

Molecular and morphological diversity of monothalamous foraminifera from South Georgia and the Falkland Islands: Description of four new species

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Abstract

Based on molecular and morphological data, we describe three new genera and four new species of monothalamids from the sublittoral zone (21–250 m) in South Georgia fjords that belong to different monothalamid clades. *Limaxia alba* gen. nov. sp. nov. (Clade A) has an elongate, subcylindrical test, 359–688 µm long, with some detritus attached to the organic wall. *Hilla argentea* gen. nov. sp. nov. (Clade Y) has a cylindrical, finely agglutinated test, 535–755 µm long. *Pseudoconqueria lenticularis* gen. nov. sp. nov. branches separately. It has a spindle-shaped, finely agglutinated test, 280–574 µm long. *Bathyallogromia olivacea* sp. nov. (Clade C) has an ovate organic-walled test, 369–433 µm long. We present the first genetic data on two monothalamid species originally described from South Georgia, *Hippocrepinella alba* (Clade C) and *Hippocrepinella hirudinea* (Clade D), as well as a single sequence for *C. delacai* (Clade J) originally described from McMurdo Sound, Antarctica. In addition, we report nine undescribed species branching in six different monothalamid clades (A, B, BM, C, J, Y), eight of them sampled around South Georgia and one collected from the Falkland Islands near Stanley.

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Introduction

South Georgia is a sub-Antarctic island situated at the northeastern edge of the Scotia Sea in the Atlantic part of the Southern Ocean. The island is 170-km long, 40-km wide, with mountainous, Alpine-type topography and more

than half of its surface covered by glaciers (Frakes, 1966; Mukasa and Dalziel, 1996). It is surrounded by a large shelf and coastal regions are influenced by the Antarctic Circumpolar Current (AAC) and the Antarctic Polar Front (APF) (Whitehouse et al., 2008). The geographic isolation of South Georgia combined with the influence of nutrient rich

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waters have resulted in high levels of biodiversity, which is reflected in the recent creation around it of one of the World's largest marine protected areas, spanning more than one million km² (Hogg et al., 2016).

The Falkland Islands are located on the Patagonian shelf, some 1450 km west of South Georgia and about 460 km to the east of the South American continent. They are affected by the Falkland Current (FC) that comprises Sub-Antarctic water and is a branch of the ACC (Upton and Shaw, 2002). The northern part of the Patagonian Shelf is dominated by opposing flows of the FC and the Brazil Current (BC), a branch of the Atlantic South Equatorial Current composed of subtropical water (Hsu et al., 2018). The Falkland Islands are at the boundary between southern temperate and sub-Antarctic ecosystems. Shallow-water temperatures reach up to 10 °C in summer (Arkhipkin et al., 2004), much higher than near-surface waters around South Georgia, which do not exceed 5 °C (Whitehouse et al., 2008).

The first reports about shallow-water benthic foraminifera from South Georgia and the Falkland Islands were published by Heron-Allen and Earland (1932a,b) and Earland (1933, 1934). These surveys were based on sediment samples collected during the Discovery expeditions and described a mixture of calcareous and agglutinated species. Some descriptions refer to single-chambered monothalamids that build an agglutinated test. However, no delicate, soft-walled species were recognised in these early studies; their tests would not have withstood storage in alcohol or the harsh sample processing methods described by Earland (1934). Monothalamids are usually under-represented in traditional, morphology-based studies. In particular, organic-walled or finely-agglutinated taxa with delicate, flexible test walls are either ignored or not preserved in dried sediment residues. As a result, many studies only include monothalamids with sturdy agglutinated tests, which represent a small subset of monothalamid diversity.

A gap of more than eighty years separates these first surveys from recent taxonomic studies conducted on South Georgia foraminiferal fauna by Dejardin et al., (2018). This recent morphology-based analysis included 58 genera and 60 species of hard-shelled calcareous and agglutinated foraminifera. The authors identified 24 species previously described by Earland (1933), among them 13 that are typical of South Georgia assemblages.

The first study that combined molecular and morphological data for benthic foraminifera from around South Georgia and the Falkland Islands was conducted by Majewski et al., (2021) and concerned the Cassidulinidae, a family

of calcareous, multichambered foraminifera in the order Rotaliida. The authors examined the evolution and dispersal of Cassidulinidae in Antarctic and sub-Antarctic coastal zones. Some of the investigated species seem to be endemic to Antarctica while others might be the result of hybridisation between Antarctic and sub-Antarctic populations. Another taxonomic study that combined molecular and morphological data described six new species in the genus *Gromia* (Rhizaria, Cercozoa), a group of testate marine protists related to the foraminifera (Gooday et al., 2022). Four were from South Georgia and two from the Falklands. Some of the species were found only in samples from these islands, but others were also represented in Patagonia.

The molecular diversity of monothalamid foraminifera in the Southern Ocean has been investigated in a number of studies (Pawlowski et al., 2002a,b, 2005, 2008; Majewski et al., 2015) and several species have been described from the abyssal Weddell Sea (Gooday et al., 2004; Gooday and Pawlowski, 2004; Cedhagen et al., 2009) and from coastal locations in Admiralty Bay, West-Antarctica (Sinniger et al., 2008; Pawlowski and Majewski, 2011) and Terra Nova Bay, Ross Sea (Sabbatini et al., 2004). The morphological diversity of the monothalamid community in Admiralty Bay from 8 m down to 254 m has been reviewed by Majewski et al., 2007 and Majewski, 2010.

The present study explores the genetic and morphological diversity of sub-Antarctic monothalamid foraminifera from South Georgia and one site near the Falkland Islands, based on specimens collected in 2019 during an expedition aboard the yacht *Saoirse*. Our results show that monothalamids are highly diverse in our study area. The species recognized belong to seven previously-defined monothalamid clades (Pawlowski et al., 2002a) and one new monothalamid lineage. Several species have ranges that extend across the ACC and also exist around Antarctica, while others have close relatives in the Northern hemisphere. The bar-coding approach used in this study will also improve the interpretation of metabarcoding datasets in future biodiversity surveys.

Material and methods

Sampling, sample processing and morphological methods

Samples were collected around South Georgia during November and December 2019 in Fortuna, Stromness and

Fig. 1. Map of sampling localities in the Falkland Islands and on the north coast of South Georgia. Map data from google map (upper), <https://freevectormaps.com> (middle), as well as *South Georgia and The Shackleton Crossing map 1: 200 000*, published by British Antarctic Survey in 2017 and *Nautical chart BA 3588 Approaches to Stromness and Cumberland Bays 1: 50 000*, published by UK Hydrographic Office (lower). Position of the southern Antarctic Circumpolar Current front (SACCF), the Polar Front (PF), the Subantarctic Front (SAF) and the Falkland Current (FKC) after Hsu et al. (2018). The SACCF and SAF mark the southern and northern limits, respectively, of the Antarctic Circumpolar Current (ACC).

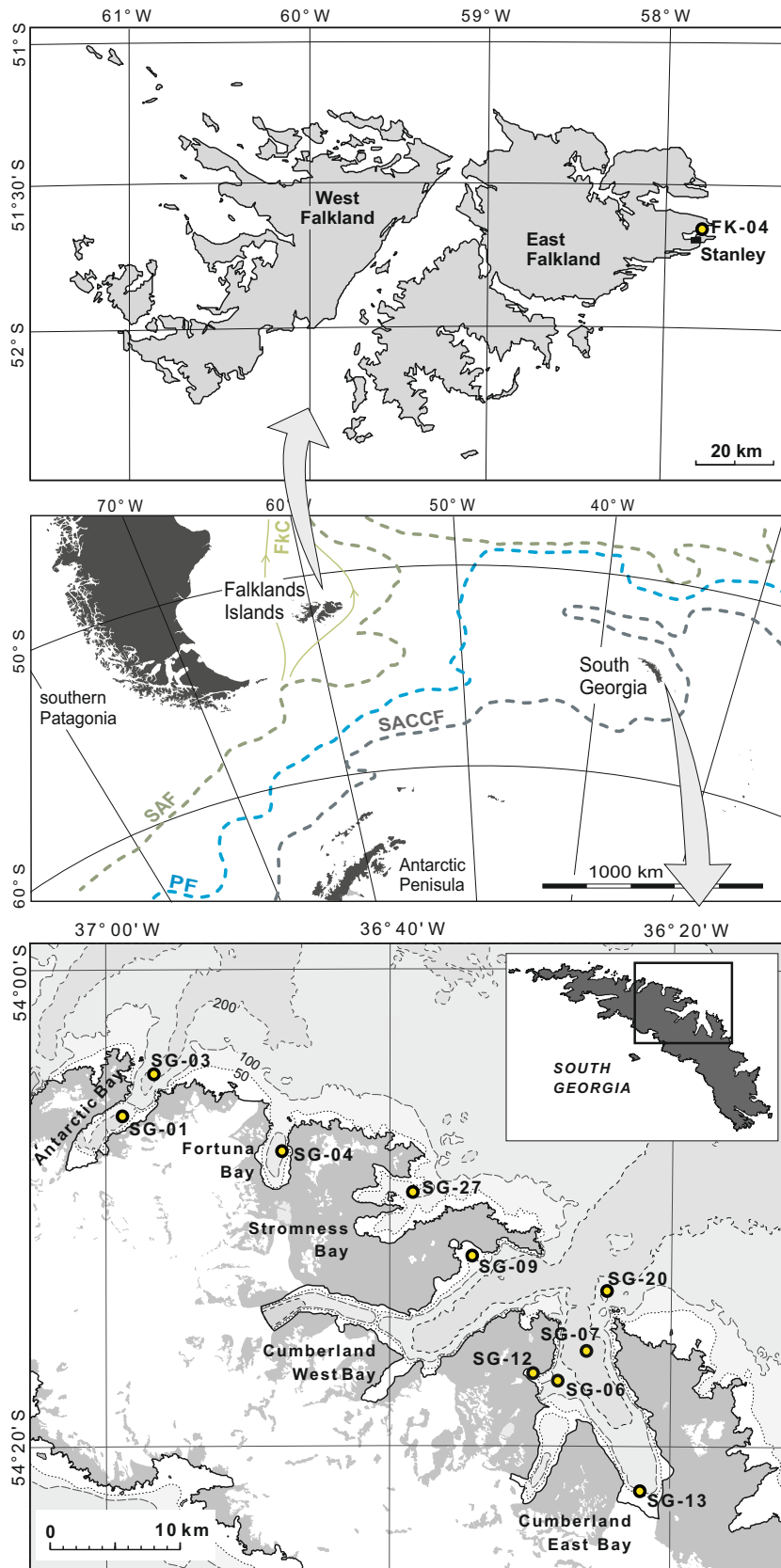


Table 1. Data for sampling sites in South Georgia and the Falkland Islands.

Station	Location	Latitude °S	Longitude °W	Depth (m)
SG-01	Antarctic Bay	54° 06.200'	36° 58.800'	111
SG-03	Antarctic Bay	54° 04.250'	36° 56.812'	250
SG-04	Fortuna Bay	54° 07.658'	36° 47.598'	135
SG-06	Cumberland East Bay	54° 17.299'	36° 28.247'	121
SG-07	Cumberland East Bay	54° 16.052'	36° 26.277'	250
SG-09	Cumberland West Bay	54° 12.044'	36° 34.253'	60
SG-12	Cumberland East Bay	54° 16.980'	36° 29.977'	21
SG-13	Cumberland East Bay	54° 21.936'	36° 22.486'	28
SG-20	outer Cumberland Bay	54° 13.586'	36° 25.234'	106
SG-27	Stromness Bay	54° 09.372'	38° 38.426'	136
FK-04	Sparrow Cove	51° 39.150'	57° 48.546'	9

Cumberland East and West bays between 21 m and 250 m water depths. The Falkland Island sample was collected in December 2019 in Sparrow Cove outside Stanley at 9 m depth (Fig. 1, Table 1). A Van Veen grab deployed from the *Saoirse* was used in all cases, and the surface sediment removed with a spoon and washed on deck through sieves with mesh sizes of 500, 250, 125 and 63 µm. The residues were transferred to plastic jars with ambient seawater and stored at 4 °C. On South Georgia, the samples were examined as soon as possible after collection in the British Antarctic Survey's King George Point Laboratory. The different residues were sorted for foraminifera in seawater in Petri dishes that were kept chilled using a freezer pack. Specimens for genetic analyses were preserved in RNAlater; those for morphological analyses and type specimens were preserved in Nalgene tubes filled with 4% formalin buffered with borax.

Following the expedition, the foraminifera for genetic analysis were transported to Geneva, where they were photographed using a Leica M205 C microscope fitted with a Leica DFC 450 C camera. Specimens to be described morphologically were transported to Southampton where they were photographed using an Olympus SZX7 stereomicroscope and an Olympus BH2 compound microscope, in both cases equipped with a Canon 60D SRL digital camera.

DNA extraction, PCR amplification and sequencing

Fifty-five foraminiferal specimens were extracted individually using guanidine lysis buffer (Pawlowski, 2000). Semi-nested PCR amplification was carried out for the SSU rDNA barcoding fragment of foraminifera (Pawlowski and Holzmann, 2014) using forward primers s14F3 (acgcamgtgtgaaacttg) -s20r (gacggcggtgtgtacaa) for the first and primers s14F1 (aaggcaccacaagaacgc)-s20r for the second amplification. The reverse primer sB (tgatcctctgcaaggttcacctac) was used for amplification of isolates 20851–20855, 20866–20868 and 20870–20874. Thirty-five and 25 cycles were performed for the first and the second PCR, with an annealing temperature of 50 °C

and 52 °C, respectively. 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 resulting sequences were deposited in the NCBI/GenBank database. Isolate and Accession numbers are specified in Table 2.

