Journal of Paleontology, page 1 of 23

0022-3360/24/1937-2337
doi: 10.1017/jpa.2024.1

JOURNAL OF PALEONTOLOGY A PUBLICATION OF THE Paleontological Society

Slit-bearing gastropods in the Jane Longstaff Collection at the Natural History Museum, London from the Visean (Carboniferous) of Dalry, Ayrshire, Scotland

Baran Karapunar,[1,2,3,4]* Jonathan A. Todd,[5] and Alexander Nützel[2,3,4]

[1]Institute for Geology, Universität Hamburg, Hamburg, Germany <B.Karapunar@leeds.ac.uk>
[2]SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.
[3]Department of Earth and Environmental Sciences, Palaeontology and Geobiology, Ludwig-Maximilians-Universität München, Munich, Germany <nuetzel@snsb.de>
[4]GeoBio-Center, Ludwig-Maximilians-Universität München, Munich, Germany.
[5]The Natural History Museum, London, UK <j.todd@nhm.ac.uk>

Non-technical Summary.—Natural history museums house numerous previously undescribed species and unknown information hidden in their collections. We describe lower Carboniferous slit-bearing gastropods (Pleurotomariida and Goniasmatidae) from previously unreported gastropod collections made by Jane Longstaff (Jane Donald), one of the pioneering paleontologists of Paleozoic gastropods in the late nineteenth and early twentieth centuries. The gastropods were collected from an old quarry near Dalry, Ayrshire, Scotland. The collection consists largely of microgastropods, many of which are unusually well preserved including delicate ornament and larval shells. The collection yields ten species, three of them representing new species. The new data on earliest whorls and other shell features such as the selenizone (the shell region formed by the closure of the shell slit) improved the classification. The new findings confirm that the genus *Neilsonia* belongs to Pleurotomariida and is distinct from the morphologically convergent *Peruvispira* (Goniasmatidae). The similarities between *Biarmeaspira* and *Baylea* support previous opinions that they are closely related. Furthermore, the collection yields the oldest record of *Biarmeaspira*, which was previously known only from the Permian. The angulated selenizone (as in *Biarmeaspira*) evidently evolved several times in Pleurotomariida and the repeated appearance of this character in different groups needs further studies using phylogenetic methods.

Abstract.—Natural history museums house numerous previously undescribed species and unknown information hidden in their collections. We describe lower Carboniferous slit-bearing gastropods (order Pleurotomariida, subclass Vetigastropoda; and family Goniasmatidae, subclass Caenogastropoda) from previously unreported gastropod collections made by Jane Longstaff (Jane Donald), one of the pioneering paleontologists of Paleozoic gastropods in the late nineteenth and early twentieth centuries. The gastropods were collected from the Lower Limestone Formation (Visean, Brigantian) near Dalry, Ayrshire, Scotland. The collection consists largely of microgastropods, many of which are unusually well-preserved including delicate ornament and protoconchs (larval shells). Three new pleurotomariidan species are described—*Biarmeaspira heidelbergerae* new species, *Neilsonia seussae* new species, *Tapinotomaria longstaffae* new species—in addition to seven species belonging to *Borestus* Thomas, 1940, *Stegocoelia* (*Stegocoelia*) Donald, 1889, *Stegocoelia* (*Hypergonia*) Donald, 1892, *Donaldospira* Batten, 1966, and *Platyzona* Knight, 1945. The caenogastropod-type protoconch is documented for the first time in *Hypergonia*, which is therefore placed in Goniasmatidae. The new data confirm that *Neilsonia* Thomas, 1940 (type genus of Neilsoniinae) belongs to Pleurotomariida and is distinct from the morphologically convergent *Peruvispira* Chronic, 1949 (Goniasmatidae). The selenizone morphology is identical in *Biarmeaspira* Mazaev, 2006 and *Baylea* de Koninck, 1883 during their early ontogeny, and *Biarmeaspira* develops an angulation on the selenizone (the diagnostic feature) in late ontogeny. This corroborates earlier suggestions that *Biarmeaspira* evolved from *Baylea*. *Biarmeaspira heidelbergerae* n. sp. is the first Carboniferous record of *Biarmeaspira*, which was previously only known from the Permian. The angulated selenizone evidently evolved several times in Pleurotomariida and the repeated appearance of this character in different groups (e.g., Phymatopleuridae, Eotomariidae, Pleurotomariidae) needs further studies using phylogenetic methods.

UUID: http://zoobank.org/92ae9a99-5774-4ee9-bf5d-9a9319494ef6

*Corresponding author.

Introduction

Jane Longstaff (née Mary Jane Donald) was one of the pioneering specialists on Paleozoic gastropods of the late nineteenth and early twentieth centuries (Creese and Creese, 1994; Wyse Jackson and Spencer Jones, 2007). She is best known for her work on Carboniferous gastropods, especially on Murchisoniidae (Donald, 1889, 1899, 1902, 1906; Longstaff, 1926), Loxonematidae (Donald, 1905a, b; Longstaff, 1909, 1933), Zygopleuridae, and Pleurotomariida (Longstaff, 1912), but also for her taxonomic work on Elizabeth Gray's lower Paleozoic gastropod collection (Longstaff, 1924; Cleevely et al., 1989). Upon her death in 1935, her collections were donated by her nephew M. H. Donald to The Natural History Museum (Cox, 1936). The Longstaff collection from Dalry in The Natural History Museum was noticed during a study on slit-band gastropods (order Pleurotomariida) in the museum's collections. The Longstaff collection studied herein was found in three separate glass vials, each containing dozens of specimens, which had been taxonomically sorted and placed in different drawers according to their systematics.

An early study of the fossiliferous Carboniferous deposits near Dalry (Glencart, Upper Limestone Formation, Namurian) reported an exquisitely preserved, moderately diverse benthic fauna including sponges, bivalves, brachiopods, and gastropods (Young, 1884). Carboniferous gastropods from Dalry (at Glencart and Law) are quite remarkable in composing mainly of small-sized individuals. With their creamy white color, they look more like shells of younger, 'Tertiary' strata (Young, 1884; Donald, 1898). High-spired gastropod taxa including Zygopleuridae and slit-bearing Murchisoniidae (some now classified as Goniasmatidae) were described in a series of papers by Donald (1889, 1898; Longstaff, 1917, 1926, 1933) from the Upper Limestone Formation at Dalry. Some bellerophontids from this site were figured by Weir (1931). Low-spired slit-band gastropods (order Pleurotomariida) from the Upper Limestone Formation at Dalry were previously mentioned (Young, 1884) but only a single taxon, *Baylea parva* (Thomas, 1940), was described in detail (Thomas, 1940). Although several murchisoniids from the Lower Limestone Formation (Visean) at Dalry (Law Quarry) were described (Donald, 1892, 1895, 1898), low-spired slit-band gastropods (order Pleurotomariida) have not been reported. The aim of the present paper is to describe slit-bearing gastropod taxa (Pleurotomariida and Goniasmatidae) in the Longstaff collection from the Visean (lower Carboniferous) of Dalry that have not been studied in detail so far.

The earliest paleontological studies on the Carboniferous slit-bearing gastropods from the United Kingdom were conducted by Phillips (1836, 1841). These early works were followed by comprehensive studies on Carboniferous Goniasmatidae and Murchisonioidea from Ireland, Scotland, and England by Longstaff (Donald, 1885, 1887, 1889, 1892, 1895, 1898; Longstaff, 1912, 1917, 1926, 1933) and Pleurotomariida from Scotland by Thomas (1940). Batten (1966a, b) described a diverse gastropod fauna from the Visean Hotwells Limestone of Somerset (England), which yielded 98 species, 46 of which belonged to the slit-bearing groups. The most recent work on British Carboniferous gastropods was done by Peel (2016), who described a slightly younger (Namurian) gastropod fauna from Cheshire (England) also yielding a substantial proportion of slit-bearing groups (10 of 27 species; Peel, 2016). Pleurotomariida and Goniasmatidae were also major groups in other Carboniferous gastropod faunas (e.g., Belgium: de Koninck, 1883; Russia: Mazaev, 2001, 2002, 2011; Germany: Amler, 2006; Australia: Yoo, 1988, 1994; Morocco: Heidelberger et al., 2009; United States: Thein and Nitecki, 1974; Batten, 1995; Hoare et al., 1997; Kues and Batten, 2001; Karapunar et al., 2022). Herein, we discuss the relationship of the studied slit-bearing gastropod fauna from Dalry to other lower Carboniferous faunas.

Material and methods

The material was collected by Jane Longstaff (Jane Donald) from the Blackhall Limestone Member of the Lower Limestone Formation at Law [Quarry], Dalry, Ayrshire, Scotland. Etheridge (1881, p. 25) noted that "Law Quarry is situated on the Cubeside farm, about 2 miles north-west of Dalry [Ayrshire], and only a few hundred feet from the edge of the great mass of bedded traps [now the Clyde Plateau Volcanic Formation] which stretch from Dalry to Largs." Cubeside Farm is at 55.71994°N, −4.75926°W and Law Hill is a short distance to the east southeast (Fig. 1.2).

