



Cold-seep ostracods from the western Svalbard margin: direct palaeo-indicator for methane seepage?

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Abstract. Despite their high abundance and diversity, microfossil taxa adapted to a particular chemosynthetic environment have rarely been studied and are therefore poorly known. Here we report on an ostracod species, *Rosaliella svalbardensis* gen. et sp. nov., from a cold methane seep site at the western Svalbard margin, Fram Strait. The new species shows a distinct morphology, different from other eucytherurine ostracod genera. It has a marked similarity to *Xylocythere*, an ostracod genus known from chemosynthetic environments of wood falls and hydrothermal vents. *Rosaliella svalbardensis* is probably an endemic species or genus linked to methane seeps. We speculate that the surface ornamentation of pore clusters, secondary reticulation, and pit clusters may be related to ectosymbiosis with chemoautotrophic bacteria. This new discovery of specialized microfossil taxa is important because they can be used as an indicator species for past and present seep environments (<http://zoobank.org/urn:lsid:zoobank.org:pub:6075FF30-29D5-4DAB-9141-AE722CD3A69B>).

1 Introduction

It is important to understand causes behind changes in the activity of release of methane in the geological past because methane is a ~25 times more powerful greenhouse gas than carbon dioxide, and it constitutes an important factor in regional and global climate change (Nisbet and Chappellaz, 2009; Consolaro et al., 2015; Hopcroft et al., 2017). Reconstructions of deep-sea seep activities in the geological past have often been based on $\delta^{13}\text{C}$ values measured in foraminiferal shells, but the signals are often caused by secondary mineralization of diagenetic carbonate, making inferences about timing of seepage events difficult (Uchida et al., 2008; Consolaro et al., 2015; Szybor and Rasmussen, 2017a). So far, apart from certain macrofossils (e.g. vesicomid bivalves), very few other indicator species for the de-

tection of past methane seepage in sedimentary records have been described (e.g. Sen Gupta et al., 1997; Bernhard et al., 2001). Because of their large size and low abundance compared to microfossils, quantitative studies of deep-sea macrofaunas are difficult.

Methane hydrate provinces are widely distributed in the Arctic Ocean (Biastoch et al., 2011). The stability of methane hydrate is known to be sensitive to climate change (Berndt et al., 2014). In turn, methane seepage may have contributed to rapid climate change (Nisbet and Chappellaz, 2009; Dickens, 2011). Release of methane creates a unique chemosynthetic ecosystem (Van Dover et al., 2003), and thus there may be unique microfossil communities or endemic microfossil species providing unequivocal indications for palaeo-methane seepage.

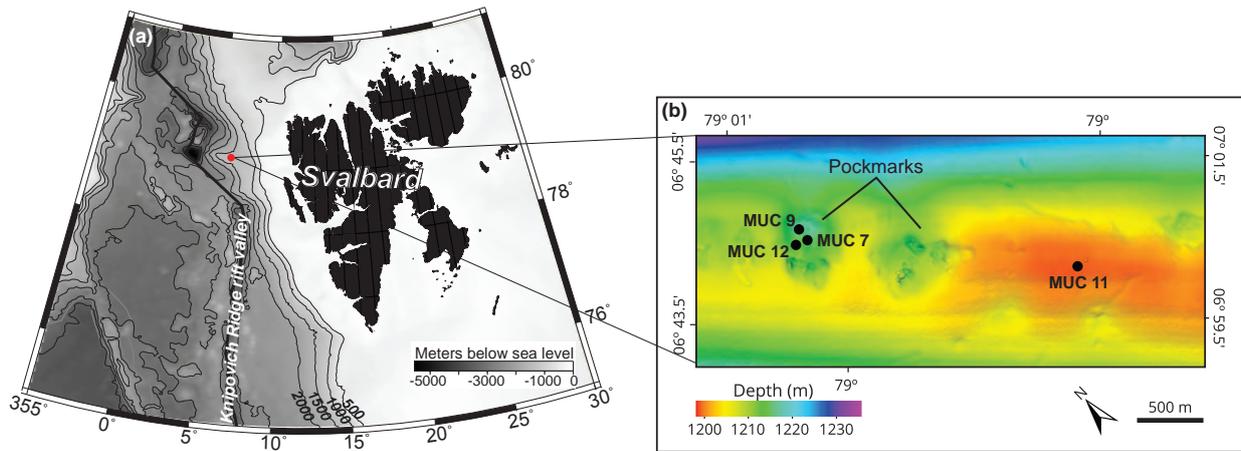


Figure 1. Locality maps. (a) Map of Svalbard and the research area marked by red dot. (b) Details of research area showing positions of the multicore stations. Pockmark bathymetry data are from Bünz et al. (2012).

