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Monothalamous foraminiferans and gromiids (Protista) from western Svalbard: A preliminary survey

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Abstract

Monothalamous foraminifera were abundant in sediment samples from fjords and offshore areas around western Svalbard (water depth range 26–2472 m). The >500 μm fractions of samples from the inner parts of fjords yielded numerous delicate "allogromiids" (organic-walled) "saccamminids" and "psammosphaerids" (agglutinated), including species assigned to *Cylindrogullmia*, *Gloiogullmia*, *Nemogullmia* and *Toxisarcon*. Larger, more robust, tubular agglutinated species were abundant in the outer reaches of Tempelfjord, Isfjord and Van Meijenfjord (*Hyperammina subnodosa*, *Hippocrepinella crassa*), on the current-influenced upper slope off Isfjord (*Pelosina variabilis*, *Rhabdammina abyssorum*), and the deeper part of the continental slope off Isfjord (e.g. *Hyperammina crassatina*). Oval and sausage-shaped organisms resembling gromiids (probably relatives of the foraminifera) were sometimes abundant in the fjords. Finer size fractions (63–500 μm) of fjord samples yielded a rich variety of monothalamous species. Among the allogromiids, *Micrometula* sp. was widely distributed, while *Tinogullmia* sp. and an undescribed species were restricted to single stations in Kongsfjord and Van Meijenfjord, respectively. Saccamminids common in the finer fractions included *Conqueria* spp., *Psammophaga* sp., and undescribed species with silvery, white and brownish tests. Many of the smaller allogromiids and saccamminids in our Svalbard samples resemble species found in the Gullmarfjord on the Swedish west coast.

Key words: *Arctic, allogromiids, foraminifera, fjords, gromiids, saccamminids*

Introduction

Foraminifera are ubiquitous members of marine, soft-bottom communities, particularly in cold-water, deep-sea and high-latitude settings where they frequently constitute a substantial proportion of benthic standing stocks and biomass (e.g. Tendal & Hessler 1977; Thies 1991; Snider et al. 1984; Gooday et al. 1996; Korsun et al. 1998; Kuznetzov & Burministrova 1997). Monothalamous (single-chambered) species are often a conspicuous component of these assemblages. They include species with relatively simple, soft-walled, agglutinated or organic-walled tests and others that belong to larger, more robust, agglutinated genera such as *Bathysiphon*, *Hyperammina*, *Pelosina* and *Rhabdammina*. These taxa are considered to be modern representatives of the basal foraminiferal radiation and, therefore, have considerable phylogenetic importance (e.g. Pawlowski et al. 2003a). In recent years, detailed studies have been conducted of monothalamous foraminifera in Explorers Cove, Antarctica (e.g. Gooday et al. 1996; Pawlowski et al. 2002a), as well as at deep-water sites in the Northeast Atlantic, Indian and Pacific Oceans (Gooday et al. 2001, 2004; Gooday 2002). They remain frequently overlooked, however, in shallow-water habitats. Records from coastal Arctic settings are largely confined to

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recent reports by Korsun and colleagues, in which a number of species were recognized but not identified (Korsun 2002 and references therein).

Multilocular calcareous and agglutinated foraminifera from the fjords of western and northern Svalbard are well known from previous investigations (Hald & Korsun 1997; Korsun & Hald 2000; Korsun 2002). Thies (1991) identified some large monothalamous taxa in her study of foraminifera in the northern North Atlantic. Some of her samples were collected on the continental slope west of Svalbard (>622 m water depth). Szymelfenig et al. (1995) included foraminifera in a study of intertidal meiobenthos around the shores of Svalbard, but did not differentiate species. In the present study, we examined samples from several fjords along the west coast of the archipelago, and from deeper sites on the adjacent continental shelf and slope, in order to obtain foraminifera for molecular genetic and ultrastructural work. Because living specimens were required for these purposes, the samples (>500 and 125–500 μm fractions) were sorted immediately and without fixation. These extensive collections yielded large numbers of monothalamous foraminifera, comprising a mixture of allogromiids, psammosphaerids, saccamminids and large agglutinated species. We later examined the finer size fractions (>63 μm) of fixed sediment from three selected sites in order to document the smaller species. Our main aim was to provide a descriptive overview of monothalamous foraminifera around western Svalbard. Additionally, we asked (1) how similar are these Arctic assemblages to those from other sublittoral settings and (2) can their distribution patterns be related to known environmental parameters? We hope this survey will provide a framework for future more detailed studies of Arctic monothalamous foraminifera and their relationship to similar faunas in Explorers Cove and other southern hemisphere sites.

Physical setting

The archipelago of Svalbard is situated between 76 and 80°N and is bordered by the Arctic Ocean to the north, the Barents Sea to the south and east, and the Norwegian Sea to the west (Figure 1A). The landmass is dominated by sedimentary rocks (Steel & Worsley 1984). The islands are incised by fjords with a typical glacial morphology that includes troughs and sills. Modern glaciation covers approximately 40% of the terrain. Many outlet glaciers reach sea level, feeding icebergs and, in summer, meltwater into the fjords.

The study area includes the continental slope and shelf off the western coast of Svalbard and three fjords, Isfjord (including its tributary, Tempelfjord), Kongsfjord and Van Miejenfjord (Figure 1A). The continental margin west of Svalbard is characterized by a narrow shelf with a typical glacial morphology represented by shallow banks between glacial troughs, the latter forming a continuation of the east–west trending fjords. The continental slope has a relatively steep gradient of 4–5°. Due to strong currents, the sediments are predominantly coarse grained, especially on banks and along the shelf break. The fjord basins are dominated by muddy sediments. Extremely fluid, unconsolidated glaciomarine muds, settled as meltwater fallout, accumulate in fjord heads in the vicinity of tidewater glacier termini.

The oceanography of the western coast of Svalbard is influenced by saline (35.0–35.1‰) and relatively warm (1–7°C) Atlantic water transported northward along the shelf break by the West Spitzbergen Current, an end member of the Gulf Stream. The sea ice conditions vary with the season and degree of exposure to storm waves, and in response to the oceanic circulation around the archipelago (Dowdeswell & Dowdeswell 1989). A continuous cover of fast ice forms in the major fjord systems and other sheltered coastal areas by about late November and is usually retained until late May or June (Wadhams 1981). Pack ice may be present along the western coast of Svalbard between November and April, but its density is minimal compared with other parts of the archipelago due to the presence of the warm West Spitzbergen Current (Vinje 1985).

Fjords that lack sills have extensive water exchange with the adjacent ocean. Atlantic water easily penetrates into such fjords and, owing to its high salinity, normally remains in the lower part of the water column (Węslawski et al. 1991). A hyposaline (30–34‰) surface layer forms in the fjords during the melt season and cold (<−1°C) local water forms during sea ice formation in autumn and winter. In silled fjords that have limited exchange with the ocean, this cold water is trapped in depressions and may persist until next winter. Even in fjord basins isolated by shallow sills, oxygen deficiency has never been observed.

The inner basin of Kongsfjord (80 m water depth) is isolated by a 25m sill. Several large glaciers calve into this small area, producing extensive meltwater plumes. During the present study, glaciomarine mud was recovered at all stations (0773–0776; Figure 1B) located in the basin. Negative temperatures were recorded below 60 m water depth. A sample obtained in the outer basin of Kongsfjord (Stn 0777, 115 m water depth) seaward of the sill

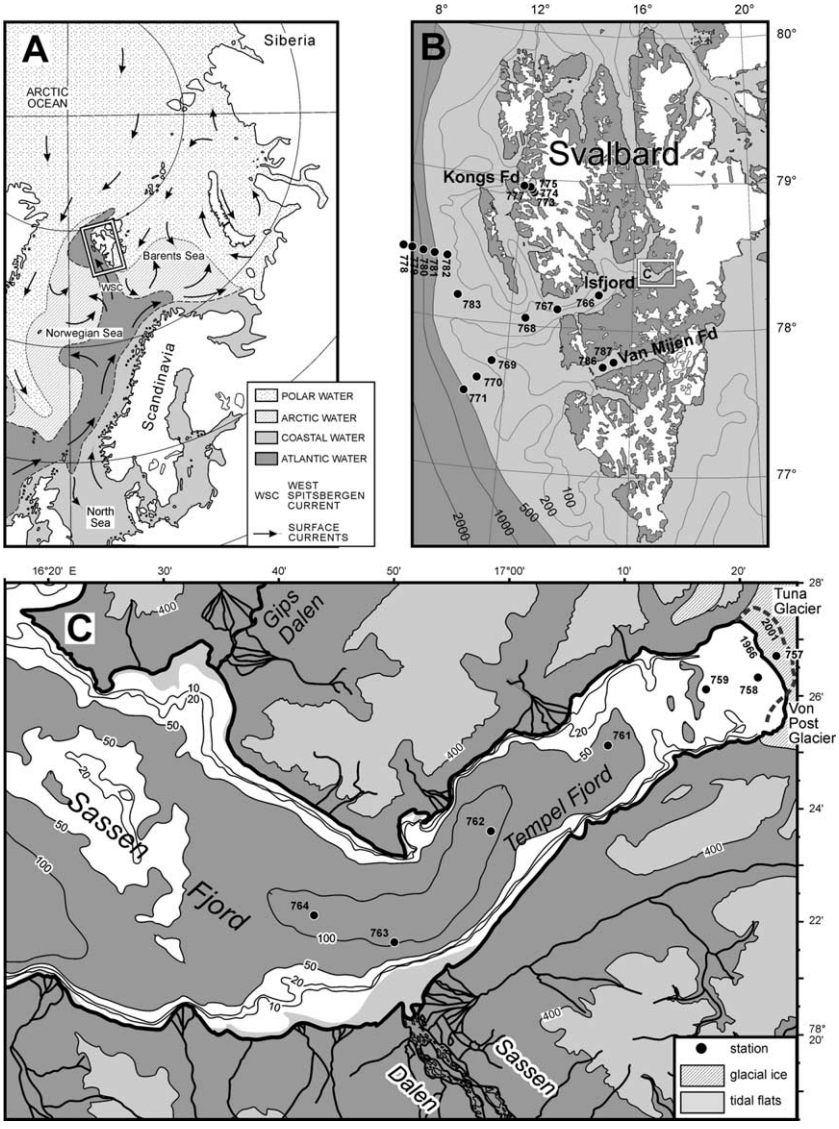

Figure 1. Locality map.

was characterized by a positive bottom-water temperature and marine mud.

Isfjord, the largest fjord of Svalbard, lacks sills in its outer reaches (200–400 m water depth) and thus has a good water exchange with the ocean. Bottom temperatures are always positive here. Sediments are typical marine muds. Tempelfjord (110 m water depth), a tributary of Isfjord, is partially isolated from the main basin by a sill depth of 80 m water depth. A transect of seven stations was sampled along the axis of this fjord (Figure 1C). Two large outlet glaciers feed meltwater into the fjord head. Glaciomarine mud extends 7 nautical miles (about 13 km) from the termini (Stns 0757–0762). The sediment is marine mud at the two outer stations (0763, 0764). We recorded negative temperatures below 65 m water depth. However, the presence of cold bottom waters is probably not typical of Tempelfjord. Korsun & Hald (2000) never observed negative bottom-water temperatures during their year-long survey period.

