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3 **1 A silicified Early Triassic marine assemblage from Svalbard**
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2
3 12 **Abstract**
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5 13 Understanding how the marine biosphere recovered from the late Permian mass extinction
6 14 event is a major evolutionary question. The quality of the global fossil record of this interval
7 15 is, however, somewhat poor due to preservational, collection and sampling biases. Here we
8 16 report a new earliest Induan (*Hindeodus parvus* Zone) marine assemblage from the
9 17 Deltadalen Member of the Vikinghøgda Formation, central Spitsbergen, which fills a critical
10 18 gap in knowledge. The fully silicified fossils comprise the oldest silicified assemblage known
11 19 from the Triassic and provide critical new systematic data. For its age, the assemblage is
12 20 exceptionally diverse with 14 species of bivalves and gastropods, as well as conodonts and
13 21 ammonoids. Four new bivalve species (*Austrotindaria antiqua*, *A. svalbardensis*, *Nucinella*
14 22 *taylori* and *N. nakremi*) and one new gastropod species (*Glabrocingulum parvum*) are
15 23 described, and five families are recorded in the Induan for the first time. Some of the
16 24 common and globally widespread Early Triassic taxa, such as *Unionites*, are also present and
17 25 their exceptional preservation reveals key morphological characters that are documented for
18 26 the first time. Taxonomic and ecological revisions based on these new data suggest that
19 27 shallow-infaunal deposit-feeders were a dominant component of pre-Spathian benthic
20 28 communities. The gastropods and bivalves all possessed a planktotrophic larval stage, which
21 29 may have been a particular advantage in the wake of the late Permian mass extinction.

22 30 **Keywords:** extinction; Early Triassic; diversification; Mollusca; Protobranchia;
23 31 chemosymbiosis.
24 32

33 Introduction

34 The aftermath of the late Permian mass extinction represents a key interval in the
35 diversification of marine biota. Even though 78% of marine genera are estimated to have
36 gone extinct during the late Permian event no novel phyla or classes and only one new mode
37 of life originated during the extinction aftermath (Erwin et al. 1987; Foster & Twitchett
38 2014). The re-diversification of benthic groups in the wake of the extinction, e.g. bivalves
39 (Nakazawa & Runnegar 1973; Komatsu et al. 2004; Fraiser & Bottjer 2005; Hautmann 2007;
40 Posenato 2008) and gastropods (Erwin & Pan 1996; Nützel 2005; Gründel & Nützel 2012), is
41 typically described as occurring in the Middle Triassic, resulting in the traditional view of a
42 ‘delayed’ post-Permian recovery. The Early Triassic fossil record is, however, notoriously
43 poor, as evidenced by an unusually high number of Lazarus taxa, due to the typical mouldic
44 preservation of shells (Nakazawa & Runnegar 1973; Wheeley & Twitchett 2005), their small,
45 easily overlooked, sizes (Hautmann & Nützel 2005), as well as the substantial regional and
46 latitudinal sampling bias towards low (tropical) palaeolatitudes of Palaeotethys (Foster &
47 Twitchett 2014).

48 Better preserved benthic fossil assemblages have been reported from the Induan of
49 South China (Kaim et al. 2010; Hautmann et al. 2011; 2015) and Primorye, Russia (Shigeta et
50 al. 2009), and from the Olenekian of the western USA (Batten & Stokes 1987; Hautmann &
51 Nützel 2005; Nützel & Schulbert 2005; Pruss et al. 2015) and Pakistan (Wasmer et al. 2012;
52 Kaim et al. 2013). In addition, a partially silicified fauna is known from the Griesbachian of
53 Oman (Twitchett et al. 2004; Wheeley & Twitchett 2005; Oji & Twitchett 2015). Studies of
54 those assemblages have shown that a greater number of bivalve, gastropod and crinoid
55 lineages survived the late Permian mass extinction event and/or were present in the Early
56 Triassic than previously thought. These partially silicified and better preserved assemblages
57 still lack key diagnostic characters of many taxa, however, especially the internal morphology
58 of bivalve shells, making taxonomic assignments often equivocal.

59 Better preserved early Induan (Griesbachian) fossil assemblages from palaeotropical
60 localities have been critical in demonstrating that taxonomically and ecologically diverse
61 benthic ecosystems reappeared locally in some settings by the second conodont zone of the
62 Triassic in Neotethys (Twitchett et al. 2004). At higher latitudes, however, early Induan
63 shelly benthic assemblages are rarely reported and typically consist of poorly preserved
64 cosmopolitan generalists, such as *Claraia*, *Unionites*, *Lingularia* and *Warthia* (Spath 1930;
65 Mørk et al. 1999; Zonneveld et al. 2007). In these regions, trace fossils are typically used as a

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3 66 measure of documenting ecosystem collapse and recovery (following Twitchett 2006) and
4 67 demonstrate that rapid local recovery of the infauna took place within the earliest Induan
5 68 (Twitchett & Barras 2004; Beatty et al. 2008; Zonneveld et al. 2010). From their analysis of
6 69 global fossil occurrences, Foster & Twitchett (2014) also concluded that during the Induan
7 70 the benthic fauna of the extratropical northern palaeolatitudes contained a greater ecological
8 71 diversity than that of the palaeotropics.

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13 72 Here, we describe the first silicified fossil assemblage from the Lower Triassic of the
14 73 northern palaeolatitudes. The assemblage was recovered from the lower Griesbachian of
15 74 central Spitsbergen, Svalbard, making it the oldest silicified assemblage known from the
16 75 Mesozoic. It is the first fully silicified assemblage of Early Triassic age and the exquisite
17 76 preservation of the internal and external morphology of the bivalve and gastropod shells
18 77 provides critical new taxonomic data that have major implications for our understanding of
19 78 the response of marine ecosystems to the late Permian mass extinction event and of the
20 79 stratigraphic ranges of several molluscan families.

26 27 28 81 **Materials**

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30
31 82 The fossil assemblage described herein was recovered from two carbonate concretions,
32 83 collected by WJF & RJT in 2013 from 11.9 and 12.6 m above the base of the Deltadalen
33 84 Member of the Vikinghøgda Formation, Lusitaniadalen, Svalbard (N78° 17' 54.8", E016° 43'
34 85 59.3"; Fig. 1). The fossils were extracted in the laboratory by first mechanically
35 86 disaggregating 3kg samples to expose larger fossils. Remaining rock fragments were then
36 87 dissolved using the buffered formic acid technique of Jeppsson & Anehus (1995). To
37 88 maximise yield, the residue was collected at ca. 12-hour intervals, washed thoroughly with
38 89 tap water to remove any excess solution and to avoid crystal growth, and dried. The buffered
39 90 solution was renewed every 48 hours. Heavy liquid separation (Mitchell & Heckert 2010)
40 91 was used to separate the fossils from the remaining residue. The specimens are housed in the
41 92 Natural History Museum, London.

49 50 51 94 **Geological setting**

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53
54 95 During the Early Triassic, the Svalbard archipelago was situated at ca. 45-50°N in the
55 96 southern part of the Boreal Ocean (Fig. 1; Hounslow et al. 2008). In central Spitsbergen, the
56 97 Vikinghøgda Formation, described by Mørk et al. (1999), records deposition through the

1
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3 98 latest Permian and entire Early Triassic in a siliciclastic, open-marine, shelf setting. It is
4
5 99 divided into three members, of which the Deltadalen Member is the lowest (Mørk et al.
6
7 100 1999). At the study site in Lusitaniadalen, the basal 1.6 m of the Deltadalen Member is
8
9 101 composed of bedded, well-bioturbated, fine- to medium-grained, glauconitic sandstones that
10
11 102 are very similar to the underlying Kapp Starostin Formation except that they lack diagenetic
12
13 103 chert nodules (Mørk et al. 1999; Nabbefeld et al. 2010). These sandstones contain a diverse
14
15 104 trace fossil assemblage, indicating a fully functional benthic ecosystem that was living under
16
17 105 well-oxygenated conditions (Nabbefeld et al. 2010). In contrast, the body fossil assemblage is
18
19 106 limited, comprising mainly the phosphatic-shelled lingulid brachiopods, which may indicate
20
21 107 preservational bias.

22
23 108 The sandstones record the onset of marine transgression (Mørk et al. 1999; Nabbefeld
24
25 109 et al. 2010) with the base of the overlying laminated, silty mudstones marking significant
26
27 110 deepening. Several horizons of cemented siltstones and tabular concretions are found in the
28
29 111 lower few metres of this mudstone-dominated interval and contain coarser laminae with
30
31 112 abundant ichthyoliths and disarticulated lingulid shells. Occasional, 1-5cm thick, fine-
32
33 113 grained, pyritic and glauconitic, graded, cemented sandstones, interpreted as distal
34
35 114 tempestites, also occur within the laminated silty mudstones. Biomarker data support the
36
37 115 interpretation based on field observations that deposition took place under anoxic and
38
39 116 periodically euxinic conditions during transgression and maximum flooding, with evidence of
40
41 117 phytoplankton blooms in the surface waters likely driven by nutrient influx (Nabbefeld et al.
42
43 118 2010).

44
45 119 From ca. 10m above the base of the mudstones, the lithologies become noticeably
46
47 120 coarser with a greater proportion of interbedded siltstones and very fine sandstones,
48
49 121 presumably due to progradation or sealevel fall. The coarser, heterolithic beds are
50
51 122 bioturbated, initially by mm-diameter *Planolites* and then with the addition of *Skolithos* and
52
53 123 *Arenicolites* ca. 1.5 m higher, indicative of environmental amelioration and deposition under
54
55 124 more persistently oxygenated conditions. Ichnofabric index remains low (ii2-3), however,
56
57 125 and the burrows are small (diameters <5mm) and do not penetrate deeply, indicating that the
58
59 126 environment was probably still not fully optimal for benthic colonisation. Earliest Triassic
60
127 ammonoids, conodonts and a moderate benthic assemblage have already been recorded from
128
129 the *Planolites*-dominated interval (Mørk et al. 1999). One of the concretions that yield the
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silicified assemblage documented in this study derives from that same horizon, 12.6 m above
the base of the formation. The second concretion was collected from ca. 65 cm lower (Fig. 1).

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3 131 The age of the Deltadalen Member is well constrained by biostratigraphy (ammonoids
4 132 and conodonts) and magnetostratigraphy, with deposition recorded from the upper
5 133 Changhsingian, prior to the late Permian mass extinction event, through most of the Induan
6 134 (Mørk et al. 1999; Hounslow et al. 2008; Nakrem et al. 2008). Locally, the late Permian
7 135 extinction event is recorded by the disappearance of prolific bioturbation just below the top of
8 136 the glauconitic sandstones, 1.6m above the base of the member (Nabbefeld et al. 2010). From
9 137 conodont evidence, Nakrem et al. (2008) inferred that the Permian/Triassic boundary occurs
10 138 between 5 m and 11 m above the base of the Deltadalen Member. *Claraia* cf. *wangi* is
11 139 recorded 10.1 m above the base of the member at Lusitaniadalen, indicative of a Griesbachian
12 140 age. The silicified assemblages described herein are of earliest Griesbachian (earliest Induan)
13 141 age, and are assigned to the upper part of the *Otoceras boreale* Zone, which corresponds to
14 142 the basal Triassic *Hindeodus parvus* Conodont Zone (Orchard 2007).
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144 Systematic palaeontology

145
146 Phylum **Brachiopoda** Duméril, 1805

147 Class **Lingulata** Goryansky & Popov, 1985

148 Order **Lingulida** Waagen, 1885

149 Family: **Discinidae** Gray, 1840

150 Genus **Orbiculoidea** d'Orbigny, 1847
151

152 **Type species.** *Orbicula forbesii* Davidson, 1848; Silurian, Wenlock; West Midlands, England.
153

154 **Diagnosis.** The generic diagnosis follows Mergl (2006). Shell thin, strongly dorsibiconvex,
155 subcircular, with subtrapezoidal outline of the posterior part. Ornament on both valves
156 composed of regular raised concentric fila separated by broader interspaces. Dorsal valve is
157 conical to subconical with subcentral apex; ventral valve with subcentral apex. Ventral valve
158 depressed conical with subcentral apex. Pedicle track narrow, tapering posteriorly and
159 anteriorly closed by shallow listrium; foramen in posterior end of listrium with short internal
160 tube.
161

162 Species **Orbiculoidea winsnesi** Gobbet, 1963

163 (Fig. 2A)

164 1963 *Orbiculoidea winsnesi* Gobbett, p. 46; Plate 1; Figs 4-5.
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3 165 **Material.** One dorsal valve from LD-04 ([NHMUK PI BE 3238](#)).

4
5 166 **Description.** Shell outline is sub-circular, with its length slightly greater than the width. The
6
7 167 [dorsal](#) valve is inflated to an apex, which is located about a third of the diameter from the
8
9 168 anterior margin. Shell smooth, except for fine concentric growth lines.

10
11 169 **Remarks.** Extant solitary discinids are sessile, epifaunal, invertebrates that attach to hard
12
13 170 surfaces with a sucker-like pedicle (Mergl 2010). They have been attaching to shelled
14
15 171 invertebrates since the Ordovician (Mergl 2010), and one of the specimens described herein
16
17 172 is attached to an ammonoid. Discinids are suspension feeders and their co-occurrence with
18
19 173 lingulids in laminated black shales has led some authors to interpret them as being tolerant of
20
21 174 low-oxygen conditions (Savoy 1992; Hallam 1995; Mergl 2010).

22 175 **Mode of Life.** Surficial, stationary, attached, suspension feeder (Mergl 2010).

23 176

24 177

Phylum **Mollusca** Linnaeus, 1758

26 178

Class **Bivalvia** Linnaeus, 1758

28 179

Order **Pterioida** Newell, 1965

30 180

Family **Myalinidae** Frech, 1891

32 181

Genus **Promyalina** Kittl, 1904

34 182

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36
37 183 **Type species.** *Promyalina hindi* Kittl, 1904; Permian, Changhsingian; near Sarajevo, Bosnia-
38
39 184 Herzegovina.

40 185 **Diagnosis.** Outline mytiliform and less triangular than *Myalina*; dorsal margin slightly
41
42 186 convex, moderately thickened; narrow beak present. Left valve inflated below the umbo.
43
44 187 Inequivalve with the right valve being less inflated and less curved.

45 188

46 189

Species **Promyalina schamarae** (Bittner, 1899)

48 190

(Fig. 2C-G)

50 191

1899 *Myalina schamarae* Bittner. p. 19; Plate 4; Figs 20-25.

52 192

2009 *Promyalina schamarae*; Kumagai & Nakazawa. p. 157; Fig 144, 4-5.

53 193

54 194

Material. Three specimens from LD-04 ([NHMUK PE PEI 5484](#); [NHMUK PI MB 1202](#);
[NHMUK PI MB 1205](#)) and seven specimens from LD-05 ([NHMUK PI MB 1188](#); [NHMUK](#)

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3 195 [PI MB 1203-1204](#); [NHMUK PE PEI 5475-5476](#); [NHMUK PE PEI 5500](#); [NHMUK PE PEI](#)
4 196 [5503](#)).

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6
7 197 **Description.** Shell is small, mytiliform, inequilateral, prosocline, higher than long, and
8 198 moderately inflated. Umbo is small, terminal and prosogyrate. Posterior dorsal margin is
9 199 straight. Posterior margin is slightly convex, forming a rounded posteroventral margin.
10 200 Anterior margin is long, nearly straight or weakly acute and partly depressed near the umbo.

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14 201 **Remarks.** The internal characters of the shells cannot be observed because all the specimens
15 202 are articulated. Externally, the shells resemble *Promyalina schamarae* from the Griesbachian
16 203 Lazurnaya Bay Formation, Russia (Shigeta et al. 2009), and [are](#) therefore assigned to this
17 204 species. These specimens differ from *P. groenlandica* (Newell 1955), as the beak does not
18 205 project beyond the dorsal margin, and from *P. spathi* in having a more convex anterior
19 206 margin.