This former quarry exposed the Trearne facies (Richey, 1947) of the Blackhall Limestone Member (formerly known in Ayrshire as the Dockra Limestone), Lower Limestone Formation (formerly Lower Limestone Series) of the Clackmannan Group. This member is assigned to the Brigantian substage of the Visean (Monro, 1999; Waters et al., 2007). The stratigraphic position of the Lower Limestone Formation is given in Figure 1. Etheridge (1881, p. 25) described the limestone, which he identified as the Hurlet Limestone, a correlation not accepted now (Monro, 1999), at this site as "12 feet or so in thickness." A revised isopachyte map of the Trearne facies of the Irvine district was given by Monro (1999, fig. 13). The Trearne facies (Richey, 1947) forms an oval west-east oriented carbonate shoal within the widespread and otherwise more argillaceous Lugton carbonate facies, although it was only elevated 1–2 m above the latter sediments and was perhaps partly formed by the baffling action of dense crinoid stands with frequent coral thickets (*Siphonodendron* McCoy, 1849) preventing ingress of terrigenous sediment (Brown, 1977; Monro, 1999). The Blackhall Limestone was deposited during a marine transgression and is apparently the most fossiliferous of the Visean limestones of the surrounding area, with a highly diverse fauna consisting of chaetetid sponges, corals, brachiopods, fenestellid and trepostome bryozoans, crinoid stems, the echinoid *Archaeocidaris* McCoy, 1844, infaunal and epifaunal bivalves, gastropods, and occasional trilobites as well as fish scales and teeth (Monro, 1999, table 13).

Donald (1898, p. 47) stated that "the shells from Law … were obtained from fissures and partings in limestone and shales, where the rock had become rotten in situ through the percolation of surface-water in recent times." Etheridge (1881, p. 25) reported that the limestone "is very hard and compact where solid and unweathered. The bed is highly charged with siliceous matter, as a large percentage of the contained fossils

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

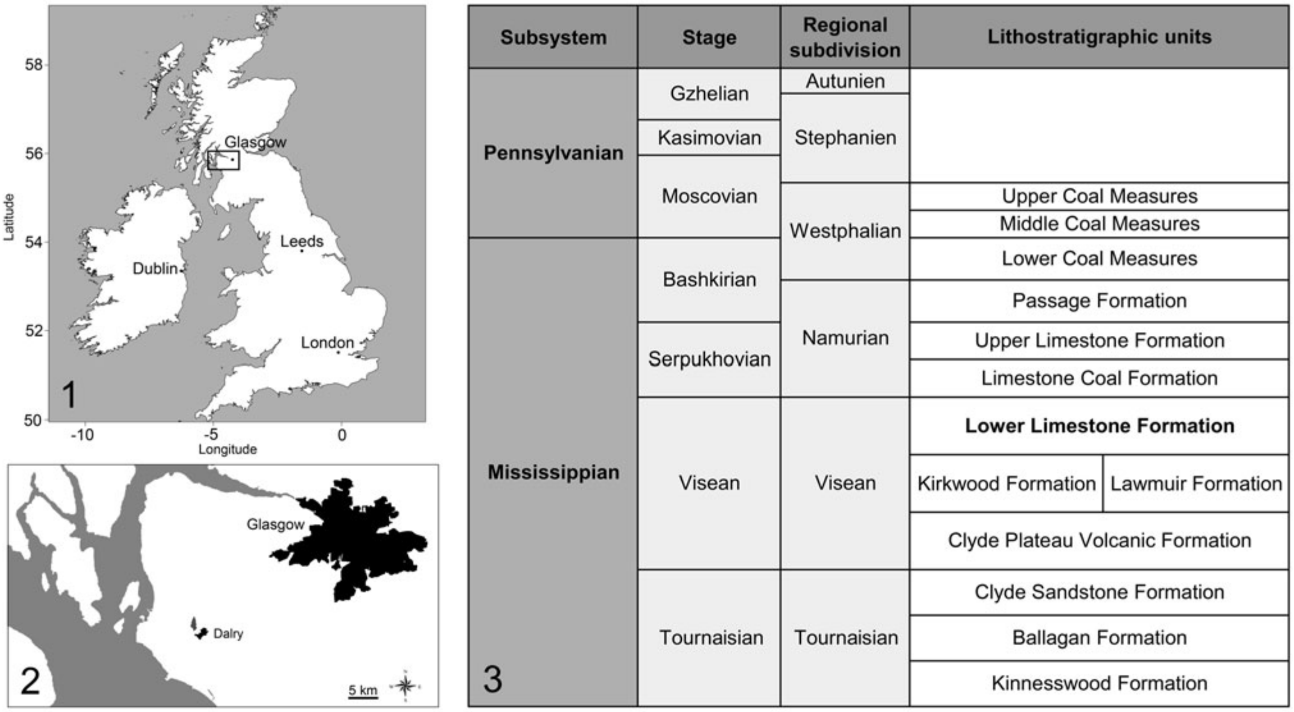

Figure 1. (**1**) Map of the United Kingdom and Ireland. (**2**) Detail of the map, with the location of the collection near Dalry denoted by a gastropod figure. (**3**) Stratigraphic table of the rock units near Dalry (modified from Monro, 1999); the studied specimens come from the Lower Limestone Formation (Visean, Brigantian).

have been changed into some form of silica." Referring to small gastropods, he noted that "The fossils are obtained by washing the disintegrated material found in ledges of the quarry-face and in fissures and pockets made by the natural jointing of the rock." The other lower Carboniferous outcrop at Glencart (55.7097°N, -4.675°W) near Dalry yields similar white-creamy colored fossils that were also recovered from argillaceous and limestone deposits (Young, 1884; Donald, 1898), but these belong to the Upper Limestone Formation (Namurian). The gastropod shells are recrystallized, and testing with dilute acetic acid indicates that they are silicified.

Specimens were photographed with a digital microscope camera after coating them with ammonium chloride (if not stated otherwise). Some specimens were coated with gold for SEM photography.

The higher classification of taxa follows the latest published consensus on gastropod classification (Bouchet et al., 2017) and modifications to it (Karapunar et al., 2022). Terms used in the descriptions follows the terminology given by Cox (1960a). Abbreviations used in descriptions are: L, length; W, width.

Repository and institutional abbreviation.—All specimens are stored in The Natural History Museum, London, England (NHMUK).

Systematic paleontology

Class Gastropoda Cuvier, 1795
Subclass Vetigastropoda Salvini-Plawen, 1980
Order Pleurotomariida Cox and Knight, 1960
Superfamily Eotomarioidea Wenz, 1938
Family Eotomariidae Wenz, 1938
Genus *Biarmeaspira* Mazaev, 2006

Type species.—Biarmeaspira verideclinata Mazaev, 2006; by original designation.

Remarks.—Mazaev (2006) erected the genus *Biarmeaspira* for taxa similar to *Baylea* de Koninck, 1883 that share a similar early ontogenetic shell, surface ornamentation (dominant spiral ornament), growth line on ramp (opisthocyrt subsuturally then prosocyrt), and whorl profile but with an angulated selenizone (Mazaev, 2006, 2015, 2016, 2017; Karapunar et al., 2022). The *Biarmeaspira* spp. from the Permian of Russia more closely resemble *Baylea* spp. deposited in the same basins (Mazaev, 2006, 2015, 2016, 2017) than *Biarmeaspira heidelbergerae* new species. With its surface ornament, *Biarmeaspira heidelbergerae* n. sp. has a close affinity to the Carboniferous species *Baylea yvanii* Léveillé, 1835 (the type species of *Baylea*; Kase, 1988, fig. 3.1, 3.6–3.9; Lindström and Peel, 2005, fig. 1A) and especially to *Baylea leveillei* de Koninck, 1883 (Fig. 2; Amler, 2006, fig. 1i, j). *Baylea leveillei* might have given rise to *Biarmeaspira heidelbergerae* n. sp. There is a possibility that different *Baylea* lineages gave rise to an angulated selenizone multiple times during their evolutionary history.

