A silicified Early Triassic marine assemblage from Svalbard

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Abstract

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

Keywords: extinction; Early Triassic; diversification; Mollusca; Protobranchia; chemosymbiosis.

Introduction

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

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

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

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

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

Materials

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

Geological setting

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

4

98 latest Permian and entire Early Triassic in a siliciclastic, open-marine, shelf setting. It is

99 divided into three members, of which the Deltadalen Member is the lowest (Mørk et al.

100 1999). At the study site in Lusitaniadalen, the basal 1.6 m of the Deltadalen Member is

101 composed of bedded, well-bioturbated, fine- to medium-grained, glauconitic sandstones that

102 are very similar to the underlying Kapp Starostin Formation except that they lack diagenetic

103 chert nodules (Mørk et al. 1999; Nabbefeld et al. 2010). These sandstones contain a diverse

104 trace fossil assemblage, indicating a fully functional benthic ecosystem that was living under

105 well-oxygenated conditions (Nabbefeld et al. 2010). In contrast, the body fossil assemblage is

106 limited, comprising mainly the phosphatic-shelled lingulid brachiopods, which may indicate

107 preservational bias.

108 The sandstones record the onset of marine transgression (Mørk et al. 1999; Nabbefeld

109 et al. 2010) with the base of the overlying laminated, silty mudstones marking significant

110 deepening. Several horizons of cemented siltstones and tabular concretions are found in the

111 lower few metres of this mudstone-dominated interval and contain coarser laminae with

112 abundant ichthyoliths and disarticulated lingulid shells. Occasional, 1-5cm thick, fine-

113 grained, pyritic and glauconitic, graded, cemented sandstones, interpreted as distal

114 tempestites, also occur within the laminated silty mudstones. Biomarker data support the

115 interpretation based on field observations that deposition took place under anoxic and

116 periodically euxinic conditions during transgression and maximum flooding, with evidence of

117 phytoplankton blooms in the surface waters likely driven by nutrient influx (Nabbefeld et al.

118 2010).

119 From ca. 10m above the base of the mudstones, the lithologies become noticeably

120 coarser with a greater proportion of interbedded siltstones and very fine sandstones,

121 presumably due to progradation or sealevel fall. The coarser, heterolithic beds are

122 bioturbated, initially by mm-diameter *Planolites* and then with the addition of *Skolithos* and

123 *Arenicolites* ca. 1.5 m higher, indicative of environmental amelioration and deposition under

124 more persistently oxygenated conditions. Ichnofabric index remains low (ii2-3), however,

125 and the burrows are small (diameters <5mm) and do not penetrate deeply, indicating that the

126 environment was probably still not fully optimal for benthic colonisation. Earliest Triassic

127 ammonoids, conodonts and a moderate benthic assemblage have already been recorded from

128 the *Planolites*-dominated interval (Mørk et al. 1999). One of the concretions that yield the

129 silicified assemblage documented in this study derives from that same horizon, 12.6 m above

130 the base of the formation. The second concretion was collected from ca. 65 cm lower (Fig. 1).

131   The age of the Deltadalen Member is well constrained by biostratigraphy (ammonoids

132 and conodonts) and magnetostratigraphy, with deposition recorded from the upper

133 Changhsingian, prior to the late Permian mass extinction event, through most of the Induan

134 (Mørk et al. 1999; Hounslow et al. 2008; Nakrem et al. 2008). Locally, the late Permian

135 extinction event is recorded by the disappearance of prolific bioturbation just below the top of

136 the glauconitic sandstones, 1.6m above the base of the member (Nabbefeld et al. 2010). From

137 conodont evidence, Nakrem et al. (2008) inferred that the Permian/Triassic boundary occurs

138 between 5 m and 11 m above the base of the Deltadalen Member. *Claraia* cf. *wangi* is

139 recorded 10.1 m above the base of the member at Lusitaniadalen, indicative of a Griesbachian

140 age. The silicified assemblages described herein are of earliest Griesbachian (earliest Induan)

141 age, and are assigned to the upper part of the *Otoceras boreale* Zone, which corresponds to

142 the basal Triassic *Hindeodus parvus* Conodont Zone (Orchard 2007).

143

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.

165   **Material.** One dorsal valve from LD-04 (NHMUK PI BE 3238).

166   **Description.** Shell outline is sub-circular, with its length slightly greater than the width. The

167   dorsal valve is inflated to an apex, which is located about a third of the diameter from the

168   anterior margin. Shell smooth, except for fine concentric growth lines.

169   **Remarks.** Extant solitary discinids are sessile, epifaunal, invertebrates that attach to hard

170   surfaces with a sucker-like pedicle (Mergl 2010). They have been attaching to shelled

171   invertebrates since the Ordovician (Mergl 2010), and one of the specimens described herein

172   is attached to an ammonoid. Discinids are suspension feeders and their co-occurrence with

173   lingulids in laminated black shales has led some authors to interpret them as being tolerant of

174   low-oxygen conditions (Savoy 1992; Hallam 1995; Mergl 2010).

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

176
177   Phylum **Mollusca** Linnaeus, 1758

178   Class **Bivalvia** Linnaeus, 1758

179   Order **Pterioida** Newell, 1965

180   Family **Myalinidae** Frech, 1891

181   Genus ***Promyalina*** Kittl, 1904

182

183   **Type species.** *Promyalina hindi* Kittl, 1904; Permian, Changhsingian; near Sarajevo, Bosnia-

184   Herzegovina.

185   **Diagnosis.** Outline mytiliform and less triangular than *Myalina*; dorsal margin slightly

186   convex, moderately thickened; narrow beak present. Left valve inflated below the umbo.

187   Inequivalve with the right valve being less inflated and less curved.

188

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

190   (Fig. 2C-G)

191   1899   *Myalina schamarae*   Bittner. p. 19; Plate 4; Figs 20-25.

192   2009   *Promyalina schamarae*; Kumagae & Nakazawa. p. 157; Fig 144, 4-5.

193   **Material.** Three specimens from LD-04 (NHMUK PE PEI 5484; NHMUK PI MB 1202;

194   NHMUK PI MB 1205) and seven specimens from LD-05 (NHMUK PI MB 1188; NHMUK

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195 PI MB 1203-1204; NHMUK PE PEI 5475-5476; NHMUK PE PEI 5500; NHMUK PE PEI
196 5503).

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

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

207 **Mode of life.** Surficial, stationary, attached, suspension feeder (Stanley 1972).

208

209   Order **Solemyoida** Dall, 1889
210   Family **Nucinellidae** Vokes, 1956

211

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

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

223
224   Genus *Nucinella* Wood, 1851

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

226 **Diagnosis.** Nucinellids with external ligament.

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*.

232 Species ***Nucinella taylori*** sp. nov.
233 (Fig. 3)

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

9

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.

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

Other Material. Two specimens from LD-04 (NHMUK PI MB 1221-1222).

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

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

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

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

11

324 lateral secondary ridge creating a secondary socket, this specimen has two hinge teeth and a

325 lateral tooth (i.e. the normal right valve arrangement). An alternative interpretation is that this

326 specimen represents an earlier ontogenetic stage, but this is rejected because even though the

327 specimen is slightly smaller, its lateral tooth is more prominent than in a typical left valve

328 arrangement and both the subumbonal and lateral teeth appear to fit with the expected

329 corresponding valve arrangement. In addition, it has been reported that in the early stages of

330 nucinellid development the second lateral tooth is very small and closer to the subumbonal

331 teeth than later in ontogeny (Bernard, 1898), which is not the case with this specimen.

