



Zootaxa 3859 (1): 001–066  
www.mapress.com/zootaxa/

Copyright © 2014 Magnolia Press

# Monograph

ISSN 1175-5326 (print edition)

**ZOOTAXA**

ISSN 1175-5334 (online edition)

<http://dx.doi.org/10.11646/zootaxa.3859.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:24FCAAE1-AB7C-4FAD-8698-D0C9F12400EC>

# ZOOTAXA

3859

## **Bivalves from the latest Jurassic-earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard**

KRZYSZTOF HRYNIEWICZ<sup>1,3</sup>, CRISPIN T.S. LITTLE<sup>2</sup> & HANS ARNE NAKREM<sup>1</sup>

<sup>1</sup>Natural History Museum, University of Oslo, 1172 Blindern, 0318 Oslo, Norway.

E-mail: [krzysztof.hryniewicz@nhm.uio.no](mailto:krzysztof.hryniewicz@nhm.uio.no); [h.a.nakrem@nhm.uio.no](mailto:h.a.nakrem@nhm.uio.no)

<sup>2</sup>School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK. E-mail: [earctsl@leeds.ac.uk](mailto:earctsl@leeds.ac.uk)

<sup>3</sup>Corresponding author



Magnolia Press  
Auckland, New Zealand

Accepted by N. Malchus: 28 Jul. 2014; published: 2 Sept. 2014

Licensed under a Creative Commons Attribution License <http://creativecommons.org/licenses/by/3.0>

KRZYSZTOF HRYNIEWICZ, CRISPIN T.S. LITTLE & HANS ARNE NAKREM  
**Bivalves from the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard**  
(*Zootaxa* 3859)

66 pp.; 30 cm.

2 Sept. 2014

ISBN 978-1-77557-483-5 (paperback)

ISBN 978-1-77557-484-2 (Online edition)

FIRST PUBLISHED IN 2014 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: [zootaxa@mapress.com](mailto:zootaxa@mapress.com)

<http://www.mapress.com/zootaxa/>

© 2014 Magnolia Press

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

## Table of content

Abstract . . . . .	4
Introduction . . . . .	4
Material and methods . . . . .	6
Class Bivalvia Linnaeus, 1758 . . . . .	7
Subclass Protobranchia Pelseneer, 1889 . . . . .	7
Order Solemyoida Dall, 1889 . . . . .	7
Family Solemyidae Gray, 1840 . . . . .	7
Genus <i>Solemya</i> Lamarck, 1818 . . . . .	8
<i>Solemya (Petrasma) cf. woodwardiana</i> Leckenby, 1859 . . . . .	8
Family Nucinellidae Vokes, 1956 . . . . .	12
Genus <i>Nucinella</i> Wood, 1851 . . . . .	12
<i>Nucinella svalbardensis</i> sp. nov. . . . .	12
Order Nuculoida Dall, 1889 . . . . .	13
Superfamily Nuculoidea Gray, 1824 . . . . .	15
Family Nuculidae Gray, 1824 . . . . .	15
Genus <i>Dacromya</i> Agassiz, 1839 . . . . .	15
<i>Dacromya chetaensis</i> Sanin, 1976 . . . . .	15
Family Mallettiidae H. Adams & A. Adams, 1858 . . . . .	16
Genus <i>Mesosaccella</i> Chavan, 1946 . . . . .	16
<i>Mesosaccella rogovi</i> sp. nov. . . . .	17
<i>Mesosaccella toddi</i> sp. nov. . . . .	19
Subclass Autobranchia Grobben, 1894 . . . . .	22
Superorder Pteriomorphia Beurlen, 1944 . . . . .	22
Order Pectinida Gray, 1854 . . . . .	22
Pectinida gen. et sp. indet. . . . .	22
Family Buchiidae Cox, 1953 . . . . .	22
Genus <i>Buchia</i> Rouillier, 1845 . . . . .	22
<i>Buchia</i> spp. . . . .	23
Family Oxytomidae Ichikawa, 1958 . . . . .	23
Genus <i>Oxytoma</i> Meek, 1864 . . . . .	23
<i>Oxytoma octavia</i> (d'Orbigny, 1850) . . . . .	23
Superfamily Pectinoidea Rafinesque, 1815 . . . . .	26
Family Pectinidae Rafinesque, 1815 . . . . .	26
Genus <i>Camptonectes</i> Agassiz in Meek, 1864 . . . . .	26
<i>Camptonectes (Costicamptonectes) aff. milnelandensis</i> Fürsich, 1982 . . . . .	27
<i>Camptochlamys (Camptochlamys) clathratus</i> (Roemer, 1836) . . . . .	27
<i>Camptonectes</i> spp. . . . .	28
Order Limida Waller, 1978 . . . . .	28
Family Limidae Rafinesque, 1815 . . . . .	28
Genus <i>Pseudolimea</i> Arkell in Douglas & Arkell, 1932 . . . . .	28
<i>Pseudolimea arctica</i> (Zakharov, 1966) . . . . .	28
Superorder Heteroconchia Gray, 1854 . . . . .	30
Clade Heterodonta Neumayr, 1884 . . . . .	30
Order Lucinida Neumayr, 1884 . . . . .	30
Family Lucinidae Fleming, 1828 . . . . .	30
Genus <i>Tehamatea</i> Kiel, 2013 . . . . .	31
<i>Tehamatea rasmusseni</i> sp. nov. . . . .	31
Family Thyasiridae Dall, 1901 . . . . .	35
Genus <i>Cretaxinus</i> gen. nov. . . . .	35
<i>Cretaxinus hurumi</i> sp. nov. . . . .	37
Order Venerida Gray, 1854 . . . . .	41
Family Arcticiidae Newton, 1891 . . . . .	41
Genus <i>Pseudotrapezium</i> Fischer, 1887 . . . . .	41
<i>Pseudotrapezium aff. groenlandicum</i> Spath, 1936 . . . . .	41
Subclass Anomalodesmata Dall, 1889 . . . . .	43
Order Pholadomyoida Newell, 1965 . . . . .	43
Family Pholadomyidae Gray, 1847 . . . . .	43
Genus <i>Goniomya</i> Agassiz, 1842 . . . . .	43
<i>Goniomya literata</i> (J. Sowerby, 1819) . . . . .	43
Discussion . . . . .	44
Acknowledgments . . . . .	46
References . . . . .	47

## Abstract

The bivalve fauna from the latest Jurassic–earliest Cretaceous hydrocarbon seep deposits from central Spitsbergen, Svalbard comprises at least 17 species, four of which belong to chemosymbiotic taxa often found at seeps. These are the solemyid *Solemya* (*Petrasma*) cf. *woodwardiana*; *Nucinella svalbardensis* **sp. nov.**, which belongs to a group of large *Nucinella* species known from seeps and deep water environments; the lucinid bivalve, *Tehamatea rasmusseni* **sp. nov.**, included in a genus widely distributed in other Jurassic–Cretaceous seeps; and *Cretaxinus hurumi* **gen. et sp. nov.**, which is the oldest known thyasirid and is discussed in relation to other large seep-restricted genera in this family. The remaining species in the fauna belong to ‘background’ genera known from coeval normal marine sediments, mostly from the Boreal area. These include the nuculid *Dacromya chetaensis*, two new malletiids (*Mesosaccella rogovi* **sp. nov.** and *M. toddi* **sp. nov.**), the oxytomiid *Oxytoma octavia*, at least three *Buchia* species, at least two pectinids, including *Camptonectes* (*Costicamptonectes*) aff. *milnelandensis* and *Camptonectes* (*Camptochlamys*) *clatrathus*, the limid *Pseudolimea arctica*, the arcticid *Pseudotrapezium* aff. *groenlandicum*, and the pholadomyid *Goniomya literata*. The large number of ‘background’ species in the bivalve fauna is probably a reflection of the shallow-water setting of the Svalbard seeps. This might also explain the lack of the seep-restricted modiomorphid bivalve *Caspiconcha* from the fauna. With solemyids, *Nucinella*, lucinids and thyasirids, the latest Jurassic–earliest Cretaceous bivalve seep fauna of Svalbard contains typical representatives of the Mesozoic bivalve seep faunas, both long established and young evolutionary colonists.

**Key words:** *Nucinella*, *Solemya*, lucinids, thyasirids, Jurassic, Cretaceous, background fauna, evolution, new genus, new species

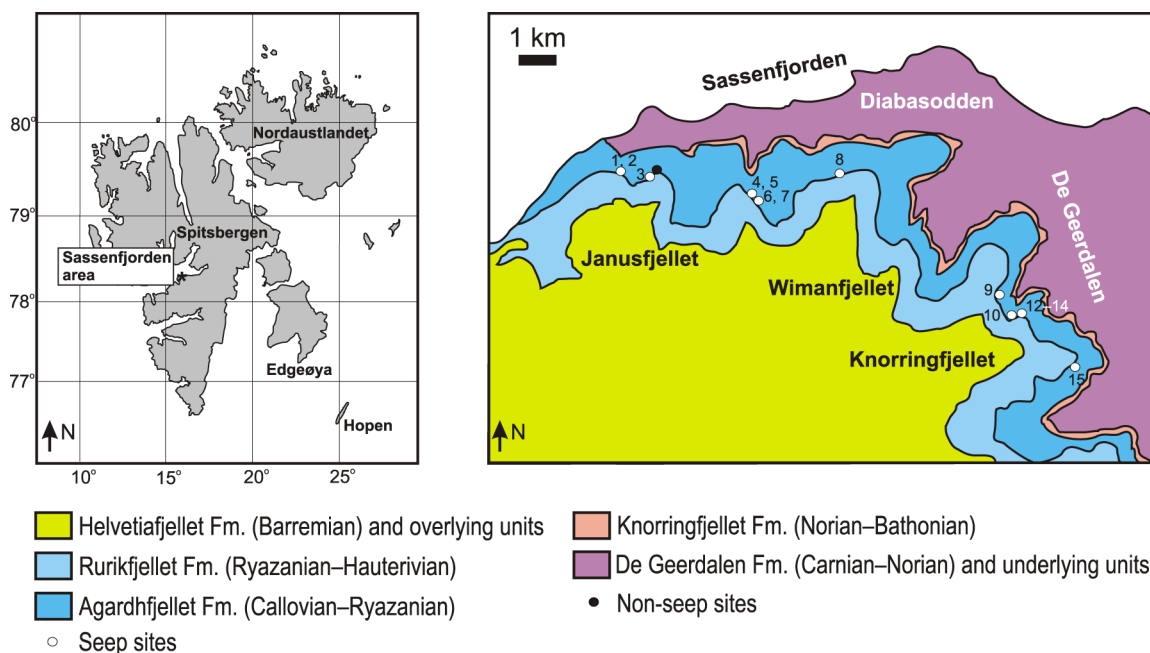
## Introduction

Bivalves are one of the major groups of animals found in chemosynthesis-based ecosystems in modern oceans (e.g. Van Dover 2000; Dando 2010; Taylor & Glover 2010; Watanabe *et al.* 2010) and chemosymbiotic bivalve species often represent a dominant element of such assemblages (Sibuet & Olu 1998; Van Dover *et al.* 2003; Levin 2005; Dupperon 2010). The evolutionary history of bivalves in hydrocarbon seep environments is long and can be traced back to the Devonian (Peckmann *et al.* 1999; Aitken *et al.* 2002; Campbell 2006). However, most of the well studied seep bivalve faunas are from Eocene or younger circum-Pacific settings. These are dominated by bathymodiolin and vesicomid bivalves, often associated with solemyids, lucinids and thyasirids (Squires & Goedert 1991; Squires & Gring 1996; Goedert *et al.* 2003; Amano & Kiel 2007; Saether *et al.* 2010; Amano & Ando 2011; Gill & Little 2013; Kiel & Amano 2013). Knowledge of pre-Eocene bivalve seep faunas is less complete (e.g. Amano *et al.* 2007; Kiel *et al.* 2008a; Kiel *et al.* 2010; Jenkins *et al.* 2013; Kiel 2013), which partially reflects the smaller number of Mesozoic and particularly Palaeozoic seep sites available for study. Pre-Eocene bivalve seep faunas are composed predominantly of solemyids, *Nucinella*, lucinids and thyasirids (Kiel 2010). In addition, some Late Jurassic to Late Cretaceous seep faunas contained species of the large obligate seep modiomorphid genus *Caspiconcha*, which possibly had chemosymbionts (e.g. Kelly *et al.* 2000; Kiel *et al.* 2010; Jenkins *et al.* 2013; Kiel *et al.* 2013).

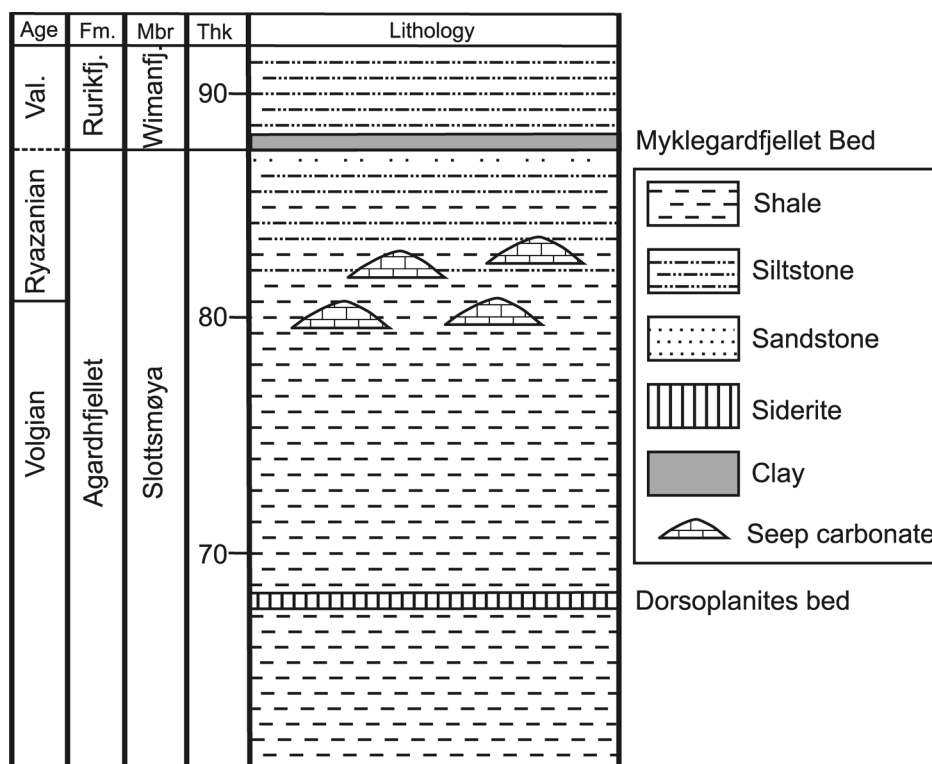
This paper is a systematic study of the bivalve fauna from the latest Jurassic–earliest Cretaceous hydrocarbon seep deposits from central Spitsbergen, Svalbard. It is part of a wider taxonomic treatment of macrofossils from these sites, including, so far, ammonites (Wierzbowski *et al.* 2011), cephalopod arm hooks (Hammer *et al.* 2013), lingulate brachiopod (Holmer & Nakrem 2012) and serpulids (Vinn *et al.* in press). Aside from these the Svalbard seep carbonates also contain belemnoid guards, crustaceans, echinoderms, gastropods, rhynchonellate brachiopods, scaphopods and sponges (Hammer *et al.* 2011) as well as agglutinated and calcareous foraminiferans (Hjálmaradóttir *et al.* 2012). The initial list of bivalve taxa in Hammer *et al.* (2011) comprised 14 bivalve species, all of which were left in open nomenclature. This paper extends that number to more than 17, and presents systematic descriptions for most of them; the buchiid bivalves will be dealt with in a separate paper.

**Geological background.** Bivalve specimens have been found in 13 out of 15 seep carbonates in the Sassenfjorden area, Central Spitsbergen, Svalbard (Fig. 1). The seeps are hosted by the Slottsmøya Member, which is composed mainly of grey to black organic-rich shales with lesser silty beds and carbonate concretions, and was deposited on the middle to outer shelf (Nagy *et al.* 1988; Dypvik *et al.* 1991; Collignon & Hammer 2012). Based on ammonite faunas, the seep deposits are of Late Volgian to latest Ryazanian age (Fig. 2; Wierzbowski *et al.* 2011). The Volgian and Ryazanian are regional stages applied around the Jurassic–Cretaceous transition in the Boreal realm, where Tithonian and Berriasian standards are not applicable, due to strong ammonite provincialism

(e.g. Zakharov & Rogov 2008; Rogov & Zakharov 2009). The Tithonian–Berriasian boundary, and thus the boundary between the Jurassic and Cretaceous, is positioned within the Taimyrensis Zone of the Upper Volgian, so the uppermost Volgian and Ryazanian equates to the Berriasian, and are hence Cretaceous in age (Houša *et al.* 2007). All of the Volgian seeps previously described from Svalbard are therefore of latest Tithonian age and all the Ryazanian seeps are of Berriasian age (Wierzbowski *et al.* 2011).



**FIGURE 1.** Map showing location of the bivalve-bearing seep carbonates in central Spitsbergen, Svalbard. Modified from Dallmann *et al.* (2001).



**FIGURE 2.** Lithological profile of the Slottsmøya Member, Agardhfjellet Formation at the Janusfjellet section. Modified from Wierzbowski *et al.* (2011). Fm.—Formation; Mbr—Member; Rurikfj.—Rurikfjellet; Thk—Thickness; Val.—Valanginian; Wimanfj.—Wimanfjellet.

## Material and methods

The fossil seep bivalves were collected during six field seasons to Svalbard between 2007 and 2012. All the specimens housed in the Natural History Museum, University of Oslo, have collection numbers with a PMO prefix in Appendix 1; one specimen with the JUE prefix is stored in the collections of the Joetsu University of Education, Joetsu, Japan. Specimens used for comparison are housed in the British Geological Survey, Keyworth, UK (prefix BGS); Geological Survey of Denmark and Greenland, Copenhagen, Denmark (prefix GGU); Museum of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Sciences of the USSR (prefix 150) and Sedgwick Museum, Cambridge, UK (prefix SM). The bivalves show variable preservation, coming from heavily indurated seep limestones. Most of the shells are recrystallized to blocky calcite, except for the pteriomorph bivalves, which have some original shell material preserved. However, internal and/or external moulds are well preserved and from these silicone rubber casts were made, revealing important internal and external shell details. For photography, the fossils were covered with ‘black gold opaque’ and the silicone rubber casts were made as dark as possible. Both were then whitened with ammonium chloride to increase contrast. Photography was done using a Nikon D3100 camera with AF-S Micro Nikkor 60 mm 1:2.8 G ED lens. The resulting digital images were edited using Adobe Photoshop CS4 and mounted on plates using Corel Draw 12. Specimens were measured using callipers with a 0.1 mm error and the resulting data were analysed using the PAST software (Hammer *et al.* 2001).

**TABLE 1.** Distribution of discussed species in the Svalbard seeps.

Taxon/Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Solemya (Petrasma) cf. woodwardiana</i>	+		+		+			+	+			+			
<i>Nucinella svalbardensis</i>	+	+	+		+				+			+	+	+	+
<i>Dacromya chetaensis</i>												+			
<i>Mesosaccella rogoi</i>	+	+	+		+			+	+			+	+		+
<i>Mesosaccella toddi</i>	+		+						+			+			
Pectinida gen. et sp. indet.			+												
<i>Buchia</i> spp.		+	+	+	+		+	+	+	+		+	+		+
<i>Oxytoma octavia</i>			+		+			+	+			+			+
<i>Camptonectes (Costicamptonectes) aff. milnelandensis</i>								+							
<i>Camptonectes (Camptochlamys) clathratus</i>								+							
<i>Camptonectes</i> spp.	+		+	+				+	+						
<i>Pseudolimea arctica</i>									+						
<i>Tehamatea rasmusseni</i>									+						
<i>Cretaxinus hurumi</i>									+						
<i>Pseudotrapezium aff. groenlandicum</i>		+	+		+			+	+			+			
<i>Goniomya literata</i>			+						+						

**Classification and terminology.** The higher-taxa nomenclature and classification of bivalves used here follow that of Bieler *et al.* (2010). Open nomenclatural rules are those of Matthews (1973) and Bengtson (1988). Ligament demipads in solemyid bivalves are used as defined by Bailey (2011, p. 18) and references therein. Posterior sulcus and submarginal sulcus of the thyasirid bivalves are used here accordingly to the definition by Oliver & Killeen (2002). Where sulcus of other bivalve families is discussed, just the term ‘sulcation’ is used. Dorsal furrow is understood in the way it was used by Yonge (1977) for anomiiids.

Institutional abbreviations used in the text:

BGS—British Geological Survey, Keyworth, UK;

JUE—Joetsu University of Education, Joetsu, Japan;

PMO—Natural History Museum, University of Oslo, Norway;  
SM—Sedgwick Museum, Cambridge, UK.

Morphological abbreviations used in the text, on the figures and in the appendices:

AAMS—anterior adductor muscle scar;  
Aau—anterior auricle;  
Acth—anteriormost cardinal tooth;  
APRS—anterior pedal retractor scar;  
BT—buttress;  
Ca—carina;  
Card—cardinal teeth;  
Ch—chondrophore;  
Ct—ctenolium;  
Es—escutcheon;  
GL—growth line;  
GLD—growth line deflections;  
H—shell height;  
L—shell length;  
Lat—lateral tooth;  
LD—ligament demipads;  
LGv—ligament groove;  
Lh—length of the hinge plate;  
Lig—ligament;  
Lu—lunule;  
PaL—pallial line;  
PAMS—posterior adductor muscle scar;  
Parea—posterior area;  
Pau—posterior auricle;  
Pl—length of the posterior part of the shell;  
Plh—length of the posterior part of the hinge plate;  
PPRS—posterior pedal retractor scar;  
Ps—posterior sulcus;  
Rib—primary radial ornamental rib;  
Rp—number of primary ribs;  
Sms—submarginal sulcus;  
Srib—secondary radial ornamental rib;  
Ua—umbonal angle;  
W—width of both valves;  
?AMS—possible adductor muscle scar;  
?DF—possible dorsal furrow;  
?ManLS—possible mantle lobe scars;  
?MS—unidentified muscle scar.

### **Class Bivalvia Linnaeus, 1758**

#### **Subclass Protobranchia Pelseneer, 1889**

#### **Order Solemyoida Dall, 1889**

#### **Family Solemyidae Gray, 1840**

## Genus *Solemya* Lamarck, 1818

**Type species.** *Solemya mediterranea* (Lamarck, 1818) = *Tellina togata* Poli, 1795 (by subsequent designation, Children, 1823).

**Remarks.** Our species is included in *Solemya* Lamarck, 1818, because of its internal ligament (Taylor *et al.* 2008; Kamenev 2009; Oliver *et al.* 2011). It is not a member of the genus *Acharax* Dall, 1908, because this taxon has an external ligament positioned above the thickened shell margin, developed probably as a support for the ligament nymphs (Amano & Ando 2011; Oliver *et al.* 2011; Taviani *et al.* 2011). *Solemya* has an internal ligament with a distinct resilium supported on a chondrophore.

Fossil solemyids are morphologically very conservative, having a cylindrical shape with inequilaterally positioned beaks and an elongated shell anterior (e.g. Logan 1967; Duff 1978; Liljedahl 1984; Cope 1996; Kiel *et al.* 2008a; Bailey 2011). This conservatism (e.g. Taylor & Glover 2010) is maintained not only at the genus, but also at the species level, as testified by the presence of cryptic modern species of *Acharax* (Neulinger *et al.* 2006). Thus, the taxonomy of solemyids is difficult, and there are few characters useful for species discrimination.

## Subgenus *Petrasma* Dall, 1908

**Type species.** *Solemya borealis* Totten, 1834

**Remarks.** We have included our species in the subgenus *Petrasma* Dall, 1908, because of the presence of a chondrophore supporting an oblique buttress adjoining the anterior side of the posterior adductor muscle scar, and small ligament demipads elongated along the dorsal margin and developed in front of the chondrophore. A buttress in front of the posterior adductor muscle scar is also present in the subgenera *Solemyarina* Iredale, 1931, *Zesolemya* Iredale, 1939, and *Austrosolemya* Taylor, Glover & Williams 2008, all of which have large ligament demipads perpendicular to the dorsal margin in front of the chondrophore (e.g. Kamenev 2009, fig. 4–6). For more detailed discussion of subgeneric differences in the genus *Solemya* see Taylor *et al.* (2008), Kamenev (2009) and Oliver *et al.* (2011).

## *Solemya* (*Petrasma*) cf. *woodwardiana* Leckenby, 1859

(Figure 3)

1859 cf. *Solemya woodwardiana* sp. nov.—Leckenby, p. 14, pl. 3, fig. 7.

1978 cf. *Solemya woodwardiana* Leckenby—Duff, p. 31, pl. 1, figs. 34–44.

? 1990 *Solemya* cf. *woodwardiana* Leckenby—Wignall, p. 8.

? 1993 *Solemya* cf. *woodwardiana* Leckenby—Wignall & Pickering, p. 328.

2011 Solemyid—Hammer *et al.*, fig. 7h, tab. 2.

**Material examined.** 26 specimens, articulated to partially articulated; mostly internal moulds with only small portions of shell preserved. See Appendix 1 for the list of specimens.

**Dimensions.** 14–62 mm in length, 4.2–32 mm in width, 4–23.5 mm in height. See Figure 4 A–C and Appendix 2A for details.

**Description.** Shell medium to large, elongated and narrow. Anterior margin broadly rounded, with anteriormost extremity positioned roughly in middle of curvature. Dorsal and ventral margin parallel to subparallel. Valves of some partially articulated specimens rotated along ligament line, which gives a false impression of shell widening anteriorly. Posterior margin evenly rounded, with curvature more pronounced than that of anterior margin. Umbones weak, opisthogyrate. External ornament composed of radial ridges projecting from umbonal area towards shell margins and commarginal growth lines, preserved as weak and broad wrinkles. Radial ridges are two to three times as wide as interridge spaces. On internal moulds external radial ornament is weaker. Anterior adductor muscle scar weak and positioned close to anterior shell extremity, supported by dorsal margin. Anterior adductor muscle scar rarely preserved well enough to define shape, but when present forms a broad arch pointing anteriorly, with its posteroventral margin running dorsally, passing into oblique and elongated portion, probably representing a visceral mass integument attachment scar. Posterior adductor muscle scar well impressed, especially on larger specimens, egg-shaped, with acute end pointing towards umbo. Anterior margin of posterior adductor



muscle scar supported by well-developed buttress, running obliquely in dorsal direction and connected with chondrophore. Dorsal margin of posterior adductor muscle scar supported on a chondrophore; posterodorsal margin of posterior adductor muscle scar projecting above chondrophore. Hinge edentulous. Ligament internal, supported on a chondrophore, with small ligament demipads parallel to dorsal margin anterior of chondrophore.

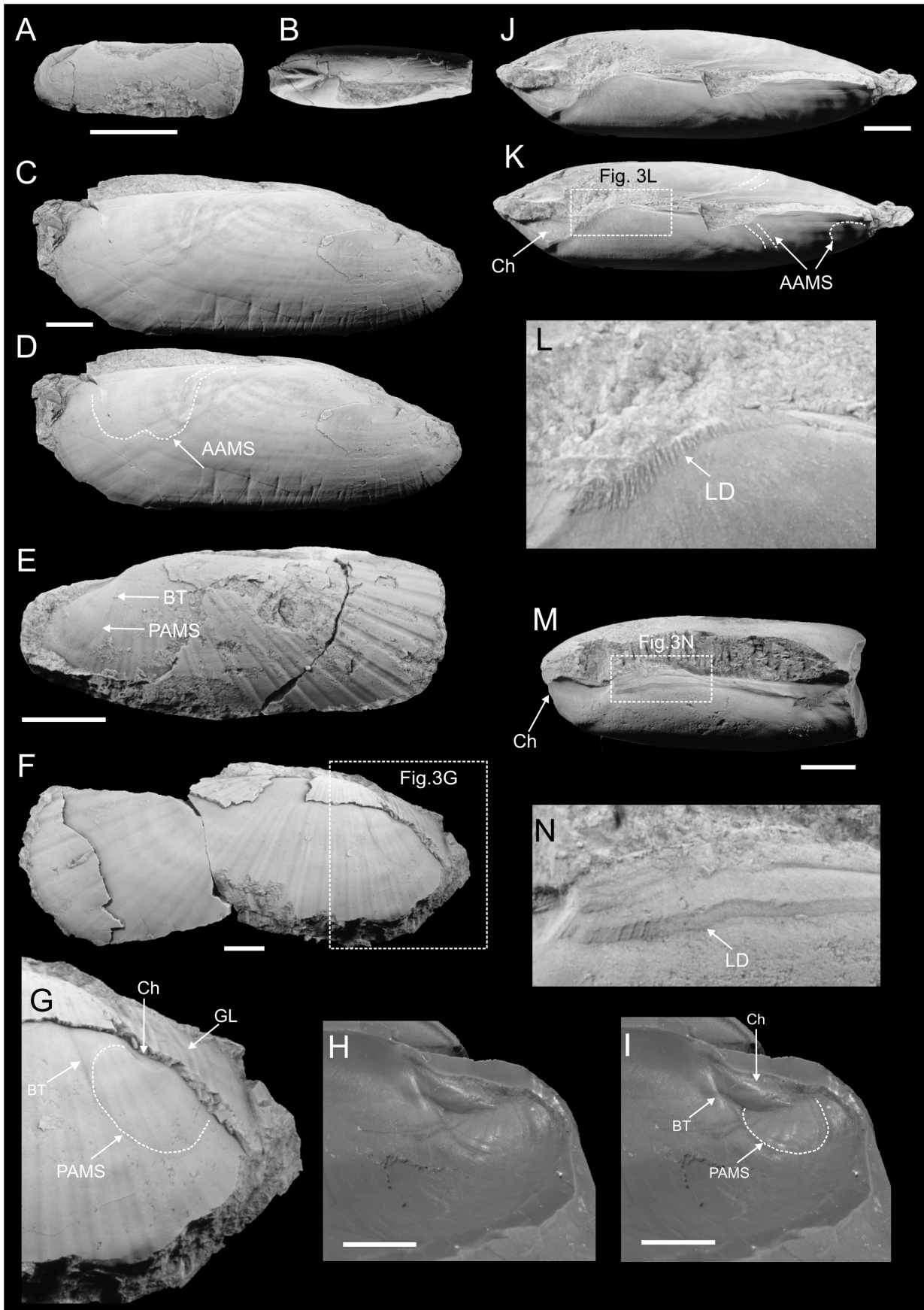
**Remarks.** We compare our species with *Solemya woodwardiana* Leckenby, 1859, from the Callovian of England, due to the overall similar shape and shell proportions. Duff (1978) noted the presence of a chondrophore and a buttress running along the anterior edge of posterior adductor muscle scar in *S. woodwardiana*. However, we leave our material in open nomenclature, because not all important solemyid characters are sufficiently defined in the Callovian *S. woodwardiana*. A similar species, identified as *S. cf. woodwardiana*, comes from the Kimmeridgian organic-rich facies of England (Wignall 1990) and Scotland (Wignall & Pickering 1993). *Solemya* species with shapes similar to *S. woodwardiana* are common in the Boreal Jurassic and Cretaceous (Figure 4A). *Unio togata* from the Moscow area in Russia (Trautschold 1858, p. 550, pl. 4, fig. 3) is a solemyid, with a characteristic notch in the subumbonal area, possibly indicating a presence of a buttress in front of PAMS. Trautschold (1858), probably unaware of Lamarck's (1818) designation of the genus *Solemya*, synonymized his finds with the recent solemyid *Tellina togata* Poli, 1795 = *Solemya togata* (Poli, 1795). Another solemyid with a shape comparable to the Svalbard seep specimens is *Solemya strigata* Lahusen, 1886, from the Bajocian around the Olenek and Lena River mouths (Lahusen 1886; Zakharov & Shurigin 1978). A solemyid with similar shape and proportions was also noted from the Volgian of East Greenland by Fürsich (1982). *Solemya cf. woodwardiana* differs from the *Solemya voltzii* (Roemer, 1839) from the Toarcian Posidonienschiefer of Germany by having beaks positioned closer to the posterior than that species. A species described by Lindström (1865) as *Solenomya torelli* from the Jurassic of Svalbard is more elongated than most of the specimens of *S. cf. woodwardiana*, and Lindström's brief diagnosis lacks any information about the ligament morphology. There is no certainty about the stratigraphic position of this species, since there is no Jurassic sediments cropping out in the Adventfjorden [Advent Bay] area of Svalbard, where Lindström's specimens are said to come from.

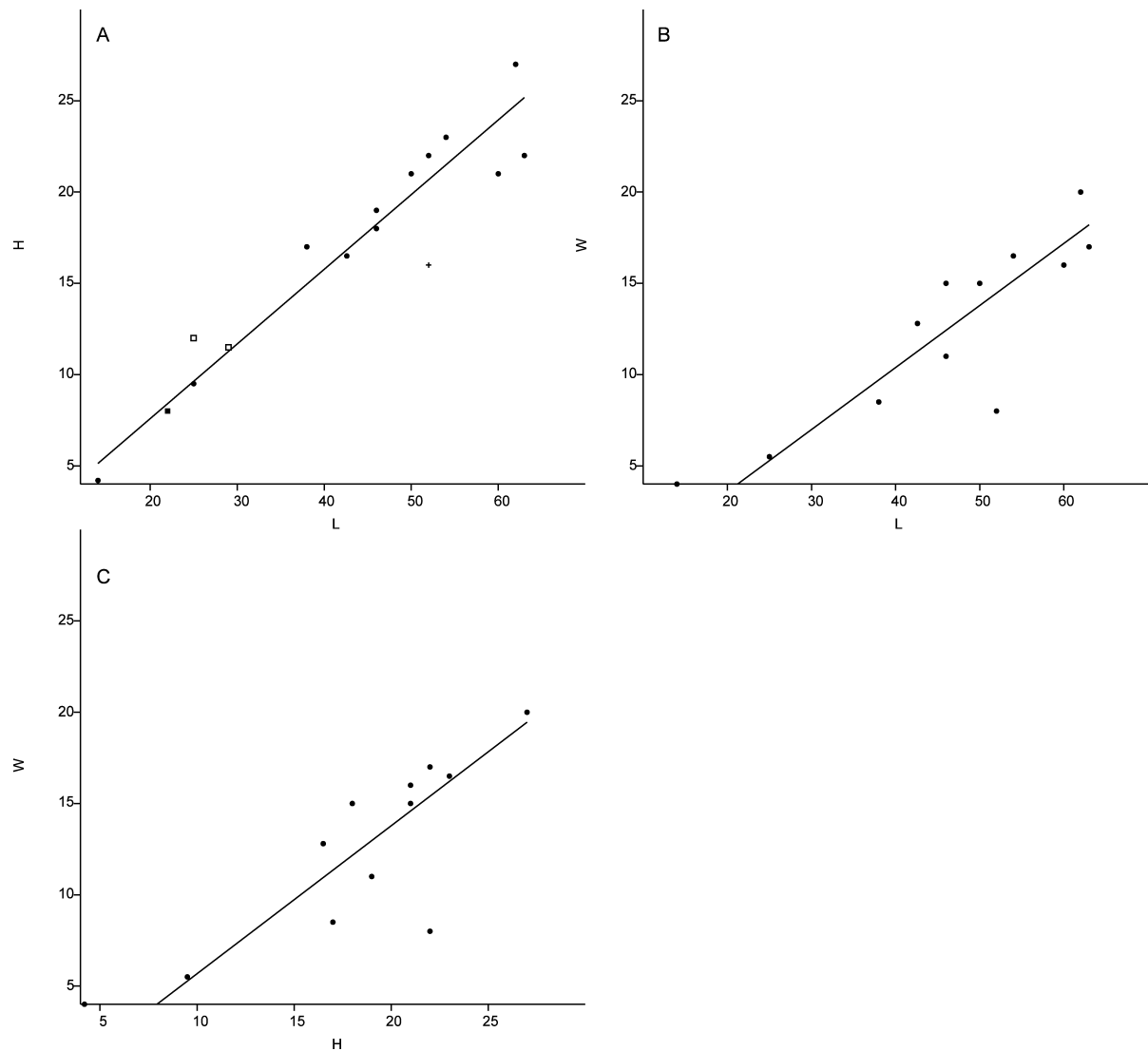
The external ornament of modern solemyids, especially of the thin-shelled species, is likely to be subjected to early diagenetic modification due to shell dissolution. The external shell shape and proportions can also be subjected to some variation due to plasticity and deformation of the organic-rich shell during burrowing (e.g. Stanley 1970; Taylor & Glover 2010), and by later compaction. Therefore, ascribing a bivalve fossil to the solemyids based on elongated shape only can be problematic. For example, *Solenomya (?) hoeli* from the Upper Jurassic of Svalbard (Sokolov & Bodylevsky 1931; Birkenmajer *et al.* 1982) has a very similar shape and proportions to our *Solemya cf. woodwardiana* specimens, and also has a radial ornament. However, detailed investigation of Sokolov & Bodylevsky's type specimen reveals that the radial pattern on the anterior part of the shell is in fact caused by cracking. Sokolov & Bodylevsky (1931) failed to notice very a fine radial ornament on the anterior and posterior margins of their type, which shows that *Solenomya (?) hoeli* is not a solemyid and instead belongs to the genus *Musculus* Roeding, 1798.