Ostracoda are small crustaceans that have bivalve-like calcified shells. They are diverse: > 20 000 living species are estimated, and, among them, ~ 8000 species have been described (Horne et al., 2002; Rodriguez-Lazaro and Ruiz-Muñoz, 2012). Most species are sensitive to changes in various environmental factors (e.g. temperature, salinity, oxygen, organic matter supply) (Horne et al., 2002; Schellenberg, 2007; Yasuhara and Cronin, 2008; Mesquita-Joanes et al., 2012). Their calcified shells are abundantly preserved in marine sediments (Yasuhara et al., 2017). Thus, ostracods are a widely used microfossil group in the reconstruction of various palaeoceanographic and palaeoclimatological changes. They have been successfully applied in the reconstruction of past sea-level, temperature, salinity, and other environmental changes (Frenzel and Boomer, 2005; Yasuhara and Seto, 2006; Iwatani et al., 2012; Cronin, 2015). However, methane seep ostracods remain poorly investigated, and any ostracod species, genera, or faunas endemic or specific in methane seep environments have not been known until now (Karanovic and Brandão, 2015).

Here we report on deep-sea ostracods from Vestnesa Ridge in the eastern Fram Strait, carefully collected from an active pockmark generated by strong and persistent release of methane from the seafloor (e.g. Bünz et al., 2012; Szytybor and Rasmussen, 2017a, b). We discovered *Rosaliella svalbardensis* gen. et sp. nov., and this species or genus is likely endemic to methane seepage environments; thus, their well-calcified microfossil shells can be useful indicators of methane release in the past and present.

2 Materials and methods

The samples were collected with a video-guided multicorer (MUC) during the RV *Poseidon* cruise 419 to Vestnesa Ridge in August 2011 (Fig. 1). In total three sites within the cold-

seep pockmark (MUC 7, 9, 12) and one control station outside the pockmark (MUC 11) were sampled (Fig. 1; Table 1). The cores of MUC 7 and MUC 12 were taken in bacterial mats, while MUC 9 was retrieved from a field of (chemosynthetic) tubeworms. Each of the cores was subsampled on board. The cores were cut into 1 cm thick slices, preserved in alcohol stained with rose bengal, and kept cool until further processing. For this study, the core top 1 cm slices were used. In the laboratory the samples were wet-sieved (0.063, 0.1, and 1 mm) and then dried. We used the > 100 µm size fraction for ostracod analysis. This sieve size allows one to obtain adult and late-stage juvenile specimens of most species. All ostracod specimens in a sample were picked, mounted on microfossil slide, and identified to species level. The number of specimens refers to valves.

Uncoated ostracod specimens were digitally imaged with a Hitachi S-3400N variable pressure scanning electron microscope (SEM) in low-vacuum mode, at the Electron Microscope Unit, The University of Hong Kong. Figured specimens are deposited in the National Museum of Natural History (Washington, DC, USA; catalogue numbers USNM 696651–696672). M. Yasuhara's personal catalog number (Seep1–15, 17–23) is indicated in parentheses. For the higher classification scheme, we mainly refer to the World Ostracoda Database (Brandão et al., 2017), Whatley et al. (1993), and Horne et al. (2002).

Abbreviations

LV, left valve; RV, right valve; L, length; H, height.

3 Systematic palaeontology

Subclass **Podocopa** Sars, 1866

Order **Podocopida** Sars, 1866

Table 1. Sample and locality information.

Site	Sample	Date	Latitude (N)	Longitude (E)	Depth (m)	Note
POS419-675	MUC9	28/8/2011	79°00.466'	06°54.279'	1241	Siboglinidae field
POS419-676	MUC11	28/8/2011	78°59.774'	06°58.064'	1191	Control site
POS419-678	MUC12	29/8/2011	79°00.417'	06°54.131'	1235	Bacterial mat, strongly bubbling
POS419-658	MUC7	24/8/2011	79°00.415'	06°54.229'	1204	<i>Beggiatoa</i> mat

Suborder **Cytherocopina** Baird, 1850

Superfamily **Cytheroidea** Baird, 1850

Family **Cytheruridae** Müller, 1894

Genus ***Rosaliella*** gen. nov.

Derivation of name. In honour of Rosalie F. Maddocks (University of Houston, USA) for her work on ostracods from chemosynthetic environments.

Type species. *Rosaliella svalbardensis* gen. et sp. nov.

Diagnosis. A large, oval-shaped Cytheruridae genus with primary reticulation and pore clusters (i.e. secondary reticulation). No ventrolateral or dorsolateral ridge on valve surface. Caudal process lacking. Hingement peratodont type (Bate, 1972). Subcentral muscle scars composed of one boomerang-shaped frontal scar and a vertical row of four elongate adductor scars.

