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Authors(s)	Foster, William J., Danise, Silvia, Twitchett, Richard J.
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A silicified Early Triassic marine assemblage from Svalbard

William J. Foster^{a,b,c,*}, Silvia Danise^{b,d} and Richard J. Twitchett^c

^aJackson School of Geosciences, University of Texas, Austin, TX 78712, USA; ^bEarth Sciences, Plymouth University, Plymouth, PL4 8AA, UK; ^cDepartment of Earth Sciences, Natural History Museum, London, SW7 5BD, UK; ^dDepartment of Geology, University of Georgia, Athens, GA 30602, USA

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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.

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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, such as 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) and their small, easily overlooked sizes (Hautmann & Nützel 2005), as well as the substantial regional and latitudinal sampling bias towards

low (tropical) palaeolatitudes of the 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 1986; 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

*Corresponding author. Email: w.j.foster@gmx.co.uk

diverse benthic ecosystems reappeared locally in some settings by the second conodont zone of the Triassic in the 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 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 to be found, 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 stratigraphical ranges of several molluscan families.

Material and methods

The fossil assemblage described herein was recovered from two carbonate concretions, collected by WJF and 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 3 kg samples to expose larger fossils. Remaining rock fragments were then dissolved using the buffered formic acid technique of Jeppsson & Anehus (1995). To maximize yield, the residue was collected at *c.* 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 (NHMUK).

Geological setting

During the Early Triassic, the Svalbard archipelago was situated at *c.* 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 latest Permian and entire Early Triassic in a siliciclastic, open-marine, shelf setting. It is divided into three members, of which the Deltadalen Member is the lowest (Mørk *et al.* 1999). At the study site in Lusitaniadalen, the basal 1.6 m of the Deltadalen Member is composed of bedded, well-bioturbated, fine- to medium-grained, glauconitic sandstones that are very similar to the underlying Kapp Starostin Formation except that they lack diagenetic chert nodules (Mørk *et al.* 1999; Nabbefeld *et al.* 2010). These sandstones contain a diverse trace fossil assemblage, indicating a fully functional benthic ecosystem that was living under well-oxygenated conditions (Nabbefeld *et al.* 2010). In contrast, the body fossil assemblage is limited, comprising mainly the phosphatic-shelled lingulid brachiopods, which may indicate preservational bias.

The sandstones record the onset of marine transgression (Mørk *et al.* 1999; Nabbefeld *et al.* 2010), with the base of the overlying laminated, silty mudstones marking significant deepening. Several horizons of cemented siltstones and tabular concretions are found in the lower few metres of this mudstone-dominated interval and contain coarser laminae with abundant ichthyoliths and disarticulated lingulid shells. Occasional, 1–5 cm thick, fine-grained, pyritic and glauconitic, graded, cemented sandstones, interpreted as distal tempestites, also occur within the laminated silty mudstones. Biomarker data support the interpretation based on field observations that deposition took place under anoxic and periodically euxinic conditions during transgression and maximum flooding, with evidence of phytoplankton blooms in the surface waters likely driven by nutrient influx (Nabbefeld *et al.* 2010).

From *c.* 10 m above the base of the mudstones, the lithologies become noticeably coarser with a greater proportion of interbedded siltstones and very fine sandstones, presumably due to progradation or sea level fall. The coarser, heterolithic beds are bioturbated, initially by millimetre-diameter *Planolites* and then with the addition of *Skolithos* and *Arenicolites* about 1.5 m higher, indicative of environmental amelioration and deposition under more persistently oxygenated conditions. The ichnofabric index remains low (ii2–3), however, and the burrows are small (diameters <5 mm) and do not penetrate deeply, indicating that the environment was probably still not fully optimal for benthic colonization. Earliest Triassic ammonoids, conodonts and a moderate benthic assemblage have already been recorded from the *Planolites*-dominated interval (Mørk *et al.* 1999). One of the concretions that yield the silicified assemblage documented in this study derives from that same horizon, 12.6 m above the base of the formation. The second concretion was collected from *c.* 65 cm lower (Fig. 1).

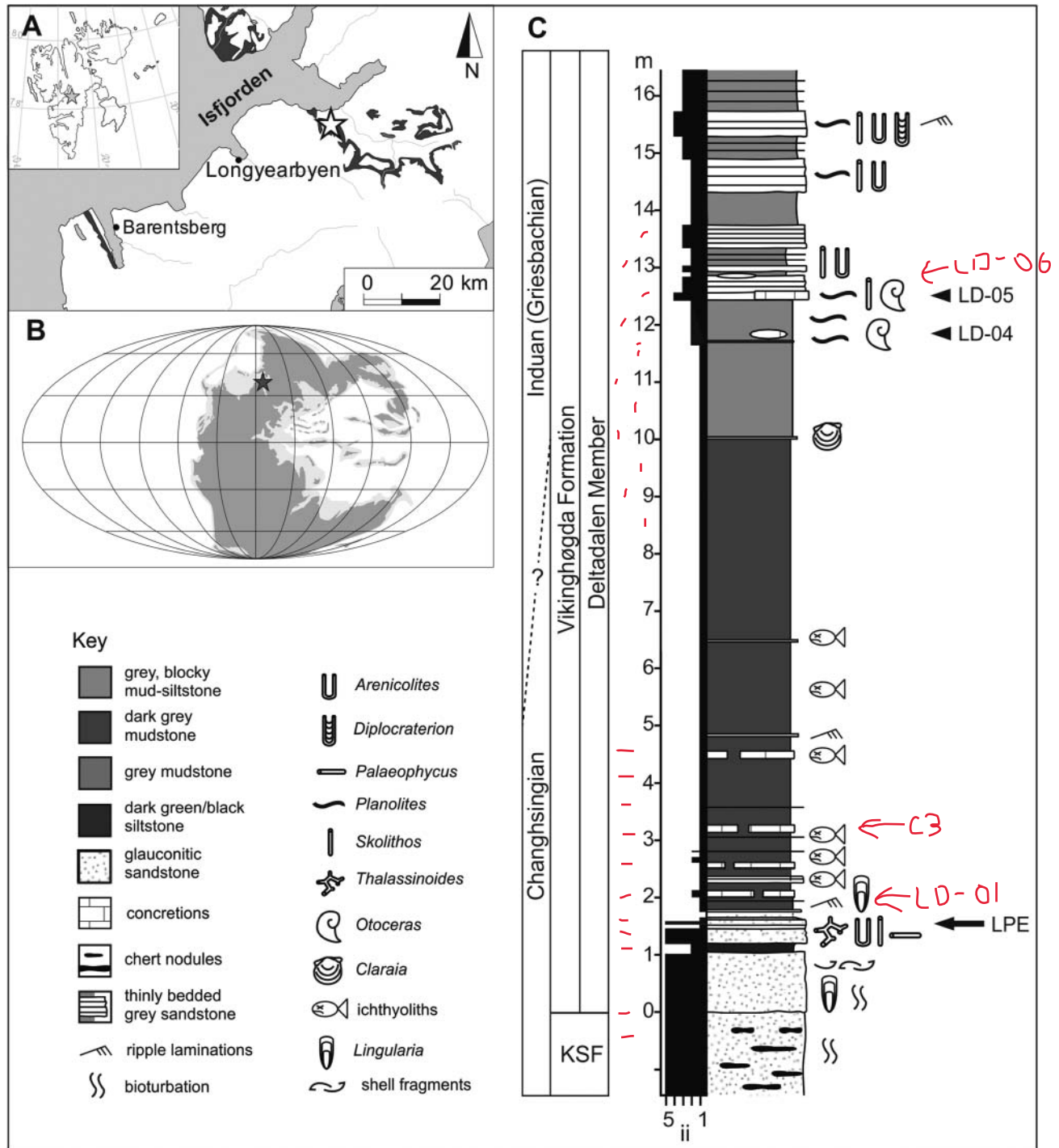


Figure 1. Locality and stratigraphy of the studied section in Lusitaniadalen. **A**, locality map of the Lusitaniadalen section; **B**, palaeogeographical position; **C**, stratigraphical column indicating the position of the sampled concretionary levels (LD-04 and LD-05) and disappearance of bioturbation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

The age of the Deltadalen Member is well constrained by biostratigraphy (ammonoids and conodonts) and magnetostratigraphy, with deposition recorded from the upper Changhsingian, prior to the late Permian mass extinction

event, through most of the Induan (Mørk *et al.* 1999; Hounslow *et al.* 2008; Nakrem *et al.* 2008). Locally, the late Permian extinction event is recorded by the disappearance of prolific bioturbation just below the top of the

glauconitic sandstones, 1.6 m above the base of the member (Nabbefeld *et al.* 2010). From conodont evidence, Nakrem *et al.* (2008) inferred that the Permian/Triassic boundary occurs between 5 and 11 m above the base of the Deltadalen Member. *Claraia* cf. *wangi* is recorded 10.1 m above the base of the member at Lusitaniadalen, indicative of a Griesbachian age. The silicified assemblages described herein are of earliest Griesbachian (earliest Induan) age, and are assigned to the upper part of the *Otoceras boreale* Zone, which corresponds to the basal Triassic *Hindeodus parvus* Conodont Zone (Orchard 2007).

Systematic palaeontology

Phylum **Brachiopoda** Duméril, 1805
 Class **Lingulata** Goryansky & Popov, 1985
 Order **Lingulida** Waagen, 1885
 Family **Discinidae** Gray, 1840
 Genus ***Orbiculoidea*** d'Orbigny, 1847

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

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

Orbiculoidea winsnesi Gobbet, 1963
 (Fig. 2A)

1963 *Orbiculoidea winsnesi* Gobbett: 46, pl. 1, figs 4, 5.

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

Description. Shell outline is subcircular, with its length slightly greater than the width. The dorsal valve is inflated to an apex, which is located about a third of the diameter from the anterior margin. Shell smooth, except for fine concentric growth lines.

Remarks. Extant solitary discinids are sessile, epifaunal invertebrates that attach to hard surfaces with a sucker-like pedicle (Mergl 2010). They have been attaching to shelled invertebrates since the Ordovician (Mergl 2010), and one of the specimens described herein is attached to an ammonoid. Discinids are suspension feeders, and their co-occurrence with lingulids in laminated black shales

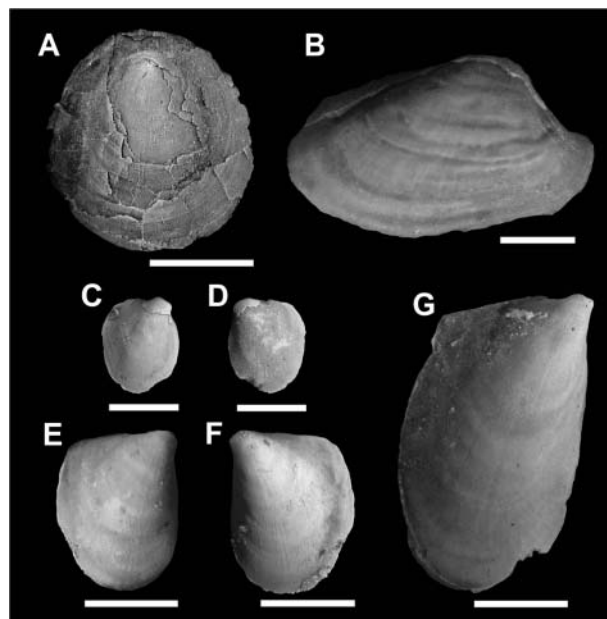


Figure 2. A, *Orbiculoidea winsnesi* Gobbet, 1963, NHMUK PI BE 3238, dorsal view, dorsal valve; B, *Austrotindaria? canalen-sis* (Catullo, 1846), NHMUK PI MB 1198, external view, left valve; C–G, *Promyalina schamarae* (Bittner, 1899), external view; C, D, NHMUK PI MB 1204; C, right valve; D, left valve.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

has led some authors to interpret them as being tolerant of low-oxygen conditions (Savoy 1992; Hallam 1995; Mergl 2010).

Mode of life. Surficial, stationary, attached, suspension feeder (Mergl 2010).

Phylum **Mollusca** Linnaeus, 1758
 Class **Bivalvia** Linnaeus, 1758
 Order **Pterioidea** Newell, 1965
 Family **Myalinidae** Frech, 1891
 Genus ***Promyalina*** Kittl, 1904

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

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

Promyalina schamarae (Bittner, 1899)
 (Fig. 2C–G)

1899 *Myalina schamarae* Bittner 19, pl. 4, figs 20–25.

2009 *Promyalina schamarae* (Bittner); Kumagae & Nakazawa: 157, fig. 144, 4–5.

Material. Three specimens from LD-04 (NHMUK PEI 5484; NHMUK PI MB 1202; NHMUK PI MB 1205) and seven specimens from LD-05 (NHMUK PI MB 1188; NHMUK PI MB 1203–1204; NHMUK PEI 5475–5476; NHMUK PEI 5500; NHMUK PEI 5503).

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

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

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

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

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

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

Genus **Nucinella** Wood, 1851

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

Diagnosis. Nucinellids with external ligament.

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

Nucinella taylori sp. nov.
(Fig. 3)

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

Holotype. Disarticulated left valve, NHMUK PI MB 1206, LD-04; length = 1.6 mm, height = 1.6 mm.

Paratypes. Disarticulated right valve, NHMUK PI MB 1209, LD-04; length = 1.6 mm, height = 1.6 mm; disarticulated right valve, NHMUK PI MB 1210, LD-05; length = 2.1 mm, height = 2.3 mm.

Other material. Two specimens from LD-04 (NHMUK PI MB 1207–1208) and three specimens from LD-05 (NHMUK PEI 5500; NHMUK PEI 5506; NHMUK PEI 5517). Fifty-three prodissococonch valves from LD-04 (NHMUK PI MB 1211–1217; NHMUK PEI 5481) and 36 prodissococonch valves from LD-05 (NHMUK PI MB 1218).

Derivation of name. Named after Dr John Taylor (Natural History Museum, London, UK) in recognition of his work on chemosymbiotic bivalve molluscs.