The early ontogenetic development of the type species, *Biarmeaspira verideclinata*, was well documented (Mazaev, 2006, pl. 4). Similar to *Biarmeaspira heidelbergerae* n. sp.,

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

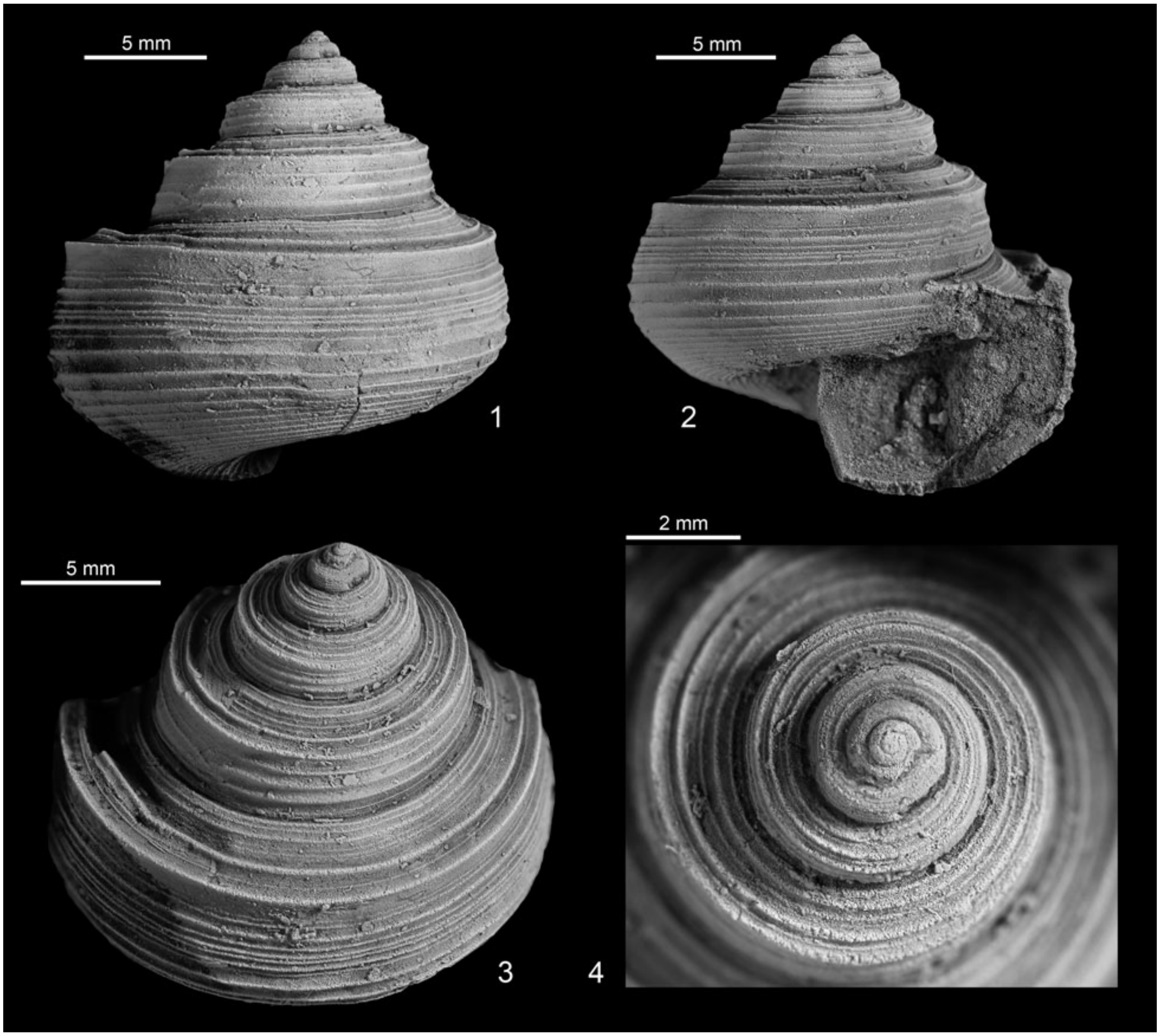

Figure 2. *Baylea leveillei* de Koninck, 1883, Tournaisian, Tournai, Belgium, NHMUK PI G 18629.

Biarmeaspira veridéclinata has a concave selenizone in early ontogeny, the abapical edge of the selenizone represents the whorl angulation, and it develops an angulation within the selenizone in later ontogenetic stages. However, the *Biarmeaspira* spp. later included by Mazaev (2015), e.g., *Biarmeaspira striata* Mazaev, 2015, develop a whorl angulation before the appearance of the selenizone, and the selenizone appears on the whorl angulation, hence these species have an angulated selenizone from its first appearance onward. These *Biarmeaspira* spp. (Mazaev, 2015) are distinctly different from *Baylea* spp. in their early ontogenetic development and resemble the early ontogenetic development of *Lineacingulum* Karapunar and Nützel, 2021, *Sisenna* Koken, 1896, and *Nodocingulum* Karapunar and Nützel, 2021 (see Karapunar and Nützel, 2021 for early ontogenetic development of these genera). Hence, *Biarmeaspira* might be polyphyletic in its current composition.

Biarmeaspira heidelbergerae new species
Figures 3, 4

Holotype.—NHMUK PI PG 10235; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Paratypes.—Four paratypes, NHMUK PI PG 10236–10239; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Diagnosis.—Shell small to medium in size, wortheniform, with gradate profile, with smooth, low-spired early whorls. Pleural angle 90–95°. Later whorls ornamented with spiral cords of various strength; number of cords increasing gradually through ontogeny. Selenizone appearing on third whorl, high on whorl face. Selenizone concave in early ontogeny, developing a median cord, which turns into whorl angulation in later ontogeny. Ramp gently sloping, with almost horizontal subsutural shoulder; ramp concave between subsutural shoulder and selenizone. Lower whorl face slightly concave, subparallel to axis. Transition to base rounded. Base convex, narrowly phaneromphalous, ornamented with spiral cords.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

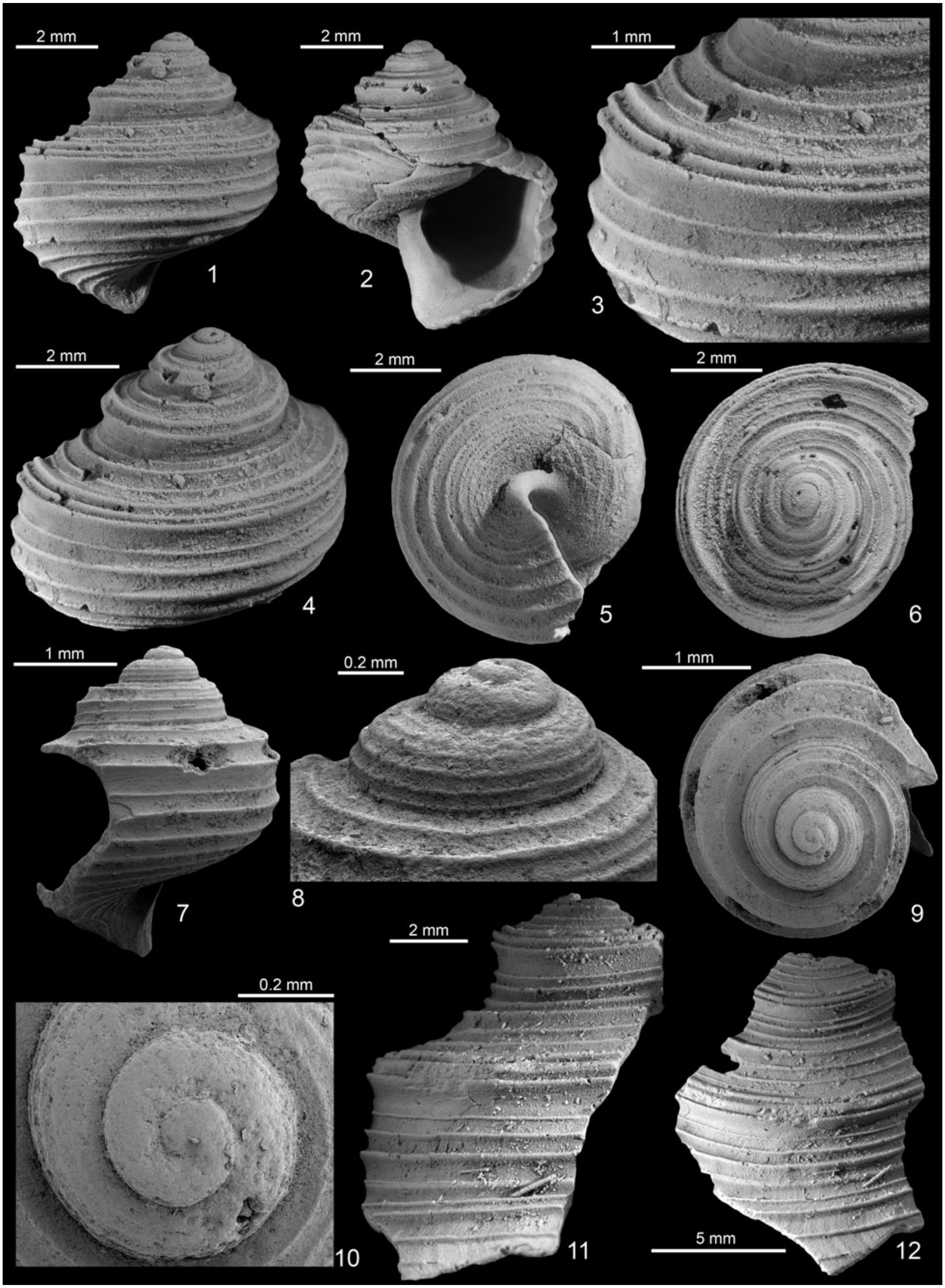

Figure 3. *Biarmeaspira heidelbergerae* n. sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean). (**1–6**) Holotype, NHMUK PI PG 10235. (**7–10**) Paratype, NHMUK PI PG 10236. (**11, 12**) Fragment of the largest specimen in the collection, NHMUK PI PG 10241.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

