



## Taxonomy and palaeoecology of two Late Pleistocene species of vesicomyid bivalves from cold methane seeps at Svalbard (79°N)

Jesper Hansen<sup>1</sup>, Ulrike Hoff<sup>2</sup>, Kamila Szybor<sup>2</sup> and Tine L. Rasmussen<sup>2</sup>

<sup>1</sup>*Akvaplan-niva AS, Framcenteret, High North Research Centre, NO-9296 Tromsø, Norway; and*

<sup>2</sup>*CAGE, Centre for Arctic Gas Hydrate, Environment and Climate, Department of Geosciences, UiT, The Arctic University of Norway, NO-9037 Tromsø, Norway*

Correspondence: J. Hansen; e-mail: [jesper@akvaplan.niva.no](mailto:jesper@akvaplan.niva.no)

(Received 2 January 2017; editorial decision 21 February 2017)

### ABSTRACT

Two species of the bivalve family Vesicomyidae have recently been sampled in marine sediment cores at a cold methane seepage site on Vestnesa Ridge, located in the eastern Fram Strait at 79°N. The specimens were dated to between 16,400 and 14,800 calibrated YBP and are the northernmost known representatives of the family. *Archivesica arctica* n. sp., a comparatively small species within the genus, is described for the first time. *Isorropodon nyeggaensis* has previously been known solely from the area of the type locality on the Norwegian continental margin at 64°N. Both species were, as typical for vesicomyids, living in the sulphide-rich reducing habitats occurring at cold seeps. Both the specimens of *A. arctica* from the Vestnesa Ridge and the specimens reported previously from the Gakkel Ridge north of Russia occurred exclusively in sediments dated to a cold event during the deglaciation named Heinrich event H1, c. 18,000–15,000 YBP. Despite great efforts, sampling of living specimens in modern active methane seeps in the Arctic has not been successful. It appears that not only the availability of hydrogen sulphide, but also the increased bottom-water temperatures, characterizing H1 in the Arctic, restricted the occurrence of vesicomyids to this short time interval.

### INTRODUCTION

Vestnesa Ridge on the continental slope off northwestern Spitsbergen (Svalbard Archipelago) in the eastern Fram Strait (Fig. 1) is one of the northernmost known areas of deep-water cold methane seeps (Hustoft *et al.*, 2009; Bünz *et al.*, 2012). Since the discovery of pockmarks and acoustic anomalies at the Vestnesa Ridge in the early 1990s (Vogt *et al.*, 1994), the area has been a subject of multiple geophysical and environmental studies (e.g. Pimenov *et al.*, 2000; Hustoft *et al.*, 2009; Ambrose *et al.*, 2015; Plaza-Faverola *et al.*, 2015; Hong *et al.*, 2016; Szybor & Rasmussen, 2016). The activity of the seeps has changed through time and appears to have been at its maximum during the relatively warm Bølling-Allerød Interstadial (Szybor & Rasmussen, 2016). The Greenland Sea Intermediate Water, with temperatures about  $-0.9$  °C, presently influences the benthic fauna in the area (Aagaard, Swift & Carmack, 1985).

Within this cold-seep environment, fossil shells of large chemosymbiotic bivalves belonging to the two families Thyasiridae and Vesicomyidae have been found in the seep-influenced deposits. The vesicomyids, especially, are known to be associated with methane seeps, hydrothermal vents and accumulations of organic debris in deep water, where they obtain nutrients from sulphide-oxidizing chemoautotrophic bacteria hosted in their gills (see Barry & Kochevar, 1999 and references therein). The vesicomyid fauna from the Vestnesa Ridge has previously been documented by Ambrose *et al.* (2015) and the species were then tentatively identified as *Isorropodon* sp. and *Phreagena* s. l.

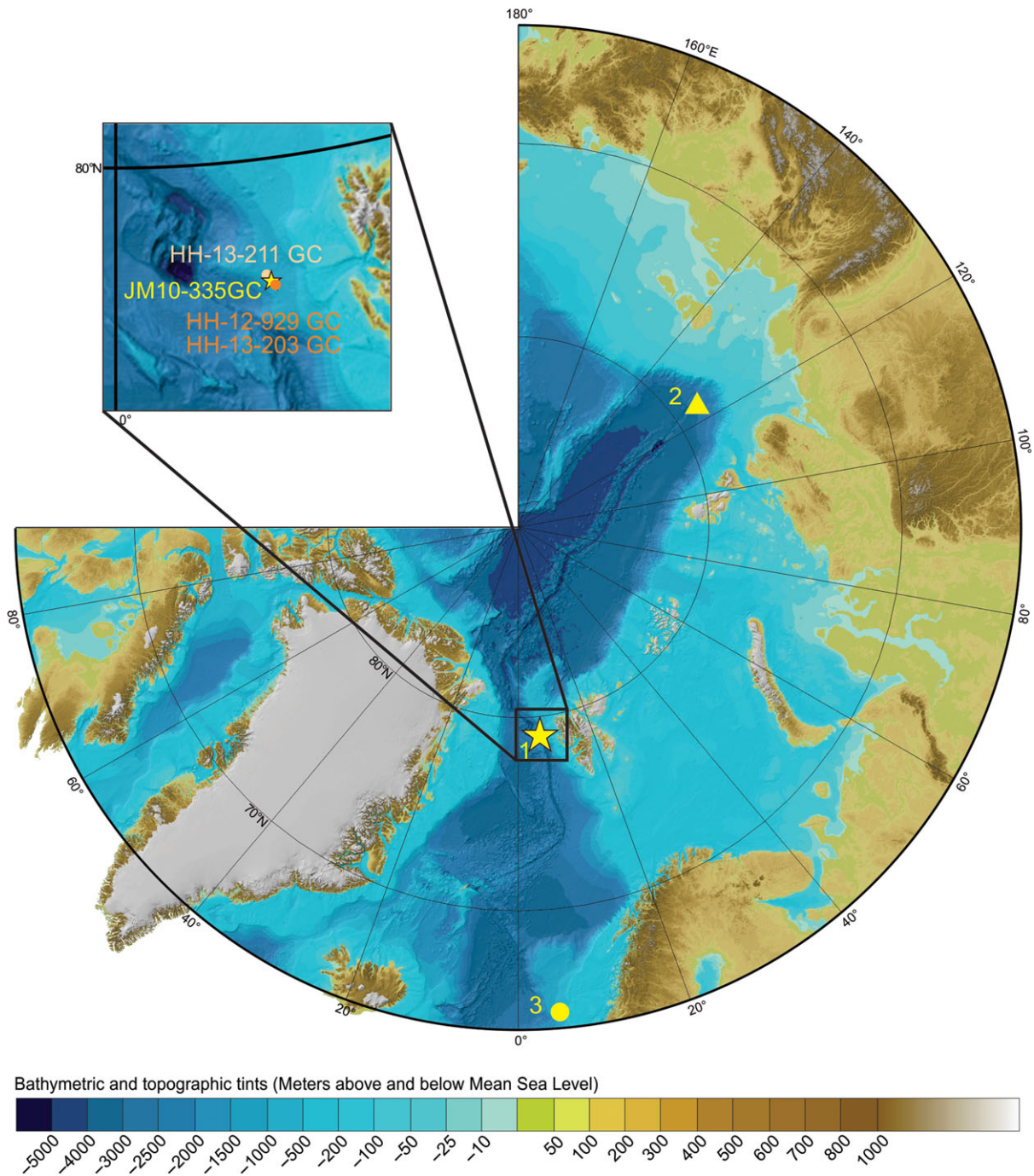
Here we describe and discuss the vesicomyid taxa retrieved in marine sediment cores from the Arctic methane seeps at 1,197 m water depth on Vestnesa Ridge off northwestern Spitsbergen (Szybor & Rasmussen, 2016), including a new species of the genus *Archivesica* Dall, 1908. The environmental factors possibly controlling the distribution of these species in time and space are discussed. In addition, we briefly discuss the genus *Archivesica* in the light of published phylogenetic studies on the family and evaluate which species should be included in the genus.

### MATERIAL AND METHODS

In June 2010, gravity core JM10-335GC was taken at Vestnesa Ridge, eastern Fram Strait, during a cruise with RV *Jan Mayen* (now RV *Helmer Hanssen*) (79°00.173'N; 06°55.335'E; 1,197 m water depth; Fig. 1). The core was taken from an active pockmark from within a rising gas flare.

Density and magnetic susceptibility of the core were measured before it was opened. After opening the core, the halves were X-rayed, XRF-scanned and visually described. In the following, one of the core halves was sampled for chemical investigations (e.g. oxygen and carbon isotopes) and the study of the foraminiferal assemblages, while the other half was stored as an archive.