Remarks. *Rosaliella* gen. nov. is most similar to species of *Xylocythere*. Both *Xylocythere* and *Rosaliella* have well-developed primary reticulation and pore clusters and similar subcentral muscle scars and hingement (e.g. see Maddocks and Steineck, 1987; Steineck et al., 1990, for *Xylocythere*). Especially the type species of both genera (i.e. *Rosaliella svalbardensis* gen. et sp. nov. and *Xylocythere turnerae* Maddocks and Steineck, 1987) have substantial similarity, for example, in the general patterns of primary reticulation and pore conuli distribution. However, *Xylocythere* species have a ventrolateral ridge and a spine on their posterior end, a more rectangular outline, and a less inflated shell (Maddocks and Steineck, 1987; Steineck et al., 1990). In contrast, *Rosaliella* does not have any ridge or spine, and has an oval outline and more inflated shell. In internal view, *Xylocythere* species have enlarged (tooth-like) anterior and posterior ends of median hinge bar in LV (Maddocks and Steineck, 1987; Steineck et al., 1990), but *Rosaliella* lacks such a tooth-like structure at each end of the median hinge bar in LV. Because these differences are substantial, we erect *Rosaliella* gen. nov. as an independent genus from *Xylocythere*. The type species *Rosaliella svalbardensis* is also similar to *Laocoonella commensalis* (de Vos, 1953) in surface ornamentation (de Vos, 1953; de Vos and Stock, 1956). But *Rosaliella svalbardensis* is much larger than *Laocoonella commensalis*. In addition, hingement of *Lao-*

coonella is more similar to that of *Xylocythere* (in lacking denticulation at least in an end of median hinge bar; see de Vos, 1953; Maddocks and Steineck, 1987), rather than that of *Rosaliella*. Thus, we consider that they are not conspecific or congeneric. *Rosaliella* is distinct from species of other eucytherurine genera. For example, *Rosaliella* is different from *Cytheropteron* by lacking ala and caudal process, although both genera have very similar hingement and subcentral muscle scars and some deep-sea *Cytheropteron* species lack ala (e.g. see Yasuhara et al., 2009, Yasuhara and Okahashi, 2015, for *Cytheropteron*). Some species of *Eucytherura* (e.g. *Eucytherura pacifica* Ayress, Whatley, Downing and Millson, 1995) have well-developed primary reticulation and pore clusters and very weakly developed caudal process similar to *Rosaliella* (Ayress et al., 1995; Yasuhara et al., 2009). However, *Rosaliella* differs from *Eucytherura* by lacking ridge, spine, and tubercle, and by having arched hingement (hingement is straight or sinuous in *Eucytherura*) and a comparatively less calcified shell (e.g. see Ayress et al., 1995; Yasuhara et al., 2009, for *Eucytherura*).

Rosaliella svalbardensis gen. et sp. nov.
(Figs. 2–3)

Derivation of name. From the type locality, Svalbard.

Holotype. Adult female RV, USNM 696652 (Seep2) (Fig. 2f–j).

Paratypes. Adult female LV, USNM 696651 (Seep1) (Fig. 2a–e); adult female LV, USNM 696653 (Seep20) (Fig. 2k–n); adult female RV, USNM 696654 (Seep21) (Fig. 2o–q); adult male LV, USNM 696655 (Seep3) (Fig. 3a–d); adult male RV, USNM 696656 (Seep4) (Fig. 3e–i); A-1 juvenile LV, USNM 696657 (Seep5) (Fig. 3j); A-1 juvenile RV, USNM 696658 (Seep6) (Fig. 3k); A-2 juvenile LV, USNM 696659 (Seep7) (Fig. 3l); A-2 juvenile RV, USNM 696660 (Seep8) (Fig. 3m).

Type locality and horizon. POS419-678, MUC 12B, 0–1 cm depth; Vestnesa Ridge, western Svalbard margin, Fram Strait, Arctic Ocean; 79°00.417' N, 06°54.131' E; 1235 m water depth (Table 1).