**Occurrence.** *Solemya woodwardiana*: Callovian of England (Leckenby 1859; Duff 1978). *Solemya cf. woodwardiana*: Kimmeridgian of England (Wignall 1990) and Scotland (Wignall & Pickering 1993); seeps 1, 3, 5, 8, 9 and 12 (Upper Volgian–uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1).

**Palaeoecology.** We assume that the Svalbard seep *Solemya cf. woodwardiana* was chemosymbiotic, as are all known modern members of the family. Since species similar to *Solemya cf. woodwardiana* are present in organic-rich, offshore facies of the Middle and Upper Jurassic of Northern Europe and the Arctic (Trautschold 1858; Lahusen 1886; Duff 1978; Zakharov & Shurigin 1978; Wignall 1990; Wignall & Pickering 1993), we infer that Svalbard species did not have any particular affiliation with seep environments and had a broad ecological tolerance, populating high redox potential environments.

Solemyids are widespread in modern oceans from intertidal to abyssal depths (Taylor & Glover 2010). The genus *Solemya* s.l. is a member of shelf and slope faunas (Coan *et al.* 2000; Coan & Scott 2012), where it is present in soft substrates enriched in organic matter, like reduced sediments (e.g. Conway *et al.* 1992), wood debris accumulations (Reid 1980), sea grass beds (e.g. Taylor *et al.* 2008) and carrion falls (Fujiwara *et al.* 2009). The deepest confirmed record of *Solemya* s.l. comes from 1510 m in Sagami Bay (Kamenev 2009), and it possibly occurs as deep as 1697 m in the Eastern Mediterranean (Rodrigues *et al.* 2011).





**FIGURE 4.** Measurements of *Solemya (Petrasma)* cf. *woodwardiana* Leckenby 1859, from Svalbard seep sites, and associated species from Europe (in mm). (A) Height to length. (B) Width to length. (C) Width to height. Full circles represent *S. (P.)* cf. *woodwardiana* from Svalbard, open squares represent *S. woodwardiana* from Callovian of England (Duff 1978), full square represents *Unio togata* from the Jurassic of Central Russia (Trautschold 1858) and a cross represents *Solenomya torelli* from unidentified strata of Svalbard (Lindström 1865).



**FIGURE 3.** *Solemya (Petrasma)* cf. *woodwardiana* Leckenby, 1859. (A–B) Lateral view of right valve and dorsal view of articulated specimen with shell preserved. (C–D) Lateral view of left valve internal mould. Note weak anterior adductor muscle scar and very weak radial ornament. (E) Lateral view of right valve internal mould with shell partially preserved. Note strong radial ornament on the shell, weak on the mould, and posterior adductor muscle scar with buttress supporting the anterior side. (F–G) Lateral view of left valve internal mould with some shell preserved in dorsal and anterior margins. Note posterior adductor muscle scar with buttress supporting its anterior side and dorsally bound by a chondrophore and weak growth lines on the posterior shell margin. (H–I) Silicone rubber cast of an internal mould showing shape of posterior adductor muscle scar and its relation to chondrophore and buttress. Note posterior adductor muscle scar surrounding the dorsal side of chondrophore and passing above the posterior end of the chondrophore. (J–K, M) Dorsal views of articulated internal moulds showing chondrophore and anterior adductor muscle scar. (L, N) Enlarged part of the dorsal margin showing ligament demipads. (A–B) PMO 224.956, (C–D, H–L) PMO 217.249, (E) PMO 217.260, (F–G) PMO 217.176, (M–N) PMO 217.245. Scale bars 5 mm.

*Solemya* s.l. is a burrower, especially favouring muddy, silty and sandy bottoms. Burrowing takes place anterior-first and leads to formation of U-to Y-shaped tubes, reinforced with mucus (Stanley 1970; Reid 1980; Stewart & Cavanaugh 2006). While resting in its burrow, the animal uses its foot in a pumping action, supplying water enriched in reduced compounds from the lower shafts of the burrow to their gills (Reid 1980). All investigated *Solemya* s.l. species live in symbiosis with thiotrophic Gammaproteobacteria (Stewart & Cavanaugh 2006; Taylor & Glover 2010). A gutless condition has been confirmed in some species (e.g. Reid 1980; Conway *et al.* 1992; Kamenev 2009), while others retain the gut (e.g. Taylor *et al.* 2008; Oliver *et al.* 2011) and have limited ability for particulate feeding (Krueger *et al.* 1992). Coan *et al.* (2000) noticed that gutless species of *Solemya* s.l. are more common in environments with extreme organic content.

## Family Nucinellidae Vokes, 1956

### Genus *Nucinella* Wood, 1851

**Type species.** *Pleurodon ovalis* Wood, 1840

**Remarks.** *Nucinella* has sometimes been placed in the family Manzanellidae Chronic, 1952 (e.g. Amano *et al.* 2007; Kiel *et al.* 2008a). However, the Permian genus *Manzanella* Girty, 1909, is longer than high, with roughly equidistantly positioned beaks. Furthermore, it is dimyarian, with anterior and posterior adductor muscle scars roughly equal in size (Chronic 1952). This contrasts with the genus *Nucinella* Wood, 1851, which is monomyarian and has a very short posterior shell margin (e.g. Allen & Sanders 1969). A dimyarian condition was previously postulated for the supposed sister genus *Huxleyia* Adams, 1860 (e.g. Habe 1958; pl. 9, fig. 16; La Perna 2004, p. 571). However, investigation of *Huxleyia habooba* Oliver & Taylor, 2012, and *Huxleyia sulcata* Adams, 1860, revealed no sign of a posterior adductor muscle, which supports separation of *Nucinella* and *Huxleyia* into a separate family Nucinellidae (Oliver & Taylor 2012), with Manzanellidae restricted to the genus *Manzanella*.

### *Nucinella svalbardensis* sp. nov.

(Figure 5 A–N)

2011 *Nucinella* sp.—Hammer *et al.*, fig. 7f–g, tab. 2.

**Etymology.** After the archipelago of Svalbard.

**Type locality.** Seep 9, Knorringsfjellet, Spitsbergen, 78°18'49.9"N 16°10'58.9"E.

**Type material.** Holotype: PMO 217.171; a well preserved articulated internal mould showing external shape and anterior muscle scar arrangement. Paratypes: PMO 217.217; an articulated internal mould and silicone rubber casts showing lateral teeth morphology. PMO 224.978; an articulated internal mould with shell partially preserved, showing external ornament of commarginal growth lines. PMO 224.981; an articulated internal mould and silicone rubber cast showing shape of cardinal teeth, as well as lateral teeth length. PMO 225.020; an articulated internal mould and silicone rubber casts showing lateral teeth length. PMO 225.042; an articulated internal mould with shell partially preserved showing the shape of the posteriormost cardinal teeth.

**Material examined.** 98 specimens; mostly articulated or semiarticulated shells or moulds. See Appendix 1 for list of specimens.

**Dimensions.** 3.5–23 mm in length, 1.2–9.1 mm in height, 1–8.2 mm in width. See Figure 6A–C and Appendix 2B for details.

**Diagnosis.** A very large species of *Nucinella* with rounded posteroventral margin, and sabre-shaped lateral teeth, two in the right valve, one in the left.

**Description.** Shell very large, moderately inflated, equivalve, inequilateral, covered with commarginal growth lines. Umbo opisthogyrate, weakly projecting above dorsal margin, situated around ¼ of shell length. Anterodorsal margin weakly and evenly convex, passing smoothly into broadly arched anterior margin. Curvature of anterior margin even and symmetrical, with extremity around half distance from dorsal to ventral sides. Ventral margin weakly convex, roughly parallel to dorsal margin. Posterior extremity asymmetrically rounded, with ventral part of arch smoother than dorsal. Posterodorsal margin weakly concave, hosting deep ligament pit. Anterior adductor

muscle scar elongated, attached to, and slightly projecting over, pallial line. Ventral part of anterior adductor muscle scar convex. Dorsal part of anterior adductor muscle scar narrow and long, connected with anterior part of lateral tooth; elongation possibly representing anterior pedal retractor scar, merged with anterior adductor muscle scar. Entire surface of anterior adductor muscle scar covered with commarginal lines. Surface of internal moulds covered with fine radial striae. Pallial line entire. Cardinal teeth diverse in shape; specimen measuring *ca.* 27 mm in length has eight teeth in left valve and seven in the right valve. Innermost cardinal teeth of right valve strong and long. Teeth get progressively smaller towards anterior and posterior extremities of hinge plate. Anteriormost cardinal tooth small, button-shaped. Lateral teeth long, thickest close to their anterior extremities, giving them characteristic sabre-like shape. In all specimens with investigated lateral teeth two laterals of right valve form a socket hosting single lateral of left valve. The socket is deepest close to anteriormost margin. Ligament external, dorsal to cardinal teeth. Detailed shape unknown.

**Remarks.** *Nucinella svalbardensis* **sp. nov.** can be distinguished from *Nucinella gigantea* Amano, Jenkins & Hikida, 2007, from the Cenomanian to Campanian hydrocarbon seeps of Hokkaido (Amano *et al.* 2007; Kiel *et al.* 2008a) by its rounded posteroventral margin, less projecting beaks and greater shell inflation. The cardinal dentition of *N. svalbardensis* is similar to that of *N. gigantea*. The slightly larger number of teeth in *N. svalbardensis* compared to *N. gigantea* can be explained by the larger size of the former species, since the number of cardinal teeth is a function of specimen size, as shown by La Perna (2004) in other species of *Nucinella*. According to Amano *et al.* (2007) a single lateral is present in the both left and right valve of *N. gigantea*, unlike in *N. svalbardensis*. A possible fossil nucinellid from the Triassic (Norian) seeps in Oregon (Peckmann *et al.* 2011) has been only tentatively identified and comparison with *N. svalbardensis* is at the present not possible. *Nucinella svalbardensis* can be distinguished from non-seep Mesozoic species by its much larger size. The Hettangian *Nuculina liasina* Bistram, 1903, of Val Solda (Bistram 1903) is much smaller than *N. svalbardensis*, reaching only a couple of millimetres in length. *Nucinella birkelundi* Clausen & Wignall, 1990, from the Kimmeridgian of Southern England (Clausen & Wignall 1990), is much smaller, in addition to being much higher, being 1.5 times high as long.

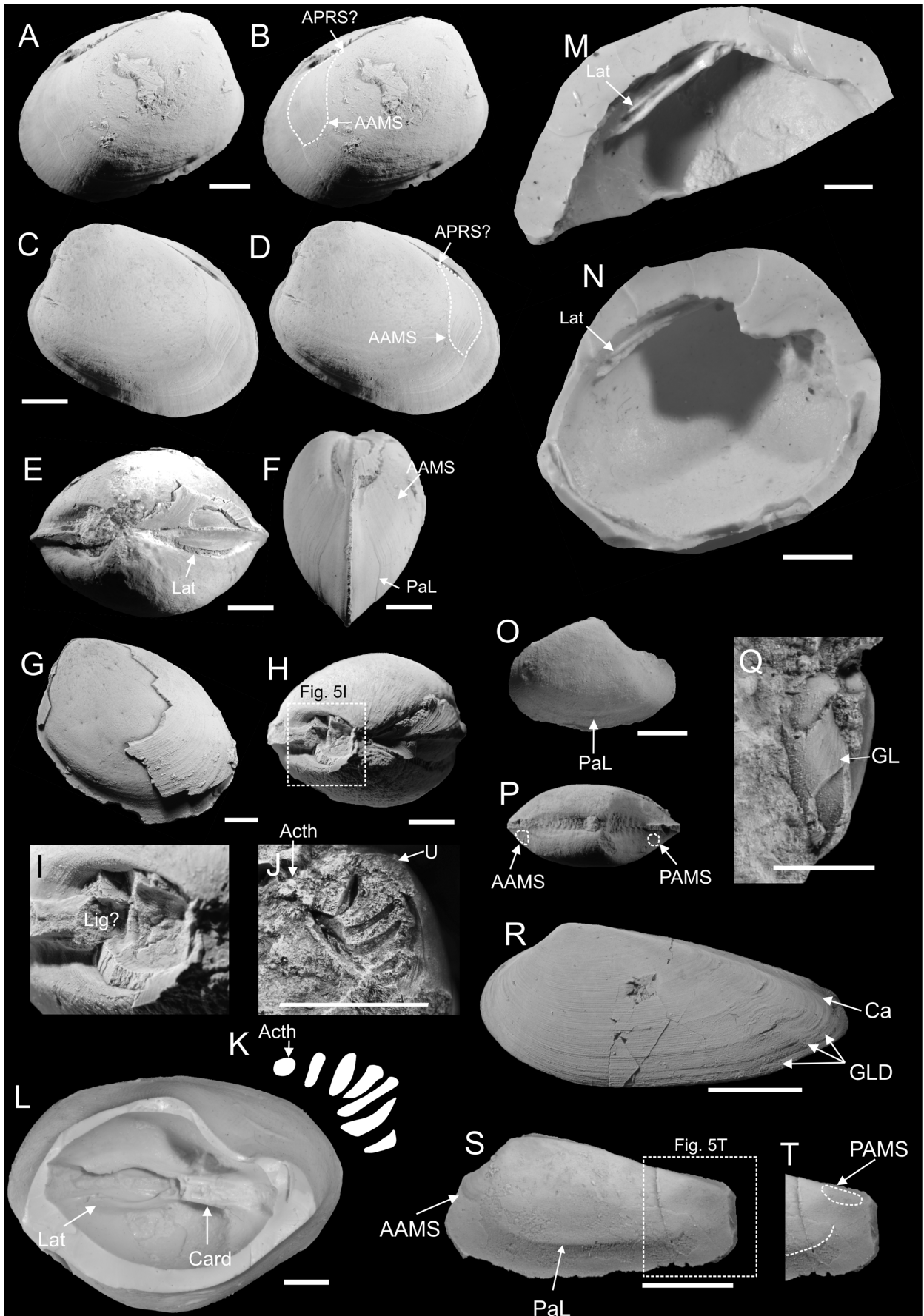
**Occurrence.** Seeps 1, 2, 3, 5, 9, 12, 13, 14 and 15 (Upper Volgian–uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1).

**Palaeoecology.** There are a number of reasons to suggest that *Nucinella svalbardensis* was a chemosymbiotic shallow burrower. First, chemosymbiosis was suggested by McLeod *et al.* (2010) for the Recent species *Nucinella maoriana* (Hedley, 1904) because of the presence of light organic carbon in its tissues. Second, the presence of bacterial structures in the gills of *Nucinella owenensis* Oliver & Taylor, 2012, led Oliver & Taylor (2012) to infer that chemosymbiosis may be common within the family, although some species are known to be active deposit feeders (Oliver & Taylor 2012). Third, large species of *Nucinella* are common in fossil hydrocarbon seep deposits, suggesting a chemosymbiotic relationship (Amano *et al.* 2007; Kiel *et al.* 2008a; Hammer *et al.* 2011; Peckmann *et al.* 2011); *N. svalbardensis*, being up to 32 mm in length, is the largest species of *Nucinella* currently known. However, some of the non-seep deep marine *Nucinella* species are also quite large, being up to 25 mm long (Thiele & Jaekel 1931; Matsukuma *et al.* 1982; La Perna 2005). Hence, a relationship between size and seep-association in *Nucinella* is not straightforward.

In addition to seeps, *Nucinella* can be found in a range of other shallow to deep marine modern environments (Allen & Sanders 1969; Matsukuma *et al.* 1982; Okutani & Iwasaki 2003; La Perna 2004), including organic-rich sediments in fjords (McLeod *et al.* 2010), and at oxygen-minimum zones (Oliver & Taylor 2012). As a fossil it occurs in a range of post-Triassic marine deposits (i.e. Wood 1851; Bistram 1903; Vokes 1956; Clausen & Wignall 1990; Studencka *et al.* 1998; Harries & Little 1999; Schneider 2008).

## Order Nuculoida Dall, 1889

### Superfamily Nuculoidea Gray, 1824



## Family Nuculidae Gray, 1824

### Genus *Dacromya* Agassiz, 1839

**Type species.** *Nucula lacryma* J. de C. Sowerby, 1824.

### *Dacromya chetaensis* Sanin, 1976

(Figure 5 O–Q)

1976 *Dacromya chetaensis* nov. sp.—Sanin, p. 26, pl. 6, figs. 10–11; pl. 7, figs. 1–6.

**Material examined.** Three specimens; articulated internal moulds with some preserved shell material. See Appendix 1 for the list of specimens.

**Dimensions.** 7–11.5 mm in length, 5.1–7.25 mm in height, 3.1–5.25 mm in width. See Appendix 2C for details.

**Description.** Shell small, with tear-drop shaped outline. Preserved shell fragments thin, with fine, densely spaced commarginal growth lines. Moderately to strongly inflated, with greatest width medially. Shell height around two-thirds of length, reaching a maximum medially and gradually diminishing towards anterior and posterior extremities. Anterior part of shell longer than posterior, arcuate, gently tapering. Anterodorsal margin weakly convex, more inclined than anteroventral margin. Ventral margin very gently rounded. Posterior shell part shorter than anterior, rostrate, rounded, and curved dorsally. Posterodorsal margin concave, hosting deep escutcheon. Beaks opisthogyrate, lunule elongated, sunken close to beaks, emerging towards anterior. Dentition taxodont with more than 10 teeth in anterior row and 7 to 10 teeth in posterior row. Cardinal area and ligament not preserved. Anterior and posterior adductor muscle scars circular, small, adhering to pallial line and positioned close to shell extremities on inside of pallial line. Posterior adductor muscle scar connected to beak with grooves, most likely formed during descending muscle growth. Pallial line entire.

**Remarks.** We include this species into *Dacromya chetaensis* Sanin, 1976, based on its shell proportions, gently arched anterior margin and external ornament. It differs from *Dacromya venusta* (Sauvage, 1871) from the Kimmeridgian of England (Clausen & Wignall 1990) in having a more rounded anterior margin, less sloping anterodorsal margin and an external ornament of commarginal growth lines. *Dacromya chetaensis* is less elongated, has more pointed umbones and shorter rostrum than *D. gigantea* Zakharov & Shurigin, 1974, from the Aalenian of the Taimyr Peninsula (Zakharov & Shurigin 1974; 1978).

**Occurrence.** Seep 12 (Upper Ryazanian), Slottsmøya Member, Svalbard (Tab. 1). Known also from the Volgian–Valanginian of the Khatanga Depression, Northern Siberia (Sanin 1976).



**FIGURE 5.** (A–N) *Nucinella svalbardensis* sp. nov. (A–D) Lateral views of holotype showing shape of the articulated internal mould, anterior adductor muscle scar and possible anterior pedal retractor scar, rounded posterior margin and fine radial striations on internal mould surface. (E) Dorsal view showing weakly opisthogyrate umbo and deep ligament pit on the posterodorsal margin. (F) Anterior view showing anterior adductor muscle scar projecting weakly beyond pallial line. (G) Lateral view showing commarginal ornament on external shell surface. (H–I) Dorsal view of partially articulated specimen showing length of the cardinal teeth and relation of the possible ligament to the cardinal dentition. (J–K) Lateral view of the cardinal part of the hinge plate showing arrangement and shape of the cardinal teeth. (L) Ventral view of silicone rubber cast of the dorsal margin of articulated internal mould showing sabre-shaped lateral teeth and interlocked cardinal teeth. (M–N) Silicone rubber casts of right valve internal moulds showing two lateral teeth. (O–Q) *Dacromya chetaensis* Sanin, 1976. (O–P) Lateral and dorsal views showing shape of internal mould, taxodont dentition, anterior and posterior adductor muscle scars. (Q) Posterodorsal shell margin showing weak growth lines. (R–T) *Mesosaccella rogoi* sp. nov. (R) Lateral view of holotype left valve shell surface showing characteristic growth-line deflections around the posterior margin and carina subparallel to the dorsal margin. (S–T) Lateral view of left valve internal mould showing anterior adductor muscle scar, weak posterior adductor muscle scar and pallial line. (A–F) PMO 217.171, (G) PMO 224.978, (H–I) PMO 225.042, (J–K) PMO 224.981, (L–M) PMO 217.217, (N) PMO 225.020, (O–P) PMO 217.581, (Q) PMO 226.600, (R) PMO 224.971, (S–T) PMO 217.229. Scale bars 5 mm.

**Palaeoecology.** *Dacromya chetaensis* was probably a mobile shallow burrowing deposit feeder without a siphon, as indicated by the lack of a pallial sinus. The streamlined shell with a blunt, weakly pointed anterior and short, rostrate posterior shows that it was probably an efficient burrower. In Siberia it is associated with sandy mudstones that were deposited in a low energy, shallow water setting (Sanin 1976). This mode of life is typical for Recent nuculids, which are shallow burrowers using palps to collect sediment, which they process for organic material (Stanley 1970).

## Family Malletiidae H. Adams & A. Adams, 1858

### Genus *Mesosaccella* Chavan, 1946

**Type species.** *Nucula foersteri* Müller, 1847

**Remarks.** The genus *Mesosaccella* is probably a bucket taxon, as it contains species with a wide range of external morphological features. This diversity is encapsulated into three morphogroups. The first comprises roughly oval, variably elongated and non-carinate species with ornament composed only of growth lines, including *M. elliptica* (Goldfuss, 1837) from the Rhaetian–Pliensbachian of Europe (Palmer 1973; Hodges 2000), *M. morrisoni* (Deshayes, 1853) from the Callovian of England and France (Duff 1978) and *M. choroschovensis* (Borissjak, 1904) from the Volgian of Russia and Greenland (Borissjak 1904; Fürsich 1982). The second *Mesosaccella* morphogroup comprises elongated species with slightly pointed posteriors, external ornament of growth lines, with or without weak commarginal ridges, and growth line deflections on the posterior parts of the shell. This group includes our *M. rogovi* sp. nov., *M. grovei* (Lartet, 1872) and *M. larteti* Chavan, 1947, from the Campanian of Palestine (Chavan 1947), as well as species currently classified within other genera, but also fitting the definition of *Mesosaccella*, such as *Leda striatula* Forbes, 1845, from the Cretaceous of India (Forbes 1845, p. 148, pl. XVII, fig. 14). The third *Mesosaccella* morphogroup comprises short and inflated forms with pointed posteriors, strong commarginal ornament fading on the anterior and posterior parts of the shell and carination of the posterior shell area. This group includes our *M. toddi* sp. nov., and species described as *Nuculana speetoniensis* Woods, 1899, and *Nuculana lineata* J. de C. Sowerby, 1836, by Woods (1899).

### *Mesosaccella rogovi* sp. nov.

(Figures 5 R–T, 7 A–F)

2011 Malletiid sp. 1—Hammer *et al.*, fig. 7n–o, tab. 2.

**Etymology.** After Mikhail A. Rogov, Russian palaeontologist specializing in Jurassic stratigraphy of the Arctic.

**Type locality.** Seep 9, Knorringsfjellet, Spitsbergen, 78°18'49.9"N 16°10'58.9"E.

**Type material.** Holotype: PMO 224.971; a well preserved left valve showing the shape and characteristic ornament of posterodorsal margin. Paratypes: PMO 217.229; a partially preserved articulated internal mould showing anterior adductor muscle scar, posterior adductor muscle scar and weak pallial line. PMO 217.371; a well preserved articulated internal mould with fragments of shell, which shows weak ridges formed by growth line deflections, a carina and lancet-shaped escutcheon; the mould shows the pallial line and weak imprints of the external ridges. PMO 217.539; a partial right valve with cardinal area showing continuous tooth row.

**Material examined.** 89 specimens, mostly articulated valves or internal moulds with portions of the shell remaining. See Appendix 1 for the list of specimens.

**Diagnosis.** Elongated, lancet-shaped species with posterior part more than four times the length of the anterior part. Up to three weak posterior ridges formed by growth line deflections on the posterior part of the shell. A carina subparallel to the posterodorsal margin runs from the umbo to the posterior shell extremity.

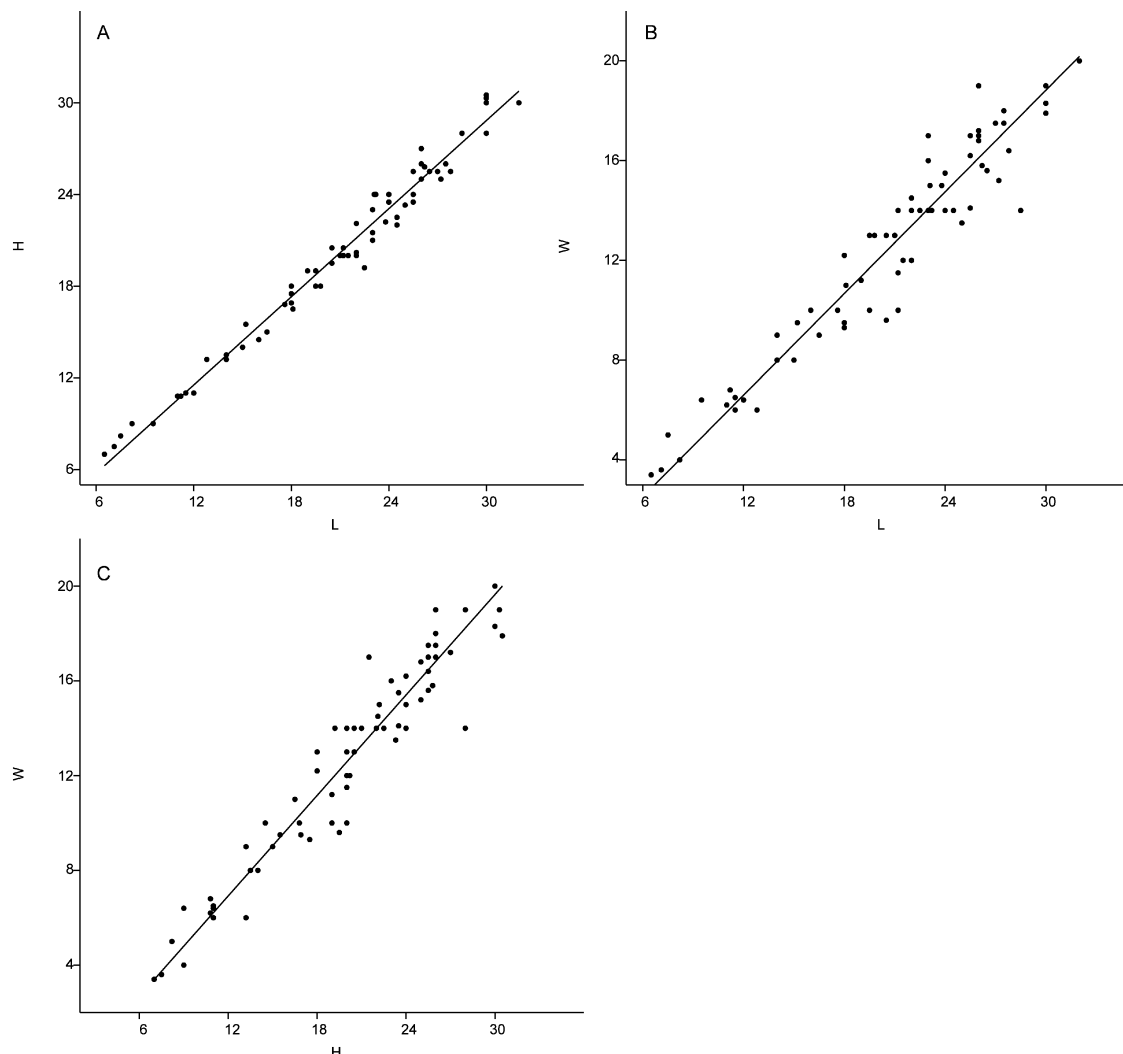
**Dimensions.** 3.5–23 mm in length, 1.2–9.1 mm in height, 1–8.2 mm in width. See Figure 8 A–D and Appendix 2D for details.

**Description.** Medium to large, up to 23 mm long, 9.1 mm high and 8.2 mm wide, elongated ( $H/L \approx 0.42$ ), lancet-shaped, weakly inflated ( $W/L \approx 0.32$ ,  $W/H \approx 0.77$ ); greatest height and width around medial plane. Elongated

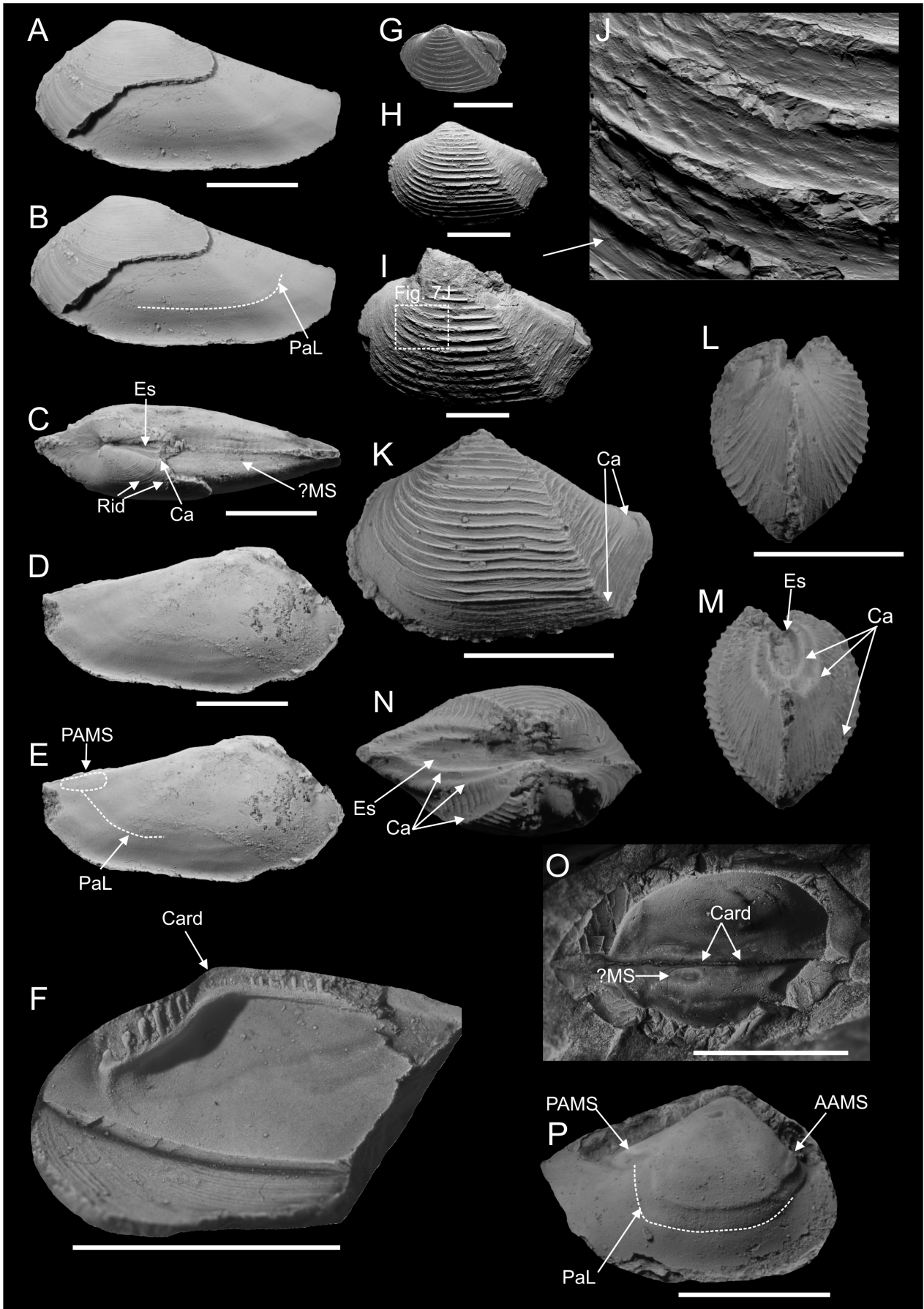


shape especially well expressed in posterior part, which occupies around 80% of total length ( $Pl/L \approx 0.79$ ). Shell shape parameters remain relatively constant throughout ontogeny. External ornament of narrowly-spaced, commarginal growth lines, strongest in median part of shell and weaker towards both anterior and posterior. Towards posterior, disappearance of concentric ridges marked by up to three closely spaced ridges composed of series of growth line deflections. A single carina runs subparallel to posterodorsal margin. Escutcheon shallow, pointed anteriorly, presumably lancet-shaped. Anterodorsal margin straight to weakly convex, without well demarcated lunule. Anterior margin rounded to blunt. Anteroventral margin rounded, passing into weakly rounded ventral margin. Ventral margin passes into weakly convex posteroventral margin. Posterior end pointed, dorsally sloping and passing into long, posterodorsal margin; parallel to dorsal carina. Beaks prosogyrate. Dentition taxodont, teeth orthomorphodont. Anterior and posterior teeth rows meet below umbo. Posterior teeth much smaller than anterior teeth. Specimen 20 mm long has up to 38 teeth in posterior row and *ca.* 11 teeth in anterior row. Anterior adductor muscle scar small, rounded. Posterior adductor muscle scar elongated, more impressed anteriorly, progressively fading towards posterior. In some specimens weak elongated muscle scars of uncertain origin visible along dorsal margin. Pallial line weakly impressed, parallel to commissure; pallial sinus very shallow to absent, and weakly impressed.

**Remarks.** *Mesosaccella rogoi* differs from *M. morrisi* (Deshayes, 1853) in being more elongated, having stronger commarginal ornament and, in addition, showing a weak dorsal carina and growth line deflections in the posterior shell areas (cf. Duff 1978). *Mesosaccella elliptica* (Goldfuss, 1837) has a shape closer to *M. rogoi*, but it lacks the distinctive commarginal ornament deflections in the posterior part of the shell and the dorsal carina



**FIGURE 6.** Measurements of *Nucinella svalbardensis* sp. nov. (in mm). (A) Height to length. (B) Width to length. (C) Width to height.



(Hodges 2000). *Mesosaccella choroschovensis* (Borissjak, 1904) is much shorter and more oval than *M. rogovi*, with a gently rounded posterior end and lacks the ridges of *M. rogovi*. *Leda striatula* Forbes, 1845, has a similar growth line deflection to *M. rogovi* in the posterior area. However, it is both less elongated and has a stronger carina than *M. rogovi*. *Mesosaccella rogovi* is as elongated as both *M. grovei* (Lartet, 1872) and *M. larteti* Chavan, 1947, but it is more inequilateral than the former and has much weaker commarginal ornament than the latter.