The largest macrofossils were located and picked out during visual examination just after the core sections were split. At about 275 cm core depth, a main shell layer was visible on X-ray photographs. Smaller specimens were retrieved during sieving of 1-cm



**Figure 1.** Map showing the known occurrences of *Archivesica arctica* n. sp. and *Isorropodon nyeggaensis*. 1 (star): Vestnesa Ridge; both species occur. 2 (triangle): Gakkel Ridge adjacent to Laptev Sea; *A. arctica* occurs. 3 (dot): Nyegga seep area on Vøring Plateau; type locality of *I. nyeggaensis*. Enlargement of Vestnesa seepage area shows cores from which both species were collected; star marks location of type core JM10-335GC. Bathymetry from IBCAO (Jakobsson *et al.*, 2012).

thick sample slices for foraminiferal assemblage investigations (size fraction >1 mm).

For a more detailed description of the core handling, methodologies, datings and age model of core JM10-335GC, see Szybor & Rasmussen (2016).

The studied vesicomid molluscs, including the type specimens, are deposited in the geological collections (TSGF numbers) at the Tromsø University Museum, UiT—the Arctic University of Norway, Norway.

Full citation of taxonomic authorities is provided in Supplementary Material.

Abbreviations:

H, valve height

L, valve length

W, combined valve width

LV, left valve

RV, right valve

## SYSTEMATIC DESCRIPTIONS

**Order Veneroida H. & A. Adams, 1856**  
**Superfamily Glossoidea Gray, 1847**  
**Family VESICOMYIDAE Dall & Simpson, 1901**  
**Subfamily PLIOCARDIINAE Woodring, 1925**

**Genus *Archivesica* Dall, 1908**

*Archivesica* Dall, 1908: 418 (type species by original designation)

*Callocardia gigas* Dall, 1896; Recent, Gulf of California).

*Phreagena* Woodring, 1938: 50.

*Akebiconcha* Kuroda, 1943: 17.

*Laubiericoncha* Cosel & Olu, 2008: 931.

**Remarks:** The definition and number of species included in the genus *Archivesica* have changed since its description. Dall (1908) originally erected *Archivesica* as a subgenus of *Vesicomya* Dall, 1886. It was subsequently raised to genus level, with *Akebiconcha* Kuroda, 1943 as a subgenus, by Keen (1969). Bernard (1974) proposed to synonymize *Ectenagena* Woodring, 1938 and *Akebiconcha* with *Archivesica* as a subgenus of *Calyptogena* Dall, 1891, while Boss & Turner (1980) as well as other authors (e.g. Barry *et al.*, 1997, Barry & Kochevar, 1999; Kojima, Fujikura & Okutani, 2004) synonymized the genus with *Calyptogena*. Others, like Krylova & Janssen (2006), Krylova & Sahling (2006) and Johnson *et al.* (2016), maintained that until more was known about the molecular phylogeny, all the genera should be kept as independent of each other. Amano & Kiel (2007) disagreed and argued, based on both morphology of the hinge and available molecular studies, that *Phreagena* Woodring, 1938 and *Akebiconcha* are synonyms of *Archivesica*, though Johnson *et al.* (2016) argued that valid morphological differences could most likely be found in the soft tissue. The synonymization of the genera was later followed up by Amano & Suzuki (2010), who added *Laubiericoncha* Cosel & Olu, 2008 as a synonym of *Archivesica*, though no reason was given. Others, such as Okutani, Fujikura & Kojima (2000) and Okutani *et al.* (2011), maintained that *Archivesica* was a subgenus of *Calyptogena*, although *Calyptogena* was revised and given a more restricted definition by Krylova & Sahling (2006).

Molecular studies have in the last two decades changed our understanding of the phylogenetic relationship within the family Vesicomylidae (see Peek *et al.*, 1997; Goffredi *et al.*, 2003; Kojima *et al.*, 2004; Amano & Kiel, 2007; Okutani *et al.*, 2009; Krylova & Sahling, 2010; Okutani *et al.*, 2011; Audzijonyte *et al.*, 2012; Decker *et al.*, 2012; Martin & Goffredi, 2012; Krylova *et al.*, 2015; Johnson *et al.*, 2016). These studies have revealed that a great deal of the morphologically based genera are paraphyletic and need to be redefined.

In agreement with Amano & Suzuki (2010), Huber (2015) recently argued, based on the available molecular phylogenetic studies, that the genera *Akebiconcha* and *Laubiericoncha* are junior synonyms of *Archivesica*. However, unlike those authors, he agreed with Krylova & Janssen (2006) in keeping *Phreagena* as a valid genus, although including only the fossil type species *Phreagena lasia* Woodring, 1938, while transferring all the other species to *Archivesica*. *Phreagena lasia*, he noted, lacked a pallial sinus and showed differences in shell texture and hinge morphology. However, in their short redescription of the holotype, Krylova & Janssen (2006) noted a shallow pallial sinus as well as a subumbonal pit, both also typical for *Archivesica*. At present, the most comprehensive studies of vesicomylid phylogeny are those published by Audzijonyte *et al.* (2012) and Johnson *et al.* (2016). Their results, as well as those of Decker *et al.* (2012), Martin & Goffredi (2012), Valdes, Sellanes & D'Elia (2012) and Krylova *et al.* (2015), support the notion that *Laubiericoncha* is paraphyletic within the *Archivesica/Phreagena* group, while *Akebiconcha* is placed at the outer edge of the group. As Johnson *et al.* (2016) did not provide any unambiguous morphological characteristics by which to distinguish *Archivesica* from *Phreagena*, and we do not find that the four genera *Akebiconcha*, *Archivesica*, *Laubiericoncha* and *Phreagena* are well separated

from each other in the phylogenetic trees, we follow Amano & Suzuki (2010) in placing *Akebiconcha*, *Laubiericoncha* and *Phreagena* as junior synonyms of *Archivesica*. The sequenced *Calyptogena* species form a strong clade, well separated both genetically and morphologically from *Archivesica* (Krylova & Sahling, 2006; Audzijonyte *et al.*, 2012; Decker *et al.*, 2012; Johnson *et al.*, 2016). Morphologically, they are distinguished by the absence of a pallial sinus, by having a broad 3b tooth, a right nymphal ridge and by having only one demi-branch (Krylova & Sahling, 2006; Amano & Kiel, 2007). Therefore, we agree that there are strong arguments for keeping *Archivesica* an independent genus. An extensive emended diagnosis for the genus was given by Amano & Kiel (2007).

**Recent species included:** *Callogonia angulata* Dall, 1896; *Vesicomya chumi* Jaeckel & Thiele in Thiele & Jaeckel, 1931; *Calyptogena diagonalis* Barry & Kochevar, 1999; *Calyptogena (Archivesica) edisonensis* Okutani, Kojima & Kim, 2004; *Ectenagena extenta* Krylova & Moskalev, 1996; *Calyptogena (Archivesica) fortunata* Okutani *et al.* 2011; *Calyptogena (Archivesica) ganuda* Okutani & Soh, 2005; *Callocardia gigas* Dall, 1896; *Akebiconcha kawamurai* Kuroda, 1943 (syn. *Calyptogena solidissima* Okutani, Hashimoto & Fujikura, 1992); *Calyptogena (Ectenagena) laubieri* Okutani & Métivier, 1986; *Calyptogena (Archivesica) magnocutellus* Okutani, Kojima & Iwasaki, 2002; *Laubiericoncha myriamiae* Cosel & Olu, 2008; *Calyptogena nankaiensis* Okutani, Kojima & Ashi, 1996; *Archivesica nanshaensis* Xu & Shen, 1991; *Calyptogena (Ectenagena) nautili* Okutani & Métivier, 1986; *Archivesica ochotica* Scarlato, 1981; *Calyptogena okutanii* Kojima & Ohta, 1997; *Calyptogena parkardana* Barry *et al.*, 1997; *Laubiericoncha puertodeseadoi* Signorelli & Pastorino, 2015; *Calyptogena similis* Okutani, Kojima & Ashi, 1997; *Calyptogena soyoae* Okutani, 1957 (syn. *Calyptogena (Archivesica) kilmeri* Bernard, 1974); *Akebiconcha soyoae ochotensis* Scarlato, 1981; *Vesicomya (Archivesica) suavis* Dall, 1913; *Calyptogena (Archivesica) tsubasa* Okutani, Fujikura & Kojima, 2000.