332 Transposed hinges have been reported in a number of bivalve families, but this is the first

333 reported occurrence in a species of Nucinellidae.

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

335
336 Order **Nuculanoida** Carter et al., 2000

337 Family **Neilonellidae** Schileyko, 1989

338 **Diagnosis**. Hinge plate with taxodont teeth in two series, sometimes separated by narrow,

339 plain area, without resilifer; ligament predominantly external, opisthodetic to amphidetic,

340 weak.

341 **Remarks**. The Neilonellidae are very similar to the Nuculanidae, but the lack of a resilifer in

342 mature adults supports their separation (Coan & Valentich-Scott 2012). The new specimens

343 described herein differ from the Malletiidae in lacking conspicuous gapes, and from the

344 Tindariidae in having a short gap in the dentition below the beaks (Di Geronimo & La Perna

345 1997). The family is currently known from the Jurassic to present in all oceans, especially in

346 deep water and soft substrates (Coan & Valentich-Scott 2012).

347

348 Genus *Austrotindaria* Fleming, 1948

349 **Type species.** *Austrotindaria wrighti* Fleming 1948; Holocene, Quaternary; Southland, New

350 Zealand.

351 **Diagnosis.** Delicate almost smooth shell, with weak concentric sculpture. A short, edentulous

352 gap between the posterior and anterior hinge plates. No pallial sinus and without rostrum.

353 **Remarks**. The Neilonellidae comprises three valid genera: *Neilonella, Austrotindaria* and

354 *Pseudoneilonella* (La Perna 2007). The convex shape of the posterior margin and the

presence of an opisthodetic ligament in our specimens indicate better agreement with *Austrotindaria* than *Neilonella* (Di Geronimo & La Perna 1997; La Perna 2007). *Austrotindaria* differs from *Neilonella* and *Pseudoneilonella* by having a delicate, almost smooth, shell rather than a sturdy, sculptured shell, and by having a small elongate pit below the posterior and anterior teeth (La Perna 2007). This genus is currently known from the Miocene to Recent (La Perna 2007; Coan & Valentich-Scott 2012) and the specimens identified in his study extend the range of the genus to the beginning of the Triassic.

Species ***Austrotindaria antiqua*** sp. nov.

(Fig. 5)

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

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

1926   *Anodontophora fassaensis*; Matsushita Plate 8; Fig. 11

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

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

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

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

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

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

Diagnosis. Shell small, smooth except for concentric growth lines, subtrigonal, inequilateral, prosogyrate; taxodont hinge dentition with more than 50% fewer anterior than posterior ones, obtusely chevron-shaped teeth, hinge plate interrupted below the beak by an edentulous gap, a small rounded triangular pit below the edentulous gap; ligament opisthodetic.

Holotype. Disarticulated right valve, NHMUK PI MB 1240, LD-04; length = 4.0mm, height = 3.0mm.

Paratype. Disarticulated left valve, NHMUK PI MB 1241, LD-04; length = 4.6mm, height = 3.4mm.

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

13

384 eighteen specimens from LD-05 (NHMUK PI MB 1191; NHMUK PI MB 1196-1197;

385 NHMUK PI MB 1199; NHMUK PI MB 1242; NHMUK PE PEI 5475-5476; NHMUK PE

386 PEI 5483; NHMUK PE PEI 5494; NHMUK PE PEI 5497; NHMUK PE PEI 5499-5501;

387 NHMUK PE PEI 5504; NHMUK PE PEI 5506; NHMUK PE PEI 5515). Two prodissoconch

388 valves from LD-04 (NHMUK PI MB 1243-1244).

389 **Derivation of name.** Latin, antiqua (ancient) referring to this species being the oldest known

390 of the genus.

391 **Description.** Equivalve, inequilateral shell with a subtrigonal outline and a beak positioned

392 approximately 30% along the length of the dorsal margin from the posterior; H/L ratio 0.6-1.

393 Conspicuously tumid. Umbo prosogyrate, prominent, moderately broad, rounded and projects

394 above the hinge margin. Slightly rounded and gently sloping anterodorsal margin.

395 Posterodorsal margin almost straight to slightly rounded, gently sloping, with a slight angled

396 junction with the posterior margin. Ventral margin deeply rounded. Escutcheon short,

397 relatively broad, elliptical; lunule narrow. Shell smooth with fine concentric growth lines;

398 entire inner margin smooth. Small ligament, external, opisthodetic, with a well-defined

399 margin and well-rounded triangular pit seated beneath the edentulous gap. Hinge plate with

400 taxodont teeth in two series, sometimes separated by a narrow, plain area, without resilifer,

401 that is narrow below the beak, broadening towards the anterior and posterior ends. Robust

402 teeth, moderately long and blunt, with more than 50% fewer anterior than posterior ones.

403 Smooth ventral margin. No pallial line, sinus or muscle scars are present. As the size of the

404 shell increases the edentulous gap becomes proportionally smaller, more central and moves

405 externally.

406 **Remarks.** The external morphology of these specimens is identical to most Early Triassic

407 specimens previously described as "*Unionites*" *fassaensis*, which is one of the most

408 widespread bivalve species from the Lower Triassic and is also a problematic dustbin taxon

409 that includes a range of different morphologies. These specimens differ from the original

410 description and figures of "*Myacites*" *fassaensis* Wissmann (1841) in having a less elongated

411 posterior margin and a more prosogyrate beak. Due to poor preservation, however, little is

412 known about the internal morphology of Early Triassic specimens assigned to *U. fassaensis*,

413 which has created some uncertainty (Hautmann et al. 2013). Internally, these new specimens

414 lack the following characters that Geyer et al. (2005) determined were diagnostic of

415 *Unionites*: a nymph extending nearly half of the posterior margin; an impressed adductor

416 muscle scar; an overlap of the anterior hinge; and a deeply impressed lunule and posterior

14

417 keel. Thus, these specimens cannot be assigned to *Unionites*. The presence of taxodont hinge

418 dentition, an opisthodetic ligament and lack of ornamentation is, however, characteristic of

419 the genus *Austrotindaria*.

420   The more prosogyrate beak means that these specimens have a similar external

421 morphology to Middle Triassic *Unionites* specimens (e.g. Geyer et al. 2005), but apart from

422 possessing a faint posterior keel they lack the diagnostic criteria of *Unionites*. Furthermore,

423 the *Unionites* specimens described by Geyer et al. (2005) and from this study (see below) all

424 have a strong posterior keel. Thus, these specimens are not assigned to *Unionites*. These

425 specimens, and all previous specimens assigned to *Unionites fassaensis* that possess a

426 prosogyrate beak and lack a well-defined posterior keel, are therefore assigned to

427 *Austrotindaria antiqua* sp. nov.

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

429

430   Species ***Austrotindaria svalbardensis*** sp. nov.

431   (Fig. 6)

432   1864   *Anoplophora fassaensis*; Alberti. p. 137; Plate III; Fig. 8.

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

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

435   2015   *Unionites* cf. *fassaensis*; Hautmann et al. p. 890; Fig. 10, H.

436 **Diagnosis.** Shell small, smooth except for concentric growth lines, subtrigonal, inequilateral,

437 orthogyrate; taxodont hinge dentition with more posterior than anterior teeth, obtusely

438 chevron-shaped teeth, hinge plate interrupted below the beak by an edentulous gap, a small

439 rounded triangular pit below the edentulous gap; ligament opisthodetic.