Van Meijenfjord (115 m water depth) is nearly closed from the ocean by a shallow sill of 25 m water depth, which allows only a very modest inflow of Atlantic water. The basin retains cold local water with temperatures often less than -1°C (Gulliksen et al. 1985; Hald & Korsun 1997; Hald et al. 2001). A small tidewater glacier calves from the northern flank of the fjord mouth and several large outlet glaciers coalesce in the fjordhead. Two stations (0786, 0787) sampled in the central part of the basin were located beyond the reach of meltwater plumes emanating from the glaciers and were therefore characterized by marine mud.

Materials and methods

The material for this study was collected during the August 2001 Cruise of the RV *Jan Mayen* at 27 sites off western Svalbard (Figure 1B, C, Table I). Except at two stations where material was obtained using a Sneli sledge (Stn 0766) and Van Veen Grab (Stn 0770 deployment 2), all samples were taken using an USNEL-type box corer, surface area 0.25 m^2. Once the corer was on deck, the overlying water was drained off and the sediment surface examined. Cores with obviously disturbed or washed surfaces were rejected. In the case of acceptable cores, any large, obvious benthic foraminifera were first removed using forceps before subcores and sediment subsamples were taken for a variety of purposes. Surficial sediment (upper few centimetres) from the remaining areas of undisturbed surface was scooped off using a small beaker and immediately sieved on deck into four size fractions (>1000, 500–1000, 250–500, 125–250 μm). These were placed in a constant temperature room maintained at ambient seafloor temperature (~2°C). Additional small volumes of undisturbed surficial sediment (upper 0.5 or 1.0 cm layer) were removed using a small spoon and fixed immediately in 10% formalin buffered with Borax®.

The two coarser residues (500–1000, >1000 μm) were sorted as soon as possible on the ship under a Wild M5 binocular microscope. The two finer size fractions (125–250, 250–500 μm) were kept cool and returned to the University Courses on Svalbard (UNIS) laboratory in Longyearbyen where they were sorted for benthic foraminifera within a period of approximately 1 week. Representative specimens of all species were photographed using a Nikon CoolPix digital camera attached to the binocular microscope. Some individuals were frozen in liquid nitrogen or fixed in glutaraldehyde for subsequent molecular and ultrastructural study. Others were fixed in 10% Borax-buffered formalin for later morphological examination.

Table I. Station data.

Station	Gear	Latitude°N	Longitude°E	Water depth (m)
Tempelfjord				
0757#1	Box core	78°56.26′	17°22.95′	26
0758#1	Box core	78°26.25′	17°20.74′	46
0759#1	Box core	78°26.01′	17°16.98′	34
0761#1	Box core	78°25.05′	17°08.36′	71
0762#2	Box core	78°23.49′	16°58.06′	104
0763#1	Box core	78°21.58′	16°49.55′	80
0764#1	Box core	78°22.14′	16°40.23′	92
0765#1	Box core	78°21.58′	16°27.54′	65
Konigsfjord				
0773#1	Box core	78°53.32′	12°28.63′	70
0774#1	Box core	78°55.83′	12°23.03′	54
0775#1	Box core	78°57.78′	12°19.29′	82
0777#1	Box core	78°55.19′	12°15.03′	106
Van Meijenfjord				
0786#1	Box core	77°44.79′	14°55.00′	114
0787#1	Box core	77°45.98′	15°09.85′	107
Isfjord				
0766#1	Sneli sledge	78°15.77′	14°49.48′	246
0767#1	Sneli sledge	78°07.84′	13°29.02′	281
0767#2	Box core	78°07.84′	13°29.02′	281
0768#1	Box core	78°03.92′	12°29.57′	248
0769	Box core	77°42.61′	11°30.40′	246
0770#2	Van Veen Grab	77°38.02′	11°00.04′	313
Isfjord trough and slope				
0771	Box core	77°34.45′	10°37.46′	994
0778	Box core	78°24.05′	08°05.41′	2472
0779	Box core	78°23.59′	08°21.89′	2000
0780	Box core	78°23.39′	08°44.23′	1532
0781	Box core	78°23.98′	09°06.50′	1032
0782	Box core	78°24.02′	09°35.74′	504
0783	Box core	78°16.33′	09°45.53′	313

The analysis of fixed surficial sediment samples from three stations (0764, 0774, 0783) was conducted at the National Oceanography Centre, Southampton (NOC). Small volumes of sediment were sieved on 300, 125, and 63 μm screens, stained overnight in rose Bengal, and sorted for all stained foraminifera under a Wild M5 binocular microscope. Specimens were placed in cavity slides in glycerol and the soft-walled monothalamous species examined further and photographed under an Olympus BH2 compound photomicroscope.

In order to provide an overview of the size distribution of monothalamous foraminifera, 679 individuals from the >63 and >125 μm fractions of fixed and unfixed samples were measured (accuracy 10 μm) using a micrometer eyepiece. The measurements were made on all specimens available at NOC. These included (i) all those extracted from the three fixed samples (>63 μm fraction) that were sorted at NOC and (ii) all specimens from the unfixed samples (>125 μm) that were sorted on the ship or at UNIS and subsequently fixed and brought back to NOC for further study. Note that the remainder of the specimens sorted on the ship or in Svalbard were taken to other laboratories for particular purposes, e.g. to Geneva for molecular analyses, and were therefore not available for measurement.

Terminology

We use a number of terms for morphology-based groups of monothalamous foraminifera currently accommodated within the orders Allogromiida (organic walls) and Astrorhizida (agglutinated walls). However, we recognize that monothalamous foraminifera include a number of phylogenetic lineages that cut across these traditional taxa; for example, some lineages include species with agglutinated and organic test walls (Pawlowski et al. 2002a, 2002b). We therefore use the following terms only as informal labels.

- *Allogromiids*: monothalamous foraminifera with organic-walled tests.
- *Saccamminids*: monothalamous foraminifera with agglutinated tests and either one terminal aperture or two terminal apertures at opposite ends of the test.
- *Psammosphaerids*: monothalamous foraminifera with agglutinated, more or less spherical tests devoid of obvious apertures.
- *Astrorhiziids*: all other monothalamous agglutinated foraminifera.

The term "gromiid" is used for organisms believed to be testate protists in the genus *Gromia* or closely related to this genus. Recent molecular work (Burki et al. 2002) suggests that gromiids constitute a sister group to the foraminifera. We presume that these organisms are gromiids because they have a clear, transparent test wall, a well-developed oral capsule, and are filled with stercomata. However, confirmation of their taxonomic affinities must await molecular characterization.

A faunal reference list that includes all species referred to in the text and tables is given in Appendix A.

Results

Monothalamous foraminifera in unfixed samples: size fractions >500 μm

Templefjord, Kongsfjord and Van Meijenfjord (26–114 m water depth). The inner parts of Tempelfjord (Stns 0757–0759) and Kongsfjord (Stn 0773) yielded sparse assemblages consisting mainly of relatively small, soft-walled monothalamous forms assignable to genera such as *Cylindrogullmia* (Figure 2H), *Nemogullmia* (Figure 2L), *Phainogullmia* (Figure 3J) and *Toxisarcon* (Figure 3E) (Table II). A saccamminid with a silvery, reflective test surface (Figure 3O), and a distinctive grey psammosphaerid with a flexible test, were also present at some of these sites. *Toxisarcon* sp. and the silver saccamminid were particularly common in the inner part of Tempelfjord (Stn 0757). *Hippocrepinella crassa* (Figure 3F) and *Hippocrepinella hirudinea* (Figure 3I) occurred in samples from the outer part of Tempelfjord and Kongsfjord and the latter species was common in the Van Meijenfjord samples (Stns 0786, 0787). A distinctive feature of the assemblages in the outer part of Tempelfjord (Stns 0764, 0765) and Van Meijenfjord was the abundance of large living specimens of *Hyperammina subnodosa*. These samples also contained other large tubular agglutinated species, including *Hyperammina fragilis* in Van Meijenfjord and *Rhabdammina abyssorum* (in which we include *R. discreta*) in Tempelfjord. A small *Pelosinella*-like species (Figure 3H) was fairly common at some of the Tempelfjord stations and two large *Pelosina* species, *P. variabilis* and *P. sphaeriloculum*, occurred in samples from Tempelfjord (Stn 0765) and Kongsfjord (Stns 0775, 0777).

Several gromiid morphotypes were encountered frequently, particularly in the middle and outer parts of Tempelfjord and in Kongsfjord (Stn 0774) and Van Meijenfjord (Stn 0787). They included oval (Figure 2E) as well as more elongate, sausage-like forms (Figure 2B, D). At Stn 0761 in Tempelfjord, a