20
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24 207 **Mode of life.** Surficial, stationary, attached, suspension feeder (Stanley 1972).
25
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28
29 209 Order **Solemyoida** Dall, 1889

30 210 Family **Nucinellidae** Vokes, 1956
31
32

33
34 212 **Diagnosis.** Shell nuculoid, obliquely oval, higher than long, monomyarian with anterior
35 213 abductor muscle scar only. Hinge with subumbonal taxodont teeth and single elongate lateral
36 214 tooth on the anterior dorsal margin. Ligament mostly opisthodontic, wholly external or in a
37 215 sunken resilifer.

38
39
40 216 **Remarks.** Although living nucinellids are sometimes classified in the family Manzanellidae,
41 217 which extends back into the Permian (e.g. Coan & Valentich-Scott 2012), Oliver & Taylor
42 218 (2012) argued that the Nucinellidae and Manzanellidae should be separated on morphological
43 219 grounds and their conclusions are followed here. *Manzanella*, the type genus of
44 220 Manzanellidae, is dimyarian and subcircular in outline, with its taxodont teeth lying posterior
45 221 to beak. In contrast, *Nucinella* and *Huxleyia* (i.e. the Nucinellidae) are both monomyarian and
46 222 elliptical, with their teeth positioned anterior to the beak (Oliver & Taylor 2012).
47
48
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52 223 Genus *Nucinella* Wood, 1851
53 224

54
55 225 **Type species.** *Pleurodon ovalis* Wood, 1840; Neogene, Pliocene; Suffolk, England.

56
57 226 **Diagnosis.** [Nucinellids with external](#) ligament.
58
59
60

227 **Remarks.** Of the two genera described for the Nucinellidae, *Huxleyia* has a mostly internal
228 ligament set in a sunken resilifer, whereas *Nucinella* has an external ligament. The specimens
229 described herein have an opisthodetic or amphidetic ligament and so are assigned to
230 *Nucinella*.

231
232 Species *Nucinella taylori* sp. nov.

233 (Fig. 3)
234

235 **Diagnosis.** A small *Nucinella* having a nuculoid shape, smooth shell except for growth lines
236 with three subumbonal and two anterior pointed blade like teeth, with no triangular flat area
237 below the dentition; opisthodetic ligament.

238 **Holotype.** Disarticulated Left valve, [NHMUK PI MB 1206](#), LD-04; length = 1.6mm, height =
239 1.6mm.

240 **Paratypes.** Disarticulated Right valve, [NHMUK PI MB 1209](#), LD-04; length = 1.6mm,
241 height = 1.6mm; Disarticulated Right valve, [NHMUK PI MB 1210](#), LD-05; length = 2.1mm,
242 height = 2.3mm.

243 **Other Material.** Two specimens from LD-04 ([NHMUK PI MB 1207-1208](#)) and three
244 specimens from LD-05 ([NHMUK PE PEI 5500](#); [NHMUK PE PEI 5506](#); [NHMUK PE PEI](#)
245 [5517](#)). Fifty-three prodissoconch valves from LD-04 ([NHMUK PI MB 1211-1217](#); [NHMUK](#)
246 [PE PEI 5481](#)) and thirty-six prodissoconch valves from LD-05 ([NHMUK PI MB 1218](#)).

247 **Derivation of name.** Named after Dr. John Taylor (Natural History Museum) in recognition
248 of his work on chemosymbiotic bivalve molluscs.

249 **Description.** Shell is small, thin, inequilateral, equivalve, with a nuculoid, suboval outline.
250 Posterior dorsal margin is slightly incurved; anterior margin almost straight. Opisthogyrate,
251 beaks close to posterior margin, umbo prominent. Smooth shell, except for concentric,
252 irregularly spaced growth lines. Monomyarian: posterior adductor muscle scar absent;
253 anterior adductor large, oval. Opisthodetic ligament, prominent, external does not invade the
254 hinge plate. Hinge made by five pointed blade-like teeth as a single arched series, with the
255 anterior subumbonal teeth being smaller and wider than the posterior ones. A single, long
256 lateral tooth. Left valve with a secondary ridge creating a shallow socket.

257 Prodissoconch valves: outline nuculoid and suboval. Posterior margin is distinct, long
258 and slightly incurved. Inequilateral, with beaks close to posterior margin, and sculpture
259 consists of irregularly spaced growth laminae. Ventral valve margin has a narrow flat

260 platform. Five anterior and eleven posterior hinge teeth. Amphidetic ligament, lying between
261 the beak and anterior hinge plate.

262 **Remarks.** These specimens are most similar to the extant nucinellid *Nucinella serrei*, in their
263 small size, number of posterior and anterior hinge teeth and opisthodetic ligament. These
264 specimens, however, lack a flat triangular area below the teeth dentition and a small circular
265 pit at the end of the lateral tooth, which supports their separation.

266 The majority of extant *Nucinella* range from intertidal to 500m deep (la Perna 2005),
267 but some species have been described from water depths exceeding 3000m (Oliver & Taylor
268 2012). A large fossil *Nucinella* species has been described from a Late Cretaceous cold-seep
269 deposit (Amano et al. 2007), showing that this genus may inhabit a wide range of sulphide-
270 rich environmental settings. Bacterial symbiosis with sulphur-oxidizing bacteria is confirmed
271 for *N. owenensis* and has been inferred for all species of the Nucinellidae (Oliver & Taylor
272 2012). *Nucinella taylori* sp. nov. supplants *N. birkelundi* from the Late Jurassic (Clausen &
273 Wignall 1990) and *Nucinella?* sp. from the Late Triassic (Nützel & Kaim 2014) as the oldest
274 known species of *Nucinella*, and extends the range of the genus to the basal Triassic *H.*
275 *parvus* Conodont Zone.

276 The prodissoconch valves are very similar to adult specimens of *Nucinella taylori* sp.
277 nov. except that they have more hinge teeth, which appears to reflect their pre-metamorphosis
278 stage of development. The position of the ligament in the prodissoconch valves also differs to
279 adult specimens of *N. taylori* sp. nov. in being amphidetic rather than opisthodetic, but this
280 character is known to change after metamorphosis (Bernard, 1898). The prodissoconch
281 valves most resemble *N. taylori* sp. nov. rather than *N. nakremi* sp. nov., but may represent
282 larval stages for either or both species.

283 **Mode of Life.** Shallow infaunal, fully motile, slow, chemosymbiotic (Oliver & Taylor 2012).

284

285 Species *Nucinella nakremi* sp. nov.

286 (Fig. 4)

287 **Diagnosis:** A small *Nucinella* having a nuculoid shape, smooth shell except for growth lines.
288 Prosogyrate beak, one to three subumbonal teeth. Ligament amphidetic and does not invade
289 the hinge plate.

290 **Holotype.** Disarticulated left valve, NHMUK PI MB 1219, LD-04; length = 1.1mm, height =
291 1.1mm.

292 **Paratype.** Disarticulated left valve, [NHMUK PI MB 1220](#), LD-04; length = 0.9mm, height =
293 0.8mm (transposed hinge).

294 **Other Material.** Two specimens from LD-04 ([NHMUK PI MB 1221-1222](#)).

295 **Derivation of name.** Named after Dr. Hans Arne Nakrem in recognition of his work on
296 Permian and Triassic fossils from Svalbard.

297 **Description.** Shell small, nuculoid and ovate. Posterior dorsal margin distinct, slightly
298 incurved; posterior margin rounded. Inequilateral, prosogyrate, with beaks close to anterior
299 margin. Umbo prominent. Smooth, thin shell with very weak growth lines. Monomyarian:
300 posterior adductor muscle scar absent; anterior adductor large, oval. One to two subumbonal,
301 pointed blade-like teeth plus one anterior tooth. Ligament amphidetic, prominent, external
302 does not invade the hinge plate. One left valve (LV) specimen with a long lateral tooth, and
303 another LV specimen with a weak secondary ridge creating a shallow socket.

304 **Remarks.** These specimens differ from other described nucinellid species in having fewer
305 hinge teeth, a more elliptical shape and a prosogyrate beak. Such differences may occur
306 during the ontogeny of *Nucinella* (e.g. Bernard, 1898) and so are not sufficient for
307 assignment to a separate genus. These specimens are, however, considered to represent a
308 separate species rather than an intermediate ontogenetic stage between the protoconch and
309 adult stage of *Nucinella taylori*. During ontogeny, the shape, size and position of nucinellid
310 subumbonal teeth also vary: in earlier stages of development they are more rounded and later
311 they develop a chevron-blade shape with the older teeth making space below the beak for
312 thinner, newer ones (Bernard, 1898; La Perna, 2004). In contrast, the subumbonal teeth of
313 specimens assigned to *N. nakremi* and *N. taylori* have comparable shapes, and so indicate a
314 similar stage of development. Furthermore, because the position of the ligament in
315 nucinellids is fixed after metamorphosis (Bernard, 1898; La Perna 2004), and the only
316 subsequent ontogenetic change is an increase in ligament size with age, the differences in
317 ligament position between *N. nakremi* and *N. taylori* cannot be ontogenetic. If the specimens
318 assigned to *N. nakremi* were included as an intermediate ontogenetic stage of *N. taylori*, the
319 ontogenetic pattern would not match any known nucinellid (cf. Bernard, 1898; La Perna,
320 2004), and, therefore, the differences in the subumbonal teeth and the position of the ligament
321 support their separation.

322 A specimen of *N. nakremi* sp. nov. includes an example of a transposed hinge on a
323 left valve (Fig. 4D). Instead of the normal left valve arrangement of three hinge teeth and a

1
2
3 324 lateral secondary ridge creating a secondary socket, this specimen has two hinge teeth and a
4 325 lateral tooth (i.e. the normal right valve arrangement). An alternative interpretation is that this
5 326 specimen represents an earlier ontogenetic stage, but this is rejected because even though the
6 327 specimen is slightly smaller, its lateral tooth is more prominent than in a typical left valve
7 328 arrangement and both the subumbonal and lateral teeth appear to fit with the expected
8 329 corresponding valve arrangement. In addition, it has been reported that in the early stages of
9 330 nucinellid development the second lateral tooth is very small and closer to the subumbonal
10 331 teeth than later in ontogeny (Bernard, 1898), which is not the case with this specimen.
11 332 Transposed hinges have been reported in a number of bivalve families, but this is the first
12 333 reported occurrence in a species of Nucinellidae.

13 334 **Mode of Life.** Shallow infaunal, fully motile, slow, chemosymbiotic (Oliver & Taylor, 2012).

14 335

15 336 Order **Nuculanoida** Carter et al., 2000

16 337

17 338 Family **Neilonellidae** Schileyko, 1989

18 339 **Diagnosis.** Hinge plate with taxodont teeth in two series, sometimes separated by narrow,
19 340 plain area, without resilifer; ligament predominantly external, opisthodetic to amphidetic,
20 341 weak.

21 342 **Remarks.** The Neilonellidae are very similar to the Nuculanidae, but the lack of a resilifer in
22 343 mature adults supports their separation (Coan & Valentich-Scott 2012). The new specimens
23 344 described herein differ from the Mallettiidae in lacking conspicuous gapes, and from the
24 345 Tindariidae in having a short gap in the dentition below the beaks (Di Geronimo & La Perna
25 346 1997). The family is currently known from the Jurassic to present in all oceans, especially in
26 347 deep water and soft substrates (Coan & Valentich-Scott 2012).

27 348

28 349 Genus **Austrotindaria** Fleming, 1948

29 350 **Type species.** *Austrotindaria wrighti* Fleming 1948; Holocene, Quaternary; Southland, New
30 351 Zealand.

31 352 **Diagnosis.** Delicate almost smooth shell, with weak concentric sculpture. A short, edentulous
32 353 gap between the posterior and anterior hinge plates. No pallial sinus and without rostrum.

33 354 **Remarks.** The Neilonellidae comprises three valid genera: *Neilonella*, *Austrotindaria* and
34 355 *Pseudoneilonella* (La Perna 2007). The convex shape of the posterior margin and the

1
2
3 355 presence of an opisthodontic ligament in our specimens indicate better agreement with
4 356 *Austrotindaria* than *Neilonella* (Di Geronimo & La Perna 1997; La Perna 2007).
5 357 *Austrotindaria* differs from *Neilonella* and *Pseudoneilonella* by having a delicate, almost
6 358 smooth, shell rather than a sturdy, sculptured shell, and by having a small elongate pit below
7 359 the posterior and anterior teeth (La Perna 2007). This genus is currently known from the
8 360 Miocene to Recent (La Perna 2007; Coan & Valentich-Scott 2012) and the specimens
9 361 identified in his study extend the range of the genus to the beginning of the Triassic.
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17 363 Species *Austrotindaria antiqua* sp. nov.

18
19 364 (Fig. 5)

20
21 365 1899 *Anodontophora (Myacites) fassaensis*; Bittner. p. 22; Plate. III, Figs 28-33.

22
23 366 1908 *Anoplophoria (Myacites) fassaensis*; von Wittenburg p. 33; Fig. 15.

24
25 367 1926 *Anodontophora fassaensis*; Matsushita Plate 8; Fig. 11

26
27 368 1963 *Unionites fassaensis*; Ciriacks. p. 81; Plate 16; Fig. 13.

28
29 369 1985 *Unionites fassaensis*; var. *brevis* Neri & Posenato p. 94; Plate 2; Fig 8.

30
31 370 2009 *Unionites fassaensis*; Kumagae & Nakazawa p. 166; Fig. 145, 5-9.

32
33 371 2014 *Unionites? Fassaensis*; Pan et al. p. 151; Fig. 5, G-H.

34
35 372 2015 *Unionites fassaensis*; Hofmann et al. p. 8; Fig. 4, K.

36
37 373 2015 cf. *Unionites fassaensis*; Foster et al. p. 381, Fig. 4, L.

38
39 374 **Diagnosis.** Shell small, smooth except for concentric growth lines, subtrigonal, inequilateral,
40 375 prosogyrate; taxodont hinge dentition with more than 50% fewer anterior than posterior ones,
41 376 obtusely chevron-shaped teeth, hinge plate interrupted below the beak by an edentulous gap,
42 377 a small rounded triangular pit below the edentulous gap; ligament opisthodontic.

43
44 378 **Holotype.** Disarticulated right valve, NHMUK PI MB 1240, LD-04; length = 4.0mm, height
45 379 = 3.0mm.

46
47 380 **Paratype.** Disarticulated left valve, NHMUK PI MB 1241, LD-04; length = 4.6mm, height =
48 381 3.4mm.

49
50 382 **Other Material.** Eight specimens from LD-04 (NHMUK PI MB 1194; NHMUK PE PEI
51 383 5479; NHMUK PE PEI 5486-5488; NHMUK PE PEI 5513; NHMUK PE PEI 5520) and

1
2
3 384 eighteen specimens from LD-05 ([NHMUK PI MB 1191](#); [NHMUK PI MB 1196-1197](#);
4 385 [NHMUK PI MB 1199](#); [NHMUK PI MB 1242](#); [NHMUK PE PEI 5475-5476](#); [NHMUK PE](#)
5 386 [PEI 5483](#); [NHMUK PE PEI 5494](#); [NHMUK PE PEI 5497](#); [NHMUK PE PEI 5499-5501](#);
6 387 [NHMUK PE PEI 5504](#); [NHMUK PE PEI 5506](#); [NHMUK PE PEI 5515](#)). Two prodissoconch
7
8 388 valves from LD-04 ([NHMUK PI MB 1243-1244](#)).

9
10
11 389 **Derivation of name.** Latin, antiqua (ancient) referring to this species being the oldest known
12
13 390 of the genus.

14
15 391 **Description.** Equivalve, inequilateral shell with a subtrigonal outline and a beak positioned
16
17 392 approximately 30% along the length of the dorsal margin from the posterior; H/L ratio 0.6-1.
18
19 393 Conspicuously tumid. Umbo prosogyrate, prominent, moderately broad, rounded and projects
20
21 394 above the hinge margin. Slightly rounded and gently sloping anterodorsal margin.
22
23 395 Posterodorsal margin almost straight to slightly rounded, gently sloping, with a slight angled
24
25 396 junction with the posterior margin. Ventral margin deeply rounded. Escutcheon short,
26
27 397 relatively broad, elliptical; lunule narrow. Shell smooth with fine concentric growth lines;
28
29 398 entire inner margin smooth. Small ligament, external, opisthodetic, with a well-defined
30
31 399 margin and well-rounded triangular pit seated beneath the edentulous gap. Hinge plate with
32
33 400 taxodont teeth in two series, sometimes separated by a narrow, plain area, without resifer,
34
35 401 that is narrow below the beak, broadening towards the anterior and posterior ends. Robust
36
37 402 teeth, moderately long and blunt, with more than 50% fewer anterior than posterior ones.
38
39 403 Smooth ventral margin. No pallial line, sinus or muscle scars are present. As the size of the
40
41 404 shell increases the edentulous gap becomes proportionally smaller, more central and moves
42
43 405 externally.