440 **Holotype.** Disarticulated right valve, NHMUK PI MB 1223, LD-04; length = 1.8mm, height

441 = 1.3mm.

442 **Paratype.** Disarticulated left valve, NHMUK PI MB 1231, LD-04; length = 1.5mm, height =

443 1.0mm.

444 **Other Material.** Twenty-one specimens from LD-04 (NHMUK PI MB 1190; NHMUK PI

445 MB 1192-1193; NHMUK PI MB 1224-1230; NHMUK PI MB 1232-1233; NHMUK PI MB

446 1235-1236; NHMUK PE PEI 5478; NHMUK PE PEI 5482; NHMUK PE PEI 5489;

447 NHMUK PE PEI 5505; NHMUK PE PEI 5509-5510; NHMUK PE PEI 5512; NHMUK PE

448 PEI 5520) and twelve specimens from LD-05 (NHMUK PI MB 1189; NHMUK PI MB 1197;

449 NHMUK PI MB 1200; NHMUK PE PEI 5476; NHMUK PE PEI 5491-5492; NHMUK PE

450 PEI 5496; NHMUK PE PEI 5498; NHMUK PE PEI 5503-5504; NHMUK PE PEI 5517).

451 Twenty-four prodissoconch valves from LD-04 (NHMUK PI MB 1234; NHMUK PI MB

452 1237; NHMUK PI MB 1238; NHMUK PE PEI 5520) and five prodissoconch valves from

453 LD-05 (NHMUK PI MB 1239).

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

455 **Description.** Shell outline subtrigonal, equivalve, inequilateral with beak positioned

456 approximately 60% of the distance along the dorsal margin from the posterior; H/L ratio 0.6-

457 1; conspicuously tumid. Orthogyrate umbo, prominent, moderately broad, rounded and

458 projected above the hinge margin. Anterodorsal margin slightly rounded and gently sloping.

459 The posterodorsal margin is almost straight to slightly rounded and gently sloping. Ventral

460 margin is smooth and deeply rounded. Escutcheon is short, relatively broad, elliptical; lunule

461 narrow. No sculpture except for fine concentric growth lines; entire inner margin is smooth.

462 Prodissoconch is smooth, broadly subovate, with H/L ratio of 0.6-0.9. Ligament small,

463 external with well-defined margin, opisthodetic, with a well-rounded triangular pit seated

464 beneath the edentulous gap. Hinge plate with taxodont teeth in two series; separated by

465 narrow, plain area, without resilifer, narrow below the beak, broadening towards the anterior

466 and posterior ends. Teeth are robust, moderately long and blunt, with more posterior than

467 anterior teeth, separated by an edentulous gap. As the size of the shell increases the

468 edentulous gap becomes proportionally smaller, more central and moves externally. No

469 pallial line, sinus or muscle scars present.

470 **Remarks.** These specimens differ from *Austrotindaria antiqua* sp. nov. in having a more

471 equal number of anterior to posterior teeth and an orthogyrate beak. The direction of the beak

472 also separates these specimens from unequivocal species of *Unionites*. In the specimens

473 described here and other *Austrotindaria* species the beak is orthogyrate to posteriorly

474 opisthogyrate, whereas in *Unionites* it is prosogyrate. Based on this key character, most

475 specimens previously assigned to *Unionites fassaensis,* and similar Early Triassic specimens

476 with an orthogyrate beak and no internal morphological detail preserved, are herein assigned

477 to *Austrotindaria svalbardensis* sp. nov.

478   These specimens have a very similar shape, size and ornamentation to the type species

479 of *Austrotindaria* (*A. wrighti* Flemming), however, they differ in possessing a small, rounded,

16

480   triangular pit below the edentulous gap and differ from other *Austrotindaria* species, e.g. *A.*
481   *mawheraensi*s, 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*; Kashiyama & 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

17

510 not belong to the genus *Unionites*. The external features of these specimens are most similar

511 to species of Neilonellidae, e.g. *Austrotindaria benthicola* (Dell, 1956). *Austrotindaria* is the

512 only genus of the Neilonellidae that is reported from the Early Triassic, and these specimens

513 are, therefore, tentatively assigned to it. Without observation of the internal characters an

514 unequivocal generic assignment cannot be made. The posterior margin is more elongate than

515 in *Austrotindaria svalbardensis* sp. nov., and these specimens are therefore considered to

516 represent a separate species.

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

518
519 Family **Malletiidae** Adams & Adams, 1858

520 (Fig. 7)

521 **Diagnosis.** Subequilteral to inequilateral; usually with elongate, compressed posterior end;

522 sculpture of commarginal striae or ribs; anterior and posterior gapes present; hinge plate

523 weak, with fine taxodont teeth in two series, sometimes separated by plain area, without

524 resilifer; ligament external, opisthodetic to amphidetic, weak; pallial sinus large.

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

526 **Description**. Shell is equilateral, elliptical, H/L ratio of 0.7, and moderately inflated. Umbo is

527 broad, orthogyrate, with beak positioned centrally. Shell smooth except for concentric growth

528 lines. Hinge plate has three anterior and three posterior teeth in two series separated by a

529 large plain area with a groove. Ligament is predominantly external, amphidetic and weak.

530 **Remarks.** The Malletiidae are very similar to the Nuculanidae, but the lack of a resilifer in

531 mature adults supports their separation (Coan & Valentich-Scott 2012). These specimens do

532 not belong to the Neilonellidae because they possess a small conspicuous gape between the

533 valves. The Malletiidae is a long-ranging family known from the Ordovician to the Recent,

534 and three genera (*Malletia, Palaeoneilo* and *Taimyrodon*) belonging to the family have

535 previously been reported from the Lower Triassic (e.g. He et al. 2007; Wasmer et al. 2012).

536 Externally, these specimens resemble the larval shells of *Paleoneilo*? *fortistriata* figured by

537 Wasmer et al. (2012), but they have far fewer hinge teeth. There are also equal numbers of

538 anterior to posterior hinge teeth in these specimens, whereas in *P. fortistriata* there are many

539 more posterior than anterior teeth (Wasmer et al. 2012).

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

18

541

Order **Unionoida** Stoliczka, 1871

Family **Anthracosiidae** Amalitsky, 1892

Genus *Unionites* Wissmann, 1841

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

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

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

(Fig. 8)

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

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

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

Material. Seven specimens from LD-04 (NHMUK PI MB 1245-1247; NHMUK PE PEI 5480; NHMUK PE PEI 5485; NHMUK PE PEI 5507; NHMUK PE PEI 5519) and nine specimens from LD-05 (NHMUK PI MB 1195; NHMUK PI MB 1197; NHMUK PI MB 1201; NHMUK PE PEI 5495; NHMUK PE PEI 5506; NHMUK PE PEI 5508; NHMUK PE PEI 5516).

570 **Description.** Outline elongate-elliptical. Shell equivalved, inflated below the umbo, and

571 inequilateral with beak positioned approximately 85% along the length of the dorsal margin

572 from the posterior. Lower part of anterior dorsal margin projects slightly beyond plane of

573 commissure. Posterodorsal margin is almost straight to slightly round and gently sloping.

574 Lunule is long and narrow, with deeply impressed escutcheon. Umbo is prosogyrate and rises

575 above the hinge margin. Ornamented with fine concentric growth lines. The entire inner

576 margin is smooth. Prodissoconch is smooth and orbicular.