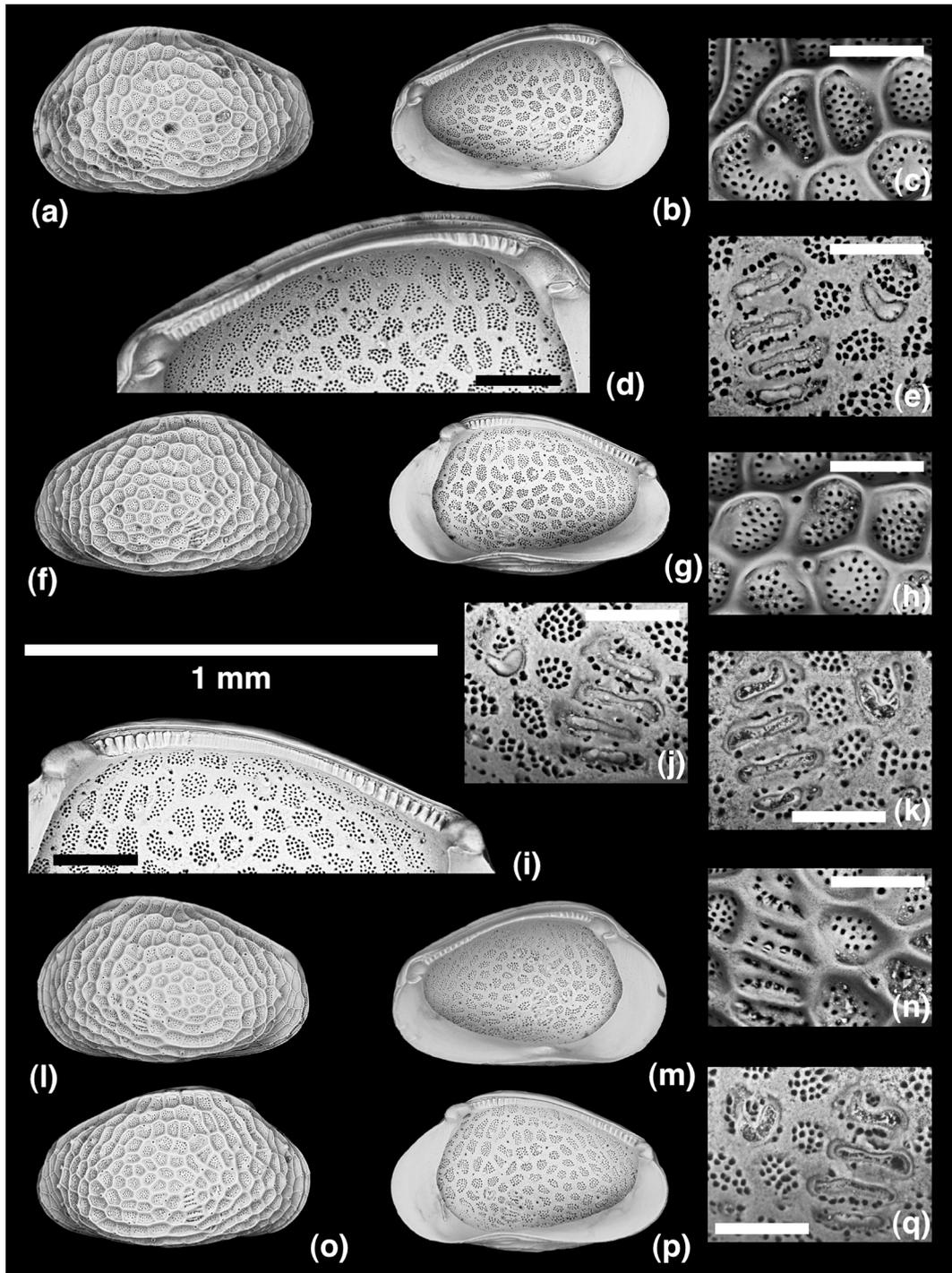


Figure 2. Scanning electron microscopy images of *Rosaliella svalbardensis* gen. et sp. nov. (a–e) USNM 696651 (Seep1), paratype, adult, female, LV, POS419-678, MUC 12B, 0–1 cm depth. (f–j) USNM 696652 (Seep2), holotype, adult, female, RV, POS419-678, MUC 12B, 0–1 cm depth. (k–n) USNM 696653 (Seep20), paratype, adult, female, LV, POS419-658, MUC 7, 0–1 cm depth. (o–q) USNM 696654 (Seep21), paratype, adult, female, RV, POS419-658, MUC 7, 0–1 cm depth. (a, c, f, h, l, n, o) Lateral views. (b, d, e, g, i, j, k, k, p, q) Internal views. Scale bars: 1 mm for (a, b, f, g, l, m, o, p); 100 μ m for (d, i); 50 μ m for (c, e, h, j, k, n, q). 1 mm scale bar in the middle part of the figure. Other scale bars in each panel.