**Fossil species included:** *Archivesica kamoi* Amano & Kiel, 2010 (Pliocene); *Phreagena lasia* Woodring, 1938 (Pliocene); *Archivesica marincovichii* Kiel & Amano, 2010 (Oligocene); *Archivesica redwoodia* Kiel & Amano, 2010 (Miocene); *Archivesica sakoi* Amano *et al.*, 2014 (Miocene); *Archivesica shikamai* Amano & Kiel, 2010 (Pliocene); '*Calyptogena*' *shiretensis* Uozumi in Uozumi & Ishikawa, 1967 (Miocene).

**Species questionably included:** *Calyptogena bosoensis* Kanie & Kuramochi, 2001 (Pliocene); *Archivesica georgemorei* Amano & Kiel, 2007 (Oligocene?); *Calyptogena gibbera* Crickmay, 1929 (Pliocene-Pleistocene); *Archivesica knapptonensis* Amano & Kiel, 2007 (U. Oligocene); *Calyptogena nipponica* Oinomikado & Kanehara, 1938 (Miocene-Pliocene).

***Archivesica arctica* n. sp.**

(Figs 2–4; Table 1)

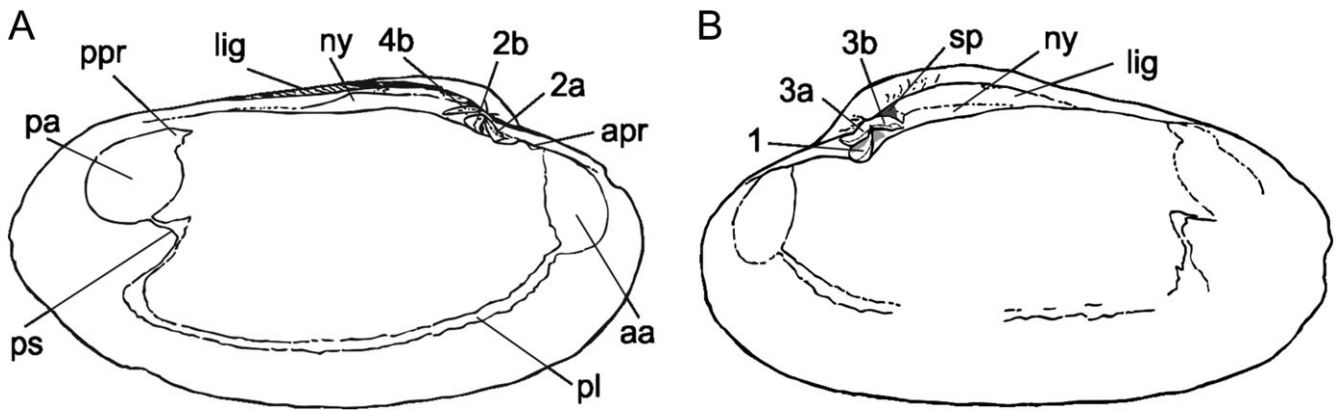
*Archivesica* sp.—Sirenko *et al.*, 1995: fig. 8. Kim *et al.*, 2006: fig. 5.

*Phreagena* s. l.—Ambrose *et al.*, 2015: fig. 6B (not 6A as stated in figure text).

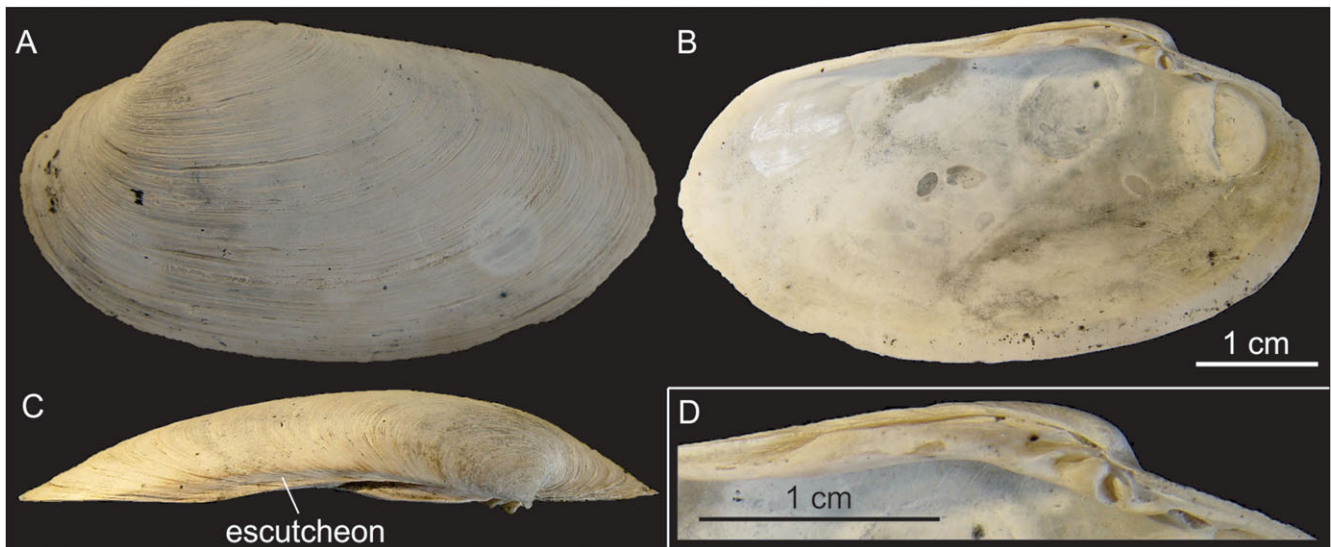
Vesicomylid bivalve—Szybor & Rasmussen, 2016: fig. 3.

**Type material:** Holotype, LV, TSGF 18357, core depth 275–277 cm; paratype 1, RV, TSGF 18358, core depth 275–277 cm; paratype 2, RV, TSGF 18359, core depth 270–273 cm; paratype 3, RV, TSGF 18360, core depth 275–277 cm; paratype 4, LV, TSGF 18361, core depth 275–277 cm; paratype 5, LV, TSGF 18362, core depth 278–279 cm; paratype 6, LV, TSGF 18363, core depth 277–278 cm; paratype 7, RV, TSGF 18364, core depth 275–277 cm; paratype 8, RV, TSGF 18365, core depth 281–282 cm; paratype 9, LV, TSGF 18366, core depth 275–277 cm. Type locality: core JM10-335GC (79°00.173'N, 06°55.335'E, 1,197 m water depth, 270–282 cm core depth), Vestnesa Ridge, Fram Strait, NW Spitsbergen, Svalbard Archipelago.





**Figure 2.** Line drawings of the interiors of valves of *Archivesica arctica* n. sp. **A.** Holotype (TSGF 18357), LV. **B.** Paratype 1 (TSGF 18358), RV. Abbreviations: aa, anterior adductor scar; Apr, anterior pedal retractor scar; lig, ligament; ny, nymph; pa, posterior adductor scar; pl, pallial line; ppr, posterior pedal retractor scar; ps, pallial sinus; sp, subumbonal pit; 1, ventral cardinal tooth; 2a, anterior ramus of subumbonal cardinal tooth; 2b, posterior ramus of subumbonal cardinal tooth; 3a, anterior ramus of subumbonal cardinal tooth; 3b, posterior ramus of subumbonal cardinal tooth; 4b, posterodorsal cardinal tooth.



**Figure 3.** *Archivesica arctica* n. sp. **A–D.** Holotype (TSGF 18357), LV. **A.** Exterior. **B.** Interior. **C.** Dorsal view. **D.** Close up of hinge. Core JM10-335GC, Vestnesa Ridge, Fram Strait, NW Spitsbergen, Svalbard Archipelago, 79°00.173'N, 06°55.335'E, water depth 1,197 m.