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

Prodissococonch valves: outline nuculoid and suboval. Posterior margin is distinct, long and slightly incurved. Inequilateral, with beaks close to posterior margin, and sculpture consists of irregularly spaced growth laminae. Ventral valve margin has a narrow flat platform. Five anterior and 11 posterior hinge teeth. Amphidetic ligament, lying between the beak and anterior hinge plate.

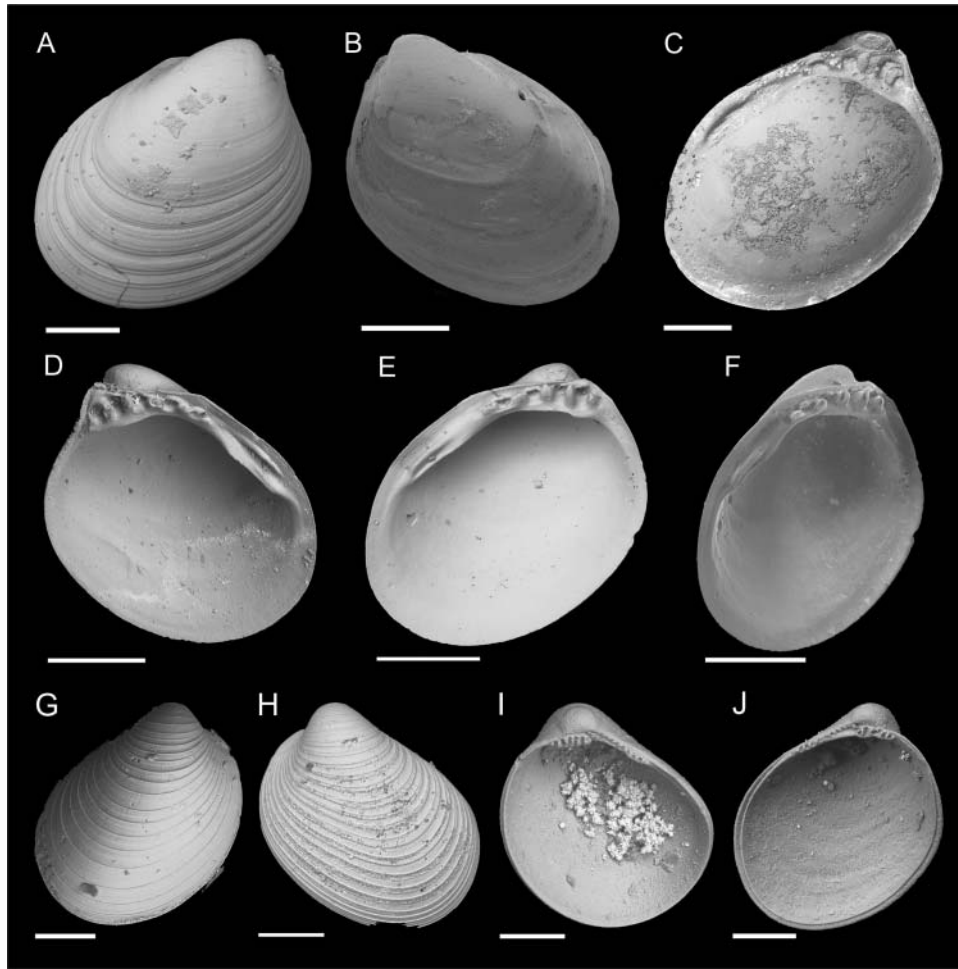


Figure 3. *Nucinella taylori* sp. nov. **A**, holotype, NHMUK PI MB 1206, external view, left valve; **B**, paratype, NHMUK PI MB 1209, external view, right valve; **C**, paratype, NHMUK PI MB 1210, internal view, right valve; **D**, holotype, NHMUK PI MB 1206, internal view, left valve; **E**, **F**, paratype, NHMUK PI MB 1209, internal view, right valve; **G–J**, prodissococonchs 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 bars: A–F = 500 μ m; G–J = 100 μ m.

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

The majority of extant *Nucinella* range from intertidal to 500 m deep (La Perna 2005), but some species have been described from water depths exceeding 3000 m (Oliver & Taylor 2012). A large fossil *Nucinella* species has been described from a Late Cretaceous cold-seep deposit (Amano *et al.* 2007), showing that this genus may inhabit a wide range of sulphide-rich environmental settings. Bacterial symbiosis with sulphur-oxidizing bacteria is confirmed for *N. owenensis* and has been inferred for all species of the Nucinellidae (Oliver & Taylor 2012).

Nucinella taylori sp. nov. supplants *N. birkelundi* from the Late Jurassic (Clausen & Wignall 1990) and *Nucinella?* sp. from the Late Triassic (Nützel & Kaim 2014) as the oldest known species of *Nucinella*, and extends the range of the genus to the basal Triassic *H. parvus* Conodont Zone.

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

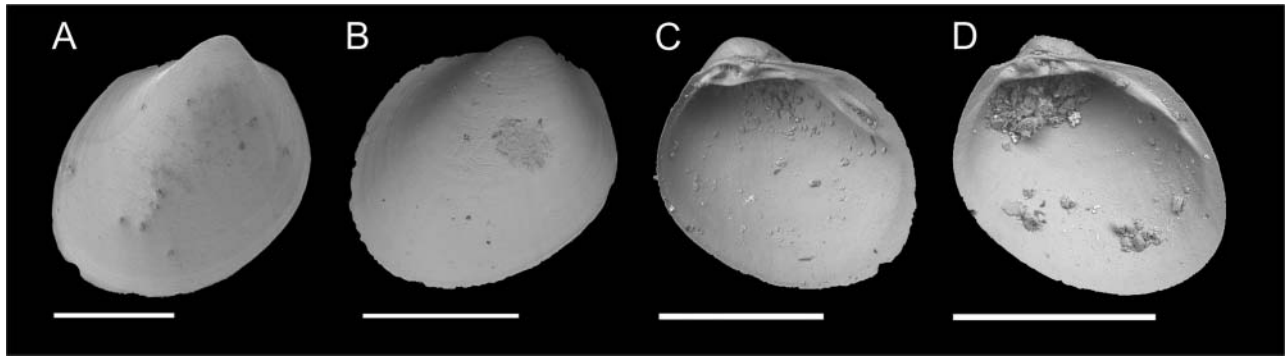


Figure 4. *Nucinella nakremi* sp. nov. **A**, holotype, NHMUK PI MB 1219, external view, left valve; **B**, paratype, NHMUK PI MB 1220, external view, left valve; **C**, holotype, NHMUK PI MB 1219, interior view, left valve; **D**, paratype, NHMUK PI MB 1220, interior view (transposed hinge), left valve. Scale bars = 500 μ m.

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

Nucinella nakremi sp. nov.
(Fig. 4)

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

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

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

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 *Nucinella 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 lateral secondary ridge creating a secondary socket, this specimen has two hinge teeth and a lateral tooth (i.e. the normal right valve arrangement). An alternative interpretation is that this specimen represents an earlier ontogenetic stage, but this is rejected because even though the specimen is slightly smaller, its lateral tooth is more prominent than in a typical left valve arrangement and both the subumbonal and lateral teeth appear to fit with the expected corresponding valve arrangement. In addition, it has been reported that in the early stages of nucinellid development the second lateral

tooth is very small and closer to the subumbonal teeth than later in ontogeny (Bernard 1898), which is not the case with this specimen. Transposed hinges have been reported in a number of bivalve families, but this is the first reported occurrence in a species of Nucinelidae.

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

Order *Nuculanoida* Carter *et al.*, 2000
Family *Neilonellidae* Schileyko, 1989

Diagnosis. Hinge plate with taxodont teeth in two series, sometimes separated by narrow, plain area, without resilifer; ligament predominantly external, opisthodontic to amphidetic, weak.

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

Genus *Austrotindaria* Fleming, 1948

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

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

Remarks. The Neilonellidae comprises three valid genera: *Neilonella*, *Austrotindaria* and *Pseudoneilonella* (La Perna 2007). The convex shape of the posterior margin and the presence of an opisthodontic 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.

Austrotindaria antiqua sp. nov.
(Fig. 5)

- 1899 *Anodontophora* (*Myacites*) *fassaensis* (Wissmann); Bittner: 22, pl. 3, figs 28–33.
- 1908 *Anoplophoria* (*Myacites*) *fassaensis* (Wissmann); von Wittenburg: 33, fig. 15.
- 1926 *Anodontophora fassaensis* (Wissmann); Matsushita: pl. 8, fig. 11.
- 1963 *Unionites fassaensis* (Wissmann); Ciriacks: 81, pl. 16, fig. 13.
- 1988 *Unionites fassaensis* var. *brevis* Neri & Posenato: 94, pl. 2, fig. 8.
- 2009 *Unionites fassaensis* (Wissmann); Kumagae & Nakazawa: 166, fig. 145, 5–9.
- 2014 *Unionites?* *fassaensis* (Wissmann); Pan *et al.*: 151, fig. 5G, H.
- 2015 *Unionites fassaensis* (Wissmann); Hofmann *et al.*: 8, fig. 4K.
- 2015 cf. *Unionites fassaensis* (Wissmann); Foster *et al.*: 381, fig. 4L.

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 opisthodontic.

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

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

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 18 specimens from LD-05 (NHMUK PI MB 1191; NHMUK PI MB 1196–1197; NHMUK PI MB 1199; NHMUK PI MB 1242; NHMUK PE PEI 5475–5476; NHMUK PE PEI 5483; NHMUK PE PEI 5494; NHMUK PE PEI 5497; NHMUK PE PEI 5499–5501; NHMUK PE PEI 5504; NHMUK PE PEI 5506; NHMUK PE PEI 5515). Two prodissococonch valves from LD-04 (NHMUK PI MB 1243–1244).

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

Description. Equivalve, inequilateral shell with a subtrigonal outline and a beak positioned approximately 30% along the length of the dorsal margin from the posterior; H/L ratio 0.6–1. Conspicuously tumid. Umbo prosogyrate, prominent, moderately broad, rounded and projects above the hinge margin. Slightly rounded and gently sloping anterodorsal margin. Posterodorsal margin almost straight to slightly rounded, gently sloping, with a slight angled junction with the posterior margin. Ventral margin deeply rounded. Escutcheon short, relatively broad, elliptical;

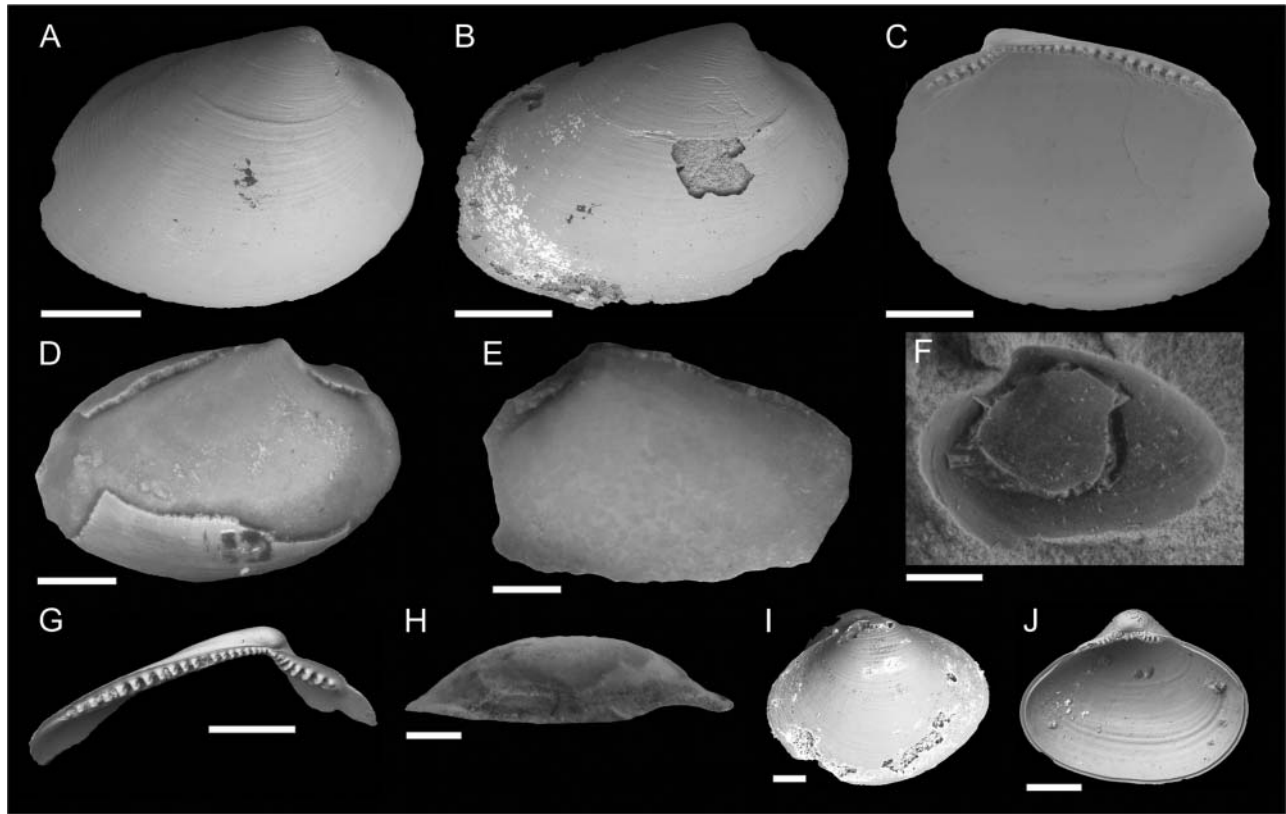


Figure 5. *Austrotindaria antiqua* sp. nov. **A**, holotype, NHMUK PI MB 1240, external view, right valve; **B**, paratype, NHMUK PI MB 1241, external view, right valve; **C**, holotype, NHMUK PI MB 1240, internal view, right valve; **D**, NHMUK PI MB 1191, external view, right valve; **E**, NHMUK PI 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 bars: A–C, G = 500 μ m; D–F = 1 mm; I, J = 100 μ m.

lunule narrow. Shell smooth with fine concentric growth lines; entire inner margin smooth. Small ligament, external, opisthodetic, with a well-defined margin and well-rounded triangular pit seated beneath the edentulous gap. Hinge plate with taxodont teeth in two series, sometimes separated by a narrow, plain area, without resilifer, that is narrow below the beak, broadening towards the anterior and posterior ends. Robust teeth, moderately long and blunt, with more than 50% fewer anterior than posterior ones. Smooth ventral margin. No pallial line, sinus or muscle scars are present. As the size of the shell increases the edentulous gap becomes proportionally smaller and more central, and moves externally.