Phylogenetic analysis

The obtained sequences were added to 115 monothalamid sequences (Table 2) that are part of the publicly available 18S database of monothalamous foraminifera (NCBI/Nucleotide; <https://www.ncbi.nlm.nih.gov/nucleotide/>). All sequences were aligned using the default parameters of the Muscle automatic alignment option as implemented in SeaView vs. 4.3.3 (Gouy, et al., 2010). Based on the obtained preliminary alignment, the new sequences were assigned to established monothalamous clades (Pawlowski et al., 2002a). Three partial alignments were generated subsequently, including the representatives of selected clades and new sequences. Because of the high genetic variability between clades (Pawlowski et al., 2002a), separate alignments allow a better resolution of tree topology. The alignment of clades A, B, BM (Fig. 2) contains 74 sequences with 1442 sites used for analysis. The alignment of clades C, D (Fig. 3) contains 82 sequences with 1649 sites used for analysis. The alignment of clades J, Y, (Fig. 4) contains 43 sequences with 1644 sites used for analysis.

The phylogenetic trees were 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 + G + I substitution model being selected for all analyses. The initial trees are based on BioNJ. Bootstrap values (BV's) are based on 100 replicates.

Pairwise genetic distances have been calculated using MEGA7, with a Maximum Composite Likelihood method

Table 2. Information on isolate, accession numbers and sampling localities of monothalamid taxa.

Taxa	Isolate	Accession number	Sampling site	Additional remarks
CladeA				
<i>Limaxia alba</i>	21,300	OM422947	UK, South Georgia, SG-13	
<i>Limaxia alba</i>	21,301	OM422948	UK, South Georgia, SG-13	
<i>Limaxia alba</i>	21,302	OM422949	UK, South Georgia, SG-13	
<i>Limaxia alba</i>	21,303	OM422950	UK, South Georgia, SG-13	
<i>Limaxia alba</i>	21,304	OM422951	UK, South Georgia, SG-13	
<i>Limaxia alba</i>	21,305	OM422952	UK, South Georgia, SG-13	
<i>Limaxia alba</i>	21,252	OM422953	UK, South Georgia, SG-01	
specimen	k49	OM422946	Sweden, Tjaerno	
undet.monothalamid	1083	OM422934	Antarctica, New Harbor	Crithionina like
undet.monothalamid	1086	OM422935	Antarctica, New Harbor	Crithionina like
undet.monothalamid	1212	AJ307744	Antarctica, New Harbor	Cylindrogullmia like
undet.monothalamid	1916	OM422933	Antarctica, New Harbor	pink sphere
undet.monothalamid	2226	AJ514858	Antarctica, New Harbor	elongate
undet.monothalamid	2227	AJ514848	Antarctica, New Harbor	elongate
undet.monothalamid	2887	OM422936	Norway, Svalbard	agglutinated
undet.monothalamid	3022*	OM422851	Antarctica, New Harbor	Cylindrogullmia like
undet.monothalamid	3118	OM422937	Antarctica, McMurdo	coarsley agglutinated, attached
undet.monothalamid	3132	HE998678	Antarctica, McMurdo	coarsley agglutinated, attached
undet.monothalamid	3133	OM422938	Antarctica, McMurdo	coarsley agglutinated, attached
undet.monothalamid	3208*	HG425220, OM422852	Antarctica, McMurdo	Cylindrogullmia like
undet.monothalamid	3523	OM422939	Weddell Sea, abyssal	Allogromia like
undet.monothalamid	3552	OL772090	Weddell Sea, abyssal	Allogromia like
undet.monothalamid	3794	OM422941	Antarctica, Terranova Bay	organic walled, oval
undet.monothalamid	3795	OM422942	Antarctica, Terranova Bay	oval, white, sticky
undet.monothalamid	3807	HG425219	Antarctica, Terranova Bay	oval, white, sticky
undet.monothalamid	11211*	OM422853	Norway, Skagerrak	Nemogullmia like
undet.monothalamid	20,866	OM422943	UK, South Georgia, SG-06	elongate, white, finely agglutinated
undet.monothalamid	21,391	OM422944	UK, South Georgia, SG-01	Crithionina like
undet.monothalamid	21,407	OM422945	UK, South Georgia, SG-04	Crithionina like
environmental foraminiferal clone	McM20	AY179179	Antarctica, McMurdo	
CladeB				
<i>Bowseria arctowskii</i>	3015	LN873609	Antarctica, New Harbor	
<i>Bowseria arctowskii</i>	4026	LN873614	Antarctica, Ross Ice Shelf	
<i>Pelosina variabilis</i>	2842	OM422916	Norway, Svalbard	
<i>Pelosina variabilis</i>	2852	HG425217	Norway, Svalbard	
<i>Psammosphaera</i> sp.	3786	OM422922	Antarctica, Terranova Bay	
<i>Psammosphaera</i> sp.	3801	OM422919	Antarctica, Terranova Bay	
<i>Psammosphaera</i> sp.	3802	OM422920	Antarctica, Terranova Bay	
<i>Psammosphaera</i> sp.	3803	OM422921	Antarctica, Terranova Bay	
<i>Psammosphaera</i> sp.	3929	OM422923	Antarctica, Terranova Bay	
<i>Psammosphaera</i> sp.	14167*	OM422908	Antarctica, McMurdo	
<i>Psammosphaera</i> sp.	14168*	OM422909	Antarctica, McMurdo	
<i>Psammosphaera</i> sp.	14170*	OM422910	Antarctica, McMurdo	
<i>Psammosphaera</i> sp.	17521*	OM422911, OM422912	Chile, Beagle Channel	
<i>Psammosphaera</i> sp.	17734*	OM422913	Chile, Beagle Channel	
Psammosphaera sp.	21,357	OM422924	UK, South Georgia, SG-09	
Psammosphaera sp.	21,358	OM422925	UK, South Georgia, SG-09	
Psammosphaera sp.	21,359	OM422926	UK, South Georgia, SG-09	
Psammosphaera sp.	21,376	OM422927	UK, South Georgia, SG-09	
<i>Psammosphaera</i> sp.	A213	AJ307747	Antarctica, New Harbor	

Table 2. (continued)

Taxa	Isolate	Accession number	Sampling site	Additional remarks
<i>Psammosphaera</i> sp.	c1	OM422928	Chile, Beagle Channel	
undet.monothalamid	1195	OM422914	Antarctica, New Harbor	red, bean like sarcode
undet.monothalamid	2125	OM422915	Antarctica, New Harbor	
undet.monothalamid	3909	OM422917	Antarctica, Ross Ice Shelf	Cylindrogullmia like
undet.monothalamid	4067	OM422918	France, Mediterranean Sea	
CladeBM				
<i>Bathysiphon argenteus</i>	1780	AJ514836	Sweden, Gullmar Fjord	
<i>Bathysiphon flexilis</i>	1784	AJ514837	Sweden, Gullmar Fjord	
<i>Micrometula</i> sp.	5053*	OM422838	Canada, Vancouver, Howe Sound	
<i>Micrometula</i> sp.	5057*	OM422839	Canada, Vancouver, Howe Sound	
<i>Micrometula</i> sp.	7602*	OM422840	Chile, Beagle Channel, 20 m	
<i>Micrometula</i> sp.	7603*	OM422841	Chile, Beagle Channel, 20 m	
<i>Micrometula</i> sp.	7605*	OM422842	Chile, Beagle Channel, 20 m	
<i>Micrometula</i> sp.	7606*	OM422843	Chile, Beagle Channel, 20 m	
<i>Micrometula</i> sp.	7609*	OM422844	Chile, Beagle Channel, 20 m	
<i>Micrometula</i> sp.	7632*	OM422845	Chile, Beagle Channel, 20 m	
<i>Micrometula</i> sp.	17179*	OM422846	Chile, Beagle Channel	
<i>Micrometula</i> sp.	17423*	OM422847	Chile, Beagle Channel	
<i>Micrometula</i> sp.	17424*	OM422848	Chile, Beagle Channel	
<i>Micrometula</i> sp.	17425*	OM422849	Chile, Beagle Channel	
<i>Micrometula</i> sp.	17554*	OM422850	Chile, Beagle Channel	
<i>Micrometula</i> sp.	20,851	OM422854	UK, South Georgia, SG-07	
<i>Micrometula</i> sp.	20,852	OM422855	UK, South Georgia, SG-07	
<i>Micrometula</i> sp.	20,853	OM422856	UK, South Georgia, SG-07	
CladeC				
<i>Abyssalia foliformis</i>	19,733	MK748285	Abyssal Eastern Pacific, Clarion-Clipperton Zone	
<i>Bathyallogromia olivacea</i>	21,323	OM422961	UK, South Georgia, SG-27	
<i>Bathyallogromia olivacea</i>	21,324	OM422962	UK, South Georgia, SG-27	
<i>Bathyallogromia olivacea</i>	21,325	OM422963	UK, South Georgia, SG-27	
<i>Bathyallogromia olivacea</i>	21,326	OM422964	UK, South Georgia, SG-27	
<i>Bathyallogromia</i> sp.	5396*	OM422905	Denmark, North Greenland Sea	
<i>Bathyallogromia weddellensis</i>	3334*	OM422904	Antarctica	
<i>Bathyallogromia weddellensis</i>	3338*	FR875101	Antarctica	
<i>Bathyallogromia weddellensis</i>	3339*	FR875100	Antarctica	
<i>Bathyallogromia weddellensis</i>	3553*	FR875102	Antarctica	
specimen	528	AJ514843	Sweden, Tjaerno	
specimen	1764	OL873223	Sweden, Gullmar Fjord	
<i>Hippocrepinella alba</i>	3906	OM422965	Antarctica, Ross Ice Shelf	
<i>Hippocrepinella alba</i>	17541*	OM422907	Chile, Beagle Channel	
<i>Hippocrepinella alba</i>	20,870	OM422966	UK, South Georgia, SG-01	
<i>Hippocrepinella alba</i>	20,872	OM422967	UK, South Georgia, SG-01	
<i>Hippocrepinella alba</i>	20,873	OM422968	UK, South Georgia, SG-01	
<i>Hippocrepinella alba</i>	20,874	OM422969	UK, South Georgia, SG-01	
<i>Gloiogullmia eurystoma</i>	526	AJ317981	Sweden, Tjaerno	
<i>Gloiogullmia eurystoma</i>	2882	LT796823, OL890664	Norway, Svalbard	
<i>Gloiogullmia eurystoma</i>	2885	OM422954	Norway, Svalbard	

Table 2. (continued)

Taxa	Isolate	Accession number	Sampling site	Additional remarks
<i>Hippocrepina indivisa</i>	4643	FR875143	Norway, Svalbard	
<i>Hippocrepina indivisa</i>	4724	LT796825	Norway, Svalbard	
<i>Hippocrepina indivisa</i>	17534*	OM422906	Chile, Beagle Channel	
<i>Hippocrepina indivisa</i>	17,539	MK748304	Chile, Beagle Channel	
<i>Leptammina flavofusca</i>	5174	LT796826	Weddell Sea, abyssal	
<i>Leptammina flavofusca</i>	5226	FM209499	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>	2836*	OM422894	Norway, Svalbard	
<i>Pilulina argentea</i>	2837	OL873224	Norway, Svalbard	
<i>Pilulina argentea</i>	2840	OL873237	Norway, Svalbard	
<i>Semipsammina mattaeformis</i>	18,239	LT854195	Abyssal Eastern Pacific, Clarion-Clipperton Zone	
<i>Shinkaiya contorta</i>	18,252	LT576124	Abyssal Eastern Pacific, Clarion-Clipperton Zone	
<i>Shinkaiya lindsayi</i>	n.a.	EU649778	Pacific, Japan Trench	
<i>Syngammina corbicula</i>	2270	HE998679	Atlantic, Cap Verde Plateau	
<i>Technitella</i> sp.	R5*	FR754395, FR754396	Norway, Oslo Fjord	
<i>Toxisarcon alba</i>	WC18H	AJ307750	Uk, Scotland, Loch Linnhe	
<i>Toxisarcon synsuicida</i>	1370	FR875140	Sweden, Tjaerno	
<i>Toxisarcon taimyr</i>	14,533	KF931124	Russia, Kara Sea	
<i>undet. monothalamid</i>	1188	AJ307751	Antarctica, New Harbor	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	1828*	OM422895	Antarctica, New Harbor	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	1829*	OM422896, OM422897	Antarctica, New Harbor	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	1918*	OM422898, OM422899	Antarctica	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	3415*	OM422900, OM422901	Weddell Sea, abyssal	Allogromia like
<i>undet. monothalamid</i>	3416*	OM422902, OM422903	Weddell Sea, abyssal	Allogromia like
<i>undet. monothalamid</i>	21,294	OM422955	UK, South Georgia, SG-09	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	21,298	OM422956	UK, South Georgia, SG-09	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	21,299	OM422957	UK, South Georgia, SG-09	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	21,382	OM422958	UK, South Georgia, SG-27	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	21,384	OM422959	UK, South Georgia, SG-27	Gloiogullmia like, agglutinated
<i>undet. monothalamid</i>	21,400	OM422960	UK, South Georgia, SG-03	Gloiogullmia like, agglutinated
CladeD				
<i>Hippocrepinella hirudinea</i>	1157	AJ307764	Antarctica, McMurdo	
<i>Hippocrepinella hirudinea</i>	3009*	LN873684, LN873685	Antarctica, McMurdo	
<i>Hippocrepinella hirudinea</i>	7863*	LN873689, LN873692	Antarctica, Admiralty Bay	
<i>Hippocrepinella hirudinea</i>	7808*	LN87369, LN873690	Antarctica, Admiralty Bay	
<i>Hippocrepinella hirudinea</i>	14310*	LN873681, LN873682, LN873683	Antarctica, New Harbor	