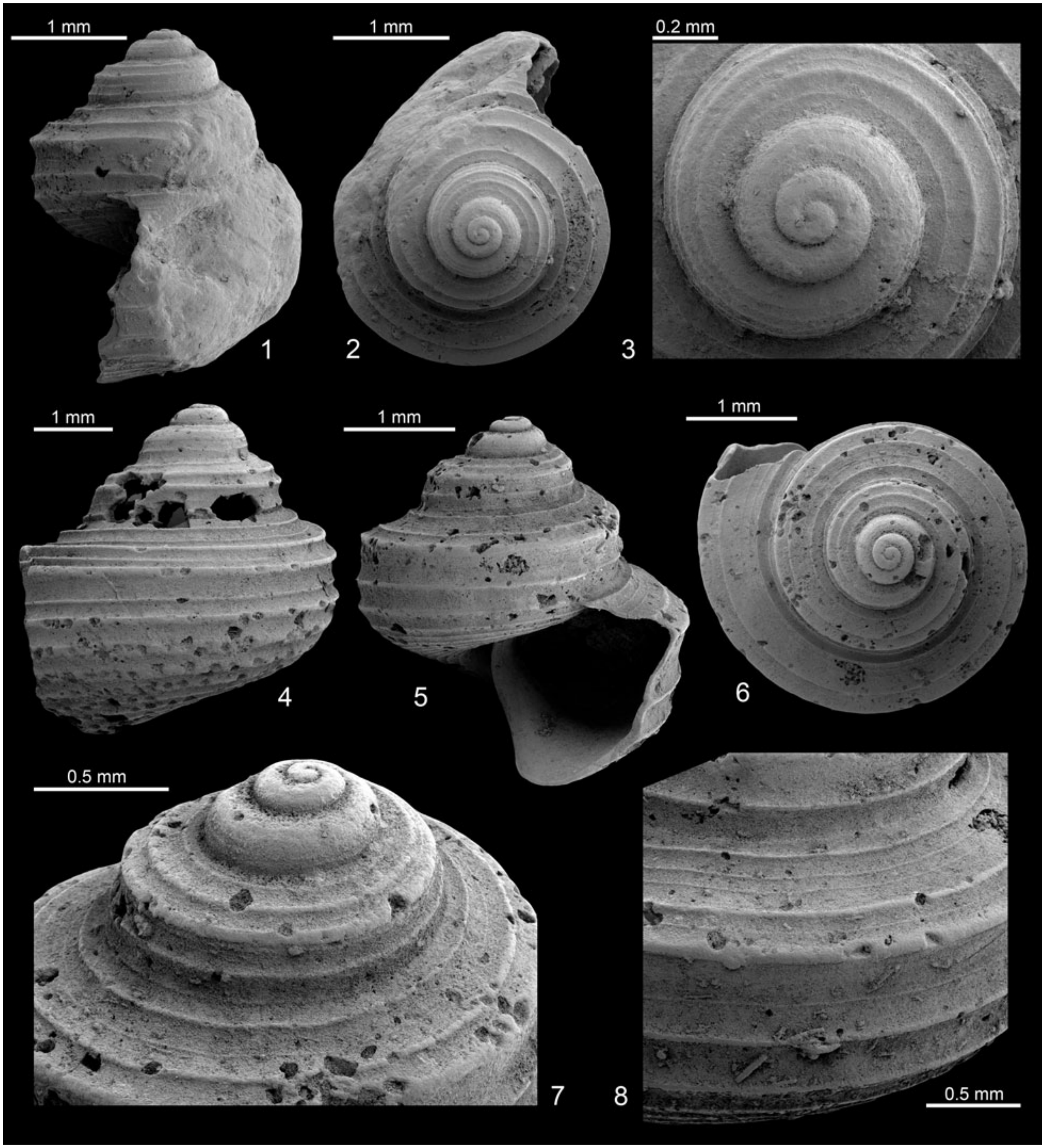

Figure 4. *Biarmeaspira heidelbergerae* n. sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), paratypes. (**1–3**) NHMUK PI PG 10237. (**4**) NHMUK PI PG 10239. (**5–8**) NHMUK PI PG 10238.

Occurrence.—Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Description.—Shell small to medium in size, approximately as high as wide (holotype H: 6.8 mm, W: 6.5 mm), wortheniform, with gradate profile; holotype with six whorls; largest fragment suggests that it could reach eight whorls (Fig. 3). First whorl W: 0.26 mm. First one and one-half whorls smooth, convex, very low-spired, trochospirally coiled. Second and third whorls convex, ornamented with up to six spiral cords of approximately equal strength. Selenizone appears on third whorl, high on whorl face. Whorl face of later whorls ornamented with spiral cords of various strengths; number of cords gradually increasing through ontogeny, with new spiral cords appearing weak between the lowermost cord on ramp and selenizone, gradually increasing in strength. Interspace between spiral cords wide, concave. Sixth whorl of holotype with two strong and one weaker spiral cord each, on ramp and on lateral whorl face. The largest fragment (of likely the seventh whorl) with three strong and one weak spiral cord on ramp and on lateral whorl face. Ramp gently sloping, almost horizontal at subsutural shoulder, which is formed by the adapical strong spiral cord, concave between subsutural shoulder and selenizone. Selenizone concave on early whorls, inclining, situated on whorl angulation, bordered by two strong spiral cords. Selenizone with distinct median spiral cord on later whorls, which turns into an angulation. Lower whorl face slightly concave, subparallel to axis, ornamented like upper whorl face, with suture situated on the lowermost spiral cord of lateral whorl face. Transition to base rounded. Base convex, narrowly phaneromphalous, ornamented with spiral cords, which decrease in strength toward umbilicus. Outer lip angulated; basal and inner lip convex.

Etymology.—Named after paleontologist Doris Heidelberger, for her work on Devonian gastropods.

Other material.—19 specimens, some fragmentary, NHMUK PI PG 419(1–17), PI PG 10240, PI PG 10241 [shell fragment]; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

LSID.—urn:lsid:zoobank.org: act:984272B9-9554-49F8-BB4F-A0914EF6BF33.

Remarks.—The present species closely resembles *Baylea yvanii* and *Baylea leveillei* in whorl ornamentation. *Baylea yvanii* is distinctly higher spired, with more spiral cords and without a median cord on its selenizone (Lindström and Peel, 2005, fig. 1A). *Baylea leveillei* differs in having more spiral cords, both in early and late ontogeny, and the median cord on its selenizone does not turn into an angulation in late ontogeny (Fig. 2). *Baylea parva* (Thomas, 1940) from the Upper Limestone Formation (Namurian) at Dalry is higher spired with more convex early whorls and a more inclined ramp.

Subfamily Neilsoniinae Knight, 1956

Genus *Neilsonia* Thomas, 1940

Type species.—*Neilsonia roscobiensis* Thomas, 1940; by original designation.

Remarks.—*Neilsonia* and *Peruvispira* Chronic, 1949 were considered to be closely related taxa and placed within Neilsoniinae (Knight et al., 1960). *Neilsonia* was differentiated from *Peruvispira* by having a distinct axial ornament toward the adapical suture forming subsutural nodes (e.g., Knight et al., 1960). As previously discussed by Karapunar et al. (2022), similar ornamentation can be seen in members of *Peruvispira* (e.g., *Peruvispira oklahomaensis* Karapunar and Nützel in Karapunar et al., 2022). Accordingly, the only distinction between the two genera is the relatively lower position of the selenizone in *Neilsonia*. Additionally, the lunulae are much more widely spaced and stronger in *Neilsonia* compared to the closely spaced fine lunulae of *Peruvispira*. Karapunar et al. (2022) documented a protoconch reflecting planktotrophic larval development in *Peruvispira* and removed *Peruvispira* from the vetigastropod subfamily Neilsoniinae and placed it in the caenogastropod family Goniasmatidae. The protoconch-teleoconch boundary of *Neilsonia seussae* new species is not well demarked nor can be obscured by preservation but *Neilsonia seussae* n. sp. has a larger initial whorl (0.28 mm) similar to nonplanktotrophic pleurotomariids (e.g., 0.33–0.36 mm: *Worthenia tabulata* Conrad, 1835; 0.28 mm: *Paragoniozona yanceyi* Karapunar and Nützel in Karapunar et al., 2022) and unlike the goniasmatid *Peruvispira* (first whorl diameter 0.19 mm: *Peruvispira oklahomaensis*; 0.15 mm: *Peruvispira* sp. of Karapunar et al., 2022). The large initial whorl supports the placement of *Neilsonia* within Pleurotomariida.

Neilsonia seussae new species

Figures 5, 6

Holotype.—NHMUK PI PG 10242; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Paratypes.—Five paratypes, NHMUK PI PG 10243–10247; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Diagnosis.—Shell small, conical, higher than wide. Pleural angle 50–60°. First two whorls rounded, smooth, low-trochospirally coiled. Selenizone appearing at midwhorl, shifting toward abapical suture on later whorls. Whorl face convex on early whorls and flat on later whorls. Whorl face above selenizone slightly convex to flat, steeply inclining, ornamented with equally and widely spaced prosocline/prosocyrt axial ribs; ribs strongly curving backward near selenizone. Selenizone concave, broad (one-quarter of whorl face), steeply inclining, situated low on whorl face somewhat above suture, with equally spaced lunulae. Lower whorl face narrow, concave, with fine axial riblets. Transition to base with angulation. Suture incised. Base flat, narrowly phaneromphalous, with sinuous radial riblets. Aperture subquadrate.