44
45 406 **Remarks.** The external morphology of these specimens is identical to most Early Triassic
46
47 407 specimens previously described as "*Unionites*" *fassaensis*, which is one of the most
48
49 408 widespread bivalve species from the Lower Triassic and is also a problematic dustbin taxon
50
51 409 that includes a range of different morphologies. These specimens differ from the original
52
53 410 description and figures of "*Myacites*" *fassaensis* Wissmann (1841) in having a less elongated
54
55 411 posterior margin and a more prosogyrate beak. Due to poor preservation, however, little is
56
57 412 known about the internal morphology of Early Triassic specimens assigned to *U. fassaensis*,
58
59 413 which has created some uncertainty (Hautmann et al. 2013). Internally, these new specimens
60
61 414 lack the following characters that Geyer et al. (2005) determined were diagnostic of
62
63 415 *Unionites*: a nymph extending nearly half of the posterior margin; an impressed adductor
64
65 416 muscle scar; an overlap of the anterior hinge; and a deeply impressed lunule and posterior

1
2
3 417 keel. Thus, these specimens cannot be assigned to *Unionites*. The presence of taxodont hinge
4 418 dentition, an opisthodontic ligament and lack of ornamentation is, however, characteristic of
5 419 the genus *Austrotindaria*.

6
7
8 420 The more prosogyrate beak means that these specimens have a similar external
9 421 morphology to Middle Triassic *Unionites* specimens (e.g. Geyer et al. 2005), but apart from
10 422 possessing a faint posterior keel they lack the diagnostic criteria of *Unionites*. Furthermore,
11 423 the *Unionites* specimens described by Geyer et al. (2005) and from this study (see below) all
12 424 have a strong posterior keel. Thus, these specimens are not assigned to *Unionites*. These
13 425 specimens, and all previous specimens assigned to *Unionites fassaensis* that possess a
14 426 prosogyrate beak and lack a well-defined posterior keel, are therefore assigned to
15 427 *Austrotindaria antiqua* sp. nov.

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18 428 **Mode of Life.** Shallow infaunal, fully motile, slow, miner (Stanley 1968).

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24 429

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26 430 Species *Austrotindaria svalbardensis* sp. nov.

27
28 431 (Fig. 6)

29
30 432 [1864 *Anoplophora fassaensis*; Alberti. p. 137; Plate III; Fig. 8.](#)

31
32 433 1930 *Nucula* sp. juv. ind; Spath. p. 53; Plate XII; Fig 12.

33
34 434 2013b *Unionites fassaensis*; Hofmann et al. p. 887; Fig. 8, 17-18.

35
36 435 2015 *Unionites* cf. *fassaensis*; Hautmann et al. p. [890](#); Fig. 10, H.

37
38 436 **Diagnosis.** Shell small, smooth except for concentric growth lines, subtrigonal, inequilateral,
39 437 orthogyrate; taxodont hinge dentition with more posterior than anterior teeth, obtusely
40 438 chevron-shaped teeth, hinge plate interrupted below the beak by an edentulous gap, a small
41 439 rounded triangular pit below the edentulous gap; ligament opisthodontic.

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43
44 440 **Holotype.** Disarticulated right valve, [NHMUK PI MB 1223](#), LD-04; length = 1.8mm, height
45 441 = 1.3mm.

46
47
48 442 **Paratype.** Disarticulated left valve, [NHMUK PI MB 1231](#), LD-04; length = 1.5mm, height =
49 443 1.0mm.

50
51
52 444 **Other Material.** Twenty-one specimens from LD-04 ([NHMUK PI MB 1190](#); [NHMUK PI](#)
53 445 [MB 1192-1193](#); [NHMUK PI MB 1224-1230](#); [NHMUK PI MB 1232-1233](#); [NHMUK PI MB](#)
54 446 [1235-1236](#); [NHMUK PE PEI 5478](#); [NHMUK PE PEI 5482](#); [NHMUK PE PEI 5489](#);

1
2
3 447 [NHMUK PE PEI 5505](#); [NHMUK PE PEI 5509-5510](#); [NHMUK PE PEI 5512](#); [NHMUK PE](#)
4 [PEI 5520](#)) and twelve specimens from LD-05 ([NHMUK PI MB 1189](#); [NHMUK PI MB 1197](#);
5 [NHMUK PI MB 1200](#); [NHMUK PE PEI 5476](#); [NHMUK PE PEI 5491-5492](#); [NHMUK PE](#)
6 [PEI 5496](#); [NHMUK PE PEI 5498](#); [NHMUK PE PEI 5503-5504](#); [NHMUK PE PEI 5517](#)).
7
8 450
9
10 451 Twenty-four prodissoconch valves from LD-04 ([NHMUK PI MB 1234](#); [NHMUK PI MB](#)
11 [1237](#); [NHMUK PI MB 1238](#); [NHMUK PE PEI 5520](#)) and five prodissoconch valves from
12
13 453 LD-05 ([NHMUK PI MB 1239](#)).

14
15 454 **Derivation of name.** Named after the Svalbard archipelago.

16
17 455 **Description.** Shell outline subtrigonal, equivalve, inequilateral with beak positioned
18 approximately 60% of the distance along the dorsal margin from the posterior; H/L ratio 0.6-
19 456 1; conspicuously tumid. Orthogyrate umbo, prominent, moderately broad, rounded and
20 457 projected above the hinge margin. Anterodorsal margin slightly rounded and gently sloping.
21 458 The posterodorsal margin is almost straight to slightly rounded and gently sloping. Ventral
22 459 margin is smooth and deeply rounded. Escutcheon is short, relatively broad, elliptical; lunule
23 460 narrow. No sculpture except for fine concentric growth lines; entire inner margin is smooth.
24 461 Prodissoconch is smooth, broadly subovate, with H/L ratio of 0.6-0.9. Ligament small,
25 462 external with well-defined margin, opisthodontic, with a well-rounded triangular pit seated
26 463 beneath the edentulous gap. Hinge plate with taxodont teeth in two series; separated by
27 464 narrow, plain area, without resilifer, narrow below the beak, broadening towards the anterior
28 465 and posterior ends. Teeth are robust, moderately long and blunt, with more posterior than
29 466 anterior teeth, separated by an edentulous gap. As the size of the shell increases the
30 467 edentulous gap becomes proportionally smaller, more central and moves externally. No
31 468 pallial line, sinus or muscle scars present.
32 469

33
34 470 **Remarks.** These specimens differ from *Austrotindaria antiqua* sp. nov. in having a more
35 471 equal number of anterior to posterior teeth and an orthogyrate beak. The direction of the beak
36 472 also separates these specimens from unequivocal species of *Unionites*. In the specimens
37 473 described here and other *Austrotindaria* species the beak is orthogyrate to posteriorly
38 474 opisthogyrate, whereas in *Unionites* it is prosogyrate. Based on this key character, most
39 475 specimens previously assigned to *Unionites fassaensis*, and similar Early Triassic specimens
40 476 with an orthogyrate beak and no internal morphological detail preserved, are herein assigned
41 477 to *Austrotindaria svalbardensis* sp. nov.

42
43 478 These specimens have a very similar shape, size and ornamentation to the type species
44 479 of *Austrotindaria* (*A. wrighti* Flemming), however, they differ in possessing a small, rounded,
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480 triangular pit below the edentulous gap and differ from other *Austrotindaria* species, e.g. *A.*
 481 *mawheraensis*, in lacking a weak posterior rostrum. For these reasons, they are therefore
 482 considered a separate species.

483 **Mode of Life.** Shallow infaunal, fully motile, slow, miner (Stasek 1961; Stanley 1968).

484

485

Species *Austrotindaria? canalensis* (Catullo, 1846)

486

(Fig. 2B)

487 1846 *Tellina canalensis* Catullo p. 56; Plate 4; Fig. 4.

488 1899 *Anodontophora (Myacites) canalensis*; Bittner p.23; Plate III; Figs 34-38.

489 1908 *Anoplophoria canalensis*; von Wittenburg p.281; Plate 5; Fig. 6.

490 1963 *Unionites canalensis*; Ciriacks p. 81; Plate 16; Fig. 11-12.

491 1985 *Unionites canalensis*; Neri & Posenato, p. 94; Plate 2; Fig.8.

492 2004 *Unionites* aff. *canalensis*; Kashiyaama & Oji p. 214; Fig 8, F.

493 2009 *Unionites canalensis*; Kumagae & Nakazawa p. 166; Fig. 145, 1-4.

494 2015 *Unionites canalensis*; Hofmann et al. p 481. Fig. 4, J.

495 2015 cf. *Unionites canalensis*; Foster et al. p. 381; Fig.4, K.

496 **Material.** Three specimens from LD-05 (NHMUK PI MB 1198; NHMUK PE PEI 5493;

497 NHMUK PE PEI 5500).

498 **Description.** Outline sub-ovate to elongate, equivalve, inflated below the umbo; inequilateral
 499 with beak lying approximately 62% along the dorsal margin length from posterior; H/L ratio
 500 0.4-0.7. Posterior margin elongated and almost straight, anterior margin narrowly rounded.
 501 Escutcheon and lunule indistinct. Umbo orthogyrate, prominent, moderately broad, rounded,
 502 projecting above the hinge margin. Ornamented externally with fine concentric growth lines;
 503 entire inner margin smooth.

504 **Remarks.** The internal characters and hinge in these specimens were not observed and have
 505 not been reported for *Unionites canalensis*. Externally, the shell is virtually identical to those
 506 that are typically assigned to *U. canalensis* (e.g. Hofmann et al. 2015), with a medially placed
 507 umbo that is a diagnostic feature of *U. canalensis* (Catullo, 1846) and an orthogyrate beak. In
 508 contrast, all other species of *Unionites* have a more anteriorly located umbo, and the beak in
 509 *Unionites* is prosogyrate (Geyer et al. 2005). Thus, these Early Triassic specimens clearly do

1
2
3 510 not belong to the genus *Unionites*. The external features of these specimens are most similar
4
5 511 to species of Neilonellidae, e.g. *Austrotindaria benthicola* (Dell, 1956). *Austrotindaria* is the
6
7 512 only genus of the Neilonellidae that is reported from the Early Triassic, and these specimens
8
9 513 are, therefore, tentatively assigned to it. Without observation of the internal characters an
10
11 514 unequivocal generic assignment cannot be made. The posterior margin is more elongate than
12
13 515 in *Austrotindaria svalbardensis* sp. nov., and these specimens are therefore considered to
14
15 516 represent a separate species.

16
17 517 **Mode of Life.** Shallow infaunal, fully motile, slow, miner (Stanley 1968).

18

19 519 Family **Mallettiidae** Adams & Adams, 1858

20
21 520

(Fig. 7)

22
23 521 **Diagnosis.** Subequilateral to inequilateral; usually with elongate, compressed posterior end;
24
25 522 sculpture of commarginal striae or ribs; anterior and posterior gapes present; hinge plate
26
27 523 weak, with fine taxodont teeth in two series, sometimes separated by plain area, without
28
29 524 resilifer; ligament external, opisthodontic to amphidetic, weak; pallial sinus large.

30 525 **Material.** Three larval shells from LD-04 ([NHMUK PI MB 1248-1250](#)).

31
32 526 **Description.** Shell is equilateral, elliptical, H/L ratio of 0.7, and moderately inflated. Umbo is
33
34 527 broad, orthogyrate, with beak positioned centrally. Shell smooth except for concentric growth
35
36 528 lines. Hinge plate has three anterior and three posterior teeth in two series separated by a
37
38 529 large plain area with a groove. Ligament is predominantly external, amphidetic and weak.

39 530 **Remarks.** The Mallettiidae are very similar to the Nuculanidae, but the lack of a resilifer in
40
41 531 mature adults supports their separation (Coan & Valentich-Scott 2012). These specimens do
42
43 532 not belong to the Neilonellidae because they possess a small conspicuous gape between the
44
45 533 valves. The Mallettiidae is a long-ranging family known from the Ordovician to the Recent,
46
47 534 and three genera (*Malletia*, *Palaeoneilo* and *Taimyrodon*) belonging to the family have
48
49 535 previously been reported from the Lower Triassic (e.g. He et al. 2007; Wasmer et al. 2012).
50
51 536 Externally, these specimens resemble the larval shells of *Paleoneilo? fortistriata* figured by
52
53 537 Wasmer et al. (2012), but they have far fewer hinge teeth. There are also equal numbers of
54
55 538 anterior to posterior hinge teeth in these specimens, whereas in *P. fortistriata* there are many
56
57 539 more posterior than anterior teeth (Wasmer et al. 2012).

58
59 540 **Mode of Life.** Shallow infaunal, fully motile, slow, miner (Stanley 1968).

541

542

Order **Unionoida** Stoliczka, 1871

543

Family **Anthracosiidae** Amalitsky, 1892

544

Genus **Unionites** Wissmann, 1841

545 **Type species.** *Unionites muensteri* Wissmann 1841; Carnian, Late Triassic; South Tyrol,
546 Italy.

547 **Diagnosis.** The generic diagnosis follows Geyer *et al.* (2005). Shell suboval to elongate-
548 elliptical or rectangular to trapeziform; equivalve, inequilateral. Umbo prosogyrate. Shell
549 surface smooth except for growth rugae, or with rather fine commarginal riblets and, rarely, a
550 faint radial ornamentation. Anterior hinge margin of right valve projects beyond the plane of
551 commissure, fitting into a recess in the opposite valve. Small subumbonal groove limits this
552 shell projection posteriorly. Posterior lateral tooth of right valve generally distinct, engaging
553 below posterior dorsal margin of left valve. Hinge of left valve with anterior platform that
554 bears depression for corresponding anterior hinge margin of right valve, followed posteriorly
555 by small, tuberculiform subumbonal tooth. Narrow groove extends parallel to margin at distal
556 part of anterior hinge margin and corresponds to anterior lateral tooth of right valve. Lower
557 part of posterior dorsal margin slightly projects beyond plane of commissure, fitting above
558 posterior lateral tooth of right valve. Ligament fixed on nymph, which extends about half the
559 length of the posterior dorsal margin.

560 Species ***Unionites aff. subrectus*** (Bittner, 1901)

561 (Fig. 8)

562 aff. 1901 *Anodontophora subrecta* Bittner, p. 100; Plate 7; Figs. 28-30.

563 aff. 2003 *Unionites subrectus*; Szente & Vörös, p. 131; Plate Biv-II; Figs. 25-26.

564 2009 *Triaphorus aff. multiformis*; Kumagae & Nakazawa p. 171; Fig. 145, 18-25.

565 **Material.** Seven specimens from LD-04 ([NHMUK PI MB 1245-1247](#); [NHMUK PE PEI](#)
566 [5480](#); [NHMUK PE PEI 5485](#); [NHMUK PE PEI 5507](#); [NHMUK PE PEI 5519](#)) and nine
567 specimens from LD-05 ([NHMUK PI MB 1195](#); [NHMUK PI MB 1197](#); [NHMUK PI MB](#)
568 [1201](#); [NHMUK PE PEI 5495](#); [NHMUK PE PEI 5506](#); [NHMUK PE PEI 5508](#); [NHMUK PE](#)
569 [PEI 5516](#)).

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2
3 570 **Description.** Outline elongate-elliptical. Shell equivalved, inflated below the umbo, and
4 571 inequilateral with beak positioned approximately 85% along the length of the dorsal margin
5 572 from the posterior. Lower part of anterior dorsal margin projects slightly beyond plane of
6 573 commissure. Posterodorsal margin is almost straight to slightly round and gently sloping.
7
8 574 **Lunule** is long and narrow, with deeply impressed **escutcheon**. Umbo is prosogyrate and rises
9 575 above the hinge margin. Ornamented with fine concentric growth lines. The entire inner
10 576 margin is smooth. Prodissoconch is smooth and orbicular.