Table 2. (continued)

Taxa	Isolate	Accession number	Sampling site	Additional remarks
<i>Hippocrepinella hirudinea</i>	21,241	OM422931	UK, South Georgia, SG-04	
<i>Hippocrepinella hirudinea</i>	21,242	OM422932	UK, South Georgia, SG-04	
<i>Hippocrepinella</i> sp.	530	AJ307765	Sweden, Tjaerno	
<i>Hippocrepinella</i> sp.	2857	OM422929	Norway, Svalbard	
<i>Hippocrepinella</i> sp.	2865	OM422930	Norway, Svalbard	
<i>Hippocrepinella</i> sp.	4821*	OM422893	Norway, Svalbard	
<i>Hippocrepinella</i> sp.	14,308	LN873677	Antarctica, New Harbor	
<i>Hippocrepinella</i> sp.	14,309	LN873680	Antarctica, New Harbor	
<i>Hippocrepinella</i> sp.	17,369	MG980267	Chile, Beagle Channel	
<i>Hippocrepinella</i> sp.	17,371	MG980269	Chile, Beagle Channel	
<i>Hippocrepinella</i> sp.	17,372	MG980272	Chile, Beagle Channel	
<i>Hippocrepinella</i> sp.	17,373	MG980277	Chile, Beagle Channel	
<i>Hippocrepinella</i> sp.	18576*	OL772077, OL772078	Pacific, abyssal: 12° 25.196'N, 116°, 37.474'W, t	
CladeJ				
<i>Capsammina patelliformis</i>	10,069	FJ646884	Portugal, Nazaré Canyon	
<i>Capsammina patelliformis</i>	10,070	FJ646885	Portugal, Nazaré Canyon	
<i>Crithionina delacai</i>	189	AJ317988	Antarctica, McMurdo	
<i>Crithionina delacai</i>	21,390	OM422882	UK, South Georgia, SG-04	
<i>Crithionina granum</i>	156	AJ317987	Sweden, Kosterfjord	
<i>Crithionina</i> sp.	21,354	OM422880	UK, South Georgia, SG-12	
<i>Crithionina</i> sp.	21,355	OM422881	UK, South Georgia, SG-12	
<i>Crithionina</i> sp.	2008	AJ514861	Antarctica, New Harbor	
<i>Crithionina</i> sp.	K55	OM422883	Sweden, Tjaerno	
CladeY				
<i>Hilla argentea</i>	21,333	OM422871	UK, South Georgia, SG-20	
<i>Hilla argentea</i>	21,334	OM422872	UK, South Georgia, SG-20	
<i>Hilla argentea</i>	21,335	OM422873	UK, South Georgia, SG-20	
<i>Hilla argentea</i>	21,336	OM422874	UK, South Georgia, SG-20	
<i>Hilla argentea</i>	21,337	OM422875	UK, South Georgia, SG-20	
undet. monothalamid	2091	OM422864	Antarctica	finely agglutinated, flask like
undet. monothalamid	2878	OM422879	Norway, Svalbard	
undet. monothalamid	3994	OM422865	UK, Scotland, Dunstaffnage	elongate, finely agglutinated
undet. monothalamid	4008	OM422866	UK, Scotland, Dunstaffnage	elongate, finely agglutinated
undet. monothalamid	7937	OM422867	Chile, Beagle Channel	finely agglutinated, flask like
undet. monothalamid	9296*	OM422884	Japan, Yokosuka	yellow-green colour
undet. monothalamid	9300*	OM422885	Japan, Yokosuka	yellow-green colour
undet. monothalamid	9323*	OM422886	Japan, Yokosuka	yellow-green colour
undet. monothalamid	20,867	OM422868	UK, South Georgia, SG-06	finely agglutinated, flask like
undet. monothalamid	20,868	OM422869	UK, South Georgia, SG-06	finely agglutinated, flask like
undet. monothalamid	21,362	OM422870	UK, South Georgia, SG-20	finely agglutinated, flask like
undet. monothalamid	21,385	OM422876	Falkland Islands, FK-04	elongate, finely agglutinated, yellow

Table 2. (continued)

Taxa	Isolate	Accession number	Sampling site	Additional remarks
undet. monothalamid	21,387	OM422877	Falkland Islands, FK-04	elongate, finely agglutinated, yellow
undet. monothalamid	21,388	OM422878	Falkland Islands, FK-04	elongate, finely agglutinated, yellow
<i>Pseudoconqueria lenticularis</i>	20,854	OM422857	UK, South Georgia, SG-07	
<i>Pseudoconqueria lenticularis</i>	20,855	OM422858	UK, South Georgia, SG-07	
<i>Pseudoconqueria lenticularis</i>	21,328	OM422859	UK, South Georgia, SG-03	
<i>Pseudoconqueria lenticularis</i>	21,329	OM422860	UK, South Georgia, SG-03	
<i>Pseudoconqueria lenticularis</i>	21,330	OM422861	UK, South Georgia, SG-03	
<i>Pseudoconqueria lenticularis</i>	21,331	OM422862	UK, South Georgia, SG-03	
<i>Pseudoconqueria lenticularis</i>	21,332	OM422863	UK, South Georgia, SG-03	
environmental foraminiferal clone		93623_SOJABIO	JX297937	Sea of Japan, 550 m, 44.56 N; 137.12 E
undet. monothalamid	FF279*	OM422887, OM422888, OM422889	New Zealand	agglutinated, Saccammina-like
undet. monothalamid	17973*	OM422890, OM422891, OM422892	Iceland	soft walled

Taxa printed in bold indicate those investigated for the current paper

*PCR products cloned prior to sequencing.

and uniform rates among sites applied to the analysis (Kumar et al., 2016).

Results

Systematic descriptions

Rhizaria Cavalier-Smith, 2002.

Retaria Cavalier-Smith, 1999.

Foraminifera D'Orbigny, 1826.

Monothalamids Pawlowski et al., 2013.

The type material is deposited in the Natural History Museum, London, registration numbers NHMUK PM ZF 9930–9945.

Hilla gen. nov.

Diagnosis. Test elongate, approximately cylindrical, <1 mm in length with single terminal aperture. Wall very fine-grained with distinct silvery reflection.

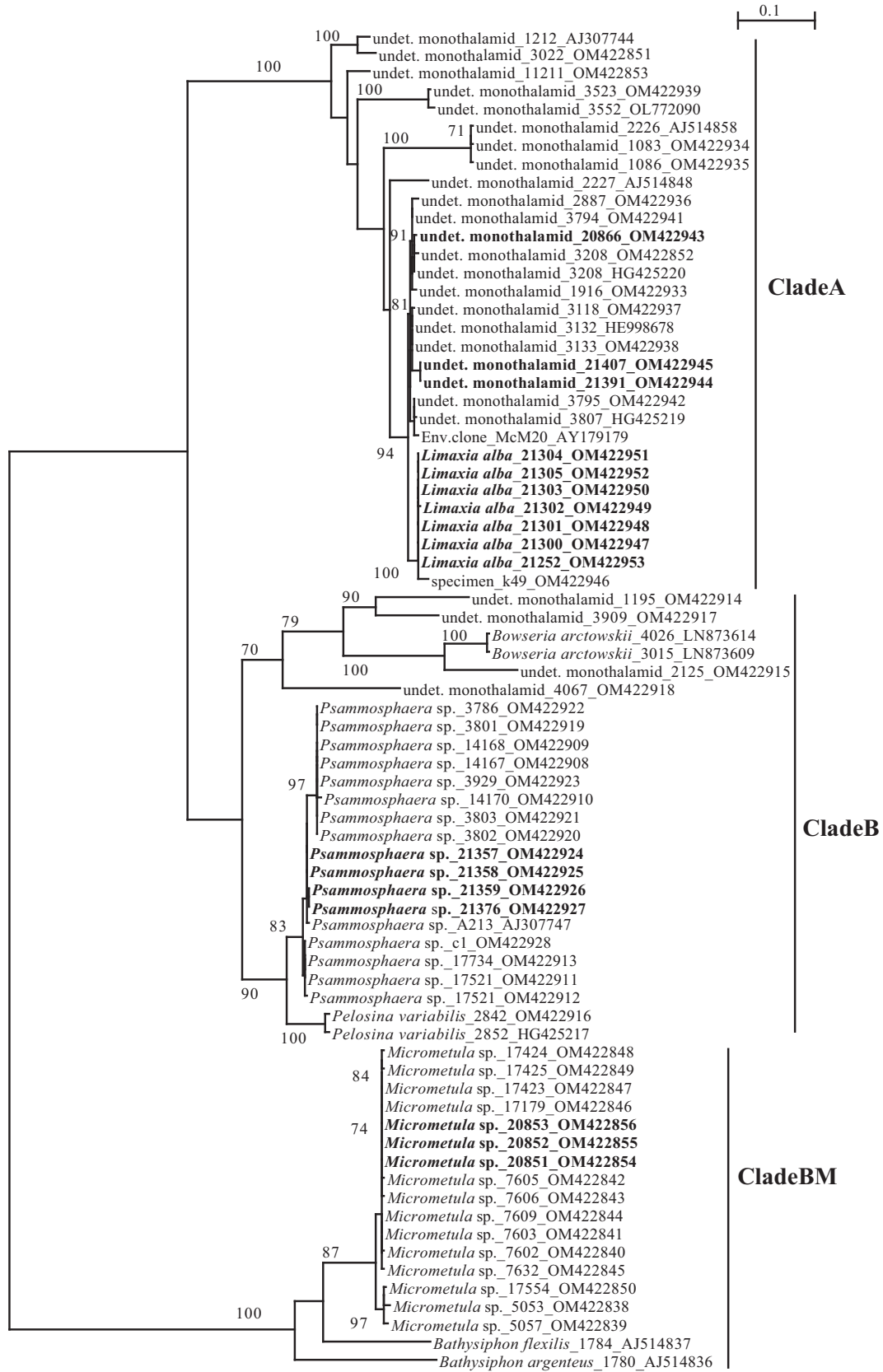
Type species. *Hilla argentea* gen. & sp. nov.

Etymology. Latin *Hilla* (feminine), meaning a small sausage.

ZooBank registration: urn:lsid:zoobank.org:pub:54405A13-5B30-4949-A168-769C2807E07B.

Remarks. Monothalamids (saccamminids) with silvery, reflective test surfaces are reported in a number of shallow- and

deeper-water settings. Höglund (1947) described *Pilulina argentea*, a species resembling ‘small balls of silver or perhaps rather of unpolished, slightly oxidized aluminium’, from the Skagerak (500–700 m depth). A ‘silver saccamminid’ resembling *P. argentea* was briefly described by Gooday et al., (1996) from Explorers Cove, Antarctica. Gooday (1986) illustrated some small, undescribed, globular saccamminids with a silvery surface sheen from the bathyal NE Atlantic (1330 m depth). These ‘silver saccamminids’ all have a more or less globular shape, and are therefore morphologically quite distinct from the new genus, which has an elongate, cylindrical test. Majewski et al. (2005) reported a variety of undescribed ‘silver saccamminids’ with either one or two apertures from West Spitzbergen fjords, including forms with more elongate, albeit somewhat irregular, morphologies (Fig. 3.4 in Majewski et al., 2005). They also recognised several morphotypes with a silvery sheen that they assigned to the genus *Phainogullmia*. Those illustrated in Fig. 3.10 of Majewski et al. (2005) were approximately cylindrical in shape and a few hundreds of microns in length. Sausage-shaped monothalamids with reflective surfaces are also known from the bathyal Arabian Sea (Gooday et al., 2008). However, these elongate morphotypes are less regular in shape than our new genus and in at least some cases have two terminal apertures. Molecular analysis of *Pilulina argentea* shows that it branches as sister to *Gloio-gullmia eurystoma* (Clade C, Fig. 3) and has no close relationship to *H. argentea* (Clade Y, Fig. 4). The only other ‘silver’



saccamminids for which genetic data exists are two morphotypes (one ovoid, the other elongate) from under the Ross Ice Shelf, both of which branch close to *Cribrothalammina alba* (Pawlowski et al., 2005; as *Hippocrepinella alba*) and are therefore unrelated to the new genus.

Hilla argentea gen. & sp. nov.

Figs. 5, 6, 13.

Diagnosis. As for genus.

Etymology. Latin *argentea*, meaning silver or silvery.

ZooBank registration: urn:lsid:zoobank.org:pub:54405A13-5B30-4949-A168-769C2807E07B.

Type material: Station SG-20, entrance to Cumberland Bay; 54° 13.536' S, 36° 24.792' W, water depth 144 m. The holotype (reg. no. NHMUK PM ZF 9930) and 4 paratypes (reg. no. NHMUK PM ZF 9931–9934) are preserved in 10% formalin.

Other material. Station SG-20. Five sequenced specimens (isolates 21333–21337).

