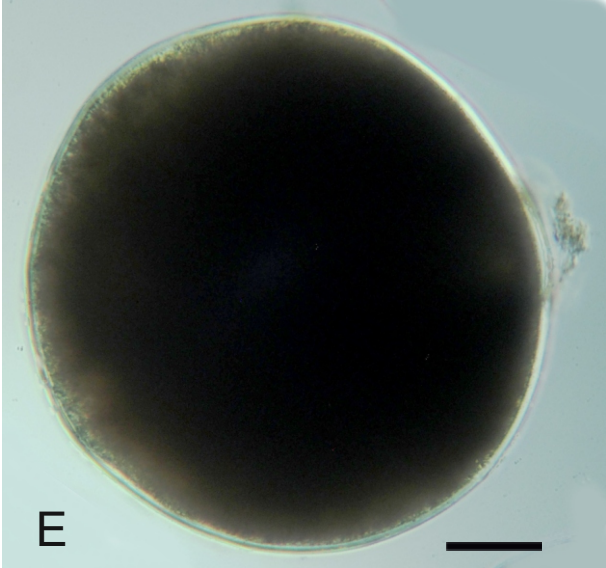
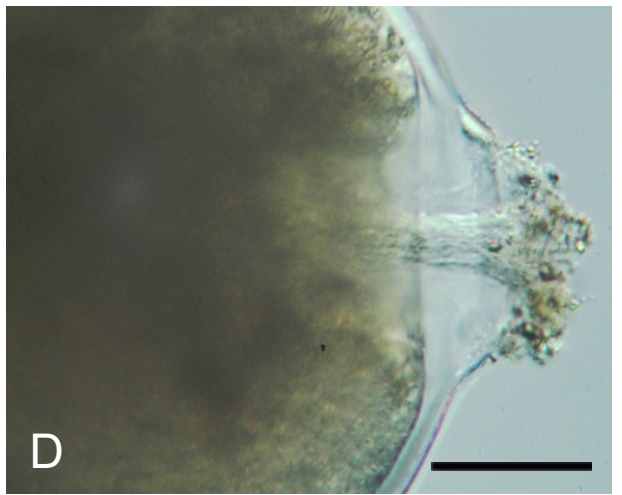
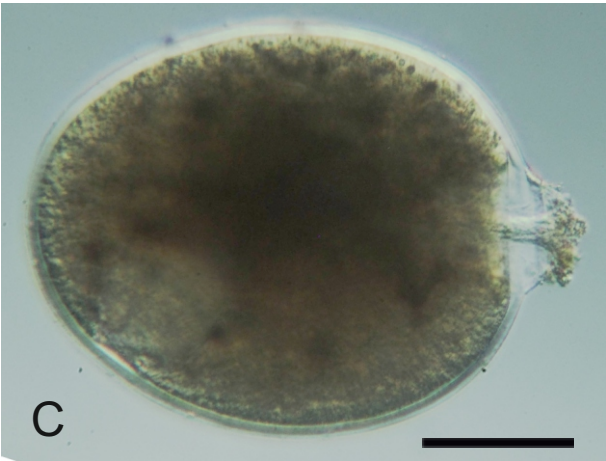
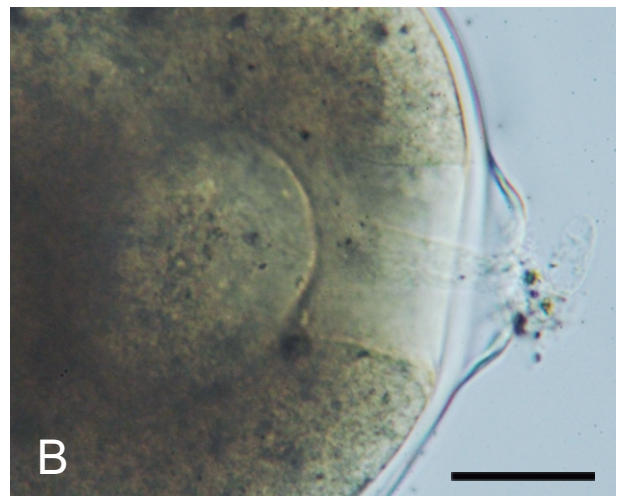
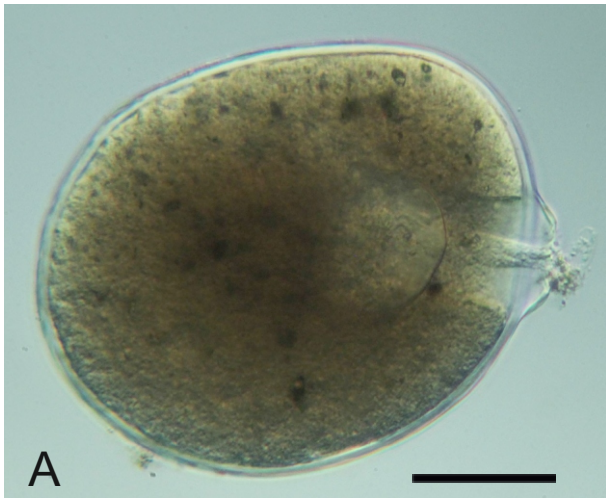


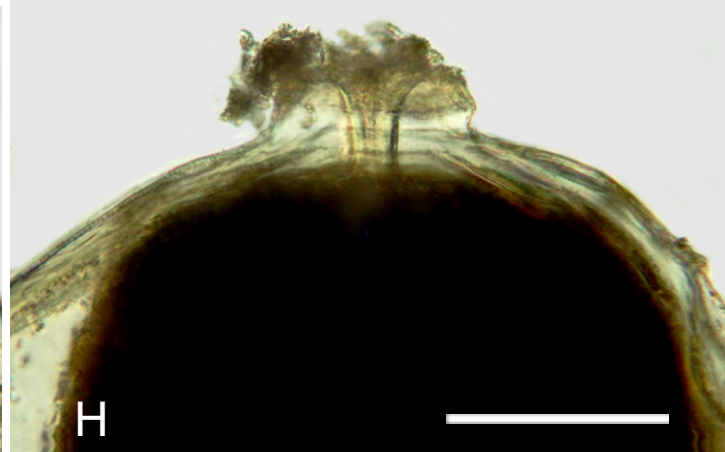
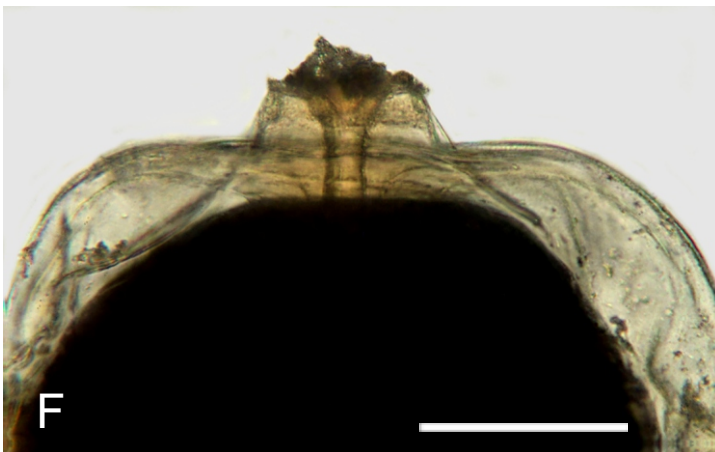
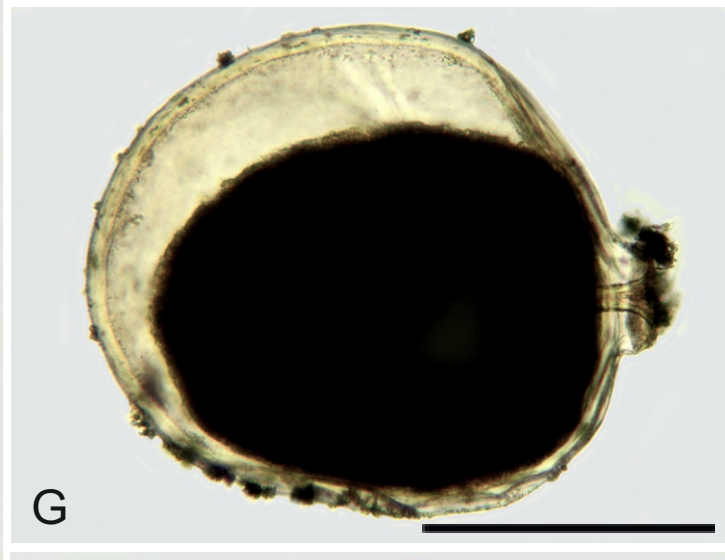
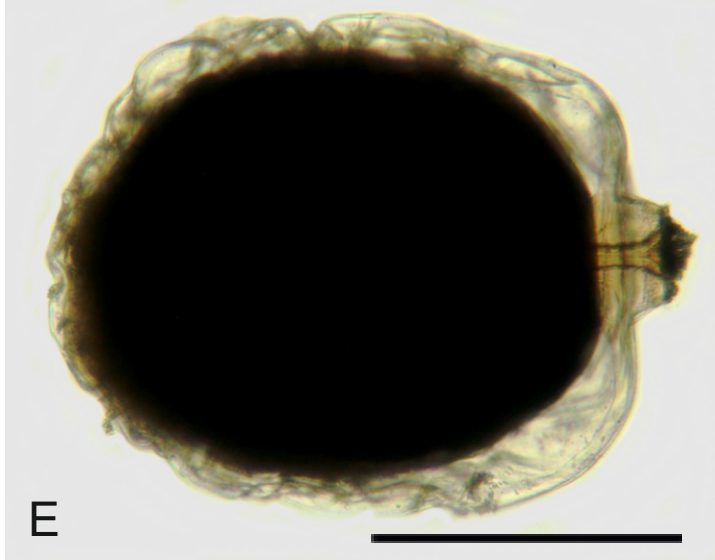
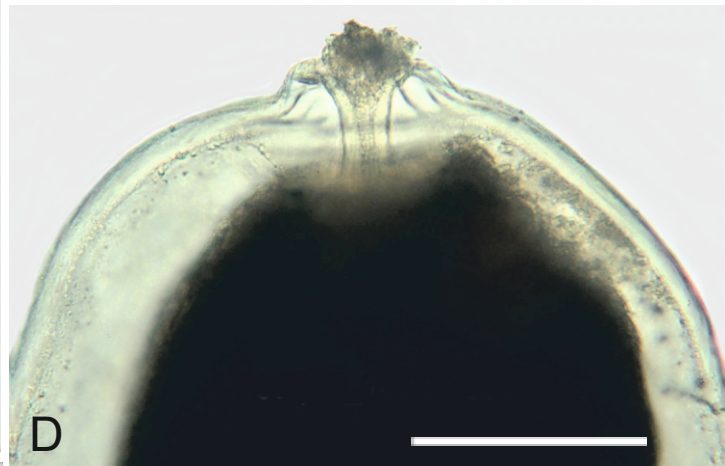
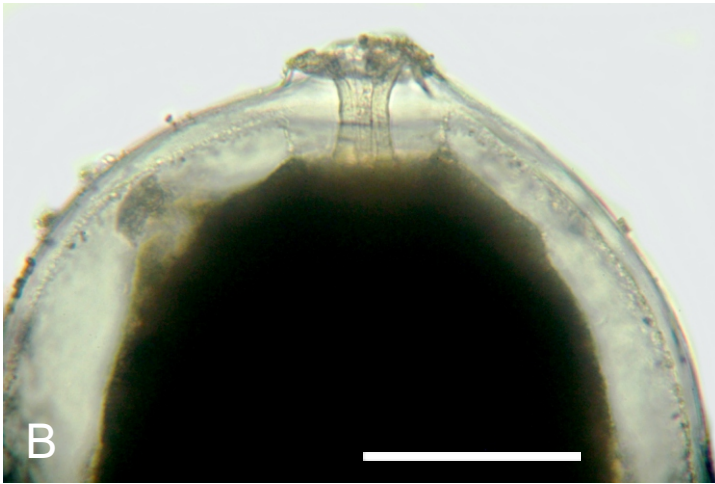




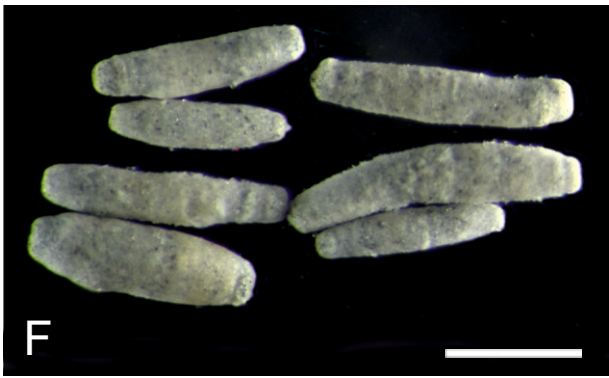
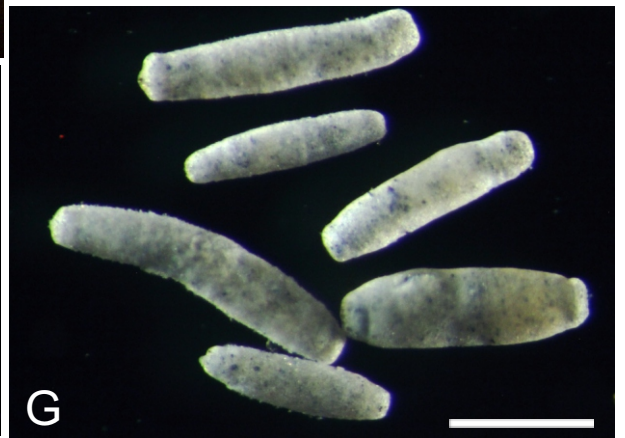
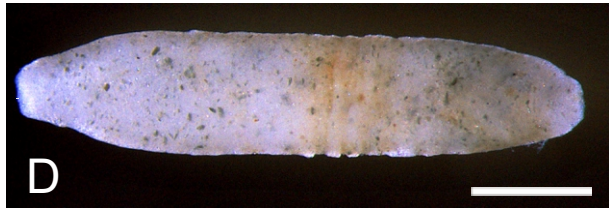
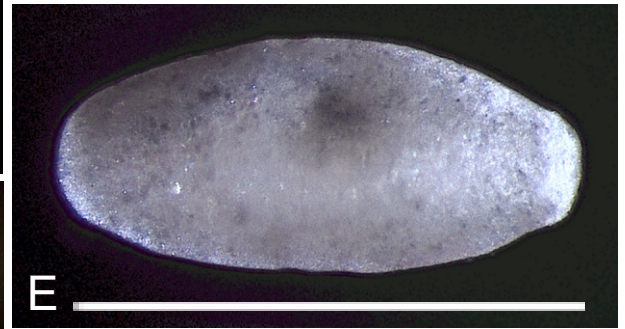