Remarks. The external morphology of these specimens is identical to most Early Triassic specimens previously described as ‘*Unionites*’ *fassaensis*, which is one of the most widespread bivalve species from the Lower Triassic and is also a problematic dustbin taxon that includes a range of different morphologies. These specimens differ from the original description and figures of ‘*Myacites*’ *fassaensis* Wissmann, 1841 in having a less elongated posterior margin and a more prosogyrate beak. Due to poor

preservation, however, little is known about the internal morphology of Early Triassic specimens assigned to *U. fassaensis*, which has created some uncertainty (Hautmann *et al.* 2013). Internally, these new specimens lack the following characters that Geyer *et al.* (2005) determined were diagnostic of *Unionites*: a nymph extending nearly half of the posterior margin; an impressed adductor muscle scar; an overlap of the anterior hinge; and a deeply impressed lunule and posterior keel. Thus, these specimens cannot be assigned to *Unionites*. The presence of taxodont hinge dentition, an opisthodetic ligament and lack of ornamentation are, however, characteristic of the genus *Austrotindaria*.

The more prosogyrate beak means that these specimens have a similar external morphology to Middle Triassic *Unionites* specimens (e.g. Geyer *et al.* 2005), but apart from possessing a faint posterior keel they lack the diagnostic criteria of *Unionites*. Furthermore, the *Unionites* specimens described by Geyer *et al.* (2005) and from this study (see below) all have a strong posterior keel. Thus, these specimens are not assigned to *Unionites*. These specimens, and all previous specimens assigned to *Unionites fassaensis* that possess a prosogyrate beak and lack a

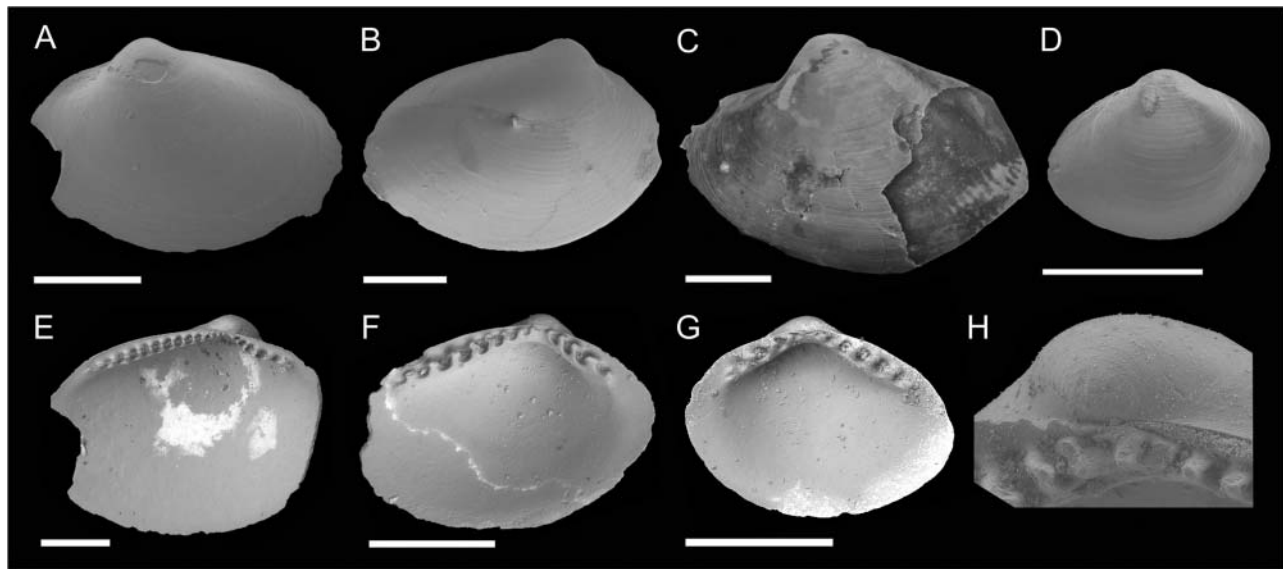


Figure 6. *Austrotindaria svalbardensis* sp. nov. **A**, paratype, NHMUK PI MB 1231, external view, left valve; **B**, holotype, NHMUK PI MB 1223, external view, right valve; **C**, NHMUK PI MB 1190, left valve, external view; **D**, larval shell, NHMUK PI MB 1234, external view, right valve; **E**, 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 bars = 500 μ m.

well-defined posterior keel, are therefore assigned to *Austrotindaria antiqua* sp. nov.

Mode of life. Shallow infaunal, fully motile, slow, miner (Stanley 1968).

Austrotindaria svalbardensis sp. nov.
(Fig. 6)

1864 *Anoplophora fassaensis* (Wissmann); Alberti: 137, pl. 3, fig. 8.

1930 *Nucula* sp. juv. ind; Spath: 53, pl. 7, fig. 12.

2013a *Unionites fassaensis* (Wissmann); Hofmann *et al.*: 887, fig. 8, 17–18.

2015 *Unionites* cf. *fassaensis*; Hautmann *et al.*: 890, fig. 10H.

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

Holotype. Disarticulated right valve, NHMUK PI MB 1223, LD-04; length = 1.8 mm, height = 1.3 mm.

Paratype. Disarticulated left valve, NHMUK PI MB 1231, LD-04; length = 1.5 mm, height = 1.0 mm.

Other material. Twenty-one specimens from LD-04 (NHMUK PI MB 1190; NHMUK PI MB 1192–1193;

NHMUK PI MB 1224–1230; NHMUK PI MB 1232–1233; NHMUK PI MB 1235–1236; NHMUK PE PEI 5478; NHMUK PE PEI 5482; NHMUK PE PEI 5489; NHMUK PE PEI 5505; NHMUK PE PEI 5509–5510; NHMUK PE PEI 5512; NHMUK PE PEI 5520) and 12 specimens from LD-05 (NHMUK PI MB 1189; NHMUK PI MB 1197; NHMUK PI MB 1200; NHMUK PE PEI 5476; NHMUK PE PEI 5491–5492; NHMUK PE PEI 5496; NHMUK PE PEI 5498; NHMUK PE PEI 5503–5504; NHMUK PE PEI 5517). Twenty-four prodissoconch valves from LD-04 (NHMUK PI MB 1234; NHMUK PI MB 1237; NHMUK PI MB 1238; NHMUK PE PEI 5520) and five prodissoconch valves from LD-05 (NHMUK PI MB 1239).

Derivation of name. Named after the Svalbard archipelago.

Description. Shell outline subtrigonal, equivalve, inequilateral with beak positioned approximately 60% of the distance along the dorsal margin from the posterior; Height/Length (H/L) ratio 0.6–1; conspicuously tumid. Orthogyrate umbo, prominent, moderately broad, rounded and projected above the hinge margin. Anterodorsal margin slightly rounded and gently sloping. The posterodorsal margin is almost straight to slightly rounded and gently sloping. Ventral margin is smooth and deeply rounded. Escutcheon is short, relatively broad, elliptical; lunule narrow. No sculpture except for fine concentric growth lines; entire inner margin is smooth. Prodissoconch is smooth, broadly subovate, with H/L ratio of 0.6–0.9. Ligament small, external with well-defined margin,

opisthodontic, with a well-rounded triangular pit seated beneath the edentulous gap. Hinge plate with taxodont teeth in two series; separated by narrow, plain area, without resilifer, narrow below the beak, broadening towards the anterior and posterior ends. Teeth are robust, moderately long and blunt, with more posterior than anterior teeth, separated by an edentulous gap. As the size of the shell increases the edentulous gap becomes proportionally smaller, more central and moves externally. No pallial line, sinus or muscle scars present.

Remarks. These specimens differ from *Austrotindaria antiqua* sp. nov. in having a more equal number of anterior to posterior teeth and an orthogyrate beak. The direction of the beak also separates these specimens from unequivocal species of *Unionites*. In the specimens described here and other *Austrotindaria* species the beak is orthogyrate to posteriorly opisthogyrate, whereas in *Unionites* it is prosogyrate. Based on this key character, most specimens previously assigned to *Unionites fassaensis*, and similar Early Triassic specimens with an orthogyrate beak and no internal morphological detail preserved, are herein assigned to *Austrotindaria svalbardensis* sp. nov.

These specimens have a very similar shape, size and ornamentation to the type species of *Austrotindaria* (*A. wrighti* Fleming); however, they differ in possessing a small, rounded, triangular pit below the edentulous gap, and differ from other *Austrotindaria* species, such as *A. mawheraensis*, in lacking a weak posterior rostrum. For these reasons, they are therefore considered a separate species.

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

Austrotindaria? canalensis (Catullo, 1846)
(Fig. 2B)

1846 *Tellina canalensis* Catullo: 56, pl. 4, fig. 4.

1899 *Anodontophora (Myacites) canalensis* (Catullo); Bittner: 23, pl. 3, figs 34–38.

1908 *Anoplophoria canalensis* (Catullo); von Wittenburg: 281, pl. 5, fig. 6.

1963 *Unionites canalensis* (Catullo); Ciriacks: 81, pl. 16, figs 11, 12.

1988 *Unionites canalensis* (Catullo); Neri & Posenato: 94, pl. 2, fig. 8.

2004 *Unionites* aff. *canalensis* (Catullo); Kashiyama & Oji: 214, fig. 8F.

2009 *Unionites canalensis* (Catullo); Kumagae & Nakazawa: 166, fig. 145, 1–4.

2015 *Unionites canalensis* (Catullo); Hofmann *et al.*: 481, fig. 4J.

2015 cf. *Unionites canalensis* (Catullo); Foster *et al.*: 381, fig. 4K.

Material. Three specimens from LD-05 (NHMUK PI MB 1198; NHMUK PE PEI 5493; NHMUK PE PEI 5500).

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

Remarks. The internal characters and hinge in these specimens were not observed and have not been reported for *Unionites canalensis*. Externally, the shell is virtually identical to those that are typically assigned to *U. canalensis* (e.g. Hofmann *et al.* 2015), with a medially placed umbo that is a diagnostic feature of *U. canalensis* (Catullo, 1846) and an orthogyrate beak. In contrast, all other species of *Unionites* have a more anteriorly located umbo, and the beak in *Unionites* is prosogyrate (Geyer *et al.* 2005). Thus, these Early Triassic specimens clearly do not belong to the genus *Unionites*. The external features of these specimens are most similar to species of Neilonellidae, such as *Austrotindaria benthicola* (Dell, 1956). *Austrotindaria* is the only genus of the Neilonellidae that is reported from the Early Triassic, and these specimens are, therefore, tentatively assigned to it. Without observation of the internal characters, an unequivocal generic assignment cannot be made. The posterior margin is more elongate than in *Austrotindaria svalbardensis* sp. nov., and these specimens are therefore considered to represent a separate species.

Mode of life. Shallow infaunal, fully motile, slow, miner (Stanley 1968).

Family **Mallettiidae** Adams & Adams, 1858 gen. et
sp. indet.
(Fig. 7)

Diagnosis. Subequilateral to inequilateral; usually with elongate, compressed posterior end; sculpture of commarginal striae or ribs; anterior and posterior gapes present; hinge plate weak, with fine taxodont teeth in two series, sometimes separated by plain area, without resilifer; ligament external, opisthodontic to amphidetic, weak; pallial sinus large.

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

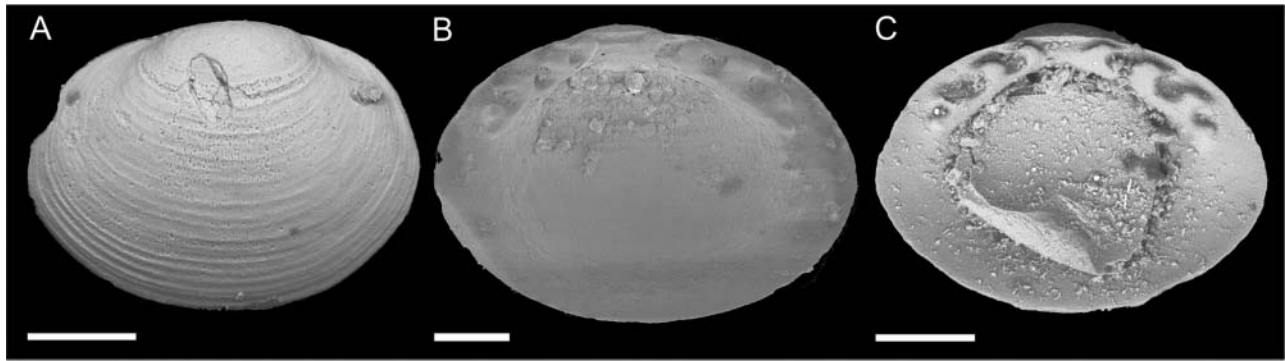


Figure 7. Malletiidae gen et sp. indet., larval shells. **A**, NHMUK PI MB 1249, external view; **B**, NHMUK PI MB 1249, internal view; **C**, NHMUK PI MB 1248, internal view. Scale bars = 100 μ m.

Description. Shell is equilateral, elliptical, H/L ratio of 0.7, and moderately inflated. Umbo is broad, orthogyrate, with beak positioned centrally. Shell smooth except for concentric growth lines. Hinge plate has three anterior and three posterior teeth in two series separated by a large plain area with a groove. Ligament is predominantly external, amphidetic and weak.

Remarks. Malletiidae are very similar to Nuculanidae, but the lack of a resilifer in mature adults supports their separation (Coan & Valentich-Scott 2012). These specimens do not belong to the Neilonellidae because they possess a small conspicuous gap between the valves. The Malletiidae is a long-ranging family known from the Ordovician to the Recent, and three genera (*Malletia*, *Palaeoneilo* and *Taimyrodon*) belonging to the family have previously been reported from the Lower Triassic (e.g. He *et al.* 2007; Wasmer *et al.* 2012). Externally, these specimens resemble the larval shells of *Paleoneilo? fortistriata* figured by Wasmer *et al.* (2012), but they have far fewer hinge teeth. There are also equal numbers of anterior to posterior hinge teeth in these specimens, whereas in *P. fortistriata* there are many more posterior than anterior teeth (Wasmer *et al.* 2012).