Description. The test is approximately cylindrical, ranging in length from 535 μm to 755 μm (mean 647 μm) in the type specimens (Table 3). The maximum width ranges from 74 to 104 μm (mean 85 μm) and usually varies somewhat along the length of an individual specimen, with minimum values of 67 to 93 μm (mean 82 μm). The abapertural end is evenly rounded and the apertural end tapers into a short tubular or nipple-like extension. The end is open, possibly damaged, in paratype 2 (Fig. 5E), but more often, notably in paratype 1, it appears to be partially closed (Fig. 6E). The test wall is very finely agglutinated, basically pale greyish but with a distinct silvery reflection. In optical sections of individual specimens, it has an even thickness of 4.6–5.5 μm (paratype 4) to 7.3–8.2 μm (holotype). The cell body is usually separated from the test wall by a narrow space of inconsistent width, but otherwise fills most of the test lumen. The cytoplasm, as viewed through the test wall, appears finely granular without any obvious large inclusions, apart from a single nucleus (diameter 36.6–51.2 μm), visible in the holotype (Fig. 6G) and two of the paratypes. In paratype 3, a peduncle-like strand of cytoplasm extends inward from the aperture inside a peduncular sheath (Fig. 6F). A similar feature is weakly developed in paratype 4 (Fig. 6D).

Molecular characteristics. *Hilla argentea* specimens from South Georgia are part of the monothalamid Clade Y (Fig. 4) and form a relatively well-supported (87% BV) group that branches as sister to a clade containing undescribed monothalamids from South Georgia (20867, 20868), Antarctica (2091) and the Beagle Channel (7937). However, this branching is not supported by the BV. The partial SSU rDNA sequences of *H. argentea* contain 806 nucleotides and the GC content is 43.7%.

Remarks. The silvery, reflective surface of the test serves to distinguish *Hilla argentea* from other finely-agglutinated, tubular monothalamids, including *Conqueria laevis* Gooday and

Pawlowski, 2004, described from the abyssal Weddell Sea, and *Hippocrepinella alba* (Heron-Allen and Earland, 1932), described from South Georgia. The surface of the former species has a 'slight satin-like sheen' (Gooday and Pawlowski, 2004), and the latter has a whitish, non-reflective test surface (Nyholm, 1956). Both are generally larger (up to 1.4 and 2.8 mm, respectively) and morphologically more variable than the new species (Heron-Allen and Earland, 1932; Nyholm, 1956; Gooday and Pawlowski, 2004).

Pseudoconqueria gen. nov.

Diagnosis. Test < 600 μm in length and asymmetrically lenticular (spindle-shaped), apertural end slightly produced, with single terminal aperture. Test wall very fine-grained, opaque, with whitish, non-reflective surface.

ZooBank registration: urn:lsid:zoobank.org:pub:54405A13-5B30-4949-A168-769C2807E07B.

Type species. *Pseudoconqueria lenticularis* gen. & sp. nov.

Remarks. The asymmetrical, spindle-like test morphology distinguishes *Pseudoconqueria* from other elongate monothalamids with whitish, finely agglutinated walls, such as *Hippocrepinella*, *Cribrothalammina* and *Conqueria*. These genera are also generally larger and display a greater degree of variability than the new genus (Heron-Allen and Earland, 1932; Earland, 1934; Nyholm, 1956; Gooday and Pawlowski, 2004), as well as being genetically distinct from it.

Pseudoconqueria lenticularis gen. & sp. nov.

Figs. 7, 8, 13.

Diagnosis. As for genus.

Etymology. English lenticular (lens-shaped), derived from Latin lenticularis.

ZooBank registration: urn:lsid:zoobank.org:pub:54405A13-5B30-4949-A168-769C2807E07B.

Type material: Station SG-03, Antarctic Bay; 54° 06.200' S, 36° 58.800' W, water depth 111 m. The holotype (reg. no. NHMUK PM ZF 9935) and 2 paratypes (reg. no. NHMUK PM ZF 9936–9937) are preserved in 10% formalin.

Other material. Station SG-03. Five sequenced specimens (isolates 21328–21332). Station SG-07. Two sequenced specimens (isolates 20854, 20855). Sea of Japan. Environmental clone 93623_SOJABIO (Lejzerowicz et al., 2013).

Description. The test is subfusiform to somewhat lenticular in shape, widest in front of the midpoint, tapering towards apertural end and more gradually towards the abapertural end. Specimens range from almost straight to gently curved. The holotype is 503 μm long, 74 μm wide at the widest point, tapering to 34 μm near the abapertural end. The corresponding dimensions for the paratypes are 448 μm , 68 μm and 28 μm (paratype 1) and 535 μm , 89 μm and 27 μm (paratype 2). The overall dimensions of the 17 specimens (including the types) that were studied morphologically are: length = 280–574 μm (mean 467.8 \pm 82.8 μm), maximum width = 70–102 μm (mean 69.7 \pm 14.4 μm). The length/width ratio ranges from 5.64 to 7.53 (mean 6.76 \pm 0.53). The apertural end typically

Fig. 2. PhyML phylogenetic tree based on the 3' end fragment of the SSU rRNA gene, showing the evolutionary relationships of 74 monothalamid foraminiferal sequences belonging to Clades A, B, BM. Taxa marked in bold indicate those for which sequences were acquired for the present study. The tree is unrooted. Specimens are identified by their isolate numbers (1st) and accession numbers (2nd). Numbers at nodes indicate bootstrap values (BV). Only BV >70% are shown.

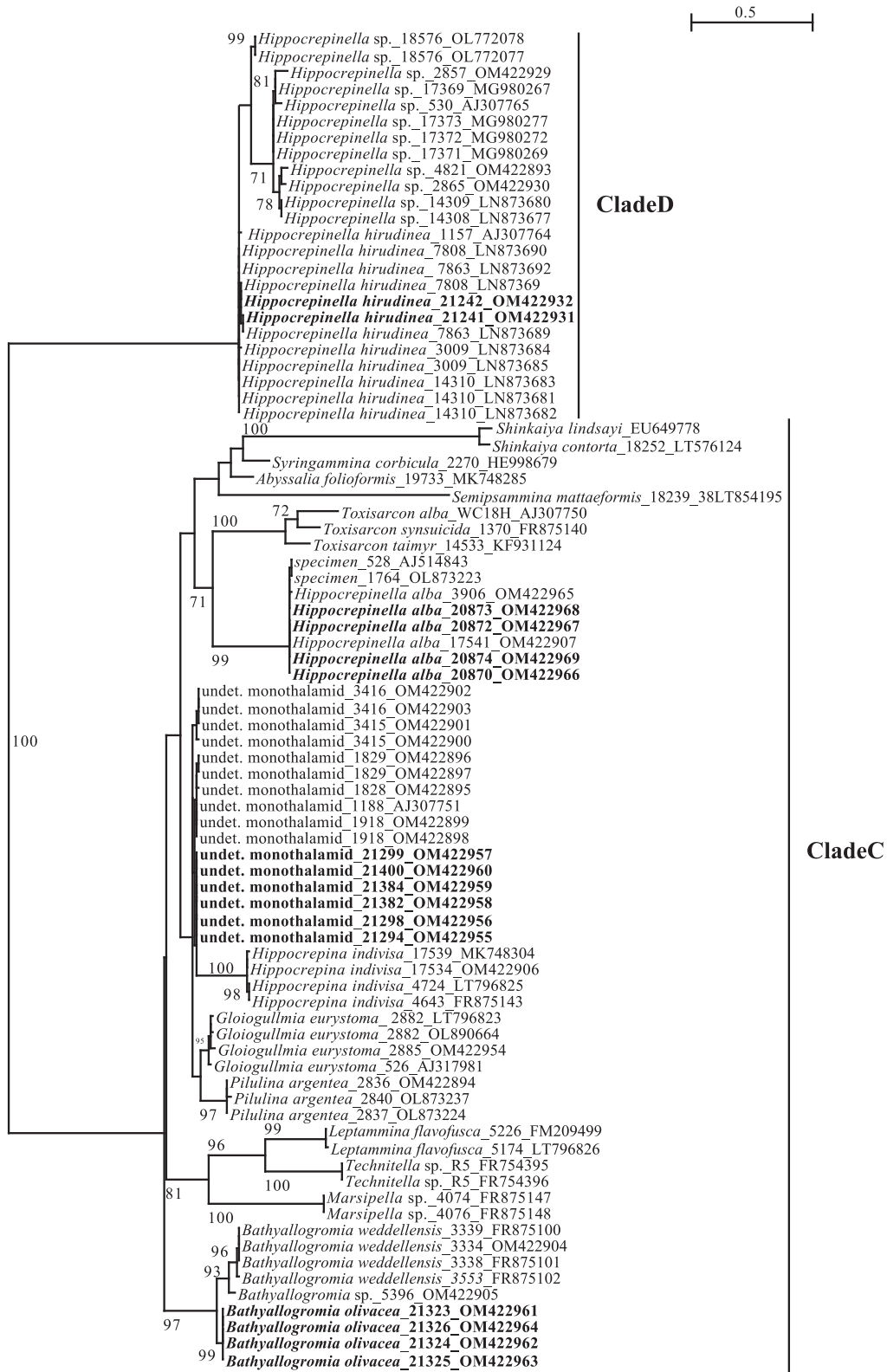


Fig. 3. PhyML phylogenetic tree based on the 3' end fragment of the SSU rRNA gene, showing the evolutionary relationships of 82 monothalamid foraminiferal sequences belonging to Clades C, D. Taxa marked in bold indicate those for which sequences were acquired for the present study. The tree is unrooted. Specimens are identified by their isolate numbers (1st) and accession numbers (2nd). Numbers at nodes indicate bootstrap values (BV). Only BV > 70% are shown.

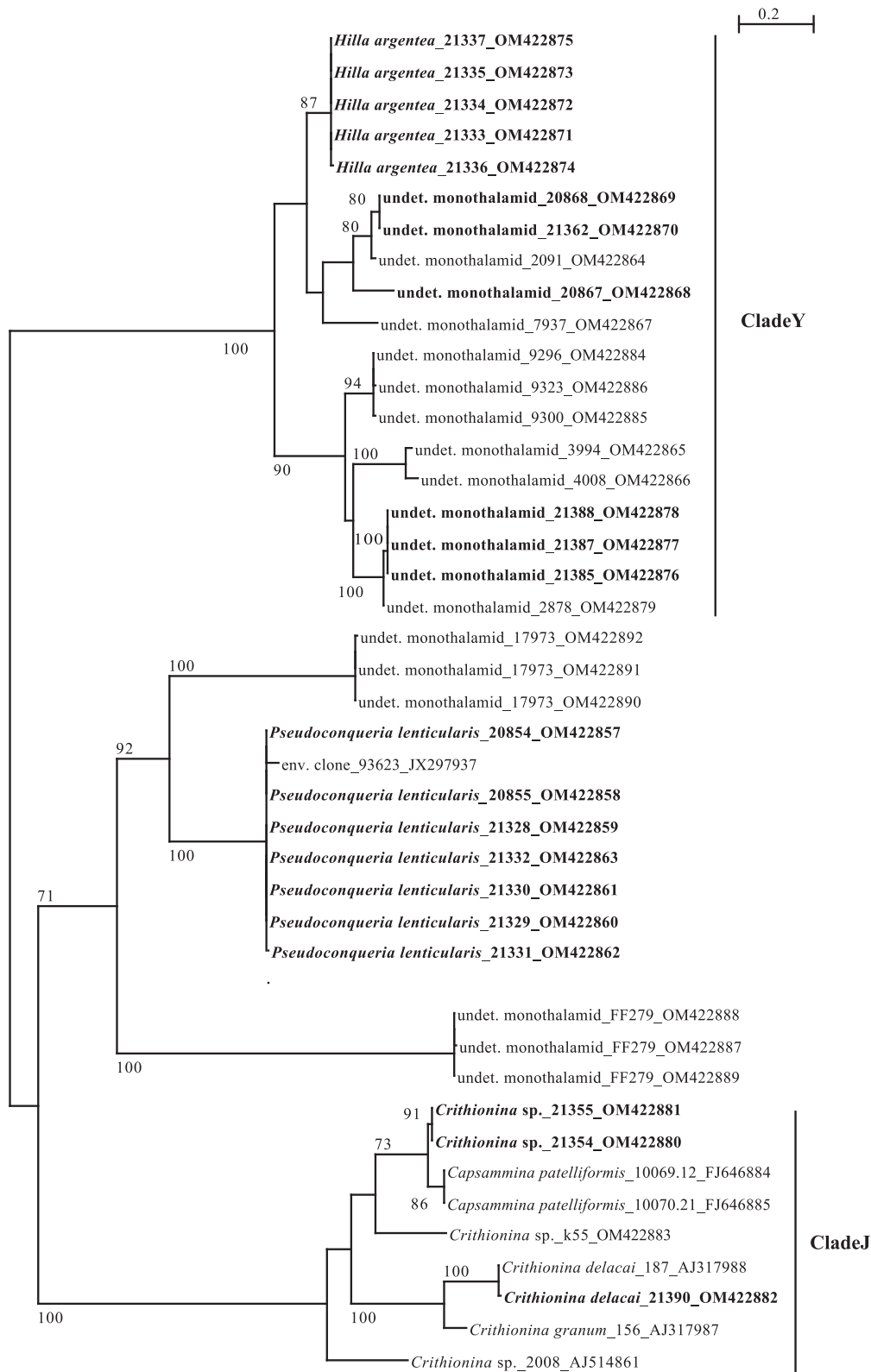


Fig. 4. PhyML phylogenetic tree based on the 3' end fragment of the SSU rRNA gene, showing the evolutionary relationships of 43 monothalamid foraminiferal sequences belonging to Clades J, Y and a new monothalamid lineage. Taxa marked in bold indicate those for which sequences were acquired for the present study. The tree is unrooted. Specimens are identified by their isolate numbers (1st) and accession numbers (2nd). Numbers at nodes indicate bootstrap values (BV). Only BV > 70% are shown.