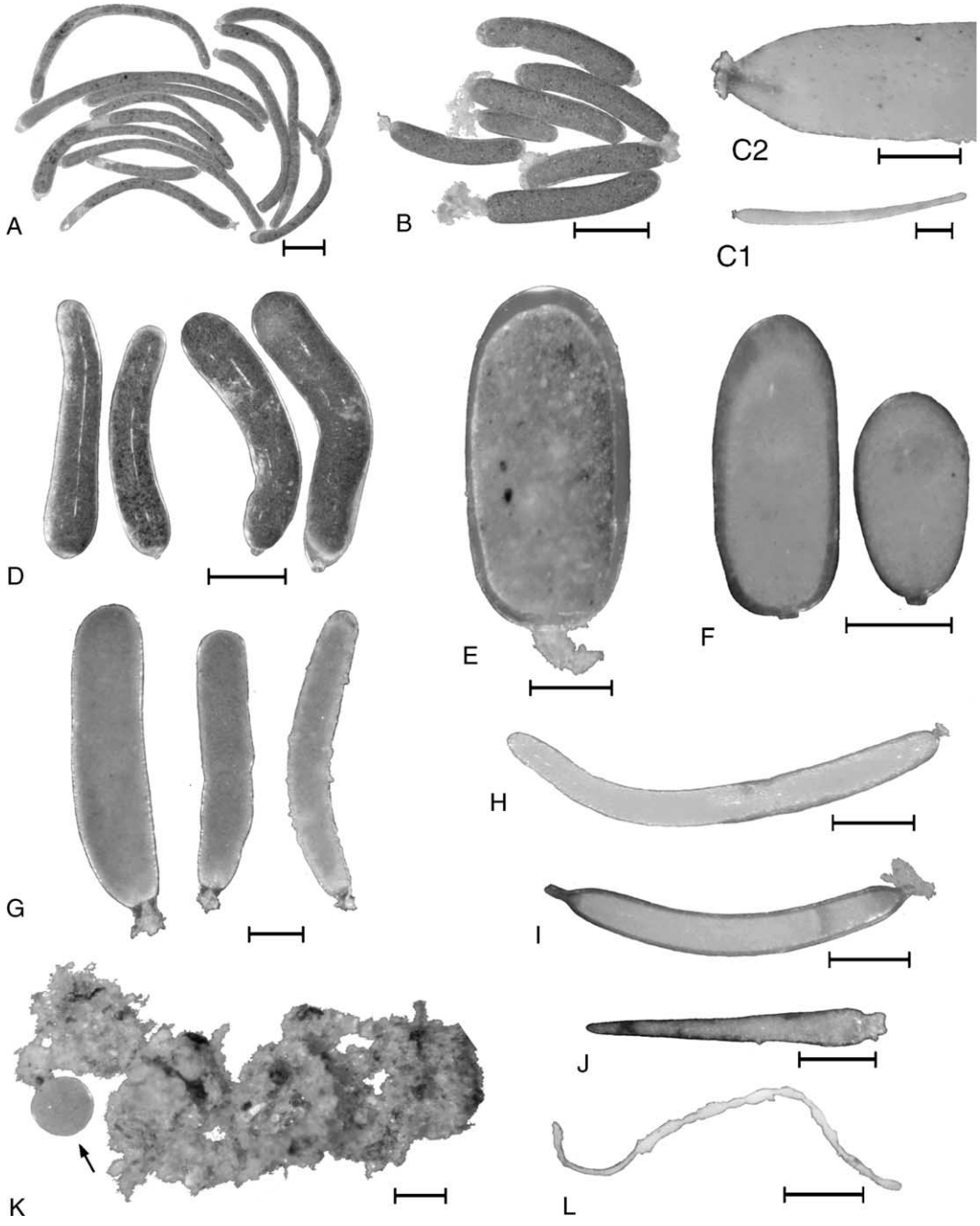

Figure 2. Gromiids and allogromiids; all specimens are from unfixed samples sorted for live foraminifera in Svalbard. (A) Very long, slender gromiid, Stn 0762. (B) Elongate slender gromiid, Stn 0758. (C) Yellow allogromid (new lineage), Stn 0764. (D) Elongate dark gromiid, Stn 0770. (E) Oval gromiid, Stn 0787. (F) Allogromiid sp. 2, Stn 0787. (G) *Gloiogullmia* sp., Stn 0757. (H) *Cylindrogullmia* sp. 2, Stn 0762. (I) *Tinogullmia* sp., Stn 0776. (J) *Micrometula* sp., Stn 0787. (K) Allogromiid sp. 1 (inside mudball), Stn 0763. (L) *Nemogullmia* sp., Stn 0757. Scale bars: A, B, C1, D, L = 100 μm; C2, E–K = 25 μm.

very elongate curved gromiid (Figure 2A) was particularly abundant.

Isfjord (246–313 m water depth). Samples from deeper water in the outer part of Isfjord yielded fewer allogromiids, psammosphaerids and saccamminids than the other fjord samples. However, certain taxa (e.g. *Nemogullmia*, *Toxisarcon*, *Hippocrepinella* spp.) were sometimes present and gromiids occurred at most stations. *Hyperammina subnodosa* was abundant in an epibenthic (Sneli) sledge sample from Stn 0766 and occurred in smaller numbers at several other stations; these large tubes provided a substrate for attached tests of *Crithionina* spp. and *Hemisphaerammina* sp. Large, typical specimens of *Pelosina variabilis* and *P. sphaeriloculum* were also obtained at Stn 0766. *Rhabdammina abyssorum* was common in a Van

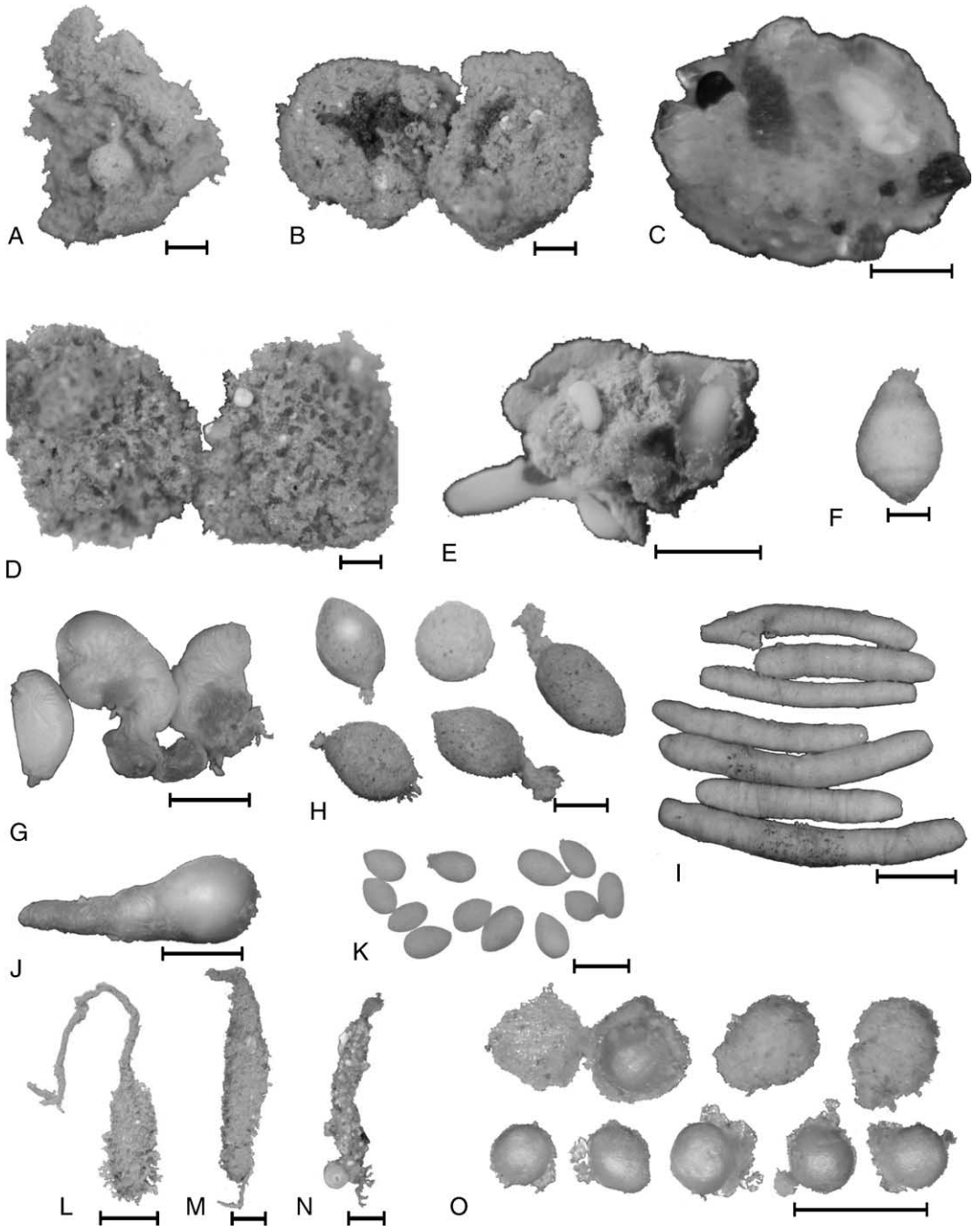

Figure 3. Monothalamous agglutinated foraminifera; all specimens are from unfixed samples sorted for live foraminifera in Svalbard. (A) Saccamminid with long neck inside mudball, Stn 0762. (B) Mudball with stercomata, Stn 0779. (C) *Psammosphaera fusca*, Stn 0770. (D) Komokiacean, Stn 0779. (E) *Toxisarcon* sp., Stn 0757. (F) *Hippocrepinella crassa*, Stn 0775. (G) ?*Phainogullmia* sp., Stn 0757. (H) *Pelosinella*-like species, Stn 0762. (I) *Hippocrepinella hirudinea*, Stn 0786. (J) *Phainogullmia* sp., Stn 0757. (K) Small white Saccamminid, Stn 0774. (L), (M) *Pelosina fusiformis*, Stn 0783. (N) *Pelosina variabilis*, specimen studded with foraminiferal tests, Stn 0779. (O) Silver saccamminid, Stn 0757. Scale bars: E, G–J, L, N = 100 μm; A–D, F, K, M = 25 μm.

Veen grab sample from Stn 0770 and the large spherical species *Psammosphaera fusca* (Figure 3C) also occurred at this site.

Isfjord trough and slope (313–2477 m water depth). In contrast to the fjords, samples from the continental slope yielded only occasional allogromiids, saccamminids and gromiids. *Rhabdammina abyssorum* was a dominant species at the two shallowest stations (0782, 0783; 504 and 313 m water depth, respectively) where numerous individuals were visible on the surfaces of box cores. *Pelosina variabilis* was also common in these samples. The box core from Stn 0771 (994 m water depth) was of poor quality and

Table II. Monothalamous foraminifera in unfixed size fractions >500 µm. Because the samples were unstained and not completely sorted, only qualitative information is included.

Station	Allogromiids								Saccamminids								Psammosphaerids			Gromiids						Pelosina							Other large monothalamous species															
	Nonogullmia	*Cylindrogullmia* sp.1	*Cylindrogullmia* sp.2	*Gloiogullmia* sp.	Allogromiid sp.1	Allogromiid sp.2	Allogromiid sp.17	Yellow allogromiid	*Toxisarcon*	*Phainogullmia* sp.	Silver saccamminid	Small, oval saccamminid	Saccamminid with neck inside mudball	Grey saccamminid	Grey/silver 2 apertures	*Technitella* sp.	Grey flexible	Smooth no aperture	Distinctive species	Very long and slender	Elongate and slender	Elongate and fat	Oval	Elongate dark gromiidsl	Other gromiids	*P. fusiformis*	*P. variabilis*	P. cf. *sphaeriloculum*	*Pelosinella* sp.	*P. arborescens*	*Pelosina* thin form	Others	*Astrorhiza cornuta*	*Bathysiphon* spp.	*Hyperammina subnodosa*	*Hyp. friabilis.*	*Hyp. fragilis*	*Hyp. crassatina*	*Hippocrepinella crassa*	*Hippo. hirudinea*	*Psamm. erecta*	*Rhabdammina abyssorum*	*Psammosphaera fusca*	Mudball with stercomata	*Crithionina* spp.	*Hemisphaerammina* spp.	Chain – like komokiacean	*Edgertonia* – like komoki
Tempelfjord																																																
0757/1	x	x		x					C	x	C						x	x			x								x																			
0758/1	x	x									x						x				x								x																			
0759/1												x			x		x				x		x						x										x									
0761/1								x												C			x						x																x			
0762/2			x										x						x	x	x	x						x	x			x							x	x								
0763/1	x				x		x				x										x	x																	x									
0764/1								x	x											x	x	x	x						x						C					x		x						
0765/1																											x	x							A					x		x						
Kongsfjord																																																
0773																													x			x																
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0775	x				x				x																			x	x			x							x									
0776	x								x		x																					x														x		
0777									x		x				x		x				x							x	x										x	x								
Van Meijenfjord																																																
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Isfjord trough & slope																																																
0783																										C		x		x	x				x	x	x					A						
0782/1																										C				x	x		x	x	x	x	x					A			x	x		
0771/1																																x	x											x				
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0780/1																									x						x			x			x	x				x		C	x	x	x	x
0779/1																			x								x				x							A				x		C	x	x		x
0778/1																																						A						x	x			

x, present; C, common component of assemblage; A, abundant (dominant) component.
*Sneli sledge; **Van Veen grab.