577 A small subumbonal groove limits the shell projection posteriorly. Short lateral tooth,

578 left valve possesses a weak secondary ridge creating a shallow socket. Hinge of left valve has

579 an anterior platform that bears a depression for the corresponding anterior hinge margin of

580 the right valve, posterior to this is a small, tuberculiform subumbonal tooth fitting above

581 posterior lateral tooth of right valve. Ligament is fixed to a nymph, which extends about half

582 the length of the posterior dorsal margin. Isomyarian muscle scars with a deeply impressed

583 anterior adductor muscle scar.

584 **Remarks.** Insufficient knowledge of the internal morphology of Early Triassic bivalves in

585 general, and *Unionites* in particular, has created uncertainty regarding their systematic

586 position. Based on their external morphology alone these specimens would be assigned to

587 *Triaphorus* aff. *multiformis* (Kumagae & Nakazawa 2009), but they possess the following

588 characters that are diagnostic of *Unionites*: the anterior hinge margin of the right valve

589 overlaps that of the left; a nymph that extends nearly half the length of the posterior hinge

590 margin; an impressed anterior adductor muscle scar; a deeply impressed lunule; and a long

591 and narrow escutcheon. Thus, these specimens are assigned to *Unionites*.

592 These specimens differ from *U. brevis, U. fassaensis, U. letticus, U. griesbachi, U.*

593 *borealis,* and *U. rhomboidalis* because their length greatly exceeds their height. They are

594 most similar to *U. subrectus* described from the Middle Triassic of Hungary by Szente &

595 Vörös (2003), except they have a more elliptical outline.

596 **Mode of Life.** Shallow infaunal, facultatively motile, unattached, suspension feeder

597 (Hautmann et al. 2013).

598

599 Order **Trigoniida** Dall, 1889

600 Family **Myophoriidae** Bronn, 1849

601 Genus *Neoschizodus* Gieberl, 1855

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

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

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

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

Material. Five specimens from LD-04 (NHMUK PI MB 1251; NHMUK PE PEI 5489; NHMUK PE PEI 5519; NHMUK PE PEI 5522) and eight specimens from LD-05 (NHMUK PE PEI 5476-5477; NHMUK PE PEI 5499; NHMUK PE PEI 5501; NHMUK PE PEI 5518; NHMUK PE PEI 5521). Fifty-nine prodissoconch valves from LD-04 (NHMUK PI MB 1252; NHMUK PI MB 1254; NHMUK PI MB 1255-1260; NHMUK PE PEI 5480; NHMUK PE PEI 5484; NHMUK PE PEI 5486; NHMUK PE PEI 5511; NHMUK PE PEI 5513; NHMUK PE PEI 5520) and fourteen prodissoconch valves from LD-05 (NHMUK PI MB 1253; NHMUK PE PEI 5514).

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

The larval shells have a similar external morphology to the adult shells, with a short and subumbonal hinge and short, narrow nymphs running down the anterior and posterior 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;

22

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).

692

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

694 Family **Eotomariidae** Wenz, 1938

695 Subfamily **Eotomariinae** Wenz, 1938

23

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 <45° 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.

721

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.

24

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

Other Material. Ten specimens from LD-04 (NHMUK PI MG 1468; NHMUK PI MG 1471; NHMUK PI MG 1495; NHMUK PI MG 1500-1501; NHMUK PI MG 1513-1515; NHMUK PE PEI 5519-5520) and fourteen specimens from LD-05 (NHMUK PI MG 1476; NHMUK PI MG 1482; NHMUK PI MG 1484; NHMUK PI MG 1493; NHMUK PI MG 1530; NHMUK PE PEI 5493; NHMUK PE PEI 5502; NHMUK PE PEI 5514). Fourteen juvenile shells from LD-04 (NHMUK PI MG 1516-1517; NHMUK PI MG 1519-1529; NHMUK PE PEI 5486).

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

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

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

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

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

762   The Vetigastropoda have a diverse range of living habits including being described in
763 association with wood-fall communities (Kiel et al. 2008). The specimens in this study do
764 occur in association with wood, however, no direct relationship was observed. Eotomariidae
765 recorded from Zechstein reefs are described as motile algal grazers that were probably
766 confined to a hard substrate (Hollingworth & Pettigrew 1988). The lack of evidence of a hard
767 substrate in their depositional environment, however, suggests that these specimens probably
768 had a similar life habit to deep-sea vetigastropods that typically consume sediment (Hickman
769 1988).

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

771

772   Order **Ptenoglossa** Gray, 1853

773   Family **Pseudozygopleuridae** Knight, 1930

774   (Fig. 12)

775 **Material.** Three larval shells from LD-04 (NHMUK PI MG 1532-1534).

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

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

791 Zygopleuridae have smooth whorls with fine riblets at the sutures (Nützel & Mapes 2001;

792 Kaim 2004) or straight ribs in the Ampezzopleurinae (Nützel 1998; 2005). Protoconchs of the

793 Ladinulidae are similar to those of the Pseudozygopleuridae but can be differentiated due to

794 their vertical costellae (Bandel 2006). These specimens are, therefore, representatives of the

795 Pseudozygopleuridae. No teleoconch is apparently present in these specimens as the sculpture

796 of the prodissoconch is uninterrupted.

797   The Pseudozygopleuridae is primarily a Palaeozoic family. Apart from the Early

798 Triassic specimens described herein, the only other Mesozoic pseudozygopleurid is

799 *Plocezyga* from the Jurassic of Poland (Kaim 2004). Those specimens attributed to *Plocezyga*

800 by Kaim (2004), however, lack a protoconch with the diagnostic sigmoidal

801 pseudozygopleurid ornamentation described by Hoare & Sturgeon (1978; 1980). Instead they

802 have a reticulate pattern, shouldered whorls and transverse costae on the protoconch,

803 indicating that they belong to a different genus and family.

804   Nützel (1998) used the diameter, ornamentation and whorl number of the protoconch)

805 to separate planktotrophic from non-planktotrophic pseudozygopleurid species. The

806 specimens recorded in this study have small protoconch I diameters (0.12-0.14mm), and the

807 same ornamentation and number of whorls as pseudozgopleurid larval shells interpreted as

808 planktotrophic by Mapes & Nützel (2009), which suggest that they too had a planktotrophic

809 larval lifestyle. A teleoconch was not developed in any of the specimens, which may indicate

810 that the adults were unable to live in this environment.

811

812   Order **Architectibranchia** Haszprunar, 1985

813   Family **Tubiferidae** Cossmann, 1895

814   Genus *Sinuarbullina* Gründel, 1997

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

816 Poland.

817 **Diagnosis.** The generic diagnosis follows Gründel and Nützel (2012). The shell is fusiform

818 with a distinctly elevated spire. The teleoconch whorls have a subsutural ramp. The transition

819 from the ramp to the outer whorl face is either rounded or angular, sometimes demarcated

820 abapically by a spiral concavity. Whorls are smooth in most species, although faint spiral

821 furrows occur on the base in a few of them. Growth lines are prosocyrt on the outer whorl

822 face but strongly curving in an abapertural direction and opisthocyrt at the ramp. The aperture

823 is relatively low for the group, teardrop-shaped and lack columnellar fold. The protoconch is

824 trans- to medioaxial.

Remarks. Pan et al. (2003) described *Jiangxispira* as a new genus using the following

826 diagnostic features: 1) a small, high-spired, slender, fusiform shell; 2) teleoconch whorls with

827 narrow shoulder; and 3) a heterostrophic, discoidal, transaxial protoconch. These characters

828 are all within the diagnostic features of the genus *Sinuarbullina* Gründel (1997), and

829 *Jiangxispira* is, therefore, a junior synonym of *Sinuarbullina*.