Table 3. Test dimensions of type specimens. All measurements in microns.

Specimen	Length	Width max	Width min
Holotype	203	104	92.9
Paratype 1	687	74.3	66.9
Paratype 2	595	74.3	91.0
Paratype 3	535	100	92.9
Paratype 4	665	74.3	66.9

merges with a short neck. In the holotype, where the neck is fairly well developed, it is around 21 μm long and 17 μm wide (Fig. 7C, D). In other specimens the neck may be shorter or hardly developed at all, possible as a result of breakage. The abapertural end is narrowly rounded. The test wall is pale greyish and has a dull, non-reflective surface. It is very finely agglutinated, with a scattering of tiny dark particles and a few reflective particles (about 1–2 μm in size) visible using a compound microscope and reflected light (20x objective). The wall is largely opaque and little can be seen of the interior when the

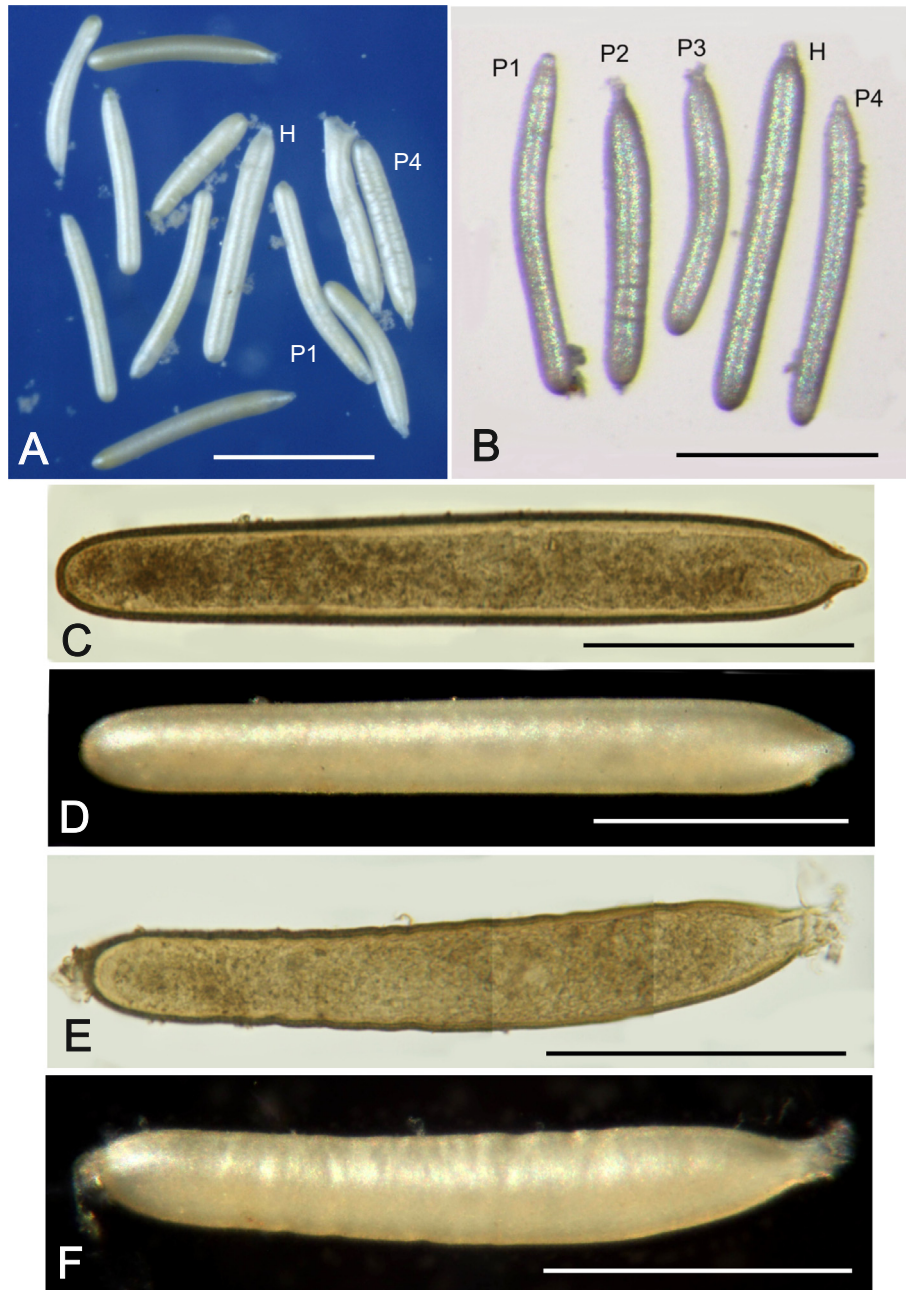


Fig. 5. *Hilla argentea*. (A) Freshly collected, unfixed specimens photographed in South Georgia soon after collection. The Holotype (H) and Paratypes 1, 3 and 4 (P1, P3, P4) are indicated; paratype 2 cannot be confidently identified. (B) Holotype and paratypes photographed in Southampton using a combination of reflected and transmitted light. (C, D) Holotype photographed using a compound microscope with Nomarski interference optics (C) and reflected light (D). Scale bars = 0.50 mm (A, B), 0.25 mm (C–F).

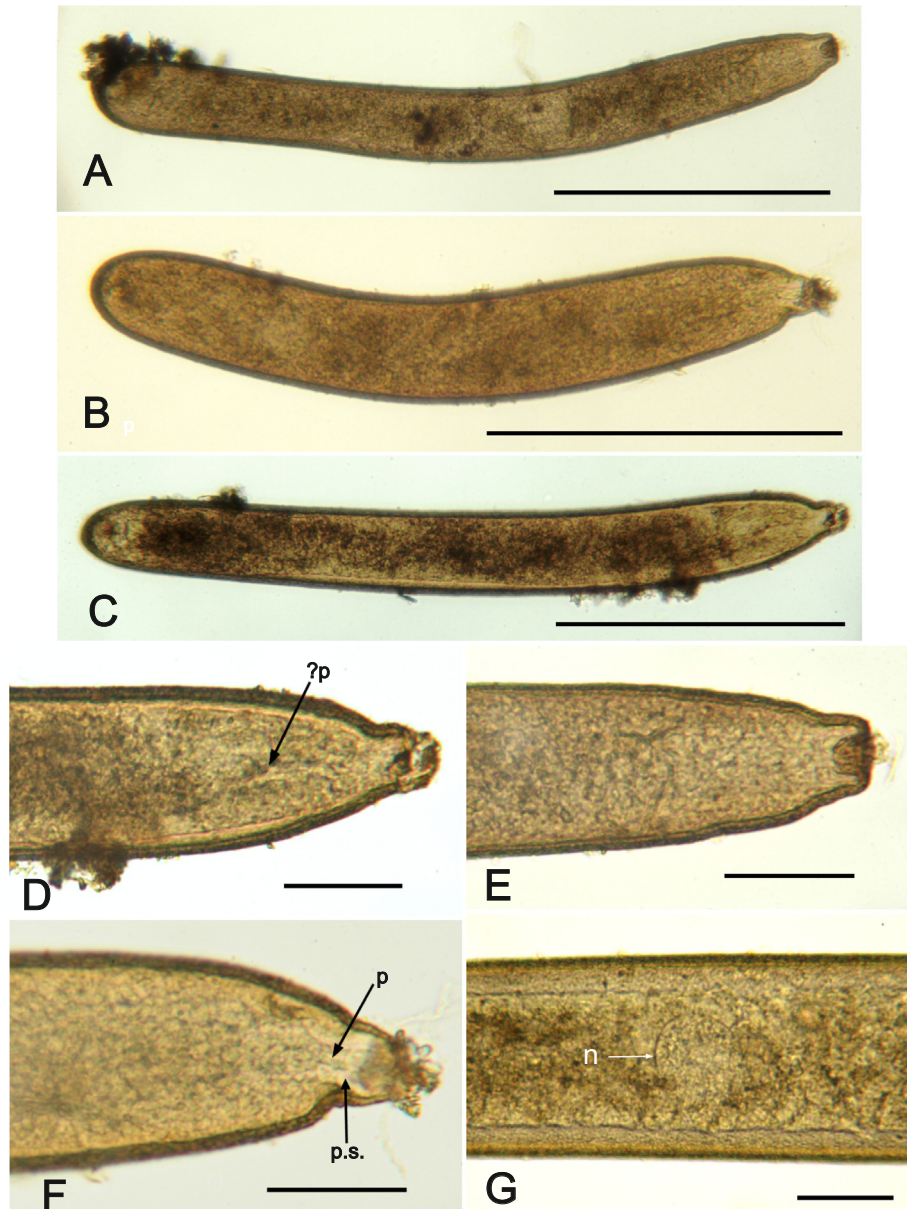


Fig. 6. *Hilla argentea*. (A) Paratype 1. (B) Paratype 3. (C) Paratype 4. (D–F) Details of apertural ends. (D) Paratype 4. (E) Paratype 1. (F) Paratype 3. (G) Detail of holotype showing nucleus. N = nucleus; p = peduncle; p.s. = peduncular sheath. Scale bars = 0.50 mm (A–C); 50 μ m (D–G).

test is viewed in glycerol using transmitted light (Fig. 8A, C, E). However, the wall can be dimly discerned in optical section; it ranges in thickness from approximately 8.3 to 10.4 μ m towards the apertural end and 3.1 to 4.2 μ m at the abapertural end.

Molecular characteristics. *Pseudoconqueria lenticularis* forms a new monothalamid lineage supported by 100% BV (Fig. 4). The species branches next to undescribed monothalamids from Iceland (17973) supported by 92% BV. The sister to this group is an undetermined monothalamid from New Zealand (FF279), but the support for this relation is rather weak (71%BV). Sequence length of *P. lenticularis* ranges from

929 to 1086 nucleotides and the GC content ranges from 43.6% to 44.4%.

Remarks. In terms of its test morphology and composition, *Pseudoconqueria lenticularis* is closest to *Conqueria laevis* Gooday and Pawlowski, 2004. Some of the small specimens of *C. laevis* included in Fig. 1 of Gooday and Pawlowski (2004) have a similar general appearance to the new species. However, our specimens are more lenticular and relatively wider than *C. laevis* (length/width ratio 5.6–7.5 compared to 6.8–15.8). *Pseudoconqueria lenticularis* also resembles an undetermined fusiform saccamminid from Admiralty Bay, West-Antarctica (Fig.4.15 in Majewski et al., 2007). The fusi-

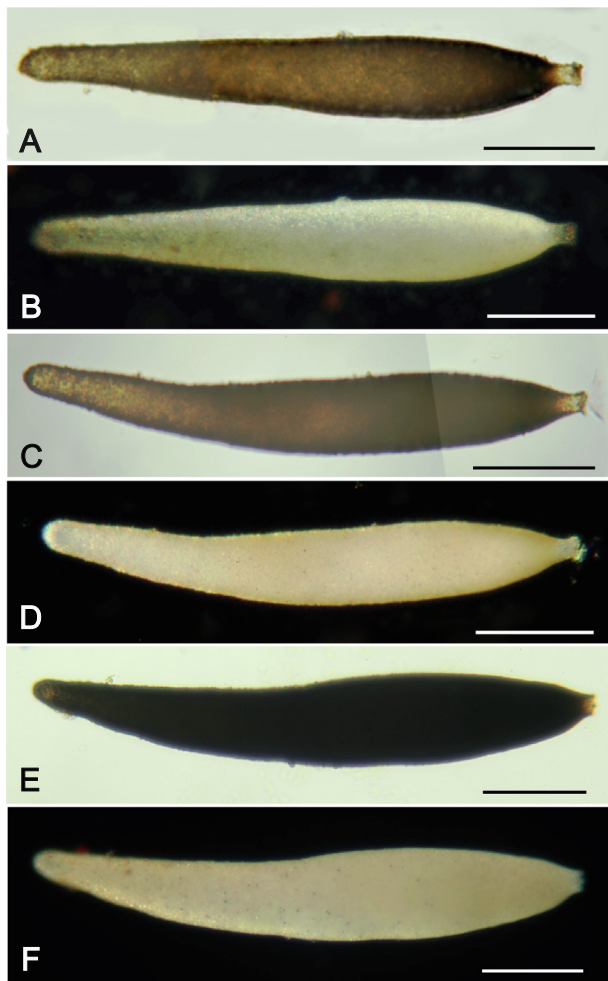


Fig. 7. *Pseudoconqueria lenticularis*. (A–D) Freshly collected, unfixed specimens photographed soon after collection in South Georgia. (E, F) Preserved specimens. Holotype (H) and Paratypes 2 (P2) are indicated; Paratype 1 could not be confidently identified. Scale bars = 0.50 mm (E, F).

form saccamminid has an aperture placed on a short neck and its test is finely agglutinated although darker than in *P. lenticularis*. The figured specimen in Majewski et al. (2007) is also larger (1600 μm long, 300 μm wide).