Mode of life. Shallow infaunal, fully motile, slow, miner (Stanley 1968).

Order **Unionoida** Stoliczka, 1871
Family **Anthracosiidae** Amalitzky, 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.

Unionites aff. *subrectus* (Bittner, 1901)
(Fig. 8)

aff. 1901 *Anodontophora subrecta* Bittner: 100, pl. 7, figs 28–30.

aff. 2003 *Unionites subrectus* (Bittner); Sente & Vörös: 131, pl. Biv-II, figs 25, 26.

2009 *Triaphorus* aff. *multiformis* Kiparisova; Kumagai & Nakazawa: 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).

Description. Outline elongate-elliptical. Shell equivalved, inflated below the umbo, and inequilateral with beak positioned approximately 85% along the length of the dorsal margin from the posterior. Lower part of anterior dorsal margin projects slightly beyond plane of commissure. Posterodorsal margin is almost straight to

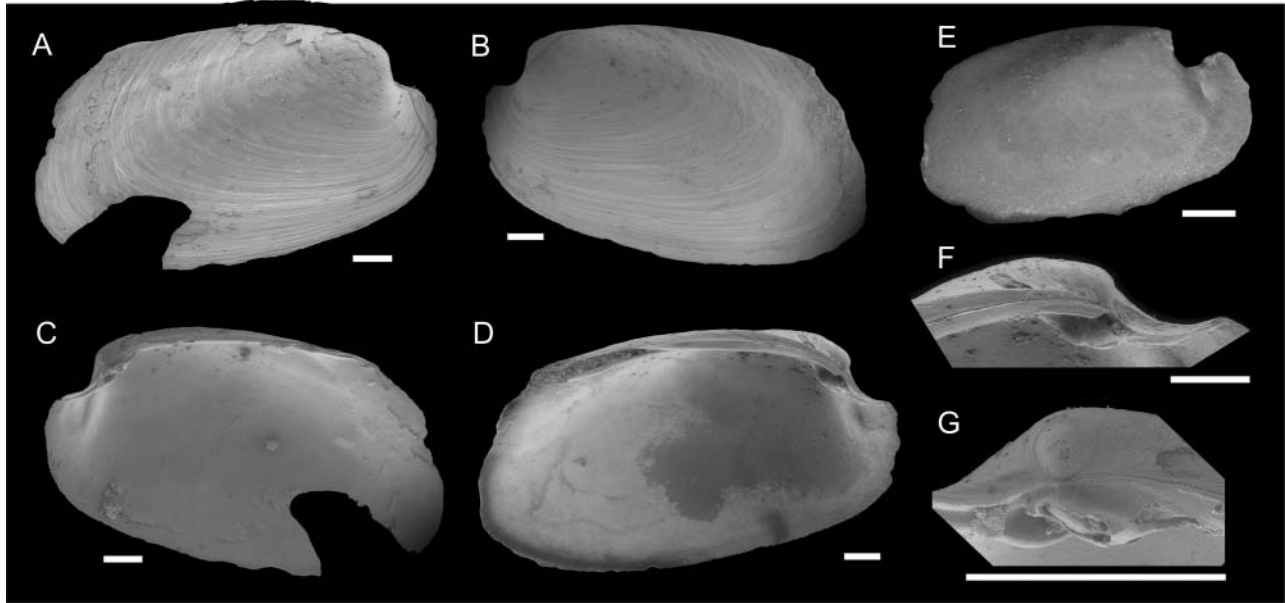


Figure 8. *Unionites* aff. *subrectus* (Bittner, 1901). **A**, NHMUK PI MB 1246, external view, right valve; **B**, NHMUK PI MB 1245, external view, left valve; **C**, NHMUK PI MB 1246, internal view, right valve; **D**, NHMUK PI MB 1245, internal view, left valve; **E**, NHMUK PI MB 1195, external view,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

slightly round and gently sloping. Lunule is long and narrow, with deeply impressed escutcheon. Umbo is prosogyrate and rises above the hinge margin. Ornamented with fine concentric growth lines. The entire inner margin is smooth. Prodissoconch is smooth and orbicular.

A small subumbonal groove limits the shell projection posteriorly. Short lateral tooth, left valve possesses a weak secondary ridge creating a shallow socket. Hinge of left valve has an anterior platform that bears a depression for the corresponding anterior hinge margin of the right valve; posterior to this is a small, tuberculiform subumbonal tooth fitting above posterior lateral tooth of right valve. Ligament is fixed to a nymph, which extends about half the length of the posterior dorsal margin. Isomyarian muscle scars with a deeply impressed anterior adductor muscle scar.

Remarks. Insufficient knowledge of the internal morphology of Early Triassic bivalves in general, and *Unionites* in particular, has created uncertainty regarding their systematic position. Based on their external morphology alone these specimens would be assigned to *Triaphorus* aff. *multiformis* (Kumagai & Nakazawa 2009), but they possess the following characters that are diagnostic of *Unionites*: the anterior hinge margin of the right valve overlaps that of the left; a nymph that extends nearly half the length of the posterior hinge margin; an impressed anterior adductor muscle scar; a deeply impressed lunule; and a long and narrow escutcheon. Thus, these specimens are assigned to *Unionites*.

These specimens differ from *U. brevis*, *U. fassaensis*, *U. letticus*, *U. griesbachi*, *U. borealis* and *U. rhomboidalis* because their length greatly exceeds their height. They are most similar to *U. subrectus* described from the Middle Triassic of Hungary by Szente & Vörös (2003), except for their more elliptical outline.

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

Order **Trigoniida** Dall, 1889

Family **Myophoriidae** Bronn, 1849

Genus ***Neoschizodus*** Giebel, 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,

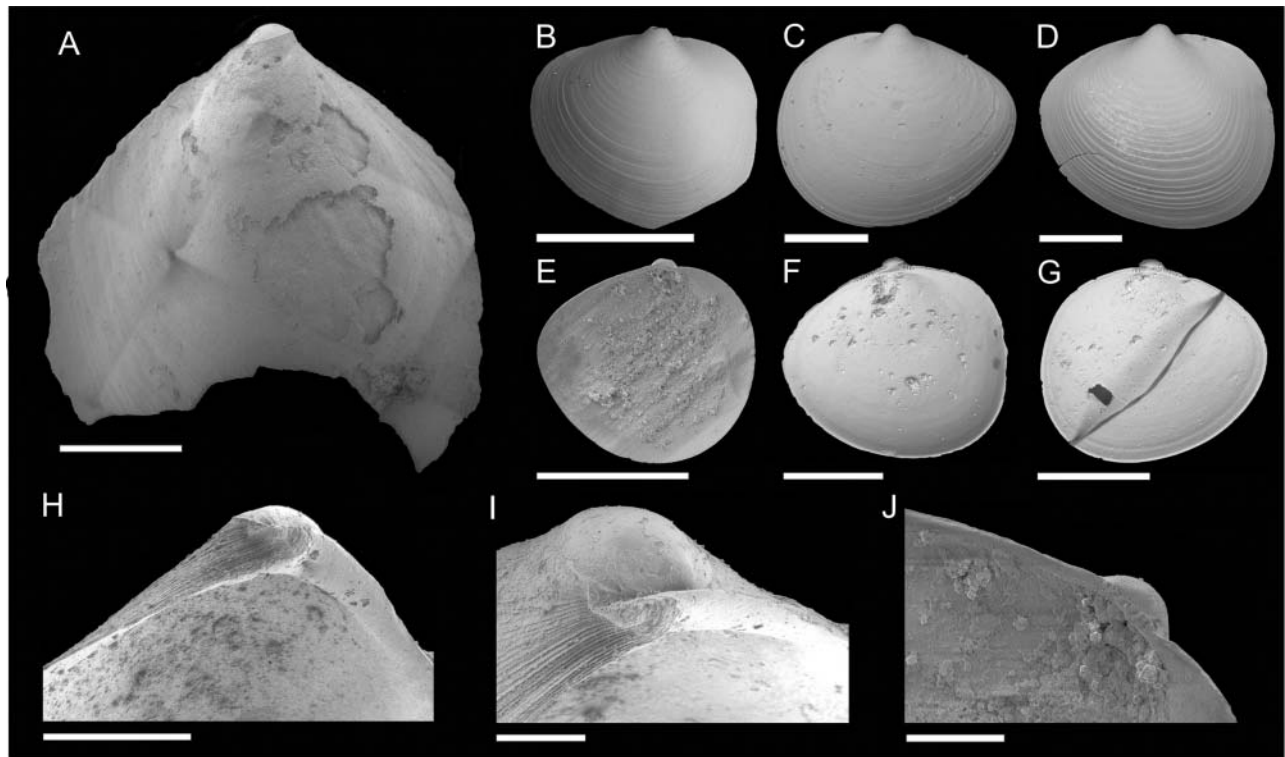


Figure 9. *Neoschizodus laevigatus* (Goldfuss, 1837). **A**, NHMUK PI MB 1251, external view, left valve; **B–G, J**, larval shells; **B**, NHMUK PI MB 1256, external view, right valve; **C**, NHMUK PI MB 1259, external view, left valve; **D**, NHMUK PI MB 1257, external view, right valve; **E**, NHMUK 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 bars: **A** = 2 mm; **B–G, I** = 200 µm; **H** = 1 mm; **J** = 50 µm.

however, have a similar external morphology to other Early and Middle Triassic specimens assigned to *Neoschizodus* (e.g. Kumagai & Nakazawa 2009) and are, therefore, referred to this genus.

Neoschizodus laevigatus (Goldfuss, 1837)
(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 prodissococonch 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 14 prodissococonch 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 prodissococonch is smooth with fine concentric growth lines.

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

One of the adult specimens preserves a prodissococonch (Fig. 9I) and its morphology is identical to that of the other prodissococonchs that were found as isolated specimens. The hinge plate of the prodissococonchs was not observed to be myophorian – instead the hinge dentition is typical of a taxodont – but it is not known how a myophorian hinge plate develops through ontogeny (Newell & Boyd 1975). Hautmann & Nützel (2005) suggested that,

in bivalves, the presence of a small prodissoconch I and a relatively large prodissoconch II indicates a planktotrophic larval stage. Therefore, a planktotrophic larval stage is interpreted for these specimens.

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

Class **Gastropoda** Cuvier, 1795
Order **Amphigastropoda** Simroth, 1906
Family **Euphemitidae** Knight, 1956
Genus **Warthia** Waagen, 1880

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

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

Warthia zakharovi Kaim, 2009
(Fig. 10)

2009 *Warthia zakharovi* Kaim: 141, figs 132–134.

Material. One hundred and thirty-eight specimens from LD-04 (NHMUK PI MG 1468–1473; NHMUK PI MG 1495–1496; NHMUK PI MG 1502–1511; NHMUK PE PEI 5478–5482; NHMUK PE PEI 5484–5490; NHMUK PE PEI 5505; NHMUK PE PEI 5507; NHMUK PE PEI 5509–5513; NHMUK PE PEI 5519–5520; NHMUK PE PEI 5522), and 193 specimens from LD-05 (NHMUK PI MG 1467; NHMUK PI MG 1474–1481; NHMUK PI MG 1483; NHMUK PI MG 1485–1494; NHMUK PI MG 1497–1499; NHMUK PI MG 1512; NHMUK PE PEI 5475–5477; NHMUK PE PEI 5483; NHMUK PE PEI 5491–5504; NHMUK PE PEI 5506; NHMUK PE PEI 5508; NHMUK PE PEI 5514–5518; NHMUK PE PEI 5521).

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

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

Remarks. The shell of *Warthia* is usually entirely involute and overgrows the umbilicus. In some of our smaller specimens, the umbilicus is still visible, but in larger specimens it has become overgrown during subsequent

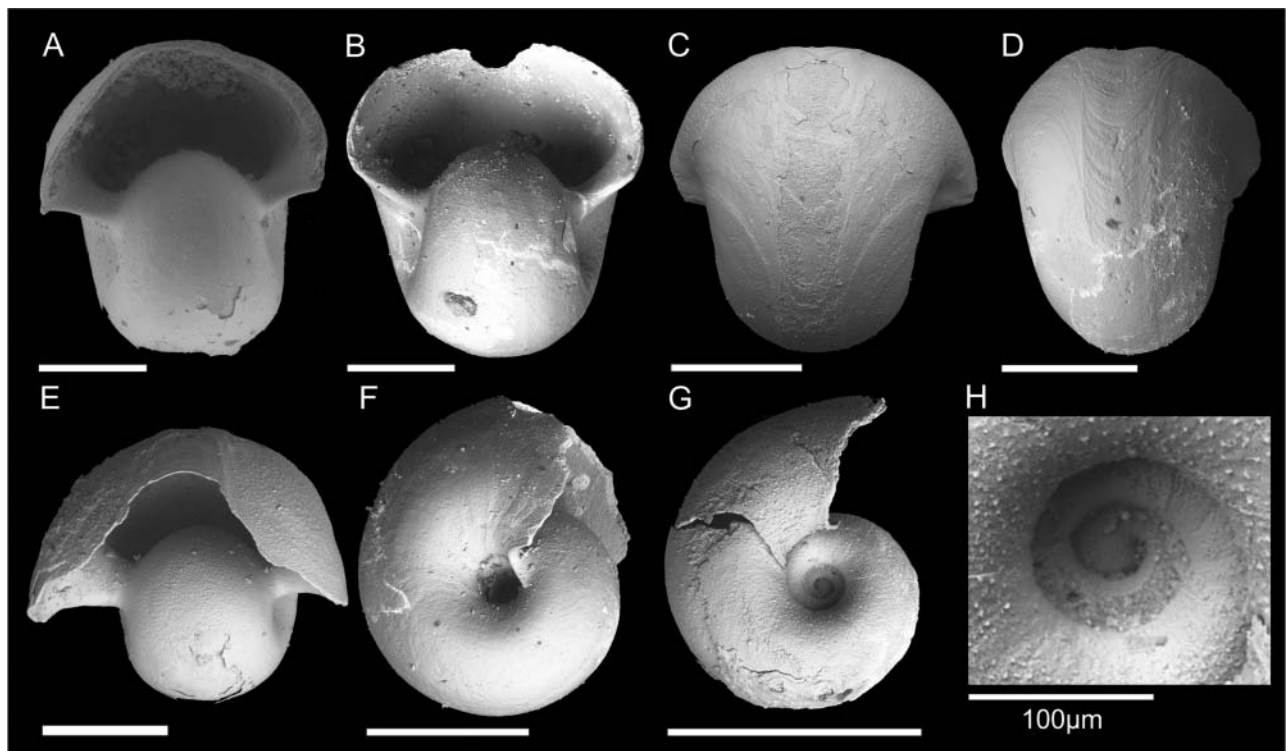


Figure 10. *Warthia zakharovi* Kaim, 2009. A, NHMUK PI MG 1502, apertural view; B, C, NHMUK PI MG 1505; B, apertural view; C, lateral view; D, E, NHMUK PI MG 1509; D, lateral view; E, apertural view; F, NHMUK PI MG 1508, apical view; G, H, NHMUK PI MG 1504; G, apical view; H, protoconch. Scale bars =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

growth. Even though our specimens lack an inductural layer and have growth lines that have not previously been recorded in Early Triassic *Warthia* species, in Permian species of *Warthia* visible growth lines or wrinkles have been recorded (e.g. *W. micromphala* and *W. stricta*; Waterhouse 1963) and, therefore, we consider our specimens to belong to *Warthia*.