**Occurrence.** Seeps 1, 2, 3, 5, 8, 9, 12, 13 and 15 (Upper Volgian–uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1).

**Palaeoecology.** *Mesosaccella rogovi* was probably a shallow burrower, like other protobranch bivalves (Stanley 1970; Sanders & Allen 1985; Zardus 2002). The elongated and streamlined shell indicates it was an efficient burrower, and the very shallow pallial sinus implies the presence of a short siphon, developed either for respiration or for feeding from the sediment-water interface (e.g. Hodges 2000, text-fig. 32). Some protobranchs inhabiting modern vent and seep environments are believed to benefit from the concentration of chemosynthetically produced organic matter in the sediments, and possibly even feed on bacterial mats (e.g. Allen 1993; Sahling *et al.* 2002). We assume *M. rogovi* might have done the same.

### ***Mesosaccella toddi* sp. nov.**

(Figure 7 G–P)

2011 Malletiid sp. 2—Hammer *et al.*, tab. 2.

**Etymology.** After Jonathan A. Todd, curator of the Mesozoic and Cenozoic mollusc collection in the Natural History Museum, London. Study of this collection helped the work on the fossils described in this paper.

**Type locality.** Seep 9, Knorringfjellet, Spitsbergen, 78°18'49.9"N 16°10'58.9"E.

**Type material.** Holotype: PMO 224.861; a large, complete shell. Paratypes: PMO 225.031 Fragment of the cardinal area showing taxodont dentition. PMO 224.862; an internal mould showing weak anterior adductor muscle scar and posterior adductor muscle scar and pallial line with shallow pallial sinus. PMO 217.609; a small, complete shell. PMO 217.610; a small, complete shell. PMO 217.616; a large, well preserved shell showing external commarginal and rosette-shaped ornament.

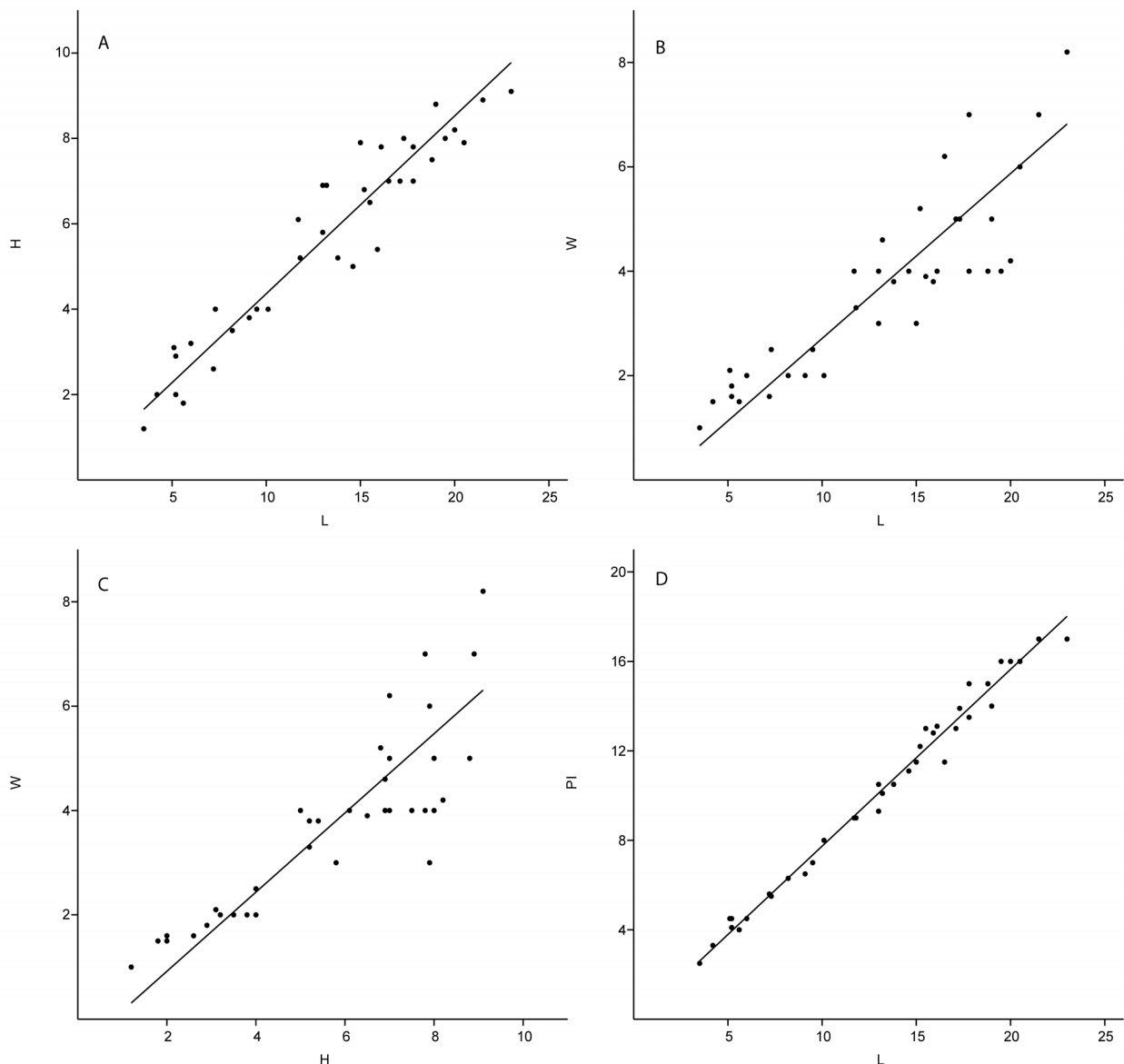
**Material examined.** 35 specimens, articulated valves and internal or external moulds. See Appendix 1 for the list of specimens.

**Diagnosis.** Inflated and thick-shelled with posterior part approximately twice the length of the anterior part, and with three strong posterior carinae. External ornament of strong commarginal ridges fading towards posterior and anterior and crossed obliquely by commarginal growth lines. Interridge spaces occupied by rows of rosette-shaped ornamentation, fading anteriorly and posteriorly.

**Dimensions.** 6–12.5 mm in length, 4–8.2 mm in height, 3–7.1 mm in width. See Figure 9 A–D and Appendix 2E for details.



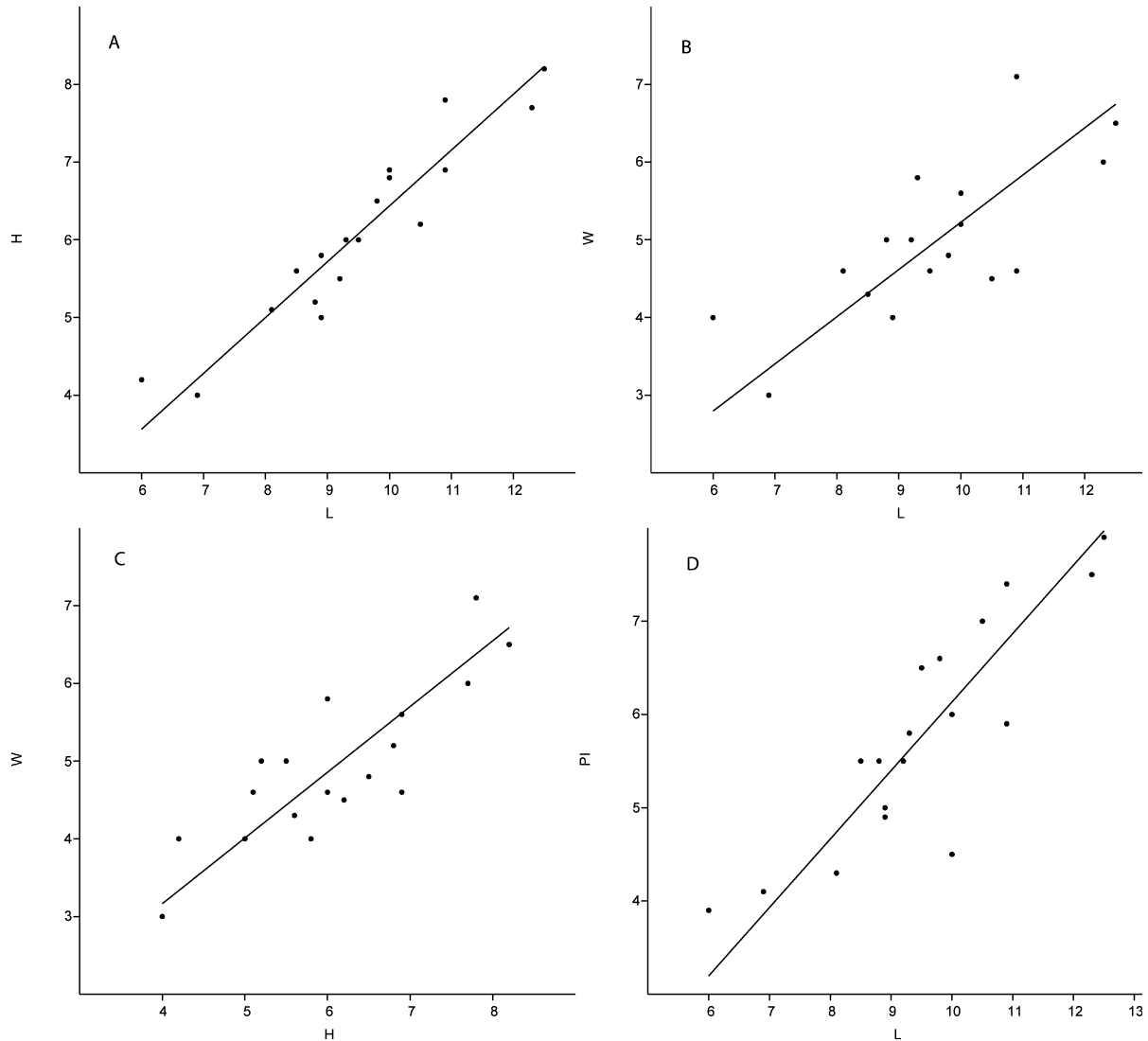
**FIGURE 7.** (A–F) *Mesosaccella rogovi* sp. nov. (A–B) Lateral view of a internal mould showing pallial line. Fragment of the shell shows concentric growth lines. (C) Dorsal view of specimen with partially preserved shell showing weak carina, escutcheon, unidentified muscle scars and ridges formed by growth line deflections. (D–E) Lateral view of right valve internal mould showing weak posterior adductor muscle scar and weak pallial line with very shallow pallial sinus. (F) Internal view of the right valve showing anterior and posterior dental rows and cardinal dentition. (G–P) *Mesosaccella toddi* sp. nov. (G–K) Left valve lateral views of articulated specimens. (J) Details of external ornament showing characteristic commarginal ridges and rosette-shaped ornament in interr ridge spaces (arrowed). (K) Holotype showing strong posterior carinae. (L–M) Anterior and posterior views of holotype. Note three carinae and escutcheon visible in the posterior view. (N) Dorsal view of holotype showing three carinae and their relation to wide and shallow escutcheon. (O) Internal view of the dorsal margin of articulated specimen showing cardinal-most teeth and unidentified muscle scars. (P) Lateral view of right valve internal mould showing relatively strong, circular anterior adductor muscle scar and elongated posterior adductor muscle scar, as well as strong pallial line with shallow pallial sinus. (A–E) PMO 217.371, (F) PMO 217.539, (G) PMO 217.609, (H) PMO 217.610, (I–J) PMO 217.616, (K–N) PMO 224.861, (O) PMO 225.031, (P) PMO 224.862. Scale bars 5 mm (A–F, K–P), 2 mm (G–I).



**FIGURE 8.** Measurements of *Mesosaccella rogoi* sp. nov. (in mm). (A) Height to length. (B) Width to length. (C) Width to height. (D) Posterior length to length.

**Description.** Shell small to medium in size, up to 12.5 mm long, 8.2 mm high, and 7.1 mm wide, elongated ( $H/L \approx 0.72$ ), and inflated ( $W/L \approx 0.52$ ,  $W/H \approx 0.81$ ), with more inflated specimens more frequent than less inflated. Moderately inequilateral ( $Pl/L \approx 0.72$ ) throughout observed ontogeny. Orthogyrate beaks, passing into broadly curved anterodorsal margin through shallow concavity directly in front of beaks. Anterodorsal margin bends down and gets more tightly rounded to form broadly arcuate anterior margin, which gets progressively less curved and passes smoothly into ventral margin. Ventral margin gently rounded, deepest approximately below beaks. Posterior to first carina ventral margin oblique, with shallow sinus developed on larger specimens, connected to shallow, but well defined sulcus. Posterior shell extremity pointed, supported on second carina. Posterodorsal shell margin straight, joining beak through very small and shallow concavity directly behind it. External ornament of weak commarginal growth lines, obscured in shell mid-flank by strong, commarginal ridges transecting growth lines obliquely. Interridge spaces occupied by rows of rosette-shaped ornament arranged in regular intervals. Posterior area ornamented only by growth lines and rosettes; delineated by two strong carinae. First carina forms angle of  $ca. 55^\circ$  with anteroposterior axis and visible throughout observed ontogeny. Second carina forms approximate angle of  $27^\circ$  with anteroposterior axis and also visible throughout ontogeny. Escutcheon wide, shallow, bounded by third

carina. Dentition taxodont with long and straight teeth arranged in rows along hinge line. Specimen approximately 9 mm in length has nine teeth in anterior row and 16 teeth in posterior row. No resilifer; teeth joining below beak to form single teeth row. Anterior adductor muscle scar circular and well impressed; rather small. In specimen *ca.*9 mm long anterior adductor muscle scar is 1 mm in diameter. Anterior adductor muscle scar positioned slightly above anteroposterior axis. Posterior adductor muscle scar poorly visible, small, elongated, positioned above pallial sinus. Five pairs of elongated muscle scars present directly underneath hinge plate: two in anterior part of hinge plate, one underneath cardinal area and two pairs of longer muscle scars present underneath posterior part of hinge plate. Some of these may represent pedal muscle attachments. Pallial line well impressed; pallial sinus shallow.



**FIGURE 9.** Measurements of *Mesosaccella toddi* sp. nov. (in mm). (A) Height to length. (B) Width to length. (C) Width to height. (D) Posterior length to length.

**Remarks.** Protobranch bivalves with a shell shape similar to *M. toddi* are known from several other Cretaceous localities. Woods (1899) listed several carinated species from the Cretaceous of England which he assigned to the genus *Nuculana* Link, 1807. In our opinion these belong to both *Nuculana* and *Mesosaccella*. For example, no resilifer is visible on the drawings of *N. lineata* in Woods (1899, pl. 1, fig. 31d), which excludes this species from *Nuculana*. *Nuculana speetoniensis* (Woods 1899, p. 3, pl. 1, figs. 6–7) from the Lower Cretaceous Speeton Clay has a very similar shell shape to *M. toddi*, the main difference between them being the shorter and less pointed posterior margin of *N. speetoniensis*. *Nuculana lineata* J. de Sowerby, 1836 (Woods 1899, p. 7, pl. 1, figs. 28–32), from the Lower Cretaceous of Southern England has a similar shape and ornament to *M. toddi*, having commarginal ridges fading on the anterior and posterior shell parts, but can be distinguished from *M. toddi* by

being less inflated and having a rounded posterior with less pronounced carinae. In the Aptian of Spitsbergen Sokolov & Bodylevsky (1931, p. 66, pl. 12, figs. 4–6) recorded *Leda angulatostrata*, which has a very similar shell shape to *M. toddi*, the main difference being *L. angulatostrata* has a less pronounced posterior carination than *M. toddi*. In our opinion *L. angulatostrata* also belongs to *Mesacella*.

**Occurrence.** Seeps 1, 3, 9 and 12 (Upper Volgian–latest Ryazanian), Slottsmøya Member, Svalbard (Tab. 1).

**Palaeoecology.** *Mesosacella toddi* was probably a shallow burrowing deposit feeder, like *M. rogoi*. The inflated shell of *M. toddi*, its relatively short posterior and shallow pallial sinus suggests, however, that this species was a slow burrower living underneath the sediment-water interface. The strong commarginal ornament and relatively thick shell may have been adaptations for burrowing in coarser sediment, like silt and sand (e.g. Marshall 1978), or it might have been an adaptation for living in acidic environment (e.g. Allen 1993). As for *M. rogoi*, *M. toddi* might have fed on chemosynthetically produced organic matter.

## Subclass Autobranchia Grobben, 1894

## Superorder Pteriomorphia Beurlen, 1944

## Order Pectinida Gray, 1854

### Pectinida gen. et sp. indet.

(Figure 10 A–B)

2011 Ostreoidean—Hammer *et al.*, tab. 2.

**Material examined.** Five specimens; fragmented and delaminated shells. See Appendix 1 for the list of specimens.

**Description.** Shell thin, roughly round in shape, only weakly inflated. Right valve thin, flat, visible only in cross-section. Left valve thin, weakly convex and larger than right valve; irregularly shaped, no sign of attachment found. Beak weakly incurved, accompanied by a shallow ventrally directed furrow. Weak muscle scar probably represent an adductor muscle scar. Shell ornamented by weak commarginal folds.

**Remarks.** The lack of a well demarcated external ligament, the thinness of the shells and the nature of cementation precludes our specimens belonging to the Ostreida Ferrusac, 1822. Instead, the flat right valve facing the substrate and a larger covering left valve indicates that our specimens belong either to the Anomiidae Rafinesque, 1815, or the Dimyidae, Fischer, 1886 (e.g. Coan *et al.* 2000; Coan & Scott 2012). An anomiid origin is probably more likely because the dorsal furrow resembles the shell fusion scar characteristic for anomiids (Yonge 1977). However, the lack of well preserved right valves and adductor muscle scars means we cannot unequivocally include our specimens into either the Anomiidae and Dimyidae at present.

**Palaeoecology.** Our species was most likely a filter-feeder attached to hard substrates. Modern anomiids are shallow water forms, attached by a byssus protruding through a foramen in the lower valve (e.g. Yonge 1977). Recent Dimyidae is a cementing group found in deep water and cryptic habitats (e.g. Waller 2012). In the Mesozoic both groups were fairly common in shallow water habitats (e.g. Fürsich & Werner 1989; Hodges 1991; Todd & Palmer 2002).

## Family Buchiidae Cox, 1953

## Genus *Buchia* Rouillier, 1845

**Type species.** *Avicula mosquensis* von Buch, 1844

## ***Buchia* spp.**

2011 *Buchia* sp.—Hammer *et al.*, fig. 7i, tab. 2.

**Material examined.** 156 specimens. See Appendix 1 for the list of specimens.

**Remarks.** Species of the genus *Buchia* are considered valuable index fossils in Oxfordian to Hauterivian strata and are used for biostratigraphic subdivisions (e.g. Jeletzky 1966; Kauffman 1973; Zakharov 1981; Surlyk & Zakharov 1982). The Svalbard seep buchiids probably represent *Buchia okensis* (Pavlow, 1907), *Buchia volgensis* (Lahusen, 1888) and *Buchia* cf. *inflata* (Lahusen, 1888). A separate paper is planned to formally describe them, and their stratigraphic significance in relation to the ammonite stratigraphy of Wierzbowski *et al.* (2011).

**Palaeoecology.** *Buchia* species were epifaunal byssally attached suspension-feeders (e.g. Wignall & Pickering 1993, fig. 7), often clustering around hard structures (e.g. shells, rocks) providing a substrate for byssal attachment (Fürsich 1982). The species of the genus had a broad ecological tolerance and were present in a variety of shallow to deep marine facies (e.g. Sokolov & Bodylevsky 1931; Håkansson *et al.* 1981; Fürsich 1982; 1984; Oschmann 1988; Kelly 1984; Wignall & Pickering 1993) and are suggested to have been opportunists (Fürsich 1984; Wignall 1990).

## **Family Oxytomidae Ichikawa, 1958**

### **Genus *Oxytoma* Meek, 1864**

**Type species.** *Avicula muensteri* Bronn, 1830

### ***Oxytoma octavia* (d'Orbigny, 1850)**

(Figure 10 C–G)

1850 *Avicula Octavia* sp. nov.—d'Orbigny, p. 61.

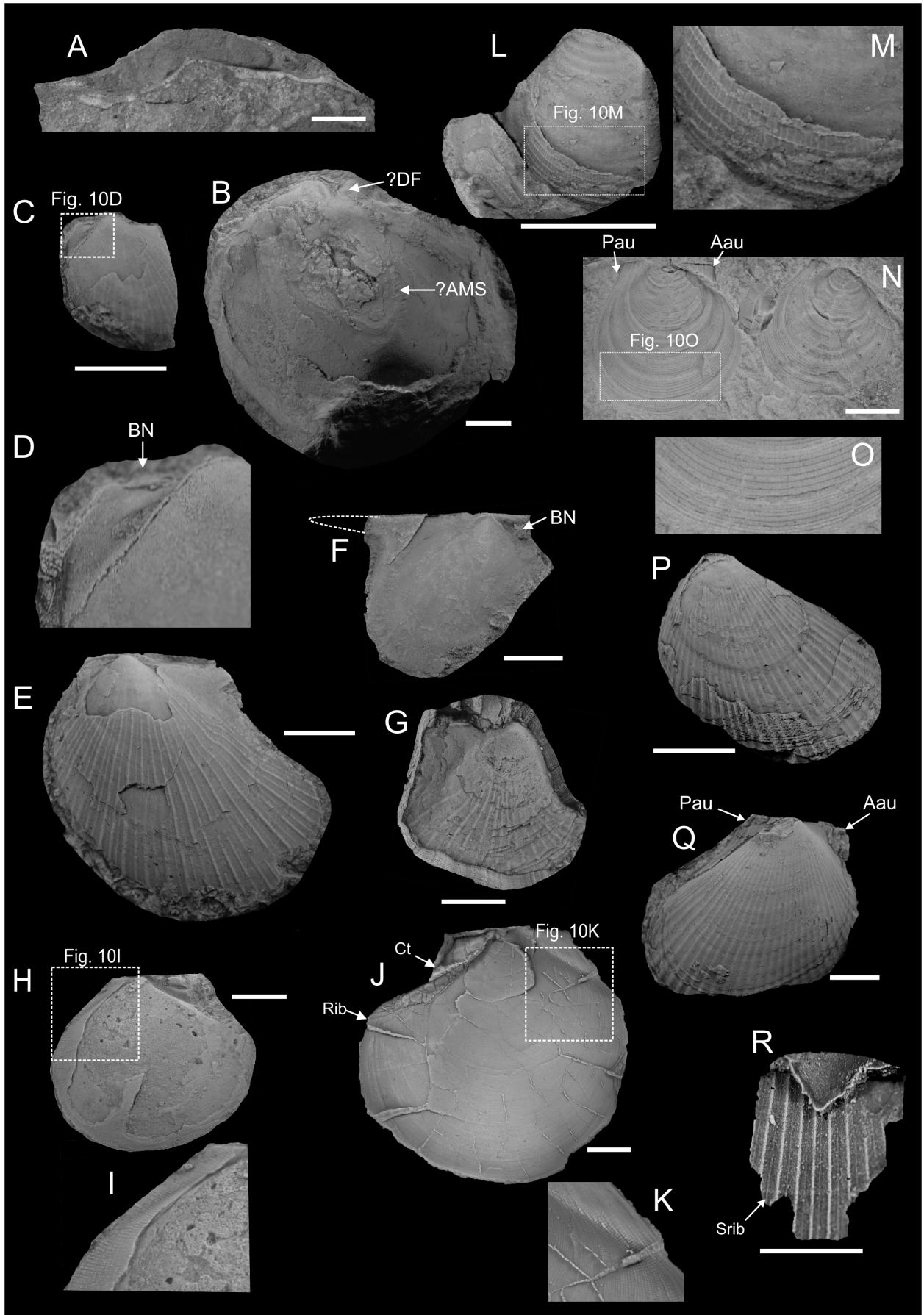
1984 *Oxytoma* (*Oxytoma*) *octavia* (d'Orbigny)—Kelly, p. 61, pl. 5, figs. 1–9 and references therein.

2011 *Oxytoma* sp.—Hammer *et al.* 2011, fig. 7q, tab. 2.

**Material.** 37 specimens, all single valves with completely or partially preserved shells. Four right valves, 33 left valves. See Appendix 1 for the list of specimens.

**Dimensions.** 7–24.5 mm in length, 7–23.5 mm in height. See Figure 11 A–C and Appendix 2F for details.

**Description.** Adult shell more than 24 mm long, inequivalved with left valve significantly larger than right. Left valve oval and weakly posteroventrally elongated; thin, inequilateral, moderately inflated, ornament of 15–20 radial primary ribs, intercalated with secondary riblets and occasionally very weak tertiary riblets. Primary radial ribs dense, but thin, on early shell growth stages, progressively thicker during ontogeny. On internal moulds ribs visible only on later growth stages. Inter-rib spaces around five times wider than primary ribs. Secondary ribs appear on shell in late growth stages, but on internal moulds are present only on ventral margins of larger specimens. Ribs occasionally show disturbances and deflections. Shell growth lines weak; no nodes present at radial ribs intersections. Beak weakly prosogyrate, hinge line straight. Posterior auricle present; in investigated specimens not projecting beyond posterior valve margin, demarcated from the rest of valve by weak, oblique sulcus. Anterior auricle absent, groove in inner shell surface below anterior part of hinge line visible on outer shell surface as an oblique, elongated ridge. Right valve thin, circular to weakly oval in outline; inequilateral, flat to weakly inflated. Radial ribs present on external shell surface, absent on internal moulds. Beak weakly prosogyrate, hinge line straight, posterior auricle moderately long, projecting beyond posterior valve margin; indistinct sulcus demarcating auricle from rest of valve. Anterior auricle straight, triangular, acute, around a fifth to a sixth of hinge line length. Triangular and moderately deep byssal notch developed below anterior auricle, with main axis slightly oblique to the hinge line. Ctenolium not observed.





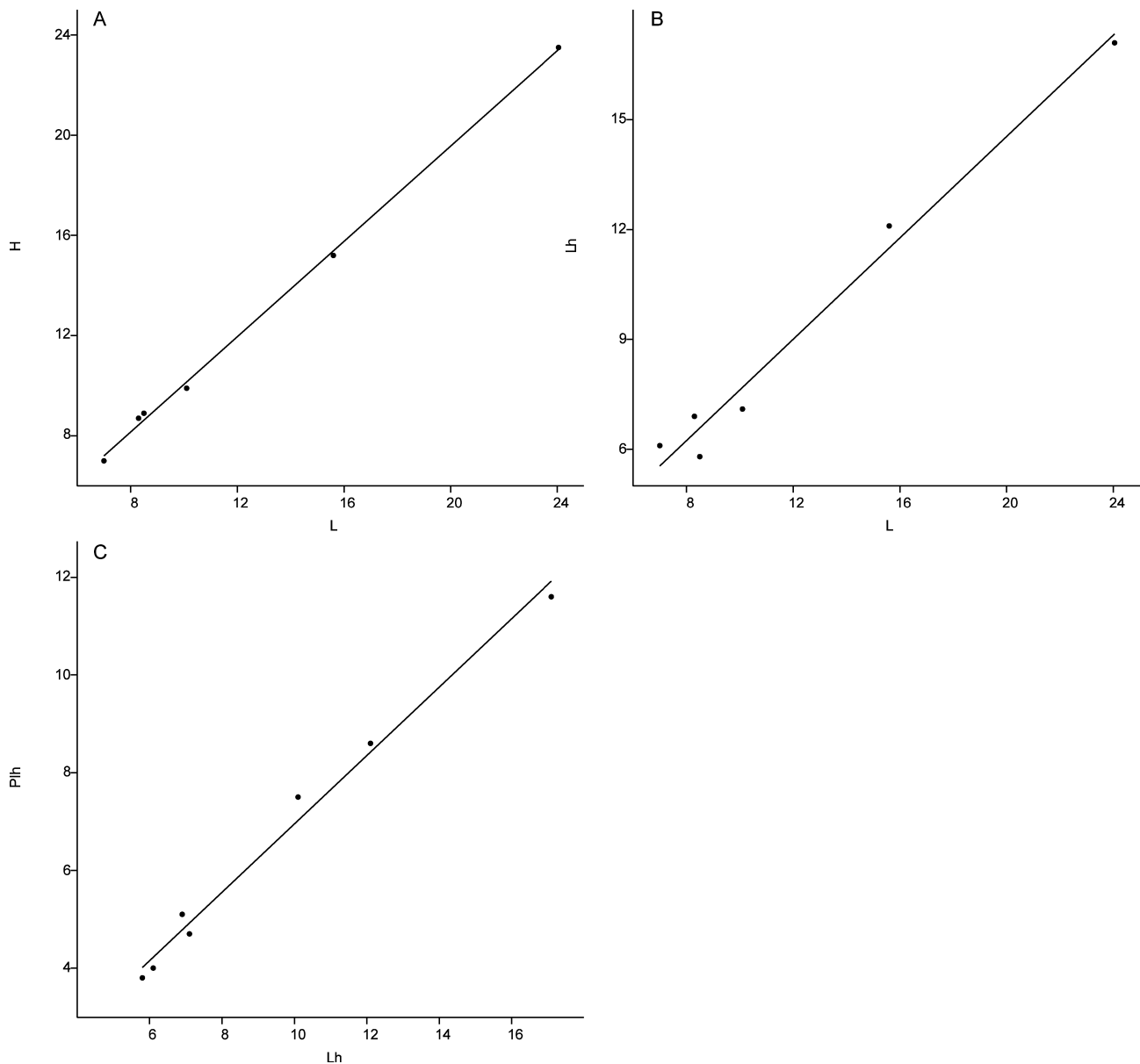
**Remarks.** Our specimens are synonymized with *Oxytoma octavia* (d’Orbigny, 1850) due to their strong secondary ribs on the right valve, which is markedly smaller than the left valve. *Oxytoma octavia* is inequivalved and characterized by having 12 to 20 primary ribs on the left valve (12 to 19 in Kelly 1984, p. 62), separated by distinct secondary and tertiary riblets (e.g. Kelly 1984, text-fig. 40). The rather similar *O. inequivalve* (J. Sowerby, 1819), widespread from the Lower Jurassic up to the Kimmeridgian (e.g. Gerasimov 1955; Ichikawa 1958; Cox 1965; Duff 1978; Wierzbowski *et al.* 1981; Pugaczewska 1986; Clausen & Wignall 1990) has a left valve with a similar number of radial ribs to *O. octavia* and with inter-rib spaces containing variably strong secondaries and tertiaries (e.g. Duff 1978, p. 55). The difference between *O. octavia* and *O. inequivalve* lies in the presence of primary and secondary ribbing on the right valve in *O. octavia* contrasting with the smooth or weakly striated right valve of *O. inequivalve* (Duff 1978; Kelly 1984). The right valves of our specimens are small and circular, which suggests an inequivalve condition, separating our species from *O. expansa* (Phillips, 1829) which is approximately equivalved (e.g. Arkell 1931, p. 191). Our specimens are much less inequilateral and have a very different style of ribbing than *O. (Boreioxytoma) aucta* Zakharov, 1966, from the Volgian of Siberia (Zakharov 1966), which has seven to nine widely spaced primary ribs (Zakharov 1966, pl. I: 6, pl. II:1).

**Occurrence.** Seeps 3, 5, 8 and 9 (Upper Volgian–uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1). Occurs in the Volgian–Ryazanian of Europe, Greenland, Russia and Siberia (de Loriol & Pellat 1867; Lewinski 1922; Spath 1936; 1947; Gerasimov 1955; Zakharov 1966; Fürsich 1982; Birkenmajer *et al.* 1982; Kelly 1984).

**Palaeoecology.** *Oxytoma octavia* was a byssally attached filter feeder. This mode of life is shared by many other pteriomorphs (Stanley 1970). The long posterior auricle likely sheltered the posterior exhalant current from being swept back into the shell by water currents, as in pteriids (Stanley 1970). Because of the relatively thin valves, *O. octavia* was more likely preserved in less agitated environments, where it was living attached to loose shells and local carbonate hardgrounds. A pseudoplanktonic mode of life and attachment to drifting algal fronds is also possible for *O. octavia*, an interpretation supported by the lack of articulated specimens in the studied material.



**FIGURE 10.** (A–B) Pectinida gen. et. sp. indet. (A) Cross section of an articulated specimen. (B) Internal mould of the upper valve. Note possible adductor muscle scar and a line close to the dorsal margin, representing a possible dorsal furrow. (C–G) *Oxytoma octavia* (d’Orbigny, 1850). (C) Lateral view of a small left valve internal mould with fragments of the shell preserved showing weak radial ornament. (D) Enlarged view of anterodorsal portion area showing weak byssal notch. (E) Lateral view of a large left valve showing well developed radial ornament composed of primary and secondary ribs. (F) Lateral view of a right valve; lack of ornament is caused by shell delamination. Note very weak posterior sulcus and flattening of the valve. Probable shape of auricle is shown with dashed line (evidence from other partial specimens). (G) Plasticine cast of right valve external mould. Note radial ornament composed of primary and secondary ribs. (H–K) *Camptonectes (Costicamptonectes)* aff. *milnelandensis* Fürsich, 1982. (H–I) Right valve internal mould with shell partially preserved showing some divaricating ornament preserved close to the posterior shell margin. (J–K) External mould of right valve of a specimen from the Dorsoplanites bed, showing radial ribs close to the anterior shell margin and divaricating ornament preserved close to the posterior shell margin. (L–O) *Camptonectes (Camptochlamys) clathratus* (Roemer, 1836). (L–M) Lateral view of poorly preserved left valve showing cancellate external ornament in ventral margin. (N–O) Lateral view of a disarticulated and compressed shell from the Dorsoplanites bed showing cancellate ornament. Note distinct anterior auricle in the right valve. (P–R) *Pseudolimea arctica* (Zakharov, 1966). (P) Lateral view of left valve internal mould with some shell preserved around the ventral margin, with V-shaped ribs on the outer shell surface and corresponding rounded ribs on the internal mould. (Q) Lateral view of right valve, with anterior and posterior auricles and lack of secondary ribs caused by shell delamination. (R) Silicone rubber cast of small area of shell surface showing detail of external ornament, with large primary ribs and smaller secondary riblets in the interrib spaces. (A) PMO 226.609, (B) PMO 226.610, (C–D) PMO 217.562, (E) PMO 217.555, (F) PMO 217.214, (G) PMO 217.570, (H–I) PMO 226.606, (J–K) PMO 226.604, (L–M) PMO 226.605, (N–O) PMO 226.603, (P) PMO 217.194, (Q) PMO 217.353, (R) PMO 217.370. Scale bars 5 mm (A–I), 10 mm (J–R).



**FIGURE 11.** Measurements of *Oxytoma octavia* (d'Orbigny, 1850) (in mm). (A) Height to length. (B) Length of hinge line to length. (C) Length of the posterior part of the hinge line to total length of the hinge line.

**Superfamily Pectinoidea Rafinesque, 1815**

**Family Pectinidae Rafinesque, 1815**

**Genus *Camptonectes* Agassiz in Meek, 1864**

**Type species.** *Pecten lens* Sowerby, 1818

**Subgenus *Costicamptonectes* Fürsich, 1982**

**Type species.** *Camptonectes (Costicamptonectes) milnelandensis* Fürsich, 1982

### ***Camptonectes (Costicamptonectes) aff. milnelandensis* Fürsich, 1982**

(Figure 10 H–K)

1982 aff. *Camptonectes (Costicamptonectes) milnelandensis* sp. nov.—Fürsich, p. 50, figs. 23 C–D, F, G.

**Material examined.** Two poorly preserved right valves. In addition a single external mould with silicone rubber cast from the Dorsoplanites bed (PMO 226.604). See Appendix 1 for the list of specimens.