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12
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14
15 577 A small subumbonal groove limits the shell projection posteriorly. Short lateral tooth,
16 578 left valve possesses a weak secondary ridge creating a shallow socket. Hinge of left valve has
17 579 an anterior platform that bears a depression for the corresponding anterior hinge margin of
18 580 the right valve, posterior to this is a small, tuberculiform subumbonal tooth fitting above
19 581 posterior lateral tooth of right valve. Ligament is fixed to a nymph, which extends about half
20 582 the length of the posterior dorsal margin. Isomyarian muscle scars with a deeply impressed
21 583 anterior adductor muscle scar.

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23
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25
26 584 **Remarks.** Insufficient knowledge of the internal morphology of Early Triassic bivalves in
27 585 general, and *Unionites* in particular, has created uncertainty regarding their systematic
28 586 position. Based on their external morphology alone these specimens would be assigned to
29 587 *Triaphorus* aff. *multiformis* (Kumagae & Nakazawa 2009), but they possess the following
30 588 characters that are diagnostic of *Unionites*: the anterior hinge margin of the right valve
31 589 overlaps that of the left; a nymph **that** extends nearly half the length of the posterior hinge
32 590 margin; an impressed anterior adductor muscle scar; a deeply impressed lunule; and a long
33 591 and narrow escutcheon. Thus, these specimens are assigned to *Unionites*.

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40 592 These specimens differ from *U. brevis*, *U. fassaensis*, *U. letticus*, *U. griesbachi*, *U.*
41 593 *borealis*, and *U. rhomboidalis* because their length greatly exceeds their height. They are
42 594 most similar to *U. subrectus* described from the Middle Triassic of Hungary by Szente &
43 595 Vörös (2003), except they have a more elliptical outline.

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45
46
47 596 **Mode of Life.** Shallow infaunal, facultatively motile, unattached, suspension feeder
48 597 (Hautmann et al. 2013).

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51 598

52
53 599 Order **Trigoniida** Dall, 1889

54
55 600 Family **Myophoriidae** Bronn, 1849

56
57 601 Genus **Neoschizodus** Giebel, 1855

602 **Type species.** *Lyrodon laevigatum* (Goldfuss, 1837), Anisian, Middle Triassic, Rüdersdorf,
603 Germany.

604 **Diagnosis.** The diagnosis follows Newell & Boyd (1975). Orthogyrous to moderately
605 prosogyrous shell with slightly incurved beak. Posterior ridge angular to subangular in
606 transverse profile. Myophorian hinge; teeth and sockets smooth or bearing transverse
607 striations.

608 **Remarks.** These specimens have most of the required diagnostic criteria for assignment to
609 *Neoschizodus*: an orthogyrate to moderately prosogyrate shell with an incurved beak and a
610 posterior ridge angular to subangular in transverse. The nymph, teeth and umbonal platform
611 were not present in these specimens so it is not known whether these specimens possess the
612 myophorian hinge that is also diagnostic of this genus. These specimens do, however, have a
613 similar external morphology to other Early and Middle Triassic specimens assigned to
614 *Neoschizodus* (e.g. Kumagae & Nakazawa 2009) and are, therefore, referred to this genus.

615
616 Species *Neoschizodus laevigatus* Gieberl, 1855
617 (Fig. 9)

618 **Material.** Five specimens from LD-04 ([NHMUK PI MB 1251](#); [NHMUK PE PEI 5489](#);
619 [NHMUK PE PEI 5519](#); [NHMUK PE PEI 5522](#)) and eight specimens from LD-05 ([NHMUK](#)
620 [PE PEI 5476-5477](#); [NHMUK PE PEI 5499](#); [NHMUK PE PEI 5501](#); [NHMUK PE PEI 5518](#);
621 [NHMUK PE PEI 5521](#)). Fifty-nine prodissoconch valves from LD-04 ([NHMUK PI MB 1252](#);
622 [NHMUK PI MB 1254](#); [NHMUK PI MB 1255-1260](#); [NHMUK PE PEI 5480](#); [NHMUK PE](#)
623 [PEI 5484](#); [NHMUK PE PEI 5486](#); [NHMUK PE PEI 5511](#); [NHMUK PE PEI 5513](#); [NHMUK](#)
624 [PE PEI 5520](#)) and fourteen prodissoconch valves from LD-05 ([NHMUK PI MB 1253](#);
625 [NHMUK PE PEI 5514](#)).

626 **Description.** Shell is trigonally subovate, equivalve, inflated below the umbo, inequilateral,
627 slightly higher than long. Umbo is small and orthogyrate, with an elevated, subangular to
628 rounded, umbonal ridge. Indistinct posterior ridge. Anterodorsal margin recurvate, passing to
629 widely arched ventral margin, posterodorsal margin straight, entire inner margin smooth.
630 Smooth sculpture except for faint concentric growth lines.

631 The larval shells have a similar external morphology to the adult shells, with a short
632 and subumbonal hinge and short, narrow nymphs running down the anterior and posterior
633 margins. The prodissoconch is smooth with fine concentric growth lines.

634 **Remarks.** *Neoschizodus laevigatus* is a cosmopolitan Early and Middle Triassic species with
 635 a high variability in its morphological characters. The shell shape and indistinct posterior
 636 ridge means that the present specimens agree with the characters of *N. laevigatus*, and similar
 637 specimens identified from the Early Triassic (e.g. Kumagae & Nakazawa 2009; Hautmann et
 638 al. 2011).

639 One of the adult specimens preserves a prodissoconch (Fig. 9I) and its morphology is
 640 identical to the other prodissoconchs that were found as isolated specimens. The hinge plate
 641 of the prodissoconchs was not observed to be myophorian, instead the hinge dentition is
 642 typical of a taxodont, but it is not known how a myophorian hinge plate develops through
 643 ontogeny (Newell & Boyd 1975). Hautmann & Nützel (2005) suggest that, in bivalves, the
 644 presence of a small prodissoconch I and a relatively large prodissoconch II indicates a
 645 planktotrophic larval stage. Therefore, a planktotrophic larval stage is interpreted for these
 646 specimens.

647 **Mode of Life.** Shallow infaunal, facultatively motile, unattached, suspension feeder
 648 (Hautmann et al. 2013).

649

650 Class **Gastropoda** Cuvier, 1795

651 Order **Amphigastropoda** Simroth, 1906

652 Family **Euphemitidae** Knight, 1956

653 Genus *Warthia* Waagen, 1880

654 **Type species.** *Warthia brevisinunata* Waagen, 1880; Middle Permian, Salt Range, Pakistan.

655 **Diagnosis.** The generic diagnosis follows Waterhouse (1963). Deeply involute planispirally
 656 coiled bellerophont gastropod, distinguished by absence of spiral ornament. Sinus is broad,
 657 usually with a short slit. Selenizone obscured by inductural layer. Ornament of faint growth
 658 lines and growth wrinkles. Umbilicus generally filled.

659 Species *Warthia zakharovi* Kaim, 2009

660 (Fig. 10)

661 2009 *Warthia zakharovi* Kaim, p. 141; Fig. 132-134.

662 **Material.** One-hundred and thirty-eight specimens from LD-04 ([NHMUK PI MG 1468-1473](#);
 663 [NHMUK PI MG 1495-1496](#); [NHMUK PI MG 1502-1511](#); [NHMUK PE PEI 5478-5482](#);

664 [NHMUK PE PEI 5484-5490](#); [NHMUK PE PEI 5505](#); [NHMUK PE PEI 5507](#); [NHMUK PE](#)
 665 [PEI 5509-5513](#); [NHMUK PE PEI 5519-5520](#); [NHMUK PE PEI 5522](#)) and one-hundred and
 666 ninety-three specimens from LD-05 ([NHMUK PI MG 1467](#); [NHMUK PI MG 1474-1481](#);
 667 [NHMUK PI MG 1483](#); [NHMUK PI MG 1485-1494](#); [NHMUK PI MG 1497-1499](#); [NHMUK](#)
 668 [PI MG 1512](#); [NHMUK PE PEI 5475-5477](#); [NHMUK PE PEI 5483](#); [NHMUK PE PEI 5491-](#)
 669 [5504](#); [NHMUK PE PEI 5506](#); [NHMUK PE PEI 5508](#); [NHMUK PE PEI 5514-5518](#);
 670 [NHMUK PE PEI 5521](#)).

671 **Diagnosis.** *Warthia* with wide shell in comparison to its thickness and weakly depressed
 672 selenizone.

673 **Description.** Shell globular, almost as long as wide. Slit short and broad at base of U-shaped
 674 sinus. Weakly depressed selenizone. In well-preserved specimens growth lines can be
 675 observed. Aperture is arched around earlier whorls, and curved inwards by the selenizone.

676 **Remarks.** The shell of *Warthia* is usually entirely involute and overgrows the umbilicus. In
 677 some of our smaller specimens, the umbilicus is still visible, but in larger specimens it has
 678 become overgrown during subsequent growth. Even though our specimens lack an inductural
 679 layer and have growth lines that have not previously been recorded in Early Triassic *Warthia*
 680 species, in Permian species of *Warthia* visible growth lines or wrinkles have been recorded
 681 (e.g. *W. micromphala* and *W. stricta*; Waterhouse 1963) and, therefore, we consider our
 682 specimens to belong to *Warthia*.

683 The question of whether bellerophontids had a planktonic larval stage is unresolved
 684 (Nützel & Mapes 2001). The protoconch in bellerophontids may be very small, less than one
 685 whorl, and is succeeded by the teleoconch (Frýda 1999), and in our specimens the initial
 686 whorl is overgrown almost immediately. The small size (<0.05mm), bilateral symmetry and
 687 lack of ornamentation in the initial whorls of *Warthia zakharovi* recorded in this study (Fig.
 688 10H), are comparable to the embryonic shells of *Bellerophon* from the late Silurian that
 689 Frýda (1999) interpreted as indicating planktotrophy. A planktotrophic larval stage is,
 690 therefore, inferred for *Warthia zakharovi*.

691 **Mode of Life.** Surficial, fully motile, slow, surface deposit feeder (Linsley 1977).

693 Order **Vetigastropoda** Salvini-Plawen, 1980

694 Family **Eotomariidae** Wenz, 1938

695 Subfamily **Eotomariinae** Wenz, 1938

696 Genus *Glabrocingulum* Thomas, 1940

697 **Type species.** *Glabrocingulum beggi* Thomas, 1940, Carboniferous, Scotland.

698 **Diagnosis.** Low- to moderately high-spired and turbiniform shell shape. The upper whorl
699 surface forming an angle of <math><45^\circ</math> with the selenizone located on the upper edge of whorl face.
700 Sutures sharply defined. Upper whorl face with both spiral and collabral ornament; most
701 strongly developed near the suture, weakest near the selenizone. Anomphalus to widely
702 phaneromphalus, with or without funicle.

703 **Remarks.** These specimens resemble the Permian genera *Wannerispira*, *Ananias* and
704 *Glabrocingulum*, and the Triassic genus *Kamupena*. They differ from *Wannerispira* by
705 possessing a selenizone in the upper third of the whorl, and only having two rather than three
706 strong spiral ribs; from *Ananias* by being low- rather than high-spired and having a less
707 conspicuous and thinner concave band below the selenizone; and from *Kamupena* by lacking
708 a strong umbilical callus plug. These specimens also differ from other neilsoniines by having
709 spiral ribs, no axial ornamentation and by being less elongated. Another genus with a
710 comparable whorl profile is *Rhaphistomella*, which has been considered as a synonym of
711 *Glabrocingulum* (Batten 1989; Erwin & Pan 1996), but it differs from these specimens by the
712 absence of a prominent medial concave band and a more strongly nodulose keel under the
713 suture. These specimens are therefore assigned to the genus *Glabrocingulum*.

714 *Wannerispira* is the only other unequivocal eotomariid genus to have been reported
715 from the Early Triassic (Kaim et al. 2010; Hautmann et al. 2015) and belongs to the
716 Subfamily Neilsoniinae. Since *Glabrocingulum*, in contrast, is dextral, low- rather than high-
717 spired, and with a moderately deep slit developing into a selenizone with rounded margins, it
718 belongs within the Subfamily Eotomariinae. These specimens represent the first Early
719 Triassic record of the Subfamily Eotomariinae and are the first Early Triassic record of the
720 genus *Glabrocingulum*, which is rarely recorded after the Permian period.

722 Species *Glabrocingulum parvum* sp. nov.

723 (Fig. 11)

724 **Diagnosis.** Moderately low-spired shells with faint spiral ornament without sutural nodes.
725 Broad selenizone in relation to whorl height with sharp edges. Deeply concave selenizone.
726 Funicle absent or weakly formed.

727 **Holotype.** Dextral shell, NHMUK PI MG 1531; height = 2.5mm, width = 3.0mm.

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3 728 **Paratype.** Dextral shell, NHMUK PI MG 1518; height = 2.0mm, width = 2.0mm.

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5 729 **Other Material.** Ten specimens from LD-04 (NHMUK PI MG 1468; NHMUK PI MG 1471;
6 730 NHMUK PI MG 1495; NHMUK PI MG 1500-1501; NHMUK PI MG 1513-1515; NHMUK
7 731 PEI 5519-5520) and fourteen specimens from LD-05 (NHMUK PI MG 1476; NHMUK
8 732 PI MG 1482; NHMUK PI MG 1484; NHMUK PI MG 1493; NHMUK PI MG 1530;
9 733 NHMUK PEI 5493; NHMUK PEI 5502; NHMUK PEI 5514). Fourteen juvenile
10 734 shells from LD-04 (NHMUK PI MG 1516-1517; NHMUK PI MG 1519-1529; NHMUK PE
11 735 PEI 5486).

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17 736 **Derivation of name.** Latin, parvum (small), referring to its small size.

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19 737 **Description.** Shell is dextral, turbiniform, low-spired, with simple sutures. The upper whorl
20 738 surface is slightly concave and gently sloping, and bears the selenizone between sharply
21 739 protruding edges, with the lower of the edges on the shell periphery. Selenizone is concave
22 740 and moderately deep. Narrow, concave band immediately below the lower rib. Whorl profile
23 741 below the lower rib is gently convex. Basal angulation is relatively sharply defined, but
24 742 convex; base with a rounded circum-umbilical shoulder; small umbilical chink. Aperture is a
25 743 rounded trapezoid; inner lip is reflexed; peristome interrupted by a slit in the outer lip. Shell
26 744 ornamented with closely, irregular spaced fine spiral lirae. Growth lines visible with small
27 745 knobs at the intersection of spiral ribs, otherwise no axial ornamentation observed. On the top
28 746 of the keel, near the suture, the growth lines form small nodules.

29 747 Protoconch: openly coiled; first two whorls smooth; third whorl possesses ~15 evenly
30 748 spaced, rounded, spiral threads; peristome uninterrupted (Fig. 11F).

31 749
32 750 **Remarks.** These specimens resemble *Glabrocingulum texanum* Batten (1989) with the
33 751 selenizone being located in the upper third of the whorl and lacking axial ornamentation.
34 752 They differ from *G. texanum* in having a broader selenizone in relation to whorl height; a
35 753 more concave selenizone with sharper edges; a weakly developed funicle or none at all; and
36 754 in being moderately low-spired. The uncoiling that has been described for some *G. texanum*
37 755 specimens from the Permian of the southwestern US (Batten 1989) was not observed. These
38 756 specimens are also considerably smaller (Max size H=3.6mm, W=4.6mm) than the type
39 757 material of *G. texanum* (Max size H=8.7mm, W=9.9mm), which may be a consequence of
40 758 environmental stress in the immediate aftermath of extinction event and an expression of the
41 759 Lilliput effect in this genus (cf. Twitchett 2007). Due to their excellent preservation, these

specimens reveal the morphology of the larval stages, which [show a similar ontogenetic development as other species of *Glabrocingulum* \(e.g. Pan and Shen, 2008\)](#).