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

Mode of life. Surficial, fully motile, slow, surface deposit feeder (Linsley 1977).

Order **Vetigastropoda** Salvini-Plawen, 1980

Family **Eotomariidae** Wenz, 1938

Subfamily **Eotomariinae** Wenz, 1938

Genus ***Glabrocingulum*** Thomas, 1940

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

Diagnosis. Low- to moderately high-spined and turbiniform shell shape. The upper whorl surface forming an angle of <45° with the selenizone located on the upper edge of whorl face. Sutures sharply defined. Upper whorl face with both spiral and collabral ornament; most strongly developed near the suture, weakest near the selenizone. Anomphalus to widely phaneromphalus, with or without funicle.

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

These specimens are therefore assigned to the genus *Glabrocingulum*.

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

***Glabrocingulum parvum* sp. nov.**

(Fig. 11)

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

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

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

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 14 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-spined, 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

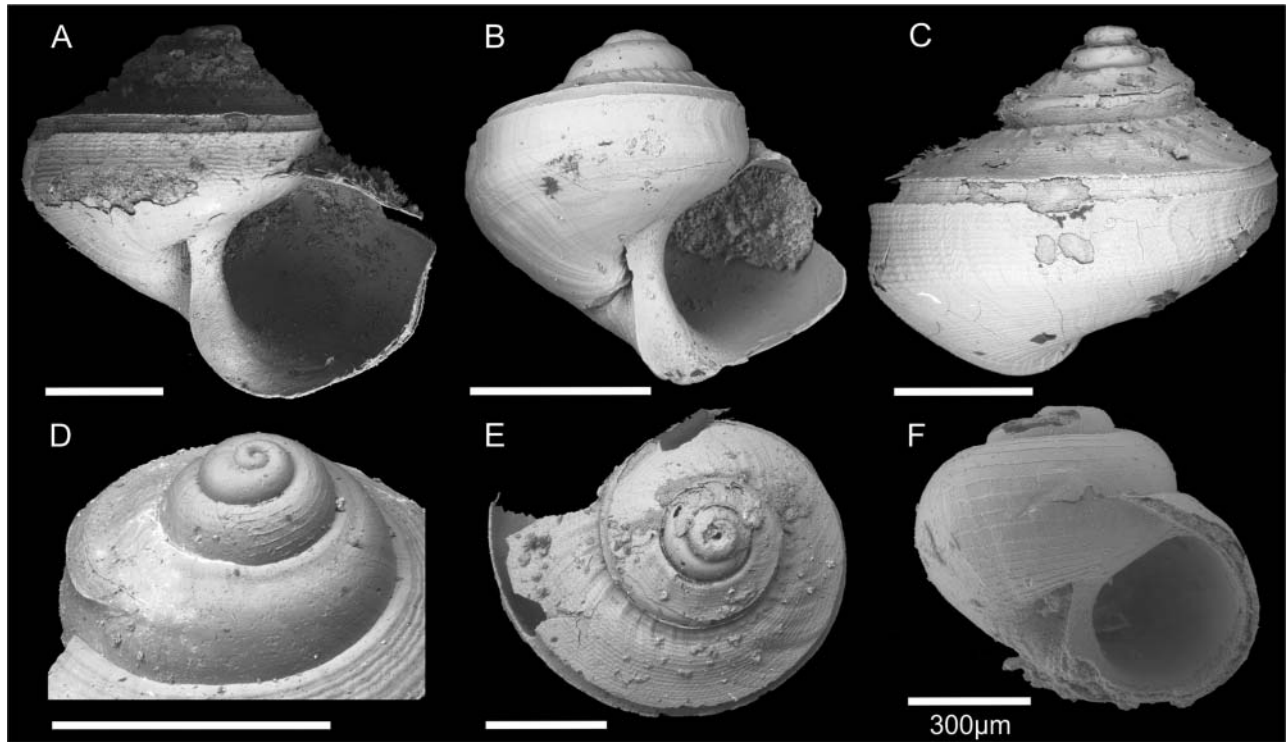


Figure 11. *Glabrocingulum parvum* sp. nov. **A, B**, apertural view; **A**, holotype, NHMUK PI MG 1531; **B**, paratype, NHMUK PI MG 1518; **C–E**, NHMUK PI MG 1531; **C**, lateral view; **D**, side view of initial whorls; **E**, apical view; **F**, apertural view of a larval shell, NHMUK PI MG 1520. Scale bars = 1 mm, except F.

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 south-western US (Batten 1989) was not observed. These specimens are also considerably smaller (max. size: H = 3.6 mm, W = 4.6 mm) than the type material of *G. texanum* (max. size: H = 8.7 mm, W = 9.9 mm), which may be a consequence of environmental stress in the immediate aftermath of an extinction event and an expression of the Lilliput effect in this genus (cf. Twitchett 2007). Due to their excellent preservation, these specimens reveal the morphology of the larval stages, which show a similar ontogenetic development to other species of *Glabrocingulum* (e.g. Pan & Shen 2008).

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

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

Order **Ptenoglossa** Gray, 1853
Family **Pseudozygopleuridae** Knight, 1930 gen.
et sp. indet.
(Fig. 12)

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

Description. Teleoconch not observed. Protoconch is conical, elongate and composed of five whorls. The initial whorl is smooth and has a diameter of 0.08 mm. Collabral ornamentation is initiated on the second whorl, continues

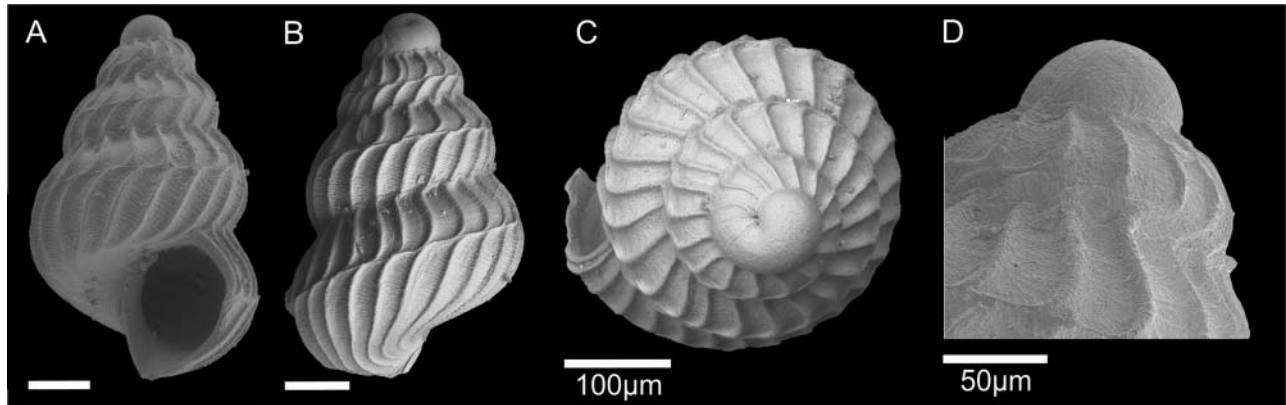


Figure 12. Pseudozygopleuridae gen et sp. indet., larval shell. **A, B**, NHMUK PI MG 1532; **A**, apertural view; **B**, lateral view; **C**, NHMUK PI MG 1533, apical view; **D**, side view of initial whorl, NHMUK PI MG 1532. Scale bars = 100 μm .

to the base of the protoconch, and consists of narrow costellae that intersect at or just below the mid-whorl. Costellae are sigmoidal: on the upper part of the whorls they are slightly curved and oriented at 40° to the shell axis, and on the lower part of the whorls they are oriented at 200° to the shell axis. Growth lines are visible as faint collabral ribs between, and perpendicular to, the costellae. Aperture is circular, with a small columellar fold. Four whorls are present in these specimens.

Remarks. Hoare & Sturgeon (1978) showed that protoconchs of species of Pseudozygopleuridae are very similar, but can be readily differentiated from those of the Zygopleuridae. Diagnostic characters of pseudozygopleurid protoconchs that are present in these specimens include an elongate, conical shape with 3–5 whorls; smooth initial whorl with collabral ornamentation from the second whorl; and narrow opisthocline to sigmoidal transverse costellae that are equally spaced, extend up and below from the suture and curve uniformly to the mid-whorl (Hoare & Sturgeon 1978). In contrast, protoconchs of the Zygopleuridae have smooth whorls with fine riblets at the sutures (Nützel & Mapes 2001; Kaim 2004) or straight ribs in the Ampezzopleurinae (Nützel 1998, 2005). Protoconchs of the Ladinulidae are similar to those of the Pseudozygopleuridae but can be differentiated due to their vertical costellae (Bandel 2006). These specimens are, therefore, representatives of the Pseudozygopleuridae. No teleoconch is apparently present in these specimens as the sculpture of the prodissoconch is uninterrupted.

Pseudozygopleuridae is primarily a Palaeozoic family. Apart from the Early Triassic specimens described herein, the only other Mesozoic pseudozygopleurid is *Plocezyga* from the Jurassic of Poland (Kaim 2004). The specimens attributed to *Plocezyga* by Kaim (2004), however, lack a protoconch with the diagnostic sigmoidal pseudozygopleurid ornamentation described by Hoare & Sturgeon

(1978, 1980). Instead they have a reticulate pattern, shouldered whorls and transverse costae on the protoconch, indicating that they belong to a different genus and family.

Nützel (1998) used the diameter, ornamentation and whorl number of the protoconch to separate planktotrophic from non-planktotrophic pseudozygopleurid species. The specimens recorded in this study have small protoconch I diameters (0.12–0.14 mm), and the same ornamentation and number of whorls as pseudozygopleurid larval shells interpreted as planktotrophic by Mapes & Nützel (2009), suggesting that they too had a planktotrophic larval lifestyle. A teleoconch was not developed in any of the specimens, which may indicate that the adults were unable to live in this environment.

Order **Architectibranchia** Haszprunar, 1985

Family **Tubiferidae** Cossmann, 1895

Genus ***Sinuarbullina*** Gründel, 1997

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

Diagnosis. The generic diagnosis follows Gründel & Nützel (2012). The shell is fusiform with a distinctly elevated spire. The teleoconch whorls have a subsutural ramp. The transition from the ramp to the outer whorl face is either rounded or angular, sometimes demarcated abapically by a spiral concavity. Whorls are smooth in most species, although faint spiral furrows occur on the base in a few of them. Growth lines are prosocyr on the outer whorl face but strongly curving in an abapertural direction and opisthocyr at the ramp. The aperture is relatively low for the group, teardrop-shaped and lacks a columellar fold. The protoconch is trans- to medioaxial.

Remarks. Pan *et al.* (2003) described *Jiangxispira* as a new genus using the following diagnostic features: (1) a small, high-spined, slender, fusiform shell; (2) teleoconch whorls with narrow shoulder; and (3) a heterostrophic,

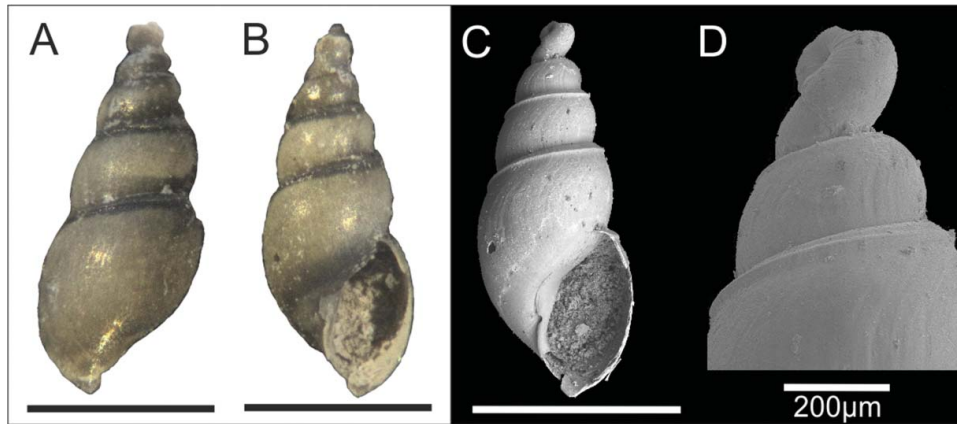


Figure 13. *Sinuarbullina yangouensis* (Pan *et al.*, 2003). **A, B**, lateral views; **C, D**, views of the protoconch. Scale bars = 1 mm, except D. Note: specimen lost by WJF after photography.

discoidal, transaxial protoconch. These characters are all within the diagnostic features of the genus *Sinuarbullina* Gründel (1997), and *Jiangxispira* is, therefore, a junior synonym of *Sinuarbullina*.