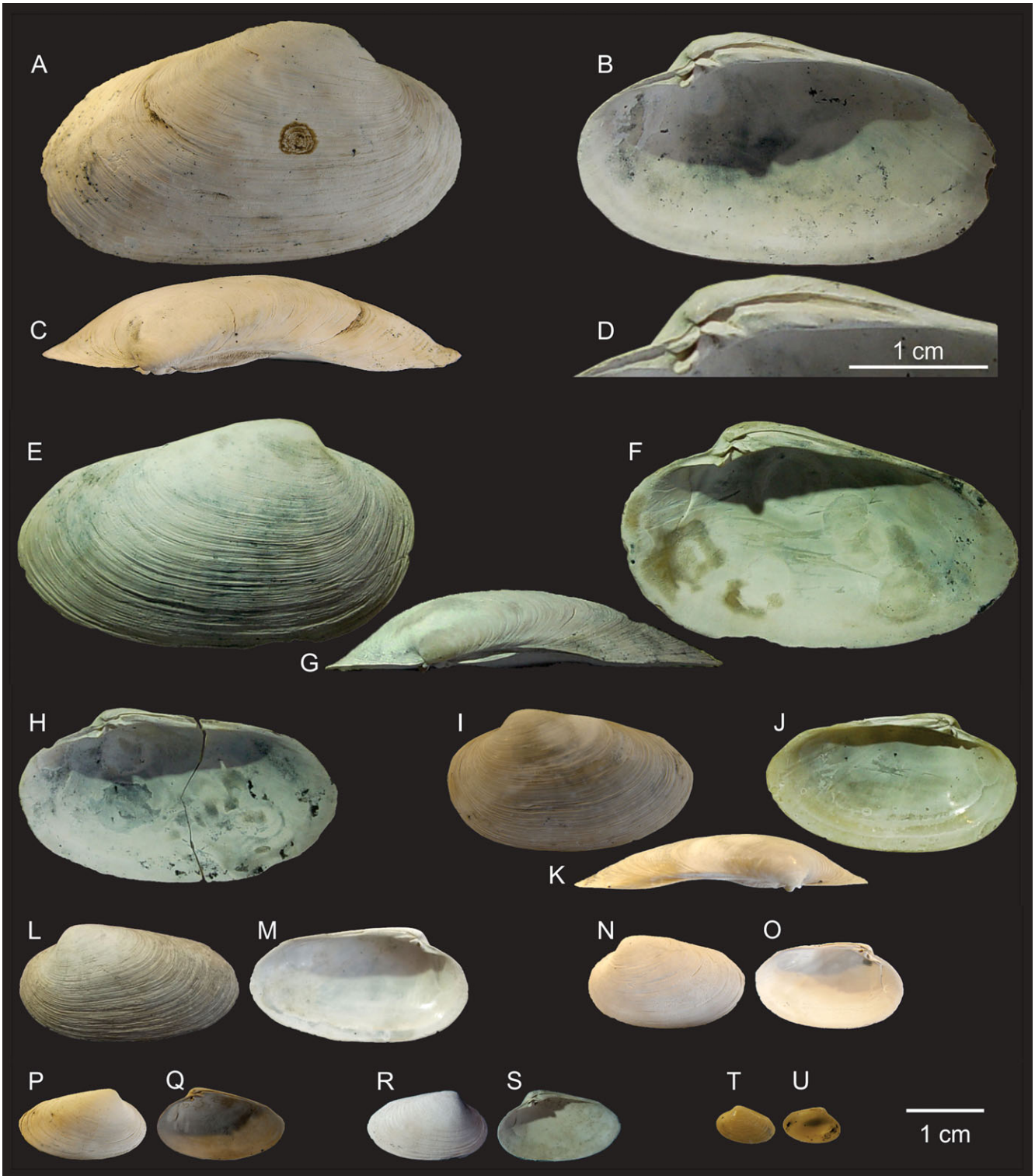
*ZooBank registration:* urn: lsid:zoobank.org:act:6A9D482D-7E65-4592-8FE6-52EC84444129.

*Etymology:* Named after the Arctic region since, so far, it is the only species that has been found in a wide part of the Arctic.

*Diagnosis:* Small, relatively thin-shelled *Archivesica* species normally with escutcheon. L/H ratio of shell 1.68–1.95. Ventral margin convex. Corner between dorsal and posterodorsal margin located at about 12–18% L from posterior margin. 3a tooth normally as large as other teeth. Pallial line subparallel to valve margin, with small, but well-developed V-shaped sinus.

*Description:* Shell small, L up to 55.6 mm (but see Remarks). Holotype: L = 54.7 mm, H = 28.0 mm. L/H of studied specimens 1.68–1.95. Shell slightly angulated oblong oval, moderately tumid, relatively thin- to moderately thick-shelled. Anterior margin usually somewhat acutely rounded well above horizontal midline, though below or at horizontal midline in smallest three specimens. Anteroventral valve margin a gently rounded to nearly straight line in ventroposterior direction, connecting to broadly rounded convex

ventral margin. Posterior margin broadly tapering to a rounded corner at horizontal midline. Posterodorsal and dorsal margin separated by weak corner 12–18% L from posterior margin. Posterior margin a nearly straight line between umbo and posterodorsal corner. Umbo shallow, with prosogyrous beak at anterior 2/7–1/4 L. Surface has dense, irregular growth waves or ridges, becoming stronger distally. Lunule absent. Narrow escutcheon present in 8 out of 10 specimens, including holotype; escutcheon bordered by sharp ridge subparallel to posterodorsal border. In remaining specimens, a superficial sulcus bordered by a rounded, weak ridge reaching to posterodorsal corner substitutes for a real escutcheon. External ligamental groove deep, 38–41% L. Ligament not preserved. Posterior ridge broadly rounded, ending at posterior extremity. Flattened or slightly sulcate area between dorsal and posterodorsal ridge. Periostracum not preserved. Hinge line short, narrow, robust. LV with short, strong anterior ramus of subumbonal cardinal tooth (2a) at 45° to hinge axis from just below umbo. A massive, triangular posterior ramus of subumbonal cardinal tooth (2b) fused with, though still well defined from, 2a. Posterior ramus 2b slightly inclined in posterior direction from umbo. Rami 2a and 2b of equal length. Posteriorly to subumbonal cardinal teeth, laminar posterodorsal cardinal tooth (4b) develops just behind umbo, running straight in ventroposterior direction. RV with strong laminar ventral cardinal



**Figure 4.** *Archivesica arctica* n. sp. **A–D.** Paratype 1 (TSGF 18358), RV. **A.** Exterior. **B.** Interior. **C.** Dorsal view. **D.** Close up of hinge. **E–G.** Paratype 2 (TSGF 18359), RV. **E.** Exterior. **F.** Interior. **G.** Dorsal view. **H.** Paratype 3 (TSGF 18360), RV interior. **I–K.** Paratype 4 (TSGF 18361), LV. **I.** Exterior. **J.** Interior. **K.** Dorsal view. **L, M.** Paratype 5 (TSGF 18362), LV. **L.** Exterior. **M.** Interior. **N, O.** Paratype 6 (TSGF 18363), LV. **N.** Exterior. **O.** Interior. **P, Q.** Paratype 7 (TSGF 18364), RV. **P.** Exterior. **Q.** Interior. **R, S.** Paratype 8 (TSGF 18365), RV. **R.** Exterior. **S.** Interior. **T, U.** Paratype 9 (TSGF 18366), LV. **T.** Exterior. **U.** Interior. All specimens from core JM10-335GC, Vestnesa Ridge, Fram Strait, NW Spitsbergen, Svalbard Archipelago, 79°00.173'N, 06°55.335'E, water depth 1,197 m.

tooth (1) starting directly below umbo, curving very gently in antero-ventral direction, with axis at 45° angle to anterodorsal margin (80° in one juvenile). Anterior ramus (3a) of subumbonal cardinal tooth usually robust, starts right above anterior end of ventral cardinal tooth,

following dorsal valve margin to umbo. Ramus 3a usually as large as other teeth, but shows considerable variation. Posterior ramus (3b) of subumbonal cardinal tooth massive, bifid, starting in posterior direction at umbo, running in crescentic or straight line in posteroventral



**Table 1.** Measurements of specimens of *Archivesica arctica* n. sp.

Specimen	Core and depth	Valve	L, mm	H, mm	L/H	Position of posterodorsal corner
Holotype TSGF 18357	JM10-335GC 275–277 cm	LV	54.7	28.0	1.95	14% L
Paratype 1 TSGF 18358	JM10-335GC 275–277 cm	RV	55.6	30.7	1.81	12% L
Paratype 2 TSGF 18359	JM10-335GC 270–273 cm	RV	51.8	29.3	1.77	15% L
Paratype 3 TSGF 18360	JM10-335GC 275–277 cm	RV	41.3	22	1.88	15% L
Paratype 4 TSGF 18361	JM10-335GC 275–277 cm	LV	32.5	17.9	1.82	14% L
Paratype 5 TSGF 18362	JM10-335GC 278–279 cm	LV	27.8	14.7	1.89	16% L
Paratype 6 TSGF 18363	JM10-335GC 277–278 cm	LV	21.8	12.5	1.74	16% L
Paratype 7 TSGF 18364	JM10-335GC 275–277 cm	RV	17.9	9.7	1.85	18% L
Paratype 8 TSGF 18365	JM10-335GC 281–282 cm	RV	15.7	9.2	1.71	17% L
Paratype 9 TSGF 18366	JM10-335GC 275–277 cm	LV	8.4	5	1.68	16% L

Position of posterodorsal corner is given in percent valve length (L) from posterior edge.

direction, meeting ventral edge of hinge line right angle, or 45° when straight. Posterior division of 3b formed at wide posteroventral end of tooth. Ramus 3a meeting with, but sharply defined from, 3b. Ligament external, opisthodontic, short, on narrow but strong nymphal plate. Lymphal ridge not developed. Subumbonal pit deep. Weakly impressed to obscure pallial line runs subparallel to valve edge, connects posteroventrally to anterior adductor scar, anteroventrally to posterior adductor scar. Pallial sinus short but well developed, V-shaped, acute, generally pointing to umbo or more in direction of anterior adductor scar. Anterior pedal retractor scar deep, separated from anterior adductor scar. Anterior adductor scar moderately impressed, with rounded subtriangular to egg-shaped outline. Posterior pedal retractor scar weakly impressed, united with equally weakly impressed posterior adductor scar. Inside of valves show very faint radiating lines. Valves whitish.