Occurrence.—Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Description.—Shell small, conical, higher than wide (holotype H: 4.4 mm, W: 3.7 mm), up to seven whorls; initial whorl W: 0.28 mm. First two whorls rounded, smooth, low-trochospirally coiled; two spiral cords appearing within third whorl, representing selenizone borders. Selenizone situated at midwhorl when it first appears, shifting toward abapical suture on later whorls. Whorl face convex on early whorls and flat on later whorls. Whorl face above selenizone slightly convex to flat, steeply inclining, ornamented with equally and widely spaced prosocline/prosocyrt axial ribs; ribs strongly curving backward near selenizone. Selenizone borders projecting; lower border more protruding so that the selenizone is steeply inclining. Selenizone concave, broad (one-quarter of whorl face), situated low on whorl face somewhat above suture, with equally spaced lunulae. Lower whorl face (below selenizone) narrow, concave, with fine axial riblets. Transition to base with angulation. Suture incised; base

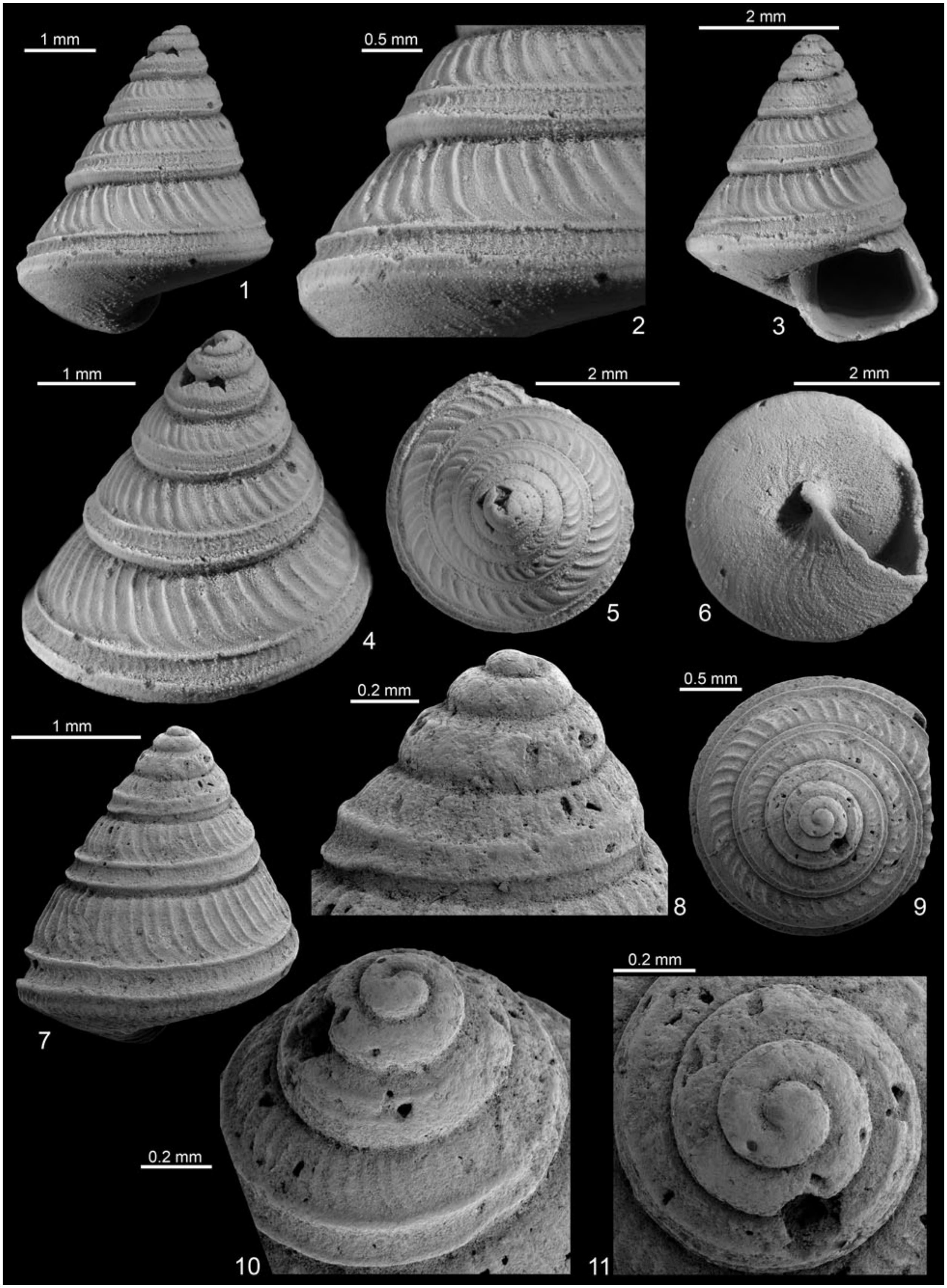

Figure 5. *Neilsonia seussae* n. sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean). (**1–6**) Holotype, NHMUK PI PG 10242. (**7–11**) Paratype, NHMUK PI PG 10243.

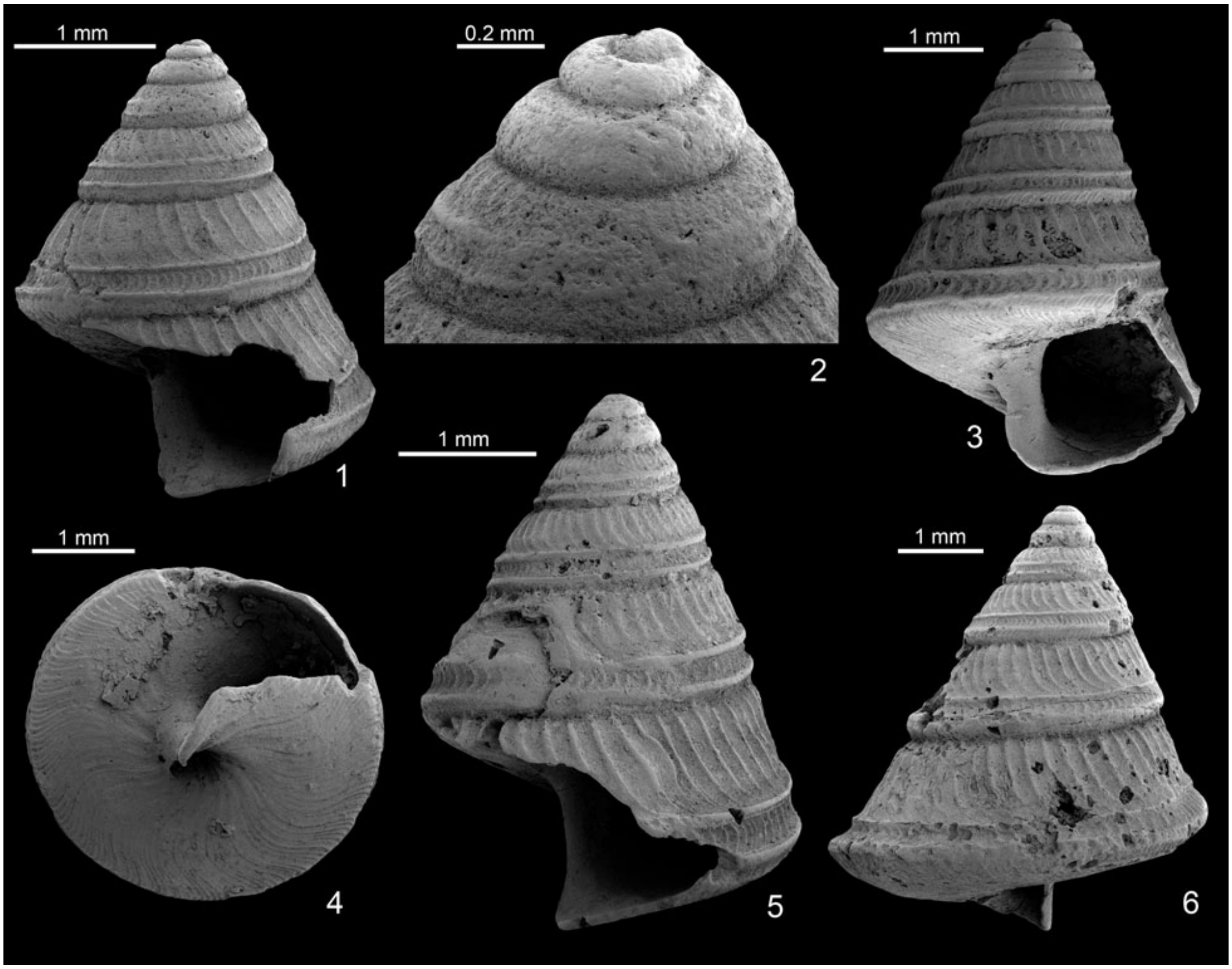

Figure 6. *Neilsonia seussae* n. sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), paratypes. (**1, 2**) NHMUK PI PG 10244. (**3, 4**) NHMUK PI PG 10245. (**5**) NHMUK PI PG 10247. (**6**) NHMUK PI PG 10246.

flat, narrowly phaneromphalous, with sinuous radial riblets (strengthened growth lines), concave near periphery, convex near umbilicus. Aperture subquadrate, with flat outer lip, flat basal lip, and convex inner lip.