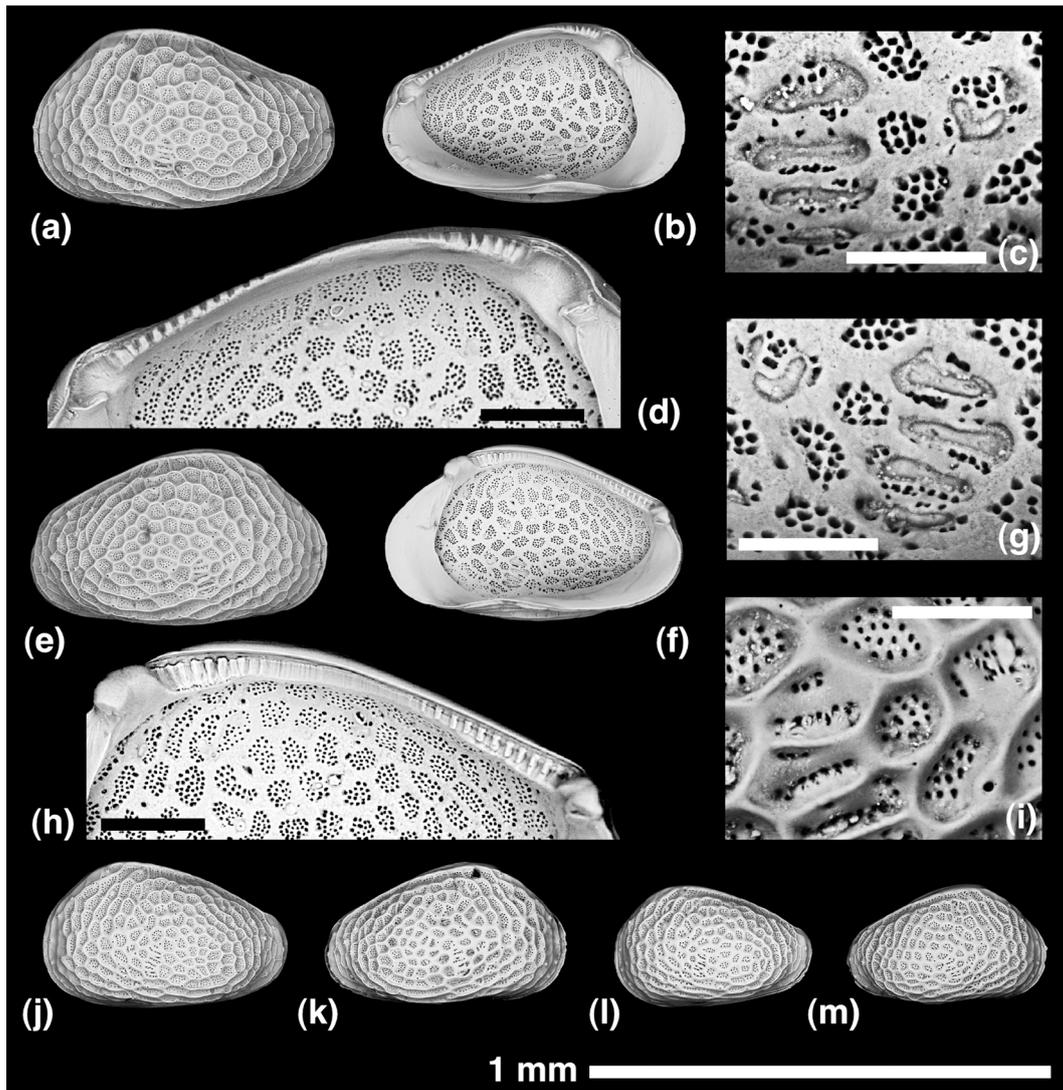


Figure 3. Scanning electron microscopy images of *Rosaliella svalbardensis* gen. et sp. nov. (a–d) USNM 696655 (Seep3), paratype, adult, male, LV, POS419-678, MUC 12B, 0–1 cm depth. (e–i) USNM 696656 (Seep4), paratype, adult, male, RV, POS419-678, MUC 12B, 0–1 cm depth. (j) USNM 696657 (Seep5), paratype, A-1 juvenile, LV, POS419-678, MUC 12B, 0–1 cm depth. (k) USNM 696658 (Seep6), paratype, A-1 juvenile, RV, POS419-678, MUC12B, 0–1 cm depth. (l) USNM 696659 (Seep7), paratype, A-2 juvenile, LV, POS419-678, MUC 12B, 0–1 cm depth. (m) USNM 696660 (Seep8), paratype, A-2 juvenile, RV, POS419-678, MUC 12B, 0–1 cm depth. (a, e, i, j, k, l, m) Lateral views. (b, c, d, f, g, h) Internal views. Scale bars: 1 mm for (a, b, e, f, j, k, l, m); 100 μ m for (d, h); 50 μ m for (c, g, i). 1 mm scale bar on the bottom right of the figure. Other scale bars in each panel.