**Dimensions.** 15–30.5 mm in length, 15–28.2 mm in height. See Appendix 2G for details.

**Description.** Shell small to medium sized, very thin, appears to get shorter at later growth stages. Right valve suborbicular, moderately inflated, with small posterior and larger anterior auricle, ventrally delineated by a deep byssal notch. Ctenolium well developed. Antero- and posterodorsal margins subequal, anterodorsal margin slightly concave. Anterior margin slightly more convex than posterior margin, ventral margin evenly rounded. Preserved ornament consists of weak divaricating radial ribs, intersected by weak but dense growth lines. Anterodorsal margin ornamented by ca. 6 subparallel radial ribs. Left valve, musculature and dentition unknown.

**Remarks.** We compare our specimens with *C. (Co.) milnelandensis* because of its ornament of commarginal growth lines accompanied by divaricate ribs and with additional radial ribs close to the anterodorsal margin. The Svalbard specimens have a slightly higher umbonal angle than comparatively sized specimens of *C. (Co.) milnelandensis* from Greenland (Fürsich 1982). However, no specimens larger than 18 mm were reported by Fürsich (1982) so we are unable to compare the ontogenetic changes of umbonal angle of specimens from both localities. In addition, the Svalbard material is composed of right valves only. Until more is known about *C. (Co.) milnelandensis* from both Greenland and Svalbard, we prefer to leave our species in open nomenclature.

**Occurrence.** *Camptonectes (Co.) milnelandensis*: Upper Callovian–Upper Oxfordian of Milne Land, East Greenland (Fürsich 1982). *Camptonectes (Co.) aff. milnelandensis*: Seep 8 (Upper Volgian), Slottsmøya Member (Tab. 1); also Dorsoplanites bed (Middle Volgian), Svalbard.

**Palaeoecology.** We assume that *C. (Co.) aff. milnelandensis* was a byssally attached suspension feeder, as indicated by the presence of a well-developed ctenolium. Byssal attachment is a characteristic feature for the genus *Camptonectes*, although larger species in the subgenus *McLearnia* Crickmay, 1930, probably lost a functional byssal attachment in maturity (e.g. Fürsich 1982). An expanded anterior auricle in pectinids is an adaptation for byssal attachment with the commissure non-perpendicular to the substrate (Stanley 1970). In such a position the auricle and anterior shell margin acts as a fulcrum and prevents the shell overturning from its set position. As in most of the pectinids, *C. (Co.) aff. milnelandensis* probably had the ability to swim to escape predation, although the umbonal angle is too acute to assume this was habitual (Stanley 1970).

### **Subgenus *Camptochlamys* Arkell, 1930**

**Type species.** *Pecten intertextus* Roemer, 1839

### ***Camptochlamys (Camptochlamys) clathratus* (Roemer, 1836)**

(Figure 10 L–O)

1836 *Pecten clathratus* sp. nov.—Roemer, p. 212, pl. 13, fig. 9.

1984 *Camptonectes (Camptochlamys) clathratus* (Roemer)—Johnson, p. 143, pl. 4, figs. 23, 26, 27, pl. 5, figs. 1–3, 6, text-figs. 131–136 and references therein.

1984 *Camptonectes (Camptochlamys) intertextus* (Roemer)—Kelly, p. 75, pl. 6, figs. 16–18.

**Material examined.** Two poorly preserved specimens. In addition, a single disarticulated specimen from the Dorsoplanites bed (PMO 226.603). See Appendix 1 for the list of specimens.

**Dimensions.** 15.8–23.8 mm in length, 15.8–23.2 mm in height. See Appendix 2H for details.

**Description.** Shell small to medium, thin. Both valves suborbicular, left valve moderately inflated, with anterior and posterior auricles subequal and not prominent. Umbonal angle ca. 100°; hinge line straight, umbones orthogyrate and not projecting. Curvature of right valve unknown. Anterodorsal margin straight to very weakly

convex, posterodorsal margin straight. Anterior and posterior margins subequal, with anterior margin slightly more rounded. Ventral margin evenly rounded. Ornament composed of series of dense commarginal lamellae intersected by fine primary ribs and secondary radial riblets. Intersection of radial and commarginal ornament forms a cancellate pattern. Specimen measuring 23.2 mm in height has three growth lines per millimeter. Musculature and dentition unknown.

**Remarks.** Our specimens have an external ornament and shell morphology within the range of *Camptonectes* (*Camptochlamys*) *clathratus* (Roemer, 1836). Similarly shaped and ornamented specimens have been recorded by Kelly (1984) as *C. (Cc.) intertextus* (Roemer, 1839), which is the younger synonym of *C. (Cc.) clathratus* according to Johnson (1984).

**Occurrence.** The species is known from Bajocian to Kimmeridgian of Western and Central Europe (Johnson 1984), and the Middle Volgian of Greenland (Fürsich 1982). It has been recorded previously from the Jurassic of Svalbard as *Pecten (Chlamys) pertextus* var. *densiradiatus* var. nov. by Sokolov & Bodylevsky (1931, p. 54, pl. 3, figs. 6a–b). Seep 8 (Upper Volgian), Slottsmøya Member (Tab. 1); also Dorsoplanites bed (Middle Volgian), Svalbard.

**Palaeoecology.** *Camptonectes (Camptochlamys) clathratus* was a byssally attached filter feeder (Johnson 1984) and in the Svalbard seeps it probably attached onto exposed carbonate substrates. The umbonal angle increase during ontogenesis (Johnson 1984) suggests that juveniles may have been attached to a firm substrate with a byssus, which was then lost in adults so they became recliners (e.g. Stanley 1970). In the Mid- to early Late Jurassic *C. (Cc.) clathratus* is often associated with shallow water corals, upon which juveniles were supposed to attach byssally, and oolitic facies, in which the adult forms reclined (Johnson 1984). The Svalbard specimens (Sokolov & Bodylevsky 1931; this study) represent both the youngest occurrence and the most offshore occurrence of the species, which suggests that it either had a broader ecological tolerance than previously suspected, or *C. (Cc.) clathratus* shifted its preference to more offshore environments around the latest Jurassic.

### ***Camptonectes* spp.**

2011 *Camptonectes* sp.—Hammer *et al.*, fig. 7j.

**Material examined.** 118 unnumbered specimens, all internal moulds with delaminated shells from seeps 1, 3, 4, 8 and 9. See Appendix 1 for the list of specimens.

**Remarks.** These specimens belong to the genus *Camptonectes*, but the absence of external shell characters means they cannot be identified to species level. They most likely belong to the two species discussed above, but it is possible that some represent individuals of contemporary Jurassic and Cretaceous species, including *Camptonectes (Camptonectes) auritus* (Schlotheim, 1813) and *Camptonectes (Camptochlamys) obscurus* (J. Sowerby, 1818).

## **Order Limida Waller, 1978**

### **Family Limidae Rafinesque, 1815**

#### **Genus *Pseudolimea* Arkell in Douglas & Arkell, 1932**

**Type species.** *Plagiostoma duplicata* (J. Sowerby, 1814)

#### ***Pseudolimea arctica* (Zakharov, 1966)**

(Figure 10 P–R)

1966 *Lima (Pseudolimea) arctica* sp.—Zakharov, p. 62, pl. 16, figs. 6–11.

1966 *Pseudolimea* aff. *parallela* Orbigny [sic]—Zakharov, p. 64, pl. 16, fig. 12.

1982 *Pseudolimea* cf. *arctica* (Zakharov)—Fürsich, p. 61, fig. 25 A.

**Material examined.** 18 specimens, all single valves; shells and internal moulds. See Appendix 1 for the list of specimens.

**Dimensions.** 18.1–34 mm in length, 16–31.5 mm in height. See Figure 12 A–C and Appendix 2I for details.

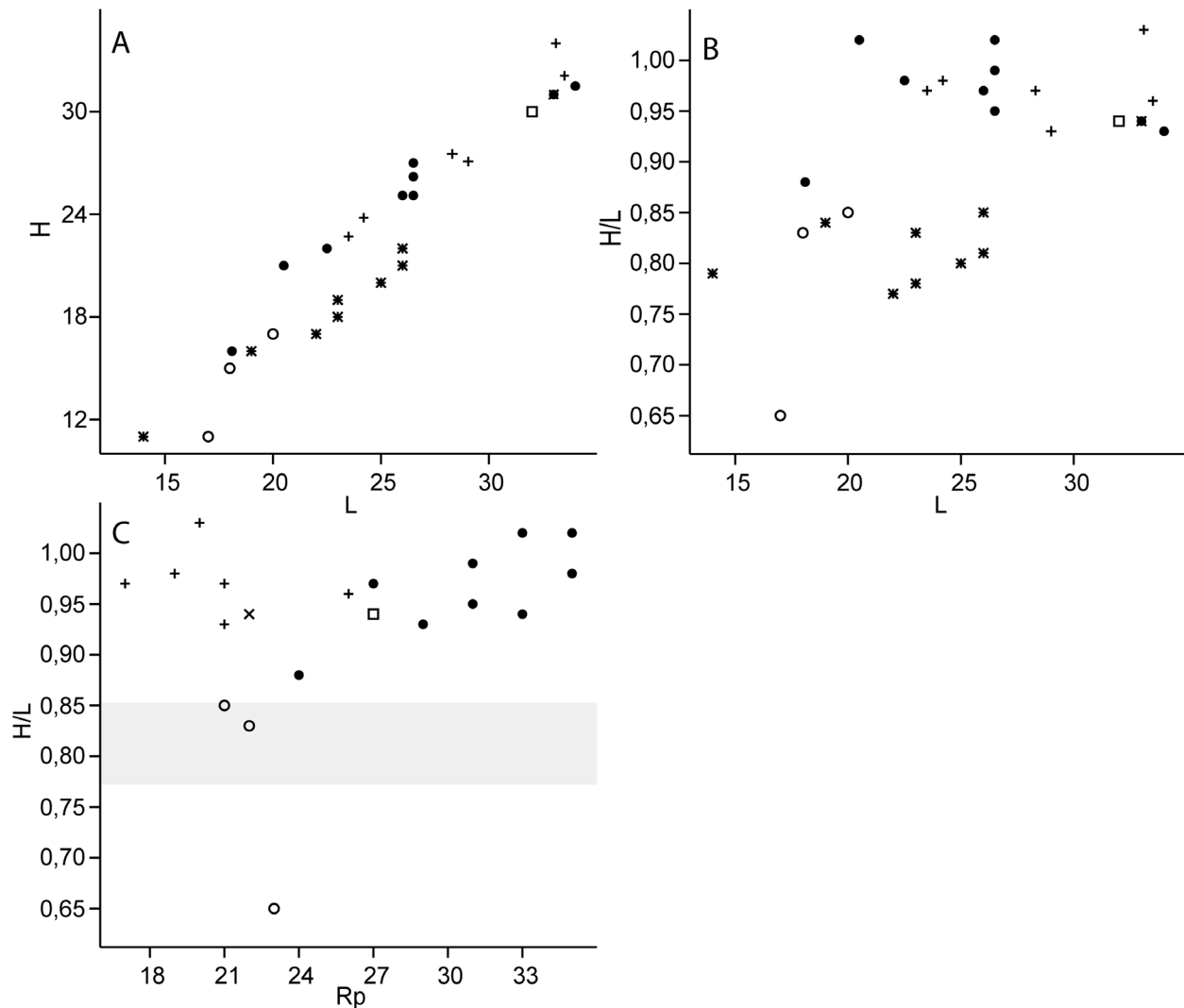
**Diagnosis.** A *Pseudolimea* with up to 35 radial, v-shaped primary ribs with weaker ribs on anterior and posterior parts of the shell. Inter-rib spaces with single smaller riblet.

**Description.** Shell small to medium, up to 34 mm long and 31.5 mm high. Shell oval, inequilateral, posteroventrally elongated, triangular, with umbonal angle around 90°. Anterodorsal margin weakly convex, passing abruptly into broadly arcuate ventral margin. Posteroventral margin tightly arcuate, passing gently into straight and long posterodorsal margin. Posterodorsal margin about twice length of anterodorsal margin. Hinge line straight, around quarter shell length, with smaller anterior and larger posterior auricles not projecting beyond shell outline. Umbo small, weakly prosogyrate beak projecting beyond hinge line. Shell ornament of 24–35 v-shaped primary ribs with intercalated weaker secondary riblets in interspaces. Radial ornament dissected by weak, commarginal growth lines visible on outer shell surface only. Internal moulds show only rounded primary ribs. Ribs start on umbo, getting progressively stronger towards ventral margin; strongest on shell mid-flank, becoming weaker close to anterior and posterior shell margins. Ribs fade and then disappear on shell anterior where ventral curvature bends up towards anterodorsal margin; on posterior margin ribs disappear where posteroventral curvature passes into straight posterodorsal shell margin. Dorsal margins and auricles ornamented by concentric growth lines only. Dentition not observed.

**Remarks.** We include this species in the Siberian Kimmeridgian–Volgian taxon *Pseudolimea arctica* (Zakharov, 1966), based on its external shell proportions and the number of ribs. Comparison of shell measurements (Fig. 12 A–C) shows that the Svalbard *Pseudolimea* specimens and *P. arctica* have an almost identical shell shape. The Svalbard specimens are more densely ribbed than *P. arctica* (Zakharov, 1966). However, more sparsely ribbed Svalbard specimens form a morphological continuity with the densely ribbed specimens of *P. arctica*, so there is no reason to separate them on rib number. Coarsely ribbed *P. arctica* specimens from Siberia overlap in rib number with *P. multicosata* Fürsich, 1982, from England, Greenland and Siberia (Tab. 10, Zakharov 1966; Fürsich 1982; Kelly 1984) and with *Lima (Mantellum) parallela* (J. Sowerby, 1812) from the Aptian–Albian of England (Woods 1904), which has no more than 23 ribs. However, both *P. multicosata* and *P. parallela* are more elongated than *P. arctica* from Siberia and Svalbard (Fig. 12 B, C). Interestingly, *Lima (Pseudolimea) aff. parallela* (J. Sowerby, 1812) *non* (d’Orbigny), from the upper Ryazanian of Siberia (Zakharov 1966) has 27 ribs and similar shell proportions to *P. arctica*, but not to *P. parallela* as shown by the data of Woods (1904), and should therefore also be included into *P. arctica*.

**Occurrence.** Seep 9 (uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1). It also occurs in the Kimmeridgian, Volgian and possibly also the Upper Ryazanian of Siberia (Zakharov 1966) and the Volgian of Greenland (Fürsich 1982).

**Palaeoecology.** *Pseudolimea arctica* probably took advantage of hard substrates present in the seeps, such as exposed carbonate and other shells, for byssal attachment. Modern limids can be found both in shallow and deep marine environments (Allen 2004). They are suspension feeders, byssally attached to rocks, shells and marine plants. They can also form ‘nests’ composed of mucus, byssal threads and various incorporated hard elements if the substrate proves unsuitable for byssal attachment (Merrill & Turner 1963). Some species possess the ability to swim by clapping their valves, and others are able to relocate using their foot and byssus (Mikkelsen & Bieler 2008). Unlike other monomyarian bivalve families, limids are not pleurothetic, i.e. they do not rest on one of the valves, but orient their commissure perpendicular to the substrate (Mikkelsen & Bieler 2008). The extinct genus *Pseudolimea* probably behaved in the same way. No association between limids and symbiotic bacteria has been recorded to date, but *Acesta oophaga* Järnegren, Schander & Young, 2007 in Järnegren *et al.* 2007, from hydrocarbon seep environments in the Gulf of Mexico has morphological adaptations for feeding on the eggs of the tubeworm *Lamellibrachia luyesi* van der Land & Nørrevang, 1975. It has a folded posterodorsal shell margin that surrounds the tubeworm plume, where eggs are being released from the tube (Järnegren *et al.* 2005). No such adaptation has been recorded in any species of *Pseudolimea*.



**FIGURE 12.** Measurements of *Pseudolimea arctica* (Zakharov, 1966) from Svalbard seep sites, and associated species from Greenland, Europe and Siberia (in mm). Full circles represent *P. arctica* from Slottsmøya Member, Svalbard, crosses represent *Lima (Pseudolimea) arctica* from Kimmeridgian of Siberia (Zakharov 1966), open square represent *P. cf. arctica* from East Greenland (Fürsich 1982), asterisks represent *Lima (Mantellum) parallela* from Aptian–Albian of England (Woods 1904), x represents *L. (P.) aff. parallela* from Upper Ryazanian of Siberia (Zakharov 1966), open circles represent *P. multicostrata* from Lower Cretaceous of eastern England (Kelly 1984). (A) Height to length. (B) Height to length (elevation) to length. (C) Height to length (elevation) to number of ribs. The grey belt represents the area presumably occupied by specimens of *L. (M.) parallela* from England (Woods 1904). The number of ribs for these specimens is not available.

## Superorder Heteroconchia Gray, 1854

### Clade Heterodonta Neumayr, 1884

### Order Lucinida Neumayr, 1884

### Family Lucinidae Fleming, 1828

### Genus *Tehamatea* Kiel, 2013

**Type species.** *Lucina ovalis* Stanton, 1895

**Remarks.** We assign our lucinid specimens to the genus *Tehamatea* Kiel, 2013, based on their external ornament

composed of commarginal growth lines only, oval external shape of the shell, reduced 3a cardinal, and the length and divergence angle of the anterior adductor muscle scar (Kiel 2013). *Tehamatea* is a Late Jurassic–Early Cretaceous seep-restricted genus known from California (Stanton 1895), the Basque-Cantabrian Basin (Agirrezabala *et al.* 2013), the Vocontian Basin and Planerskoje in Crimea (Kiel & Peckmann 2008; Kiel 2013). The similar lucinid genus *Beauvoisina* Kiel, Campbell & Gaillard, 2010, has much weaker muscle scars than the Svalbard specimens, and has a ridge developed within the lunule, a feature not seen in our material (Kiel *et al.* 2010; Kiel 2013). *Beauvoisina* also has beaks located further towards the posterior than the Svalbard specimens. Another seep-restricted lucinid genus, *Cubatea* Kiel, Campbell & Gaillard, 2010, differs from our specimens by having a much stronger anterior lateral teeth and lacking a 3b cardinal. The Late Cretaceous–Paleocene seep lucinid genus *Nymphalucina* Speden, 1970, has an external ornament composed of sparse commarginal ridges, stronger sulcation, and strong cardinal and lateral dentition (Speden 1970; Kiel 2013), all features lacking in our material. Comparable Mesozoic non-seep lucinid genera include *Jagonoma* Chavan, 1946, from the Jurassic of France (Chavan 1946; 1947; 1952), but our specimens do not belong to this genus because it has stout cardinal dentition, with thick and well-formed 3a and 3b, and an anterior adductor muscle scar that only weakly diverges from the pallial line. Another European Jurassic genus, *Discomiltha* Chavan, 1952, is on average less inflated than the Svalbard specimens, has an external ornament composed of regularly spaced, commarginal ridges and cardinal dentition of two weak denticles (e.g. Duff 1978). The Jurassic genus *Mesomiltha* Chavan, 1938, differs from our specimens with its regular commarginal ornament and more angular shape (e.g. Kelly 1992). *Discoloripes* Wellnhofer, 1964, has a similar shape to the Svalbard material, but has a much longer and club-shaped anterior adductor muscle scar (e.g. Wellnhofer 1964; Kelly 1992).

The taxonomy of Mesozoic lucinids is currently problematic, and in need of revision, because many Mesozoic and Recent species are homeomorphic and difficult to distinguish without in-depth study (e.g. Gerasimov 1955; Wellnhofer 1964; Kelly 1992). Further, many Mesozoic lucinids have been classified tentatively as “*Lucina*” (e.g. Woods 1907, p. 152–153, fig. 2–6, 10–19; Lewinski 1922, p. 78, pl. 4, fig. 4). Recent molecular phylogenetic studies show that most of the modern lucinid lineages can be traced back through the Cenozoic, but are much more difficult to recognize in the Mesozoic (Williams *et al.* 2004; Taylor *et al.* 2011).

***Tehamatea rasmusseni* sp. nov.**

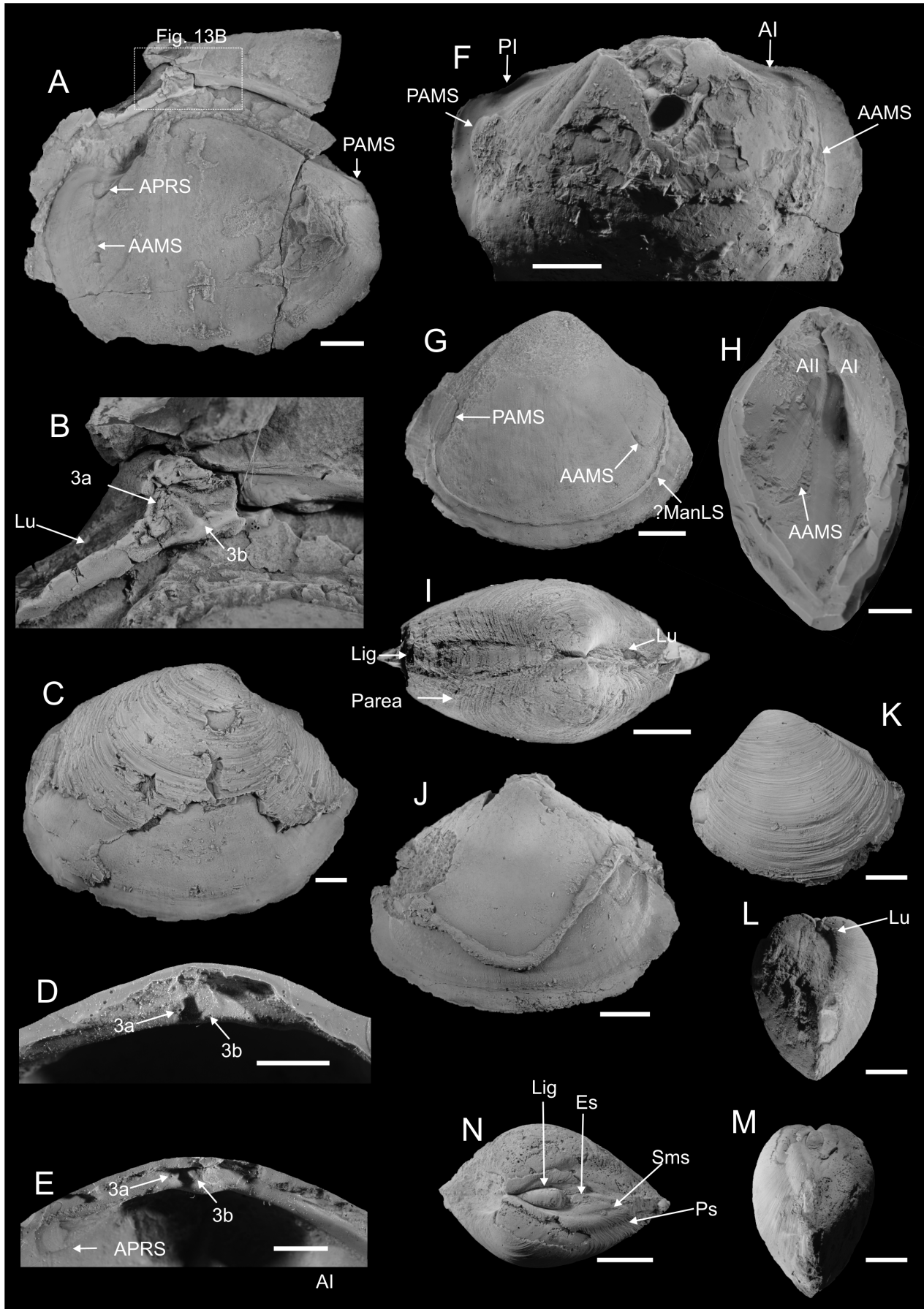
(Figure 13 A–J)

2011 Lucinid sp.—Hammer *et al.*, fig. 7d–e, tab. 2.

**Etymology.** After Jan Audun Rasmussen, curator of the Greenland collection in the Natural History Museum of Denmark, Copenhagen, study of which helped with taxonomic determinations in this paper.

**Type locality.** Seep 9, Knorringsfjellet, Spitsbergen, 78°18'49.9"N 16°10'58.9"E.

**Type material.** Holotype: PMO 217.234; a partially articulated shell the vertically displaced valves; right valve shows cardinal and anterior lateral dentition of the right valve; left valve is an internal mould, with silicone rubber cast. Paratypes: PMO 217.169; an articulated, partially preserved shell showing outline and details of external ornament. PMO 217.173; an internal mould and silicone rubber cast showing part of the right valve cardinal dentition. PMO 217.227; an articulated specimen showing the ligament and posterior sulcation. PMO 217.243; an articulated, partially preserved internal mould and silicone rubber cast showing the right valve cardinal dentition. PMO 217.247; an articulated, partially preserved internal mould showing bioimmuration trace. PMO 225.101; an internal mould with silicone rubber cast showing anterior lateral dentition. PMO 225.104; an internal mould showing anterior adductor muscle scar and posterior adductor





muscle scar and possible mantle gill scars. PMO 225.111; an internal mould with silicone rubber cast showing anterior and posterior hinge plate areas.

**Material examined.** 60 specimens, mostly articulated internal moulds, some with adhering shell, and a few single valves. See Appendix 1 for list of specimens.

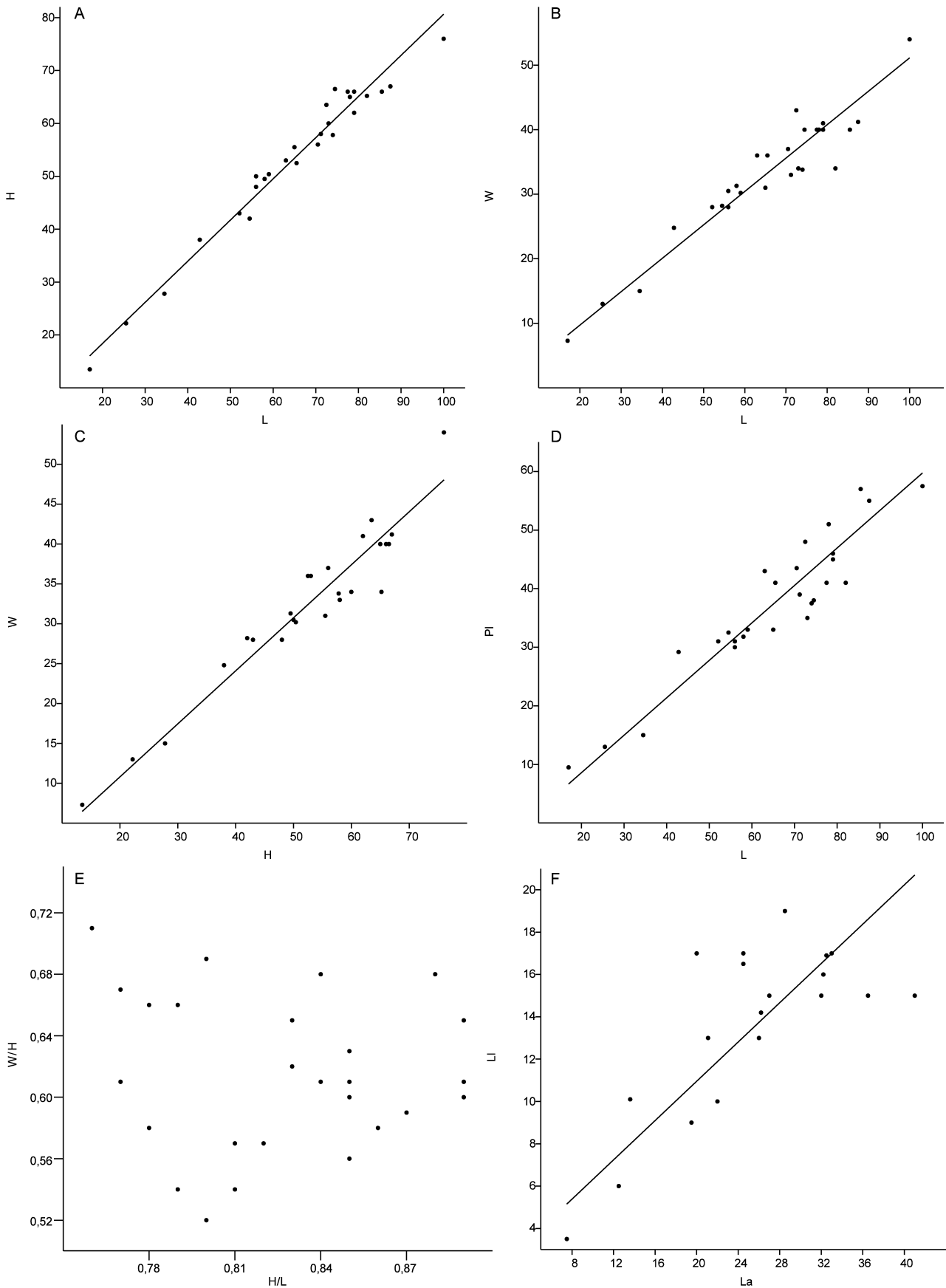
**Dimensions.** 17–100 mm in length, 13–76 mm in height, 7.3–54 mm in width. See Figure 14 A–F and Appendix 2J for details.

**Diagnosis.** Shell oval to weakly hexagonal in shape, covered with dense commarginal growth lines. Posterodorsal margin gently convex, posterior area slightly flattened. Posterior margin slightly truncated. Anterior and posterior laterals short and weak. Cardinal tooth 3a very small, 3b large, not bifid. Anterior adductor muscle scar elongated, weakly incurved. Anterior pedal retractor scar well impressed, separated from anterior adductor muscle scar. Posterior adductor muscle scar large, deeply impressed, merged with posterior pedal retractor scar.

**Description.** Shell large, up to 100 mm long, 76 mm high, and 54 mm wide. Average H/L  $\approx$  0.78, relatively constant throughout ontogeny. W/H ratio  $\approx$  0.67, also relatively constant throughout ontogeny. Shell oval to weakly hexagonal in outline, inequilateral with umbones positioned closer towards anterior; average PI/L ratio of  $\approx$  0.64. Umbones prosogyrate, not very prominent. Anterodorsal margin short and relatively straight. Lunule asymmetric, larger in left valve than in right; large, lancet-shaped and deep, occupying on average  $\approx$  0.46 of anterior shell length. Anterior margin arcuate, with dorsally tightening curvature. Ventral margin broadly rounded, smoothly passing into moderately tight posteroventral margin. Posterior margin inclined, truncated, posterodorsal margin long, weakly and evenly convex; some specimens develop weakly flattened posterior area. Ligament opisthodeltic, external, long. Hinge plate thick. AI short, thick but not prominent, positioned at anterior end of hinge plate. PI short, with socket corresponding to right valve anterior lateral tooth. Posterior laterals weak. PII unknown, presumably shallow. PIII very weak and short, oval. Cardinal dentition present. Right valve: 3a very small, opisthocline; 3b prosocline, strong, not bifid, weakly curved; at base 3b supported by a thickening of hinge plate. Left valve: 2 triangular, deepest at base, becoming weaker dorsally; 4b arcuate, prosocline. Anterior adductor muscle scar deep, striated and detached from pallial line around two thirds to three quarters of length. Ventral margin of anterior adductor muscle scar sharp, dorsal margin irregular and jagged. Anterior pedal retractor scar circular, positioned below anterior lateral teeth, weakly separated from anterior adductor muscle scar. Deep groove connecting anterior adductor muscle scar with umbonal cavity represents trace of descent during growth. Posterior adductor muscle scar deep, striated, pointed ventrally, heart-shaped, projecting beyond the pallial line for about half of diameter. Trace of descending posterior adductor muscle visible as deep grooves connecting it with umbonal cavity. Posterior pedal retractor scar not seen, presumably merged with posterior adductor muscle scar. Pallial line strong, entire; wavy below anterior adductor muscle scar. Some specimens develop dispersed pustules on internal shell surface.



**FIGURE 13.** (A–J) *Tehamatea rasmussenii* sp. nov. (A) Lateral view of holotype showing the vertical valve displacement. (B) Detail for interior of right valve showing cardinal dentition. Note long lunule, small 3a and long 3b. (C) Lateral view of exterior of right valve showing oval outline and ornament of dense commarginal growth lines. (D–E) Silicone rubber casts of right valve cardinal areas showing small 3a and large, thick 3b cardinal teeth. (F) Oblique lateral view of a right valve internal mould showing small anterior and posterior lateral teeth. (G) Lateral view right valve internal mould showing shapes and relative sizes of anterior and posterior adductor muscle scars and wavy pallial line below anterior adductor muscle scar, representing possible mantle lobe scars. (H) Silicone rubber cast of an articulated internal mould showing anterior adductor muscle scar and anterior lateral teeth. (I) Dorsal view of an articulated shell showing long external ligament, flattened posterior shell area and deep, lancet-shape, slightly asymmetric lunule. (J) Lateral view of a right valve internal mould showing bioimmuration trace. (K–N) *Cretaxinus hurumi* gen. et sp. nov. (K) Lateral view of articulated holotype left valve showing shell outline. Note very weakly sulcated posterodorsal margin extending only slightly above the shell outline. (L) Holotype anterior view showing large and deep lunule. (M–N) Holotype posterior and dorsal views respectively, showing external portion of the ligament, escutcheon and posterodorsal margin sulcation. (A–B) PMO 217.234, (C) PMO 217.169, (D) PMO 217.173, (E) PMO 217.243, (F) PMO 225.111, (G) PMO 225.104, (H) PMO 225.101, (I) PMO 217.227, (J) PMO 217.247, (K–N) PMO 217.277. Scale bars 10 mm.



**FIGURE 14.** Measurements of *Tehamatea rasmusseni* sp. nov. (in mm). (A) Height to length. (B) Width to length. (C) Width to height. (D) Posterior length to length. (E) Width to height (inflation) to height to length (elevation). (F) Length of the lunule to length.

**Remarks.** *Tehamatea rasmusseni* **sp. nov.** differs from *T. ovalis* (Stanton, 1895), from Tithonian to Albian seeps from California by the smaller size of the 3a anterior cardinal in the former (Stanton 1895; Kiel 2013). Otherwise, the two species are very similar. *Tehamatea rasmusseni* differs from another Californian seep lucinid, the Tithonian–Hauterivian *T. colusaensis* (Stanton, 1895), by the more rounded posterior margin and more equilaterally positioned beaks in *T. rasmusseni*. *Tehamatea rasmusseni* has similar dentition to *T. agirrezabalai* Kiel, 2013, from Albian seeps of northern Spain, but in comparison with that species *T. rasmusseni* has a longer and more detached anterior adductor muscle scar and less projecting beaks. *Tehamatea vocontiana* from Hauterivian seep carbonates of southern France (Lemoine *et al.* 1982) and Crimea (Kiel & Peckmann 2008) has a cardinal dentition with only an orthocline 3b developed, unlike *T. rasmusseni*, which has both 3a and 3b developed, with the 3b weakly curved and prosocline.

**Occurrence.** Seep 9 (uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1). Known only from the type locality.

**Palaeoecology.** The seep-restricted distribution of the genus *Tehamatea* (Kiel 2013), together with the clustering of *T. rasmusseni* at seep 9 and the presumed antiquity of chemosymbiosis among lucinids (Taylor & Glover 2010) strongly suggests that *T. rasmusseni* was chemosymbiotic and took advantage from the reduced compounds available in the seep environment. Lucinids are a diverse group of burrowing bivalves having obligate chemosymbiotic relationships with sulfide-oxidizing bacteria (e.g. Dando *et al.* 1986; Reid & Brand 1986; Herry *et al.* 1989; Taylor & Glover 2000; Glover *et al.* 2004). They inhabit a variety of environments, being especially diverse in tropical and temperate shallow water environments with high redox potential, like seagrass beds (Mikkelsen & Bieler 2008), mangrove swamps (Frenkiel *et al.* 1996), coral sands (Glover & Taylor 1997), reducing sediments (Dando *et al.* 1986) and sewage outfalls (Herry *et al.* 1989). Lucinids are also common at hydrocarbon seeps, from both shallow and deep water (e.g. Salas & Woodside 2002; Holmes *et al.* 2005; Taylor & Glover 2009; Oliver *et al.* 2011). An increasing number of modern lucinid genera are being reported from deep water sites, and have been recovered from organic-rich sediments in water as deep as 2570 m (Cosel 2006).