830

831 Species ***Sinuarbullina yangouensis*** (Pan et al., 2003) comb. nov.

832 (Fig. 13)

833

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

Material. Specimen lost by WJF after photography.

Description. The shell is high-spired, slender and fusiform. Teleoconch whorls have a

837 subsutural ramp. The ramp from the outer whorl face is rounded with a rib on the shell

838 periphery. Whorls are smooth, except for growth lines which are prosocyrt on the outer whorl

839 face curving in an apertural direction and become opisthocyrt towards the ramp. The surface

840 of the shell shows a colour spiral band around the subsutural ramp. The aperture is an

841 elongated teardrop shape. Protoconch is heterostrophic, sinistral, nearly discoidal with lightly

842 elevated spire 30° offset from the shell axis; protoconch has 1-2 round whorls.

Remarks. Seven species are included in *Sinuarbullina*, and *S. convexa* (='*Cylindrobullina'*

844 *convexa*) is the only accepted species from the Lower Triassic (Gründel & Nützel 2012).

845 These specimens are more slender than *S. convexa*, described from the Sinbad Limestone of

846 the western US by Batten & Stokes (1986), and better resemble *Jiangxispira yangouensis*

847 from the Induan Dayie Formation, China.

848 The shell morphology is similar to *Meekospira*, which has been interpreted as a slow-

849 moving shell dragger (Hughes 1986), but could have also been a burrower (Hollingworth &

850 Pettigrew 1988). Interpreting the feeding strategy of fossil gastropods is difficult because

851 information on the organ system, including the ctendium, is not usually preserved. The

852 ancestral condition in high-spired gastropods is presumably an algal grazer on hard substrates

853 (Declerck 1995). Given the absence of hard substrates in this study, the specimens described

854 herein were probably detritus feeders or possibly micro-carnivorous on sedentary prey as in

855 many modern shelled opisthobranchs (e.g. Lobo da Cunha et al. 2009).

28

856   **Mode of Life.** Surficial, fully motile, slow, deposit feeder.

857

858   **Discussion**

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

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

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

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

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

29

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

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

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

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

30

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

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

The importance of planktotrophy

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

956 shell development has been inferred for many Early Triassic gastropods (Nützel & Erwin

957 2002; Pan et al. 2003; Nützel & Schulbert 2005) and this selectivity has been questioned

958 (Nützel 2014). All gastropod taxa recorded in the present study (i.e., *Warthia,*

959 *Glabrocingulum, Sinuarbullina* and the Pseudozygopleuridae) are inferred to have had

960 planktotrophic larvae (Nützel & Mapes 2001, this study), and in addition, the bivalves

961 *Nucinella, Austrotindaria, Unionites* and *Neoschizodus* all possess a small prodissoconch I

962 and a relatively large prodissoconch II which imply planktotrophic larval development (cf.

963 Hautmann & Nützel 2005). Thus, we infer that the possession of planktotrophic larvae was a

964 particular advantage for benthic molluscs inhabiting shelf settings of the Boreal Ocean in the

965 earliest Triassic. This may simply be a consequence of sampling this particular depositional

966 setting, as benthic taxa with plankotrophic larvae were common in similar mid-outer shelf

967 settings during the Palaeozoic (e.g. Nützel & Mapes 2001; Frýda 2001; Bandel et al. 2002).

968 Alternatively, it may be a consequence of the extinction event and associated environmental

969 changes.

970 One possible advantage of a planktotrophic larval development is protection from

971 benthic predation (Nützel & Frýda 2003). Although predators are rarely identified in Early

972 Triassic benthic assemblages (e.g. Schubert & Bottjer 1995; Twitchett et al. 2004; Hautmann

973 et al. 2011; Hofmann et al. 2013a; 2013b; 2014; 2015; Foster and Twitchett 2014; Foster et

974 al. 2015), it is possible that some nektobenthic conodonts, ammonoids or fish may have

975 fulfilled this role or that the predators were largely non-mineralised. Fish with durophagous

976 dentitions, such as *Bobasatrania*, are locally common in the lowest Triassic of the Boreal

977 Ocean (e.g. East Greenland; Stensiö 1932), and trace fossil evidence of vagile crustaceans has

978 been recorded from the Induan of northwest Canada (Beatty et al. 2008; Zonneveld et al.

979 2010) and central Spitsbergen (WJF & RJT pers. obs.).

980 An alternative advantage is that planktotrophic larvae enable more effective dispersal

981 and a wide geographic distribution. The cosmopolitan opportunists that thrived in the wake of

982 the late Permian mass extinction (e.g. *Lingularia* and *Claraia*) all have an inferred

983 planktotrophic larval stage (Hammond & Poiner 1984; Yang et al. 2001). Possession of

984 planktotrophic larvae would have been particularly useful for Early Triassic benthic

985 invertebrates given the spatial and temporal fluctuations in benthic oxygen concentrations

986 that have been inferred for the earliest Triassic seafloor (Wignall & Twitchett 1996; Thomas

987 et al. 2004; Nabbefeld et al. 2010). Effective dispersal and wide distribution would have

988 afforded greater protection from extinction and enabled rapid colonisation of vacated seafloor

989 once harsh environmental conditions had ameliorated. The late Permian mass extinction did

990 not select against animals with planktotrophic larval development (Posenato et al. 2014;

991 Nützel 2014), and possession of that character may have been a key factor in the survival and

992 radiation of certain groups.

993   The occurrence of well-preserved planktotrophic larval shells in this newly described

994 benthic assemblage has additional palaeoenvironmental implications. First, it implies that

995 primary production in surface waters was adequate enough to sustain planktic foodwebs.

996 Second, the exquisite preservation of the earliest formed larval stages and the complete

997 absence of any signs of shell dissolution or repair (cf. Garilli et al. 2015) demonstrates that

998 neither the surface waters nor benthic habitat in this particular region were affected by ocean

999 acidification at this time, and the pH was not low enough to have curtailed biomineralization.

1000

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

Acknowledgements

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Figure 1. Locality and stratigraphy of the studied section in Lusitaniadalen. **A,** locality map of the Lusitaniadalen section; **B,** Palaeogeographic position; **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).

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.

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 = 500μm; G-J = 100 μm

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.

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,

1407   right valve; **G,** NHMUK PI MB 1242, hinge plate of left valve; **H,** NHMUK PI MB 1194,

1408   dorsal view, right valve; **I,** Articulated specimen, NHMUK PI MB 1243; **J,** Larval shell,

1409   NHMUK PI MB 1244, left valve. Scale bar: A-C, G = 500μm; D-F = 1mm; I-J = 100μm.

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1411   **Figure 6.** *Austrotindaria svalbardensis* sp. nov. **A,** Paratype, Length – 1.5mm, height –

1412   1.0mm, NHMUK PI MB 1231, external view, left valve; **B,** Holotype, Length – 1.8mm,

1413   height – 1.3mm, NHMUK PI MB 1223, external view, right valve; **C,** NHMUK PI MB 1190,

1414   left valve, external view; **D,** larval shell, NHMUK PI MB 1234, external view, right valve; **E,**

1415   NHMUK PI MB 1225, internal view, left valve; **F,** NHMUK PI MB 1227, internal view, left

1416   valve; **G,** larval shell, NHMUK PI MB 1237, internal view, right valve; **H,** Paratype,

1417   posterior and anterior hinge plate junction, NHMUK PI MB 1231. Scale bar = 500μm.