Table III. Occurrence of selected monothalamous foraminiferal species in unfixed and unstained size fractions 125–250 and 250–500 μm. Because the samples were unstained and not completely sorted, only qualitative information is included. The total number of species in each main taxonomic category may include additional species.

	Tempelfjord					Kongsfjord					Van Meijenfjord			
Station	757	758	759	761	762	763	764	773	774	775	776	777	786	787
Water depth (m)	26	46	34	71	104	80	92	70	54	82	49	106	114	107
Allogromiids														
Cylindrogullmia sp. 2	x					x	x		x					
Gloiogullmia sp.	x			x		C	x		x					
Micrometula sp.	x	x		x	x	C	x	x	x		x			x
Nemogullmia sp				x	x		x						x	
Tinogullmia sp.											x			
Allogromiid sp. 1					x	C							x	
Allogromiid sp. 17						C	x							
Allogromiid sp. 22							x							
Allogromiid sp. 26													x	x
Allogromiid sp. 32													x	
Yellow allogromiid					x									
Allogromiid species: total	4	2	1	4	4	6	7	1	4	3	5	1	5	6
Saccamminids														
Conqueria spp.	x	C	x			x	C	x	x	x	C		x	
Psammophaga sp.						x	x		x			x	x	
?*Phainogullmia* sp.													x	
Saccamminid sp. 1				x	x	x	x	x	x	C	C	C	x	x
Saccamminid sp. 1A													x	
Saccamminid sp. 2									C	x		x	x	
Saccamminid sp. 3				x		x	x	x	x	C	x	C	C	x
Saccamminid sp. 3A												C		
Saccamminid sp. 4											x	x		
Saccamminid sp. 8											x			
Saccamminid sp. 27													x	
Saccamminid sp. 28													x	
Saccamminid sp. 29													x	
Saccamminid sp. 31							x						x	
Saccamminid sp. I							C		x					
Saccamminid sp. O							x							
Silver Saccamminid	x					x								x
Toxisarcon sp.										x		x	x	
Saccamminid species: total	7	8	5	5	4	9	11	3	11	12	9	8	13	7
Psammosphaerids														
Sausage psammosphaerid									x					
Psammosphaerid sp. C							x							
Psammosphaerid sp. D									x					
Psammosphaerid sp. K									x					

Table III (*Continued*)

	Tempelfjord					Kongsfjord					Van Meijenfjord			
Station	757	758	759	761	762	763	764	773	774	775	776	777	786	787
Water depth (m)	26	46	34	71	104	80	92	70	54	82	49	106	114	107
Psammosphaerid species: total	0	0	0	0	0	0	1	0	3	0	0	0	0	0
Other monothalamous forams														
Bathysiphon sp.				x						C		x	x	x
Hippocrepinella crassa			x	x	x	C	x		x			C		
Hippocrepinella indivisa							x							
Hyperammina sp.				x										
Other monothalamous: total	0	0	1	3	1	1	2	0	1	1	0	2	1	1
Gromiids														
Oval				x		x	x		x	C	x	x	C	
Sausage-shaped	x	x	x		x	x	x		x	x		x	C	x
Very elongate				x	x		x							C
Other species					x				x					x
Gromiid species: total	1	1	1	2	3	2	3	0	3	2	1	2	3	2

x, present; C, common.

contained numerous stones with attached specimens of *Tolypammina* sp., in addition to free-living species such as *Astrorhiza cornuta* and *Saccorhiza ramosa.* Most of the foraminifera recovered from this sample appeared to be dead. The other stations on this transect (0778–0780; 2472–1532 m water depth) yielded numerous *Hyperammina crassatina* (particularly abundant at the deepest station), and an undescribed mudball with a central lumen filled with stercomata (Figure 3B). The monothalamous agglutinated foraminifera also included other species of *Hyperammina*, an undescribed *Pelosina* sp., and a small, white *Bathysiphon* sp. Chain-like komokiaceans and komokiacean mudballs, the latter possibly belonging to an *Edgertonia* species (Figure 3D), were present in the sample from 1532 m (Stn 0780).

Monothalamous foraminifera in unfixed samples: 125–500 μm size fractions

The finer fractions of samples from Tempelfjord, Kongsfjord and Van Meijenfjord contained numerous allogromiids, saccamminids, psammosphaerids and gromiids. Individual samples yielded four to 22 morphospecies (Table III). A number of these, notably *Gloiogullmia* sp., *Micrometula* sp., *Tinogullmia* sp. and many of the saccamminids, were not present in the coarser fractions. Gromiids occurred in all but one sample and were sometimes abundant, for example, at Stn 0775 and 0786. They were represented by the same oval and elongate morphotypes that were common in the >500 μm fraction. The most frequently encountered allogromiid was a small elongate tapered species of *Micrometula* (Figure 2J, 4A) that occurred in 10 out of the 14 samples examined and was particularly common at Stn 0763 in Tempelfjord. An elongate, brightly coloured (yellow-green) allogromiid (*Gloiogullmia* sp.) was encountered in five samples, four of them in Tempelfjord. A white *Cylindrogullmia* species (Figure 2H), and an elongate, thread-like species assigned to *Nemogullmia* (Figure 2L), each occurred in four samples. The only other allogromiid species identifiable at the generic level was *Tinogullmia* sp. (Figure 4B), confined to Stn 0776 in Kongsfjord. Notable among the undescribed allogromiids was a distinctive species (Allogromiid sp. 26) with two terminal apertures (Figure 4C), found only in Van Meijenfjord (Stns 0786, 0787).

Among the saccamminids, a morphotype resembling *Conqueria* Gooday & Pawlowski (Figure 4D) occurred at 10 stations. These forms, which may represent more than one species, were abundant at Stns 0758 and 0764 in Tempelfjord and Stn 0776 in Kongsfjord. Of particular interest were three tiny saccamminid morphospecies. Two of these, a silvery

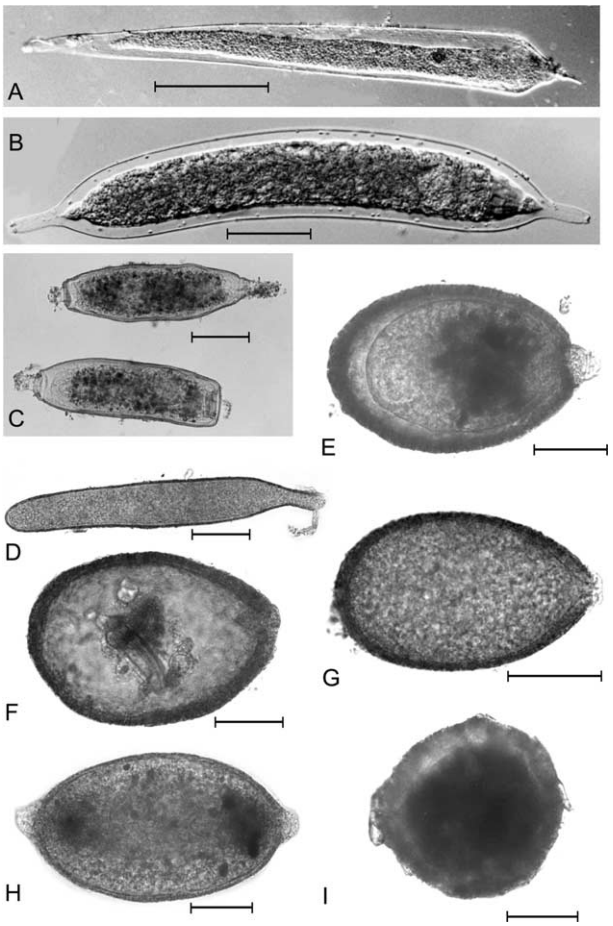

Figure 4. Monothalamous foraminifera from the unfixed (A–H) and fixed (I) samples. (A)–(C) Organic-walled allogromiids. (E)–(H) Agglutinated saccamminids. All specimens are mounted in glycerol and photographed in transmitted light. (A) *Micrometula* sp., Stn 0764. (B) *Tinogullmia* sp., Stn 0776, Kongsfjord. (C) Allogromiid sp. 26 with two terminal apertures, Stn 0786. (D) Elongate species resembling *Conqueria,* Stn 0776, Kongsfjord. (E) Saccamminid sp.1 (silver species), Stn 0777, Kongsfjord. (F) Saccamminid sp. 3 (brown species), Stn 0786, Van Meijenfjord. (G) Saccamminid sp. 2 (dull white species), Stn 0774. (H) Saccamminid sp. 29, a species with two terminal apertures, Stn 0786. (I) Psammosphaerid sp. C, Stn 0764. Scale bars: A–D = 100 μm; E–I = 50 μm.

form (Saccamminid sp. 1; Figure 4E) and a brownish form (Saccamminid sp. 3; Figure 4F), were present in samples from all three fjords and very common in the outer part of Kongsfjord. A whitish species (Saccamminid sp. 2; Figure 3K, 4G) was confined to Kongsfjord and Van Meijenfjord and was abundant at Stn 0774. Also notable among the saccamminids in all three fjords were occasional individuals of *Psammophaga*. In our unfixed material, this genus was confined to Stn 0777 in the outer part of Kongsfjord. The vast majority of the saccamminids had one terminal aperture but one rare species, Saccamminid sp. 29 from Van Meijenfjord (Figure 4H), had two terminal apertures. Several psammosphaerid species were abundant at Stn 0774 in Kongsfjord and one (Figure 4I) was common at Stn 0764 in the outer part of Tempelfjord.

Other monothalamous taxa were also important in the 125–500 μm fractions (Table III). *Hippocrepinella crassa* was common in Tempelfjord (particularly Stn 0763) and Kongsfjord (particularly Stn 0777). The other widely distributed monothalamous species was a tiny *Bathysiphon* sp., which was particularly common at Stn 0775 in Kongsfjord. Another tiny tubular species with a proloculus (*Hyperammina* sp.) was present at Stn 0761.

Monothalamous foraminifera in fixed samples

In small volumes of sediment from Tempelfjord (Stn 0764), Kongsfjord (Stn 0774) and the Isfjord trough (Stn 0783), the majority (56–72%) of stained foraminifera occurred in the 63–125 μm fraction, 22–35% in the 125–300 μm fraction, and a small but variable proportion (<1–15%) in the >300 μm fraction (Table IV). The percentage of saccamminids was fairly consistent at around 8–9% of stained foraminifera, while allogromiids and gromiids combined contributed between 2 and 10% of the assemblage. Psammosphaerids were very abundant (33%) in the sample from Kongsfjord (0774), but

Table IV. Relative abundance of different kinds of soft-shelled monothalamous foraminifera among stained foraminiferal assemblages in fixed samples from Tempelfjord (Stn 0764), Kongsfjord (Stn 0774) and Isfjord trough (Stn 0783).