Etymology.—Named after paleontologist Barbara Seuss, for her work on the Carboniferous faunas.

Other material.—18 specimens, NHMUK PI PG 412(1–18), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

LSID.—urn:lsid:zoobank.org:
act:97E2E5F2-9F4B-44E8-8B67-F93EF80D402A.

Remarks.—*Neilsonia seussae* n. sp. closely resembles *Neilsonia roscobiensis* Thomas, 1940 and *Neilsonia acuminata* Thomas, 1940 in position of selenizone and ornamentation of whorls and selenizone. *Neilsonia roscobiensis* differs in having a convex whorl face throughout ontogeny, its axial ribs fading toward the selenizone, and its selenizone being almost parallel to the axis. *Neilsonia acuminata* has a similarly flat whorl face but differs in the orientation of its selenizone, which faces abapically, and its adapical selenizone border represents the whorl periphery. *Pleurotomaria galaeottiana* de Koninck, 1844 (p. 396, pl. 35, fig. 3) from the Visean of Belgium resembles *Neilsonia seussae* n. sp. in shell and whorl morphology, ornamentation, and position of the selenizone but its selenizone is narrower according to the illustrations. The type material of *Pleurotomaria galaeottiana* needs better documentation.

As mentioned in the Remarks on *Neilsonia*, *Neilsonia* and *Peruvispira* were once considered closely related and the ornamentation pattern was used to differentiate the members of the taxa. Karapunar et al. (2022) discussed the presence of similar ornamentation in the members of both genera and suggested using the relatively lower position of the selenizone in *Neilsonia* for differentiation. Therefore, they transferred many species previously regarded as *Neilsonia* to *Peruvispira*: *Peruvispira coatesi* (Peel, 2016), *Peruvispira ganneyica* (Peel, 2016), *Peruvispira invisitata* (Hoare, Sturgeon, and Anderson, 1997), and *Peruvispira welleri* (Thein and Nitecki, 1974). In addition to their higher-positioned selenizone, these four taxa have fine and closely spaced lunulae (a character shared by the type species of *Peruvispira*). These taxa also further differ from *Neilsonia seussae* n. sp. in whorl profile and ornament pattern.

Family Phymatopleuridae Batten, 1956
Genus *Tapinotomaria* Batten, 1956

Type species.—*Tapinotomaria rugosa* Batten, 1956; by original designation.

Remarks.—Due to the morphology and ornamentation of the whorl face, selenizone ornamentation, and position of the selenizone, Karapunar et al. (2022, p. 38) placed *Tapinotomaria* in Phymatopleuridae. The early ontogeny of *Tapinotomaria* has been hitherto unknown. *Tapinotomaria longstaffae* new species has planispirally coiled early whorls. Its selenizone appears at midwhorl and shifts abapically during ontogeny. The position of selenizone on early whorls further corroborates the close relationship of *Tapinotomaria* to other phymatopleurids.

Tapinotomaria longstaffae new species
Figures 7, 8

Holotype.—NHMUK PI PG 10248; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Paratypes.—Six paratypes, NHMUK PI PG 10249–10254; Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Diagnosis.—Shell small, conical. Pleural angle 45–55°. First two whorls rounded, smooth, planispirally coiled; later whorls with spiral cords; selenizone appears within third whorl, high on whorl face, quickly shifting abapically and positioned just above suture from fourth whorl onward. Ramp slightly convex on early whorls, becoming flat, steeply inclining on last whorl. Whorl face ornamented with three or four spiral cords and axial ribs, forming a reticulate pattern; axial ribs orthocline on adapical portion of whorl face where spiral cords are present; axial ribs becoming prosocline above selenizone. Adapical border of selenizone represents whorl angulation and periphery. Selenizone strongly concave, with a median cord on early teleoconch whorls, which disappears gradually; selenizone with widely spaced, sharp lunulae; lower border of selenizone representing an angulation and transition to base. Base slightly convex, phaneromphalous, ornamented with spiral cords and sinuous radial growth lines. Aperture subcircular.

Occurrence.—Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Description.—Shell small (holotype H: 3.2 mm, W: 2.9 mm), conical, with up to five and one-half whorls. Initial whorl W: 0.23 mm; first two whorls rounded, smooth, planispirally coiled, with only slightly elevated initial whorl; spiral cord appearing on midwhorl face at end of second whorl; additional spiral cords appearing at two and one-half whorls; selenizone appearing within third whorl, high on whorl face, quickly shifting abapically and positioned just above suture from fourth whorl onward. Ramp slightly convex on fourth whorl, flat, steeply inclining on last whorl, ornamented with three to four spiral cords and axial ribs, forming a reticulate pattern. Axial ribs orthocline on adapical portion of whorl face where spiral cords are present; axial ribs becoming prosocline above selenizone; adapical border of selenizone representing whorl angulation and periphery. Selenizone strongly concave, with median cord on early teleoconch whorls, which disappears gradually; selenizone with widely spaced, sharp lunulae; lower border of selenizone representing an angulation and transition to base. Base slightly convex, phaneromphalous, ornamented with spiral cords and sinuous radial growth lines, convex near periphery, concave near umbilicus. Aperture subcircular, with rounded outer lip, convex basal lip, and rounded inner lip.

Etymology.—Named after paleontologist Mary Jane Longstaff (née Jane Donald), for her contributions to Paleozoic gastropod paleontology.

Other material.—A total of 90 specimens, NHMUK PI PG 411 (1–90), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

LSID.—urn:lsid:zoobank.org:
act:45795250-8771-430C-A1D0-54BA389888EA.

Remarks.—Among the members of *Tapinotomaria*, *Tapinotomaria rugosa* (figured by Batten, 1958) and *Tapinotomaria globosa* Batten, 1958 from the Permian of the USA resemble *Tapinotomaria longstaffae* n. sp. most closely in principal ornament. However, both taxa have one or more additional spiral cords on the ramp. The axial ribs of these Permian species are completely prosocline between the adapical suture and selenizone and thus lack an orthocline portion. The orthocline ribs on the upper whorl portion are a diagnostic feature of *Tapinotomaria longstaffae* n. sp., differentiating it from other known *Tapinotomaria* spp. *Murchisonia sulcata* McCoy, 1844 from the Carboniferous of Ireland resembles *Tapinotomaria longstaffae* n. sp. in the position of the selenizone and presence of spiral cords. However, growth lines and lunulae were not described for *M. sulcata*; hence, its generic identity is unclear and whether it is conspecific with *Tapinotomaria longstaffae* n. sp. cannot be evaluated.

Genus *Borestus* Thomas, 1940

Type species.—*Borestus wrighti* Thomas, 1940; by original designation.

Borestus similis? (de Koninck, 1883)
Figure 9

?1883 *Ptychomphalus similis* de Koninck, p. 53, pl. 25, figs. 4–6.
?1883 *Ptychomphalus suavis* de Koninck, p. 57, pl. 30, figs. 39–42.
1966a *Borestus similis*; Batten, p. 49, pl. 5, fig. 18.

Holotype.—According to Batten (1966a, p. 49) “in the de Koninck collection at the Institut Royal des Sciences Naturelles, Brussels,” type locality Visé, Belgium, type age Visean.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