**Distribution:** Methane seep deposits on Vestnesa Ridge in the Fram Strait off NW Spitsbergen, Svalbard Archipelago. [Ambrose et al. \(2015\)](#) reported the species from the cores HH-13-203 GC09 (79°00.143977'N, 06°55.683059'E, 1,210 m water depth, 242–250 cm core depth) and HH-13-211 GC16 (79°01.86696'N, 06°49.850833'E, 1,202 m water depth, 408–415 cm core depth). [Szybor & Rasmussen \(2016\)](#) additionally reported the species from core HH12-929GC (79°00.220'N, 06°56.007'E, 1,211 m water depth, 110–240 cm core depth). The specimens are dated to *c.* 16,400–14,800 calibrated YBP according to [Szybor & Rasmussen \(2016\)](#).

Methane seep deposits on Gakkel Ridge, Arctic Ocean Stn 50/1993 (trawl between 77°41.4'N, 125°55.1'E and 77°41.1'N, 125°54.2'E, water depth 1,992–1,993 m) ([Sirenko et al., 1995](#)) and core PS2720-7 in the Laptev Sea (77°46.098'N, 126°7.296'E, water depth 2,054 m) ([Rachor, 1997](#)). The Gakkel Ridge specimens were dated to 15,700 YBP ([Kim et al., 2006](#)).

**Remarks:** Based on its convex ventral margin, *A. arctica* n. sp. can be distinguished from all of these species: *A.?* *bosoensis*, *A. diagonalis*, *A. extenta*, *A. garuda*, *A.?* *gibbera*, *A.?* *knapptonensis*, *A. lasia*, *A. magnocultellus*, *A. nankaiensis*, *A. nautilei*, *A.?* *nipponica*, *A. ochotensis*, *A. okutanii*, *A. shikamai*, *A. shiretokensis*, *A. similaris* and *A. tsubasa*. The new species has a 3a tooth as strongly developed as the other teeth, which distinguishes it from the species: *A. edisonensis*, *A. fortunata*, *A. kannoi*, *A. kavamurai*, *A. marincovichi*, *A. ochotica*, *A. parkardana*, *A. redwoodia*, *A. sakoi* and *A. soyaoe*. Among the nine remaining species, the total absence of an escutcheon excludes *A. angulata*, *A. chuni*, *A. myriamae*, *A. nanshaensis*, *A. puertodeseadoi* and *A. suavis*. Of these, *A. puertodeseadoi* and *A. chuni* are very similar in outline to *A. arctica* n. sp. *Archivesica puertodeseadoi* can further be distinguished by a gently convex posterodorsal margin, a more prominent cardinal 1 and a pallial line that is not parallel to the valve margin. *Archivesica chuni* can additionally be distinguished by the position of the posterodorsal valve

corner, located about 19% L from the posteriormost valve margin, the less acute anterior margin, much shorter ligamental groove and the larger size (L up to 120 mm). *Archivesica?* *georgenoerei* from the Oligocene of Alaska can be distinguished from the new species by an L/H ratio varying between 1.13 and 1.31. It is also moderately inflated, with cardinal 1 located well in front of 3b. It is unknown if the species has a pallial sinus. *Archivesica gigas* from the Gulf of California is distinguished from the new species by the markedly shorter ligamental groove, shorter and concave pallial sinus, the shallow anterior pedal retractor scar, the more tumid and subquadrate shell, the evenly rounded posterior margin and the corner between the dorsal and posterodorsal margin is located at about 37% L. *Archivesica laubieri* from Japan differs from the new species by larger size, having a rather rounded pallial sinus, a pallial line running obliquely to the valve margin, a very short 3a tooth and ligamental groove, and by well-impressed muscle scars.

*Archivesica arctica* n. sp. was previously documented and figured from Vestnesa Ridge by [Ambrose et al. \(2015\)](#) under the name *Phreagena s. l.* It was also reported by [Szybor & Rasmussen \(2016\)](#) as 'vesicomylid bivalve' in their study on the present core JM10-335GC.

[Sirenko et al. \(1995\)](#) and [Kim et al. \(2006\)](#) mentioned the occurrence of an *Archivesica* from a trawl sample taken at 1,992–1,993 m depth at the southeastern end of the Gakkel Ridge (77°41'N, 125°55'E), north of Russia. Based on the illustrations of the species (all exterior views), this species is identical to *A. arctica* n. sp. we describe from Svalbard. The largest Gakkel Ridge specimen was 68 mm L ([Rachor, 1997](#); [Kim et al., 2006](#)) and thus larger than the largest specimen from Svalbard. The illustrated specimens are filled by carbonate concretions so the interiors are hidden. The same species was apparently also encountered in core PS2720-7 at 2,054 m water depth in the Laptev Sea at 77°46.098'N, 126°7.296'E according to [Rachor \(1997\)](#). This gives the species a known depth range between 1,197 and 2,054 m, which is a moderately deep range for the genus according to [Krylova & Sahling \(2010\)](#), even when taking into account that the global sea level was about 110 m lower at that time ([Fairbanks, 1989](#)).

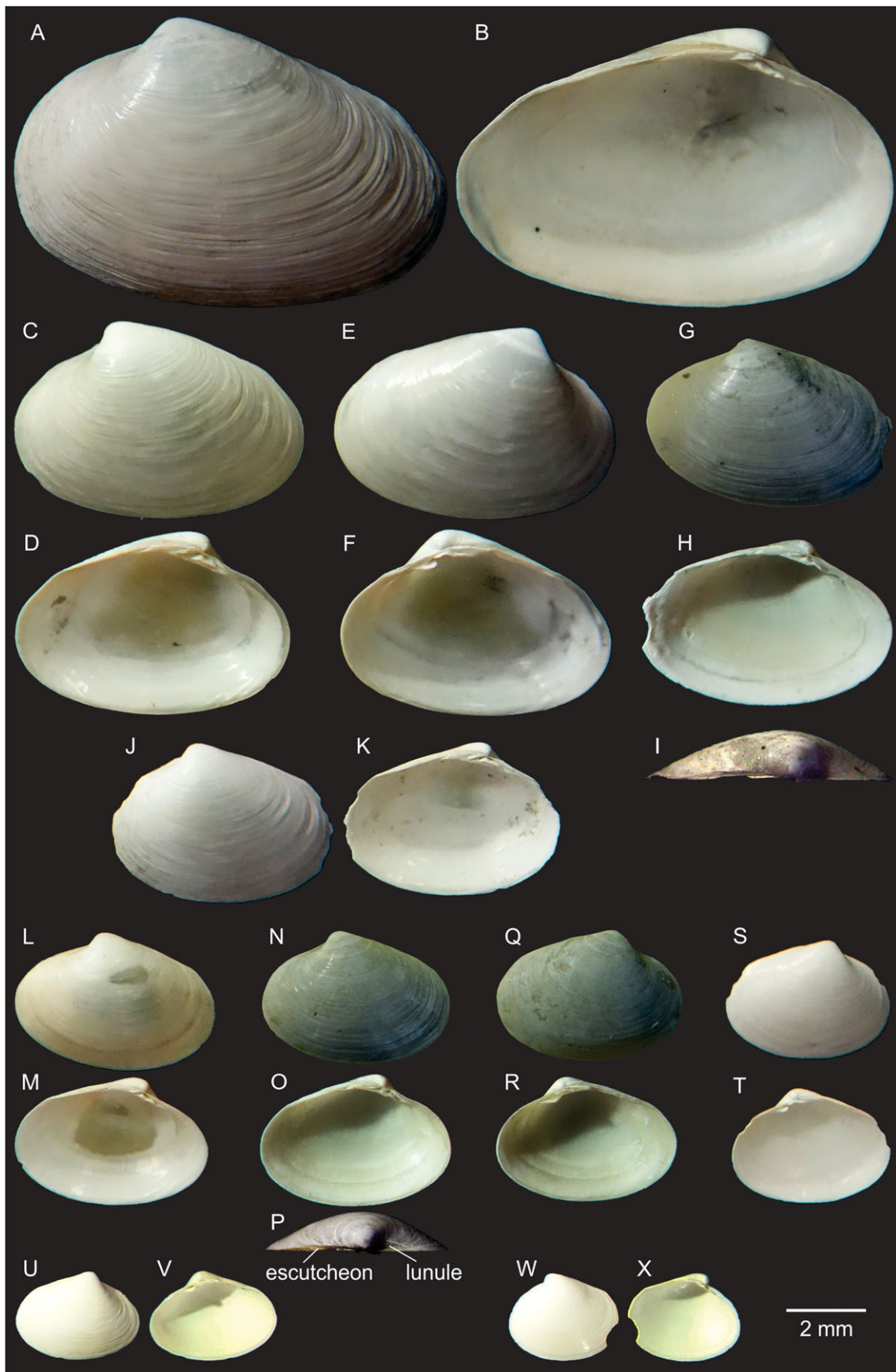
### Genus *Isorropodon* Sturany, 1896

*Isorropodon* Sturany, 1896 (type species *Isorropodon perplexum* Sturany, 1896).