The [Vetigastropoda](#) have a diverse range of living habits including being described in association with wood-fall communities (Kiel et al. 2008). The specimens in this study do occur in association with wood, however, no direct relationship was observed. Eotomariidae [recorded](#) from Zechstein [reefs](#) are described as motile algal grazers that were probably confined to a hard substrate (Hollingworth & Pettigrew 1988). [The lack of evidence](#) of a hard substrate in [their depositional environment](#), however, suggests that these specimens probably had a similar life habit to deep-sea vetigastropods that typically consume sediment (Hickman 1988).

Mode of Life. Surficial, fully motile, slow, surface deposit feeder.

Order *Ptenoglossa* Gray, 1853

Family *Pseudozygopleuridae* Knight, 1930

(Fig. 12)

Material. Three larval shells from LD-04 ([NHMUK PI MG 1532-1534](#)).

Description. Teleoconch not observed. Protoconch is conical, elongate and composed of five whorls. The initial whorl is smooth and has a diameter of 0.08mm. Collabral ornamentation is initiated on the second whorl, continues to the base of the protoconch, and consists of narrow costellae that intersect at or just below the mid-whorl. Costellae are sigmoidal: on the upper part of the whorls [they](#) are slightly curved and oriented 40° to the shell axis, and on the lower part of the whorls [they](#) are [oriented](#) 200° to the shell axis. Growth lines are visible as faint collabral ribs [between, and](#) perpendicular to, the costellae. Aperture is circular, with a small [columellar](#) fold. Four whorls are present in these specimens.

Remarks. Hoare & Sturgeon (1978) showed that protoconchs of species of *Pseudozygopleuridae* are very similar, but can be readily differentiated from those of the *Zygopleuridae*. Diagnostic characters of pseudozygopleurid protoconchs that are present in these specimens include an elongate, conical shape with 3-5 whorls; smooth initial whorl with collabral ornamentation from the second whorl; and narrow opisthoclinal to sigmoidal transverse costellae that are equally spaced, extend up and below from the suture and curve uniformly to the mid-whorl (Hoare & Sturgeon 1978). In contrast, protoconchs of the

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3 791 Zygopleuridae have smooth whorls with fine riblets at the sutures (Nützel & Mapes 2001;
4 792 Kaim 2004) or straight ribs in the Ampezzopleurinae (Nützel 1998; 2005). Protoconchs of the
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6 793 Ladinulidae are similar to those of the Pseudozygopleuridae but can be differentiated due to
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8 794 their vertical costellae (Bandel 2006). These specimens are, therefore, representatives of the
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10 795 Pseudozygopleuridae. No teleoconch is apparently present in these specimens as the sculpture
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12 796 of the prodissoconch is uninterrupted.

13 797 The Pseudozygopleuridae is primarily a Palaeozoic family. Apart from the Early
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15 798 Triassic specimens described herein, the only other Mesozoic pseudozygopleurid is
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17 799 Plocezyga from the Jurassic of Poland (Kaim 2004). Those specimens attributed to Plocezyga
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19 800 by Kaim (2004), however, lack a protoconch with the diagnostic sigmoidal
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21 801 pseudozygopleurid ornamentation described by Hoare & Sturgeon (1978; 1980). Instead they
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23 802 have a reticulate pattern, shouldered whorls and transverse costae on the protoconch,
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25 803 indicating that they belong to a different genus and family.

26 804 Nützel (1998) used the diameter, ornamentation and whorl number of the protoconch)
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28 805 to separate planktotrophic from non-planktotrophic pseudozygopleurid species. The
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30 806 specimens recorded in this study have small protoconch I diameters (0.12-0.14mm), and the
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32 807 same ornamentation and number of whorls as pseudozygopleurid larval shells interpreted as
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34 808 planktotrophic by Mapes & Nützel (2009), which suggest that they too had a planktotrophic
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36 809 larval lifestyle. A teleoconch was not developed in any of the specimens, which may indicate
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38 810 that the adults were unable to live in this environment.

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38 812 Order **Architectibranchia** Haszprunar, 1985

39 813 Family **Tubiferidae** Cossmann, 1895

40 814 Genus **Sinuarbullina** Gründel, 1997

41 815 **Type species.** *Sinuarbullina ansorgi* Gründel, 1997; Jurassic, Bathonian, NE Germany, NW
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43 816 Poland.

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45 817 **Diagnosis.** The generic diagnosis follows Gründel and Nützel (2012). The shell is fusiform
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47 818 with a distinctly elevated spire. The teleoconch whorls have a subsutural ramp. The transition
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49 819 from the ramp to the outer whorl face is either rounded or angular, sometimes demarcated
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51 820 abapically by a spiral concavity. Whorls are smooth in most species, although faint spiral
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53 821 furrows occur on the base in a few of them. Growth lines are prosocyrct on the outer whorl
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55 822 face but strongly curving in an abapertural direction and opisthocyrct at the ramp. The aperture
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3 823 is relatively low for the group, teardrop-shaped and lack columnellar fold. The protoconch is
4 824 trans- to medioaxial.

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7 825 **Remarks.** Pan et al. (2003) described *Jiangxispira* as a new genus using the following
8 826 diagnostic features: 1) a small, high-spined, slender, fusiform shell; 2) teleoconch whorls with
9 827 narrow shoulder; and 3) a heterostrophic, discoidal, transaxial protoconch. These characters
10 828 are all within the diagnostic features of the genus *Sinuarbullina* Gründel (1997), and
11 829 *Jiangxispira* is, therefore, a junior synonym of *Sinuarbullina*.

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16 831 Species *Sinuarbullina yangouensis* (Pan et al., 2003) comb. nov.
17 832 (Fig. 13)

18 833

19 834 2003 *Jiangxispira yangouensis* Pan et al. p. 44; Fig. 3, 1-7.

20 835 **Material.** Specimen lost by WJF after photography.

21 836 **Description.** The shell is high-spined, slender and fusiform. Teleoconch whorls have a
22 837 subsutural ramp. The ramp from the outer whorl face is rounded with a rib on the shell
23 838 periphery. Whorls are smooth, except for growth lines which are prosocyrts on the outer whorl
24 839 face curving in an apertural direction and become opisthocyrts towards the ramp. The surface
25 840 of the shell shows a colour spiral band around the subsutural ramp. The aperture is an
26 841 elongated teardrop shape. Protoconch is heterostrophic, sinistral, nearly discoidal with lightly
27 842 elevated spire 30° offset from the shell axis; protoconch has 1-2 round whorls.

28 843 **Remarks.** Seven species are included in *Sinuarbullina*, and *S. convexa* (=‘*Cylindrobullina*’
29 844 *convexa*) is the only accepted species from the Lower Triassic (Gründel & Nützel 2012).
30 845 These specimens are more slender than *S. convexa*, described from the Sinbad Limestone of
31 846 the western US by Batten & Stokes (1986), and better resemble *Jiangxispira yangouensis*
32 847 from the Induan Dayie Formation, China.

33 848 The shell morphology is similar to *Meekospira*, which has been interpreted as a slow-
34 849 moving shell dragger (Hughes 1986), but could have also been a burrower (Hollingworth &
35 850 Pettigrew 1988). Interpreting the feeding strategy of fossil gastropods is difficult because
36 851 information on the organ system, including the ctendium, is not usually preserved. The
37 852 ancestral condition in high-spined gastropods is presumably an algal grazer on hard substrates
38 853 (Declerck 1995). Given the absence of hard substrates in this study, the specimens described
39 854 herein were probably detritus feeders or possibly micro-carnivorous on sedentary prey as in
40 855 many modern shelled opisthobranchs (e.g. Lobo da Cunha et al. 2009).

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3 856 **Mode of Life.** Surficial, fully motile, slow, deposit feeder.
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6 858 **Discussion**

7 859 **Implications for Permian-Triassic extinction and diversification**

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11 860 The fully silicified, diverse, earliest Triassic assemblage described herein includes
12 861 gastropod and bivalve taxa that have not previously been recognised from the Early Triassic.
13 862 Some occurrences extend stratigraphic ranges back to the basal Triassic (Fig. 14), with
14 863 implications for timing and rates of diversification, whereas others show unequivocally that
15 864 some taxa that were previously thought to have become extinct during the late Permian mass
16 865 extinction event actually survived.

17
18 866 Three of the four gastropod taxa represent families that originated in the Palaeozoic,
19 867 of which two (*Warthia* and *Wannerispira*) have previously been recognised from the earliest
20 868 Griesbachian and have been interpreted as ‘dead clades walking’ (*sensu* Jablonski 2002) by
21 869 Kaim et al. (2010) and Kaim & Nützel (2011). The family Pseudozygopleuridae is recorded
22 870 in the Triassic for the first time (Fig. 14), confirming that it too survived the late Permian
23 871 extinction, and could also be interpreted in this way. As noted above, the Jurassic specimens
24 872 assigned to the Pseudozygopleuridae by Kaim (2004) do not have the expected suite of
25 873 diagnostic characters and it may be that they represent a different family. If so, then the
26 874 specimens described herein from Svalbard would represent the youngest occurrence of the
27 875 Pseudozygopleuridae.

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29 876 The other gastropod described in this study, *Sinuarbullina yangouensis*, represents
30 877 one of the oldest occurrences of the architectibranchs (*sensu* Gründel & Nützel 2012), a
31 878 group that diversified in the late Triassic and Jurassic. Although architectibranchs have been
32 879 described from the Carboniferous, the Carboniferous specimens do not have a heterostrophic
33 880 protoconch, which means that they are not true architectibranchs (Gründel & Nützel 2012).
34 881 Thus, while the oldest unequivocal architectibranchs occur in the first conodont zone of the
35 882 Triassic (this study; Pan et al. 2003), as hypothesised for other benthic invertebrate groups,
36 883 such as the articulate crinoids (Baumiller et al. 2010; Oji & Twitchett 2015), their origin may
37 884 have been Palaeozoic.

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39 885 Of the five bivalve genera identified in this study, *Promyalina*, *Unionites* and
40 886 *Neoschizodus* have previously been recorded in the earliest Induan (e.g. Hautmann et al.
41 887 2015). The occurrences of the protobranchs *Nucinella* and *Austrotindaria* represent
42 888 significant range extensions back to the Induan and are the oldest occurrences of the

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3 889 Nucinellidae and Nuculanida respectively. Recent phylogenetic analyses show that the
4 890 protobranchs rapidly diversified in the late Triassic and Jurassic (Bieler et al. 2014), but these
5 891 new occurrences demonstrate that the Nucinellidae and Neilonellidae appeared ca. 50 million
6 892 years before that, in the basal Triassic, which better supports the view of Sharma et al. (2013)
7 893 that the late Permian mass extinction event triggered protobranch diversification. Future
8 894 phylogenetic analyses will need to take into account our new findings in order to better
9 895 calibrate molluscan evolutionary trees.

10 896 The excellent preservation of the fossil assemblage described in this study has been
11 897 critical in recognising that most specimens previously assigned to *Unionites fassaensis* and
12 898 *U. canalensis* (Palaeoheterodonta) from Lower Triassic rocks worldwide are likely to have
13 899 been misidentified and better resemble the protobranch *Austrotindaria*. Other specimens from
14 900 this study are, however, unequivocally identified as *Unionites*, confirming its presence in
15 901 Svalbard during the earliest Triassic. The palaeoheterodonts *Unionites* and *Neoschizodus*
16 902 represent two lineages that were part of a major Early Triassic diversification of the
17 903 Palaeoheterodonta (Newell & Boyd 1975; Ros et al. 2011; Sharma et al. 2013; Bieler et al.
18 904 2014).

19 905 The re-assignment of most Early Triassic "*Unionites*" specimens to *Austrotindaria*
20 906 has important implications for understanding how benthic marine ecosystems functioned in
21 907 the wake of the late Permian mass extinction event, as pre-Spathian shelly benthic
22 908 assemblages are typically described as being dominated by "*Unionites*" (Fraiser & Bottjer
23 909 2007; Hofmann et al. 2013b; 2014; 2015; Foster et al. 2015). Our taxonomic re-assignment
24 910 has implications for the functional interpretation of those specimens previously described as
25 911 "*Unionites*" because the motility and feeding of *Unionites* and *Austrotindaria* are
26 912 significantly different, i.e. the former is a facultatively motile suspension-feeder and the latter
27 913 is a motile deposit-feeder. Other non-protobranch taxa with a similar morphology, e.g.
28 914 *Tellina*, also have a deposit-feeding mode of life, so this ecological reinterpretation will still
29 915 be valid even if the tentative generic reassignment from "*Unionites*" *canalensis* to
30 916 *Austrotindaria? canalensis* is subsequently revised. This new functional interpretation means
31 917 that the palaeoecology of Early Triassic benthic shelly assemblages is in better agreement
32 918 with the ichnofaunal record than previously thought (cf. Twitchett 2006), and that in many
33 919 post-extinction, pre-Spathian benthic communities the dominant functional group was
34 920 infaunal, motile, deposit-feeders.

35 921 The Middle and, especially, the Late Triassic are frequently described as being key
36 922 intervals in the radiation of extant marine invertebrate groups from both fossil and molecular

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3 923 evidence (e.g. Nakazawa & Runnegar 1973; Nützel 2005; [Hautmann, 2007](#); Posenato 2008;
4 924 Gründel & Nützel 2012; Rouse et al. 2013; Bieler et al. 2014; Hausmann & Nützel 2014).
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6 925 The poor quality of the Early Triassic fossil record is, however, widely recognised (Fraiser &
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8 926 Bottjer 2005) and it is demonstrably biased towards certain regions, palaeolatitudes and
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10 927 depositional settings (Foster & Twitchett 2014). As shown by other studies (e.g. Hautmann &
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12 928 Nützel 2005; Oji & Twitchett 2015), taxa may be overlooked because they are small, poorly
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14 929 preserved or inhabited particular depositional settings, and there is significant hidden
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16 930 diversity in the Early Triassic. The present study reinforces that view as the assemblage
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18 931 [documented herein](#) is [the first fully silicified Early Triassic fauna, comes](#) from a remote
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20 932 location, comprises mainly small-sized fossils, and demonstrates that Early Triassic diversity
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22 933 was higher than previously recognised.

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24 934 The high-fidelity silicification, which has preserved shells that were originally
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26 935 aragonitic in exquisite detail, is a key factor. A significant post-Permian reduction in the
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28 936 number of silicified assemblages has been attributed to a decline and movement offshore of
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30 937 siliceous sponges (Schubert et al. 1997), driven by changes in climate, ocean circulation and
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32 938 productivity (Kidder & Erwin 2001). Although partially silicified assemblages are known
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34 939 from the Early Triassic (e.g. Twitchett et al. 2004), which Fraiser & Bottjer (2005) argued are
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36 940 adequate for palaeoecological analyses, the present study has demonstrated the necessity of
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38 941 early, complete and high-fidelity silicification for detailed taxonomic [and ecological](#) analysis.
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40 942 Thus, it appears that there is significant hidden biodiversity in the Early Triassic and that the
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42 943 diversification of many extant marine groups probably began earlier than is presently
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44 944 recognised, with implications for both the timing and rate of evolution. The most diverse
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46 945 silicified assemblages of the earliest Induan are known from offshore settings (Twitchett et al.
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48 946 2004; this study), consistent with Schubert et al.'s (1997) hypothesis that siliceous sponges
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50 947 moved offshore after the late Permian extinction event, and so a search strategy focussing on
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52 948 those depositional settings is likely to yield critical new information, especially if regions that
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54 949 are currently under-represented are prioritised.