Sinuarbullina yangouensis (Pan, Erwin, Nützel, & Xiang-Shui, 2003) comb. nov.
(Fig. 13)

2003 *Jiangxispira yangouensis* Pan, Erwin, Nützel, & Xiang-Shui: 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 subsutural ramp. The ramp from the outer whorl face is rounded with a rib on the shell periphery. Whorls are smooth, except for growth lines which are prosocyrte on the outer whorl face curving in an apertural direction and become opisthocyrte towards the ramp. The surface of the shell shows a coloured spiral band around the subsutural ramp. The aperture is an elongated teardrop shape. Protoconch is heterostrophic, sinistral, nearly discoidal with lightly 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*' *convexa*) is the only accepted species from the Lower Triassic (Gründel & Nützel 2012). These specimens are more slender than *S. convexa*, described from the Sinbad Limestone of the western USA by Batten & Stokes (1986), and better resemble *Jiangxispira yangouensis* from the Induan Dayie Formation, China.

The shell morphology is similar to that of *Meekospira*, which has been interpreted as a slow-moving shell dragger (Hughes 1986), but could have also been a burrower (Hollingworth & Pettigrew 1988). Interpreting the feeding

strategy of fossil gastropods is difficult because information on the organ system, including the ctenidium, is not usually preserved. The ancestral ecology of high-spired gastropods is presumably as algal grazers on hard substrates (Declerck 1995). Given the absence of hard substrates in this study, the specimens described herein were probably detritus feeders or possibly micro-carnivorous on sedentary prey, like many modern shelled opisthobranchs (e.g. Lobo da Cunha *et al.* 2009).

Mode of life. Surficial, fully motile, slow, deposit feeder.

Discussion

Implications for Permian–Triassic extinction and diversification

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

Three of the four gastropod taxa represent families that originated in the Palaeozoic, of which two (*Warthia* and *Wannerispira*) have previously been recognized from the earliest Griesbachian and have been interpreted as 'dead clades walking' (*sensu* Jablonski 2002) by Kaim *et al.* (2010) and Kaim & Nützel (2011). The family Pseudozogopleuridae is recorded in the Triassic for the first time (Fig. 14), confirming that it too survived the late Permian extinction, and could also be interpreted in this way. As noted above, the Jurassic specimens assigned to the Pseudozogopleuridae by Kaim (2004) do not have the

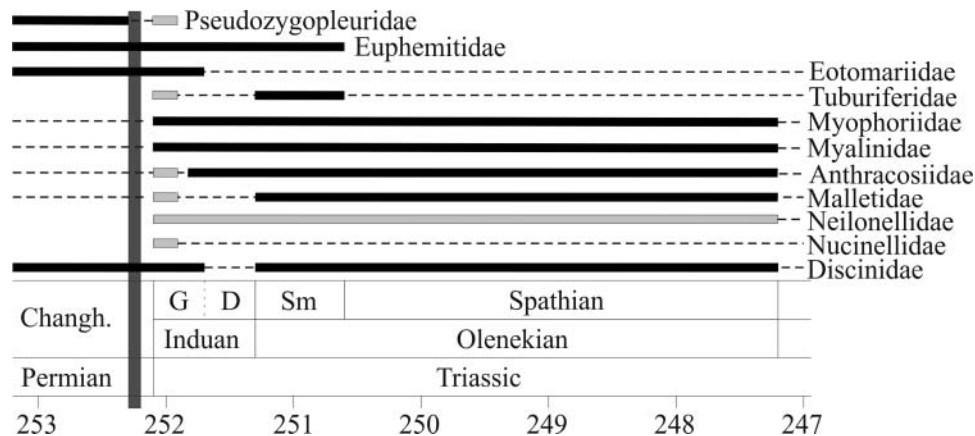


Figure 14. Ranges of benthic invertebrate families identified from the base of the Vikinghøgda Formation. Grey bars = range extensions based on this study; black bars = previously known unequivocal ranges of families; dashed lines = ghost ranges. Chang. = Changhsingian. G = Griesbachian, D = Dienerian, Sm = Smithian. Radiometric ages (bottom) after Lehrmann *et al.* (2006), Galfetti *et al.* (2007) and Shen *et al.* (2011). Late Permian mass extinction event is indicated by a vertical dark grey bar.

expected suite of diagnostic characters and it may be that they represent a different family. If so, then the specimens described herein from Svalbard would represent the youngest occurrence of the Pseudozygopleuridae.

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

Of the five bivalve genera identified in this study, *Pro-myalina*, *Unionites* and *Neoschizodus* have previously been recorded in the earliest Induan (e.g. Hautmann *et al.* 2015). The occurrences of the protobranchs *Nucinella* and *Austrotindaria* represent significant range extensions back to the Induan and are the oldest occurrences of the Nucinelidae 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 Nucinelidae and Neilonellidae appeared *c.* 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 recognizing that most specimens previously assigned to *Unionites fastaensis* 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.* 2013a, 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 – that is, the former is a facultatively motile suspension feeder and the latter is a motile deposit feeder. Other non-protobranch taxa with a similar morphology, such as *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 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 recognized (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 or 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 recognized.

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 recognized, 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 the hypothesis of Schubert *et al.* (1997) 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 prioritized.

The importance of planktotrophy

The exceptionally preserved prodissococonchs 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 shell development has been inferred for many Early Triassic gastropods (Nützel & Erwin 2002; Pan *et al.* 2003; Nützel & Schulbert 2005) and this selectivity has been questioned (Nützel 2014). All gastropod taxa recorded in the present study (i.e. *Warthia*, *Glabrocingulum*, *Sinuarbullina* and the Pseudozygo-pleuridae) are inferred to have had planktotrophic larvae (Nützel & Mapes 2001; this study), and in addition, the bivalves *Nucinella*, *Austrotindaria*, *Unionites* and *Neoschizodus* all possess a small prodissococonch I and a relatively large prodissococonch II which imply planktotrophic larval development (cf. Hautmann & Nützel 2005). Thus, we infer that the possession of planktotrophic larvae was a particular advantage for benthic molluscs inhabiting shelf settings of the Boreal Ocean in the earliest Triassic. This may simply be a consequence of sampling this particular depositional setting, as benthic taxa with planktotrophic larvae were common in similar mid-outer shelf settings during the Palaeozoic (e.g. Frýda 2001; Nützel & Mapes 2001; Bandel *et al.* 2002). Alternatively, it may be a consequence of the extinction event and associated environmental changes.

One possible advantage of a planktotrophic larval development is protection from benthic predation (Nützel & Frýda 2003). Although predators are rarely identified in Early Triassic benthic assemblages (e.g. Schubert & Bottjer 1995; Twitchett *et al.* 2004; Hautmann *et al.* 2011; Hofmann *et al.* 2013a, b, 2014, 2015; Foster & Twitchett 2014; Foster *et al.* 2015), it is possible that some nekto-benthic conodonts, ammonoids or fish may have fulfilled this role or that the predators were largely non-mineralized. Fish with durophagous dentitions, such as *Bobasatrania*, are locally common in the lowest Triassic of the Boreal Ocean (e.g. East Greenland; Stensiö 1932), and trace fossil evidence of vagile crustaceans has been recorded from the Induan of north-west Canada (Beatty *et al.* 2008; Zonneveld *et al.* 2010) and central Spitsbergen (WJF & RJT pers. obs.).

An alternative advantage is that planktotrophic larvae enable more effective dispersal and a wide geographical distribution. The cosmopolitan opportunists that thrived in the wake of the late Permian mass extinction (e.g. *Lingularia* and *Claraia*) all have an inferred planktotrophic larval stage (Hammond & Poiner 1984; Yang *et al.* 2001). Possession of planktotrophic larvae would have been particularly useful for Early Triassic benthic invertebrates given the spatial and temporal fluctuations in benthic oxygen concentrations that have been inferred for the earliest Triassic seafloor (Wignall & Twitchett 1996; Thomas *et al.* 2004; Nabbefeld *et al.* 2010). Effective dispersal and wide distribution would have afforded greater protection from extinction and enabled rapid colonization of

vacated seafloor once harsh environmental conditions had ameliorated. The late Permian mass extinction did not select against animals with planktotrophic larval development (Nützel 2014; Posenato *et al.* 2014), and possession of that character may have been a key factor in the survival and radiation of certain groups.

The occurrence of well-preserved planktotrophic larval shells in this newly described benthic assemblage has additional palaeoenvironmental implications. First, it implies that primary production in surface waters was adequate to sustain planktic food webs. Second, the exquisite preservation of the earliest formed larval stages and the complete absence of any signs of shell dissolution or repair (cf. Garrilli *et al.* 2015) demonstrates that neither the surface waters nor benthic habitat in this particular region were affected by ocean acidification at this time, and the pH was not low enough to have curtailed biomineralization.

Conclusions

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

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References

- Adams, H. & Adams, A. 1858. *The genera of recent Mollusca arranged according to their organization*. John van Voorst, London, 661 pp.
- Alberti, F. von. 1864. *Überblick über die Trias, mit Berücksichtigung ihres Vorkommens in den Alpen*. J. G. Cotta'sche Buchhandlung, Stuttgart, 353 pp.
- Amalitzky, W. 1892. Ueber die Anthracosien der Permformation Russlands. *Palaeontographica*, **39**, 125–213.
- Amano, K., Jenkins, R. G. & Hikida, Y. 2007. A new gigantic *Nucinella* (Bivalvia: Solemyoidea) from the Cretaceous cold-seep deposit in Hokkaido, northern Japan. *Veliger*, **49**, 8–90.
- Bandel, K. 2006. Families of the Cerithioidea and related superfamilies (Palaeo-Caenogastropoda; Mollusca) from the Triassic to the recent characterized by protoconch morphology-including the description of new taxa. *Freiberger Forschungshefte C*, **511**, 59–138.
- Bandel, K., Nützel, A. & Yancey, T. E. 2002. Larval shells and shell microstructures of exceptionally well preserved late Carboniferous gastropods from the Buckhorn Asphalt deposit (Oklahoma, USA). *Senckenbergiana Lethaea*, **82**, 639–689.
- Batten, R. L. 1989. Permian gastropods of the southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiridae, Gosseletinidae. *American Museums Novitates*, **2958**, 1–64.
- Batten, R. L. & Stokes, W. L. 1986. Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *American Museum Novitates*, **1864**, 1–33.
- Baumiller, T. K., Salamon, M. A., Gorzelak, P., Mooi, R., Messing, C. G. & Gahn, F. J. 2010. Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. *Proceedings of the National Academy of Sciences*, **107**, 5893–5896.
- Beatty, T. W., Zonneveld, J.-P. & Henderson, C. M. 2008. Anomalously diverse Early Triassic ichnofossil assemblages in northwest Pangea: a case for a shallow-marine habitable zone. *Geology*, **36**, 771–774.
- Bernard, F. 1898. Recherches ontogénétiques et morphologiques sur la coquille des lamellibranches. Première partie. Taxodontes et Anisomyaires. *Annales des Sciences Naturelles. Zoologie et Paléontologie*, **8**, 1–208.
- Bieler, R., Mikkelsen, P. M., Collins, T. M., Glover, E. A., Gonzalez, V. L., Graf, D. L., Harper, E. M., Healy, J., Kawachi, G. Y., Sharma, P. P., Staubach, S., Strong, E. E., Taylor, J. D., Temkin, I., Zardus, J. D., Clark, S., Guzman, A., McIntyre, E., Sharp, P. & Giribet, G. 2014. Investigating the bivalve tree of life – an exemplar-based approach combining molecular and novel morphological characters. *Invertebrate Systematics*, **28**, 32–115.
- Bittner, A. 1899. Versteinerungen aus den Trias-Ablagerungen des Süd-Ussuri-Gebietes in der ostsibirischen Küstenprovinz. *Mémoires du Comité Géologique*, **7**, 1–35.