### *Isorropodon nyeggaensis* Krylova in Krylova et al., 2011

(Fig. 5; Table 2)

*Isorropodon nyeggaensis* Krylova in [Krylova et al., 2011](#): 1139–1142, figs 5–7 (locality 10, 64°40.826'N, 05°15.710'E, 720 m water depth, Vøring Plateau, Norwegian Sea).



*Isooropodon* sp.—Ambrose *et al.*, 2015: fig. 6A (not 6B as stated in figure text).

**Material:** TSGF 18367, LV (278–279 cm core depth); TSGF 18368, LV (278–279 cm core depth); TSGF 18369, RV (278–279 cm core depth); TSGF 18370, LV (270–273 cm core depth); TSGF 18371, LV (278–279 cm core depth); TSGF 18372, LV (278–279 cm core depth); TSGF 18373, entire shell (270–273 cm core depth); TSGF 18374, RV (278–279 cm core depth); TSGF 18375, RV (281–282 cm core depth); TSGF 18376, LV (281–282 cm core depth). All from core JM10-335GC (79°00.173'N, 06°55.335'E, water depth 1,197 m, 270–282 cm below present sediment surface).

**Diagnosis:** *Isooropodon* species up to 21 mm long. Elongate to elliptical. L/H 1.24–1.56. W/L 0.20–0.26. Ventral margin gently convex to nearly straight. Glossy transparent light brown periostracum. Shallow escutcheon. Slight lunular incision. Umbo situated in anterior 30–35% of valve. Prosogyrate beaks. Stout nymph. Fibrous layer of ligament occupying 20–27% L and 61–79% of posterior lamellar layer.

**Distribution:** Methane seep deposits on Vestnesa Ridge in the Fram Strait, NW Spitsbergen, Svalbard Archipelago. Ambrose *et al.* (2015) additionally reported the species from cores HH-13-203 GC09 (79°00.143977'N, 06°55.683059'E, 1,210 m water depth, 241–250 cm core depth) and HH-13-211 GC16 (79°01.86696'N, 06°49.850833'E, 1,202 m water depth, 421–426 cm core depth). Methane seep deposits in the Nyegga seep area at 715–732 m water depth on the Vøring Plateau in the Norwegian Sea (Krylova *et al.*, 2011).

**Remarks:** Since L of the type specimens is 12.7–18.3 mm, the ten specimens from Vestnesa Ridge are smaller (2.8–11.1 mm). They also have a slightly smaller umbo and a slightly more acute posterior margin. However, the ten specimens show some variability in shape. Besides the natural variability of individuals, it also seems that some of the variability is size-related. Hence, we do not find reason to believe they are two different species.

The species was previously documented and illustrated by Ambrose *et al.* (2015). Their specimens originated from two cold seep-influenced cores, located close to our core location on the Vestnesa Ridge, and were identified as *Isooropodon* sp. Its appearance on Vestnesa Ridge shows that the species lived as far north as the Fram Strait and has a depth range from 715–1,210 m (not taking into account the influence of the eustasy and isostasy in the region).

## DISCUSSION

The Vestnesa Ridge *Archivesica* and *Isooropodon* species discussed here are, according to Krylova *et al.* (2011), the northernmost reported vesicomids. Since *A. arctica* n. sp. also lived at the Gakkel Ridge, north of Russia, it seems to have been a truly Arctic species. So far, the species is only represented by fossil valves. At Gakkel Ridge, the specimens were dated to an age of 15,700 YBP (Kim *et al.*, 2006). This is very close to the age range of the Vestnesa Ridge specimens, which Ambrose *et al.* (2015) dated to *c.* 17,707–16,680 calibrated YBP and Szybyor & Rasmussen (2016) to between 18,197 ± 189 and 17,789 ± 182

**Table 2.** Measurements of specimens of *Isooropodon nyeggaensis* Krylova in Krylova *et al.* 2011.

Specimen	Core and depth	Valve	L, mm	H, mm	L/H
TSGF 18367	JM10-335GC 278–279 cm	LV	11.1	7.3	1.52
TSGF 18368	JM10-335GC 278–279 cm	LV	7.2	4.7	1.53
TSGF 18369	JM10-335GC 278–279 cm	RV	6.9	4.6	1.50
TSGF 18370	JM10-335GC 270–273 cm	LV	6.3	4.1	1.54
TSGF 18371	JM10-335GC 278–279 cm	LV	5.4	3.8	1.42
TSGF 18372	JM10-335GC 278–279 cm	LV	4.9	3.2	1.53
TSGF 18373	JM10-335GC 270–273 cm	LV + RV	4.8	3.3	1.45
TSGF 18374	JM10-335GC 278–279 cm	RV	4.0	2.8	1.43
TSGF 18375	JM10-335GC 281–282 cm	RV	3.2	2.4	1.36
TSGF 18376	JM10-335GC 281–282 cm	LV	2.8	2.3	1.24

cal. YBP. However, Szybyor & Rasmussen (2016) found that the age of the pelagic foraminifera, used for dating, was too old and that the bivalve specimens at Vestnesa Ridge in reality are between 16,400 and 14,800 cal. YBP. This problem in dating is possibly due to the fact that the foraminiferal tests had overgrowth caused by the methane seep activity. Hence, at both places vesicomids lived when the last, cold Heinrich Event (H1) took hold of the region and led to perennial ice cover as far south as the Faroe Islands (Hoff *et al.*, 2016; Szybyor & Rasmussen, 2016). In the North Atlantic, Nordic seas and Arctic Ocean, this event took place within the time interval *c.* 18,000–15,000 YBP (Bond *et al.*, 1993; Fronval *et al.*, 1995; Cronin *et al.*, 2012). Szybyor & Rasmussen (2016) also found that the activity of the methane release increased at about that time, but that the vesicomids disappeared again before the emission decreased. Vesicomids as a family are most abundant at low latitudes between 30°S and 30°N, becoming progressively more sporadic towards the poles and nearly absent at latitudes higher than 60° (Krylova & Sahling, 2010). We take this as indication that they prefer relatively warmer bottom-water conditions, even though the report of living probable vesicomids at the Larsen Ice Shelf in Antarctica by Domack *et al.* (2005) indicates that at least one species has developed tolerance to cold environments. However, that study lacked both a taxonomic identification of the clams and a temperature profile for the bottom water. Despite the very cold surface conditions during the Heinrich event H1, the bottom-water temperatures increased due to northward advection of Atlantic water as a subsurface current below the meltwater layer (Birgel & Hass, 2004; Rasmussen & Thomsen, 2004; Rasmussen *et al.*, 2007; Ezat, Rasmussen & Groeneveld, 2014). The increase of about 2 °C in bottom-water temperatures at nearly 1,500 m water depth (Rasmussen *et al.*, 2007) seemingly made it possible for the vesicomids to settle in the Arctic for a short period. Thus, the current low bottom-water temperature at Vestnesa of about –1 °C could explain why no living specimens have been collected in the Arctic despite active methane release in the region. In addition, the type locality of *I. nyeggaensis* at Nyegga in the Norwegian Sea, which is the third northernmost known occurrence of vesicomids (Krylova *et al.*, 2011), has only revealed dead specimens. Unfortunately, these have not been dated and we therefore cannot say if they are as old as the Arctic specimens. There the bottom-water temperature is presently about –0.7 °C (Hovland & Svensen, 2006), which