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56 950

57 951 **The importance of planktotrophy**

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59 952 The exceptionally preserved prodossoconchs and protoconchs in this study provide
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953 valuable insights into the early ontogeny of these taxa. Valentine & Jablonski (1983; 1986)
954 suggested that during the late Permian extinction event there was selection against benthic
955 invertebrates with planktotrophic larval stages. More recently, however, planktotrophic larval

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3 956 shell development has been inferred for many Early Triassic gastropods (Nützel & Erwin
4 957 2002; Pan et al. 2003; Nützel & Schulbert 2005) and this selectivity has been questioned
5 958 (Nützel 2014). All gastropod taxa recorded in the present study (i.e., *Warthia*,
6 959 *Glabrocingulum*, *Sinuarbullina* and the Pseudozygopleuridae) are inferred to have had
7
8 960 planktotrophic larvae (Nützel & Mapes 2001, this study), and in addition, the bivalves
9 961 *Nucinella*, *Austrotindaria*, *Unionites* and *Neoschizodus* all possess a small prodissoconch I
10 962 and a relatively large prodissoconch II which imply planktotrophic larval development (cf.
11 963 Hautmann & Nützel 2005). Thus, we infer that the possession of planktotrophic larvae was a
12 964 particular advantage for benthic molluscs inhabiting shelf settings of the Boreal Ocean in the
13 965 earliest Triassic. This may simply be a consequence of sampling this particular depositional
14 966 setting, as benthic taxa with planktotrophic larvae were common in similar mid-outer shelf
15 967 settings during the Palaeozoic (e.g. Nützel & Mapes 2001; Frýda 2001; Bandel et al. 2002).
16 968 Alternatively, it may be a consequence of the extinction event and associated environmental
17 969 changes.

18 970 One possible advantage of a planktotrophic larval development is protection from
19 971 benthic predation (Nützel & Frýda 2003). Although predators are rarely identified in Early
20 972 Triassic benthic assemblages (e.g. Schubert & Bottjer 1995; Twitchett et al. 2004; Hautmann
21 973 et al. 2011; Hofmann et al. 2013a; 2013b; 2014; 2015; Foster and Twitchett 2014; Foster et
22 974 al. 2015), it is possible that some nektobenthic conodonts, ammonoids or fish may have
23 975 fulfilled this role or that the predators were largely non-mineralised. Fish with durophagous
24 976 dentitions, such as *Bobasatrania*, are locally common in the lowest Triassic of the Boreal
25 977 Ocean (e.g. East Greenland; Stensiö 1932), and trace fossil evidence of vagile crustaceans has
26 978 been recorded from the Induan of northwest Canada (Beatty et al. 2008; Zonneveld et al.
27 979 2010) and central Spitsbergen (WJF & RJT pers. obs.).

28 980 An alternative advantage is that planktotrophic larvae enable more effective dispersal
29 981 and a wide geographic distribution. The cosmopolitan opportunists that thrived in the wake of
30 982 the late Permian mass extinction (e.g. *Lingularia* and *Claraia*) all have an inferred
31 983 planktotrophic larval stage (Hammond & Poiner 1984; Yang et al. 2001). Possession of
32 984 planktotrophic larvae would have been particularly useful for Early Triassic benthic
33 985 invertebrates given the spatial and temporal fluctuations in benthic oxygen concentrations
34 986 that have been inferred for the earliest Triassic seafloor (Wignall & Twitchett 1996; Thomas
35 987 et al. 2004; Nabbefeld et al. 2010). Effective dispersal and wide distribution would have
36 988 afforded greater protection from extinction and enabled rapid colonisation of vacated seafloor
37 989 once harsh environmental conditions had ameliorated. The late Permian mass extinction did

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3 990 not select against animals with planktotrophic larval development (Posenato et al. 2014;
4 991 Nützel 2014), and possession of that character may have been a key factor in the survival and
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6 992 radiation of certain groups.
7

8 993 The occurrence of well-preserved planktotrophic larval shells in this newly described
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10 994 benthic assemblage has additional palaeoenvironmental implications. First, it implies that
11 995 primary production in surface waters was adequate enough to sustain planktic foodwebs.
12
13 996 Second, the exquisite preservation of the earliest formed larval stages and the complete
14
15 997 absence of any signs of shell dissolution or repair (cf. Garilli et al. 2015) demonstrates that
16 998 neither the surface waters nor benthic habitat in this particular region were affected by ocean
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18 999 acidification at this time, and the pH was not low enough to have curtailed biomineralization.
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1000

1001 **Conclusions**

1002 The fossil assemblage from the Lusitaniadalen section, Svalbard, is the first fully silicified
1003 fauna to have been described from the Early Triassic and provides new critical systematic
1004 data. The fauna includes four new bivalve species: *Nucinella taylori*, *N. nakremi*,
1005 *Austrotindaria antiqua* and *A. svalbardensis* and a gastropod species: *Glabrocingulum*
1006 *parvum*. The silicified fauna from Svalbard demonstrates that the aftermath of the late
1007 Permian mass extinction was a key interval for the diversification of the Architectibranchs,
1008 Protobranchia and Palaeoheredonta. The assignment of Early Triassic specimens previously
1009 identified as *Unionites* to *Austrotindaria* has important palaeoecological implications
1010 demonstrating that infaunal deposit-feeders dominated benthic assemblages prior to the
1011 Spathian. The gastropod and bivalve taxa recorded in the present study are inferred to have
1012 had planktotrophic larvae, and it is likely that this was an important adaptation for bivalves
1013 and gastropods in mid-outer shelf settings of the Boreal Ocean during the earliest Triassic.
1014

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For Review Only

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3 1373 **Figure 1.** Locality and stratigraphy of the studied section in Lusitaniadalen. **A**, locality map
4 1374 of the Lusitaniadalen section; **B**, Palaeogeographic position; **C**, Stratigraphic column
5 1375 indicating the position of the sampled concretionary levels (LD-04 and LD-05) and
6 1376 disappearance of bioturbation associated with marine ecosystem collapse and the Late
7 1377 Permian mass extinction (LPE; modified from Nabbefeld et al., 2010). KSF = Kapp Starostin
8 1378 Formation. ii = ichnofabric index. Palaeogeography after Blakey (2012).
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14 1380 **Figure 2.** **A**, *Orbiculoidea winsnesi* Gobbet (1963), NHMUK PI BE 3238, dorsal view,
15 1381 dorsal valve; **B**, *Austrotindaria? canalensis* (Catullo, 1846), NHMUK PI MB 1198, external
16 1382 view, left valve; **C-G**, *Promyalina schamarae* (Bittner, 1899), external view; **C-D**, NHMUK
17 1383 PI MB 1204; **C**, right valve; **D**, left valve. **E-F**, NHMUK PI MB 1203; **E**, right valve; **F**, left
18 1384 valve. **G**, NHMUK PI MB 1202, right valve. Scale bar: **A-B**, **G** = 2mm, **C-F** = 1mm.
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24 1386 **Figure 3.** *Nucinella taylori* sp. nov. **A**, Holotype, Length – 1.6mm, height – 1.5mm,
25 1387 NHMUK PI MB 1206, external view, left valve; **B**, Paratype, Length – 1.6mm, height –
26 1388 1.6mm, NHMUK PI MB 1209, external view, right valve; **C**, Paratype, Length – 2.1mm,
27 1389 height – 2.3mm, NHMUK PI MB 1210, internal view, right valve; **D**, Holotype, NHMUK PI
28 1390 MB 1206, internal view, left valve; **E-F**, Paratype, NHMUK PI MB 1209, internal view, right
29 1391 valve; **G-J**, Prodissoconchs of *N. taylori*: **G**, NHMUK PI MB 1213, external view, left valve;
30 1392 **H**, NHMUK PI MB 1211, external view, right valve; **I**, NHMUK PI MB 1214, internal view,
31 1393 left valve; **J**, NHMUK PI MB 1211, internal view, right valve. Scale bar: **A-F** = 500µm; **G-J**
32 1394 = 100 µm
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41 1396 **Figure 4.** *Nucinella nakremi* sp. nov. **A**, Holotype, Length – 1.1mm, height – 1.1mm,
42 1397 NHMUK PI MB 1219, external view, left valve; **B**, Paratype, Length – 0.9mm, height –
43 1398 0.8mm, NHMUK PI MB 1220, external view, left valve; **C**, Holotype, NHMUK PI MB 1219,
44 1399 interior view, left valve; **D**, Paratype, NHMUK PI MB 1220, interior view (transposed
45 1400 hinge), left valve. Scale bar = 500µm.
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51 1402 **Figure 5.** *Austrotindaria antiqua* sp. nov. **A**, Holotype, Length – 4.0mm, height – 3.0mm,
52 1403 NHMUK PI MB 1240, external view, right valve; **B**, Paratype, Length – 4.6mm, height –
53 1404 3.4mm, NHMUK PI MB 1241, external view, right valve; **C**, Holotype, NHMUK PI MB
54 1405 1240, internal view, right valve; **D**, NHMUK PI MB 1191, external view, right valve; **E**,
55 1406 NHMUK PI MB 1199, external view, left valve; **F**, NHMUK PI MB 1196, external view,
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3 1407 [right valve; G, NHMUK PI MB 1242, hinge plate of left valve; H, NHMUK PI MB 1194,](#)
4 1408 [dorsal view, right valve; I, Articulated specimen, NHMUK PI MB 1243; J, Larval shell,](#)
5 1409 [NHMUK PI MB 1244, left valve. Scale bar: A-C, G = 500µm; D-F = 1mm; I-J = 100µm.](#)
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10 1411 **Figure 6.** *Austrotindaria svalbardensis* sp. nov. **A**, Paratype, Length – 1.5mm, height –
11 1412 1.0mm, [NHMUK PI MB 1231](#), external view, left valve; **B**, Holotype, Length – 1.8mm,
12 1413 height – 1.3mm, [NHMUK PI MB 1223](#), external view, right valve; **C**, [NHMUK PI MB 1190,](#)
13 1414 [left valve, external view; D, larval shell, NHMUK PI MB 1234, external view, right valve; E,](#)
14 1415 [NHMUK PI MB 1225, internal view, left valve; F, NHMUK PI MB 1227, internal view, left](#)
15 1416 [valve; G, larval shell, NHMUK PI MB 1237, internal view, right valve; H, Paratype,](#)
16 1417 posterior and anterior hinge plate junction, [NHMUK PI MB 1231](#). Scale bar = 500µm.
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23 1419 **Figure 7.** Malletiidae (Adams & Adams, 1858) larval shell. **A**, [NHMUK PI MB 1249,](#)
24 1420 external view; **B**, [NHMUK PI MB 1249,](#) internal view; **C**, [NHMUK PI MB 1248,](#) internal
25 1421 view. Scale bar = 100µm.
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29 1423 **Figure 8.** *Unionites* aff. *subrectus* (Bittner, 1901). **A**, [NHMUK PI MB 1246,](#) external view,
30 1424 right valve; **B**, [NHMUK PI MB 1245,](#) external view, left valve; **C**, [NHMUK PI MB 1246,](#)
31 1425 internal view, right valve; **D**, [NHMUK PI MB 1245,](#) internal view, left valve; **E**, [NHMUK PI](#)
32 1426 [MB 1195, external view, right valve; F, hinge margin, NHMUK PI MB 1245, left valve; G,](#)
33 1427 hinge margin, [NHMUK PI MB 1246,](#) right valve. Scale bar = 1mm.
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39 1429 **Figure 9.** *Neoschizodus laevigatus* Gieberl (1855). **A**, [NHMUK PI MB 1251,](#) external view,
40 1430 left valve; **B-G, J**, larval shells; **B**, [NHMUK PI MB 1256,](#) external view, right valve; **C**,
41 1431 [NHMUK PI MB 1259,](#) external view, left valve; **D**, [NHMUK PI MB 1257,](#) external view,
42 1432 right valve; **E**, [NHMUK PI MB 1260,](#) internal view, left valve; **F**, [NHMUK PI MB 1258,](#)
43 1433 internal view, left valve; **G**, [NHMUK PI MB 1255,](#) internal view, right valve; **H-I**, beak of
44 1434 adult specimen, [NHMUK PI MB 1251](#); **J**, hinge plate of a larval shell, [NHMUK PI MB 1260.](#)
45 1435 Scale bar: A = 2mm; B-G, I = 200µm; H = 1mm; J = 50µm.
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52 1437 **Figure 10.** *Warthia zakharovi* Kaim (2009). **A**, [NHMUK PI MG 1502,](#) apertural view; **B-C**,
53 1438 [NHMUK PI MG 1505; B](#), apertural view; **C**, lateral view; **D-E**, [NHMUK PI MG 1509; D](#),
54 1439 lateral view; **E**, apertural view; **F**, [NHMUK PI MG 1508,](#) apical view; **G-H**, [NHMUK PI MG](#)
55 1440 [1504; G](#), apical view; **H**, protoconch. A-B, Scale bar = 500 µm, except H.
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3 1441
4 1442 **Figure 11.** *Glabrocingulum parvum* sp. nov. **A-B**, , apertural view; **A**, Holotype, Height –
5 1443 2.5mm, Width – 3.0mm, NHMUK PI MG 1531; **B**, Paratype, Height – 2.0mm, Width –
6 1444 2.0mm, NHMUK PI MG 1518; **C-E**, NHMUK PI MG 1531; **C**, lateral view; **D**, side view of
7 1445 initial whorls; **E**, apical view; **F**, apertural view of a larval shell, NHMUK PI MG 1520. Scale
8 1446 bar = 1mm, except F.

9 1447
10 1448 **Figure 12.** Pseudozygopleuridae Knight (1930), larval shell. **A-B**, NHMUK PI MG 1532; **A**,
11 1449 apertural view; **B**, lateral view; **C**, NHMUK PI MG 1533, apical view; **D**, side view of initial
12 1450 whorl, NHMUK PI MG 1532. Scale bar = 100µm.

13 1451
14 1452 **Figure 13.** *Sinuarbullina yangouensis* (Pan et al., 2003). **A**, lateral view; **B-C**, apertural view;
15 1453 **D**, view of the protoconch. Scale bar = 1mm, except D. Note: Specimen lost by WJF after
16 1454 photography.

17 1455
18 1456 **Figure 14:** Ranges of benthic invertebrate families identified from the base of the
19 1457 Vikinghøgda Formation. Grey bars = range extensions based on this study; Black bars =
20 1458 previously known unequivocal ranges of families; Dashed line = ghost ranges. Chang. =
21 1459 Changhsingian. Radiometric ages after: Lehrmann et al., 2006; Galfetti et al., 2007; Shen et
22 1460 al., 2011. Late Permian mass extinction event is indicated by a vertical dark grey bar.

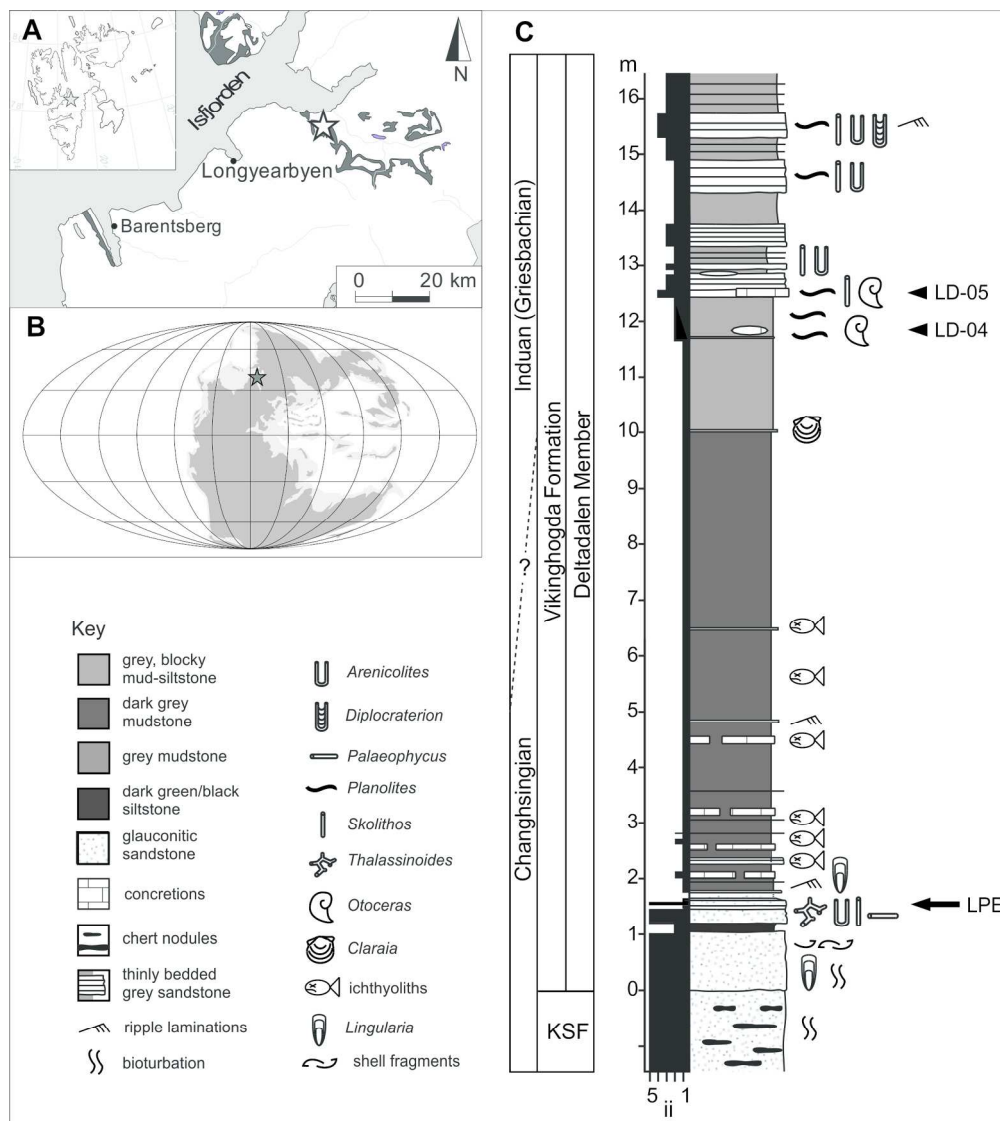


Figure 1. Locality and stratigraphy of the studied section in Lusitaniadalen. (A) locality map of the Lusitaniadalen section; (B) Palaeogeographic position and (C) Stratigraphic column indicating the position of the sampled concretionary levels (LD-04 and LD-05) and disappearance of bioturbation associated with marine ecosystem collapse and the Late Permian mass extinction (LPE; modified from Nabbefeld et al., 2010). KSF = Kapp Starostin Formation. ii = ichnofabric index. Palaeogeography after Blakey (2012).