Station	Isfjord trough (Stn 0783)	Kongsfjord (Stn 0774)	Tempelfjord (Stn 0764)
Water depth (m)	313	54	92
Sediment volume (ml)	2.7	2.5	2.7
Size fractions (μm)			
>300	15.2%	0.60%	5.49%
125–300	28.9%	35.5%	22.4%
63–125	55.9%	63.9%	72.1%
Foraminiferal group			
Calcareous	44.3%	14.6%	15.2%
Multilocular agglutinated	43.2%	34.6%	70.0%
Saccamminids	8.57%	9.25%	8.21%
Psammosphaerids	1.32%	33.1%	2.72%
Allogromiids and gromiids	2.20%	9.25%	4.19%
Total specimens	455	335	1695

uncommon (1–3%) at the other two sites. Sixteen species occurred in the 63–125 μm fraction, and an additional three species (*Micrometula* sp., Saccamminid sp. O, Psammosphaerid sp. K) were much more abundant in this finest residue.

In total, 36 monothalamous foraminiferal species and gromiids were recognized; 13–20 of these were present at individual stations (Table V). Organic-walled allogromiids were represented by two to eight species per station, the most abundant being *Micrometula* sp. (Figure 4A), which was common at the Tempelfjord site (Stn 0764). Saccamminids were the most specious group with between six and 10 species per station. Saccamminid sp. O (Figure 5A) was particularly abundant at Stn 0764 and *Psammophaga* sp. (forms A, B, D) (Figure 5B, C) were fairly common at the same locality. Psammosphaerids (e.g. Figure 4I) were very abundant in the Kongsfjord sample, particularly in the 63–125 μm fraction.

Size distribution

The maximum dimensions of 679 specimens from all stations (63–125 and >125 μm fractions; fixed and unfixed samples) ranged from 70 to 5400 μm (Figure 6). The main peak was between 80 and 240 μm, with a secondary peak at 550–1500 μm due largely to two elongate taxa, the saccamminid *Conqueria* spp. and the allogromiid *Micrometula* sp. This pattern was clearly evident in the >125 μm fraction, which included some of the larger individuals extracted from samples in Svalbard. The addition of specimens from the finer (63–125 μm) fractions of the three fixed samples analysed at NOC, enhanced the main peak at the smaller end of the size spectrum but did not alter the basic size distribution pattern.

Discussion

Monothalamous foraminifera in the Arctic

It has long been known that large monothalamous agglutinated foraminifera are abundant in some Arctic settings (Goës 1894; Kiaer 1899). Large astrorhiziids, such as *Astrorhiza arenaria*, *Hippocrepinella hirudinea*, *Hyperammina crassatina*, *Hyperammina subnodosa*, *Pelosina variabilis*, *Rhabdammina abyssorum* and "*Rhabdammina*" (=*Astrorhiza*) *cornuta* are well known from high-latitude areas in the northern hemisphere, including the Greenland–Norwegian Sea, East Greenland fjords, the Barents Sea and the Svalbard area (e.g. Cushman 1918; Spärck 1933; Thorson 1934; Tendal & Thomsen 1988; Thies 1991; Linke & Lutze 1993; Korsun 2002). Kiaer (1899) recorded a "superabundance" of *Rhabdammina abyssorum* at 330 m water depth in the Barents Sea. According to Korsun (2002), *Rhabdammina abyssorum*, *Hyperammina subnodosa* and *Pelosina variabilis* dominate foraminiferal biomass on the Barents–Kara shelf. Cushman (1918) reported that *Hyperammina subnodosa* was extremely abundant at two stations (51°N, 150 m water depth and 52°N, 162 m water depth) under the influence of the Greenland current. Linke & Lutze (1993) found dense concentrations of *Hyperammina crassatina* tubes on the surface of a box core from the East Greenland shelf. Some of our Svalbard samples yielded rich collections of these species, notably *Hyperammina subnodosa* from the outer part of Tempelfjord, *Rhabdammina abyssorum* and *Pelosina fusiformis* in the Isfjord trough, and *Hyperammina crassatina* at the deepest slope stations (Table II). Our observations provide further evidence that species of *Hyperammina*, *Pelosina* and *Rhabdammina*

Table V. Abundance of monothalamous foraminiferal and gromiid species in fixed samples from three Svalbard fjords. The sample residues were stained with rose Bengal and all stained ("live") specimens of these taxa extracted.

Fjord	Tempelfjord		Kongsfjord		Isfjord trough	
Station (water depth)	Stn 0764 (92 m)		Stn 0774 (54 m)		Stn 0783 (313 m)	
Size fraction (μm)	63–125	>125	63–125	>125	63–125	>125
Allogromiids						
Allogromiid sp 17		1				
Allogromiid sp 29	5	3				
Allogromiid sp 34	1					
Allogromiid sp 35	1					
Allogromiid sp 36	1		7		1	
Allogromiid sp G	1	3				
Allogromiid sp H				1		
Allogromiid sp I			1			
Micrometula sp.	29		3	2	3	
Thread-like species	3					
Saccamminids						
Hippocrepinella sp. C				1	2	
Psammophaga form A	4					
Psammophaga form B	9	3			6	
Psammophaga form D	7			1		
Saccamminid sp. 4			1			
Saccamminid sp. 31		1				
Saccamminid sp. A					4	
Saccamminid sp. B					1	
Saccamminid sp. E					5	1
Saccamminid sp. I		9		1		
Saccamminid sp. H						4
Saccamminid sp. J			15	2		
Saccamminid sp. N	2					
Saccamminid sp. O	78	2			1	4
Saccamminid sp. P					1	1
Saccamminid sp. Q		1				
Saccamminid sp. R	2					
Saccamminid sp. S			1			
Saccamminid sp. T						1
Saccamminid sp. U					2	
Psammosphaerids						
Psammosphaerid sp. C	15	7				
Psammosphaerid sp. D			72	30		
Psammosphaerid sp. K			1	1		
Sausage-shaped				7		
Gromiids						
Oval gromiid	1		4		1	
Elongate gromiid	1			1		

are common in some sublittoral and bathyal Arctic, soft-sediment communities.

There are fewer records of smaller, soft-walled monothalamous taxa (allogromiids, psammosphaerids and saccamminids) in Arctic settings. Linke (1989) reported an *Allogromia* sp., similar to specimens illustrated by Gooday (1986: Figure 3), from 1243 to 1427 m water depth in the Greenland–Norwegian Sea. Schewe & Soltwedel (1998) found undifferentiated allogromiids to be a significant (1–13%) component of the meiofauna in the central Arctic (864–4187 m depth). Later, Schewe & Soltwedel (2003) reported that allogromiids (dominated by *Nodellum* species) made up 4–44% of foraminifera in the northern Fram Strait (744–3020 m) with the highest proportion (>20%) being found in the shallow part of the depth range (744–1486 m). According to Wollenburg (1995) and Wollenburg & Mackensen (1998), the multilocular organic-walled species *Placopsilinella aurantiaca* accounts for up to 88% of all stained foraminifera, also in the central Arctic Ocean (1051–4427 m depth).

The only previous records of allogromiids and saccamminids from sublittoral Arctic sites are from

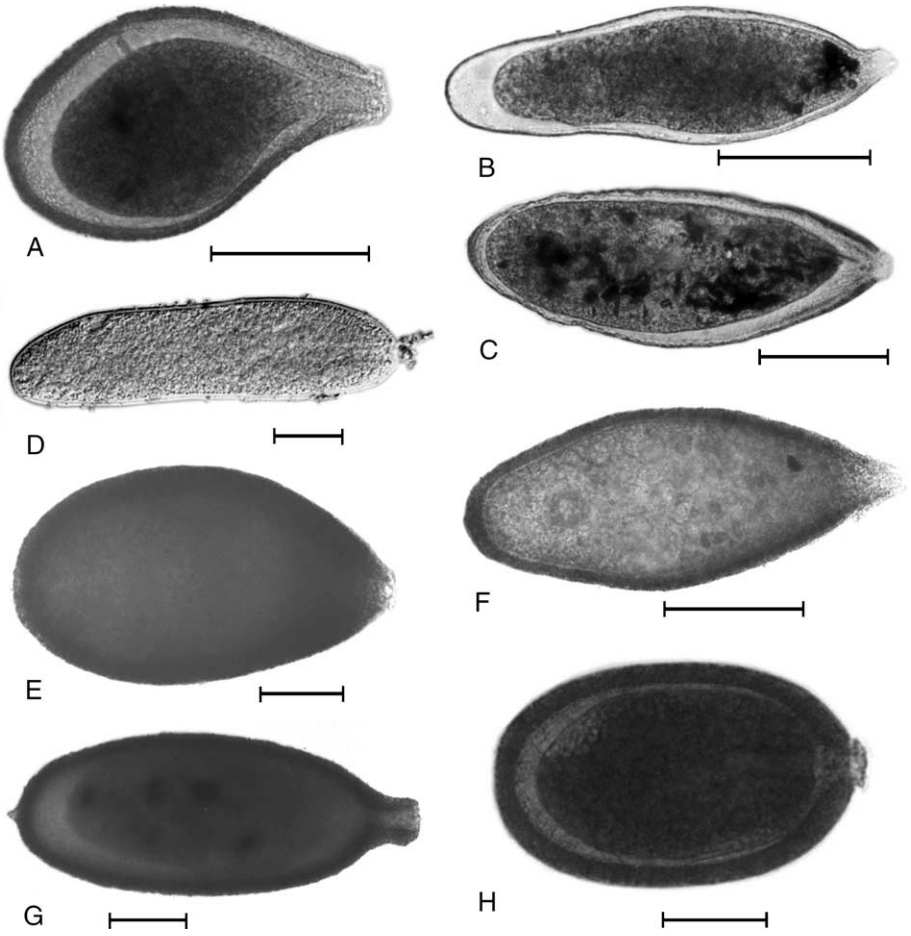

Figure 5. Monothalamous foraminifera from unfixed (D–F) and fixed (A–C, G, H) samples. All specimens are mounted in glycerol and photographed in transmitted light. (D) is an organic-walled allogromiid; the others are agglutinated saccamminids. (A) Saccamminid sp. O, Stn 0764. (B), (C) *Psammophaga* sp. form B, Stn 0764, Tempelfjord, and Stn 0783, Isfjord, respectively. (D) Delicate, elongate allogromiid (sp. 32), Stn 0786. (E) White, opaque saccamminid (sp. 4), Stn 0777. (F) Saccamminid sp. 27, Stn 0786. (G) Saccamminid sp. H, Stn 0783. (H) Saccamminid sp. J, Stn 0774.
Scale bars: A–D, F, G = 100 μm; E, H = 50 μm.