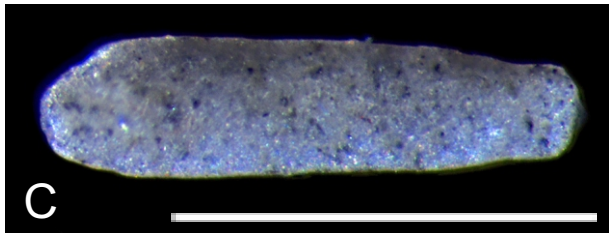
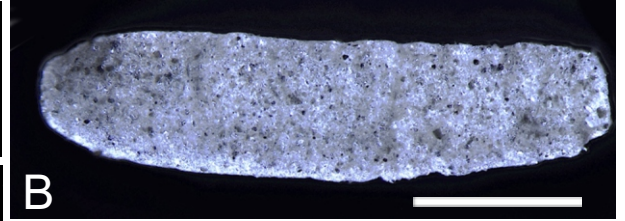
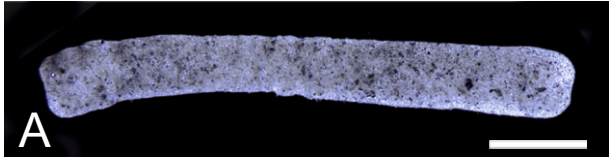












## Supplementary figures

**Figure S1.** (A–Q) Monothalamids that were not sequenced. (A) Elongate organic-walled test with white cytoplasm and single nucleus, St. 3. (B) Unknown saccamminid, St. 16. (C) Elongate saccamminid, St. 15. (D) *Technitella*-like specimen, St. 2B. (E) Organic-walled test with attached detritus, St. 6. (F) *Phainogullmia*-like specimen, St. 8. (G) Elongate saccamminid, St. 4. (H) *Hippocrepina indivisa*, St. 4. (I) *Cylindrogullmia*-like organic-walled test with agglutinated casing, St. 