179x200mm (300 x 300 DPI)

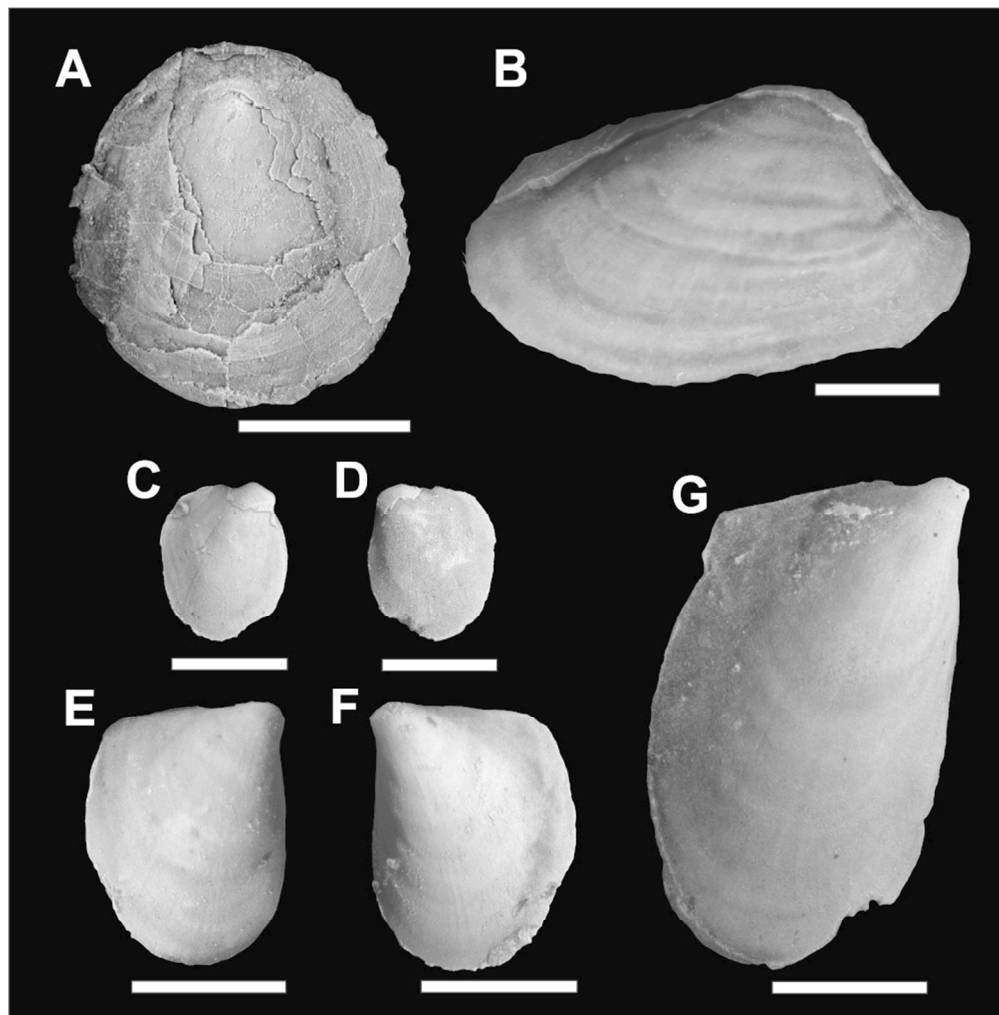


Figure 2. A, *Orbiculoidea winsnesi* Gobbet (1963), NHMUK PI BE 3238, dorsal view, dorsal valve; B, *Austrotindaria? canalensis* (Catullo, 1846), NHMUK PI MB 1198, external view, left valve; C-G, *Promyalina schamarae* (Bittner, 1899), external view; C-D, NHMUK PI MB 1204; C, right valve; D, left valve. E-F, NHMUK PI MB 1203; E, right valve; F, left valve. G, NHMUK PI MB 1202, right valve. Scale bar: A-B, G = 2mm, C-F = 1mm.

85x86mm (300 x 300 DPI)

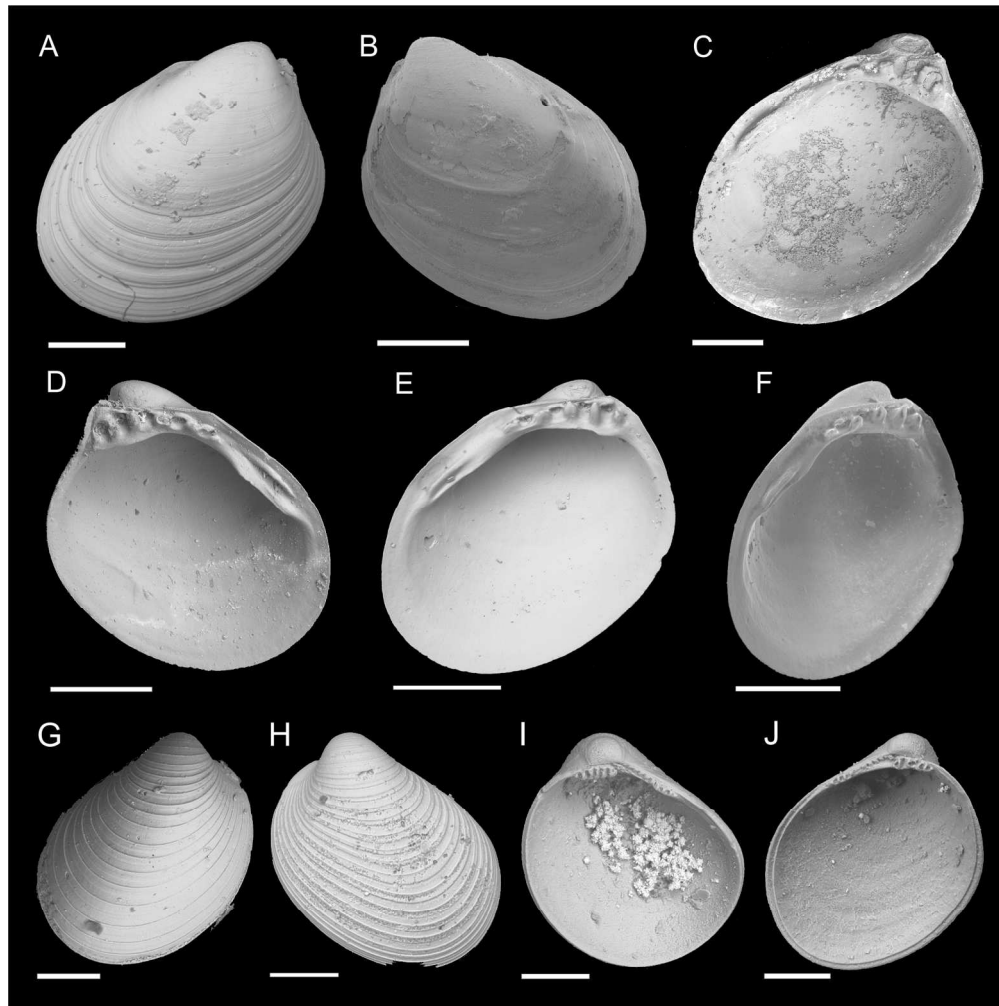


Figure 3. *Nucinella taylori* sp. nov. A, Holotype, Length – 1.6mm, height – 1.5mm, NHMUK PI MB 1206, external view, left valve; B, Paratype, Length – 1.6mm, height – 1.6mm, NHMUK PI MB 1209, external view, right valve; C, Paratype, Length – 2.1mm, height – 2.3mm, NHMUK PI MB 1210, internal view, right valve; D, Holotype, NHMUK PI MB 1206, internal view, left valve; E-F, Paratype, NHMUK PI MB 1209, internal view, right valve; G-J, Prodissoconchs of *N. taylori*: G, NHMUK PI MB 1213, external view, left valve; H, NHMUK PI MB 1211, external view, right valve; I, NHMUK PI MB 1214, internal view, left valve; J, NHMUK PI MB 1211, internal view, right valve. Scale bar: A-F = 500 μ m; G-J = 100 μ m.

170x171mm (300 x 300 DPI)

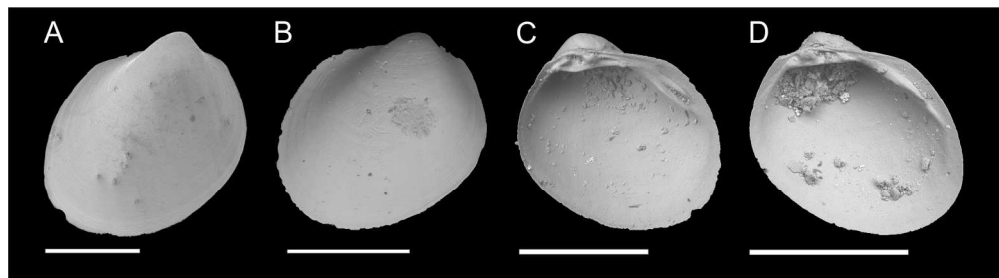


Figure 4. *Nucinella nakremi* sp. nov. A, Holotype, Length – 1.1mm, height – 1.1mm, NHMUK PI MB 1219, external view, left valve; B, , Paratype, Length – 0.9mm, height – 0.8mm, NHMUK PI MB 1220, external view, left valve; C, Holotype, NHMUK PI MB 1219, interior view, left valve; D, Paratype, NHMUK PI MB 1220, , interior view (transposed hinge), left valve. Scale bar = 500µm.

170x46mm (300 x 300 DPI)

Review Only

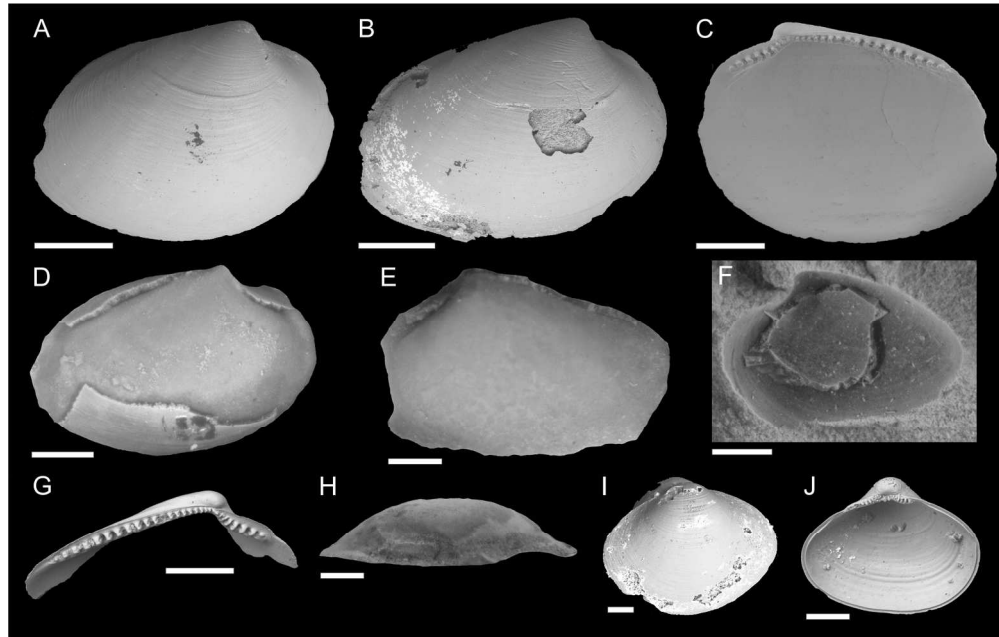


Figure 5. *Austrotindaria antiqua* sp. nov. A, Holotype, Length – 4.0mm, height – 3.0mm, NHMUK PI MB 1240, external view, right valve; B, Paratype, Length – 4.6mm, height – 3.4mm, NHMUK PI MB 1241, external view, right valve; C, Holotype, NHMUK PI MB 1240, internal view, right valve; D, NHMUK PI MB 1191, external view, right valve; E, NHMUK PI MB 1199, external view, left valve; F, NHMUK PI MB 1196, external view, right valve; G, NHMUK PI MB 1242, hinge plate of left valve; H, NHMUK PI MB 1194, dorsal view, right valve; I, Articulated specimen, NHMUK PI MB 1243; J, Larval shell, NHMUK PI MB 1244, left valve. Scale bar: A-C, G = 500 μ m; D-F = 1mm; I-J = 100 μ m.

170x108mm (300 x 300 DPI)

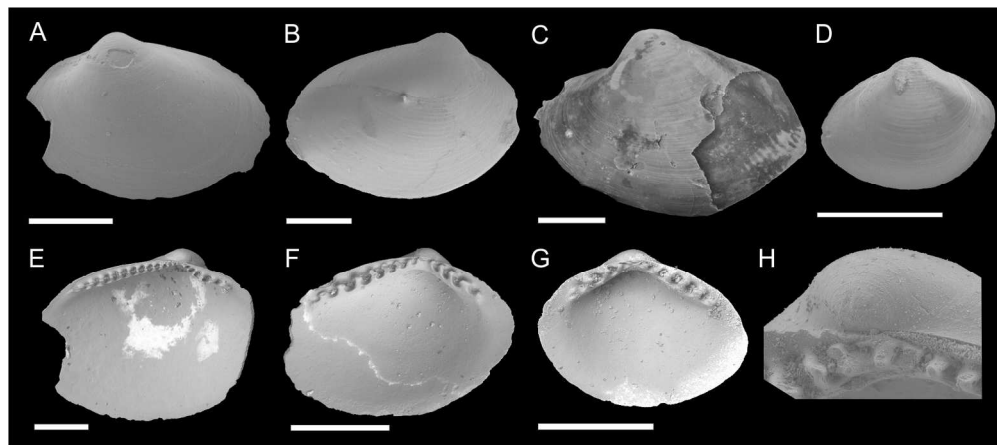


Figure 6. *Austrotindaria svalbardensis* sp. nov. A, Paratype, Length – 1.5mm, height – 1.0mm, NHMUK PI MB 1231, external view, left valve; B, Holotype, Length – 1.8mm, height – 1.3mm, NHMUK PI MB 1223, external view, right valve; C, NHMUK PI MB 1190, left valve, external view; D, larval shell, NHMUK PI MB 1234, external view, right valve; E, NHMUK PI MB 1225, internal view, left valve; F, NHMUK PI MB 1227, internal view, left valve; G, larval shell, NHMUK PI MB 1237, internal view, right valve; H, Paratype, posterior and anterior hinge plate junction, NHMUK PI MB 1231. Scale bar = 500µm.