**Figure 5.** *Isooropodon nyeggaensis* Krylova in Krylova *et al.* (2011). **A, B.** TSGF 18367, LV. **A.** Exterior. **B.** Interior. **C, D.** TSGF 18368, LV. **C.** Exterior. **D.** Interior. **E, F.** TSGF 18369, RV. **E.** Exterior. **F.** Interior. **G–I.** TSGF 18370, LV. **G.** Exterior. **H.** Interior. **I.** Dorsal view. **J, K.** TSGF 18371, LV. **J.** Exterior. **K.** Interior. **L, M.** TSGF 18372, LV. **L.** Exterior. **M.** Interior. **N–R.** TSGF 18373, complete specimen. **N.** Exterior, LV. **O.** Interior, LV. **P.** Dorsal view, LV. **Q.** Exterior, RV. **R.** Interior, RV. **S, T.** TSGF 18374, RV. **S.** Exterior. **T.** Interior. **U, V.** TSGF 18375, RV. **U.** Exterior. **V.** Interior. **W, X.** TSGF 18376, LV. **W.** Exterior. **X.** Interior. All specimens from core JM10-335GC, Vestnesa Ridge, Fram Strait, NW Spitsbergen, Svalbard Archipelago, 79°00.173'N, 06°55.335'E, water depth 1,197 m.



is in accordance with the hypothesis of temperature as the limiting factor in the distribution of vesicomimid bivalves at high latitudes.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

## ACKNOWLEDGEMENTS

We thank the reviewer Steffen Kiel for very helpful and constructive comments on the manuscript. Thanks go to Eike Rachor for helping with questions about the Gakkel Ridge shells. We would also like to thank Ivar Stokkeland (Norwegian Polar Research Institute Library) for exceptionally fast service and Andrey Sikorski (Akvaplan-niva AS) for helping to obtain Russian literature. Many thanks go to Thomas Hansen (Akvaplan-niva) for taking photos, to Elsebeth Thomsen (Tromsø University Museum) for discussions concerning the shells and to Inger Greve Alsos (Tromsø University Museum) for clarifying questions about molecular phylogeny. We thank the crew on RV *Jan Mayen* for taking the gravity core JM10-335GC. This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

## REFERENCES

- AAGAARD, K., SWIFT, J.H. & CARMACK, E.C. 1985. Thermohaline circulation in the Arctic Mediterranean Seas. *Journal of Geophysical Research*, **90**: 4833–4846.
- AUDZIJONYTE, A., KRYLOVA, E.M., SAHLING, H. & VRIJENHOEK, R.C. 2012. Molecular taxonomy reveals broad trans-oceanic distributions and high species diversity of deep-sea clams (Bivalvia: Vesicomidae: Pliocardiinae) in chemosynthetic environments. *Systematics and Biodiversity*, **10**: 403–415.
- AMANO, K. & KIEL, S. 2007. Fossil vesicomimid bivalves from the North Pacific Region. *The Veliger*, **49**: 270–293.
- AMANO, K. & SUZUKI, A. 2010. Redescription of “*Calyptogena*” *shiretokensis* Uozumi (Bivalvia: Vesicomidae) from the Miocene Rusha Formation on the Shiretoko Peninsula, Eastern Hokkaido, Japan. *Venus*, **68**: 165–171.
- AMBROSE, W.G.J.R., PANIERI, G., SCHNEIDER, A., PLAZA-FAVEROLA, A., CARROLL, M.L., ÅSTRÖM, E.K.L., LOCKE, W.L.V. & CARROLL, J. 2015. Bivalve shell horizons in seafloor pockmarks of the last glacial-interglacial transition: a thousand years of methane emissions in the Arctic Ocean. *Geochemistry, Geophysics, Geosystems*, **16**: 4108–4129. Doi:10.1002/2015GC005980.
- BARRY, J.P. & KOCHEVAR, R.E. 1999. *Calyptogena diagonalis*, a new vesicomimid bivalve from subduction zone cold seeps in the eastern north pacific. *The Veliger*, **42**: 117–123.
- BARRY, J.P., KOCHEVAR, R.E., BAXTER, C.H. & HARROLD, C. 1997. *Calyptogena packardana*, a new species of vesicomimid bivalve from cold seeps in Monterey Bay, California. *The Veliger*, **40**: 341–349.
- BERNARD, F. 1974. The genus *Calyptogena* in British Columbia with a description of a new species (Bivalvia, Vesicomidae). *Venus*, **33**: 11–22.
- BIRGEL, D. & HASS, H.C. 2004. Oceanic and atmospheric variations during the last deglaciation in the Fram Strait (Arctic Ocean): a coupled high-resolution organic-geochemical and sedimentological study. *Quaternary Science Reviews*, **23**: 29–47.
- BOND, G., BROECKER, W.S., JOHNSEN, S.J., MCMANUS, J., LABEYRIE, L., JOUZEL, J. & BONANI, G. 1993. Correlations between climate records from North Atlantic sediments and Greenland ice. *Nature*, **365**: 143–147.
- BOSS, K.J. & TURNER, R.D. 1980. The giant white clam from the Galapagos Rift, *Calyptogena magnifica* species novum. *Malacologia*, **20**: 161–194.
- BÜNZ, S., POLYANOV, S., VADAKKEPULIYAMBATTA, S., CONSOLARO, C. & MIENERT, J. 2012. Active gas venting trough hydrate-bearing sediments on the Vestnesa Ridge, offshore W-Svalbard. *Marine Geology*, **332–334**: 189–197.
- COSEL, R.V. & OLU, K. 2008. A new genus and new species of Vesicomidae (Mollusca, Bivalvia) from cold seeps on the Barbados accretionary prism, with comments on other species. *Zoosystema*, **30**: 929–944.
- CRONIN, T.M., DWYER, G.S., FRAMER, J., BAUCH, H.A., SPIELHAGEN, R.F., JACOBSSON, M., NILSSON, J., BRIGGS, W. M. JR & STEPANOVA, A. 2012. Deep Arctic Ocean warming during the last glacial cycle. *Nature Geoscience*, **5**: 631–634.
- DALL, W.H. 1908. Reports on the dredging operations off the west coast of Central America to Galapagos, to the west of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer “Albatross”, during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. 37. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer “Albatross”, from October, 1904 to March, 1905, Lieut., Commander L.M. Garrett, U.S.N., commanding. 14. The Mollusca and the Brachiopoda. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **43**: 205–487.
- DECKER, C., OLU, K., CUNHA, R.L. & ARNAUD-HAOND, S. 2012. Phylogeny and diversification patterns among vesicomimid bivalves. *PLoS ONE*, **7**: e33359. Doi:10.1371/journal.pone.0033359.
- DOMACK, E., ISHMAN, S., LEVENTER, A., SYLVA, S., WILLMOTT, V. & HUBER, B. 2005. A chemotrophic ecosystem found beneath Antarctic ice shelf. *Eos (Rome, Italy)*, **86**: 269–276.
- EZAT, M.M., RASMUSSEN, T.L. & GROENEVELD, J. 2014. Persistent intermediate water warming during cold stadials in the southeastern Nordic seas during the past 65 k.y. *Geology*, **42**: 663–666.
- FAIRBANKS, R.G. 1989. A 17,000-years glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*, **342**: 637–742.
- FRONVAL, T., JANSEN, E., BLOEMENDAL, J. & JOHNSEN, S.J. 1995. Oceanic evidence for coherent fluctuations in Fennoscandian and Laurentide ice sheets on millennium timescales. *Nature*, **374**: 443–446.
- GOFFREDI, S.K., HURTADO, L.A., HALLAM, S. & VRIJENHOEK, R.C. 2003. Evolutionary relationships of deep-sea vent and cold seep clams (Mollusca: Vesicomidae) of the “*pacifica/lepta*” species complex. *Marine Biology*, **142**: 311–320.
- HOFF, U., RASMUSSEN, T.L., STEIN, R., EZAT, M.M. & FAHL, K. 2016. Sea ice and millennial-scale climate variability in the Nordic seas 90 kyr ago to present. *Nature Communications*, **7**: 1–10. doi:10.1038/ncomms12247.
- HONG, W.-L., SAUER, S., PANIERI, G., AMBROSE, W.G.J.R., JAMES, R.H., FAVEROLA, A.P. & SCHNEIDER, A. 2016. Removal of methane through hydrological, microbial, and geochemical processes in the shallow sediments of pockmarks along eastern Vestnesa Ridge (Svalbard). *Limnology and Oceanography*. doi:10.1002/lno.10299.
- HOVLAND, M. & SVENSEN, H. 2006. Submarine pingoes: indicators of shallow gas hydrates in a pockmark at Nyegga, Norwegian Sea. *Marine Geology*, **228**: 15–23.
- HUBER, M. 2015. *Compendium of bivalves 2*, 907. Conchbooks, Harxheim, Germany.
- HUSTOFT, S., BÜNZ, S., MIENERT, J. & CHAND, S. 2009. Gas hydrate reservoir and active methane-venting province in sediments on <20 Ma young oceanic crust in the Fram Strait, offshore NW-Svalbard. *Earth and Planetary Science Letters*, **284**: 12–24.
- JAKOBSSON, M., MAYER, L.A., COAKLEY, B., DOWDESWELL, J. A., FORBES, S., FRIDMAN, B., HODNESDAL, H., NOORMETS, R., PEDERSEN, R., REBESCO, M., SCHENKE, H.-W., ZARAYSKAYA, Y., ACCETTERLA, A.D., ARMSTRONG, A., ANDERSON, R.M., BIENHOFF, P., CAMERLENGHI, A., CHURCH, I., EDWARDS, M., GARDNER, J.V., HALL, J.K., HELL, B., HESTVIK, O.B., KRISTOFFERSEN, Y., MARCUSSEN, C., MOHAMMAD, R., MOSHER, D., NGHIEM, S.V., PEDROSA, M.T., TRAVAGLINI, P.G. & WEATHERALL, P. 2012. The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. *Geophysical Research Letters*. doi:10.1029/2012GL052219.
- JOHNSON, S.B., KRYLOVA, E.M., AUDZIJONYTE, A., SAHLING, H. & VRIJENHOEK, R.C. 2016. Phylogeny and origins of chemosynthetic vesicomimid clams. *Systematics and Biodiversity*. doi:10.1080/14722000.2016.1252438.