Tempelfjord (Korsun & Hald 2000), off Novaya Zemlya tidewater glaciers (Korsun et al. 1995; Korsun & Hald 1998), in the estuary of the River Ob, western Siberia (Korsun 1999), and various areas on the Barents–Kara shelf where they may reach densities of up to 290 individuals 10 cm^3 of sediment (Korsun 2002). The Novaya Zemlya material is now known to consist entirely of tiny saccamminids (Korsun, unpub. obs.). In their study of Tempelfjord, Korsun & Hald (2000) reported that five allogromiid species (probably also saccamminids) made up 76% of live foraminifera in a sample obtained 1.4 km from the edge of the glacier. Our new survey confirms the observations of Korsun & Hald (2000) and demonstrates that these poorly known foraminiferal taxa, together with morphologically similar gromiids, are diverse and abundant around Svalbard, particularly in the fjords. We speculate that monothalamous foraminifera are an important faunal component in many areas of the Arctic. Although the specimens in our material span a wide size range, many are relatively small (<240 μm maximum dimension) (Figure 6). Earlier studies of foraminifera from the northeast Atlantic (Gooday 1986; Gooday et al. 1995) and North Pacific (Gooday et al. 2001) have noted that the majority of allogromiids and saccamminids obtained in deep-sea core samples are <200 μm maximum dimension.

Comparison with other areas

Species-level analyses of monothalamous foraminiferal assemblages are uncommon. The largest body of data comes from deep-sea sites, mainly in the North Atlantic (Gooday 2002). In sublittoral northern hemisphere settings, these protists have been documented most fully in the Skagerak, particularly the

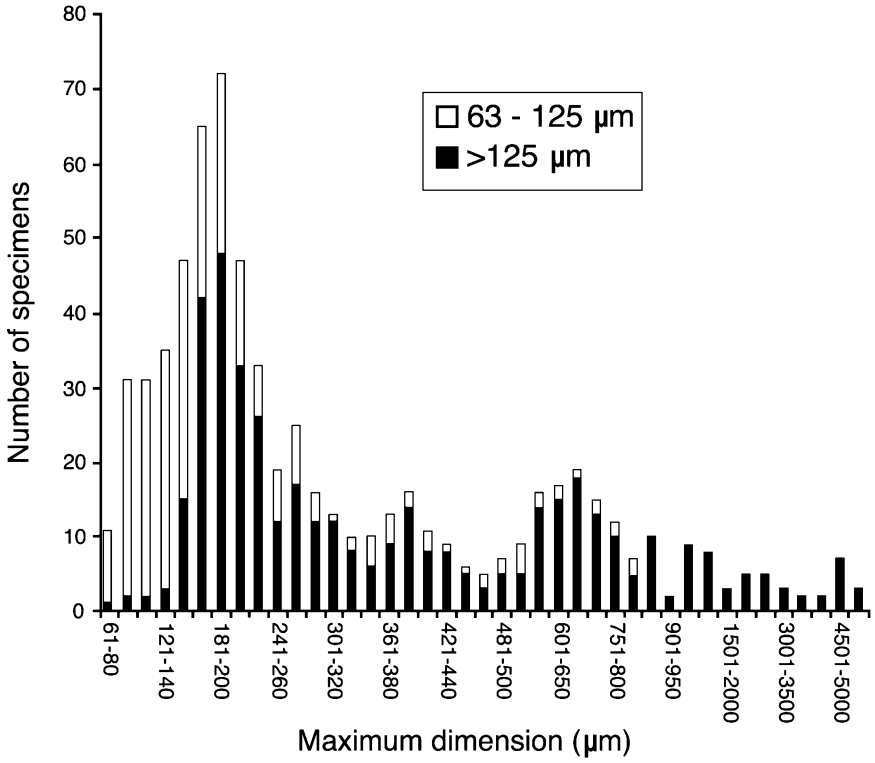

Figure 6. Size distribution of 679 specimens from all stations: 63–125 and >125 µm fractions of fixed samples and 125–250 and 250–500 µm fractions of unfixed samples.

Gullmarfjord, from where Nyholm (1952, 1953, 1954, 1955, 1974) described a number of distinctive genera. Many of Nyholm's genera (*Cylindrogullmia*, *Gloiogullmia*, *Micrometula*, *Nemogullmia*, *Tinogullmia*) have been recognized in our Svalbard samples. The species often appear closely similar to those of Nyholm, although their identity requires confirmation. Another common monothalamous foraminiferan in the Svalbard fjords is *Toxisarcon*. This genus was first described from the Swedish west coast (Cedhagen & Pawlowski 2002) and a second species occurs on the Scottish west coast (Wilding 2002). It has a flimsy, very loosely organized agglutinated test and can also exist as a naked amoeba. *Toxisarcon* would be difficult to recognize in fixed samples. A species of *Psammophaga* occurs in some of our Svalbard samples. This genus is also reported from the Ob Estuary (Korsun 1999, unpub. obs.), the western North Atlantic off Sapelo Island (Pawlowski et al. 2002b), an intertidal mudflat site in southern England (Larkin & Gooday 2004), the Black Sea (Anikeeva 2005) and Explorers Cove, McMurdo Sound, Antarctica (Gooday et al. 1996).

Monothalamous foraminifera have been studied exhaustively at a coastal (28 m water depth) site in Explorers Cove (e.g. Gooday et al. 1996; Pawlowski et al. 2002a). These Antarctic assemblages exhibit interesting parallels with the Svalbard faunas. The organic-walled allogromiids include species of *Cylindrogullmia*, *Gloiogullmia*, *Micrometula*, *Nemogullmia* and *Tinogullmia* (Gooday et al. 1996: plate 1, figures A–E therein) that are morphologically similar to those inhabiting Svalbard fjords. Among the saccamminids, a silver saccamminid, *Psammophaga* sp., and a small, whitish, flask-shaped species (Gooday et al. 1996: plate 4, figures A, C, E therein, respectively) resemble forms in our Svalbard material. Preliminary molecular evidence suggests that these morphological similarities conceal substantial genetic divergence and that at least some species are endemic to one or other of the polar regions (Pawlowski et al. 2002a). However, Arctic and Antarctic populations of two morphospecies (*Psammophaga* sp., and an unidentified allogromiid), yield very similar genetic sequences (divergence $<1\%$), suggesting that these distant populations have separated relatively recently, perhaps since the end of the last ice age (Pawlowski et al. 2003b). An important feature of the Explorers Cove assemblages is that many of the abundant larger agglutinated monothalamous species (*Astrammina rara*, *A. triangularis*, *Notodendrodes antarctikos*, *N. hyalinosphaira*, *Psammosphaera* spp.) contain an allogromid-like sarcode separated from the agglutinated wall by a distinct space (Bowser et al. 1995, 2002; Gooday et al. 1996; DeLaca et al. 2002). In our material, only Psammosphaerid sp. K has a similar organization.

Faunal trends and possible controls on distributions

The following discussion is based on the >500 μm fraction (Table II, 29 stations) and the 125–500 μm fraction (Table III, 14 stations) of the unfixed samples sorted in Svalbard. We do not consider the finer fractions (63–125 μm) because these were only analysed for three fixed samples (Table V).

We examined unmeasured volumes of surficial sediment scooped from box cores. Therefore, this study was largely qualitative. Moreover, compared with hydraulically damped samplers, such as the multicorer (Barnett et al. 1984), the bow wave associated with box corers leads to a much greater loss of surficial sediments and associated fauna (Bett et al. 1994). Some of the between-sample differences in foraminiferal assemblages may therefore reflect variations in sample quality rather than faunal changes. Nevertheless, we believe that some genuine trends are evident in our material. Most obviously, there is a tendency for test size to increase, and the proportion of small, soft-shelled species to decrease, along the two fjords (Tempelfjord and Kongsfjord) headed by tidewater glaciers, i.e. along a gradient of decreasing glacial influence and irregularly increasing water depth. The inner areas of these fjords yielded relatively small allogromiid and saccamminid species, e.g. *Cylindrogullmia* sp., *Nemogullmia* sp., *Toxisarcon* sp., and silver saccamminids, in addition to gromiids.

Some of the faunal differences between sampling areas probably reflect environmental contrasts within and between fjords. The finer fractions (125–500 μm) of samples from the inner stations (0757–0762) of Tempelfjord each yielded eight to 14 species compared with 18 and 24 species at the outer two stations (0763–0765) (Table III). In the coarser fractions (>500 μm), some species (*Cylindrogullmia* sp. 1, *Toxisarcon* sp., silver saccamminid) that were common in the inner part of Tempelfjord close to the glacier were rare or absent in the outer fjord (Table II). These faunal differences could be related to differences in sediment types, i.e. very fine-grained, fluid glaciomarine muds at Stns 0757–0762 compared with the marine muds present at Stns 0763 and 0765. On the other hand, there were relatively few differences in species living at the outermost Kongsfjord station (0777; temperature >0°C, marine muds) and those from the inner part of this fjord (Stns 0773–0776; temperature <0°C, glaciomarine muds).

Smaller gromiids, white, silver and brown saccamminids, and tiny white *Bathysiphon* spp. were generally more abundant and widespread in Kongsfjord and Van Meijenfjord than in the inner parts of Tempelfjord (Table III). Kongsfjord and Van Meijenfjord are both filled with supercool winter water <−1°C. However, there were also differences between the two fjords. A species of *Tinogullmia* (Figure 4B) was only found in Kongsfjord and an undescribed organic-walled allogromiid with two terminal apertures (Figure 4C) was confined to Van Meijenfjord. The Van Meijenfjord samples (>500 μm fractions) also yielded *Hyperamminia subnodosa*, a large agglutinated species that was common in the outer parts of Tempelfjord (Stns 0764, 0765) and Isfjord (Stn 0766) where the water temperatures were higher than in Van Meijenfjord, but was not represented in Kongsfjord. Despite its shallow sill depth (25 m water depth), there is clearly some faunal exchange between Van Meijenfjord and Isfjord, the next fjord to the north. Both of the fjordic areas where *Hyperammina subnodosa* occurs are characterized by typical marine muds in contrast to the very fine-grained glaciomarine muds found close to glacial termini.

The occurrence of large *Hyperammina*, *Rhabdammina* and *Pelosina* species in the outer parts of fjords and offshore waters (Table II) is presumably related to an enhanced food supply compared with the inner reaches of fjords. The dense standing crops of *Rhabdammina abyssorum* and *Pelosina fusiformis* at Stns 0782 and 0783 also coincide with strong current flow associated with the West Spitzbergen Current. Numerous live individuals of *Rhabdammina abyssorum*, and its two-rayed counterpart *R. discreta* (which we consider to be conspecific with *Rhabdammina abyssorum*), protruded from the surfaces of box cores collected on the upper slope off Isfjord. A similar life position was reported for this species by Linke & Lutze 1993. This and other large agglutinated foraminifera with an erect life position are probably predominately suspension feeders.