170x75mm (300 x 300 DPI)

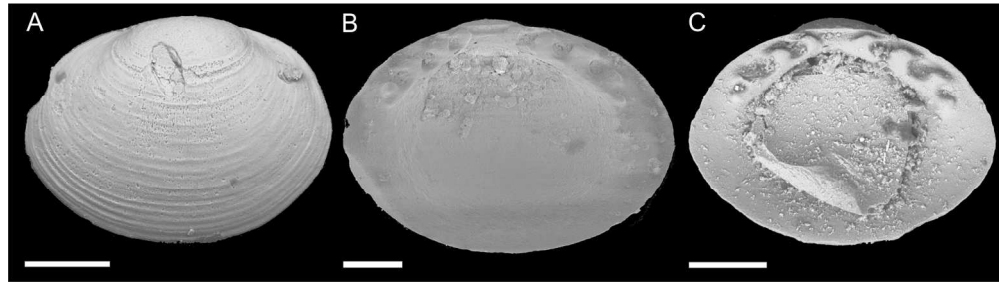


Figure 7. Malletiidae (Adams & Adams, 1858) larval shell. A, NHMUK PI MB 1249, external view; B, NHMUK PI MB 1249, internal view; C, NHMUK PI MB 1248, internal view. Scale bar = 100 μ m.

170x47mm (300 x 300 DPI)

or Review Only

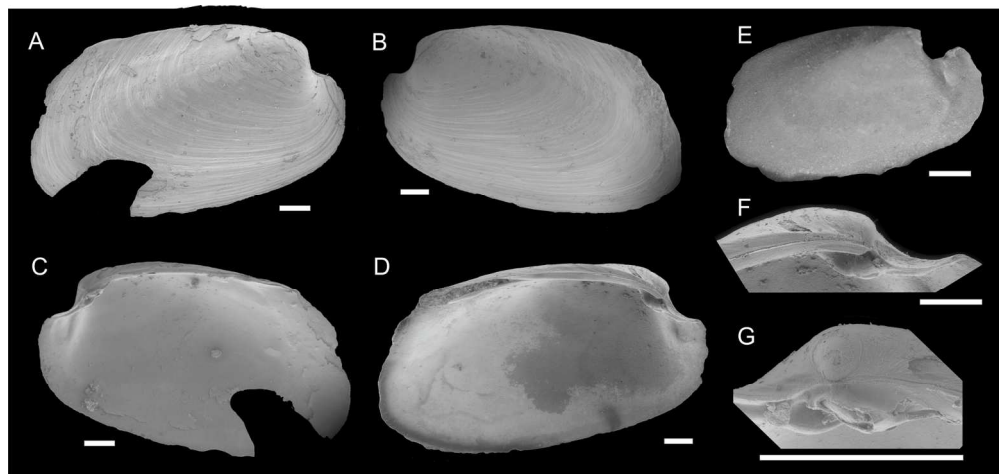


Figure 8. *Unionites* aff. *subrectus* (Bittner, 1901). A, NHMUK PI MB 1246, external view, right valve; B, NHMUK PI MB 1245, external view, left valve; C, NHMUK PI MB 1246, internal view, right valve; D, NHMUK PI MB 1245, internal view, left valve; E, NHMUK PI MB 1195, external view, right valve; F, hinge margin, NHMUK PI MB 1245, left valve; G, hinge margin, NHMUK PI MB 1246, right valve. Scale bar = 1mm.

85x40mm (600 x 600 DPI)

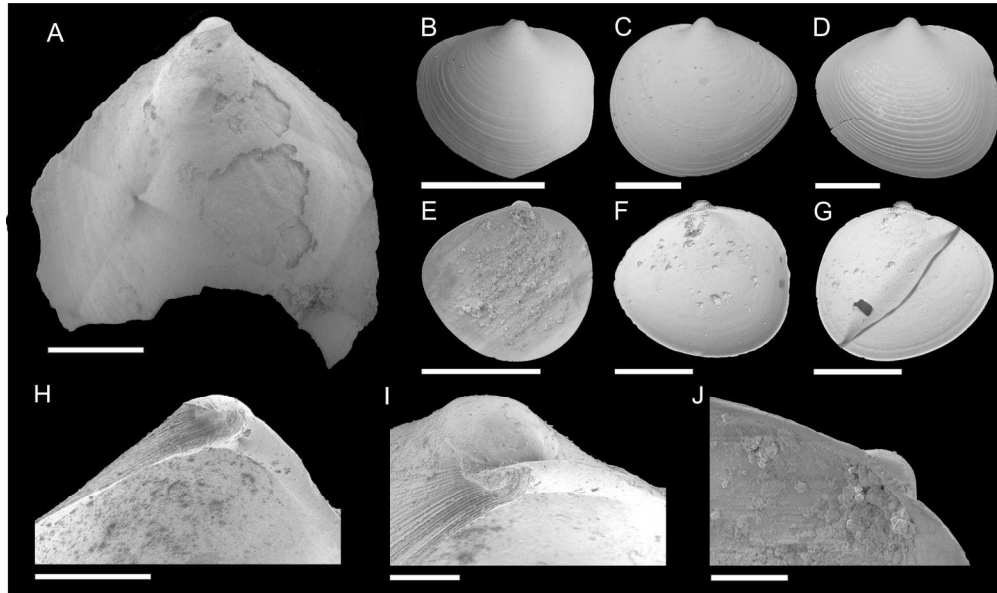


Figure 9. *Neoschizodus laevigatus* Giebel (1855). A, NHMUK PI MB 1251, external view, left valve; B-G, J, larval shells; B, NHMUK PI MB 1256, external view, right valve; C, NHMUK PI MB 1259, external view, left valve; D, NHMUK PI MB 1257, external view, right valve; E, NHMUK PI MB 1260, internal view, left valve; F, NHMUK PI MB 1258, internal view, left valve; G, NHMUK PI MB 1255, internal view, right valve; H-I, beak of adult specimen, NHMUK PI MB 1251; J, hinge plate of a larval shell, NHMUK PI MB 1260. Scale bar: A = 2mm; B-G, I = 200 μ m; H = 1mm; J = 50 μ m.

170x100mm (300 x 300 DPI)

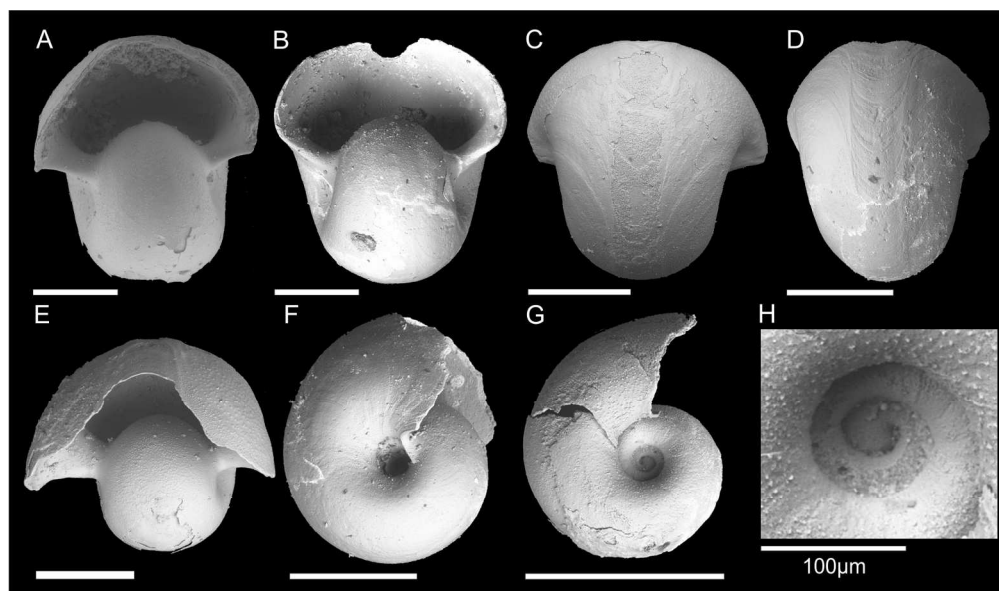


Figure 10. *Warthia zakharovi* Kaim (2009). A, NHMUK PI MG 1502, apertural view; B-C, NHMUK PI MG 1505; B, apertural view; C, lateral view; D-E, NHMUK PI MG 1509; D, lateral view; E, apertural view; F, NHMUK PI MG 1508, apical view; G-H, NHMUK PI MG 1504; G, apical view; H, protoconch. A-B, Scale bar = 500 μ m, except H.

170x100mm (300 x 300 DPI)

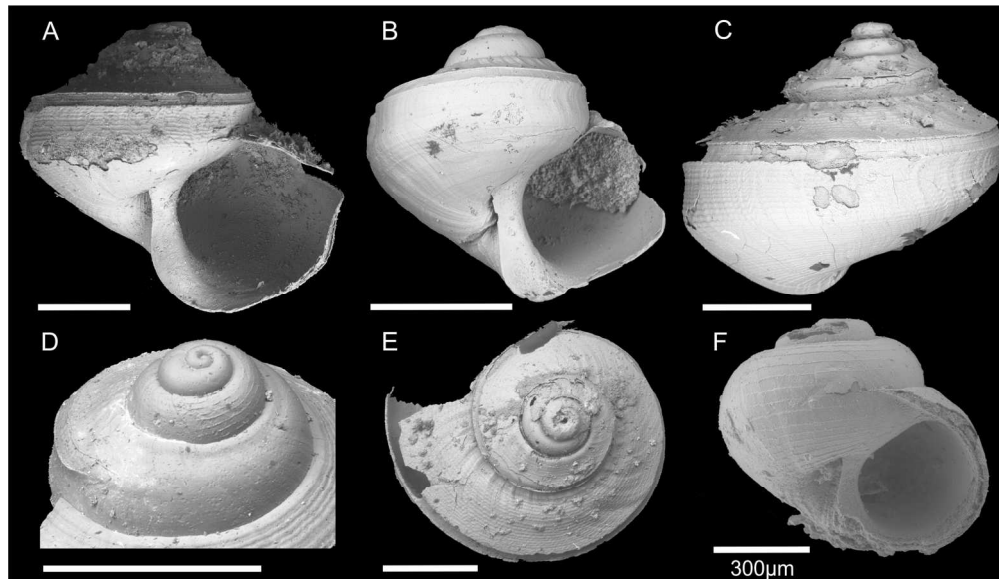


Figure 11. *Glabrocingulum parvum* sp. nov. A-B, , apertural view; A, Holotype, Height – 2.5mm, Width – 3.0mm, NHMUK PI MG 1531; B, Paratype, Height – 2.0mm, Width – 2.0mm, NHMUK PI MG 1518; C-E, NHMUK PI MG 1531; C, lateral view; D, side view of initial whorls; E, apical view; F, apertural view of a larval shell, NHMUK PI MG 1520. Scale bar = 1mm, except F.

170x98mm (300 x 300 DPI)

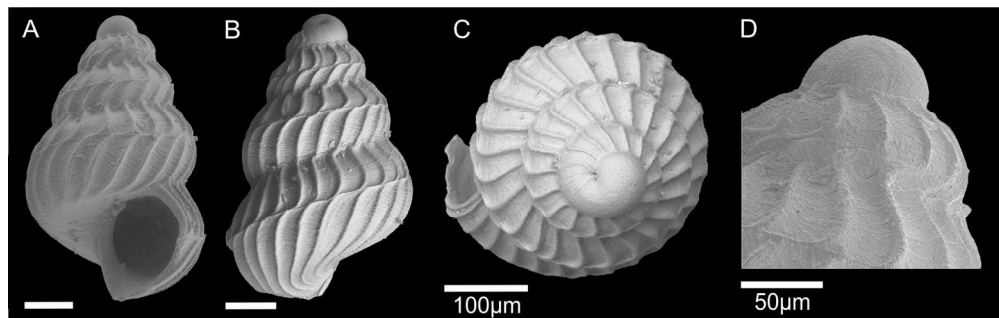


Figure 12. Pseudozygopleuridae Knight (1930), larval shell. A-B, NHMUK PI MG 1532; A, apertural view; B, lateral view; C, NHMUK PI MG 1533, apical view; D, side view of initial whorl, NHMUK PI MG 1532. Scale bar = 100µm.

159x50mm (300 x 300 DPI)

Review Only

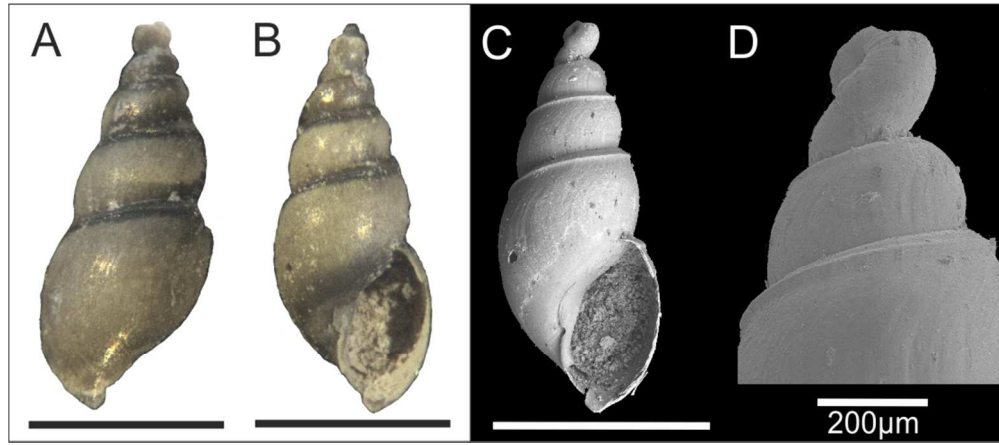


Figure 13. *Sinuarbullina yangouensis* (Pan et al., 2003). A, lateral view; B-C, apertural view; D, view of the protoconch. Scale bar = 1mm, except D. Note: Specimen lost by WJF after photography.

94x41mm (300 x 300 DPI)

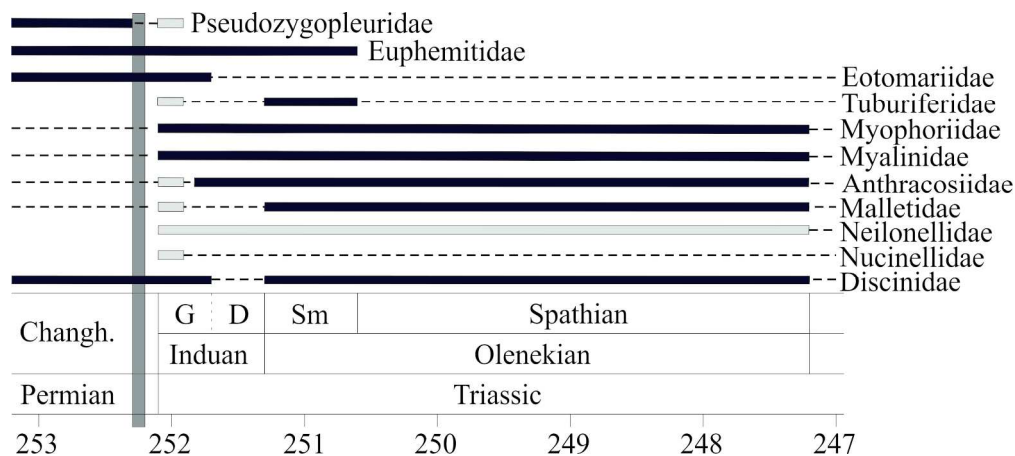


Figure 14: Ranges of benthic invertebrate families identified from the base of the Vikinghøgda Formation. Grey bars = range extensions based on this study; Black bars = previously known unequivocal ranges of families; Dashed line = ghost ranges. Chang. = Changhsingian. Radiometric ages after: Lehrmann et al., 2006; Galfetti et al., 2007; Shen et al., 2011. Late Permian mass extinction event is indicated by a vertical dark grey bar.

199x88mm (300 x 300 DPI)