Dimensions. USNM 696652 (Seep2) (holotype), L = 672 μ m, H = 404 μ m; USNM 696651 (Seep1) (paratype), L = 680 μ m, H = 411 μ m; USNM 696655 (Seep3) (paratype), L = 656 μ m, H = 395 μ m; USNM 696656 (Seep4) (paratype), L = 642 μ m, H = 382 μ m.

Diagnosis. A species of *Rosaliella* ornamented with well-developed primary and secondary reticulation.

Description. Carapace well calcified, medium in size, highest at anterior third of length. Outline oval in lateral

view; anterior margin evenly rounded in ventral half and straight in dorsal half; posterior margin rounded; dorsal and ventral margins rounded. Anterodorsal corner rounded; posterodorsal corner weakly angular. Lateral surface ornamented with well-developed, regular primary reticulation and pore clusters (i.e. secondary reticulation), and lacking any spines or ridges; normal pores situated on muri. Inner lamella broad. Hingement peratodont type; anterior and posterior terminal teeth in RV smooth; median hinge element in RV denticulate especially in posterior and anterior thirds; median hinge bar in LV denticulate in posterior and anterior

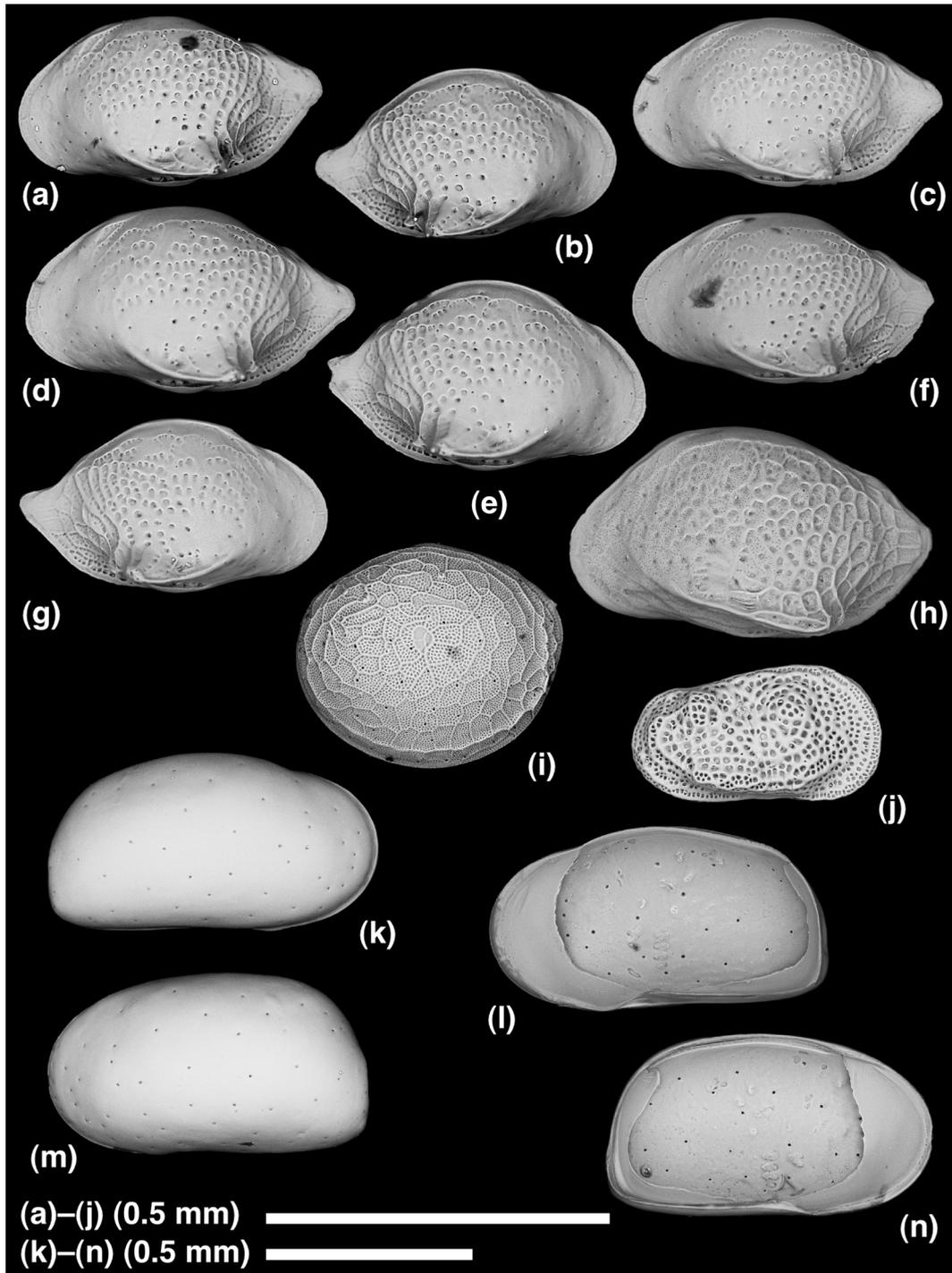


Figure 4. Scanning electron microscopy images of *Cytheropteron carolinae*, *Cytheropteron* cf. *pseudoinflatum*, *Polycope bireticulata*, *Cluthia cluthae*, and *Krithe glacialis*. **(a–g)** *Cytheropteron carolinae* Whatley and Coles, 1987. **(a)** USNM 696661 (Seep9), adult, LV, POS419-678, MUC 12B, 0–1 cm depth. **(b)** USNM 696662 (Seep10), adult, RV, POS419-678, MUC 12B, 0–1 cm depth. **(c)** USNM 696663 (Seep17), adult, LV, POS419-675, MUC 9, 0–1 cm depth. **(d)** USNM 696664 (Seep11), adult, LV, POS419-678, MUC 12B, 0–1 cm depth. **(e)** USNM 696665 (Seep12), adult, RV, POS419-678, MUC 12B, 0–1 cm depth. **(f)** USNM 696666 (Seep22), adult, LV, POS419-658, MUC 7, 0–1 cm depth. **(g)** USNM 696667 (Seep23), adult, RV, POS419-658, MUC 7, 0–1 cm depth. **(h)** *Cytheropteron* cf. *pseudoinflatum* Whatley and Eynon 1996, USNM 696668 (Seep18), adult, LV, POS419-675, MUC 9, 0–1 cm depth. **(i)** *Polycope