Conclusions

Our survey clearly establishes, for the first time, the existence of diverse assemblages of small, soft-shelled monothalamous foraminifera in sublittoral Arctic waters. Organic-walled allogromiids and agglutinated saccamminids are common in samples from western Svalbard fjords. Some of the common morphotypes (*Cylindrogullmia*, *Micrometula*, *Nemogullmia*, *Tinogullmia*) closely resemble species described from the Swedish west coast and other areas of Scandinavia. We predict that similar assemblages are widespread in sublittoral habitats around northwestern Europe and in the European Arctic. Allogromiids and saccamminids resembling those from Svalbard occur at a coastal site in Explorers Cove, Antarctica. Several gromiid-like morphospecies are also common in these samples, particularly those

from Tempelfjord. Larger and more robust monothalamous agglutinated foraminifera (mainly species of *Hyperammina*, *Pelosina* and *Rhabdammina*) are absent from the inner fjords, but very abundant in the outer reaches of Tempelfjord and Van Meijenfjord and at deeper offshore sites. These large astrorhiziids are widely reported from other temperate and high-latitude sites in the northern hemisphere.

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Appendix A: Faunal reference list

The following notes refer to species included in Tables II, III, and V; some are illustrated in figures 2–5. Note that the terms "allogromiid", "saccamminid" and "psammosphaerid" are used only as

convenient descriptive labels and do not represent phylogenetically coherent groupings (Pawlowski et al. 2003a).

Allogromiids

Cylindrogullmia sp. 1. Test ranging from elongate oval to cigar- or sausage-shaped, sometimes slightly curved and often with partial coating of muddy detritus. Apertural end produced into short tubular structure. Cytoplasm white. Similar to typical specimens of *Cylindrogullmia alba* illustrated by Nyholm (1974: figure 6) but lacks the reflective test surface of this species.

Cylindrogullmia sp. 2 (Figure 2H). Test elongate, often curved, 2–4 mm long and 60–160 μm wide, gently tapered, sometimes with one or more constrictions. Single terminal aperture at end of short tubular extension. Wall reflective; most specimens have remnants of agglutinated covering. Cytoplasm white. Most similar to the "budding specimen" of *Cylindrogullmia alba* illustrated by Nyholm (1974: figure 5) and *Cylindrogullmia* sp. of Gooday et al. (1996) from Explorers Cove, Antarctica.

Gloiogullmia sp. (Figure 2G). Fairly elongate allogromiid with cylindrical, sometimes slightly curved, test and apertural end produced into short, broad apertural structure with central protoplasmic strand. Test wall thin, transparent, sometimes with a few adhering particles. Cytoplasm distinctly greenish.

Micrometula sp. (Figure 2J, 4A). Our specimens measure 640–1100 μm long and 80–120 μm wide and are closely similar to *M. hyalostriata* Nyholm 1952.

Tinogullmia sp. (Figure 2I, 4B). Test 700–1000 μm long and 100–130 μm wide. Very similar to *T. hyalina* Nyholm 1954, except for being shorter and relatively wider. Another species resembling *T. hyalina* has recently been reported from the Black Sea (Sergeeva et al. in press).

Nemogullmia sp. (Figure 2L). Long, vermiform species with partial coating of agglutinated material. Closely resembles *Nemogullmia longevariabilis* Nyholm 1953.

Yellow Allogromid (Figure 2C). Distinctive species with slender, elongate test several mm long, widest ($\sim$400 μm) just behind the aperture and tapering gradually to a rounded proximal end. Aperture fairly featureless, although an associated endosolenial tube is well developed. Cytoplasm yellow. This species is similar in general shape to *Micrometula*, but has a simpler aperture. Molecular evidence suggests that it represents a new allogromiid lineage.

Allogromiid 1 (Figure 2K). Spherical allogromiid with reflective test wall enclosed within mudball.

Allogromiid sp. 2 (Figure 2F). Species with oval, more or less elongate test, transparent wall with reflective highlight, nipple-like apertural structure and white cytoplasm. It may be a gromiid.

Allogromiid sp. 17. Delicate allogromiid with almost spherical test, 260–400 μm diameter, single indistinct aperture, and finely granular cytoplasm.

Allogromiid sp. 22. Test 300–600 μm long and 200–280 μm wide and with slightly protruding aperture, thin, shiny wall, and white cytoplasm.

Allogromiid sp. 26 (Figure 4C). Very distinctive species, 420–740 μm long and 80–120 μm wide, with cylindrical or fusiform test produced into thin-walled apertural extensions. Cytoplasm with dark inclusions.

Allogromiid sp. 29. Test typically 180–440 μm long and 120–260 μm wide, oval with broadly rounded proximal end and rather flattened distal end. Organic wall thin and completely transparent. Cytoplasm dark, finely granular with scattered dark inclusions; endosolenial tube sometimes visible.

Allogromiid sp. 32 (Figure 5D). Large, delicate species with elongate oval test and simple aperture. Finely granular cytoplasm with well-developed endosolenial tube, separated from test wall by narrow but distinct space of even width.

Allogromiid sp. 34. Elongate, fusiform test, proximal end bluntly pointed, distal end extended into apertural neck. Wall fairly thick, appears to be basically organic but with thin, fine-grained agglutinated veneer. Cytoplasm forms distinct mass occupying only part of test interior and featureless except for prominent nucleus.

Allogromiid sp. 35. Test 340 μm long and 60 μm wide, elongate, with very delicate organic wall. Distinct cytoplasmic body featureless except for large nucleus.

Allogromiid sp. 36. Elongate species, up to 280 μm long and 100 μm wide, enclosed in delicate agglutinated sheath.

Allogromiid sp. G. Tiny delicate species with oval to droplet-shaped test, 70–120 μm diameter. Cytoplasm finely granular, separated by distinct space from test wall.

Allogromiid sp. H. Coiled, elongate test, $\sim$400 μm long and tapering from 70 μm at the distal end to $\sim$30 μm at the proximal end, with prominent aperture. Organic wall with scattered adhering particles. Cytoplasmic body rather featureless except for prominent endosolenial tube; separated from wall by distinct space.

Allogromiid sp. I. Test 200 μm long and 50 μm wide, subrectangular with one end flattened, the other broadly rounded; aperture indistinct, located at flattened end. Organic test appears to have two layers, the inner one less distinct than the outer. Cytoplasm finely granular with large nucleus.

Thread-like allogromiid. Elongate species, 740–820 μm long and 20–30 μm wide with terminal aperture. Prominent endosolenial tube associated with aperture. Closely resembles the Northeast Atlantic species illustrated by Gooday (2002: plate 1, figures 1–3).

Saccamminids

Conqueria sp. (Figure 4D). Slender test 480–800 μm long and 90–140 μm wide. Similar to the Antarctic species *C. laevis* Gooday & Pawlowski 2004 but with longer and slenderer apertural neck. Some specimens are distinctly wider and may represent a separate species. Surface pale brownish with diffuse, speckly reflection.

Silver saccamminid (Figure 3O). Test 400–500 μm in size, more or less spherical to slightly oval in shape with relatively large, circular aperture. Test surface silvery with distinct silvery reflection. Many specimens are partly or completely obscured by coating of fine sediment. This species resembles *Pilulina argentea* Höglund 1947 (see Höglund 1947: 64–65, plate 8, figures 11–14) and the "silver saccamminid" of Gooday et al. (1996) from Explorers Cove, Antarctica.

?Phainogullmia spp. (Figures 3G, J). Test generally elongated but of variable shape, ranging from irregular to oval to a more elongate carrot shape. Wall brownish with silvery reflection. The only described species of this genus, *Phainogullmia aurata* Nyholm 1955, exhibits considerable morphological variability.

Psammophaga sp. (Figures 5B, C). In Svalbard specimens of this widely distributed genus, the wall is either clearly agglutinated (form A) or transparent and predominately organic (form B). Both forms are 240–460 μm long and 60–140 μm wide with an oval outline and cytoplasm containing black mineral inclusions. A third type (form D) has an agglutinated test and is devoid of inclusions. Form A resembles *Psammophaga* sp. from Explorers Cove, Antarctica (Gooday et al. 1996). Recent evidence suggests that the Svalbard and Explorers Cove populations are also very closely related genetically (Pawlowski et al. 2003b).

Toxisarcon sp. (Figure 3E) Large, irregularly shaped species with loosely agglutinated sediment coating. Similar to *Toxisarcon synsuicidica* Cedhagen & Pawlowski 2002.

Saccamminid sp. 1 (Figure 4E). Test small and delicate, 160–360 μm long and 120–200 μm wide, varying in shape from almost round to elongate oval, sometimes with a mound-like projection associated with the aperture. Surface whitish with distinct but rather diffuse silvery reflection.

Saccamminid sp. 1A. Test 280–400 μm long and 140–200 μm wide, oval with slightly produced apertural neck. Wall silvery, slightly wrinkled.

Saccamminid sp. 2 (Figures 3K, 4G). Test small and delicate, 160–200 μm long and 90–120 μm wide, droplet-shaped with more or less pointed apertural end. Surface dull white with eggshell-like sheen. Aperture small and circular. Cytoplasm without obvious inclusions.

Saccamminid sp. 3 (Figure 4F). Test delicate, 160–320 μm long and 130–200 μm wide, generally oval but rather variable in shape and sometimes slightly asymmetrical. Aperture terminal, indistinct; in some specimens there appear to be two apertures at opposite ends of the test. Surface pale brownish with slight speckly reflection. Cytoplasm with inclusions including diatoms.

Saccamminid sp. 3A. Test 160–320 μm long and 140–220 μm wide, similar to Saccamminid sp. 3 but with thicker wall that is opaque even when immersed in glycerol.

Saccamminid sp. 4 (Figure 5E). Test small and delicate, 200–220 μm long, droplet-shaped with more or less pointed apertural end. Aperture small and circular. Wall opaque, even in glycerol; surface silvery white with a speckly sheen.

Saccamminid 8. Test 400–640 μm long and 16–240 μm wide, elongate oval, tending to be widest in front of midpoint with broadly rounded proximal end and tapered apertural end. Surface brownish with diffuse, speckly reflection, slightly wrinkled; translucent in glycerol.

Spherical saccamminid with long neck enclosed within mudball. Illustrated in Figure 3A.

Saccamminid sp. 27 (Figure 5F). Test 280–320 μm long and 120–140 μm wide, elongate oval with rounded posterior end and tapering towards apertural end, which is produced into short neck. Wall fairly thick and finely granular. Cytoplasmic body separated from wall by distinct gap.

Saccamminid sp. 28. Test 300–380 μm long and 160–220 μm wide, similar to Saccamminid sp. 27 but with strongly flattened test and wall with weak transverse wrinkles.

Saccamminid sp. 29 (Figure 4H). Test oval, 230 μm long and 120 μm wide, with two terminal apertures at opposite ends. Wall composed of plate-like grains giving reflective sheen. Cytoplasm with inclusions including mineral grains.