***Limaxia* gen. nov.**

Diagnosis. Test elongate, <1 mm in length, generally subcylindrical with bluntly pointed apertural end and single indistinct terminal aperture. Wall transparent, relatively thick, often with some particles adhering to outer surface. Cell body whitish with long peduncular sheath; stercomata absent.

Etymology. Latin: derivative of *limax* (slug), referring to the somewhat slug-like appearance.

ZooBank registration: urn:lsid:zoobank.org:act:A230A7C6-93C8-40BB-9B4D-7EF3E75D20F5.

Remarks. Compared to *Gloioquillmia* Nyholm, 1974, *Limaxia* is smaller, with an inconspicuous aperture and a simpler wall structure that comprises a single relatively thick structure rather than two ‘more or less separated, semitransparent membranes’ (Nyholm, 1974). It is also generally smaller and less elongate

than either *Bowseria* Sinniger, Lecroq, Majewski, & Pawlowski, 2008 or *Cylindrogullmia* Nyholm, 1974 and often has particles adhering to the test surface, as well as different apertural characteristics.

***Limaxia alba* gen. & sp. nov.**

Figs. 9, 10, 13.

Diagnosis. As for genus.

Etymology. Latin: *albus* (white), referring to the colour of the cell body.

ZooBank registration: urn:lsid:zoobank.org:act:78DD4C91-BA39-447F-934E-38F5C6243D0B.

Type material. Station SG-13, Cumberland East Bay; 54° 21.936' S, 36° 22.486' W, water depth 28 m. The holotype (reg. no. NHMUK PM ZF 9938) and 4 paratypes (reg. no. NHMUK PM ZF 9939–9942) are preserved in 10% formalin.

Other material. Station SG-01. One sequenced specimen (isolate 21252), Station SG-13. Six sequenced specimens (isolates 21300–21305). Sweden, Tjaerno, one sequenced specimen (isolate k49) may also belong in this species.

Description. The test is elongate, generally subcylindrical and straight or slightly curved with approximately parallel sides, but occasionally more ovoid (Fig. 9). The abapertural end is evenly rounded and the apertural end bluntly pointed. The holotype is 537 μm long and 139 μm wide at the widest point (L/W ratio = 3.86). Paratypes 1 and 2 are, respectively, 537 and 570 μm long and 141 and 137 μm wide (L/W ratios 3.80 and 4.16). The overall dimensions of the 26 specimens (including the types) that were studied morphologically are: length = 359–688 μm (mean 500.0 \pm 80.7 μm), maximum width = 116–217 μm (mean 154.7 \pm 14.4 μm). The length/width ratio ranges from 2.44 to 4.16 (mean 3.25 \pm 0.42). The test wall is transparent, often with some detritus adhering to the surface of freshly collected specimens. In optical sections the wall appears to be quite thick (6–8 μm) with little space between it and the whitish cell body, which occupies the test lumen. The aperture is indistinct but seems to be a simple opening with no obvious associated structures. In the holotype and paratype 2, an invagination (peduncular sheath) extends into the cytoplasm beneath the aperture (Fig. 10). It is about 120 μm long and 20–30 μm wide in the holotype and about 95 μm long and about 30 μm wide in paratype 2. There is no clearly defined peduncle in either of these specimens. The cytoplasm is finely granular with scattered darker inclusion, possibly mineral grains. A large nucleus (50–55 μm diameter) is sometimes visible.

Molecular characteristics. *Limaxia alba* (100%BV) is part of Clade A (Fig. 2) and branches next to undescribed monothalamids from South Georgia (20866, 21391, 21407), Antarctica (1916, 3118, 3132, 3133, 3208, 3794, 3795, 3807, env.-clone_McM20) and Svalbard (2887). The branching is strongly supported (94%BV). Sequence length of *L. alba* amounts to 873 nucleotides and the GC content is 43.2%.

Remarks. The new species is most similar to *Gloioquillmia eurystoma* Nyholm, 1974 in the shape of the test and the apparently sticky nature of the surface, as indicated by the adherence of particles to some specimens. The main differences are its smaller size (359–688 μm versus 600–2000 μm), the simpler structure of the wall, which comprises a single relatively thick layer rather than two layers (‘membranes’), and the inconspicuous aperture, which is quite different from large opening present in *G. eurystoma* (Nyholm, 1974). In molecular analyses,

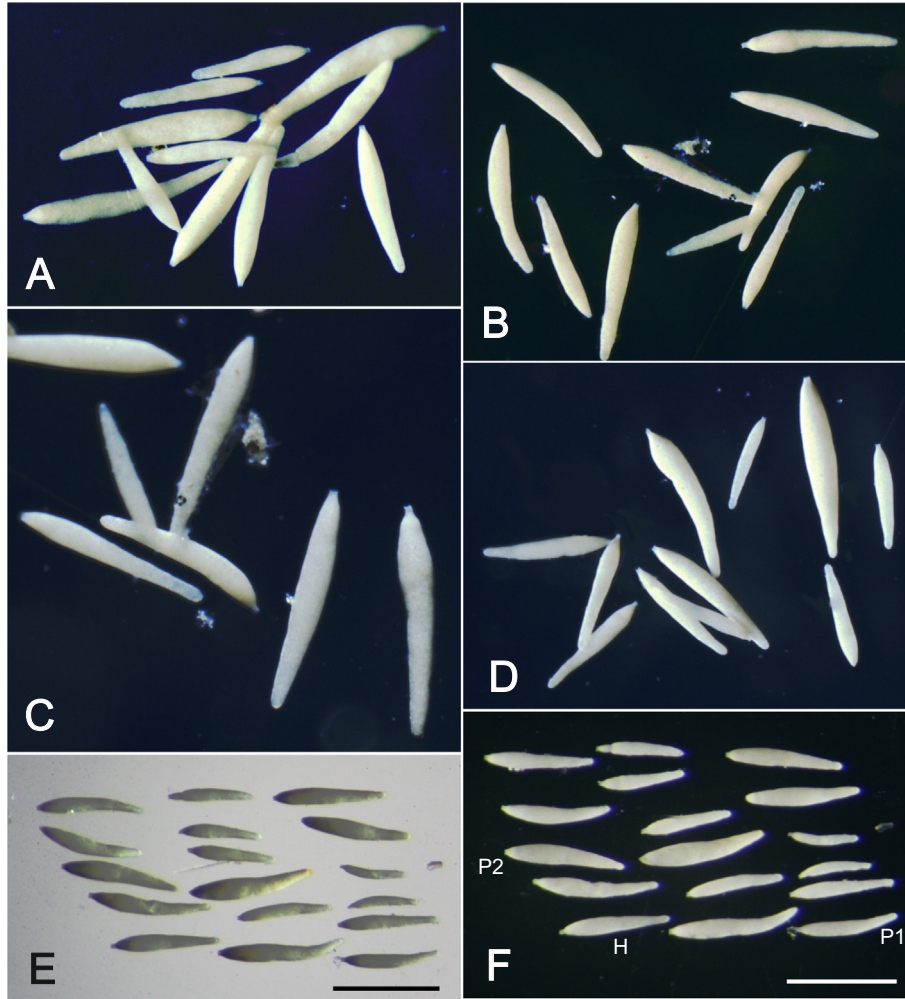


Fig. 8. *Pseudoconqueria lenticularis*. Type specimens photographed using a compound microscope with transmitted (A, C, E) and reflected (B, D, F) light. (A, B) Holotype; (C, D) Paratype 1; (E, F) Paratype 2. Scale bars = 0.10 mm.

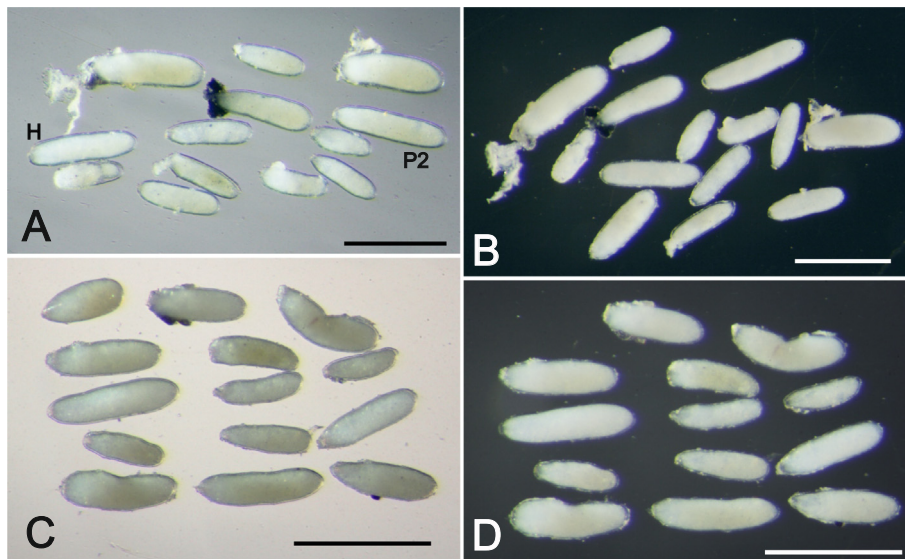


Fig. 9. *Limaxia alba*. Two collections of preserved specimens, photographed using a stereo-microscope under different lighting conditions. H = Holotype; P2 = Paratype 2; Paratype 1 could not be confidently identified. Scale bars = 0.5 mm.

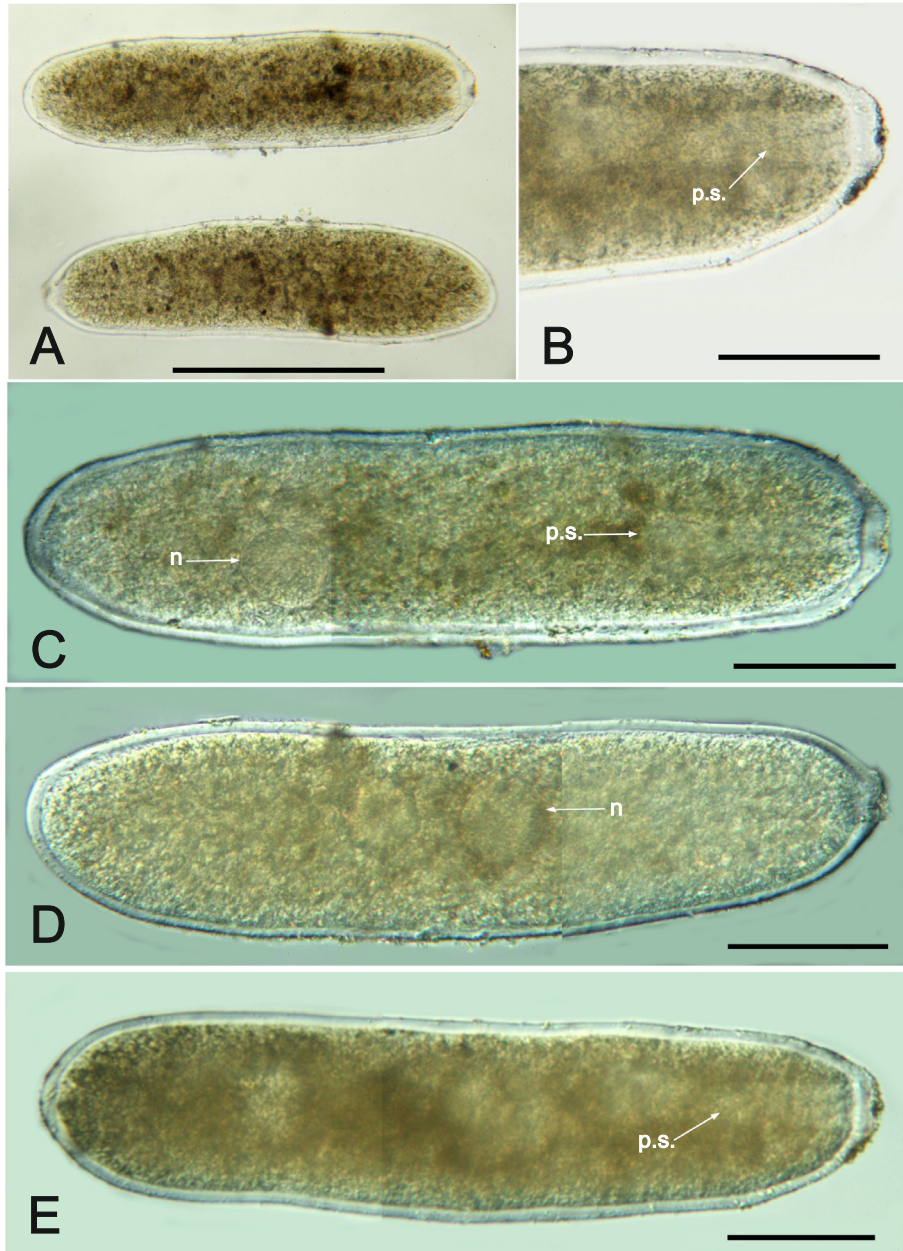


Fig. 10. *Limaxia alba*. Preserved specimens, photographed using a compound microscope with either normal (A, B) or Nomarski Interference (C–E) illumination. (A) Holotype (upper) and Paratype 1 (lower). (B) Apertural end of Holotype. (C) Holotype. (D) Paratype 1. (E) Paratype 2. n = nucleus; p.s. = peduncular sheath. Scale bars = 0.25 mm (A); 0.10 mm (B); 0.10 mm (C–E).

G. eurystoma branches as sister to *Pilulina argentea* (Clade C, Fig. 3) and is not related to *L. alba*, which is part of Clade A (Fig. 2).