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1419   **Figure 7.** Malletiidae (Adams & Adams, 1858) larval shell. **A,** NHMUK PI MB 1249,

1420   external view; **B,** NHMUK PI MB 1249, internal view; **C,** NHMUK PI MB 1248, internal

1421   view. Scale bar = 100μm.

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1423   **Figure 8.** *Unionites* aff. *subrectus* (Bittner, 1901). **A,** NHMUK PI MB 1246, external view,

1424   right valve; **B,** NHMUK PI MB 1245, external view, left valve; **C,** NHMUK PI MB 1246,

1425   internal view, right valve; **D,** NHMUK PI MB 1245, internal view, left valve; **E,** NHMUK PI

1426   MB 1195, external view, right valve; **F,** hinge margin, NHMUK PI MB 1245, left valve; **G,**

1427   hinge margin, NHMUK PI MB 1246, right valve. Scale bar = 1mm.

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1429   **Figure 9.** *Neoschizodus laevigatus* Gieberl (1855). **A,** NHMUK PI MB 1251, external view,

1430   left valve; **B-G, J,** larval shells; **B,** NHMUK PI MB 1256, external view, right valve; **C,**

1431   NHMUK PI MB 1259, external view, left valve; **D,** NHMUK PI MB 1257, external view,

1432   right valve; **E,** NHMUK PI MB 1260, internal view, left valve; **F,** NHMUK PI MB 1258,

1433   internal view, left valve; **G,** NHMUK PI MB 1255, internal view, right valve; **H-I,** beak of

1434   adult specimen, NHMUK PI MB 1251; **J,** hinge plate of a larval shell, NHMUK PI MB 1260.

1435   Scale bar: A = 2mm; B-G, I = 200μm; H = 1mm; J = 50μm.

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1437   **Figure 10.** *Warthia zakharovi* Kaim (2009). **A,** NHMUK PI MG 1502, apertural view; **B-C,**

1438   NHMUK PI MG 1505; **B,** apertural view; **C,** lateral view; **D-E,** NHMUK PI MG 1509; **D,**

1439   lateral view; **E,** apertural view; **F,** NHMUK PI MG 1508, apical view; **G-H,** NHMUK PI MG

1440   1504; **G,** apical view; **H,** protoconch. A-B, Scale bar = 500 μm, except H.

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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.

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.

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.

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
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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 = 500μm; G-J = 100 μm.

170x171mm (300 x 300 DPI)
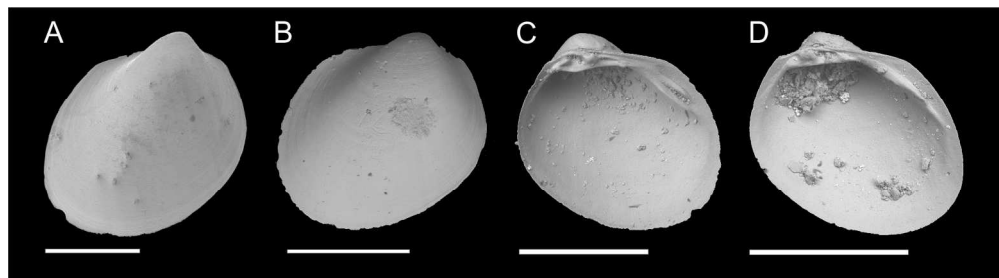
Figure 4. Nucinella nakremi sp. nov. A, Holotype, Length – 1.1mm, height – 1.1mm, NHMUK PI MB 1219, external view, left valve; B, , Paratype, Length – 0.9mm, height – 0.8mm, NHMUK PI MB 1220, external view, left valve; C, Holotype, NHMUK PI MB 1219, interior view, left valve; D, Paratype, NHMUK PI MB 1220, , interior view (transposed hinge), left valve. Scale bar = 500µm.

170x46mm (300 x 300 DPI)
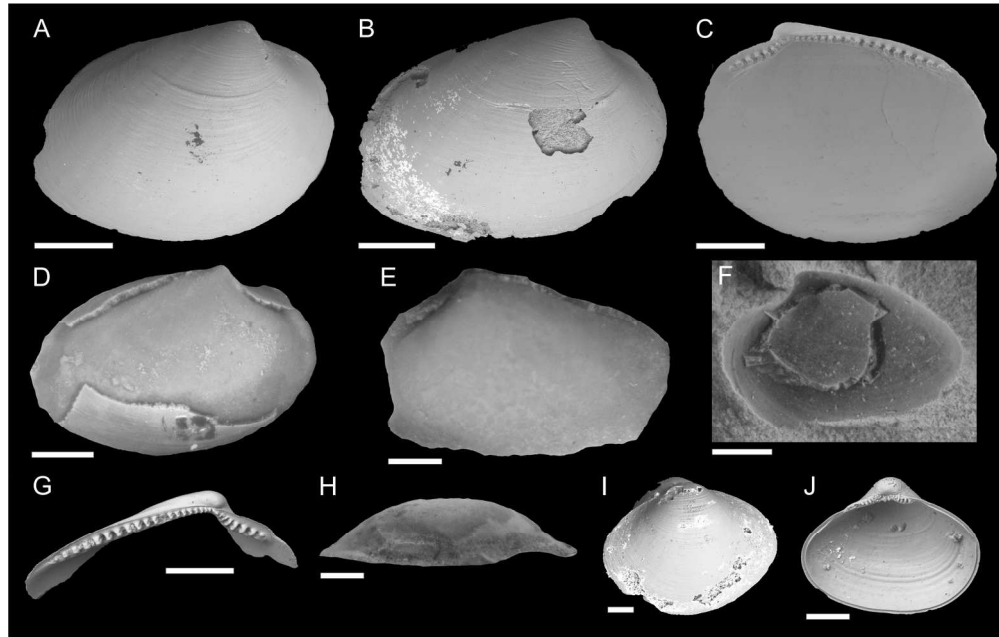
Figure 5. Austrotindaria antiqua sp. nov. A, Holotype, Length – 4.0mm, height – 3.0mm, NHMUK PI MB 1240, external view, right valve; B, Paratype, Length – 4.6mm, height – 3.4mm, NHMUK PI MB 1241, external view, right valve; C, Holotype, NHMUK PI MB 1240, internal view, right valve; D, NHMUK PI MB 1191, 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 = 500µm; D-F = 1mm; I-J = 100µm.