To reach sulfide-rich pore waters necessary to feed their symbionts, most lucinids burrow down to the oxic/dysoxic interface, where they remain stationary with their umbones facing upwards. Their muscular foot is then used to construct ventral tunnels to supply sulfide-rich water to the symbionts in the gills (Taylor & Glover 2010). Oxygenated seawater is supplied via a subvertical mucus-lined tube entering the body parallel to the anterior adductor muscle (Stanley 1970). The elongated and detached anterior adductor muscle acts as a partition separating symbiont-bearing gills from the respiratory surface of the mantle around the anterior opening (Taylor & Glover 2000).

Similar anatomical features as shown by internal shell features are found in the lucinid fossil record back to the Silurian (Boyd & Newell 1979; Fürsich 1982; Kelly 1992; Liljedahl 1992). The wavy pallial line below the anterior adductor muscle scar suggests that *T. rasmusseni* developed mantle lobes with possible respiratory function (e.g. Taylor & Glover 2000). One specimen shows traces in both valves of tubular structures that represent either shell boring activity or an organism living between the mantle and the shell (bioimmuration traces). Very similar structures have been found in other fossil seep bivalves (Kiel & Peckmann 2008; Jenkins *et al.* 2013), and have been attributed to possible polychaete worms. All specimens found are articulated or semi-articulated shells filled with carbonate micrite and were enclosed in a matrix composed of cracked and worn *Buchia* shells with some rare and disarticulated *Pseudolimea arctica*, *Oxytoma octavia* and *Camptonectes* spp. As Svalbard seeps developed in low-depositional rate environment and seabed omission was frequently the case (Hryniewicz *et al.* 2012), *Tehamatea rasmusseni* must have been a relatively deep burrower. After death, specimens remained buried for some time and were not exposed by the bottom currents until early carbonate cementation in the seep environment kept the valves in an articulated state.

## Family Thyasiridae Dall, 1901

### Genus *Cretaxinus* gen. nov.

**Type species.** *Cretaxinus hurumi* **sp. nov.**

**Etymology.** Refers to the Cretaceous occurrence of the type species, and to the genus *Axinus*.

**Diagnosis.** Shell inequilateral, triangular in outline, thin. Ornament of commarginal growth lines. Beaks

weakly prosogyrate, not very prominent. Cardinal area edentulous, with small ligament groove. No lateral teeth. Lunule long and deep. Posterior sulcus shallow, posterior fold not very prominent. Submarginal sulcus shallow; no auricle. Ligament short, thick, external, with possible small internal portion. Anterior adductor muscle scar elongated, very weak; size difficult to estimate, but relatively small. Posterior adductor muscle scar larger than anterior one, circular, well impressed. Pallial line entire.

**Remarks.** Comparison of *Cretaxinus* **gen. nov.** with other large, chemosymbiotic thyasirids (Dufour 2005) suggest it can be clearly differentiated from all of them (Tab. 2). The most noticeable feature is its subtriangular shape, which is very distinct from the shapes of the genera *Axinus* J. Sowerby, 1821, *Thyasira* Lamarck, 1818, *Parathyasira* Iredale, 1930, and *Conchocele* Gabb, 1866 (Tab. 2). Another feature distinguishing *Cretaxinus* from other thyasirids is its short, thick and external ligament set in a deep escutcheon, accompanied by a possible small internal portion. A similar feature is seen only in *Axinus*. However, *Axinus* has a totally different shape, sulci, adductor muscle proportions and external ornament (Tab. 2). The ligament of *Cretaxinus* is very distinct from that of *Thyasira*, *Parathyasira* and *Conchocele*, all of which have variably long, sunken ligaments (Tab. 2). Another major difference between *Cretaxinus* and *Axinus*, *Thyasira*, *Parathyasira* and *Conchocele* is the proportions of adductor muscle scars. In *Cretaxinus* the anterior adductor muscle scar is small and weak, and the posterior adductor muscle scar is large and well impressed; in the other genera the proportions of the muscle scars are reversed. The sulci are less distinct and somehow anteroposteriorly flattened in comparison to the sulci of the other discussed genera. The escutcheon is wider and deeper than that of *Thyasira* and *Parathyasira*.

**TABLE 2.** The main characters distinguishing *Cretaxinus* **gen. nov.** from other large chemosymbiotic thyasirid genera.

Genus	<i>Cretaxinus</i> <b>gen. nov.</b>	<i>Axinus</i> J. Sowerby, 1821	<i>Thyasira</i> Lamarck, 1818	<i>Parathyasira</i> Iredale, 1930	<i>Conchocele</i> Gabb, 1866
Shape	Subtriangular	Subhexangular	Ovate to ovate-polygonal	Ovate to ovate diamond-shaped	Subquadrangular
Ornament	Commarginal growth lines	Commarginal wavy ridges	Commarginal growth lines	Commarginal growth lines	Commarginal growth lines
Ligament	Thick and external with small internal part	Partially external	Variably sunken, short to medium	Sunken, short to medium	Thick, sunken and long
Character of posterodorsal margin	Ps, (sms), no auricle, wide and deep escutcheon	Ps, no auricle, small escutcheon	Ps, sms, auricle, variable escutcheon	Ps, no auricle, ill-defined escutcheon	Ps, (sms), no auricle, no escutcheon
Adductor muscle scars	AAMS smaller and weaker than PAMS	AAMS $\approx$ PAMS	AAMS larger than PAMS	AAMS larger than PAMS	AAMS much larger than PAMS
Reference	This study	Payne & Allen 1991; Löffler <i>et al.</i> 2006; Oliver & Holmes 2007	Payne & Allen 1991; Oliver & Killeen 2002; Oliver & Holmes 2006; Rodrigues <i>et al.</i> 2008; Zelaya 2009	Iredale 1930; Payne & Allen 1991; Oliver & Killeen 2002; Zelaya 2009	Kamenev <i>et al.</i> 2001; Okutani 2002

Knowledge of small thyasirid species is far less complete than of their large relatives (Payne & Allen 1991; Oliver & Killeen 2002) and therefore their direct comparison with *Cretaxinus* **gen. nov.** is more problematic. *Mendicula* Iredale, 1924, has a very small, oval shell (<3 mm in length) with a pointed posterior margin (Payne & Allen 1991; Oliver & Killeen 2002), unlike *Cretaxinus* **gen. nov.** Both sulci of *Mendicula* are shallow and the ligament is entirely internal (Zelaya 2010), also unlike in *Cretaxinus* **gen. nov.**, which has weak sulci but largely external ligament. *Adontorhina* Berry, 1947, apart from small, oval shells with an internal ligament, differs from *Cretaxinus* by characteristic granules on the hinge plate of the former (Scott 1986; Barry & McCormick 2007). *Axinulus* Verrill & Bush, 1898, has a small oval shell which is higher than long (Payne & Allen 1991) and a largely internal ligament, also unlike *Cretaxinus* **gen. nov.**

The current lack of taxonomically robust characters in the shells of the Thyasiridae leads to problems of generic separation within the family (e.g. Payne & Allen 1991; Oliver & Killeen 2002; Oliver & Sellanes 2005; Oliver & Holmes 2006; Rodrigues *et al.* 2008). Molecular data suggest that current thyasirid generic definitions

might be inadequate and additional morphological studies may result in redefinition of the genera (Taylor *et al.* 2007). Further, the same data show only a weak separation between larger, chemosymbiotic thyasirids and small (<10 mm) thyasirid genera without symbionts, like *Mendicula* Iredale, 1924, *Leptaxinus* Verrill & Bush, 1898, *Adontorhina* Berry, 1947, and *Axinulus* Verrill & Bush, 1898 (Dufour 2005).

***Cretaxinus hurumi* sp. nov.**

(Figures 13 K–N, 15, 16 A–G)

2011 *Thyasira* sp.—Hammer *et al.*, fig. 7a–c, tab. 2.

**Etymology.** After Jørn H. Hurum, leader of 2004–2012 Svalbard expeditions of the Natural History Museum, University of Oslo.

**Type locality.** Seep 9, Knorringfjellet, Spitsbergen, 78°18'49.9"N 16°10'58.9"E.

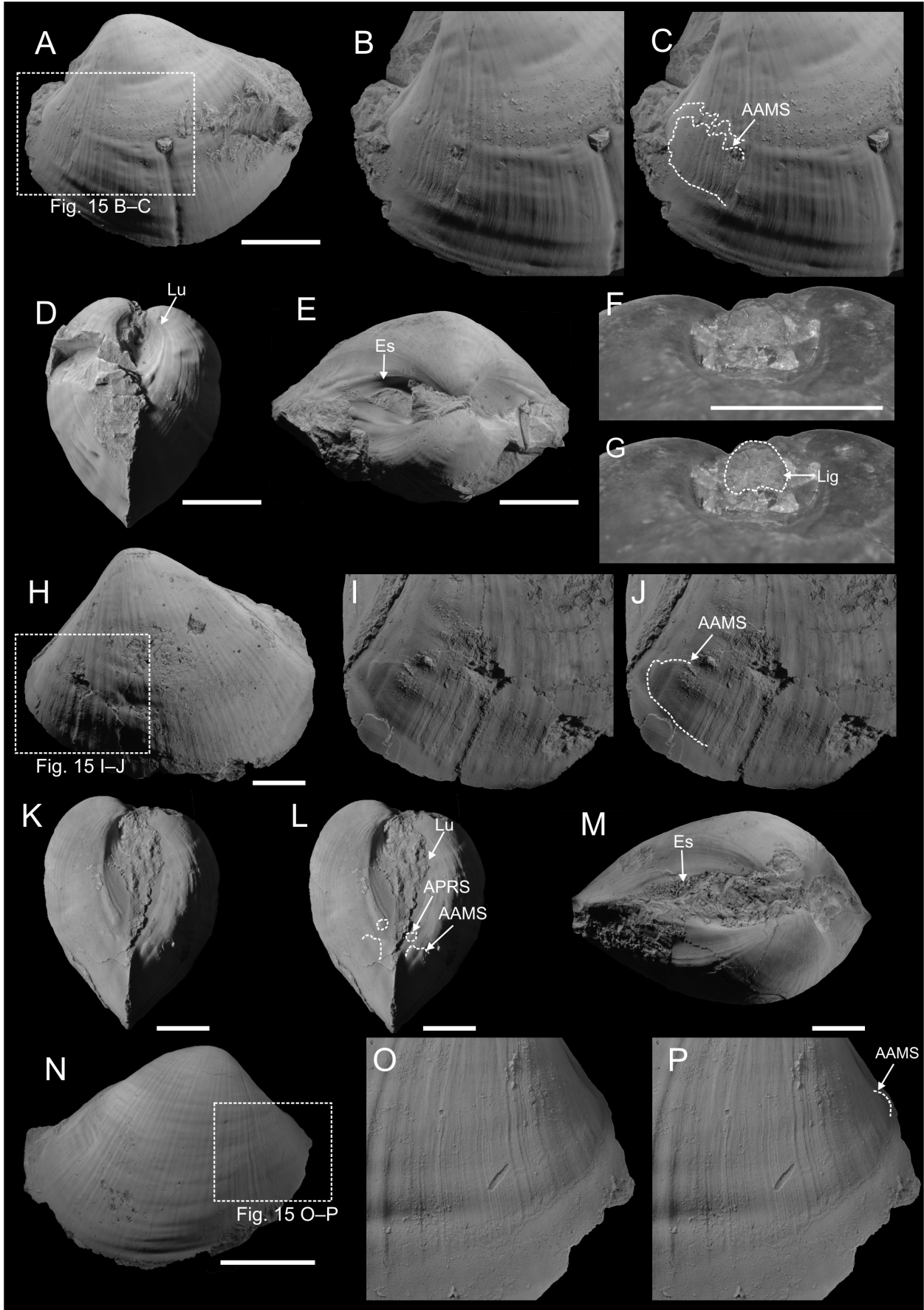
**Type material.** Holotype: PMO 217.277; an internal mould with shell partially preserved, showing a triangular outline, external ornament, a sulcated posterior margin and a thick, short, external ligament. Paratypes: PMO 217.172; an almost complete internal mould showing outline and anterior adductor muscle scar. PMO 217.175; a fragment of an internal mould and silicone rubber cast showing posterior adductor muscle scar and posterior pedal retractor. The silicone rubber cast shows the cardinal area with an elongated resilifer. PMO 217.540; complete internal mould showing the triangular outline, well impressed rounded posterior adductor muscle scar and deep escutcheon. PMO 225.128; an almost complete internal mould showing anterior adductor muscle scar and cross-section through the external ligament and ligament nymphs. PMO 225.136; an internal mould showing very weak anterior adductor muscle scar.

**Material examined.** 56 specimens, all articulated or semi-articulated internal moulds with variable amounts of shell preserved. See Appendix 1 for list of specimens.

**Dimensions.** 23–56.5 mm in length, 12.6–50 mm in height, 19–39 mm in width. See Figure 17 A–D and Appendix 2K for details.

**Diagnosis.** As for the genus.

**Description.** Shell large, subtriangular in outline, up to 56.5 mm long, 50 mm high, and 39 mm wide. Average H/L ratio  $\approx 0.85$ , W/L  $\approx 0.75$ , and W/H  $\approx 0.88$ . Shell less than 0.5 mm thick, covered with commarginal growth lines. Umbonal angle usually larger among smaller specimens, which have concave anterodorsal and posterodorsal margins. Beaks incurved, prosogyrate, not prominent, positioned closer towards the anterior, with average PI/L  $\approx 0.67$ . Umbonal angle slightly acute. Lunule large, deep, heart-shaped. Anterior margin tightly rounded, more angular in larger specimens. Ventral margin curved, with curvature deepest close to mid-line in smaller specimens, progressively displaced towards posterior during growth. Curvature shows some intraspecific variation, from deep and prominent, to shallow and gentle. Posterior extremity weakly pointed, posterodorsal margin sloping, with very weak sulcus. Smaller specimens usually have slightly concave posterodorsal margin, which is more straight in larger specimens. Escutcheon large and deep. Ligament external, thick, short, occupying 1/3 of escutcheon. Hinge plate narrow. Cardinal area with single, elongate groove, probably representing a ligament groove. Lateral dentition not observed. Anterior adductor muscle scar very weak and small, elongated along pallial line, with straight ventral margin and irregular dorsal margin; well impressed in anterior part, fading towards posterior so length of anterior adductor muscle scar cannot be fully ascertained. Anterior pedal retractor scar small and weak, circular, separated from the anterior adductor muscle scar by narrow margin, visible in one specimen only. Posterior adductor muscle scar larger than anterior adductor muscle scar, circular, deeply impressed, displaced towards hinge plate. Posterior pedal retractor small, circular, approximately same size as anterior pedal retractor scar; positioned close to hinge plate and separated from posterior adductor muscle scar by narrow distance. Pallial line entire, weak, marked by pallial muscle scars in some specimens. Internal shell surface covered with fine radial ornament, probably representing traces of descending pallial muscles.



**Remarks.** *Cretaxinus hurumi* **gen. et sp. nov.** is the oldest thyasirid species known to date. The slightly younger Valanginian to Hauterivian thyasirid is *Lucina? rouyana* d'Orbigny, 1844, from the shelf deposits of Europe and possible seep sites of Grodziszczce beds in the Carpathians (Ascher 1906, p. 164, pl. XIV, fig. 9a–c; Kiel *et al.* 2008a; Kaim *et al.* 2013), which has more of a typical *Thyasira* shape. The Albian *Lucina? sculpta* Phillips, 1829, from Southern England (Woods 1907, p. 153, pl. 24, fig. 7–9) has a very distinct shape reminiscent of the genus *Axinus* Sowerby, 1821 (Taylor *et al.* 2007). *Thyasira tanabei* Kiel, Amano & Jenkins, 2008(a) is known from Albian to Campanian hydrocarbon seeps of Hokkaido, Japan. *Thyasira tanabei* has a large anterior adductor muscle scar, unlike *C. hurumi*, but the lack of information about the ligament of *T. tanabei* makes more detailed comparison difficult. *Thyasira* sp. from the Cenomanian Kanajirasawa seep of Hokkaido (Kiel *et al.* 2008a) is known from a single, partially preserved specimen only and, therefore, is also difficult to compare to *C. hurumi*. Various Campanian thyasirid species from the Western Interior Seaway (Kauffman 1967) differ in shape from *C. hurumi*, having flattened posterior areas, narrow escutcheons, deeper sulci and more ovate shapes, reminiscent of Recent *Thyasira* species.

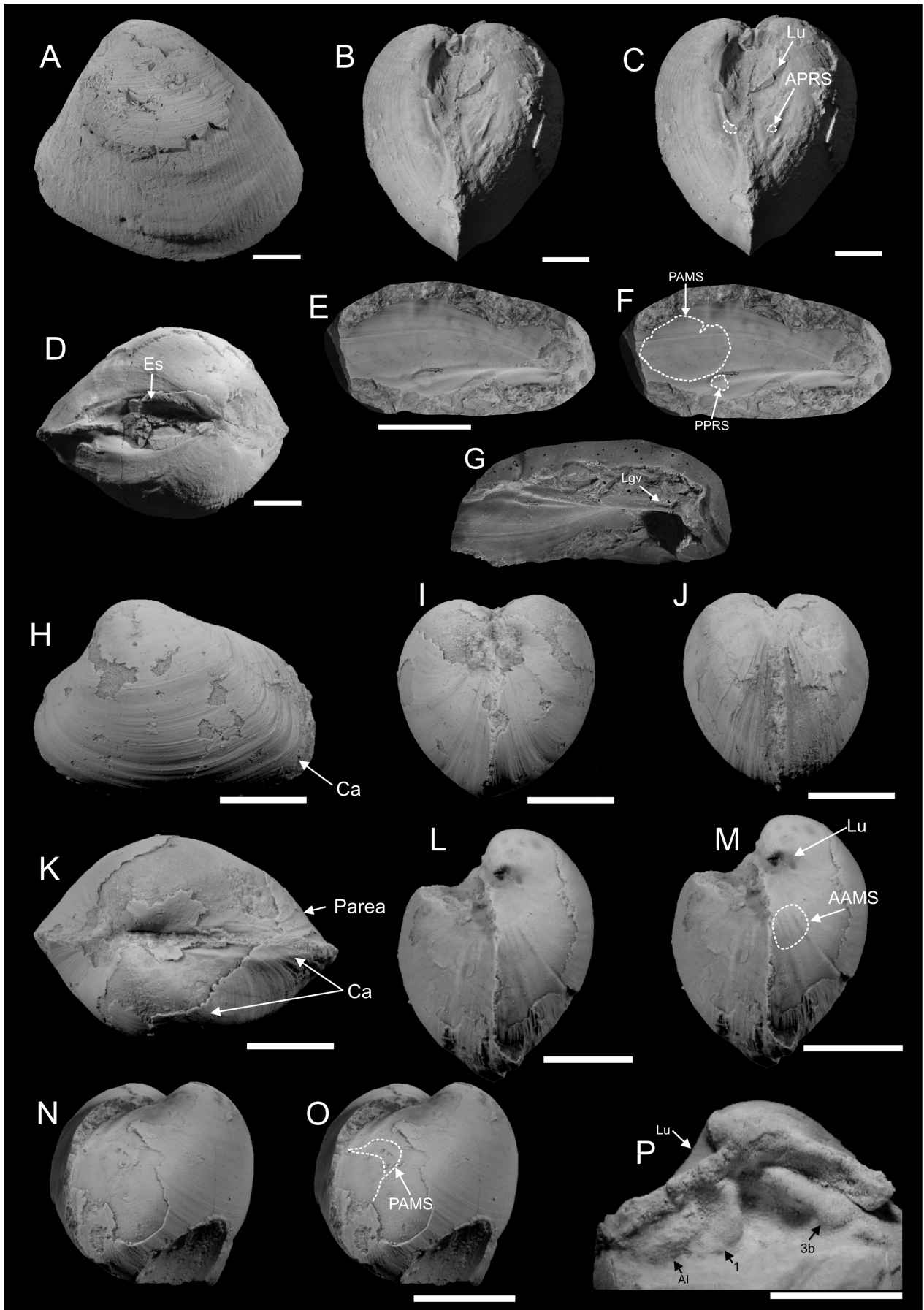
**Occurrence.** Seep 9 (uppermost Ryazanian), Slotsmøya Member, Svalbard (Tab. 1). Known only from the type locality.

**Palaeoecology.** We infer that *Cretaxinus hurumi* was a chemosymbiotic and possibly seep-restricted Mesozoic thyasirid. This is supported by the large shell size of *C. hurumi*. Among modern thyasirids chemosymbiosis is present mainly in species with two gill demibranchs (Dufour 2005) and these usually have large shells, up to around 10 mm for the genera *Axinus*, *Thyasira* and *Parathyasira*, but can reach up to 110 mm in *Conchocele* (e.g. Payne & Allen 1991; Kamenev *et al.* 2001; Oliver & Killeen 2002). Large shells provide enough space in the mantle cavity for large symbiont-bearing gills (Taylor & Glover 2010). In contrast, thyasirids with a single gill demibranch are usually asymbiotic (Dufour 2005; Taylor & Glover 2010). These asymbiotic species are much smaller, with sizes of only a few millimeters (Payne & Allen 1991; Oliver & Levin 2006). *Cretaxinus hurumi* shells are up to 56.5 mm long, and this is very large for the family, which strongly suggests the species had hypertrophied gills suitable for symbiosis with chemoautotrophic bacteria. Smaller chemosymbiotic thyasirids ( $\approx$  10 mm in length) are known from seep environments (e.g. Dando *et al.* 2004), but also occur in non-seep settings with high redox potential, such as organic-rich sediments in fjords (Dando & Spiro 1993), pulpmill effluents (Dando & Southward 1986) and in the vicinity of offshore hydrocarbon production sites (Oliver & Killeen 2002). However, the only Recent thyasirid genus which attains sizes comparable to *C. hurumi* is *Conchocele*, and this is closely associated with seeps (Kamenev *et al.* 2001; Okutani 2002; cf. Weaver 1942; Coan *et al.* 2000). Another line of evidence indicating that *C. hurumi* was both chemosymbiotic and seep-restricted comes from absence of the species in contemporary 'normal' marine sediments on Svalbard (e.g. Sokolov & Bodylevsky 1931; Weir 1933; Birkenmajer *et al.* 1982), despite being relatively abundant in the hydrocarbon seeps (Hammer *et al.* 2011).

Thyasirids are burrowers (e.g. Dando & Southward 1986; Oliver & Killeen 2002). Chemosymbiotic species dig into fine grained sediment to a depth a few times the length of the shell (Pearson 1972). In these burrows they use a vermiform foot to construct a three dimensional network of downward directed tunnels reaching up to 30 times the length of the shell, which serve as conduits for sulfide-rich pore waters from deeper interstitial levels (Dando & Southward 1986; Zuschin *et al.* 2001; Oliver & Killeen 2002; Dando *et al.* 2004; Taylor & Glover 2010). However, they are usually unable to tolerate high sulfide concentrations.



**FIGURE 15.** *Cretaxinus hurumi* **gen. et sp. nov.** (A) Lateral view of left valve of articulated internal mould, showing broadly rounded ventral margin. (B–C) Detail of anterior margin showing weak and descending anterior adductor muscle scar fading posteriorly and its serrated dorsal margin. (D) Anterior view showing shape and size of lunule. (E) Dorsal view showing shape of the posterodorsal margin and escutcheon. (F–G) Cross-section through a ligament showing its thickness. (H) Lateral view of left valve of articulated internal mould with less rounded margin than specimen shown in (A). (I–J) Detail of a anterior margin showing weak anterior adductor muscle scar fading posteriorly. (K–L) Anterior view showing shape and size of the lunule, anterior adductor and pedal retractor muscle scars. (M) Dorsal view showing shape of the posterodorsal margin and escutcheon. (N) Lateral view of right valve internal mould. (O–P) Detail of anterior margin showing very weak anterior adductor muscle scar visible only at its anteriormost portion. (A–G) PMO 225.128, (H–M) PMO 217.172, (N–P) PMO 225.136. Scale bars 10 mm.





Chemosymbiotic thyasirids are also capable of feeding on photosynthetic organic matter if conditions for chemosynthesis become unfavourable (Dando & Spiro 1993). *Cretaxinus hurumi* was probably a relatively deep burrower, based on similar lines of evidence to the lucinid *Tehamatea rasmusseni*.

## Order Venerida Gray, 1854

### Family Arcticidae Newton, 1891

#### Genus *Pseudotrapezium* Fischer, 1887

**Type species.** *Cypricardia bathonica* Morris & Lycett, 1853

#### *Pseudotrapezium* aff. *groenlandicum* Spath, 1936

(Figure 16 H–P)

1936 aff. *Pseudotrapezium groenlandicum* sp. nov.—Spath, p. 125, pl. 49, fig. 7a–c.

? 1982 aff. *Hartwellia* (*Hartwellia*) *groenlandica* (Spath)—Fürsich, p. 89.

2011 Arcticid—Hammer *et al.*, fig. 7m, tab. 2.

**Material examined.** 820 specimens, mostly articulated or semi-articulated shells and internal moulds. See Appendix 1 for list of specimens.

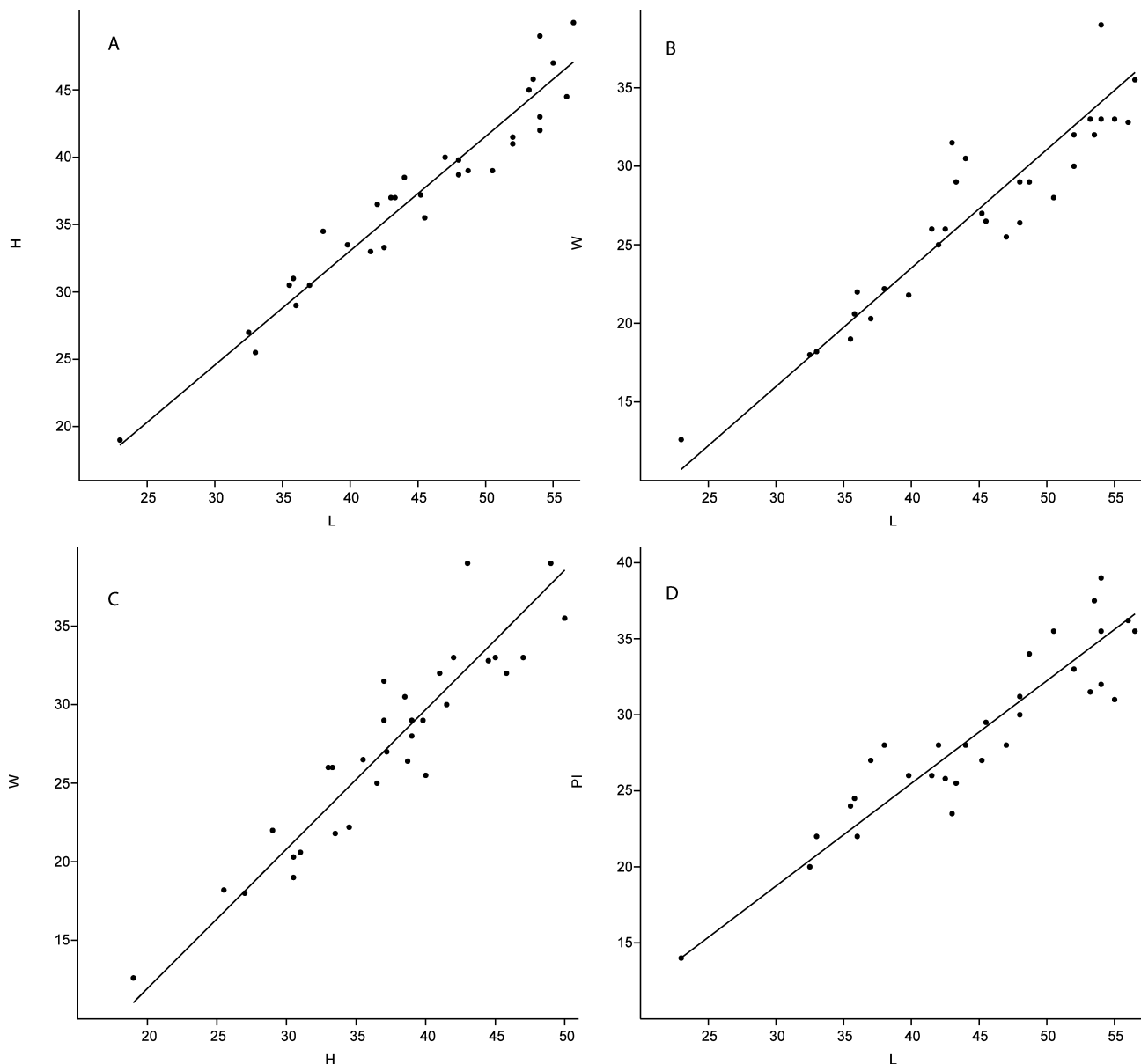
**Dimensions.** 12–15 mm in length, 9.8–11 mm in height, 8–10 mm in width. See Figure 18 A–D and Appendix 2L for details.

**Description.** Small, moderately inflated with very thin shell. Beaks prosogyrate, very strongly incurved. Lunule moderately deep. Anterior margin projecting, arcuate, passing into broadly arched ventral margin. Posterior area with two carinae, posteroventral extremity slightly rostrate where intersected by first carina, passing into truncated oblique posterior margin. Second carina weak, parallel to the posterodorsal margin. Posterodorsal margin straight. External ornament composed of very weak commarginal growth lines. Hinge plate large and thick; lateral tooth AI developed, separated from 1; 3a absent. 1 and 3b separated, diverging from umbo; 1 strong and vertical; 3b thick, anterodorsally inclined. Angle between 1 and 3b *ca.* 70°. Left valve dentition unknown. Anterior adductor muscle scar weak, elongated along pallial line, around twice as long as wide, not detached. Posterior adductor muscle scar weak, rounded. Pallial line weak, entire.

**Remarks.** We compare our specimens with *Pseudotrapezium groenlandicum* Spath, 1936, from Milne Land, East Greenland (Spath 1936) due to their thick hinge plate, similar cardinal dentition and external shape. However, the Svalbard specimens are much smaller and more thin shelled than the Greenland material, so we are not entirely sure they represent the same species and leave them in open nomenclature. Fürsich (1982) moved *P. groenlandicum* into the genus *Hartwellia* Kitchin, 1926, and redescribed it as *Hartwellia* (*H.*) *groenlandica*. *Hartwellia* was considered by Cox (1944) to be a synonym of *Pronoella* Fischer, 1887. Including *P. groenlandicum* into *Pronoella* is not justified by the hinge of our Svalbard specimens. Both *Pronoella* and *Pseudotrapezium* have relatively thick hinge plates and a similar external shape (e.g. Casey 1952), but AI and 1 are connected in *Pronoella* into a single elongate denticle and separated in *Pseudotrapezium* (Benecke 1905), showing the genera are not the same.



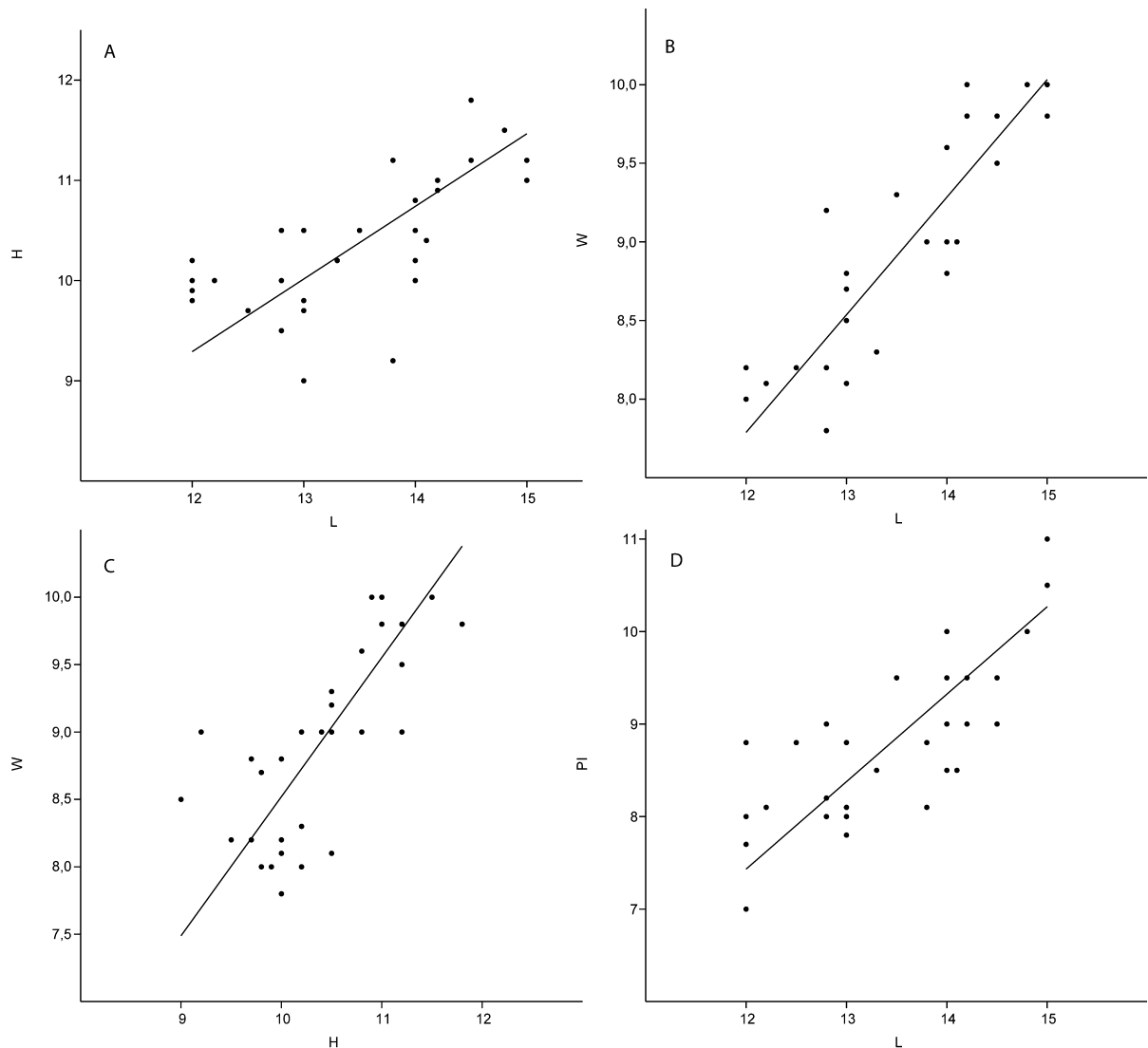
**FIGURE 16.** (A–G) *Cretaxinus hurumi* **gen. et sp. nov.** (A) Lateral view of left valve of articulated internal mould, showing a distinct, triangular shape. (B–C) Anterior views showing shape and size of lunule and anterior pedal retractor scar. (D) Dorsal view showing shape of the posterodorsal margin. (E–F) Cardinal and posterodorsal portion of left valve internal mould shell showing posterior adductor muscle scar with distinct notch on anteroventral margin and posterior pedal retractor scar. (G) Silicone rubber cast of (E–F) showing small and elongated groove, possibly ligament groove. (H–P) *Pseudotrapezium* aff. *groenlandicum* (Spath, 1936). (H) Lateral view of the shell showing the outline and carina. (I–J) Anterior and posterior views of articulated specimen with most of the shell preserved. (K) Dorsal view showing flattened posterior area, two carinae and very thin shell. (L–M) Anterior view of articulated specimen with some preserved shell, showing deep and small lunule and rounded anterior adductor muscle scar. (N–O) Oblique posterior view showing weak pallial line and weakly impressed posterior adductor muscle scar. (P) Right valve dentition and large hinge plate. (A–D) PMO 217.540, (E–G) PMO 217.175, (H–K) PMO 226.632, (L–M) PMO 226.633, (N–O) PMO 226.635, (P) JUE no. 15926. Scale bars 10 mm (A–G), 5 mm (H–P).