Bathyallogromia Gooday, Holzmann, Guiard, Cornelius, Pawlowski, 2004.

Bathyallogromia olivacea sp. nov.

Figs. 11, 12, 13.

Diagnosis. Species of *Bathyallogromia* with ovate test, length 269–433 μm , width 181–278 μm , length/width ratio 1.27–1.59 (mean 1.45). Cytoplasm in fresh specimens typically yellowish olive in colour.

Etymology. Latin: *olivacea* olive-coloured, referring to the colour of the cell body.

ZooBank registration: urn:lsid:zoobank.org:act:E747DFEE-188E-4D91-8A4A-0B4AA78F3295.

Type material: Station SG-27, Stromness Bay; 54° 09.372' S, 36° 38.426' W, water depth 136 m. The holotype (reg. no. NHMUK PM ZF 9943) and 2 paratypes (reg. no. NHMUK PM ZF 9944–9945) are preserved in 10% formalin.

Other material. Station SG-27, Stromness Bay. Four sequenced specimens (isolates 21323–21326).

Description. The test is more or less symmetrically ovate, with a circular cross section and a slightly produced apertural end

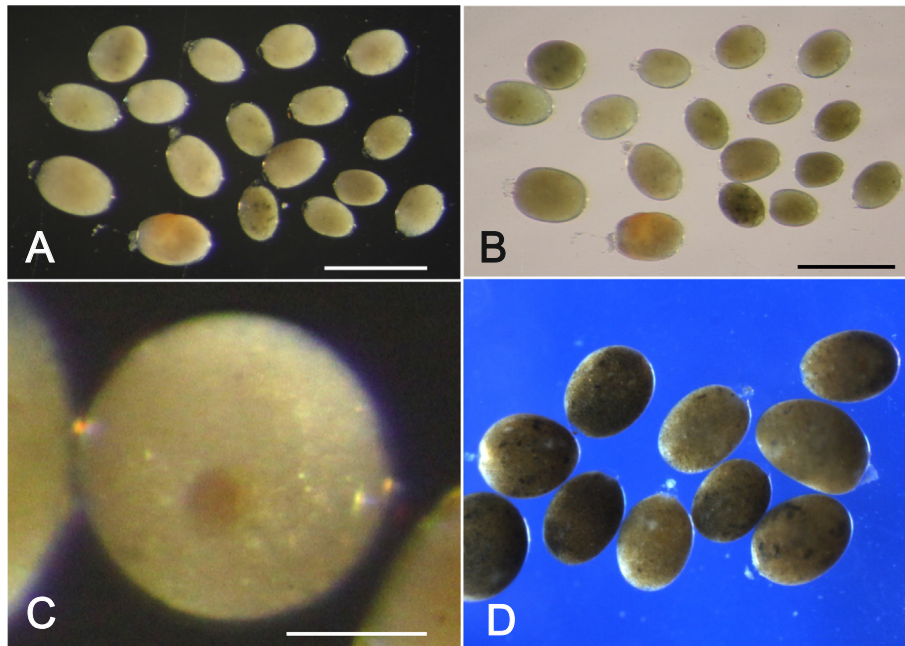


Fig. 11. *Bathyallogromia olivacea*. (A, B) Collection of preserved specimens, photographed using a stereo-microscope under different lighting conditions. The yellowish, olive-green colour of the cytoplasm is not accurately represented in these images. (C) End-on view of specimen showing opening of peduncular sheath. (D) Freshly collected, unfixed specimens photographed soon after collection. Scale bars = 0.50 mm (A, B); 0.10 mm (C). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 11). The holotype is 370 μm long (including the apertural structure) and 233 μm wide (L/W ratio = 1.59). The overall dimensions of the 17 specimens (including the types) that were studied morphologically are: length = 269–433 μm (mean 314.4 \pm 42.2 μm), maximum width = 181–278 μm (mean 217.4 \pm 26.4 μm). The length/width ratio ranges from 1.27 to 1.59 (mean 1.45 \pm 0.103). The apertural structure (Fig. 8) usually forms a low, truncated mound with sloping sides, and seems to be at least partly solid. It projects between 10 and 21 μm beyond the general outline of the test and is 53–64 μm wide near the base. This structure is more prominently developed in paratype 4, projecting approximately 45 μm beyond the general outline, with a basal width of about 85 μm (Fig. 12G,H). The aperture appears to be a simple opening, approximately 15–26 μm wide, that narrows into a channel through the apertural structure (Fig. 12F). In the holotype, a strand of cytoplasm (width 9.3–10.7 μm), the peduncle, extends through the channel and into the test, where it occupies a peduncular sheath within the cell body (Fig. 12C). The sheath, although without a peduncle, is also visible in the paratypes (Fig. 12D–H). It is approximately 42–73 μm long and 36–52 μm wide. The test wall is transparent, flexible, entirely organic, about 4.5–8.2 μm thick, and very smooth, with a reflective highlight and devoid of adhering particles. The interior is almost completely occupied by the cell body, which has an olive-green colour in fresh specimens. The cytoplasm is finely granular but includes variable numbers of mineral grains of different sizes and shapes (Fig. 12B). A single large nucleus is sometimes visible when the test is viewed in glycerol under a compound microscope (Fig. 12B). It ranges from 58.9 to 75.5 μm diameter in 4 specimens.

Molecular characteristics. *Bathyallogromia olivacea* (99% BV) branches with *B. weddellensis* (3334, 3338, 3339, 3553) from Weddell Sea, as well as *Bathyallogromia* sp. (5396) from the North Greenland Sea (Fig. 3). The genus is strongly supported (97% BV). The partial SSU rDNA sequences of *B. olivacea* contain 970 nucleotides and the GC content is 40.1%.

Remarks. The only other described species of this genus is *Bathyallogromia weddellensis* from the bathyal and abyssal Weddell Sea (Gooday et al., 2004). Compared to *B. weddellensis*, the new species is slightly longer but also slightly narrower (mean length 314 and width 217 μm versus 251 and 231 μm , respectively). As a result, the test is ovate rather than almost spherical in shape (mean length/width ratio 1.45 versus 1.09).

Molecular phylogeny

The monothalamid sequences obtained from South Georgia and the Falkland Islands cluster in seven clades, previously described by Pawłowski et al. (2002a) and one new monothalamid lineage.

Limaxia alba (100% BV) is the first morphologically described species belonging to Clade A (Fig. 2). This clade also comprises a large number of undetermined monothalamids that include three isolates from South Georgia forming a well-supported group with several undetermined monothalamids from Antarctica and Svalbard (81% BV). Clade A is strongly supported (100% BV) and branches

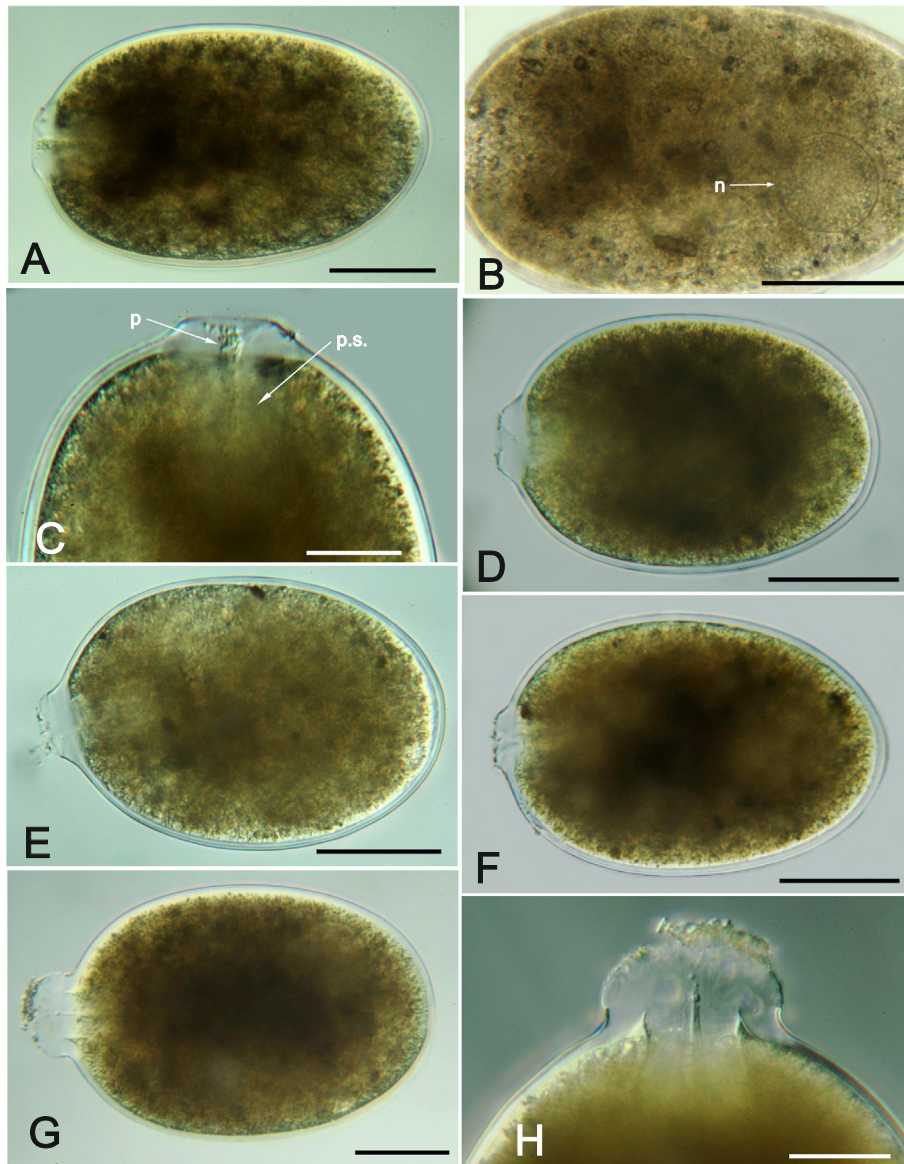


Fig. 12. *Bathyallogromia olivacea*. Preserved specimens photographed in glycerol and with Nomarski Interference illumination, except where indicated otherwise. (A–C) Holotype. (A) Entire specimen. (B) Photograph taken with normal illumination showing nucleus (n) and mineral particles in cytoplasm. (C) Apertural end showing peduncle (p) within peduncular sheath (p.s.). (D) Paratype 1. € Paratype 2. (F) Paratype 3. (G, H) Paratype 4. (G) Entire specimen. (H) Detail of apertural structure. Scale bars = 0.10 mm (A, B, D–G); 0.05 mm (C, H).

as sister to Clade B that consists of undetermined monothalamids and *Bowseria arctowskii* (70% BV) branching next to *Pelosina variabilis* and *Psammosphaera* sp. (90% BV). The genus *Psammosphaera* contains several isolates from South Georgia branching with sequences obtained from Antarctica and Patagonia (83% BV). Clade BM (100% BV) branches at the base of Clade A and Clade B and contains *Bathysiphon argenteus* and *B. flexilis* branching next to *Micrometula* sp. (87% BV). The latter genus consists of two closely related groups, one comprising sequences from South Georgia, Antarctica and Patagonia, the other comprising sequences from Patagonia and British Columbia (Canada).

Bathyallogromia olivacea (99% BV) is a member of Clade C (Fig. 3) and branches as sister to *Bathyallogromia* sp. from the East Greenland shelf and *B. weddellensis* from the Weddell Sea. The three species of *Bathyallogromia* are supported by 97% BV. In addition to *Bathyallogromia*, there are twelve monothalamids from South Georgia that branch within Clade C. Six cluster together with several other undetermined monothalamids from Antarctica, but their grouping is not well resolved. *Hippocrepinella alba* is represented by four sequences from South Georgia that are very close to specimens from Sweden and Antarctica. Finally, two monothalamid sequences from South Georgia identified as *Hippocrepinella hirudinea* branch together

with other representatives of this species from Antarctica, within Clade D.

Hilla argentea (87% BV) clusters within Clade Y (Fig. 4) and branches as sister to undescribed monothalamids from South Georgia, Antarctica and Patagonia. Clade Y includes also the sequences of six other monothalamids from South Georgia. Three of them branch closely to the isolate 2091 from McMurdo Sound and isolate 7937 from Admiralty Bay near the Antarctic Peninsula. The other three sequences form a strongly supported clade (100%) with isolate 2878 from Svalbard.

Two sequences of *Crithionina* sp. from South Georgia branch in Clade J as sister to a deep-sea species *Capsamina patelliformis*. However, their branching is only weakly supported (73% BV). We also obtained a sequence of *Crithionina delacei* from South Georgia, branching together with *C. delacei* from McMurdo, Antarctica.

Pseudoconqueria lenticularis represents a new monothalamid lineage and branches next to an undescribed monothalamid from Iceland (92% BV).

Remarks on the genus *Hippocrepinella*

Heron-Allen and Earland (1932) and Earland (1934) described two important monothalamid species from South Georgia, *Hippocrepinella hirudinea* and *H. alba*, both of which have subsequently been reported from different parts of the world. They were assigned to the same genus based on the presence in both of an elongate, thick-walled, finely-agglutinated test with apertures at both ends. *Hippocrepinella hirudinea* is the type species of the genus, while *H. alba* was established by Goldstein and Barker (1988) as the type species of a new genus, *Cribrothalammina*. However, their re-description of the species was based on specimens from Sapelo Island, Georgia, in which gametes were released from an array of distinctive pore during part of the life cycle. Our molecular data clearly show that *H. hirudinea* and *H. alba* are unrelated genetically (Fig. 3), and at the same time genetic data for *Cribrothalammina alba* from Sapelo Island (accession number AJ318225) show that it branches in a different clade (Pawlowski et al., 2002a) and is not related to *Hippocrepinella alba* from South Georgia. The designation of *Hippocrepinella alba* as type species of the genus *Cribrothalammina* is therefore problematic. A taxonomic revision is required in order to resolve the resulting muddle, but for the moment we refer to the South Georgia species by its original name, *Hippocrepinella alba*.