- Bittner, A.** 1901. Lamellibranchiaten aus der Trias des Bakonyerwaldes. In: Resultaten der Wissenschaftlichen Erforschung des Balatonsees, 1. *Palaeontologie der Umgebung des Balatonsees*, 2, 1–107.
- Blakey, R.** 2012. *Global Paleogeography*. [updated at: <http://www2.nau.edu/rcb7/globaltext2.html>, accessed July 2014]
- Bronn, H. G.** 1849. *Index Palaeontologicus oder Übersicht der bis jetzt bekannten fossilen Organismen. Zweite Abtheilung. Enumerator palaeontologicus: systematische Zusammenstellung und geologische Entwicklungs-Gesetze der organischen Reiche*. Schweizerbart, Stuttgart, 776 pp.
- Carter, J. G., Campbell, D. C., & Campbell, M. R.** 2000. Cladistic perspectives on early bivalve evolution. Pp. 44–79 in E. M. Harper, J. D. Taylor & J. A. Crame (eds) *The Evolutionary Biology of the Bivalvia*. The Geological Society of London, London.
- Catullo, T. A.** 1846. Memoria geognostico-paleozoica sulle Alpi Venete. *Memorie della Societ'a Italiana delle scienze residente in Modena*, 24, 1–158.
- Ciriacks, K. W.** 1963. Permian and Eotriassic bivalves of the Middle Rockies. *Bulletin of the American Museum of Natural History*, 125, 1–98.
- Clausen, C. K. & Wignall, P. B.** 1990. Early Kimmeridgian bivalves of southern England. *Mesozoic Research*, 2, 97–149.
- Coan, E. V. & Valentich-Scott, P.** 2012. *Bivalve seashells of tropical West America. Marine bivalve mollusks from Baja California to northern Peru*. Santa Barbara Museum of Natural History Monographs 6, Santa Barbara, CA, 1258 pp.
- Cossmann, M.** 1895. *Essais de paléontologie comparée, Vol. 1*. Comtoir Géologique, Paris, 159 pp.
- Cuvier, G.** 1795. Second mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2, 433–449.
- Dall, W. H.** 1889. On the hinge of pelecypods and its development with an attempt toward a better subdivision of the group. *American Journal of Sciences, Series 3*, 38, 445–462.
- Davidson, T.** 1848. Mémoire sur les brachiopods du Système silurien supérieur de l'Angleterre. *Bulletin de la Société géologique de France, série 2*, 5, 309–338, 370–374.
- Declerck, C. H.** 1995. The evolution of suspension feeding in gastropods. *Biological Reviews*, 70, 549–569.
- Dell, R. K.** 1956. The archibenthal Mollusca of New Zealand. *Dominion Museum Bulletin*, 18, 1–235.
- Di Geronimo, I. & La Perna, R.** 1997. Pleistocene bathyal molluscan assemblages from southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 103, 1–10.
- Dumeril, A. M. C.** 1805. *Zoologie analytique ou method naturelle de classification des animaux*. Allais, Paris, xxiv, 364 pp.
- Erwin, D. H. & Pan, H.-Z.** 1996. Recoveries and radiations: gastropods after the Permo-Triassic mass extinction. *Geological Society, London, Special Publications*, 102, 223–229.
- Erwin, D. H., Valentine, J. W. & Sepkoski, J. J.** 1987. A comparative study of diversification events; the early Paleozoic versus the Mesozoic. *Evolution*, 41, 1177–1186.
- Fleming, C. A.** 1948. New species and genera of marine Mollusca from the Southland fiords. *Transactions of the Royal Society of New Zealand*, 77, 72–92.
- Foster, W. J. & Twitchett, R. J.** 2014. Functional diversity of marine ecosystems after the late Permian mass extinction event. *Nature Geoscience*, 7, 233–238.
- Foster, W. J., Danise, S., Sedlacek, A., Price, G. D., Hips, K. & Twitchett, R. J.** 2015. Environmental controls on the post-Permian recovery of benthic, tropical marine ecosystems in western Palaeotethys (Aggtelek Karst, Hungary). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 440, 374.
- Fraiser, M. L. & Bottjer, D. J.** 2005. Restructuring in benthic level-bottom shallow marine communities due to prolonged environmental stress following the end-Permian mass extinction. *Comptes Rendus Palevol*, 4, 583–591.
- Fraiser, M. L. & Bottjer, D. J.** 2007. When bivalves took over the world. *Paleobiology*, 33, 397–413.
- Frech, F.** 1891. Die devonischen Aviculiden Deutschlands, ein Beitrag zur Systematik und Stammesgeschichte der Zweischaler. *Abhandlungen zur Geologischen Spezialkarte von Preußen und den Thüringischen Staaten*, 9, 1–253.
- Fryda, J.** 1999. Higher classification of Paleozoic gastropods inferred from their shell ontogeny. *Journal of Czech Geological Society*, 44, 137–154.
- Fryda, J.** 2001. Discovery of a larval shell in Middle Paleozoic subulitoidean gastropods with description of two new species from the Early Devonian of Bohemia. *Bulletin of the Czech Geological Survey*, 76, 29–37.
- Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard, A., Brühwiler, T., Goudemand, N., Weissert, H., Hochuli, P. A., Cordey, F. & Guodun, K.** 2007. Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages and ammonoid biochronozones. *Earth and Planetary Science Letters*, 258, 593–604.
- Garilli, V., Rodolfo-Metalpa, R., Scuderi, D., Brusca, L., Parrinello, D., Rastrick, S. P., Foggo, A., Twitchett, R. J., Hall-Spencer, J. M. & Milazzo, M.** 2015. Physiological advantages of dwarfing and surviving extinctions in high-CO₂ oceans. *Nature Climate Change*, 5, 678–682.
- Geyer, G., Hautmann, M., Hagdorn, H., Ockert, W. & Streng, M.** 2005. Well-preserved mollusks from the Lower Keuper (Ladinian) of Hohenlohe (Southwest Germany). *Paläontologische Zeitschrift*, 79, 429–460.
- Giebel, C.** 1855. Kritisches über die Myophorien des Muschelkalkes. *Zeitschrift für die gesamten Naturwissenschaften*, 5, 34.
- Gobbett, D. J.** 1963. Carboniferous and Permian brachiopods of Svalbard. *Norsk Polarinstitutt Skrifter*, 127, 1–201.
- Goldfuss, G. A.** 1837. *Petrefacta Germaniae tam ea, quae in museo universitatis regiae Borussicae Fridericae Wilhelmae Rhenanae servantur quam alia quaecunque in museis Hoeninghusino, Muensteriano aliisque extant, iconibus et descriptionibus illustrata*. Verlag lithographische Anstalt Arnz and Co, Düsseldorf, 312 pp.
- Goryansky, V. Y. U. & Popov, L. E.** 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells. *Paleontologicheskii Zhurnal*, 1985, 3–14.
- Gray, J. E.** 1840. *Synopsis of the contents of the British Museum*. British Museum, London, 370 pp.
- Gray, J. E.** 1853. On the division of ctenobranchous gastropodous Mollusca into larger groups and Families. *Annals and Magazine of Natural History*, (2), 11, 124–132.
- Gründel, J.** 1997. Heterostrophia (Gastropoda) aus dem Dogger Norddeutschlands und Nordpolens. III. Opisthobranchia. *Berliner geowissenschaftliche Abhandlungen*, 25, 177–223.
- Gründel, J. & Nützel, A.** 2012. On the early evolution (Late Triassic to Late Jurassic) of the Architectibranchia (Gastropoda: Heterobranchia), with a provisional classification. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 264, 31–59.
- Hallam, A.** 1995. Oxygen-restricted facies of the basal Jurassic of North West Europe. *Historical Biology*, 10, 247–257.

- Hammond, L. & Poiner, I. R.** 1984. Genetic structure of three populations of the 'living fossil' brachiopod *Lingula* from Queensland, Australia. *Lethaia*, **17**, 139–143.
- Haszprunar, G.** 1985. The Heterobranchia – a new concept of the phylogeny of the higher Gastropoda. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **23**, 15–37.
- Hausmann, I. M. & Nützel, A.** 2015. Diversity and palaeoecology of a highly diverse Late Triassic marine biota from the Cassian Formation of north Italy. *Lethaia*, **48**, 235–255.
- Hautmann, M.** 2007. Steuerungsfaktoren globaler Biodiversifizierungsmuster am Beispiel frühmesozoischer Muscheln. *Beringeria*, **37**, 61–74.
- Hautmann, M. & Nützel, A.** 2005. First record of a heterodont bivalve (Mollusca) from the Early Triassic: palaeoecological significance and implications for the 'Lazarus Problem'. *Palaeontology*, **48**, 1131–1138.
- Hautmann, M., Smith, A. B., McGowan, A. J. & Bucher, H.** 2013. Bivalves from the Olenekian (Early Triassic) of southwestern Utah: systematics and evolutionary significance. *Journal of Systematic Palaeontology*, **11**, 263–293.
- Hautmann, M., Bucher, H., Brühwiler, T., Goudemand, N., Kaim, A. & Nützel, A.** 2011. An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. *Geobios*, **44**, 71–85.
- Hautmann, M., Bagherpour, B., Broose, M., Frisk, Å., Hofmann, R., Baud, A., Nützel, A., Goudemand, N. & Bucher, H.** 2015. Competition in slow motion: the unusual case of benthic marine communities in the wake of the end-Permian mass extinction. *Palaeontology*, **58**, 871–901.
- He, W., Feng, Q., Weldon, E. A., Gu, S., Meng, Y., Zhang, F. & Wu, S.** 2007. A late Permian to Early Triassic bivalve fauna from the Dongpan section, southern Guangxi, South China. *Journal of Paleontology*, **81**, 1009–1019.
- Hickman, C. S.** 1988. Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. *Malacological Review*, **4**, 17–34.
- Hoare, R. D. & Sturgeon, M. T.** 1978. The Pennsylvanian a gastropod genera *Cyclozyga* and *Helminthozyga* and the classification of the Pseudozygopleuridae. *Journal of Paleontology*, **52**, 850–858.
- Hoare, R. D. & Sturgeon, M. T.** 1980. The Pennsylvanian pseudozygopleurid gastropod genus *Gamizyga* n. gen. from Ohio and West Virginia. *Journal of Paleontology*, **54**, 159–187.
- Hofmann, R., Hautmann, M. & Bucher, H.** 2013a. A new paleoecological look at the Dinwoody Formation (Lower Triassic, western USA): intrinsic versus extrinsic controls on ecosystem recovery after the end-Permian mass extinction. *Journal of Paleontology*, **87**, 854–880.
- Hofmann, R., Hautmann, M. & Bucher, H.** 2015. Recovery dynamics of benthic marine communities from the Lower Triassic Werfen Formation, northern Italy. *Lethaia*, **48**, 474–496.
- Hofmann, R., Hautmann, M., Wasmer, M. & Bucher, H.** 2013b. Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica*, **58**, 149–173.
- Hofmann, R., Hautmann, M., Brayard, A., Nützel, A., Bylund, K. G., Jenks, J. F., Vennin, E., Olivier, N. & Bucher, H.** 2014. Recovery of benthic marine communities from the end-Permian mass extinction at the low latitudes of eastern Panthalassa. *Palaeontology*, **57**, 547–589.
- Hollingsworth, N. & Pettigrew, T.** 1988. Zechstein reef fossils and their palaeoecology. *The Palaeontological Association Field Guides to Fossils*, **3**, 1–72.
- Hounslow, M. W., Peters, C., Mørk, A., Weitschat, W. & Vigran, J. O.** 2008. Biomagnetostratigraphy of the Vikinghøgda Formation, Svalbard (Arctic Norway), and the geomagnetic polarity timescale for the lower Triassic. *Geological Society of America Bulletin*, **120**, 1305–1325.
- Hughes, R. N.** 1986. *A functional biology of marine gastropods*. Crook Helm, London, 245 pp.
- Jablonski, D.** 2002. Survival without recovery after mass extinctions. *Proceedings of the Natural Academy of Sciences*, **99**, 8139–8144.
- Jeppsson, L. & Anehus, R.** 1995. A buffered formic acid technique for conodont extraction. *Journal of Paleontology*, **69**, 790–794.
- Kaim, A.** 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Acta Palaeontologica Polonica*, **62**, 3–183.
- Kaim, A.** 2009. Gastropods. *National Museum of Nature and Science Monographs*, **38**, 141–155.
- Kaim, A. & Nützel, A.** 2011. Dead bellerophontids walking – the short Mesozoic history of the Bellerophontoidea (Gastropoda). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **308**, 190–199.
- Kaim, A., Nützel, A., Hautmann, M. & Bucher, H.** 2013. Early Triassic gastropods from Salt Range, Pakistan. *Bulletin of Geosciences*, **88**, 505–516.
- Kaim, A., Nützel, A., Bucher, H., Brühwiler, T. & Goudemand, N.** 2010. Early Triassic (Late Griesbachian) gastropods from south China (Shanggan, Guangxi). *Swiss Journal of Geosciences*, **103**, 121–128.
- Kashiyama, Y. & Oji, T.** 2004. Low-diversity shallow marine benthic fauna from the Smithian of northeast Japan: paleoecologic and paleobiogeographic implications. *Paleontological Research*, **8**, 199–218.
- Kidder, D. L. & Erwin, D. H.** 2001. Secular distribution of biogenic silica through the Phanerozoic: comparison of silica-replaced fossils and bedded cherts at the series level. *The Journal of Geology*, **109**, 509–522.
- Kiel, S., Amano, K. & Jenkins, R. G.** 2008. Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan. *Acta Palaeontologica Polonica*, **53**, 525–537.
- Kittl, E.** 1904. Geologie der Umgebung von Sarajevo. *Jahrbuch der Geologischen Reichsanstalt*, **53**, 707–738.
- Knight, J. B.** 1930. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Pseudozygopleurinae. *Journal of Paleontology*, **4**, 1–89.
- Knight, J. B.** 1956. New families of Gastropoda. *Journal of the Washington Academy of Sciences*, **46**, 41–42.
- Komatsu, T., Chen, J.-H., Cao, M.-Z., Stiller, F. & Naruse, H.** 2004. Middle Triassic (Anisian) diversified bivalves: depositional environments and bivalve assemblages in the Leidapo Member of the Qingyan Formation, southern China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **208**, 207–223.
- Kumagai, T. & Nakazawa, K.** 2009. Bivalves. *National Museum of Nature and Science Monographs*, **38**, 156–172.
- La Perna, R.** 2004. *Nucinella alibrandi* (Conti, 1864) and *N. seguenzae* (Dall, 1898), the last European nucinellids (Bivalvia, Protobranchia). *Rivista Italiana di Paleontologica e Stratigrafia*, **110**, 571–577.
- La Perna, R.** 2005. A gigantic deep-sea Nucinellidae from the tropical West Pacific (Bivalvia: Protobranchia) *Zootaxa*, **88**, 1–10.
- La Perna, R.** 2007. Taxonomy of the family Neilonellidae (Bivalvia, Protobranchia): Miocene and Pliocene–Pleistocene