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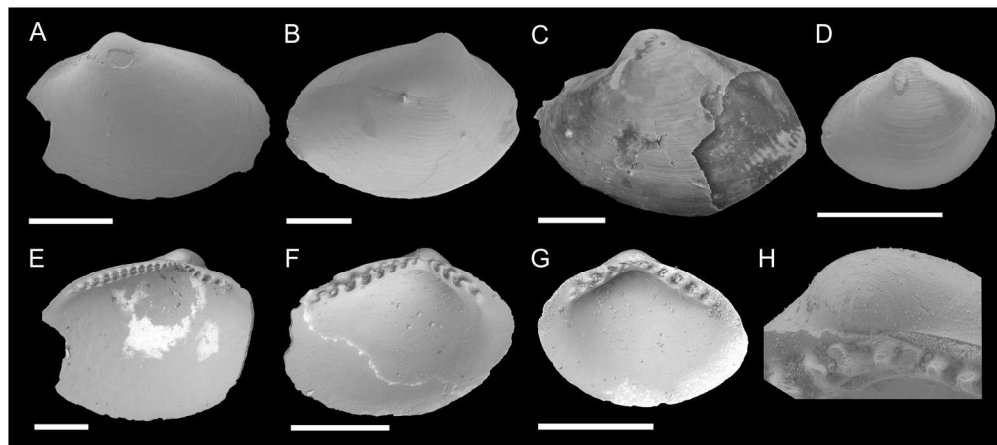
Figure 6. Austrotindaria svalbardensis sp. nov. A, Paratype, Length – 1.5mm, height – 1.0mm, NHMUK PI MB 1231, external view, left valve; B, Holotype, Length – 1.8mm, height – 1.3mm, NHMUK PI MB 1223, external view, right valve; C, NHMUK PI MB 1190, left valve, external view; D, larval shell, NHMUK PI 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)
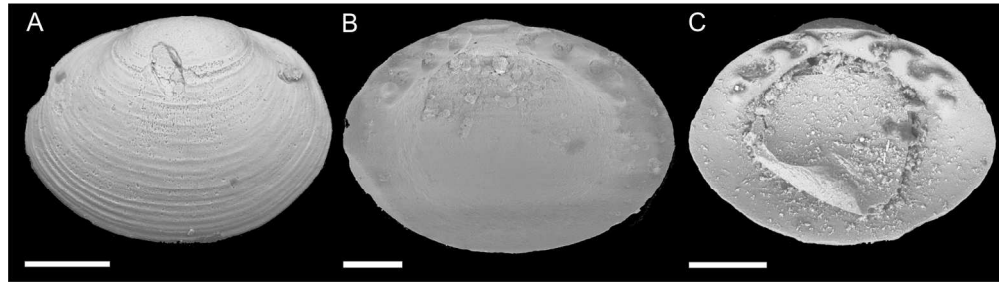
Figure 7. Malletiidae (Adams & Adams, 1858) larval shell. A, NHMUK PI MB 1249, external view; B, NHMUK PI MB 1249, internal view; C, NHMUK PI MB 1248, internal view. Scale bar = 100µm.

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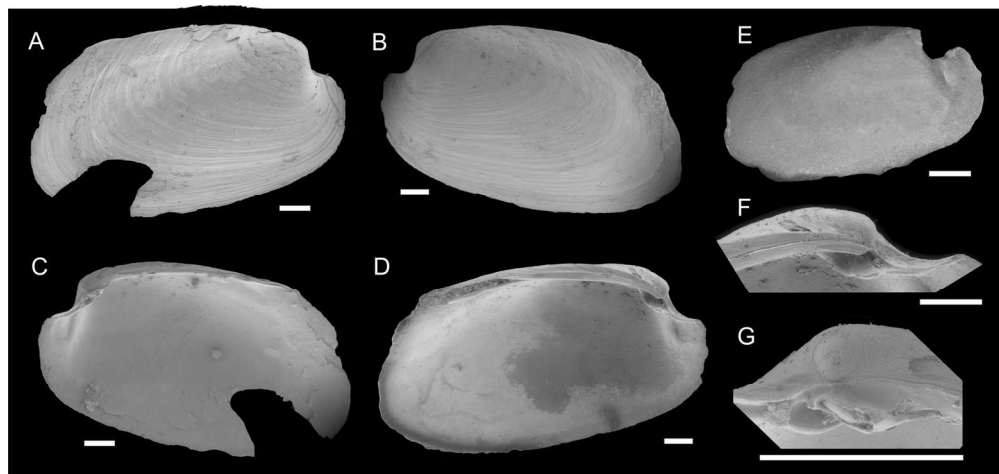
Figure 8. Unionites aff. subrectus (Bittner, 1901). A, NHMUK PI MB 1246, external view, right valve; B, NHMUK PI MB 1245, external view, left valve; C, NHMUK PI MB 1246, internal view, right valve; D, NHMUK PI MB 1245, internal view, left valve; E, NHMUK PI MB 1195, external view, right valve; F, hinge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

85x40mm (600 x 600 DPI)
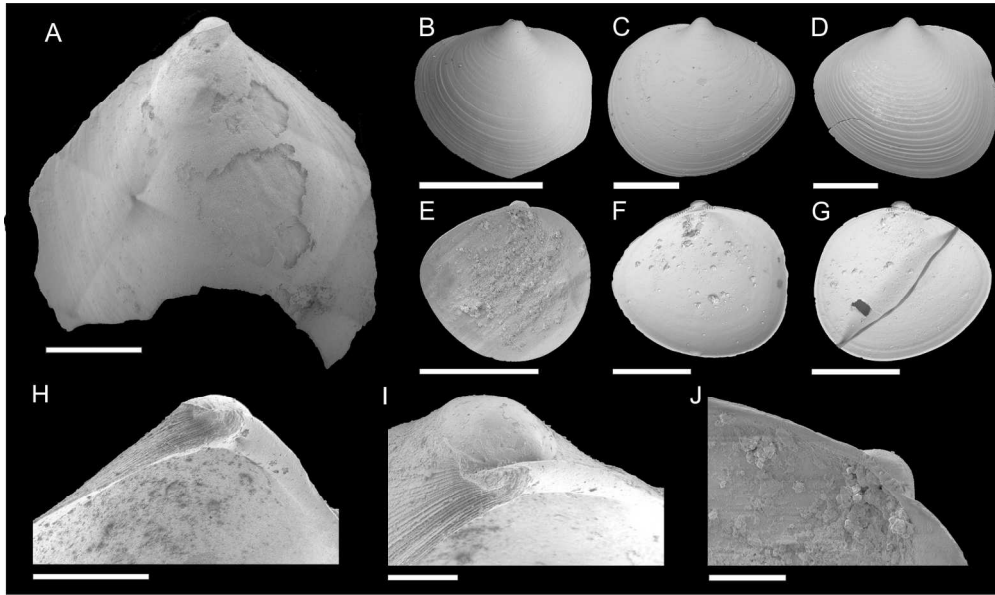
Figure 9. Neoschizodus laevigatus Gieberl (1855). A, NHMUK PI MB 1251, external view, left valve; B-G, J, larval shells; B, NHMUK PI MB 1256, external view, right valve; C, NHMUK PI MB 1259, external view, left valve; D, NHMUK PI MB 1257, external view, right valve; E, NHMUK PI MB 1260, internal view, 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 = 200µm; H = 1mm; J = 50µm.
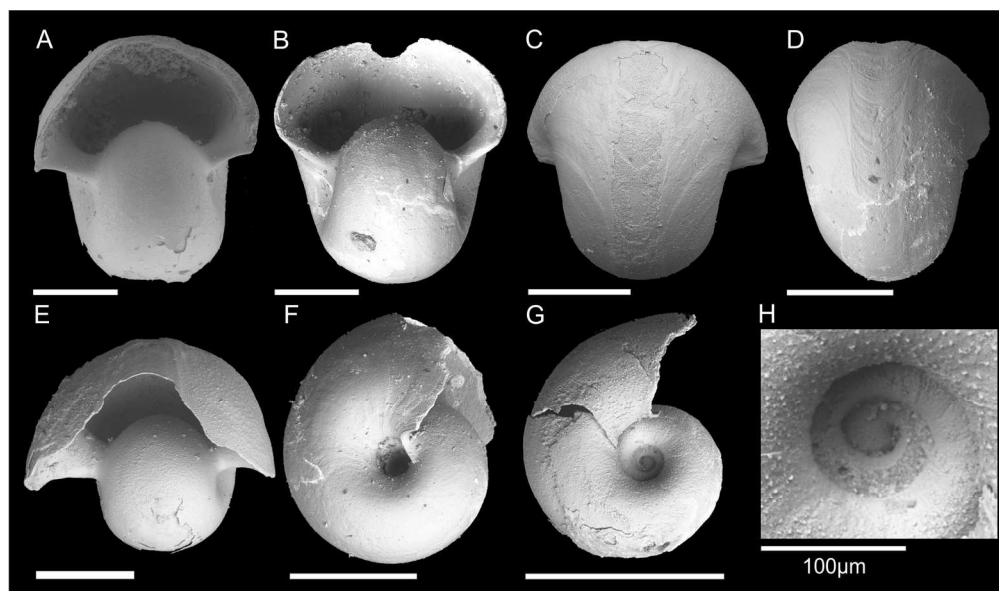
170x100mm (300 x 300 DPI)