15. (J) Spindle-like species, St. 6. (K) Organic-walled test, St. 16. (L) Bottle-shaped saccamminid, St. 4. (M) Elongate tapered saccamminid with apertural neck, St. 14. (N) Elongate saccamminid, St. 5. (O) Elongate slightly tapered organic-walled test with one aperture and containing yellow cytoplasm. (P) Small, elongate tapered organic-walled test containing whitish cytoplasm, St. 4. (Q) Small, elongate organic-walled test containing brownish cytoplasm, St. 15. (R) *Micrometula* sp., St. 4, sequenced specimen. Scale bars are not available.

**Figure S2.** Silver saccamminids. (A) St. 5, south of the island Uumanaq, water depth 240 m; the lower left elongate specimen is probably the one that was sequenced, shown in Figure 12K. (B) St 16, Lysefjord, water depth 61 m; silver saccamminid, probably the same species as shown in A. (C) St. 4, Qôrgut fjord, water depth 118 m; elongate species. (D) St. 3, Qôrgut fjord, 58 m; species with a silvery sheen and distinct aperture. Scale bars are not available.

**Figure S3.** *Pelosina*, *Pelosina*-like, and *Crithionina*-like species that were not sequenced. (A) Mudball, possibly a species of *Globipelorhiza*; St. 5. (B) Subtriangular *Pelosina* with arms; St. 14. (C, H) *Pelosina*-like test with arms, heavily encrusted with large mineral grains; St. 5 and 7, respectively. (D) Lemon-shaped *Pelosina* resembling *P. fusiformis* Earland, 1934. (E, F) Elongate fusiform *Pelosina* with smooth surface; St. 8 and 7, respectively. (G) Fusiform *Pelosina* covered in short tufts, possibly *P. variabilis* Brady, 1879; St 5. (I) Small ovate to droplet-shaped mudwalled tests with arms, possibly a *Pelosina*; St. 15. (J) *Crithionina*-like form composed of relatively large mineral grains. (K) Relatively large elongate *Pelosina*, possibly the same as *Pelosina variabilis* n. var. *constricta* of Earland (1934); St.5. Scale bars are not available.