- species of *Pseudoneilonella* Laghi, 1986 from Italy. *Veliger*, **49**, 196–208.
- Lehrmann, D. J., Ramezani, J., Bowring, S. A., Martin, M. W., Montgomery, P., Enos, P., Payne, J. L., Orchard, M. J., Hongmei, W. & Jiayong, W.** 2006. Timing of recovery from the end-Permian extinction: geochronologic and biostratigraphic constraints from south China. *Geology*, **34**, 1053–1056.
- Linnaeus, C.** 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I (Tenth Edition)*. Laurentius Salvius, Stockholm, 824 pp.
- Linsley, R. M.** 1977. Some 'laws' of gastropod shell form. *Paleobiology*, **3**, 196–206.
- Lobo da Cunha, A., Ferreira, I., Coehlo, R. & Calado, G.** 2009. Light and electron microscopy study of the salivary glands of the carnivorous opisthobranch *Philinopsis depicta* (Mollusca, Gastropoda). *Tissue and Cell*, **41**, 367–375.
- Mapes, R. H., & Nützel, A.** 2009. Late Palaeozoic mollusc reproduction: cephalopod egg-laying behavior and gastropod larval palaeobiology. *Lethaia*, **42**, 341–356.
- Matsushita, S.** 1926. Lower Triassic fossils of Kurotaki, Tosa province. *Chikyu*, **5**, 420–429.
- Mergl, M.** 2006. A review of Silurian discinoid brachiopods from historical British localities. *Bulletin of Geosciences*, **81**, 215–236.
- Mergl, M.** 2010. Discinid brachiopod life assemblages: fossil and extant. *Bulletin of Geosciences*, **85**, 27–38.
- Mitchell, J. S. & Heckert, A. B.** 2010. The setup, use and efficacy of sodium polytungstate separation methodology with respect to microvertebrate remains. *Journal of Paleontological Techniques*, **7**, 1–12.
- Mørk, A., Elvebakk, G., Forsberg, A. W., Hounslow, M. W., Nakrem, H. A., Vigran, J. O. & Weitschat, W.** 1999. The type section of the Vikinghøgda Formation: a new Lower Triassic unit in central and eastern Svalbard. *Polar Research*, **18**, 51–82.
- Nabbefeld, B., Grice, K., Twitchett, R. J., Summons, R. E., Hays, L., Böttcher, M. E. & Asif, M.** 2010. An integrated biomarker, isotopic and palaeoenvironmental study through the late Permian event at Lusitaniadalen, Spitsbergen. *Earth and Planetary Science Letters*, **291**, 84–96.
- Nakazawa, K. & Runnegar, B.** 1973. The Permian–Triassic boundary: a crisis for bivalves? *Memoirs of the Canadian Society of Petroleum Geologists*, **2**, 608–621.
- Nakrem, H. A., Orchard, M. J., Weitschat, W., Hounslow, M. W., Beatty, T. W. & Mørk, A.** 2008. Triassic conodonts from Svalbard and their Boreal correlations. *Polar Research*, **27**, 523–539.
- Neri, C. & Posenato, R.** 1988. New biostratigraphical data on uppermost Werfen Formation of Western Dolomites (Trento, Italy). *Geologisch-Paläontologische Mitteilungen*, **14**, 83–107.
- Newell, N. D.** 1965. Classification of the Bivalvia. *American Museum Novitates*, **2206**, 1–25.
- Newell, N. D.** 1955. Permian pelecypods of east Greenland. *Meddelelser om Grønland*, **110**, 1–36.
- Newell, N. D. & Boyd, D. W.** 1975. Parallel evolution in early Trigonicean bivalves. *Bulletin of the American Museum of Natural History*, **154**, 1–158.
- Nützel, A.** 1998. Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen, Reihe E*, **26**, 1–229.
- Nützel, A.** 2005. A new Early Triassic gastropod genus and the recovery of gastropods from the Permian/Triassic extinction. *Acta Palaeontologica Polonica*, **50**, 19–24.
- Nützel, A.** 2014. Larval ecology and morphology in fossil gastropods. *Palaeontology*, **57**, 479–503.
- Nützel, A. & Erwin, D. H.** 2002. *Battenizyga*, a new Early Triassic gastropod genus with a discussion of the caenogastropod evolution at the Permian/Triassic boundary. *Paläontologische Zeitschrift*, **76**, 21–27.
- Nützel, A. & Frýda, J.** 2003. Paleozoic plankton revolution: evidence from early gastropod ontogeny. *Geology*, **31**, 829–831.
- Nützel, A. & Kaim, A.** 2014. Diversity, palaeoecology and systematics of a marine fossil assemblage from the Late Triassic Cassian Formation at Settsass Scharte, N Italy. *Paläontol Z*, **88**, 406–431.
- Nützel, A. & Mapes, R. H.** 2001. Larval and juvenile gastropods from a Carboniferous black shale: palaeoecology and implications for the evolution of the Gastropoda. *Lethaia*, **34**, 143–162.
- Nützel, A. & Schulbert, C.** 2005. Facies of two important Early Triassic gastropod lagerstätten: implications for diversity patterns in the aftermath of the end-Permian mass extinction. *Facies*, **51**, 480–500.
- Oji, T. & Twitchett, R. J.** 2015. The oldest post-Palaeozoic crinoid and Permian–Triassic origins of the Articulata (Echinodermata). *Zoological Science*, **32**, 211–215.
- Oliver, P. G. & Taylor, J. D.** 2012. Bacterial symbiosis in the Nucinellidae (Bivalvia: Solemyida) with descriptions of two species. *Journal of Molluscan Studies*, **78**, 81–91.
- d'Orbigny, A.** 1847. Considérations zoologiques et géologiques sur les Brachiopodes ou Palliobranches. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **25**, 193–195, 266–269.
- Orchard, M. J.** 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**, 93–117.
- Pan, H.-Z. & Shen, S.-Z.** 2008. Late Permian (Lopingian) gastropods from the Quburga Formation at the Qubu section in the Mt. Everest (Qomolangma) region, Southern Tibet (Xizang), China. *Journal of Paleontology*, **82**, 1038–1042.
- Pan, H.-Z., Erwin, D. H., Nützel, A. & Xiang-Shui, Z.** 2003. *Jiangxispira*, a new gastropod genus from the Early Triassic of China with remarks on the phylogeny of the heterostropha at the Permian/Triassic boundary. *Journal of Paleontology*, **77**, 44–49.
- Pan, Y. H., Hu, S. X., Sha, J. G., Zhang, Q. Y., Wang, Y. Q., Zhou, C. Y., Wen, W., Huang, J. Y. & Xie, T.** 2014. Early Triassic bivalves from the Feixianguan Formation in Xingyi, Guizhou and the Ximatang Formation in Qiubei, Yunnan (southern China). *Palaeoworld*, **23**, 143–154.
- Posenato, R.** 2008. Patterns of bivalve biodiversity from Early to Middle Triassic in the Southern Alps (Italy): regional vs. global events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **261**, 145–159.
- Posenato, R., Holmer, L. E. & Prinoth, H.** 2014. Adaptive strategies and environmental significance of lingulid brachiopods across the late Permian extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **399**, 373–384.
- Pruss, S., Payne, J. L. & Westacott, S.** 2015. Taphonomic bias of selective silicification revealed by paired petrographic and insoluble analysis. *Palaaios*, **30**, 620–626.
- Ros, S., De Renzi, M., Damborenea, S. E. & Márquez-Aliaga, A.** 2011. Coping between crises: Early Triassic–Early Jurassic bivalve diversity dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **311**, 184–199.
- Rouse, G. W., Jermin, L. S., Wilson, N. G., Eeckhaut, I., Lanterbecq, D., Oji, T., Young, C. M., Browning, T.,**

- Cisternas, P., Helgen, L. E., Stuckey, M. & Messing, C. G. 2013. Fixed, free, and fixed: the fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian–Triassic origin. *Molecular Phylogenetics and Evolution*, **66**, 161–181.
- Salvini-Plawen, L. von. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, **19**, 249–278.
- Savoy, L. E. 1992. Environmental record of Devonian–Mississippian carbonate and low-oxygen facies transitions, southernmost Canadian Rocky Mountains and northwesternmost Montana. *Geological Society of America Bulletin*, **104**, 1412–1432.
- Schileyko, A. A. 1989. Morfologicheskaya evolutsiya nodotriada Protobranchia (Bivalvia) and peculiarities of abyssal members of the group [Morphological evolution of superorder Protobranchia and peculiarities of abyssal members of the group]. *Trudy Instituta Okeanologii*, **123**, 81–101.
- Schubert, J. K. & Bottjer, D. J. 1995. Aftermath of the Permian–Triassic mass extinction event: paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeography, Palaeoclimatology, Paleoecology*, **116**, 1–39.
- Schubert, J. K., Kidder, D. L. & Erwin, D. H. 1997. Silica-replaced fossils through the Phanerozoic. *Geology*, **25**, 1031–1034.
- Sharma, P. P., Zardus, J. D., Boyle, E. E., Gonzalez, V. L., Jennings, R. M., McIntyre, E., Wheeler, W. C., Etter, R. J. & Giribet, G. 2013. Into the deep: a phylogenetic approach to the bivalve subclass Protobranchia. *Molecular Phylogenetics and Evolution*, **69**, 188–204.
- Shen, S.-Z., Crowley, J. L., Wang, Y., Bowring, S. A., Erwin, D. H., Sadler, P. M., Cao, C.-Q., Rothman, D. H., Henderson, C., Ramezani, J., Zhang, H., Shen, Y., Wang, X.-D., Wang, W., Mu, L., Li, W.-Z., Tang, Y.-G., Liu, X.-L., Liu, L.-J., Zeng, Y., Jiang, Y.-F. & Jin, Y.-G. 2011. Calibrating the end-Permian mass extinction. *Science*, **334**, 1367–1372.
- Shigeta, Y., Zakharov, Y. D., Maeda, H. & Popov, A. M. 2009. Concluding remarks. *National Museum of Nature and Science Monographs*, **38**, 202.
- Simroth, H. 1906. Versuch einer neuen Deutung der Bellerophonitiden. *Sitzungsberichte der naturforschenden Gesellschaft zu Leipzig*, **1905**, 3–8.
- Spath, L. F. 1930. The Eotriassic invertebrate fauna of east Greenland. *Meddelelser Om Grønland*, **83**, 1–89.
- Stanley, S. M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs: a consequence of mantle fusion and siphon formation. *Journal of Paleontology*, **42**, 214–229.
- Stanley, S. M. 1972. Functional morphology and evolution of bysally attached bivalve mollusks. *Journal of Paleontology*, **46**, 165–212.
- Stasek, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae), with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. *Journal of Zoology*, **137**, 511–538.
- Stensiö, E. 1932. Triassic fishes from east Greenland collected by the Danish expeditions in 1929–1931. *Meddelelser om Grønland*, **83**, 1–305.
- Stoliczka, F. 1871. Cretaceous fauna of southern India, v. 3. The Pelecypoda, with a review of all known genera of this class, fossil and Recent. *Palaeontologia Indica, Series 6*, **3**, 1–537.
- Szente, I. & Vörös, A. 2003. The Pelsonian Bivalvia fauna of the Balaton Highland. *Geologica Hungarica Series: Palaeontologica, Fasciculus*, **55**, 123–138.
- Thomas, E. G. 1940. Revision of the Scottish Carboniferous Pleurotomariidae. *Transactions of the Geological Society of Glasgow*, **20**, 30–72.
- Thomas, B. M., Willink, R. J., Twitchett, R. J., Purcell, R. R., Archbold, N. W., George, A. D., Tye, S., Alexander, R., Foster, C. B. & Barber, C. J. 2004. Unique marine Permian–Triassic boundary section from Western Australia. *Australian Journal of Earth Sciences*, **51**, 423–430.
- Twitchett, R. J. 2006. The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 190–213.
- Twitchett, R. J. 2007. The Lilliput effect in the aftermath of the end-Permian extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**, 132–144.
- Twitchett, R. J. & Barras, C. G. 2004. Trace fossils in the aftermath of mass extinction events. *Geological Society, London, Special Publications*, **228**, 397–418.
- Twitchett, R. J., Krystyn, L., Baud, A., Wheeley, J. R. & Richoz, S. 2004. Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. *Geology*, **32**, 805–808.
- Valentine, J. W. & Jablonski, D. 1983. Larval adaptations and patterns of brachiopod diversity in space and time. *Evolution*, **37**, 1052–1061.
- Valentine, J. W. & Jablonski, D. 1986. Mass extinctions: sensitivity of marine larval types. *Proceedings of the National Academy of Sciences*, **83**, 6912–6914.
- Vokes, H. E. 1956. Notes on the Nucinellidae (Pelecypoda) with description of a new species from the Eocene of Oregon. *Journal of Paleontology*, **30**, 652–671.
- Waagen, W. 1880. Salt-range fossils. Vol. I, Productus-limestone fossils. Part II, Pisces—Cephalopoda: supplement. Gasteropoda. *Palaeontologia Indica*, **13**, 73–183.
- Waagen, W. 1885. Salt-range fossils. Vol. 2: fossils from the Ceratite Formation. Pisces—Ammonoidea (Cephalopoda). *Memoirs of the Geological Survey of India, Palaeontologia Indica*, **13**, 1–323.
- Wasmer, M., Hautmann, M., Hermann, E., Ware, D., Roohi, G., Ur-Rehman, K., Yaseen, A. & Bucher, H. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. *Palaeontology*, **55**, 1043–1073.
- Waterhouse, J. B. 1963. Permian gastropods of New Zealand. Part 1 – Bellerophonacea and Euomphalacea. *New Zealand Journal of Geology and Geophysics*, **6**, 88–112.
- Wenz, W. 1938. Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. Pp. 1–1639 in O. H. Schindewolf (ed.) *Handbuch der Paläozoologie, Band 6*. Borntraeger, Berlin.
- Wittenburg, P. von. 1908. Beiträge zur Kenntnis der Werfener Schichten Südtirols. *Geologische und Paläontologische Abhandlungen, Neue Folge*, **8**, 251–289.
- Wheeley, J. R. & Twitchett, R. J. 2005. Palaeoecological significance of a new Griesbachian (Early Triassic) gastropod assemblage from Oman. *Lethaia*, **38**, 37–45.
- Wignall, P. B. & Twitchett, R. J. 1996. Oceanic anoxia and the end Permian mass extinction. *Science*, **272**, 1155–1159.
- Wissman, H. L. 1841. Beiträge zur Geognosie und petrefactenkunde des Südöstlichen Tirol's. *Beiträge zur Petrefactenkunde*, **4**, 1–152.

- Wood, S. V.** 1840. A catalogue of shells from the Crag. *Annals and Magazine of Natural History*, **6**, 243–253.
- Wood, S. V.** 1851. Monograph of the Crag Mollusca with descriptions of shells from the Upper Tertiaries of the British Isles. *Palaeontographical Society Monographs*, **4**, 1–150.
- Yang, F., Peng, Y. & Gao, Y.** 2001. Study on the late Permian *Claraia* in south China. *Science in China (Series D)*, **44**, 797–807.
- Zonneveld, J.-P., Beatty, T. W. & Pemberton, S. G.** 2007. Lingulide brachiopods and the trace fossil *Lingulichnus* from the Triassic of western Canada: implications for faunal recovery after the end-Permian mass extinction. *Palaios*, **22**, 74–97.
- Zonneveld, J.-P., Gingras, M. K. & Beatty, T. W.** 2010. Diverse ichnofossil assemblages following the P–T mass extinction, Lower Triassic, Alberta and British Columbia, Canada: evidence for shallow marine refugia on the north-western coast of Pangea. *Palaios*, **25**, 368–392.