Saccamminid sp. 31. Test 260 μm long and 140 μm wide, widest in front of midpoint, tapering towards narrowly rounded proximal end; apertural end more broadly rounded with wide aperture at end of short neck. Wall thick, particularly in distal part of test.

Silver saccamminid sp. A. Tiny droplet-shaped test, 120–140 μm long and 70–80 μm wide, tapering to pointed apertural end. Wall fairly thick, composed of plate-like particles imparting a silvery reflection that is still evident after immersion in glycerol.

Saccamminid sp. B. Test 180 μm long and 120 μm wide, egg-shaped with simple aperture. Wall translucent in glycerol and retaining its reflective sheen. Cytoplasm unusual among monothalamous foraminifera from Svalbard in being packed with stercomata.

Saccamminid sp. E. Test 100–200 μm long and 80–120 μm wide, rounded to more elongate oval, in one specimen produced into short apertural neck. Wall whitish with individual grains visible under compound microscope and overlain by patchy, loosely agglutinated veneer of fine-grained material. Pale staining cytoplasm completely fills test interior.

Saccamminid sp. H (Figure 5G). Test elongate oval, 280–360 μm long and 130–170 μm wide; proximal end pointed or with short, blunt spine; distal end produced into short apertural neck. Wall thick, finely granular with dull surface, translucent in glycerol. Cytoplasmic body with a few large black inclusions.

Saccamminid sp. I. Test 160–240 μm and 120–160 μm wide, rounded to more elongate oval in shape, tapering to bluntly pointed apertural end. Wall with silvery reflection, becoming translucent in glycerol. Cytoplasm with numerous dark inclusions.

Saccamminid sp. J (Figure 5H). Test 130–230 μm long and 80–120 μm wide, oval with evenly rounded ends, terminal aperture associated with low mound-like projection. Wall thick with speckly reflection, becoming translucent in glycerol. Finely granular cytoplasm separated from wall by distinct space.

Saccamminid sp. 21. Test 160–240 μm long and 120–160 μm wide, broad to elongate oval in shape, tapering to bluntly pointed apertural end. Wall translucent in glycerol but retaining some silvery reflection.

Saccamminid sp. N. Small fusiform test, 200–220 μm long and 80 μm wide, with pointed proximal end and extended apertural neck. Wall fine grained, fairly thick. Cytoplasm with dark inclusions.

Saccamminid sp. O (Figure 5A). Test 150–220 μm long and 100–140 μm wide, droplet-shaped but with variably developed apertural neck and, in some cases, a slightly asymmetrical outline. Wall finely but distinctly granular with dull surface.

Saccamminid sp. P. Test 220–240 μm long and 120–150 μm wide, with broadly rounded proximal end, bluntly pointed distal end and wide terminal aperture. Wall composed of plate-like particles with silvery surface becoming translucent in glycerol. Cytoplasm with well-defined boundaries and filling variable proportion of test interior.

Saccamminid sp. Q. Test 220 μm long, 160 μm wide, oval with circular aperture at more pointed end. Wall thick, finely but distinctly granular, almost opaque even in glycerol.

Saccamminid sp. R. Test 130–150 μm long and 70 μm wide, droplet-shaped, tapering towards slightly extended apertural end. Wall fairly thick. Cytoplasm with brownish inclusions.

Saccamminid sp. S. Test oval, 160 μm long and 90 μm wide with prominent flared apertural neck. Wall thin and delicate. Cytoplasmic body distinct and separated from wall by large space.

Saccamminid sp. T. Test 320 μm long and 120 μm wide, oval with simple terminal aperture. Wall fairly thick, very fine grained with smooth, whitish surface becoming translucent in glycerol. Cytoplasm fills test interior.

Saccamminid sp. U. Test 140–150 μm long and 80 μm wide. Flask-shaped with short apertural neck. Organic wall overlain by agglutinated layer comprising a mix of larger and smaller particles. This species resembles Saccamminid sp. 5 of Gooday et al. (2004: figures 6D–G).

Saccamminid sp. V. Test 440–560 μm long and 100–120 μm wide, elongate, cylindrical, tapered at either end. Apertures present at both ends but one larger than the other. Wall thin, very fine grained, white becoming translucent in glycerol; surface smooth without wrinkles. Cytoplasm with well-developed endosolenial tube and scattered black particles and clear structures resembling vacuoles.

Psammosphaerids

Sausage-shaped psammosphaerid. Test 300–540 μm long and 130–200 μm wide, elongate oval to cigar-shaped (length:height ratio 2.5–3.0) with no sign of apertures. Wall generally finely agglutinated with scattered larger grains. Interior filled with cytoplasm.

Psammosphaerid sp. C (Figure 4I). More or less spherical test, 80–160 μm diameter, composed of small quartz grains, usually with some larger grains protruding. Cytoplasmic body with dark inclusions, separated from test wall by distinct space.

Psammosphaerid sp. D. Test more or less oval, 100–300 μm long and 80–200 μm wide, circular or slightly flattened in cross-section. Wall fairly coarsely agglutinated, often with larger projecting grains. Cytoplasm fills most of interior and is enclosed in organic theca.

Psammosphaerid sp. K. Test ~300 μm long and ~180 μm wide, brownish in colour, oval with thick wall, noticeably granular under compound microscope, with smooth outer surface. Interior completely filled with cytoplasm.

Grey, flexible psammosphaerid. An irregularly shaped species, resembling *Crithionina granum* in shape but with a flexible test wall.

Other monothalamous taxa

Astrorhiza cornuta Brady 1879. See Brady (1879: 43, plate 4, figures 14, 15).

Tiny *Bathysiphon*. Tiny species, <1 mm in length and ≤20 μm wide. Surface whitish grey, sometimes with silvery reflection.

Crithionina spp. Most specimens are attached to firm substrates and resemble *Crithionina goesii* and *C. mamilla* Goës 1894. A species with spicules (*Crithionina hispida* Flint 1899) was found at the deepest site (Stn 0778, 2472 m water depth). Thies (1991) reported abundant *C. hispida* from the Fram Strait (1400–1500 m water depth) and the Greenland and Lofoten basins (2000–3200 m) in the northern North Atlantic.

Hemisphaerammina spp. Low, whitish domes without apertures attached to stones and other hard substrates. Wall consists of fine particles, in some cases with scattered larger quartz grains. The internal structure was not investigated and the possibility that some specimens belong to a genus such as *Pseudowebbinella*, in which the internal cavity is subdivided, cannot be ruled out.

Hyperammina subnodosa Brady 1884. See Brady (1884: 159, plate 23, figures 11–14).

Hyperammina crassatina (Brady 1881) = *Astrorhiza crassatina* Brady 1881. See Brady (1884: plate 20, figures 1–9).

Hyperammina fragilis Brady 1884. See Brady (1884: 258, plate 23, figures 1–3, 5, 6).

Hyperammina friabilis Höglund 1947. See Höglund (1947: 71, plate 71, figures 33–42).

Tiny *Hyperammina*. Similar to the species from Explorers Cove, Antarctica, illustrated by Gooday et al. (1996) as ?*Hyperammina* sp.

Hippocrepinella crassa Heron-Allen & Earland (Figure 3F). Heron-Allen & Earland (1932: 259, plate 2, figures 1–3). Our specimens closely resemble those illustrated by Höglund (1947: 44–45, plate 1, figures 14–16).

Hippocrepinella hirudinea Heron-Allen & Earland 1932 (Figure 3I). See Heron-Allen & Earland (1932: 258, plate 1, figures 7–15). Reported by Thies (1991) from 280–1750 m water depth in the northern North Atlantic.

?Hippocrepinella C. Test 460 μm long and 130 μm wide, cigar-shaped; wall fairly thick, fine grained, brownish with weak transverse surface wrinkles and faint longitudinal grooves. Cytoplasm with scattered black inclusions, but otherwise featureless. The test shape is similar to that of *Hippocrepinella*, but the lack of obvious apertures makes a placement in this genus tentative.

Pelosina arborescens Pearcey 1910. See Pearcey (1910: 1001, plate 1, figures 1–5).

Pelosina fusiformis Earland 1933 (Figure 3L, M). Our specimens resemble those illustrated by Höglund (1947: plate 6, figure 12). This species is similar to *P. variabilis* but has a plumper test, sometimes extended out into a long, branched or unbranched tubular extension.

Pelosina variabilis Brady 1879 (Figure 3N). See Höglund (1947: plate 6, figures 5–7). Some specimens from Stn 0779 are studded with benthic and planktonic foraminiferal tests.

P. sphaeriloculum Höglund 1947 = *Pelosina variabilis* Brady *sphaeriloculum* Höglund 1947: 61, plate 6, figures 8–11. This form has a rounded test with root-like extensions.

Small *Pelosinella*-like species (Figure 3H). Test lemon-shaped, more or less pointed at both ends. It resembles the lemon-shaped *Pelosina* species illustrated by Gooday (1983: figure 5).

Psammmosphaera fusca Schultze 1875 (Figure 3C). See Brady (1884: 249–251, plate 18, figure 1).

Rhabdammina abyssorum Sars 1869 (in Carpenter 1869). See Brady (1884: 266–268, plate 21, figures 1–8, 10–13).

Dendrophyra erecta (Norman 1881) = *Psammatodendron erecta* Norman 1881. See Brady (1884: 263, plate 28, figures 12, 13, as *Hyperammina erecta*).

Psammosphaera fusca Schultze 1875 (Figure 3C). See Brady (1884: 249–251, plate 18, figure 1).

Saccorhiza ramosa (Brady 1879) = *Hyperammina ramosa* Brady 1879. See Brady (1884: 261–262, plate 23, figures 15–19, as *Hyperammina ramosa*).

Undescribed stercomata-filled mudball (Figure 3B). Resembles the specimen illustrated by Gooday et al. (1997: plate 3, figures 1–2) but has a larger, more irregularly shaped, stercomata-filled capsule.

Chain-like komokiacean. Species resembling chain-like forms such as *Catena* (Schröder et al. 1989) and undescribed taxa (Gooday 1990: plate 3).

Edgertonia-like komokiacean mudball (Figure 3D). Komokiacean mudballs are common in deep-sea samples (e.g. Gooday 1990: plate 1, figures A–D).

Gromiids

We recognized a number of gromiid-like morphotypes. The main ones are detailed below. The elongate, very elongate and dark gromiids (Figure 2A, B, D) are distinctive and represent single morphospecies, whereas the oval morphotypes are rather variable and represent a number of species.

Very elongate, slender gromiid (Figure 2A). Long, sausage-shaped gromiid, 1.5–5.4 mm long, 220–300 μm wide. Test cylindrical, gently and evenly curved with prominent apertural capsule, filled with mass of brown stercomata.

Elongate, slender gromiid (Figure 2B). Test 500–600 μm long and 120–140 μm wide with prominent oral capsule.

Elongate dark gromiid (Figure 2D).

Oval gromiid (Figure 2E). Test 300–460 μm long and 160–260 μm wide with prominent oral capsule.

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