bireticulata* Joy and Clark, 1977, USNM 696669 (Seep13), RV, POS419-678, MUC 12B, 0–1 cm depth. **(j)** *Cluthia cluthae* (Brady, Crosskey, and Robertson, 1874), USNM 696670 (Seep14), adult, RV, POS419-678, MUC 12A, 0–1 cm depth. **(k–n)** *Krithe glacialis* Brady, Crosskey, and Robertson, 1874. **(k–l)** USNM 696671 (Seep15), adult, female, RV, POS419-675, MUC 9, 0–1 cm depth. **(m–n)** USNM 696672 (Seep19), adult, female, LV, POS419-675, MUC 9, 0–1 cm depth. **(a–k, m)** Lateral views. **(l, n)** Internal views. 0.5 mm scale bars on the bottom left of the figure.

Table 2. Ostracod data summary.

Site	POS419-658	POS419-675	POS419-676	POS419-678	POS419-678
Sample	MUC 7	MUC 9	MUC 11	MUC 12A	MUC 12B
Note*	Seep w Ba	Seep w T	Control	Seep w Ba, Bu	Seep w Ba, Bu
Core depth	0–1 cm	0–1 cm	0–1 cm	0–1 cm	0–1 cm
<i>Argilloecia</i> cf. <i>robinwhatleyi</i>		2			
<i>Argilloecia</i> sp. 1 of Yasuhara et al. (2014b)		6			
<i>Australoecia posteroacuta</i>		2			
<i>Cluthia cluthae</i>		2		1	
<i>Cytheropteron carolinae</i>	2	8			9
<i>Cytheropteron higashikawai</i>			1		1
<i>Cytheropteron inflatum</i>			1		
<i>Cytheropteron perlaria</i>		1			
<i>Cytheropteron</i> cf. <i>pseudoinflatum</i>		1			
<i>Krithe glacialis</i>		24	1		
<i>Muellerina abyssicola</i>		2			
<i>Paracytherois chukchiensis</i>		6			
<i>Polycope bireticulata</i>		2			2
<i>Pseudocythere caudata</i>		11			
<i>Rosaliella svalbardensis</i> gen. et sp. nov.	2			4	22
<i>Swainocythere</i> cf. <i>chejudoensis</i>					2
<i>Thaerocythere crenulata</i>		1			
Total	4	68	3	5	36

* Control: control non-seep site; Seep w: seep site with bacteria mat (Ba), tubeworm field (T), and/or strong bubbling (Bu).

thirds, and smooth in middle part. Frontal scar boomerang-shaped; adductor muscle scars consisting of vertical row of four elongate scars.

Remarks. *Rosaliella svalbardensis* gen. et sp. nov. is most similar to *Xylocythere turnerae* Maddocks and Steineck, 1987 (see the remarks section of the genus above), but distinguished by having an oval outline and lacking a ventrolateral ridge.