**FIGURE 17.** Measurements of *Cretaxinus hurumi* **gen. et sp. nov.** (in mm). (A) Height to length. (B) Width to length. (C) Width to height. (D) Posterior length to length.

**Occurrence.** *Pseudotrachezium groenlandicum*: Lower Volgian–Lower Ryazanian of Milne Land, East Greenland (Spath 1936; Fürsich 1982). *Pseudotrachezium* aff. *groenlandicum*: seeps 2, 3, 5, 8, 9 and 12 (Upper Volgian–uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1).

**Palaeoecology.** We assume that *P.* aff. *groenlandicum* was a burrower, feeding on organic-rich sediment layer while resting in the shallow subsurface. The lack of a pallial sinus suggests that *P.* aff. *groenlandicum* possessed very short siphons, similar to its extant relative *Arctica islandica* (Linnaeus, 1767). *Arctica islandica* has very short siphons and positions its posterior extremity at the sediment-water interface for feeding on organic matter from the sediment surface (Morton 2011). As it does so it remains relatively motionless, circulating water only by means of ciliary movement (Brand & Taylor 1974). It can rebury itself into deeper sediment layers, where it remains isolated from seawater for up to seven days when it is not feeding, and respire anaerobically (Taylor 1976). The clustering of very large numbers of *P.* aff. *groenlandicum* specimens in seep 9 is difficult to explain. No association between arcticids and chemosymbiotic bacteria has been noted to date, so we do not envisage any specific trophic link between *P.* aff. *groenlandicum* and the seep environment.



**FIGURE 18.** Measurements of *Pseudotrapezium* aff. *groenlandicum* Spath, 1936 (in mm). (A) Height to length, (B) Width to length, (C) Width to height, (D) Length of the posterior to total length.

### Subclass Anomalodesmata Dall, 1889

### Order Pholadomyoidea Newell, 1965

### Family Pholadomyidae Gray, 1847

### Genus *Goniomya* Agassiz, 1842

**Type species.** *Mya angulifera* J. Sowerby, 1819. Subsequent designation Herrmannsen, 1846.

### *Goniomya literata* (J. Sowerby, 1819)

(Figure 19 A–B)

1819 *Mya? literata*—J. Sowerby, p. 45, pl. 224, fig. 1.

1931 *Goniomya arctica* nov. sp.—Sokolov & Bodylevsky, p. 76, pl. 4, fig. 8.

1934 *Goniomya literata* (J. Sowerby)—Arkell, p. 344, pl. 47, figs. 1–7 and references therein.

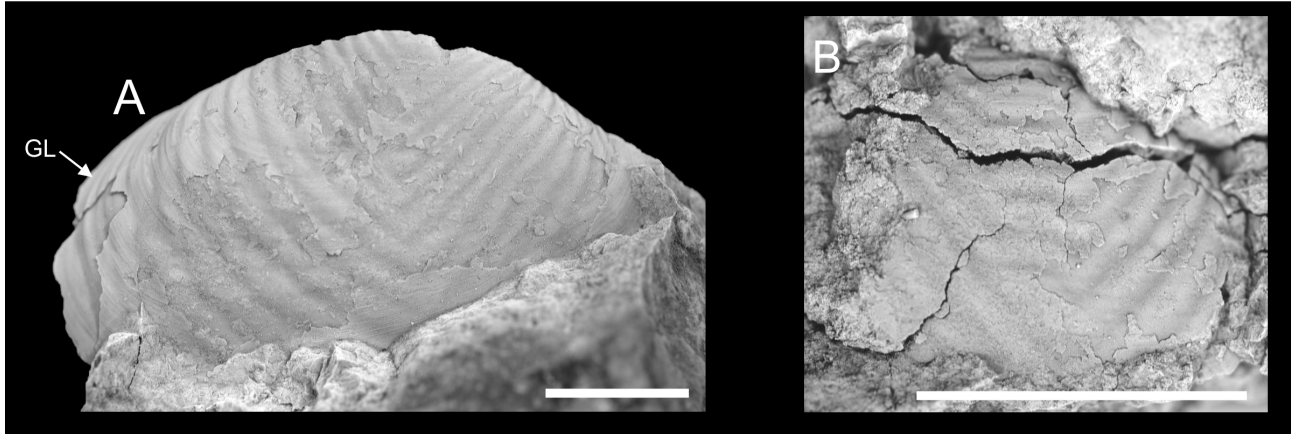
? 1982 *Goniomya* cf. *dubois* Agassiz—Birkenmajer *et al.*, pl. 43, fig. 5.

1982 *Goniomya literata* (Sowerby)—Fürsich, p. 98, figs. 35e, 36 c–d.

1985 *Goniomya literata* (Sowerby)—Bäckström & Nagy, p. 35, pl. 5, figs. 1–2 and references therein.

2011 *Goniomya* sp.—Hammer *et al.*, tab. 2.

**Material examined.** Three internal moulds with small pieces of shell. See Appendix 1 for list of specimens.



**FIGURE 19.** *Goniomya literata* (Sowerby, 1819). (A–B) Lateral views of partial right valves. (A) PMO 217.193, (B) PMO 217.358. Scale bars 10 mm.

**Description.** Shell small to medium, elongated, outline ovoid; no carina. Umbonal area positioned submedially. Umbones not preserved. Ornament of up to 13 ventrally directed chevrons, with ridges and depressions between them roughly equal in size. Chevron ridges gently rounded with both ventral and dorsal slopes inclined at an equal angle. At younger growth stages tips of chevrons often blunt so whole ornament is trapezoidal or w-shaped. Line transecting tips of chevrons slightly inclined towards shell posterior. Angle between chevron limbs between 85 and 95 degrees. Chevron ornament transected by weak, concentric growth lines. Pallial line unknown.

**Remarks.** The oval shape of our specimens with almost equilaterally positioned beaks puts them into *Goniomya literata* (J. Sowerby, 1819) (e.g. Arkell 1934; Fürsich 1982). The Svalbard specimens differs from *G. bicarinata* Fürsich, 1982, from Greenland, which has a much longer posterior and two distinct carinae running from the umbo towards the anteroventral and posteroventral margins, respectively.

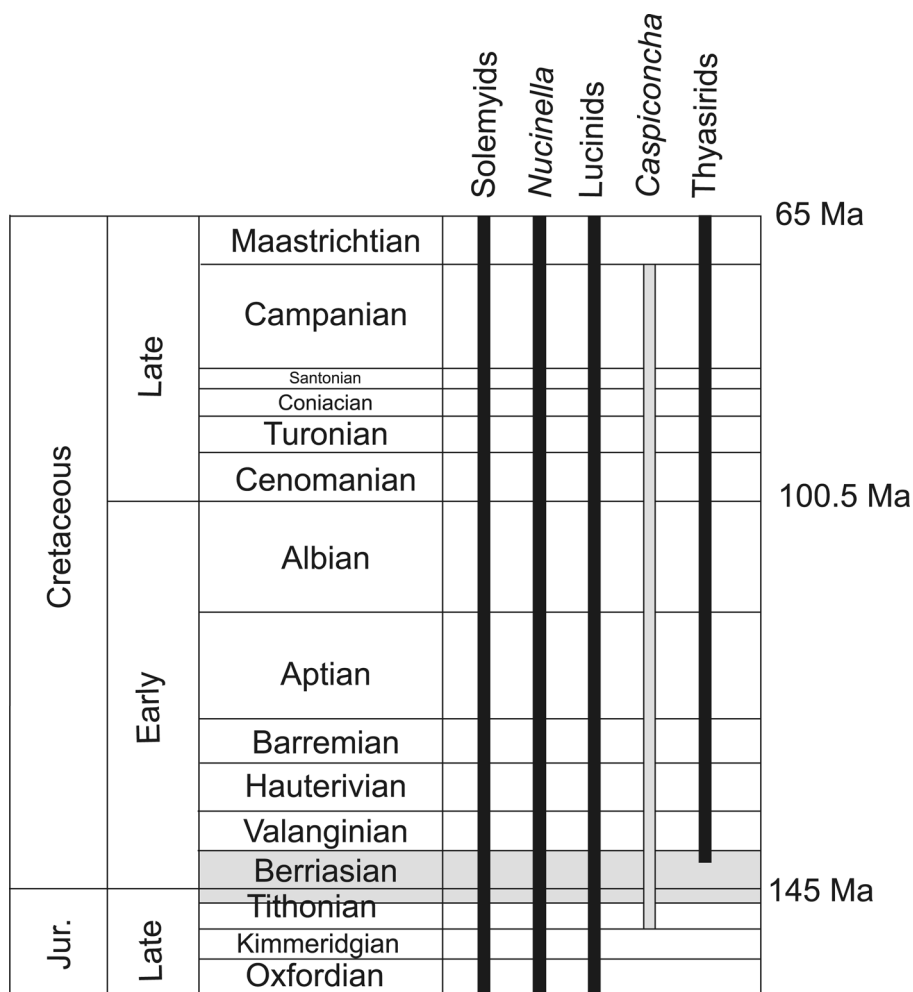
**Occurrence.** Seeps 3 and 9 (Upper Volgian–uppermost Ryazanian), Slottsmøya Member, Svalbard (Tab. 1). *Goniomya literata* is relatively wide-spread (Hallam 1976) and is known from the Middle Jurassic of England (e.g. Arkell 1934), Lithuania (Krenkel 1915), Spitsbergen (Bäckström & Nagy 1985) and the Upper Jurassic of England (Arkell 1934; Clausen & Wignall 1990), Greenland (e.g. Fürsich 1982) and Spitsbergen (Sokolov & Bodylevsky 1931). The genus *Goniomya* had much wider distribution and is common in many Jurassic fine-grained rocks (e.g. Trautschold 1865; Gerasimov 1955; Koshelkina 1962; Zakharov & Mesezhnikov 1974; Pugaczewska 1986).

**Palaeoecology.** We assume that *G. literata* was a deep-burrowing suspension feeder, by comparison with its extant relative *Pholadomya candida* J. de C. Sowerby, 1823 (Morton 1980). This species is a sluggish deep burrower, which remains stationary in the sediment with its siphons protruding towards the surface. The oblique shell ornament of *Goniomya*, comprising symmetrical ribs, is present among a variety of Late Palaeozoic and Mesozoic bivalves and was probably a shell reinforcement (e.g. Checa & Jiménez-Jiménez 2003).

## Discussion

Only two of the bivalve species in the Svalbard latest Jurassic–earliest Cretaceous hydrocarbon seep deposits, *Tehamatea rasmusseni* sp. nov. and *Cretaxinus hurumi* gen. et sp. nov., are restricted to seep environments (Kiel 2013). All of the other species found within the seeps are represented at species or generic level in Jurassic–Early Cretaceous normal-marine sediments on Svalbard (Sokolov & Bodylevsky 1931) or elsewhere in the Boreal Realm (Gerasimov 1955; Zakharov 1966; Duff 1978; Kelly 1984; Clausen & Wignall 1990). These include the likely

chemosymbiotic species *Solemya (Petrasma) cf. woodwardiana* Leckenby, 1859, and *Nucinella svalbardensis* **sp. nov.**, both of which we interpret as not being seep obligates, as they belong to genera which occur commonly in non-seep shelf settings with high redox potential (e.g. Kamenev 2009; McLeod *et al.* 2010). The large diversity of ‘background’ species, including some ‘background’ chemosymbiotic species, is a typical feature of shallow water seeps (e.g. Sahling *et al.* 2003; Dando 2010; Kiel 2010). In this respect, the composition of Svalbard bivalve seep fauna is most similar to that from the Cenomanian–Maastrichtian Tepee Buttes seeps of the Mid-Continent Seaway, USA (Howe 1987; Kauffman *et al.* 1996; Metz 2010; Kiel *et al.* 2012), which contain a diverse and abundant background fauna, but no seep-restricted bivalves. This palaeoecological similarity is not surprising as the Svalbard seeps were located in fairly shallow setting on the middle to outer shelf, as were the Tepee Buttes which formed in less than 100 m of water (Kauffman *et al.* 1996).



**FIGURE 20.** Distribution of seep-affiliated bivalve genera and families in Late Jurassic and Cretaceous hydrocarbon seeps. The gray band represents range of Svalbard hydrocarbon seeps. Black vertical column represents ranges of genus or families present in Svalbard hydrocarbon seeps, grey vertical column represents range of a genus absent in Svalbard hydrocarbon seeps. Ranges compiled from Amano *et al.* (2013), Jenkins *et al.* (2013), Kiel (2010, 2013), Kiel *et al.* (2008a, b, 2010), Peckmann *et al.* (2001) and Taylor & Glover (2010). Epoch boundaries after Ogg & Hinnov (2012).

In addition to having a large number of ‘background’ taxa the Svalbard seep bivalve assemblage differs from those of coeval Late Jurassic–Early Cretaceous seep faunas in lacking the widespread, seep-restricted modiomorphid bivalve *Caspiconcha*, which occurs in many Tithonian to Campanian sites (Jenkins *et al.* 2013). This is perhaps surprising, because the type locality of the genus comes from the only slightly younger (Barremian), palaeogeographically nearby Kuhnpasset seeps on East Greenland (Kelly *et al.* 2000). Therefore, we suppose that the absence of *Caspiconcha* from the Svalbard seeps was not a palaeobiogeographic phenomenon, an interpretation supported by the presence in the Svalbard seep fauna of other seep-restricted bivalve genera with broad distributions, i.e. *Tehamatea* (Stanton 1895; Kiel & Peckmann 2008; Agirrezabala *et al.* 2013; Kiel 2013). If

not because of palaeobiogeography, then the absence of *Caspiconcha* in the Svalbard seeps might have been down to palaeobathymetry, as seep-restricted species are mostly found in deep-water sites (Kiel 2010). However, the Kuhnpasset seeps formed on the middle to outer shelf, like the Svalbard seeps, so the reasons for the absence of *Caspiconcha* in the latter are currently opaque, and may have had more local, ecological explanations.

The Svalbard seep bivalve fauna shares several common seep-related taxa with other Late Jurassic–Early Cretaceous seep sites, including solemyids, *Nucinella* and (as noted above) lucinids. Members of this family are known at seeps from the Oxfordian and are fairly common in seeps later on, often having a seep-restricted distribution, i.e. *Tehamatea*, which ranges from the Tithonian to the Albian in seeps world-wide (Kiel *et al.* 2010; Kiel 2013). Solemyids have been recorded in Carboniferous seeps, although they are not well enough preserved to confirm this identification (Peckmann *et al.* 2001). In the Mesozoic solemyids occur in seeps from the Tithonian (Kiel *et al.* 2008b) and were then common members of later Mesozoic seep communities, occurring in the Svalbard seeps (this study), Tithonian–Albian seeps of California (Kiel *et al.* 2008b; Kaim *et al.* in press), the Barremian Kuhnpasset seeps (Kelly *et al.* 2000), and the Albian–Campanian seeps of Hokkaido (Kiel *et al.* 2008a) and New Zealand (Kiel *et al.* 2013). *Nucinella* is known from seeps since the Triassic (Peckmann *et al.* 2011). Apart from Svalbard it then occurred in Barremian seeps of California (Kaim *et al.* in press), in Albian–Cenomanian seep sites from New Zealand (Kiel *et al.* 2013) and Cenomanian–Campanian seeps from Hokkaido (Amano *et al.* 2007; Kiel *et al.* 2008a). It does appear at seeps later on in the Oligocene as well (Amano *et al.* 2013). The latest Jurassic–earliest Cretaceous Svalbard seeps contain thyasirids, represented by *Cretaxinus hurumi*. Early Cretaceous seep thyasirids are rare, but have been reported i.e. from Valanginian–Hauterivian seeps from Carpathians (Ascher 1906; Kaim *et al.* 2013) and from Albian seeps from Japan and New Zealand (Kiel *et al.* 2010; 2013). Thyasirids are fairly common in Late Cretaceous and Cenozoic seeps (e.g. Goedert *et al.* 2003, Kiel *et al.* 2008a). The latest Jurassic–earliest Cretaceous bivalve seep fauna of Svalbard thus contains usual members of the Late Mesozoic seep faunas. These comprise either background solemyids and *Nucinella*, established at seeps since no later than Palaeozoic or the Early Mesozoic, respectively, or lucinids and thyasirids, radiating into seeps at least in the Late Jurassic and earliest Cretaceous, respectively (Fig. 20).

## Acknowledgments

We would like to thank all the members of the Svalbard Jurassic Research Group (SJRG), who participated in the field work between 2007 to 2012. Special thanks go to Jørn Harald Hurum, Natural History Museum, University of Oslo, the leader of the Svalbard expeditions, for allowing us to participate in the field work. Thanks also to Øyvind Hammer, Natural History Museum, University of Oslo, for explaining how to use the PAST software; Franz-Josef Lindemann, the Natural History Museum, University of Oslo, for discussions regarding open nomenclature; Kazutaka Amano, University of Joetsu, Japan, for preparing and photographing the hinge of the arcticid bivalve; and Steffen Kiel, Georg-August-Universität Göttingen, Germany, for discussions about Mesozoic seep lucinid characters. Krzysztof Hryniewicz would also like to thank Jon Todd, Natural History Museum, London, and Jan Audun Rasmussen, Natural History Museum of Denmark, Copenhagen, for help during museum visits. Special thanks go to Robert G. Jenkins, Kanazawa University, Japan, Steffen Kiel, and Nikolaus Malchus, Institut Català de Paleontologia, Bellaterra, Spain, for careful revision and comments on the manuscript.

## References

- Adams, A. (1860) On some new genera and species of Mollusca from Japan. *Annals and Magazine of Natural History*, Series 3, 5, 299–303.
- Adams, H. & Adams, A. (1858) *The genera of recent Mollusca arranged according to their organization* (2). J. Van Voorst, London, 661 pp., 138 pls.
- Agassiz, J.L.R. (1839) Mémoire sur les moules des mollusques vivants et fossiles. In: *Mémoires de la Société des Sciences Naturelles*, (2). Imprimerie de Petitpiere, Neuchâtel, 48 pp., 9 pls.
- Agassiz, L. (1842) *Études critiques sur les mollusques fossiles*. 2. *Monographie des Myes*. Imprimerie de Petitpiere, Neuchâtel, 141 pp., 48 pls.
- Agirrezabala, L.M., Kiel, S., Blumenberg, M., Schäfer, N. & Reitner, J. (2013) Outcrop analogues of pockmarks and associated methane-seep carbonates: A case study from the Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western

- Pyrenees. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 390, 94–115.  
<http://dx.doi.org/10.1016/j.palaeo.2012.11.020>
- Aitken, S.A., Collom, C.J., Henderson, C.M. & Johnston, P.A. (2002) Stratigraphy, paleoecology, and origin of Lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco, Africa. *Bulletin of Canadian Petroleum Geology*, 50, 217–243.  
<http://dx.doi.org/10.2113/50.2.217>
- Allen, J.A. (1993) A new deep-water hydrothermal species of *Nuculana* (Bivalvia: Protobranchia) from the Guaymas Basin. *Malacologia*, 35, 141–151.
- Allen, J.A. (2004) The Recent species of the genera *Limatula* and *Limea* (Bivalvia, Limacea) present in the Atlantic, with particular reference to those in deep water. *Journal of Natural History*, 38, 2591–2593.  
<http://dx.doi.org/10.1080/00222930310001647442>
- Allen, J.A. & Sanders, H.L. (1969) *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. *Malacologia*, 7, 381–396.
- Amano, K. & Ando, H. (2011) Giant fossil *Acharax* (Bivalvia: Solemyidae) from the Miocene of Japan. *The Nautilus*, 125, 207–212.
- Amano, K., Jenkins, R.G. & Hikida, Y. (2007) A new gigantic *Nucinella* (Bivalvia: Solemyoidea) from the Cretaceous cold-seep deposit in Hokkaido, Northern Japan. *The Veliger*, 49, 84–90.
- Amano, K., Jenkins, R.G., Sako, Y., Ohara, M. & Kiel, S. (2013) A Palaeogene deep-sea methane-seep community from Honshu, Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 387, 126–133.  
<http://dx.doi.org/10.1016/j.palaeo.2013.07.015>
- Amano, K. & Kiel, S. (2007) Fossil vesicomid bivalves from the North Pacific region. *The Veliger*, 49, 270–293.
- Arkell, W.J. (1930) British Corallian Lamellibranchia. Part IV: *Palaeontographical Society Monographs*, 88, 133–180, pls. 13–20.
- Arkell, W.J. (1931) British Corallian Lamellibranchia. Part V. *Palaeontographical Society Monographs*, 88, 181–228, pls. 21–28.
- Arkell, W.J. (1934) British Corallian Lamellibranchia. Part VIII. *Palaeontographical Society Monographs*, 88, 325–350, pls. 45–49.
- Ascher, E. (1906) Die Gastropoden, Bivalven und Brachiopoden der Grödischer Schichten. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, 19, 135–167.
- Bailey, J.B. (2011) Paleobiology, paleoecology, and systematics of Solemyidae (Mollusca: Bivalvia: Protobranchia) from the Mazon Creek lagerstätte, Pennsylvanian of Illinois. *Bulletins of American Paleontology*, 382, 1–72, pls. 1–5.
- Bäckström, S.A. & Nagy, J. (1985) Depositional history and fauna of a Jurassic phosphorite conglomerate (the Brentskardhaugen Bed) in Spitsbergen. *Norsk Polarinstitutt Skrifter*, 183, 5–44, pls. 1–8.
- Barry, P.J. & McCormick, G.P. (2007) Two new species of *Adontorhina* Berry, 1947 (Bivalvia: Thyasiridae) from the Porcupine Bank, off the west coast of Ireland. *Zootaxa*, 1526, 37–49.
- Benecke, E.W. (1905) Die Versteinerungen der Eisenerzformation von Deutsch-Lothringen und Luxemburg. *Abhandlungen der geologischen Spezialkarte von Elsass-Lothringen, neue Folge*, 6, 1–591, pls. 1–59.
- Bengtson, P. (1988) Open nomenclature. *Palaeontology*, 31, 223–227.
- Berry, S.S. (1947) New Mollusca from the Pleistocene of San Pedro, California—III. *Bulletins of American Paleontology*, 31, 256–275.
- Beurlen, K. (1944) Beiträge zur Stammesgeschichte der Muscheln. *Mathematisch-Naturwissenschaftliche Abteilung der Bayerischen Akademie der Wissenschaften zu München, Sitzungsberichte*, 1–2, 133–145.
- Bieler, R., Carter, J.G. & Coan, E.V. (2010) Classification of bivalve families. In: Bouchet, P. & Rocroi, J.-P. (Eds.), Nomenclator of bivalve families. *Malacologia*, 52, 1–184.  
<http://dx.doi.org/10.4002/040.052.0201>
- Birkenmajer, K., Pugaczewska, H. & Wierzbowski, A. (1982) The Janusfjellet Formation (Jurassic–Lower Cretaceous) at Myklegardfjellet, east Spitsbergen. *Palaeontologia Polonica*, 43, 107–140, pls. 37–46.
- Bistram, A. Freiherr von (1903) Beiträge zur Kenntnis der Fauna des unteren Lias in der Val Solda. Geologisch-paläontologische Studien in den Comasker Alpen, I. *Berichte der naturforschenden Gesellschaft zu Freiburg*, 13, 116–214, pls. 1–8.
- Borissjak, A. (1904) Die Pelecypoden der Jura-Ablagerungen im Europäischen Russland. I. Nuculidae. *Mémoires du Comité Géologique, Nouvelle Série*, 11, 1–49, pls. 1–3.
- Boyd, D.W. & Newell, N.D. (1979) Permian pelecypods from Tunisia. *American Museum Novitates*, 2686, 1–22, pls. 1–3.
- Brand, A.R. & Taylor, A.C. (1974) Pumping activity of *Arctica islandica* (L.) and some other common bivalves. *Marine Behavior and Physiology*, 3, 1–15.  
<http://dx.doi.org/10.1080/10236247409378492>
- Bronn, H.G. (1830) *Gaea Heidelbergensis, oder mineralogische Beschreibung der Gegend von Heidelberg*. Karl Groos, Heidelberg & Leipzig, xii + 237 pp.
- Buch, L. von (1844) Über einige neue Versteinerungen aus Moskau. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte*, 536–539, pl. 6.
- Campbell, K. (2006) Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past developments and

- future research directions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232, 362–347.  
<http://dx.doi.org/10.1016/j.palaeo.2005.06.018>
- Casey, R. (1952) Some genera and subgenera, mainly new, of Mesozoic heterodont Lamellibranchs. *Proceedings of the Malacological Society of London*, 29, 121–176.
- Chavan, A. (1938) Essai critique de la classification des lucines. *Journal de Conchylogie*, 82, 215–241.
- Chavan, A. (1946) L'évolution des faunes marines des Mollusques dans le Nord-Ouest de l'Europe, de la fin du Crétacé à celle de l'Éocène. *Bulletin de la Société Géologique de France*, 16, 193–212.
- Chavan, A. (1947) La faune campanienne du Mont des Oliviers d'après les matériaux Vignal-Massé. *Journal de Conchyliologie*, 87, 125–196.
- Chavan, A. (1952) Les pélecypodes des sables astartiens de Cordebugle (Calvados). *Mémoires Suisses de Paléontologie*, 69, 1–132.
- Checa, A.G. & Jiménez-Jiménez, A.P. (2003) Evolutionary morphology of oblique ribs of bivalves. *Palaeontology*, 46, 709–724.  
<http://dx.doi.org/10.1111/1475-4983.00317>
- Children, J.G. (1823) Lamarck's genera of shells. *Quarterly Journal of Science, Literature & Arts*, 14, 298–322.
- Chronic, H. (1952) Molluscan fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. *Geological Society of America Bulletin*, 63, 95–166.  
[http://dx.doi.org/10.1130/0016-7606\(1952\)63\[95:mfftpk\]2.0.co;2](http://dx.doi.org/10.1130/0016-7606(1952)63[95:mfftpk]2.0.co;2)
- Clausen, C.K. & Wignall, P.B. (1990) Early Kimmeridgian bivalves of southern England. *Mesozoic Research*, 2, 97–149.
- Coan, E.V., Scott, P.V. & Bernard, F.R. (2000) Bivalve seashells of Western North America. Marine bivalve molluscs from Arctic Alaska to Baja California. *Santa Barbara Museum of Natural History Monographs*, 2, vii + 764 pp.
- Coan, E.V. & Scott, P.V. (2012) Bivalve seashells of tropical West America. Marine bivalve molluscs from Baja California to Northern Peru. *Santa Barbara Museum of Natural History Monographs*, 4, vii + 1258 pp.
- Collington, M. & Hammer, Ø. (2012) Petrography and sedimentology of the Slottsmøya Member at Janusfjellet, central Spitsbergen. *Norwegian Journal of Geology* 92, 89–101.
- Conway, N.M., Howes, B.L., McDowell Capuzzo, J.E., Turner, R.D. & Cavanaugh, C.M. (1992) Characterization and site description of *Solemya borealis* (Bivalvia; Solemyidae), another bivalve-bacteria symbiosis. *Marine Biology*, 112, 601–613. <http://dx.doi.org/10.1007/bf00346178>
- Cope, J.C.W. (1996) Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales. *Palaeontology*, 39, 979–1025.
- Cosel, R. von (2006) Taxonomy of tropical West African bivalves. VI. Remarks on Lucinidae (Mollusca, Bivalvia), with description of six new genera and eight new species. *Zoosystema*, 28, 805–851.
- Cox, L.R. (1944) On the Jurassic Lamellibranch genera *Hartwellia* and *Pronoella*. *Geological Magazine*, 81, 100–112.  
<http://dx.doi.org/10.1017/s0016756800074896>
- Cox, L.R. (1953) Lower Cretaceous gastropods, lamellibranchia and annelids from Alexander Island (Falkland Island Dependencies). *Scientific Reports (Falkland Islands Dependencies Survey)*, 4, 1–14 pp, 2 pls.
- Cox, L.R. (1965) Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. *Bulletin of the British Museum (Natural History)*, Supplement 1, 1–209, pls. 1–30.
- Crickmay, C.H. (1930) Fossils from Harrison Lake area, British Columbia. *Bulletin of the National Museum of Canada*, 63, 33–66, pls. 1–15.
- Dall, W.H. (1889) On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group. *American Journal of Science*, 38, 445–461.  
<http://dx.doi.org/10.2475/ajs.s3-38.228.445>
- Dall, W.H. (1901) Synopsis of the Lucinacea and of the American species. *Proceedings of the United States National Museum*, 23, 779–833, pls. 39–42.  
<http://dx.doi.org/10.5479/si.00963801.23-1237.779>
- Dall, W.H. (1908) Reports on the dredging operations off the west coast of Central America to the Galapagos to the west coast 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. XXXVII; 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, commanding. XUV; Reports on the Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology*, 43, 205–487, pls. 1–22.
- Dallmann, W.K., Major, H., Haremo, P., Andresen, A., Kjærnet, T. & Nøttvedt, A. (2001) Geological map of Svalbard 1:100000, sheet C9G Adventdalen. With explanatory text. *Norsk Polarinstitut Temakart*, 31/32, 4–55.
- Dando, P. (2010) Biological communities at marine shallow-water vent and seep sites. In: Kiel, S. (Ed.), *The Vent and Seep Biota. Aspects from Microbes to Ecosystems*. Topics in Geobiology, Springer, Dordrecht, Heidelberg, London, New York, pp. 333–378.  
[http://dx.doi.org/10.1007/978-90-481-9572-5\\_11](http://dx.doi.org/10.1007/978-90-481-9572-5_11)
- Dando, P.R. & Southward, A.J. (1986) Chemoautotrophy in bivalve mollusks of the genus *Thyasira*. *Journal of the Marine Biological Association of the United Kingdom*, 66, 915–926.  
<http://dx.doi.org/10.1017/s0025315400048529>



- Dando, P.R. & Spiro, B. (1993) Varying nutritional dependence of the thyasirid bivalves *Thyasira sarsi* and *T. equalis* on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios of tissue carbon and shell carbonate. *Marine Ecology Progress Series*, 92, 151–158.  
<http://dx.doi.org/10.3354/meps092151>
- Dando, P.R., Southward, A.J. & Southward, E.C. (1986) Chemoautotrophic symbionts in the gills of the bivalve mollusk *Lucinoma borealis* and the sediment chemistry of its habitat. *Proceedings of the Royal Society of London B*, 227, 227–247.  
<http://dx.doi.org/10.1098/rspb.1986.0021>
- Dando, P.R., Southward, A.J. & Southward, E.C. (2004) Rates of sediment sulphide oxidation by the bivalve mollusk *Thyasira sarsi*. *Marine Ecology Progress Series*, 280, 181–187.  
<http://dx.doi.org/10.3354/meps280181>
- Deshayes, G.P. (1853) *Traité élémentaire de Conchyliologie I, (2)*. Victor Masson, Paris, 273–368, i–xii.
- Douglas, J.A. & Arkell, W.J. (1932) The stratigraphical distribution of the Cornbrash: II. The North-Eastern Area. *Quarterly Journal of the Geological Society*, 88, 112–170.  
<http://dx.doi.org/10.1144/gsl.jgs.1932.088.01-04.08>
- Duff, K.L. (1978) Bivalvia from the English lower Oxford Clay (Middle Jurassic). *Palaeontographical Society Monographs*, 132, 1–137, pls. 1–13.
- Dufour, S. (2005) Gill anatomy and the evolution of symbiosis in bivalve family Thyasiridae. *Biological Bulletin*, 208, 200–212.  
<http://dx.doi.org/10.2307/3593152>
- Dupperon, S. (2010) The diversity of deep-sea mussels and their bacterial symbioses *In: Kiel, S. (Ed.), The Vent and Seep Biota. Aspects from Microbes to Ecosystems*. Topics in Geobiology, Springer, Dordrecht, Heidelberg, London, New York, pp. 137–167.  
[http://dx.doi.org/10.1007/978-90-481-9572-5\\_6](http://dx.doi.org/10.1007/978-90-481-9572-5_6)
- Dypvik, H., Nagy, J., Eikland, T.A., Backer-Owe, K. & Johansen, H. (1991) Depositional conditions of the Bathonian to Hauterivian Janusfjellet Subgroup, Spitsbergen. *Sedimentary Geology*, 72, 55–78.  
[http://dx.doi.org/10.1016/0037-0738\(91\)90123-u](http://dx.doi.org/10.1016/0037-0738(91)90123-u)
- Férrusac, A.E. de. (1822) *Tableaux systematiques des animaux mollusques*. A. Bertrand, Paris, 111 pp.
- Fischer, P. (1886) *Manuel de Conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossils. 10. Classes des pélecypodes*. F. Savy, Paris, 897–1008.  
<http://dx.doi.org/10.5962/bhl.title.13213>
- Fischer, P. (1887) *Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles. 10. Classes des pélecypodes*. F. Savy, Paris, 1009–1140.  
<http://dx.doi.org/10.5962/bhl.title.13213>
- Fleming, J. (1828) *A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, mollusca, and radiata of the United Kingdom; including the indigenous, extirpated, and extinct kinds, together with periodical and occasional visitants*. Bell and Bradfute, Edinburgh: i–xxiii, 1–565.  
<http://dx.doi.org/10.5962/bhl.title.12859>
- Forbes, E. (1845) Report on the fossil Invertebrata from Southern India, collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London. Series 2*, 7, 97–174, pls. 7–19.  
<http://dx.doi.org/10.1144/transgslb.7.97>
- Frenkiel, L., Gros, O. & Mouëza, M. (1996) Gill structure in *Lucina pectinata* (Bivalvia: Lucinidae) with reference to hemoglobin in bivalves with symbiotic sulphur-oxidizing bacteria. *Marine Biology*, 125, 511–524.
- Fujiwara, Y., Okutani, T., Yamanaka, T., Kawato, M., Mizota, C., Fujikura, K., Yamamoto, T. & Okoshi, K. (2009) *Solemya pervernicosa* lives in sediment underneath submerged whale carcasses: its biological significance. *Venus*, 68, 27–37.
- Fürsich, F.T. (1982) Upper Jurassic bivalves from Milne Land, East Greenland. *Gronlands Geologiske Undersøgelse*, 144, 1–126.
- Fürsich, F.T. (1984) Palaeoecology of boreal invertebrate faunas from the Upper Jurassic of Central East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 48, 309–364.  
[http://dx.doi.org/10.1016/0031-0182\(84\)90050-6](http://dx.doi.org/10.1016/0031-0182(84)90050-6)
- Fürsich, F.T. & Werner, W. (1989) Taxonomy and ecology of *Juranomia calcibyssata* gen. et sp. nov, a widespread anomiid bivalve from the Upper Jurassic of Portugal. *Geobios*, 22, 325–337.  
[http://dx.doi.org/10.1016/s0016-6995\(89\)80135-4](http://dx.doi.org/10.1016/s0016-6995(89)80135-4)
- Gabb, W.M. (1866) *Paleontology of California. Vol. 2. Cretaceous and Tertiary fossils. Sect. 1 (Tertiary Invertebrate Fossils)*. Geological Survey of California, 124 pp., 18 pls.
- Gerasimov, P.A. (1955) *Index fossils of Mesozoic of the central regions of the European part of the USSR. Part I. Lamellibranchiata, Gastropoda, Scaphopoda and Brachiopoda from the Jurassic deposits*. Gosgeoltekhizdat, Moscow, 274 pp., 50 pls. [in Russian]
- Gill, F. & Little, C.T.S. (2013) A new lucinid bivalve from hydrocarbon seeps. *Acta Palaeontologica Polonica*, 58, 573–578.  
<http://dx.doi.org/10.4202/app.2011.0092>
- Girty, G.H. (1909) Paleontology of the Manzano Group. *In: Lee, W.T. & Girty, G. (Eds.), The Manzano Group of the Rio*