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 μm, except H.
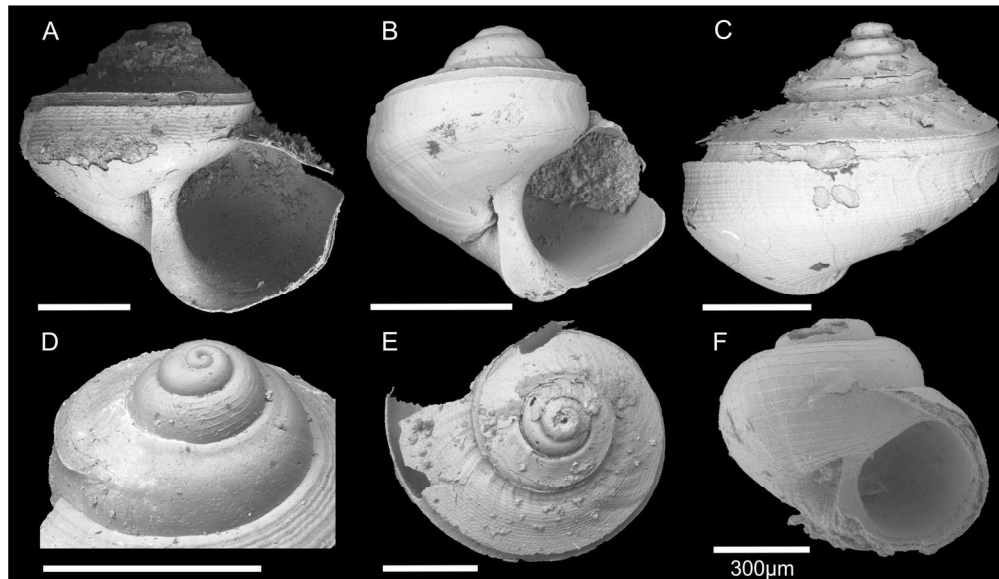
170x100mm (300 x 300 DPI)

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.
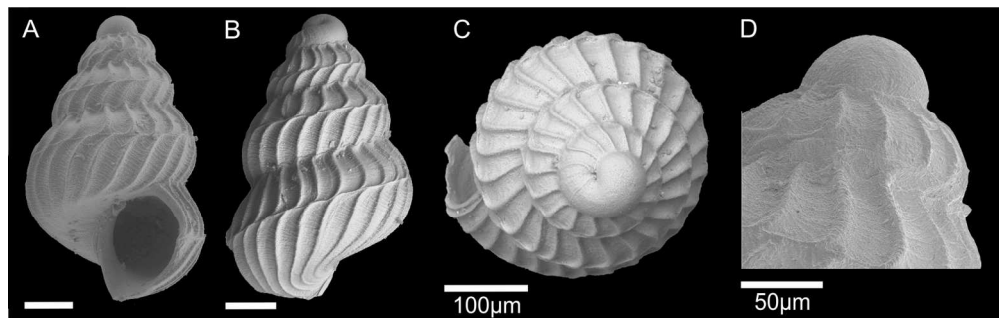
170x98mm (300 x 300 DPI)

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)

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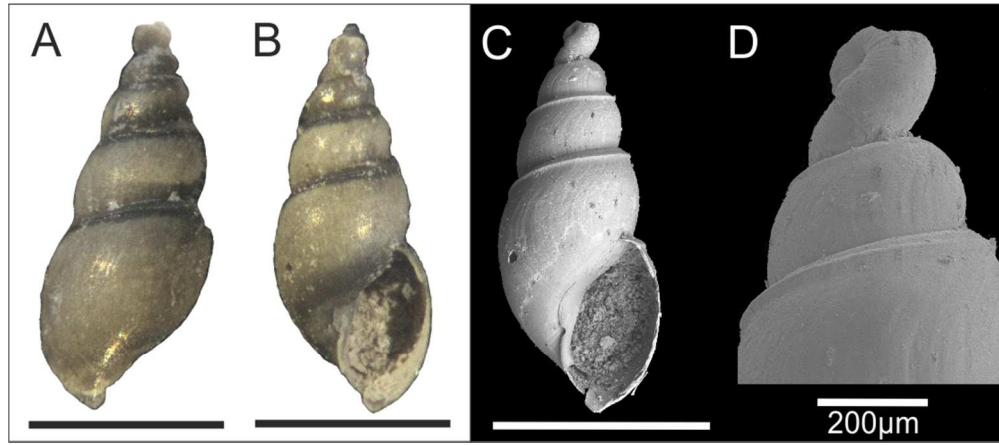42
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Figure 13. Sinuarbullina yangouensis (Pan et al., 2003). A, lateral view; B-C, apertural view; D, view of the protoconch. Scale bar = 1mm, except D. Note: Specimen lost by WJF after photography.
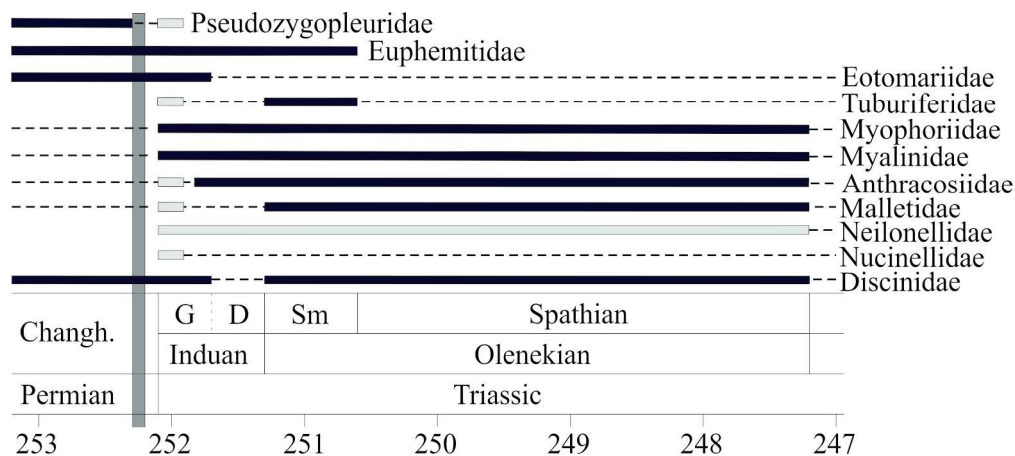
94x41mm (300 x 300 DPI)

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199x88mm (300 x 300 DPI)