Distribution. This species is known only from the methane seepage locality of Vestnesa Ridge, western Svalbard margin.

4 Results and discussion

4.1 *Rosaliella svalbardensis* as palaeo-methane seep indicator

Rosaliella svalbardensis shows clear similarity to *Xylocythere* species that are known from other chemosynthetic (i.e. wood fall and hydrothermal vent) environments (Maddocks and Steineck, 1987; Steineck et al., 1990; Van Harten, 1993; Maddocks, 2005). They are rarely found in normal soft sediments (Corrége, 1993; Karanovic and Brandão, 2015; Yasuhara et al., 2009). In these normal soft sediments, the *Xylocythere* specimens may have been transported from nearby chemosynthetic environments. Within a pockmark,

Rosaliella svalbardensis occurs in seepage sites with bacterial mats (MUC 7, 12), but it is absent in the tubeworm field (MUC 9) and in the nearby control site, 500 m from the pockmark (MUC 11) (Tables 1–2). Notably, this species shows high abundance in a site with strong bubbling of methane (MUC 12; Tables 1–2). In addition, although deep-sea ostracods from normal soft sediments are well studied in the North Atlantic, Nordic seas, and Arctic Ocean (i.e. adjacent regions to the study sites) (Whatley and Coles, 1987; Whatley et al., 1996, 1998; Didié and Bauch, 2000; Yasuhara et al., 2009, 2014a, b; Alvarez Zarikian, 2009; Yasuhara and Okahashi, 2014, 2015; Gemery et al., 2017), any similar species or genus to *Rosaliella svalbardensis* has not been reported.

Van Harten (1993) suggested that pore clusters in *Xylocythere* is related to ectosymbiosis of chemoautotrophic bacteria (also see Maddocks, 2005). We observed the same structure in *Rosaliella* (Figs. 2–3). Furthermore, *Keysercythere* recently discovered from a wood fall environment has the pore clusters even though this genus is distant from *Xylocythere* or *Rosaliella* phylogenetically, belonging to different families (Karanovic and Brandão, 2015). Thus, the pore clusters observed in these genera may be convergence and evolutionary adaptation to chemosynthetic environments.

These results indicate that *Rosaliella svalbardensis* is associated with methane seepage and probably endemic to the methane seep environment. More specifically, the habitat of this species is probably related to the presence of bacte-

rial mats. Its high abundance in an active seep site suggests that this species can be a good indicator of not only presence/absence but also of the strength of release of methane. Furthermore, *Rosaliella svalbardensis* has relatively large and well-calcified valves and a distinct morphology (Figs. 2–3). Thus, this species can be used as a direct palaeo-indicator for methane seepage allowing reconstructions of long-term changes in seepage activity. It is likely that fossil valves of this species will be discovered from long sediment cores from methane seep sites.

4.2 Ostracod fauna in methane seep

The site from the pockmark within a tubeworm field (MUC 9) shows the highest abundance of ostracods (Table 2; Fig. 4). Almost all species from this site are also known from normal deep-sea soft sediments (Yasuhara et al., 2009, 2014a, b, 2015). A notable point is the relatively high abundance of species with secondary reticulation or pit clusters, i.e. *Cytheropteron carolinae* Whatley and Coles, 1987, *Cluthia cluthae* (Brady, Crosskey, and Robertson, 1874), *Polycope bireticulata* Joy and Clark, 1977 (Fig. 4). They also occur in other cold-seep sites and are absent in the control site (Table 2). Thus, we may suggest that these secondary reticulation and pit clusters are related to ectosymbiosis of chemoautotrophic bacteria, like the pore clusters in *Xylocythere* (Van Harten, 1993; Maddocks, 2005). However, as noted above, these species are also known from normal deep-sea soft sediments (Freiwald and Mostafawi, 1998; Yasuhara et al., 2009, 2014b; Gemery et al., 2017). This hypothesis remains speculative and further research is needed.

5 Conclusions

1. *Rosaliella svalbardensis* gen. et sp. nov. is described. This species can be a useful indicator of palaeo-methane release.
2. The hypothesis that pore clusters, secondary reticulation, and pit clusters are related to ectosymbiosis of chemoautotrophic bacteria merits further investigation.
3. Macroevolution of chemosynthetic taxa in seep, vent, and organic fall habitats remains poorly understood (Smith et al., 2015). Thus, discovery of specialized taxa for the chemosynthetic environments is important especially in microfossil taxa that have abundant and excellent fossil records in deep-sea sediments and that are widely used in palaeoceanographic research.

Data availability. All data are included in this paper itself.

Competing interests. The authors declare that they have no conflict of interest.

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