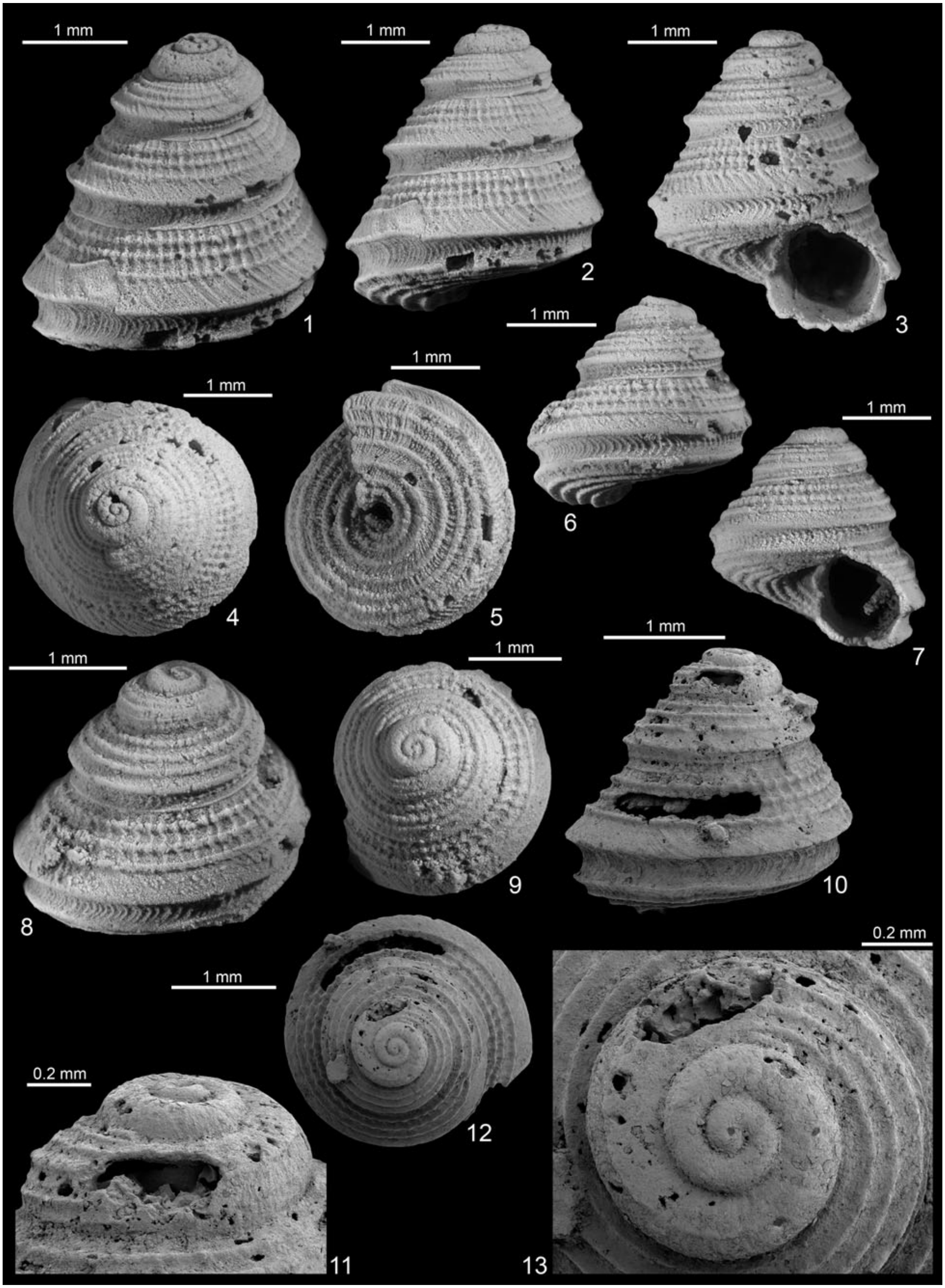

Figure 7. *Tapinotomaria longstaffae* n. sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean). (**1–5**) Holotype, NHMUK PI PG 10248. (**6–9**) Paratype, NHMUK PI PG 10249. (**10–13**) Paratype, NHMUK PI PG 10250.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

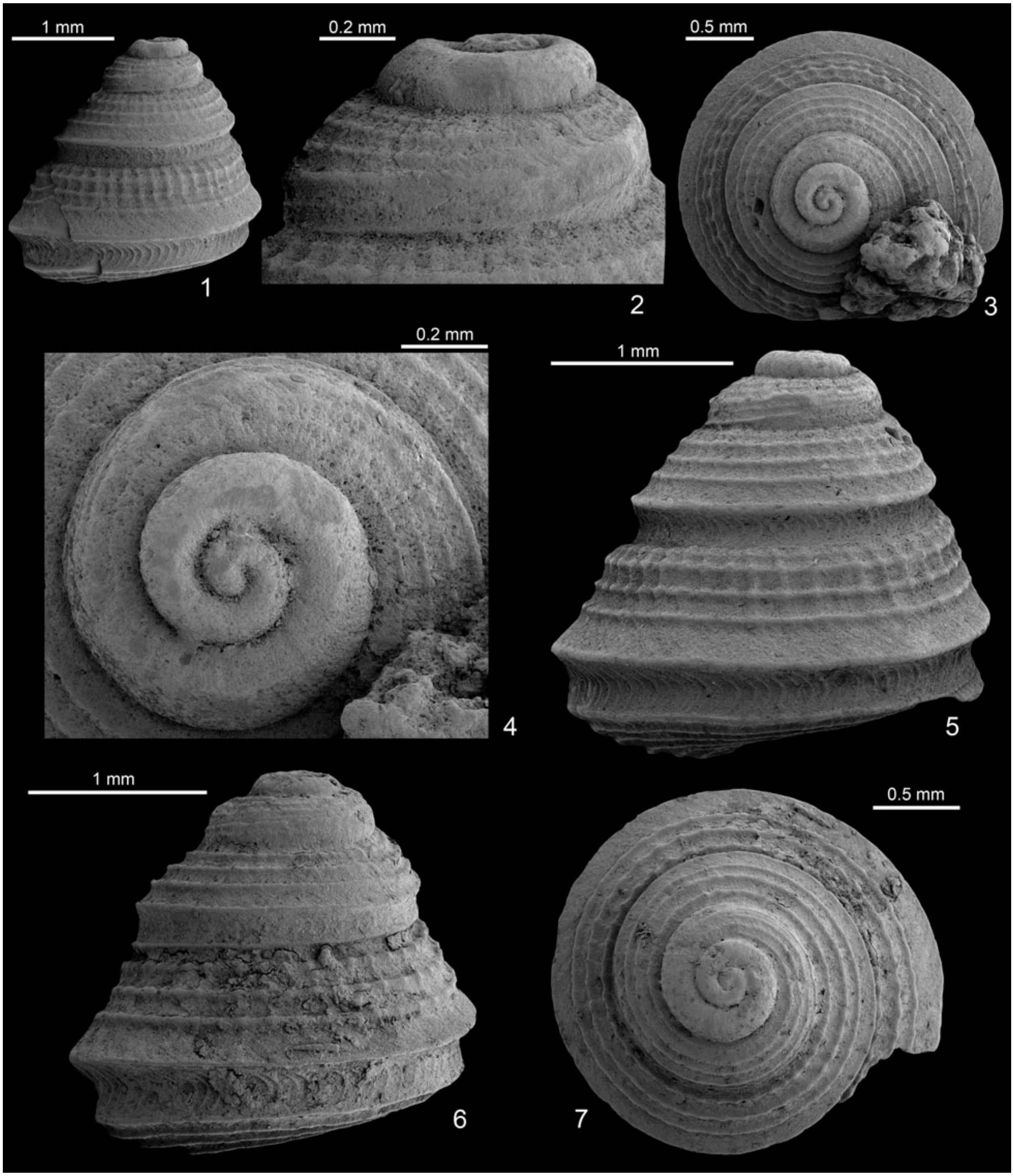

Figure 8. *Tapinotomaria longstaffae* n. sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), paratypes. (**1–5**) NHMUK PI PG 10251. (**6, 7**) NHMUK PI PG 10252.

Description.—Shell small, wortheniform, with six whorls; spire gradate. Pleural angle 67°. Initial whorl W: 0.28 mm; first two whorls convex, smooth, low-trochospirally coiled; spiral cords appearing on third whorl. Ramp sloping at ∼44°, slightly concave, with subsutural spiral cord and orthocline axial ribs, and nodes at intersections; faint second spiral cord below subsutural cord present on the last quarter of the last whorl; transition to lateral whorl face with pronounced median whorl angulation. Lateral whorl face slightly concave, parallel to shell axis, with selenizone situated at midheight, ornamented with prosocyrt axial ribs above and below selenizone. Selenizone flat, sunken, with regularly spaced sharp lunulae, bordered by two slightly projecting spiral cords. Transition to base with angulation. Base with reticulate ornament of radial riblets and spiral cords; radial riblets sinusoidal, opisthocyrt near angulation, prosocyrt near umbilicus; base anomphalous.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