- Grande valley, New Mexico*. U.S. Geological Survey Bulletin, 389, 41–141, pls. 6–12.
- Glover, E.A. & Taylor, J.D. (1997) New species and records of *Rastafaria* and *Megaximus* (Bivalvia: Lucinidae) from the Western Indian Ocean and Red Sea, with reappraisal of *Megaximus*. *Journal of Conchology*, 36, 1–18.  
<http://dx.doi.org/10.1093/mollus/70.3.283>
- Glover, E.A., Taylor, J.D. & Rowden, A.A. (2004) *Bathyaustriella thionipta*, a new lucinid bivalve from a hydrothermal vent on the Kermadec Ridge, New Zealand, and its relationship to shallow water taxa (Bivalvia: Lucinidae). *Journal of Molluscan Studies*, 70, 283–295.
- Goedert, J.L., Thiel, V., Schmale, O., Rau, W.W., Michaelis, W. & Peckmann, J. (2003) The Late Eocene ‘Whiskey Creek’ methane-seep deposit (western Washington State) Part I: geology, palaeontology and molecular geobiology. *Facies*, 48, 223–240.  
<http://dx.doi.org/10.1007/bf02667541>
- Goldfuss, G.A. (1837) *Petrefacta Germaniae 2 (3)*. Arnz, Düsseldorf, 84 pp., pls. 141–224, 25 pls.
- Gray, J.E. (1824) *A supplement to the appendix of Captain Perry's voyage for the discovery of a north west passage in the years 1819–1820, containing an account of the subjects of natural history. Appendix X. Natural history, shells*. J. Murray, London, ccxi–ccxlvii.
- Gray, J.E. (1840) Shells of molluscan animals. In: *Synopsis of the contents of the British Museum*, ed. 42. Woodfall & Son, London, pp. 105–152.
- Gray, J.E. (1847) A list of the genera of Recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London*, 15, 129–219.
- Gray, J. E. (1854) A revision of the arrangement of the families of bivalve shells (Conchifera). *The Annals and Magazine of Natural History*, Series 2, 13, 408–418.  
<http://dx.doi.org/10.1080/03745485709496364>
- Grey, M., Haggart, J.W. & Smith, P.L. (2008) A new species of *Buchia* (Bivalvia: Buchiidae) from British Columbia with an analysis of buchiid bipolarity. *Journal of Paleontology*, 82, 391–397.  
<http://dx.doi.org/10.1666/07-002.1>
- Grobben, C. (1894) Zur Kenntniss der Morphologie, der Verwandtschaftsverhältnisse und des Systems der Mollusken. *Kaiserliche Akademie der Wissenschaften (Mathematisch-Naturwissenschaftlichen Classe), Sitzungsberichte*, 103, 61–86.
- Habe, T. (1958) Report on the Mollusca chiefly collected by the S.S. Soyo-Maru of the Imperial Fisheries Experimental Station on the continental shelf bordering Japan during the years 1922–1930. Part 3. Lamellibranchia (1). *Publications of the Seto Marine Biological Laboratory, Kyoto University*, 6, 241–279.
- Hallam, A. (1976) Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia*, 9, 245–259.  
<http://dx.doi.org/10.1111/j.1502-3931.1976.tb01317.x>
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1). Available from: [http://palaeoelectronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeoelectronica.org/2001_1/past/issue1_01.htm) (accessed 12. Jan. 2013)
- Hammer, Ø., Nakrem, H.A., Little, C.T.S., Hryniewicz, K., Sandy, M., Hurum, J.H., Druckenmiller, P., Knutsen, E.M. & Høyberget, M. (2011) Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 306, 15–26.  
<http://dx.doi.org/10.1016/j.palaeo.2011.03.019>
- Hammer, Ø., Hryniewicz, K., Hurum, J.H., Høyberget, M., Knutsen, E.M. & Nakrem, H.A. (2013) Large onychites (cephalopod hooks) from the Upper Jurassic of the Boreal Realm. *Acta Palaeontologica Polonica*, 58, 827–835.  
<http://dx.doi.org/10.4202/app.2012.0020>
- Håkansson, E., Birkelund, T., Piasecki, S. & Zakharov, V.A. (1981) Jurassic–Cretaceous boundary strata of the extreme Arctic. *Bulletin of the Geological Society of Denmark*, 30, 11–42.
- Harries, P.J. & Little, C.T.S. (1999) The early Toarcian (Early Jurassic) and the Cenomanian–Turonian (Late Cretaceous) mass extinctions: similarities and contrasts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 154, 39–66.  
[http://dx.doi.org/10.1016/s0031-0182\(99\)00086-3](http://dx.doi.org/10.1016/s0031-0182(99)00086-3)
- Hedley, C.F.L.S. (1904) Notes on Australian Mollusca. Part VIII. *The Proceedings of the Linnean Society of New South Wales*, 29, 182–212, pls. 8–10.
- Herrmannsen, A.N. (1846) *Indicis generum malacozoorum primordia. Nomina subgenerum, generum, familiarum, tribuum, ordinum, classium; adjectis auctoribus, temporibus, locis systematicis atque literariis, etymis, synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda. Vol. I*. Cassellis, i–xxvii, 637 pp.
- Herry, A., Diouris, M. & Le Pennec, M. (1989) Chemoautotrophic symbionts and translocation of fixed carbon from bacteria to host tissues in the littoral bivalve *Loripes lucinalis* (Lucinidae). *Marine Biology*, 101, 305–312.  
<http://dx.doi.org/10.1007/bf00428126>
- Hjálmsarsdóttir, H.R., Nakrem, H.A. & Nagy, J. (2012) Foraminifera from Late Jurassic–Early Cretaceous hydrocarbon seep carbonates, central Spitsbergen, Svalbard—preliminary results. *Norwegian Journal of Geology*, 92, 157–165.
- Hodges, P. (1991) The relationship of the Mesozoic bivalve *Atreta* to the Dimyidae. *Palaeontology*, 34, 963–970.
- Hodges, P. (2000) The Early Jurassic Bivalvia from the Hettangian and Lower Sinemurian of South-West Britain. *Palaeontographical Society Monographs*, 154, 1–64 + vii, pls. 1–6.
- Holmer, L.E. & Nakrem, H.A. (2012) The lingulid brachiopod *Lingularia* from lowermost Cretaceous hydrocarbon seep

- bodies, Sassenfjorden area, central Spitsbergen, Svalbard. *Norwegian Journal of Geology*, 92, 167–174.
- Holmes, A.M., Oliver, P.G. & Sellanes, J. (2005) A new species of *Lucinoma* (Bivalvia: Lucinoidea) from a methane gas seep off the southwest coast of Chile. *Journal of Conchology*, 38, 673–682.
- Houša, V., Pruner, P., Zakharov, V.A., Kostak, M., Chadima, M., Rogov, M.A., Šlechta, S. & Mazuch, M. (2007) Boreal–Tethyan correlation of the Jurassic–Cretaceous boundary interval by magneto- and biostratigraphy. *Stratigraphy and Geological Correlation*, 15, 297–309.  
<http://dx.doi.org/10.1134/s0869593807030057>
- Howe, B. (1987) *Tepee Buttes: A petrological, paleontological, paleoenvironmental study of Cretaceous submarine spring deposits*. Master's thesis, Boulder, University of Colorado, 218 pp.
- Hryniewicz, K., Hammer, Ø., Nakrem, H.A. & Little, C.T.S. (2012) Microfacies of the Volgian–Ryazanian (Jurassic–Cretaceous) hydrocarbon seep carbonates from Sassenfjorden, central Spitsbergen, Svalbard. *Norwegian Journal of Geology*, 92, 113–131.
- Ichikawa, K. (1958) Zur Taxonomie und Phylogenie der triadischen "Pteriidae" (Lamellibranch.) mit besonderer Berücksichtigung der Gattungen *Claraia*, *Eumorphotis*, *Oxytoma* und *Monotis*. *Palaeontographica* (A), 111, 131–212, pls. 21–24.
- Iredale, T. (1924) Results from Roy Bell's Molluscan collections. *Proceedings of the Linnean Society of New South Wales*, 49, 179–278.
- Iredale, T. (1930) More notes on the marine Mollusca of New South Wales. *Records of the Australian Museum*, 17, 384–407.  
<http://dx.doi.org/10.3853/j.0067-1975.17.1930.773>
- Iredale, T. (1931) Australian Molluscan notes. No. 1. *Records of the Australian Museum*, 18, 201–235, pls. 22–25.  
<http://dx.doi.org/10.3853/j.0067-1975.18.1931.725>
- Iredale, T. (1939) Mollusca. Part I. *Scientific Reports of the Great Barrier Reef Expedition 1928–1929*, 5, 209–245, pls. 1–7.
- Järnægren, J., Schander, C., Sneli, J.-A., Rønningen, V. & Young, C.M. (2007) Four genes, morphology and ecology: distinguishing a new species of *Acesta* (Mollusca; Bivalvia) from the Gulf of Mexico. *Marine Biology*, 152, 43–55.  
<http://dx.doi.org/10.1007/s00227-007-0651-y>
- Järnægren, J., Tobias, C.R., Macko, S.A. & Young, C.M. (2005) Egg predation fuels unique species association at deep-sea hydrocarbon seeps. *Biological Bulletin*, 209, 87–93.  
<http://dx.doi.org/10.2307/3593126>
- Jeletzky, J.A. (1966) Upper Volgian (latest Jurassic) ammonites and buchias of Arctic Canada. *Geological Survey of Canada Bulletin*, 128, 1–51, pls. 1–8.
- Jenkins, R., Kaim, A., Little, C.T.S. Iba, Y., Tanabe, K. & Campbell, K.A. (2013) Worldwide distribution of the modiomorphid bivalve genus *Caspiconcha* in Late Mesozoic hydrocarbon seeps. *Acta Palaeontologica Polonica*, 58, 357–382.  
<http://dx.doi.org/10.4202/app.2011.0026>
- Johnson, A.L.A. (1984) The palaeobiology of the bivalve families Pectinidae and Propeamussidae in the Jurassic of Europe. *Zitteliana*, 11, 1–235, pls. 1–11.
- Kaim, A., Skupien, P. & Jenkins, R.G. (2013) A new Lower Cretaceous hydrocarbon seep locality from the Czech Carpathians and its fauna. *Palaeogeography, Palaeoecology, Palaeoclimatology*, 390, 42–51.  
<http://dx.doi.org/10.1016/j.palaeo.2013.03.010>
- Kaim, A., Jenkins, R.G., Tanabe, K. & Kiel, S. (in press) Mollusks from late Mesozoic seep deposits, chiefly in California. *Zootaxa*.
- Kamenev, G.M. (2009) North Pacific species of the genus *Solemya* Lamarck, 1818 (Bivalvia: Solemyidae) with notes on *Acharax johnsoni* (Dall, 1891). *Malacologia*, 51, 233–261.  
<http://dx.doi.org/10.4002/040.051.0202>
- Kamenev, G.M., Nadtochy, V.A. & Kuznetsov, A.P. (2001) *Conchocele bisecta* (Conrad, 1849) (Bivalvia: Thyasiridae) from cold-water methane-rich areas of the Sea of Okhotsk. *The Veliger*, 44, 84–94.
- Kauffman, E.G. (1967) Cretaceous *Thyasira* from the western interior of Northern America. *Smithsonian Miscellaneous Collections*, 152, 1–159.
- Kauffman, E.G. (1973) Cretaceous Bivalvia. In: Hallam, A. (Ed.), *Atlas of palaeobiogeography*. Elsevier Scientific, New York, 531 pp.
- Kauffman, E.G., Arthur, M.A., Howe, B. & Scholle, P.A. (1996) Widespread venting of methane-rich fluids in Late Cretaceous (Campanian) submarine springs (Tepee Buttes), Western Interior Seaway, U.S.A. *Geology*, 24, 799–802.  
[http://dx.doi.org/10.1130/0091-7613\(1996\)024<0799:wvomrf>2.3.co;2](http://dx.doi.org/10.1130/0091-7613(1996)024<0799:wvomrf>2.3.co;2)
- Kelly, S.R.A. (1984) Bivalvia of the Spilsby Sandstone and the Sandringham Sands (Late Jurassic–Early Cretaceous) of Eastern England. Part 1. *Palaeontographical Society Monographs*, 137, 1–94, pls. 1–20.
- Kelly, S.R.A. (1992) Bivalvia of the Spilsby Sandstone and the Sandringham Sands (Late Jurassic–Early Cretaceous) of Eastern England. Part 2. *Palaeontographical Society Monographs*, 146, 95–123, xiii–xiv, pls. 21–27.
- Kelly, S.R.A., Blanc, E., Price, S.P. & Witham, A.G. (2000) Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland. In: Harper, E.M., Taylor, J.D. & Crame, J.A. (Eds.), *The evolutionary Biology of the Bivalvia*. Geological Society of London, Special Publications, London, pp. 227–246.
- Kiel, S. (2010) On the potential generality of depth-related ecologic structure in cold-seep communities: Evidence from Cenozoic and Mesozoic examples. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 295, 245–257.

- <http://dx.doi.org/10.1016/j.palaeo.2010.05.042>
- Kiel, S. (2013) Lucinid bivalves from ancient methane seeps. *Journal of Molluscan Studies*, 79, 346–363.  
<http://dx.doi.org/10.1093/mollus/eyt035>
- Kiel, S. & Amano, K. (2013) The earliest bathymodiolin mussels: an evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA. *Journal of Paleontology*, 87, 589–602.  
<http://dx.doi.org/10.1666/12-135>
- Kiel, S., Amano, K. & Jenkins, R.G. (2008a) Bivalves from Cretaceous cold seep deposits on Hokkaido, Japan. *Acta Palaeontologica Polonica*, 53, 525–537.  
<http://dx.doi.org/10.4202/app.2008.0310>
- Kiel, S., Birgel, D., Campbell, K.A., Crampton, J.S., Schiøler, P. & Peckmann, J. (2013) Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 390, 17–34.  
<http://dx.doi.org/10.1016/j.palaeo.2012.10.033>
- Kiel, S., Campbell, K.A., Elder, W. & Little, C.T.S. (2008b) Jurassic and Cretaceous gastropods from hydrocarbon seeps in forearc basin and accretionary prism settings, California. *Acta Palaeontologica Polonica*, 53, 679–703.  
<http://dx.doi.org/10.4202/app.2008.0412>
- Kiel, S., Campbell, K.A. & Gaillard, C. (2010) New and little known mollusks from ancient chemosynthetic environments. *Zootaxa*, 2390, 26–48.
- Kiel, S. & Peckmann, J. (2008) Palaeoecology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula. *Palaios*, 23, 751–759.
- Kiel, S., Wiese, F. & Titus, A.L. (2012) Shallow-water methane-seep faunas in the Cenomanian Western Interior Seaway: no evidence for onshore-offshore adaptations to deep-sea vents. *Geology*, 40, 839–842.  
<http://dx.doi.org/10.1130/g33300.1>
- Kitchin, F.L. (1926) A new genus of lamellibranchs (*Hartwellia* gen. nov.) from the Upper Kimmeridge Clay of England. *The Annals and Magazine of Natural History*, 10, 433, pl. 19.  
<http://dx.doi.org/10.1080/00222932608633540>
- Koshelkina, Z.V. (1962) *Field atlas of the guide faunas of the Jurassic of the Vilyuy Syncline and Periverkhoyansk border depression*. North-Western Integrated Institute of Science and Exploration of the Siberian Branch of the Soviet Academy of Sciences, Magadan, 63 pp, 34 pls. [in Russian]
- Krenkel, E. (1915) Die Kelloway-Fauna von Popilani in Westrussland. *Palaeontographica*, 61, 191–368, pls. 19–28.
- Krueger, D.M., Dubilier, N., Cavanaugh, C.M. (1992) Chemoautotrophic symbiosis in the tropical clam *Solemya occidentalis* (Bivalvia: Protobranchia): ultrastructural and phylogenetic analysis. *Marine Biology*, 126, 55–64.  
<http://dx.doi.org/10.1007/bf00571377>
- Lahusen, J. (1886) Die Inoceramen-Schichten an dem Olenek und der Lena. *Mémoires L'académie Impériale des Sciences de St.-Petersbourg*, 23 (7), 1–12, pls. 1–2.
- Lahusen, J. (1888) Über die russischen Aucellen. *Mémoires du Comité Géologique (St Petersburg)*, 8, 1–46, pls. 1–5.
- Lamarck, J.B. (1818) *Histoire naturelle des animaux sans vertèbres*. Vol. 5, Deterville, Paris, 612 pp.
- La Perna, R. (2004) *Nucinella alibrandi* (Conti, 1864) and *N. seguenzae* (Dall, 1898): the last European nucinellids (Bivalvia: Protobranchia). *Rivista Italiana di Palaeontologia e Stratigrafia*, 110, 571–577.
- La Perna, R. (2005) A gigantic deep-sea Nucinellidae from the tropical West Pacific (Bivalvia: Protobranchia). *Zootaxa*, 881, 1–10.
- Lartet, L. (1872) Essai sur la géologie de la Palestine et des contrées avoisinantes: telles que l'Égypte et l'Arabie, comprenant les observations recueillies dans le cours de l'expédition du duc de Luynes a la Mer Morte. Suivi de Propositions de géologie et de botanique données par la faculté (3). *Annales des Sciences géologiques*, 1–96, pls. 9–12.
- Leckenby, J. (1859) On the Kelloway Rock of Yorkshire Coast. *Quarterly Journal of the Geological Society*, 15, 4–15.  
<http://dx.doi.org/10.1144/gsl.jgs.1859.015.01-02.07>
- Lemoine, M., Arnaud-Vanneau, A., Arnaud, H., Létolle, R., Mavel, C. & Thieuloy, J.-P. (1982) Indices possible de paléo-hydrothermalisme marin dans le Jurassique et le Crétacé des Alpes occidentales (océan téthysien et sa marge continentale européenne): essai d'inventaire. *Bulletin de la Société Géologique de France*, 24, 641–647.
- Levin, L. (2005) Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. *Oceanography and Marine Biology: An Annual Review*, 43, 1–46.  
<http://dx.doi.org/10.1201/9781420037449.ch1>
- Lewinski, J. (1922) Monographie géologique et paléontologique du Bolonien de la Pologne. *Mémoires de la Société Géologique de France*, 56, 1–56, pls. 1–8.
- Liljedahl, L. (1984) *Janeia silurica*, a link between nuculoids and solemyoids (Bivalvia). *Palaeontology*, 27, 693–698.
- Liljedahl, L. (1992) The Silurian *Ilonia prisca*, oldest known deep-burrowing suspension-feeding bivalve. *Journal of Paleontology*, 66, 206–210.
- Lindström, G. (1865) Om Trias-och Juraförsteningar från Spetsbergen. *Kungliga Svenska Vetenskaps-Akademiens Handlingar Bandet*, 6, 3–20, pls. 1–3.
- Link D.H.F. (1807) *Beschreibung der Naturalien-Sammlung der Universität zu Rostock, 3 abt.* Adlers Erben, Rostock, 101–165.  
<http://dx.doi.org/10.5962/bhl.title.69815>

- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, iridines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima*. Laurentius Salvius, Holmiae, 824 pp.
- Linnaeus, C. (1767) *Systema Naturae. Editio duodecima. 1. Part 2. Regnum Animale*. Laurentius Salvius, Holmiae, 533–1327.
- Logan, A. (1967) The Permian Bivalvia of Northern England. *Palaeontographical Society Monographs*, 121, 1–72, pls. 1–10.
- Löffler, S.B., Janssen, R., Gürs, K.R. & Taviani, M. (2005) The genus *Axinus* Sowerby, 1821, in the Mediterranean basin (Bivalvia: Thyasiridae). *Journal of Conchology*, 38, 581–597.
- Loriol, P. de & Pellat, A. (1867) Monographie paléontologique et géologique de l'étage Portlandien des environs de Boulogne-sur-Mer. *Mémoires de la Société de Physique et d'Histoire naturelle de Genève*, 19, 1–200, pls. 1–11.
- Marshall, B.A. (1978) The genus *Neilo* in New Zealand (Mollusca: Bivalvia). *New Zealand Journal of Zoology*, 5, 425–436. <http://dx.doi.org/10.1080/03014223.1978.10428329>
- Matsukuma, A., Okutani, T. & Tsuchi, R. (1982) Three new species of Nucinelidae (Bivalvia: Protobranchia) from the Pacific coast of Japan. *Venus*, 40, 177–186.
- Matthews, S.C. (1973) Notes on open nomenclature and on synonymy lists. *Palaeontology*, 16, 713–719.
- McLeod, R.J., Wing, S.R. & Skilton, J.E. (2010) High incidence of invertebrate-chemoautotroph symbioses in benthic communities of the New Zealand fjords. *Limnology and Oceanography*, 55, 2097–2106. <http://dx.doi.org/10.4319/lo.2010.55.5.2097>
- Meek, F.B. (1864) Check list of the invertebrate fossils of North America. Cretaceous and Jurassic. *Smithsonian Miscellaneous Collection*, 7, 1–40.
- Merrill, A.S. & Turner, R.D. (1963) Nest building in the bivalve genera *Musculus* and *Lima*. *The Veliger*, 6, 55–59.
- Metz, C.L. (2010) Tectonic controls on the genesis and distribution of Late Cretaceous, Western Interior Basin hydrocarbon-seep mounds (Tepee Buttes) of North America. *The Journal of Geology*, 118, 201–213. <http://dx.doi.org/10.1086/650181>
- Mikkelsen, P.M. & Bieler, R. (2008) *Seashells of Southern Florida. Living marine mollusks of the Florida Keys and adjacent regions. Bivalves*. Princeton University Press, Princeton & Oxford, 503 pp.
- Morris, J. & Lycett, J. (1853) The Mollusca of the Great Oolite. Part 2, Bivalves. *Palaeontographical Society Monographs*, 23, 1–80, pls. 1–8.
- Morton, B. (1980) The anatomy of the 'living fossil' *Pholadomya candida* Sowerby 1823 (Bivalvia: Anomalodesmata: Pholadomyacea). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn*, 142, 7–101.
- Morton, B. (2011) The biology and functional morphology of *Arctica islandica* (Bivalvia: Arctidae) — A gerontophilic living fossil. *Marine Biology Research*, 7, 540–533. <http://dx.doi.org/10.1080/17451000.2010.535833>
- Müller, J.M. (1847) *Monographie der Petrefacten der Aachener Kreideformation (1)*. Henry & Cohen, Bonn, 48 pp., 2 pls.
- Nagy, J., Løfaldli, M. & Bäckström, S.A. (1988) Aspects of foraminiferal distribution and depositional conditions in Middle Jurassic to Early Cretaceous shales in eastern Spitsbergen. *Abhandlungen der Geologischen Bundesanstalt Wien*, 30, 287–300.
- Neulinger, S.C., Sahling, H., Süling, J. & Imhoff, J.F. (2006) Presence of two phylogenetically distinct groups in the deep-sea mussel *Acharax* (Mollusca: Bivalvia: Solemyidae). *Marine Ecology Progress Series*, 312, 161–168. <http://dx.doi.org/10.3354/meps312161>
- Neumayr, M. (1884) Zur Morphologie des Bivalvenschlosses. *Akademie der Wissenschaften Wien. Sitzungsberichte*, 88, 385–418.
- Newell, N.D. (1965) Classification of the Bivalvia. *American Museum Novitates*, 2206, 1–26.
- Newton, R.B. (1891) *Systematic List of the Frederick E. Edwards collection of British Oligocene and Miocene Mollusca, with references to the type specimens from similar horizons*. British Museum (Natural History), London, 365 pp.
- Ogg, J.G. & Hinnov, L.A. (2012) Jurassic. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (Eds.), *The Geologic Time Scale 2012. Volume 2*. Elsevier, Oxford Amsterdam Waltham, pp. 731–791.
- Okutani, T. (2002) A new thyasirid, *Conchocele novaeguineensis* n. sp. from a thanatocoenosis associated with a possible cold seep activity off New Guinea. *Venus*, 61, 141–145.
- Okutani, T. & Iwasaki, N. (2003) Noteworthy abyssal mollusks (excluding vesicomid bivalves) collected from the Nankai Trough off Shikoku by ROV Kaiko of the Japan marine Science & Technology Center. *Venus*, 62, 1–10.
- Oliver, G.P. & Holmes, A.M. (2006) New species of Thyasiridae (Bivalvia) from chemosynthetic communities in the Atlantic Ocean. *Journal of Conchology*, 39, 175–183.
- Oliver, G.P. & Holmes, A.M. (2007) A new species of *Axinus* (Bivalvia: Thyasiroidea) from the Baby Bare Seamount, Cascadia Basin, NE Pacific, with a description of the anatomy. *Journal of Conchology*, 39, 363–376.
- Oliver, G.P. & Killeen, I. J. (2002) The Thyasiridae (Mollusca: Bivalvia) of the British continental shelf and North Sea oilfields. *Biomôr Reports*, 3, 1–73.
- Oliver, G.P. & Levin, L. (2006) A new species of the family Thyasiridae (Mollusca: Bivalvia) from the oxygen-minimum zone of the Pakistan margin. *Journal of the Marine Biological Association of the United Kingdom*, 86, 411–416. <http://dx.doi.org/10.1017/s0025315406013270>
- Oliver, G.P., Rodrigues, C.F. & Cunha, M.R. (2011) Chemosymbiotic bivalves from the mud volcanoes of the Gulf of Cadiz, NE Atlantic, with descriptions of new species of Solemyidae, Lucinidae and Vesicomidae. *ZooKeys*, 113, 1–38. <http://dx.doi.org/10.3897/zookeys.113.1402>

- Oliver, G.P. & Sellanes, J. (2005) New species of Thyasiridae from a methane seepage area off Concepción, Chile. *Zootaxa*, 1092, 1–20.
- Oliver, G.P. & Taylor, J.D. (2012) Bacterial symbiosis in the Nucinellidae (Bivalvia: Solemyida) with descriptions of two new species. *Journal of Molluscan Studies*, 78, 81–91.  
<http://dx.doi.org/10.1093/mollus/eyr045>
- Orbigny, A. d' (1844) *Paléontologie française: description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France*. Victor Masson, Paris, 807 pp, pls. 271–405.
- Orbigny, A. d' (1850) *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés. Vol. 2*. Victor Masson, Paris, 427 pp.
- Oschmann, W. (1988) Upper Kimmeridgian and Portlandian marine macrobenthic associations from Southern England and Northern France. *Facies*, 18, 49–82.  
<http://dx.doi.org/10.1007/bf02536795>
- Palmer, C.P. (1973) The palaeontology of the Liassic (Lower Jurassic) clay pits at Stonehouse and Tuffley in Gloucestershire. *Geological Magazine*, 110, 249–263.  
<http://dx.doi.org/10.1017/s0016756800036086>
- Payne, C.M. & Allen, J.A. (1991) The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. *Philosophical Transactions: Biological Sciences*, 334, 481–562.  
<http://dx.doi.org/10.1098/rstb.1991.0128>
- Pearson, T.H. (1972) The effect of industrial effluent from pulp and paper mills on the marine benthic environment. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 180, 469–485.  
<http://dx.doi.org/10.1098/rspb.1972.0032>
- Peckmann, J., Gischler, E., Oschmann, W. & Reitner, J. (2001) An Early Carboniferous seep community and hydrocarbon-derived carbonates from the Harz Mountains, Germany. *Geology*, 29, 271–274.  
[http://dx.doi.org/10.1130/0091-7613\(2001\)029<0271:aecsa>2.0.co;2](http://dx.doi.org/10.1130/0091-7613(2001)029<0271:aecsa>2.0.co;2)
- Peckmann, J., Kiel, S., Sandy, M.R., Taylor, D.G. & Goedert, J.L. (2011) Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, eastern Oregon. *The Journal of Geology*, 119, 207–220.  
<http://dx.doi.org/10.1086/658199>
- Peckmann, J., Walliser, O.H., Riegel, W. & Reitner, J. (1999) Signatures of hydrocarbon venting in a Middle Devonian carbonate mound (Hollard Mound) at the Hamar Laghdad (AntiAtlas, Morocco). *Facies*, 40, 291–296.  
<http://dx.doi.org/10.1007/bf02537477>
- Pelseneer, P. (1889) Sur la classification phylogénétique des pélécy-podes. *Bulletin scientifique de la France et de la Belgique*, 20, 27–52.
- Phillips, J. (1829) *Illustrations of the geology of Yorkshire. 1<sup>st</sup> edition*. Printed for John Murray, Ablemarle Street, York, xvi + 192 pp., 24 pls.
- Poli, G.S. (1795) *Testacea utriusque Siciliae eorumque historia et anatome tabulis aenis illustrata*. Rusconi & Parma, Chiaje, Neapoli, i–lxxvi, 1–264, pls. 9–39.
- Pugaczewska, H. (1986) Bivalvia of the Polish Middle Jurassic and remarks on their paleoecology. *Acta Palaeontologica Polonica*, 31, 27–83, pls. 15–34.
- Rafinesque, C.S. (1815) *Analyse de la nature*. De l'imprimerie de Jean Barravecchia, Palermo, 225 pp.
- Reid, R.G.B. (1980) Aspects of biology of a gutless species of *Solemya* (Bivalvia: Protobranchia). *Canadian Journal of Zoology*, 58, 386–393.  
<http://dx.doi.org/10.1139/z80-050>
- Reid, R.G.B. & Brand, D.G. (1986) Sulfide-oxidising symbiosis in lucinaceans: implication for bivalve evolution. *The Veliger*, 29, 3–24.
- Rodrigues, C.F., Dupperon, S. & Gaudron, S.M. (2011) First documented record of a living solemyid bivalve in a pockmark of the Nile Deep-sea Fan (eastern Mediterranean Sea). *Marine Biodiversity Records*, 4, e10.  
<http://dx.doi.org/10.1017/s175526721100008x>
- Rodrigues, C.F., Oliver, G.P. & Cunha, M.R. (2008) Thyasiroidea (Mollusca: Bivalvia) from the mud volcanoes of the Gulf of Cadiz. *Zootaxa*, 1752, 41–56.
- Roeding, P.F. (1798) *Museum Boltenianum. Pars secunda continens Conchylia*. Trapp, Hamburg, Viii+199 pp.
- Roemer, F.J. (1836) *Die Versteinerungen des norddeutschen Oolithen-gebirges*. Hahn, Hannover, 218 pp, pls. 1–16.
- Roemer, F.J. (1839) *Die Versteinerungen des norddeutschen Oolithen-gebirges. Ein Nachtrag*. Hahn, Hannover, 56 pp, pls. 17–20.
- Rogov, M. & Zakharov, V. (2009) Ammonite- and bivalve-based biostratigraphy and Panboreal correlation of the Volgian Stage. *Science in China Series D: Earth Sciences*, 52, 1890–1909.  
<http://dx.doi.org/10.1007/s11430-009-0182-0>
- Rouillier, C. (1845) [No title. Summary of presentation at meeting]. In: Séance du 15 Janvier 1845. Bulletin de la Société Impériale des Naturalistes de Moscou, 18 (1), 289. [New genus: *Buchia*, p. 289, based on *Avicula mosquensis* von Buch, 1844; genus valid by ICZN Opinion 492.]
- Saether, P.K., Little, C.T.S., Campbell, K.A., Marshall, B.A., Collins, M. & Alfaro, A.L. (2010) New fossil mussels (Bivalvia: Mytilidae) from Miocene hydrocarbon seep deposits, North Island, New Zealand, with general remarks on vent and seep

mussels. *Zootaxa*, 2577, 1–45.