Specimens of *H. hirudinea* have also been sequenced from several Antarctic locations. Pairwise distances between the sequences of South Georgia specimens show no differences but range from 0 to 0.003 between *H. hirudinea* from South Georgia and Antarctica. Sequences of *H. hirudinea* from other localities in the Northern and Southern hemisphere (not shown in Fig. 3) reveal that this morphos-

pecies encompasses a number of cryptic species that are genetically distinct from populations in the South Georgia type area (Holzmann et al. unpublished). *Hippocrepinella alba* has representatives in Antarctica and Patagonia and very similar sequences have been obtained from Swedish isolates (Tjaerno and Gullmar Fjord) (Table 2). Pairwise distance within specimens from South Georgia ranges from 0 to 0.001. Differences between *H. alba* from South Georgia, Antarctic and Patagonia range from 0.001 to 0.005 while differences between *H. alba* from the Southern hemisphere and the Swedish isolates range from 0.004 to 0.007.

Discussion

Importance of monothalamids in coastal settings.

Many monothalamids, particularly small, delicate forms, have a poor fossil record and are commonly either disregarded in foraminiferal studies, or destroyed when sample residues are dried. When an effort is made to look for them in wet sieve residues, monothalamids are often found to be common and diverse, with many undescribed species and higher taxa revealed by morphological and genetic data (Gooday et al., 1996; Pawlowski et al., 2002b; Habura et al., 2008; Majewski et al., 2007). Unfortunately, they can be distinguished by only a limited range of morphological characteristics, such as wall composition (organic, finely or coarsely agglutinated) and consistency (flexible, rigid), and test shape (elongate, round, oval etc.). An additional problem is that many soft-walled species can change their shape during movements (Holzmann et al., 2021). A combination of morphology and genetics is therefore important when describing this poorly-known component of foraminiferal diversity.

Here we use this integrative morphological and genetic approach to reveal that the diversity of monothalamids in the sub-Antarctic fjords of South Georgia is much greater than previously appreciated. Earland (1934) had earlier described some monothalamids from this area, but only the larger forms with more robust tests, including well-known species such as *Hippocrepinella hirudinea*, that were not destroyed by the rather harsh sample processing methods he used. Based on this new material, we describe four small, delicate, but relatively common monothalamid species, three of which represent new genera. *Hilla argentea* and *Pseudoconqueria lenticularis* possess finely agglutinated tests while *Limaxia alba* has a basically organic wall with some sparse particles agglutinated to it and *Bathyallogromia olivacea* has a transparent wall entirely composed of organic material. These four species can be readily distinguished morphologically, although similar morphotypes have been described from other areas (Gooday and Pawlowski, 2004; Majewski et al., 2005). Each species branches in a different clade, which correspond to high-level taxonomic groups of monothalamids (Pawlowski et al., 2002a).

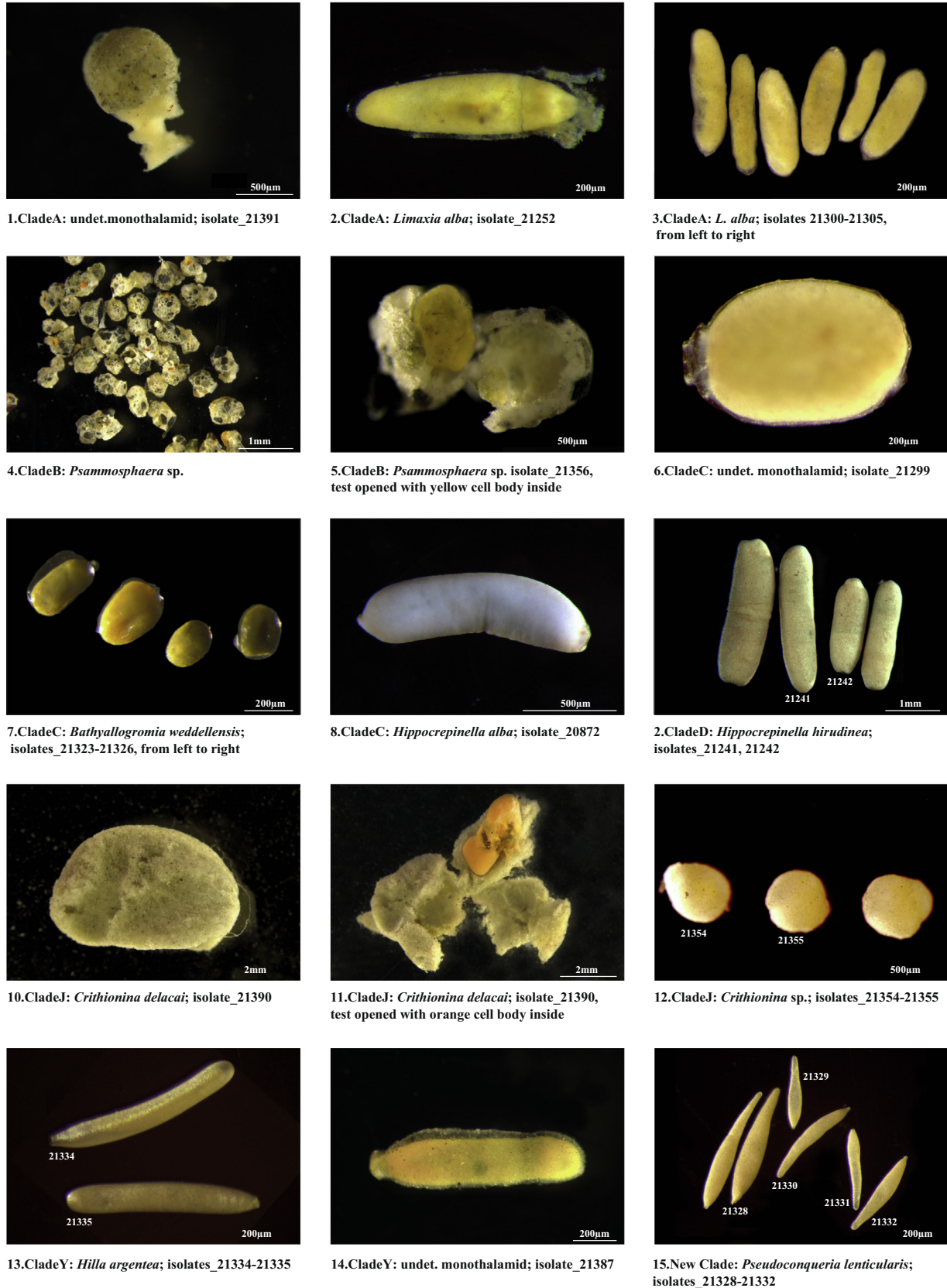


Fig. 13. Sequenced specimens belonging to Clades A, B, C, D, J, Y and the new Clade. Photographs taken with Leica M205C.

We recognize another nine monothalamid morphospecies, most of them undescribed. Some of the undetermined taxa included in our phylogenetic trees resemble described genera morphologically (Table 2, Fig. 13), but are genetically distinct. Together, these newly described and undescribed species for which we have both genetic and morphological data, in addition to those described earlier by Earland (1934) for which DNA sequences are not available, represent a level of monothalamid diversity similar to that in the Antarctic (McMurdo and New Harbor) samples of Pawlowski et al. (2002b).

Biogeography

Intensive studies over almost two centuries have generated a vast body of information regarding the distribution of hard-shelled, mainly multichambered foraminiferal morphospecies in coastal and sublittoral habitats. Foraminiferal distributions have been particularly well studied around the margins of North and Central America. The large database compiled by Culver and Buzas (1998) suggests that more than half of species are confined to one of five regions around the continent. This is consistent with the general view that morphospecies have narrower geographical ranges in coastal and sublittoral settings than in the deep sea (Gooday and Jorissen, 2012). However, although this appears to be true in many cases, there are still some morphospecies that appear to have wide ranges in shallow water (Murray, 2006).

Molecular data relevant to the issue of species ranges are much more limited but generally consistent with that derived from morphology. For example, a recent monographic treatment of the coastal genus *Ammonia* that integrated genetics and morphology concluded that most have restricted distributions, while a few occurred across different oceans (Hayward et al., 2021). Compared to the well-known, hard-shelled multichambered foraminifera, our understanding of the monothalamid biogeography is in its infancy, although with the advantage of being based to a much larger extent on genetics. The present study provides some new insights based on integrated morphological and genetic data for monothalamids from a sub-Antarctic setting.

The genus *Bathyallogromia* was first described from the abyssal Weddell Sea (Gooday et al., 2004) and *B. olivacea* is the first representative from a sublittoral fjord environment. The genus seems to be adapted to cold-water regions and has a bipolar distribution, with one undescribed species being known from 100-m depth on the East Greenland Shelf. Pairwise distance within *B. olivacea* ranges from 0 to 0.002 while the difference between *B. weddellensis* and *B. olivacea* are much greater (0.049–0.053).

Bathyallogromia olivacea and *Hilla argentea* are currently recorded only in South Georgia. On the other hand, isolate k49 from Tjaerno (Sweden) yielded a sequence that

branches with *Limaxia alba* from South Georgia, but with a pairwise distance of 0.010–0.012 compared to only 0–0.001 within the South Georgia population. Similarly, an environmental clone (93623_SOJABIO) obtained from sediment samples collected at 550 m depth in the Japan Sea (Lejzerowicz et al., 2013), branches with *Pseudoconqueria lenticularis* from South Georgia, but with a pairwise difference of 0.011–0.013 compared to only 0–0.003 within the South Georgia population. The 93623_SOJABIO clone is not associated with any morphologic information and the morphology of the Tjaerno specimen close to *L. alba* is undocumented. The lack of morphological information, combined with the relatively high genetic distances between *L. alba*, *P. lenticularis* and their respective Northern hemisphere relatives, make interpretation of these isolated sequences from localities that are geographically distant from South Georgia difficult.

Some of the undescribed monothalamids are widely distributed in the Southern Ocean. Clade C (Fig. 2, Table 2) contains species from South Georgia (isolates 21294, 21298, 21299, 21382, 21384, 21400) that are closely related to sequences from Antarctica (isolates 1188, 1828, 1829, 1918, 3415, 3416) with an overall genetic mean distance of 0.009. Another large group of closely related monothalamids branches as sister to *Limaxia alba* (Clade A, Fig. 2, Table 2). The group contains representatives from South Georgia (20866, 21391, 21407), Antarctica (1916, 3118, 3132, 3133, 3208, 3795, 3807, McM20) and also one sequence from Svalbard (isolate 2887); the overall genetic mean distance is 0.016.

Conversely, this study extends the geographical range of some monothalamid groups from Antarctic to sub-Antarctic and southern temperate regions. This is true in the case of *Psammosphaera* sp. (Clade B, Fig. 2, Table 2), a species that has been sequenced from South Georgia (isolates 21357–21359, 21376), Antarctica (isolates A213, 3801–3803, 3786, 3929, 14167, 14168, 14170) and Patagonia (c1, 17521, 17534), with an overall genetic mean distance of 0.009. Similarly, the closest relatives of *Micrometula* sp. (Clade BM, Fig. 2, Table 2) from South Georgia (isolates 20851–20853) are Patagonian specimens (isolates 7602, 7603, 7605, 7606, 7609, 7632, 17434–17425, 17179), with an overall genetic mean distance of 0.002. The genus *Micrometula* (Nyholm, 1952) is also represented in cold water regions of the Northern hemisphere, having first been described from the Gullmar Fjord, Sweden. Clade Y (Fig. 4, Table 2) contains a group of undescribed monothalamids from the Falkland Islands (isolates 21385, 21387, 21388) branching close to a sequence obtained from Svalbard (isolate 2878), the with a pairwise distance of 0.004 compared to 0 within the Falkland population.

Our South Georgia samples yielded specimens of a *Crithionina* species with a large, very poorly cemented test, that were morphologically consistent with those described from coastal waters in New Harbor, McMurdo Sound,

Antarctica as *Crithionina delacai* (Gooday et al., 1995). We obtained a single sequence from a S. Georgia specimens (Clade J, Fig. 4,) that was identical to the sequence of *C. delacai* from New Harbor. This suggests that the distribution of the species might extend beyond the Antarctic. *Crithionina delacai* is very similar morphologically to *C. granum*, a species found in Norwegian waters (Goës, 1894; Höglund, 1947). Genetic data show that these two species are closely related (Fig. 4).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

WM was responsible for organising and leading the overall South Georgia/Falklands campaign, obtaining funding, planning the sampling strategy in South Georgia, and preparing Fig. 1. JP provided additional funding. JP, MH and AJG conceived the study and picked monothalamids from the samples. AJG undertook the descriptive work, and compiled Figs. 5–12; JP was responsible for photographs taken in South Georgia and AJG for those taken in Southampton. MH was responsible for DNA extraction, amplification and sequencing, carrying out the phylogenetic analysis, preparing Figs. 2–4. MH and AJG drafted the manuscript. All authors participated in the field work and contributed to the manuscript.

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