- KEEN, A.M. 1969. Family Vesicomidae Dall, 1908. In: *Treatise on invertebrate paleontology*, Part N., Vol. 2, Bivalvia (R.C. Moore, ed.), pp. 633–634. Geological Society of America, Colorado.
- KIM, B., RACHOR, E., SIRENKO, B., APLONOV, V., STAROBOGATOV, Y. & STEIN, R. 2006. Termal discharge points on the Gakkel Ridge (Arctic Basin). Russian Academy of Sciences, Zoological Institute. *Explorations of the Fauna of the Seas*, **56**, (64): 5–14.
- KOJIMA, S., FUJIKURA, K. & OKUTANI, T. 2004. Multiple trans-Pacific migrations of deep-sea vent/seep-endemic bivalves in the family Vesicomidae. *Molecular Phylogenetics and Evolution*, **32**: 396–406.
- KRYLOVA, E.M. & JANSSEN, R. 2006. Vesicomidae from Edison Seamount (South West Pacific: Papua New Guinea: New Ireland fore-arc basin). *Archiv für Molluskenkunde*, **135**: 231–261.
- KRYLOVA, E.M. & SAHLING, H. 2006. Recent bivalve molluscs of the genus *Calyptogena* (Vesicomidae). *Journal of Molluscan Studies*, **72**: 359–395.
- KRYLOVA, E.M. & SAHLING, H. 2010. Vesicomidae (Bivalvia): current taxonomy and distribution. *PLoS One*, **5**: e9957. doi:10.1371/journal.pone.0009957.
- KRYLOVA, E.M., GEBRUK, A.V., PORTNOVA, D.A., TODT, C. & HAFIDASON, H. 2011. New species of the genus *Isoropodon* (Bivalvia: Vesicomidae: Pliocardiinae) from cold methane seeps at Nyegga (Norwegian Sea, Vøring Plateau, Storrega Slide). *Journal of the Marine Biological Association of the United Kingdom*, **91**: 1135–1144.
- KRYLOVA, E.M., KAMENEV, G.M., VLADYCHENSKAYA, I.P. & PETROV, N.B. 2015. Vesicominae (Bivalvia: Vesicomidae) of the Kuril-Kamchatka Trench and adjacent abyssal regions. *Deep-Sea Research Part II*, **111**: 198–209.
- KURODA, T. 1943. *Akebiconcha*, a new pelecypod genus. *Venus*, **13**: 14–18.
- MARTIN, A.M. & GOFFREDI, S.K. 2012. ‘Pliocardia’ krylovata, a new species of vesicomid clam from cold seeps along the Costa Rica Margin. *Journal of the Marine Biological Association of the United Kingdom*, **92**: 1127–1137.
- OKUTANI, T., FUJIKURA, K. & KOJIMA, S. 2000. New taxa and review of vesicomid bivalves collected from the northwest Pacific by deep-sea research systems of Japan Marine Science and Technology Center. *Venus*, **9**: 83–101.
- OKUTANI, T., KOJIMA, S. & ASHI, J. 1997. Further discovery of a new taxon of vesicomid clam from the Nankai Trough, off Honshu, Japan. *Venus*, **56**: 185–188.
- OKUTANI, T., KOJIMA, S., KAWATO, M., SEO, E. & FUJIKURA, K. 2011. Another new *Calyptogena* clam from deep-sea seeps off the Sanriku coast and in Sagami Bay, Japan (Mollusca: Bivalvia). *Venus*, **69**: 135–144.
- OKUTANI, T., KOSHI-ISHI, T., SATO, T., IMAI, T. & KATO, C. 2009. Vesicomid fauna in the Chishima (Kurile) Trench: occurrences of a new taxon and *Calyptogena extenta*. *Venus*, **68**: 15–25.
- PEEK, A.S., GUSTAFSON, R.G., LUTZ, R.A. & VRIJENHOEK, R.C. 1997. Evolutionary relationships of deep-sea hydrothermal vent and cold-water seep clams (Bivalvia: Vesicomidae): results from the mitochondrial cytochrome oxidase subunit I. *Marine Biology*, **130**: 151–161.
- PIMENOV, N.V., SAWICHEV, A.S., RUSANOV, I.I., LEIN, A. & IVANOV, M.V. 2000. Mikrobnyye processy cikla ugleroda na gidrotermal’nyh poljakh i holodnyh metanovyh sipah [Microbiological processes of the carbon and sulfur cycle in cold methane seeps in the North Atlantic]. *Mikrobiologiya*, **69**: 831–843. [in Russian].
- PLAZA-FAVEROLA, A., BÜNZ, S., JOHNSON, J., CHAND, S., KNIES, J., MIENERT, J. & FRANEK, P. 2015. Role of tectonic stress in seepage evolution along the gas hydrate-charged Vestnesa Ridge, Fram Strait. *Geophysical Research Letters*, **42**: 733–742.
- Rachor, E. (ed.) 1997. Scientific cruise report of the Arctic expedition ARK-XI/1 of RV “Polarstern” in 1995. German-Russian project LADI: Laptev Sea – Arctic deep basin interrelations. *Berichte zur Polarforschung*, **226**: 157 pp + appendix.
- RASMUSSEN, T.L. & THOMSEN, E. 2004. The role of the North Atlantic Drift in the millennial timescale glacial climate fluctuations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **210**: 101–116.
- RASMUSSEN, T.L., THOMSEN, E., ŚLUBOWSKA, M.A., JESSEN, S., SOLHEIM, A. & KOÇ, N. 2007. Paleooceanographic evolution of the SW Svalbard margin (76°N) since 20,000 <sup>14</sup>C yr BP. *Quaternary Research*, **67**: 100–114.
- SIRENKO, B.I., PETRYASHOV, V.V., RACHOR, E. & HINZ, K. 1995. Bottom biocoenoses of the Laptev Sea and adjacent areas. *Berichte zur Polarforschung*, **176**: 211–221.
- STURANY, R. 1896. Mollusken I (Prosobranchier und Opisthobranchier; Scaphopoden; Lamellibranchier) gesammelt von S.M. Schiff “Pola” 1890–94. *Denkschriften der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Wien*, **63**: 1–36. pls 1–2.
- SZTYBOR, K. & RASMUSSEN, T.L. 2016. Diagenetic disturbances of marine sedimentary records from methane-influenced environments in the Fram Strait as indications of variation in seep intensity during the last 35 000 years. *Boreas*. doi:10.1111/bor.12202.
- VALDES, F., SELLANES, J. & D’ELÍA, G. 2012. Phylogenetic position of vesicomid clams from a methane seep off central Chile (~36°S) with a molecular timescale for the diversification of the Vesicomidae. *Zoological Studies*, **51**: 1154–1164.
- VOGT, P.R., CRANE, K., SUNDVOR, E., MAX, M.D. & PFIRMAN, S.L. 1994. Methane-generated(?) pockmarks on young, thickly sedimented oceanic crust in the Arctic: Vestnesa ridge, Fram strait. *Geology*, **22**: 255–258.
- WOODRING, W.P. 1938. Lower Pliocene mollusks and echinoids from the Los Angeles Basin, California. *United States Geological Survey Professional Paper*, **190**: 1–67.