- Sahling, H., Galkin, S.V., Salyuk, A., Greinert, J., Foerstel, H., Piepenburg, D. & Suess, E. (2003) Depth-related structure and ecological significance of cold-seep communities—a case study from the Sea of Okhotsk. *Deep Sea Research I*, 50, 1391–1409. <http://dx.doi.org/10.1016/j.dsr.2003.08.004>
- Sahling, H., Rickert, D., Lee, R.W., Linke, P. & Suess, P. (2002) Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Marine Ecology Progress Series*, 231, 121–138. <http://dx.doi.org/10.3354/meps231121>
- Salas, C. & Woodside, J. (2002) *Lucinoma kazani* n. sp. (Mollusca: Bivalvia): evidence of a living benthic community associated with a cold seep in the Eastern Mediterranean Sea. *Deep-Sea Research I*, 49, 991–1005. [http://dx.doi.org/10.1016/s0967-0637\(02\)00010-9](http://dx.doi.org/10.1016/s0967-0637(02)00010-9)
- Sanders, H.L. & Allen, J.A. (1985) Studies on deep-sea Protobranchia (Bivalvia); the family Malletiidae. *Bulletin of the British Museum (Natural History) Zoology*, 49, 195–238.
- Sanin, V.Ya. (1976) Early Cretaceous Ctenodontida of the North of Siberia. *Transactions of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Science of USSR*, 310, 1–70. [in Russian]
- Sauvage, H.E. & Rigaux, E. (1871) Diagnoses d'espèces nouvelles des Terrains jurassiques supérieurs de Boulogne-sur-Mer (Pas de Calais). *Journal de Conchology*, 20, 165–187, pls. 8–12.
- Schlothem, E.F. von (1813) Beiträge zur Natur-geschichte der Versteinerungen in geognostischer Hinsicht. *Leonhard's Taschenbuch der Mineralogie*, 7, 3–134.
- Schneider, S. (2008) The bivalve fauna from the Ortenburg Marine Sands in the well-core “Straß” (Early Miocene, SE Germany)—taxonomy, stratigraphy, paleoecology and paleogeography. *Paläontologische Zeitschrift*, 82, 402–417. <http://dx.doi.org/10.1007/bf03184430>
- Scott, P.H. (1986) A new species of *Adontorhina* (Bivalvia: Thyasiridae) from the Northeast Pacific, with notes of *Adontorhina cyclicia* Berry, 1947. *The Veliger*, 29, 149–156.
- Sibuet, M. & Olu, K. (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities on active and passive margins. *Deep-Sea Research II*, 45, 517–567. [http://dx.doi.org/10.1016/s0967-0645\(97\)00074-x](http://dx.doi.org/10.1016/s0967-0645(97)00074-x)
- Sokolov, D. & Bodulevsky, W. (1931) Jura- und Kreidefaunen von Spitsbergen. *Skrifter om Svalbard og Ishavet*, 35, 1–151, pls. 1–14.
- Sowerby, G.B.I. (1823) *The Genera of Recent and Fossil Shells*. Van Voorst, London, 21 pp.
- Sowerby, J. (1812) *The Mineral Conchology of Great Britain I(1)*, J. Sowerby, London, i–vii, 9–32, pls. 1–9. <http://dx.doi.org/10.5962/bhl.title.14408>
- Sowerby, J. (1814) *The Mineral Conchology of Great Britain I(3)*, J. Sowerby, London, 97–178, pls. 45–78. <http://dx.doi.org/10.5962/bhl.title.14408>
- Sowerby, J. (1818) *The Mineral Conchology of Great Britain 3(1)*, J. Sowerby, London, 1–40, pls. 204–221. <http://dx.doi.org/10.5962/bhl.title.14408>
- Sowerby, J. (1819) *The Mineral Conchology of Great Britain 3(2)*, J. Sowerby, London, 41–98, pls. 222–253. <http://dx.doi.org/10.5962/bhl.title.14408>
- Sowerby, J. (1821) *The Mineral Conchology of Great Britain 4(1)*, J. Sowerby, London, 1–16, pls. 307–318. <http://dx.doi.org/10.5962/bhl.title.14408>
- Sowerby, J. de C. (1824) *The Mineral Conchology of Great Britain (5)*, J. Sowerby, London, 65–138, pls. 444–485. <http://dx.doi.org/10.5962/bhl.title.14408>
- Sowerby, J. de C. (1836) Observation on some of the strata between the chalk and the Oxford Oolite in the South-East of England. In: Fitton, W.H. (Ed.), *Transactions of the Geological Society of London*, 2, 4(2), 335–349, pls. 11–23. <http://dx.doi.org/10.1144/transgslb.4.2.103>
- Spath, L.F. (1936) The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land. II. Upper Kimmeridgian and Portlandian. *Meddelelser om Grønland*, 99, 1–180, pls. 1–50.
- Spath, L.F. (1947) Additional observations on the invertebrates (chiefly ammonites) of the Jurassic and Cretaceous of East Greenland. I. The *Hectoroceras* fauna of the S.W. Jameson Land. *Meddelelser om Grønland*, 132, 1–69, pls. 1–5.
- Speden, I.G. (1970) The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota. Part 2. Systematics of the Bivalvia. *Peabody Museum of Natural History Yale University Bulletin*, 33, 1–222.
- Squires, R.L. & Goedert, J.L. (1991) New late Eocene mollusks from localized limestone deposits formed by subduction-related methane seeps, southwestern Washington. *Journal of Paleontology*, 65, 412–416. [http://dx.doi.org/10.1130/0091-7613\(1990\)018<1182:edscil>2.3.co;2](http://dx.doi.org/10.1130/0091-7613(1990)018<1182:edscil>2.3.co;2)
- Squires, R.L. & Gring, M.P. (1996) Late Eocene chemosynthetic? bivalves from suspect cold seeps, Wagonwheel Mountains, central California. *Journal of Paleontology*, 70, 63–73.
- Stanley, S.M. (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). *The Geological Society of America Memoir*, 125, 1–296. <http://dx.doi.org/10.1130/mem125-p1>
- Stanton, T.W. (1895) Contributions to the Cretaceous paleontology of the Pacific coast: the fauna of the Knoxville beds. *United States Geological Survey Bulletin*, 133, 1–132.
- Stewart, F.J. & Cavanaugh, C.M. (2006) Bacterial endosymbioses in *Solemya* (Mollusca: Bivalvia)—model systems for studies

- of symbiont-host adaptation. *Antonie van Leeuwenhoek*, 90, 343–360.  
<http://dx.doi.org/10.1007/s10482-006-9086-6>
- Studencka, B., Gontsharova, I.A. & Popov, S.Y. (1998) The bivalve faunas as a basis for reconstruction of the Middle Miocene history of Paratethys. *Acta Geologica Polonica*, 48, 285–342.
- Surlyk, F. & Zakharov, V.A. (1982) Buchiid bivalves from the Upper Jurassic and Lower Cretaceous of East Greenland. *Palaeontology*, 25, 727–753.
- Taviani, M., Angeletti, L. & Ceregato, A. (2011) Chemosynthetic bivalves of the family Solemyidae (Bivalvia, Protobranchia) in the Neogene of the Mediterranean Basin. *Journal of Paleontology*, 85, 1067–1076.  
<http://dx.doi.org/10.1666/10-119.1>
- Taylor, A.C. (1976) Burrowing behaviour and anaerobiosis in the bivalve *Arctica islandica*. *Journal of the Marine Biological Association of the United Kingdom*, 56, 95–106.  
<http://dx.doi.org/10.1017/s0025315400020464>
- Taylor, J.D. & Glover, E.A. (2000) Functional anatomy, chemosymbiosis and evolution of the Lucinidae. In: Harper, E.M., Taylor, J.D. & Crame, J.A. (Eds.), *The evolutionary biology of the Bivalvia*. Geological Society of London, Special Publications, London, 207–225.  
<http://dx.doi.org/10.1144/gsl.sp.2000.177.01.12>
- Taylor, J.D. & Glover, E.A. (2009) New lucinid bivalves from hydrocarbon seeps of the Western Atlantic (Mollusca: Bivalvia: Lucinidae). *Steenstrupia*, 30, 127–140.
- Taylor, J.D. & Glover, E.A. (2010) Chemosymbiotic Bivalves. In: Kiel, S. (Ed.), *The vent and seep biota. Aspects from microbes to ecosystems*. Topics in Geobiology, Springer, Dordrecht, Heidelberg, London, New York, pp. 107–133.
- Taylor, J.D., Glover, E.A., Smith, L., Dyal, P. & Williams, S.T. (2011) Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). *Zoological Journal of the Linnean Society*, 163, 15–49.
- Taylor, J.D., Glover, E.A. & Williams, S.T. (2008) Ancient chemosynthetic bivalves: systematics of Solemyidae from eastern and southern Australia. *Memoirs of Queensland Museum—Nature*, 54, 75–104.
- Taylor, J.D., Williams, S.T. & Glover, E.A. (2007) Evolutionary relationships of the bivalve family Thyasiridae (Mollusca: Bivalvia), monophyly and superfamily status. *Journal of the Marine Biological Association of the United Kingdom*, 87, 565–574.  
<http://dx.doi.org/10.1017/s0025315407054409>
- Thiele, J. & Jaekel, S. (1931) Muscheln der deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 21, 159–268.
- Todd, J.A. & Palmer, T.J. (2002) The Jurassic bivalve genus *Placunopsis*: new evidence on anatomy and affinities. *Paleontology*, 45, 487–510.  
<http://dx.doi.org/10.1111/1475-4983.00247>
- Totten, J.G. (1834) Description of some new shells, belonging to the coast of New England. *American Journal of Science and Arts*, 26, 366–369.
- Trautschold, H. (1858) Recherches Géologiques aux environs de Moscou. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 23, 546–561, pls. 2, 5.
- Trautschold, H. (1865) Der Inoceramen-Thon von Ssimbirk. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 38, 1–24.
- Van der Land, J. & Nørrevang, A. (1975) The systematic position of Lamellibranchia (Annelida, Vestimentifera). *Zeitschrift für Zoologische Systematik und Evolutionforschung*, 1975, 86–101.
- Van Dover, C.L. (2000) *The ecology of deep-sea hydrothermal vents*. Princeton University Press, Princeton, New York, 352 pp.
- Van Dover, C.L., Aharon, P., Bernhard, J.M., Caylor, E., Doerries, M.B., Flickinger, W., Gillooly, W.P., Goffredi, S.K., Knick, K.E., Macko, S.A., Rapaport, S., Raulfs, E.C., Ruppel, C.D., Salerno, J.L., Seitz, R.D., Sen Gupta, B.K., Shank, T.M., Turnipseed, M. & Vrijenhoek, R.C. (2003) Blake Ridge methane seeps: characterization of a soft-sediment, chemosynthetically based ecosystem. *Deep-Sea Research Part I*, 50, 281–300.  
[http://dx.doi.org/10.1016/s0967-0637\(02\)00162-0](http://dx.doi.org/10.1016/s0967-0637(02)00162-0)
- Verrill, A.E. & Bush, K.J. (1898) Revision of the deep water Mollusca of the Atlantic Coast of North America, with description of new genera and species, Pt. 1, Bivalvia. *Proceedings of the United States National Museum*, 20, 775–901, pls. 71–97.
- Vinn, O., Hryniewicz, K., Little, C.T.S. & Nakrem, H.A. (in press) A boreal serpulid fauna from Volgian–Ryazanian (latest Jurassic–earliest Cretaceous) shelf sediments and hydrocarbon seeps from Svalbard. *Geodiversitas*.
- Vokes, H.E. (1956) Notes on Nucinellidae (Pelecypoda) with description of a new species from the Eocene of Oregon. *Journal of Paleontology*, 30, 652–671.
- Waller, T.R. (1978) Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society of London, B*, 284, 345–365.  
<http://dx.doi.org/10.1098/rstb.1978.0072>
- Waller, T.R. (2012) Morphology, phylogeny, and systematic revision of genera in the Dimyidae (Mollusca, Bivalvia, Pteriomorpha). *Journal of Paleontology*, 86, 829–851.  
<http://dx.doi.org/10.1666/12-004.1>
- Watanabe, H., Fujikura, K., Kojima, S., Miyazaki, J.-I. & Fujiwara, J. (2010) Japan: vents and seeps in close proximity. In: Kiel, S. (Ed.), *The vent and seep biota. Aspects from microbes to ecosystems*. Topics in Geobiology, Springer, Dordrecht,



- Heidelberg, London, New York, pp. 379–401.
- Weaver, C.E. (1942) Paleontology of the marine Tertiary formations of Oregon and Washington. *University of Washington Publications in Geology*, 5, 1–789.
- Weir, J. (1933) Mesozoic fossils from Spitsbergen collected by Dr. G.W. Tyrrell. *Transactions of the Royal Society of Edinburgh*, 57, 637–697, pl. 1.
- Wellnhofer, P. (1964) Zur Pelecypodenfauna der Neuburger Bankkalke (Mittel-Tithon). *Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge*, 119, 1–143, pls. 1–7, tab. 1.
- Wierzbowski, A., Hryniewicz, K., Hammer, Ø., Nakrem, H.A. & Little, C.T.S. (2011) Ammonites from hydrocarbon seep carbonate bodies from uppermost Jurassic–lowermost Cretaceous of Spitsbergen and their biostratigraphical importance. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 262, 267–288.  
<http://dx.doi.org/10.1127/0077-7749/2011/0198>
- Wierzbowski, A., Kulicki, C. & Pugaczewska, H. (1981) Fauna and stratigraphy of the Uppermost Triassic and the Toarcian and Aalenian deposits in the Sassenfjorden, Spitsbergen. *Acta Palaeontologica Polonica*, 26, 195–241, pls. 1–11.
- Wignall, P.B. (1990) Benthic palaeoecology of the late Jurassic Kimmeridge Clay of England. *Special Papers in Palaeontology*, 43, 1–74.
- Wignall, P.B. & Pickering, K.T. (1993) Palaeoecology and sedimentology across a Jurassic fault scarp, NE Scotland. *Journal of the Geological Society*, 150, 323–340.  
<http://dx.doi.org/10.1144/gsjgs.150.2.0323>
- Williams, S.T., Taylor, J.D. & Glover, E.A. (2004) Molecular phylogeny of the Lucinoidea (Bivalvia): non-monophyly and separate acquisition of bacterial chemosymbiosis. *Journal of Molluscan Studies*, 70, 187–202.  
<http://dx.doi.org/10.1093/mollus/70.2.187>
- Wood, S.V. (1840) A catalogue of the shells of the Crag. *Magazine of Natural History*, 6, 243–253.  
<http://dx.doi.org/10.1080/03745484009443291>
- Wood, S.V. (1851) Monograph of the Crag Mollusca with descriptions of shells from the Upper Tertiaries of the British Isles. Part 2. Bivalves. *Palaeontographical Society Monographs*, 4, 1–150, pls. 1–12.  
<http://dx.doi.org/10.5962/bhl.title.25879>
- Woods, H. (1899) A monograph of the Cretaceous Lamellibranchia. Vol. I. *Palaeontographical Society Monographs*, 53, 1–72, pls. 1–14.
- Woods, H. (1904) A monograph of the Cretaceous Lamellibranchia. Vol. II. *Palaeontographical Society Monographs*, 58, 1–56, pls. 1–7.
- Woods, H. (1907) A monograph of the Cretaceous Lamellibranchia. Vol. II. *Palaeontographical Society Monographs*, 61, 133–180, pls. 20–27.
- Yonge, C.M. (1977) Form and evolution in the Anomiacea (Mollusca: Bivalvia)—*Pododesmus*, *Anomia*, *Patro*, *Enigmonia* (Anomiidae): *Placunanomia*, *Placuna* (Placunidae Fam. Nov.). *Philosophical Transactions of the Royal Society of London B*, 276, 453–523.  
<http://dx.doi.org/10.1098/rstb.1977.0005>
- Zakharov, V.A. (1966) *Late Jurassic to early Cretaceous bivalve mollusks of northern Siberia*. Nauka, Moscow, 189 pp, 38 pls. [in Russian]
- Zakharov, V.A. (1981) Buchiidae and biostratigraphy of the Boreal Upper Jurassic and Neocomian. *Transactions of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Science of USSR*, 458, 1–270. [in Russian]
- Zakharov, V.A. & Mesezhnikov, M.S. (1974) The Volgian Stage of the Subarctic Ural. *Transactions of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Science of USSR*, 196, 1–214. [in Russian]
- Zakharov, V.A. & Rogov, M. (2008) Let the Volgian stage stay in the Jurassic. *Russian Geology and Geophysics*, 49, 408–412.  
<http://dx.doi.org/10.1016/j.rgg.2007.09.017>
- Zakharov, V.A. & Shurigin, B.N. (1974) Biostratigraphic and palaeobiogeographic significance of rare Middle Jurassic bivalve mollusks of the Northern Siberia. Biostratigraphy of the Boreal Mesozoic. *Transactions of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Science of USSR*, 136, 109–120, pls. 9–10. [in Russian]
- Zakharov, V.A. & Shurigin, B.N. (1978) Biogeography, facies and stratigraphy of the Middle Jurassic of Soviet Arctic (by bivalve molluscs). *Transactions of the Institute of Geology and Geophysics, Siberian Branch of the Academy of Science of USSR*, 352, 1–206. [in Russian]
- Zardus, J.D. (2002) Protobranch bivalves. *Advances in Marine Biology*, 42, 1–65.  
[http://dx.doi.org/10.1016/s0065-2881\(02\)42012-3](http://dx.doi.org/10.1016/s0065-2881(02)42012-3)
- Zelaya, D.G. (2009) The genera *Thyasira* and *Parathyasira* in the Magellan region and adjacent Antarctic waters (Bivalvia: Thyasiridae). *Malacologia*, 51, 271–290.  
<http://dx.doi.org/10.4002/040.051.0204>
- Zelaya, D.G. (2010) The new species of *Thyasira*, *Mendicula* and *Axinulus* (Bivalvia; Thyasiroidea) from Sub-Antarctic and Antarctic waters. *Polar Biology*, 33, 607–616.  
<http://dx.doi.org/10.1007/s00300-009-0736-9>
- Zuschin, M., Mandic, O., Harzhauser, M. & Pervesler, P. (2001) Fossil evidence for chemoautotrophic bacterial symbiosis in the thyasirid bivalve *Thyasira michelottii* from the Middle Miocene (Badenium) of Austria. *Historical Biology*, 15, 223–234. <http://dx.doi.org/10.1080/10292380109380594>

**APPENDIX 1.** List of non-type specimens used in this study.

Species	PMO numbers and localities
<i>Solemya (Petrasma) cf. woodwardiana</i> Leckenby, 1859	One specimen from seep 1 (224.955); three from seep 3 (224.958, 224.961–962); three from seep 5 (217.260, 224.956, 224.974); one from seep 8 (224.960); 13 from seep 9 (217.168, 217.170, 217.176–177, 217.245, 217.249, 224.963–966, 224.969–970, 224.975, 225.094); five from seep 12 (224.957, 224.959, 224.967–968, 224.990).
<i>Nucinella svalbardensis</i> <b>sp. nov.</b>	One specimen from seep 1 (225.008); one from seep 2 (217.262); 16 from seep 3 (224.988, 224.991–992, 224.997–998, 225.002–003, 225.005, 225.010, 225.012, 225.014, 225.040, 225.052, 225.062–064); eight from seep 5 (225.022, 225.026–027, 225.037–038, 225.054, 225.059–060); 45 from seep 9 (217.171, 217.178, 217.181, 217.225, 224.966, 224.976–982, 224.985–986, 224.989, 224.994–995, 225.004, 225.013, 225.015, 225.020–021, 225.030, 225.033–035, 225.041–051, 225.056, 225.058, 225.065, 225.500, 225.083, 225.106–107, 225.121); 19 from seep 12 (224.999, 225.006, 225.009, 225.011, 225.016–019, 225.023, 225.024, 225.028, 225.029, 225.032, 225.036, 225.039, 225.053, 225.055, 225.057, 225.061); 6 from seep 13 (217.150, 217.216, 217.217, 224.983, 224.993, 225.501); one from seep 14 (224.987); one from seep 15 (224.984).
<i>Dacromya chetaensis</i> Sanin, 1976	Three specimens from seep 12 (217.580–581, 226.600).
<i>Mesosaccella rogovi</i> <b>sp. nov.</b>	Nine specimens from seep 1 (217.384, 217.418–421, 217.458–461); two from seep 2 (217.586, 217.590); 24 from seep 3 (217.375–376, 217.394, 217.407, 217.415, 217.425–426, 217.446–452, 217.464–465, 217.467, 217.474, 217.475, 217.476, 217.499, 217.534, 217.536, 217.591); nine from seep 5 (217.372–374, 217.382–383, 217.396–397, 217.408, 217.455); five from seep 8 (217.377, 217.395, 217.410–411, 217.456); 28 from seep 9 (217.229, 217.538–539, 217.378, 217.379, 217.381, 217.387–390, 217.399–400, 217.405, 217.409, 217.437, 217.443–444, 217.473, 217.488–495, 217.539, 217.587); eight from seep 12 (217.423, 217.457, 217.469, 217.471, 217.480, 217.535, 217.537, 217.584); one from seep 13 (217.479); three from seep 15 (217.371, 217.386, 217.398).
<i>Mesosaccella toddi</i> <b>sp. nov.</b>	One specimen from seep 1 (217.617); one from seep 3 (224.859); 31 from seep 9 (217.219, 217.594, 217.603–604, 217.609–611, 217.615–616, 224.850–858, 224.860–868, 225.116, 225.119, 225.031, 225.650); two from seep 12 (224.620–621).
Pectinida gen. et sp. indet.	Five specimens from seep 3 (217.196, 226.609–611, 226.612).
<i>Buchia</i> spp.	One specimen from seep 4 (226.648); two from seep 9 (217.182, 226.649); 153 un-numbered specimens from seeps 2, 3, 4, 5, 7, 8, 9, 10, 12, 13 and 15.
<i>Oxytoma octavia</i> (d'Orbigny, 1850)	37 specimens; four right valves: two from seep 3 (217.214, 217.563) and two from seep 9 (217.570, 225.118); 33 left valves: 12 from seep 3 (217.333, 217.335, 217.338–339, 217.342–343, 217.345, 217.349, 217.514, 217.523, 217.554, 217.559); two from seep 5 (217.197, 217.524); eight from seep 8 (217.332, 217.336, 217.337, 217.340, 217.346, 217.556, 217.557, 217.562); 11 from seep 9 (217.334, 217.341, 217.347, 217.367, 217.440, 217.513, 217.555, 217.558, 217.570, 225.117, 225.125); one from seep 12 (217.560); one from seep 15 (217.344);.
<i>Camptonectes</i> ( <i>Costicamptonectes</i> ) aff. <i>milnelandensis</i> Fürsich, 1982	Two specimens from seep 8 (226.606–607); one from Dorsoplanites bed (226.604).
<i>Camptonectes</i> ( <i>Camptochlamys</i> ) <i>clathratus</i> (Roemer, 1836)	Two specimens from seep 8 (217.606, 226.605); one from Dorsoplanites bed (226.603).
<i>Camptonectes</i> spp.	One numbered specimen from seep 9 (217.191); 118 unnumbered specimens from seeps 1, 3, 4, 8 and 9.
<i>Pseudolimea arctica</i> (Zakharov, 1966)	18 specimens from seep 9 (217.194, 217.363, 217.368–370, 217.522, 217.551–553, 217.561, 217.566–569, 217.571–573, 225.100).
<i>Tehamatea rasmusseni</i> <b>sp. nov.</b>	60 specimens from seep 9 (217.169, 217.173, 217.227, 217.234, 217.237–238, 217.240–244, 217.246–247, 217.267, 217.272, 217.278, 225.071–082, 225.084–092, 225.094–099, 225.101–105, 225.108–115, 225.122–124, 225.126, 225.130).

.....continued on the next page

**APPENDIX 1.** (Continued)

Species	PMO numbers and localities
<i>Cretaxinus hurumi</i> <b>gen. et sp. nov.</b>	56 specimens from seep 9 (217.172, 217.179–180, 217.183, 217.215, 217.226, 217.228, 217.259, 217.263, 217.266, 217.269–270, 217.273–277, 217.540–541, 225.127–129, 225.131–162, 225.164–165).
<i>Pseudotrapezium</i> aff. <i>groenlandicum</i> Spath, 1936	Two specimens from seep 2 (226.624–226.625); two from seep 3 (226.618–619); one from seep 5 (226.626); five from seep 8 (226.620–623, 226.647); 804 from seep 9 (217.192, 226.633–635 and numerous specimens clustered in blocks 226.613–617, 226.636–647 and accompanying loose); six from seep 12 (226.627–632).
<i>Goniomya literata</i> (Sowerby, 1819)	Two specimens from seep 3 (217.193, 217.358), one from seep 9 (217.359).

**APPENDIX 2.** Measurements of bivalve species discussed in the paper.

**APPENDIX 2A** Measurements for *Solemya (Petrasma) cf. woodwardiana* Leckenby, 1859, from Svalbard compared to *Solenomya torelli*, *Solemya woodwardiana* and *Unio togata*.

Collection number	Species	Locality	Reference	L	H	W
PMO 217.168	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	–	32	23.5
PMO 217.170	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	63	22	17
PMO 217.176	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	52	22	8
PMO 217.177	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	54	23	16.5
PMO 217.245	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	–	21	14.5
PMO 217.249	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	42.6	16.5	12.8
PMO 217.260	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	25	9.5	5.5
PMO 224.955	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	60	21	16
PMO 224.956	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	14	4.2	4
PMO 224.961	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	46	19	11
PMO 224.963	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	50	21	15
PMO 224.964	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	46	18	15
PMO 224.967	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	38	17	8.5
PMO 224.970	<i>Solemya (Petrasma) cf. woodwardiana</i>	Svalbard	This study	62	27	20
s/n	<i>Solenomya torelli</i>	Svalbard	Lindström (1865)	52	16	–
SM J6008	<i>Solemya woodwardiana</i>	England	Duff (1978)	29	11.5	–
SM J12570	<i>Solemya woodwardiana</i>	England	Duff (1978)	25	12	–
s/n	<i>Unio togata</i>	Central Russia	Trautschold (1858)	22	8	–

**APPENDIX 2B.** Measurements for *Nucinella svalbardensis* **sp. nov.** (in mm).

PMO collection number	L	H	W	Pl
217.229	19	8.8	5	14
217.371	17.3	8	5	13.9
217.375	13	5.8	3	10.5
217.377	13.2	6.9	4.6	10.1
217.378	16.5	7	6.2	11.5
217.379	14.6	5	4	11.1
217.387	18.8	7.5	4	15
217.388	19.5	8	4	16
217.394	11.8	5.2	3.3	9
217.395	15	7.9	3	11.5
217.396	9.1	3.8	2	6.5
217.398	13.8	5.2	3.8	10.5
217.399	23	9.1	8.2	17
217.408	8.2	3.5	2	6.3
217.410	11.7	6.1	4	9
217.415	16.1	7.8	4	13.1
217.419	9.5	4	2.5	7
217.420	4.2	2	1.5	3.3
217.425	5.1	3.1	2.1	4.5
217.430	3.5	1.2	1	2.5
217.432	5.2	2	1.6	4.1
217.433	5.6	1.8	1.5	4
217.434	5.2	2.9	1.8	4.5
217.435	7.2	2.6	1.6	5.6
217.449	15.9	5.4	3.8	12.8
217.452	17.8	7.8	7	13.5
217.467	6	3.2	2	4.5
217.479	13	6.9	4	9.3
217.480	10.1	4	2	8
217.488	20.5	7.9	6	16
217.489	21.5	8.9	7	17
217.534	15.2	6.8	5.2	12.2
217.535	17.8	7	4	15
217.537	15.5	6.5	3.9	13
217.538	17.1	7	5	13
217.590	7.3	4	2.5	5.5
224.971	20	8.2	4.2	16

**APPENDIX 2C.** Measurements for *Dacromya chetaensis* Sanin, 1976 (in mm, ratio dimensionless).

PMO collection number	L	H	W	W/H	H/L	PI	PI/L	Anterior teeth number	Posterior teeth number
217.580	7	5.1	3.1	0.61	0.73	2.7	0.39	7	–
217.581	11.5	7.25	5.25	0.72	0.63	4.6	0.4	11	6

**APPENDIX 2D.** Measurements for *Mesosacella rogoi* sp. nov. (in mm).

PMO collection number	L	H	W	PI
217.229	19	8.8	5	14
217.371	17.3	8	5	13.9
217.375	13	5.8	3	10.5
217.377	13.2	6.9	4.6	10.1
217.378	16.5	7	6.2	11.5
217.379	14.6	5	4	11.1
217.387	18.8	7.5	4	15
217.388	19.5	8	4	16
217.394	11.8	5.2	3.3	9
217.395	15	7.9	3	11.5
217.396	9.1	3.8	2	6.5
217.398	13.8	5.2	3.8	10.5
217.399	23	9.1	8.2	17
217.408	8.2	3.5	2	6.3
217.410	11.7	6.1	4	9
217.415	16.1	7.8	4	13.1
217.419	9.5	4	2.5	7
217.420	4.2	2	1.5	3.3
217.425	5.1	3.1	2.1	4.5
217.430	3.5	1.2	1	2.5
217.432	5.2	2	1.6	4.1
217.433	5.6	1.8	1.5	4
217.434	5.2	2.9	1.8	4.5
217.435	7.2	2.6	1.6	5.6
217.449	15.9	5.4	3.8	12.8
217.452	17.8	7.8	7	13.5
217.467	6	3.2	2	4.5
217.479	13	6.9	4	9.3
217.480	10.1	4	2	8
217.488	20.5	7.9	6	16
217.489	21.5	8.9	7	17
217.534	15.2	6.8	5.2	12.2
217.535	17.8	7	4	15
217.537	15.5	6.5	3.9	13
217.538	17.1	7	5	13
217.590	7.3	4	2.5	5.5
224.971	20	8.2	4.2	16

**APPENDIX 2E.** Measurements for *Mesosaccella toddi* sp. nov (in mm).

PMO collection number	L	H	W	Pl
217.594	10.5	6.2	4.5	7
217.603	10	6.9	5.6	6
217.604	8.9	5	4	5
217.609	3.5	2.15	1.9	2.1
217.610	5.0	3	2.8	3
217.611	8.5	5.6	4.3	5.5
217.616	6.9	4.2	3.2	4.1
217.615	8.9	5.8	4	4.9
217.617	6.9	4	3	4.1
217.620	10.9	7.8	7.1	7.4
217.621	9.5	6	4.6	6.5
224.850	9.2	5.5	5	5.5
224.851	10.9	6.9	4.6	5.9
224.857	9.3	6	5.8	5.8
224.861	12.5	8.2	6.5	7.9
224.862	10	6.8	5.2	4.5
224.863	9.8	6.5	4.8	6.6
224.864	12.3	7.7	6	7.5
224.867	6	4.2	4	3.9
224.865	8.8	5.2	5	5.5
225.119	8.1	5.1	4.6	4.3

**APPENDIX 2F.** Measurements for *Oxytoma octavia* (d'Orbigny, 1850) (in mm).

PMO collection number	L	H	Lh	Plh
217.513	8.3	8.7	6.9	5.1
217.524	–	10.3	10.1	7.5
217.555	24.05	23.5	17.1	11.6
217.556	15.6	15.2	12.1	8.6
217.557	8.5	8.9	5.8	3.8
217.559	7	7	6.1	4
217.560	10.1	9.9	7.1	4.7

**APPENDIX 2G.** Measurements for *Camptonectes* (*Costicamptonectes*) aff. *milnelandensis* Fürsich, 1982 (in mm, angle in degrees).

PMO collection number	L	H	Ua
226.604	30.5	28.2	120
226.606	15	15	90

**APPENDIX 2H.** Measurements for *Camptonectes (Camptochlamys) clathratus* (Roemer, 1836) (in mm).

PMO collection number	L	H
226.603L	23.8	23.2
226.603R	22	20.6
217.606	15.8	15.8
217.608	18.5	17.5

**APPENDIX 2I.** Measurements for *Pseudolimea arctica* (Zakharov, 1966) from Svalbard compared to other specimens of *P. arctica* and *P. cf. arctica*, *P. multicosata* (Fürsich, 1982), *P. aff. parallela* (d'Orbigny), and *Lima (Mantellum) parallela* (Sowerby, 1812) (in mm, ratio and number of ribs dimensionless).

Collection number	Species	Locality	Reference	L	H	H/L	Rp
PMO 217.194	<i>Pseudolimea arctica</i>	Svalbard	This study	26.5	27	0.98	33
PMO 217.350	<i>Pseudolimea arctica</i>	Svalbard	This study	20.5	21	0.98	35
PMO 217.351	<i>Pseudolimea arctica</i>	Svalbard	This study	34	31.5	1.08	29
PMO 217.352	<i>Pseudolimea arctica</i>	Svalbard	This study	26.5	25.1	1.06	31
PMO 217.522	<i>Pseudolimea arctica</i>	Svalbard	This study	33	31	1.06	33
PMO 217.552	<i>Pseudolimea arctica</i>	Svalbard	This study	22.5	22	1.02	35
PMO 217.553	<i>Pseudolimea arctica</i>	Svalbard	This study	26.5	26.2	1.01	31
PMO 217.561	<i>Pseudolimea arctica</i>	Svalbard	This study	26	25.1	1.04	27
PMO 217.571	<i>Pseudolimea arctica</i>	Svalbard	This study	18.1	16	1.13	24
Other							
150/1556	<i>Lima (Pseudolimea) arctica</i>	Siberia	Zakharov (1966)	24.2	23.8	1.02	19
150/3670	<i>Lima (Pseudolimea) aff. parallela</i>	Siberia	Zakharov (1966)	32	30	1.07	27
150/3844	<i>Lima (Pseudolimea) arctica</i>	Siberia	Zakharov (1966)	33.1	34	0.97	20
150/3904	<i>Lima (Pseudolimea) arctica</i>	Siberia	Zakharov (1966)	33.5	32.1	1.04	26
150/449	<i>Lima (Pseudolimea) arctica</i>	Siberia	Zakharov (1966)	29	27.1	1.07	21
150/5183	<i>Lima (Pseudolimea) arctica</i>	Siberia	Zakharov (1966)	23.5	22.7	1.04	21
150/5184	<i>Lima (Pseudolimea) arctica</i>	Siberia	Zakharov (1966)	28.3	27.5	1.03	17
GGU 235522	<i>Pseudolimea arctica</i>	East Greenland	Fürsich (1982)	33	31	1.06	22
BGS AJJB1179	<i>Pseudolimea multicosata</i>	East England	Kelly (1984)	20	17	1.18	21
BGS CE3674	<i>Pseudolimea multicosata</i>	East England	Kelly (1984)	17	11	1.55	23
BGS Zu401	<i>Pseudolimea multicosata</i>	East England	Kelly (1984)	18	15	1.2	22
1	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	26	21	1.24	
2	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	26	22	1.18	
3	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	25	20	1.25	
4	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	23	19	1.21	
5	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	23	18	1.28	
6	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	22	17	1.29	
7	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	19	16	1.19	
8	<i>Lima (Mantellum) parallela</i>	England	Woods (1904)	14	11	1.27	

**APPENDIX 2J.** Measurements for *Tehamatea rasmusseni* **sp. nov** (in mm).

PMO collection number	L	H	W	La	Pl	LI
217.169	87.5	67	41.2	32.5	55	16.9
217.173	79	62	41	33	46	17
217.227	65	55.5	31	32	33	15
217.234	85.5	66	40	28.5	57	19
217.237	91.3	–	–	–	–	–
217.238	63	53	36	20	43	17
217.240	78	65	40	27	51	15
217.241	34.5	27.8	15	19.5	15	9
217.242	–	–	42.2	–	–	–
217.243	–	64.5	34	–	–	–
217.244	100	76	54	42.5	57.5	–
217.246	71.2	58	33	32.2	39	16
217.247	74	57.8	33.8	36.5	37.5	15
217.272	65.5	52.5	36	24.5	41	17
217.278	58	49.5	31.3	26.2	31.8	14.2
225.071	42.8	38	24.8	13.6	29.2	10.1
225.072	59	50.4	30.2	26	33	–
225.073	79	66	40	34	45	–
225.079	–	–	–	49	–	–
225.080	–	–	49.5	43	–	20.3
225.081	82	65.2	34	41	41	15
225.084	–	61.2	37	–	41.8	–
225.086	–	–	28.1	–	37.5	–
225.088	–	–	46	–	–	–
225.089	–	76	46	–	–	–
225.090	–	–	39	–	–	–
225.091	70.5	56	37	27	43.5	–
225.092	73	60	34	38	35	–
225.096	–	62.2	42	–	–	–
225.097	–	–	31.2	–	–	–
225.098	–	56.5	32.5	–	–	–
225.101	–	74.5	–	–	–	–
225.102	17	13.5	7.3	7.5	9.5	3.5
225.103	52.1	43	28	21.1	31	13
225.104	56	48	28	26	30	13
225.105	77.5	66	40	36.5	41	–
225.109	–	53	37.5	–	–	–
225.110	–	39.8	25.5	–	–	13
225.111	74.5	66.5	40	36.5	38	15
225.113	56	50	30.5	25	31	–
225.114	–	–	47	–	–	–
225.115	72.5	63.5	43	24.5	48	16.5
225.122	54.5	42	28.2	22	32.5	10
225.123	–	51	30.5	–	–	–
225.124	25.5	22.2	13	12.5	13	6



**APPENDIX 2K.** Measurements for *Cretaxinus hurumi* **gen. et sp. nov** (in mm).

PMO collection number	L	W	H	PI
217.172	56	32.8	44.5	36.2
217.180	23	12.6	19	14
217.183	48.7	29	39	34
217.215	50.5	28	39	35.5
217.226	43	31.5	37	23.5
217.228	54	33	42	35.5
217.259	53.5	32	45.8	37.5
217.263	42.5	26	33.3	25.8
217.269	35.5	19	30.5	24
217.274	33	18.2	25.5	22
217.277	45.2	27	37.2	27
217.540	54	39	49	39
217.541	56.5	35.5	50	35.5
225.127	35.8	20.6	31	24.5
225.128	48	29	39.8	30
225.129	37	20.3	30.5	27
225.131	43.3	29	37	25.5
225.132	52	30	41.5	33
225.133	45.5	26.5	35.5	29.5
225.136	54	39	43	32
225.139	32.5	18	27	20
225.141	53.2	33	45	31.5
225.142	39.8	21.8	33.5	26
225.145	42	25	36.5	28
225.150	48	26.4	38.7	31.2
225.151	52	32	41	33
225.153	44	30.5	38.5	28
225.154	55	33	47	31
225.157	47	25.5	40	28
225.158	38	22.2	34.5	28
225.159	36	22	29	22
225.161	41.5	26	33	26

APPENDIX 2L. Measurements for un-numbered *Pseudotrapezium* aff. *groenlandicum* Spath, 1936.

L	H	W	Pl
12	9.8	8	7
13.8	11.2	9	8.1
12	9.9	8	8.8
14.2	10.9	10	9
12.8	10.5	9.2	8
14	10.2	9	9.5
12	10	8.2	7.7
13.3	10.2	8.3	8.5
13	10.5	8.1	7.8
12.8	10	7.8	9
13.5	10.5	9.3	9.5
12.8	9.5	8.2	8.2
14	10.2	9	9.5
13.8	9.2	9	8.8
15	11.2	9.8	11
15	11	10	10.5
13	9.8	8.7	8
14.1	10.4	9	8.5
14	10	8.8	10
14	10.5	9	9
12.5	9.7	8.2	8.8
13	9.7	8.8	8.8
14	10.8	9.6	8.5
14.2	11	9.8	9.5
14.5	11.8	9.8	9.5
14	10.8	9	9
14.8	11.5	10	10
14.5	11.2	9.5	9
13	9	8.5	8.1
12.2	10	8.1	8.1
12	10.2	8	8