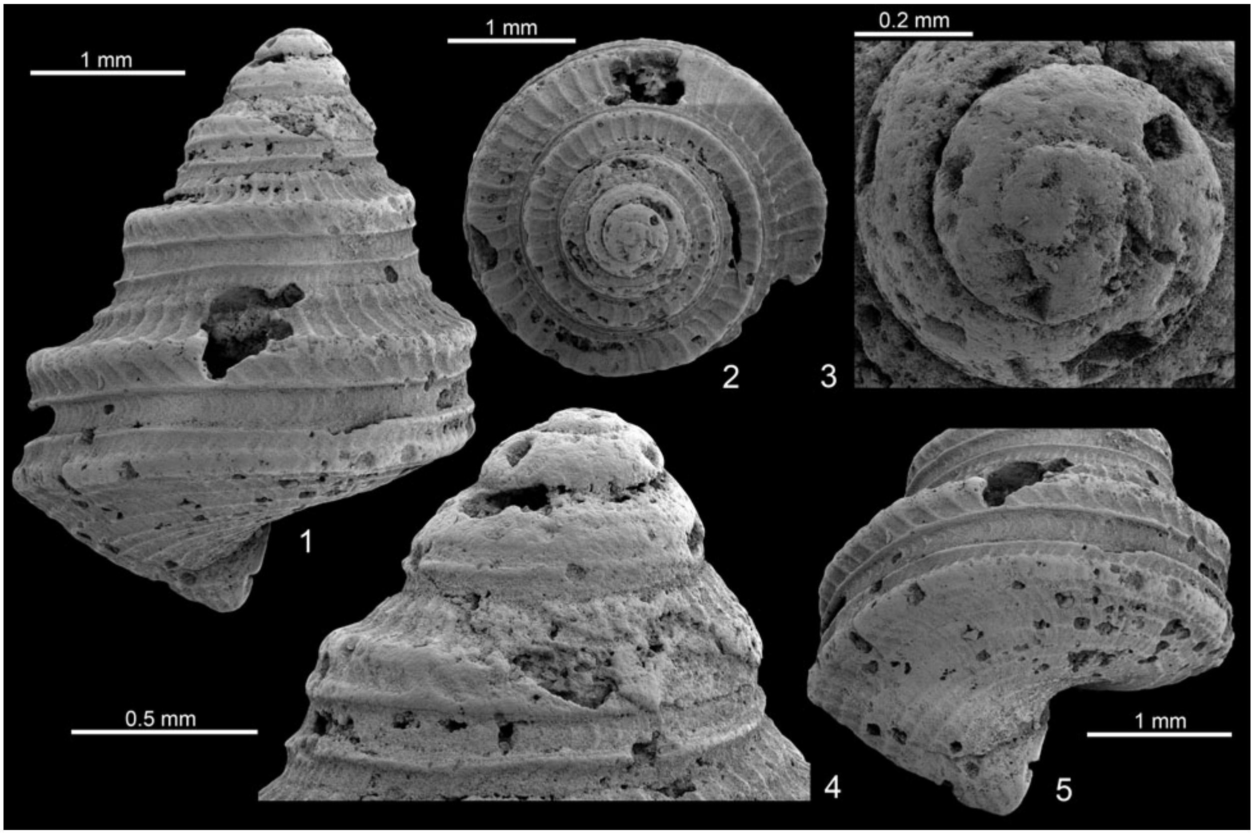

Figure 9. *Borestus similis*? (de Koninck, 1883) Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), NHMUK PI PG 10255.

Aperture subquadrate with straight inner lip, slightly convex basal lip, and angular outer lip.

Material.—A total of three specimens, NHMUK PI PG 10255, PI PG 10256(1–2); Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—*Borestus pagoda* (Newell, 1935) from the Pennsylvanian of the USA (Karapunar et al., 2022), *Borestus procerus* Thomas, 1940, and *Borestus wrighti* Thomas, 1940 from the Carboniferous of Scotland each have several spiral cords on the ramp whereas the present specimen has only one or two. *Borestus magdalenensis* Batten, 1995 from the Pennsylvanian of the USA is similar in having a subsutural spiral cord but lacks conspicuous axial ribs. *Borestus similis*, as figured by Batten (1966a, pl. 5, fig. 18) has one subsutural cord on early whorls and develops a second one on later whorls. The present specimens at hand have a faint second spiral cord on the last quarter of the last whorl and are probably also juvenile and conspecific with the specimens assigned to *Borestus similis* by Batten (1966a). According to Batten (1966a), *Borestus similis* develops two to four spiral cords and *Borestus suavis* (de Koninck, 1883) and *Borestus similis* are synonyms. Original drawings of these two species suggest that both species have a more steeply inclining ramp and develop more prominent spiral cords, therefore, the identification of our material is tentative.

Subclass Caenogastropoda Cox, 1960
Superfamily Orthonematoidea Nützel and Bandel, 2000

Family Goniasmatidae Nützel and Bandel, 2000
Genus *Stegocoelia* Donald, 1889
Subgenus *Stegocoelia* Donald, 1889

Type species.—*Murchisonia* (*Stegocoelia*) *compacta* Donald, 1889; by original designation.

Stegocoelia (*Stegocoelia*) *compacta* (Donald, 1889)
Figure 10

*1889 *Murchisonia* (*Stegocoelia*) *compacta* Donald, p. 624, pl. 20, figs. 9–13.
1926 *Hypergonia compacta*; Longstaff, p. 543, pl. 35, fig. 11.
1941 *Stegocoelia compacta*; Knight, p. 334, pl. 44, fig. 6a–e.
1966b *Stegocoelia* (*Stegocoelia*) *compacta*; Batten, p. 82, pl. 8, figs. 21, 22.

Lectotype.—NHMUK PI PG 122, lectotype (original of Donald, 1889, pl. 20, fig. 9; Knight, 1941, pl. 44, fig. 6b) subsequently designated by Longstaff (1926) and stored in NHMUK (Fig. 10A). Type locality Glencart, Dalry, Ayrshire, Scotland; type strata Upper Limestone Formation, type age Namurian. See Knight (1941) for further information on the types.

Paralectotypes.—A total of four specimens, NHMUK PI PG 123, paralectotype (original of Knight, 1941, pl. 44, fig. 6b); NHMUK PI PG 124–126, three paralectotypes from Upper Limestone Formation (Namurian), Glencart, Dalry, Ayrshire, Scotland.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

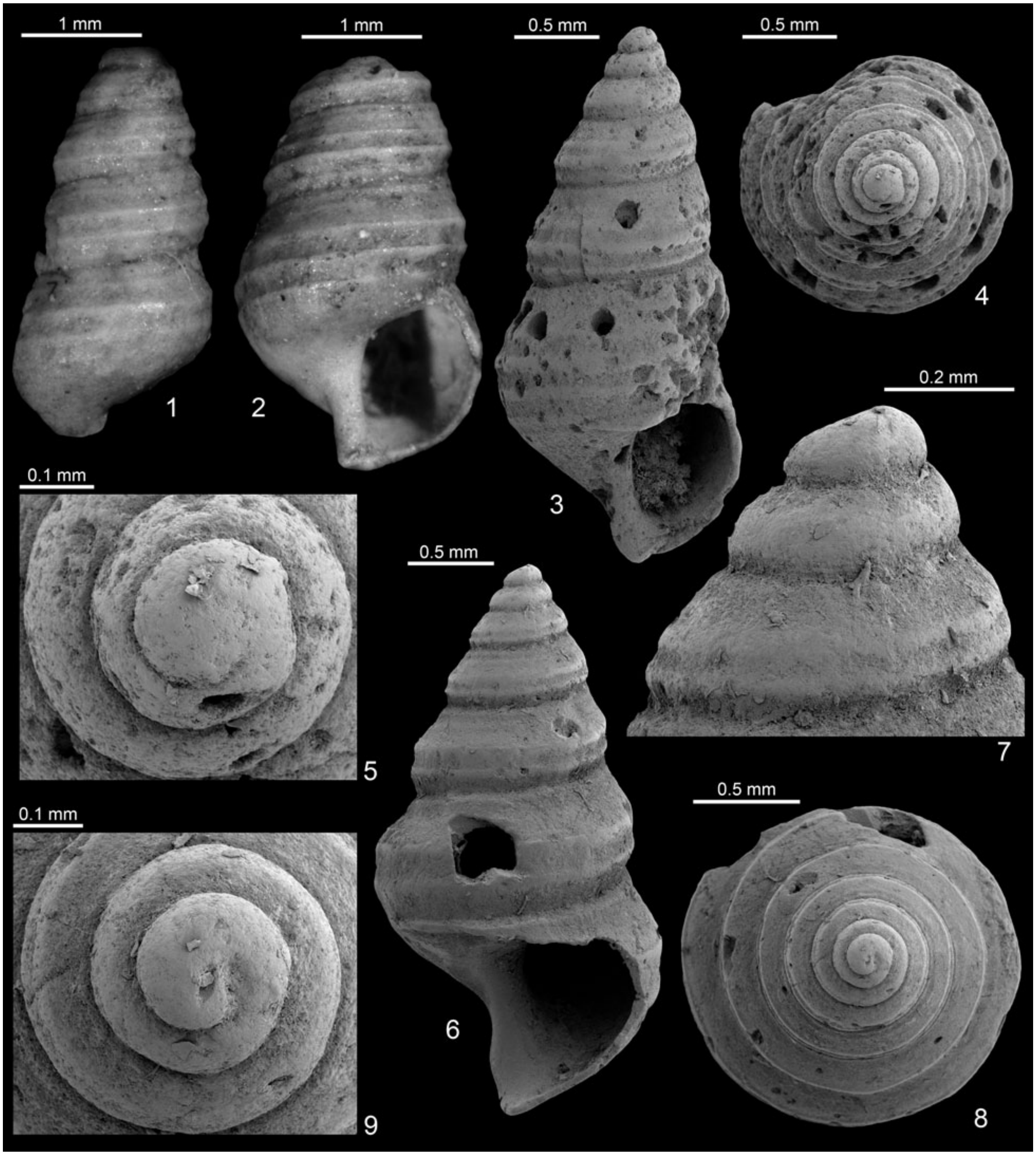

Figure 10. *Stegocoelia* (*Stegocoelia*) *compacta* (Donald, 1889). (**1**) Lectotype designated by Longstaff (1926) (original of Donald, 1889, pl. 20, fig. 9; Knight, 1941, pl. 44, fig. 6b), Glencart, Dalry, Ayrshire, Scotland; Upper Limestone Group (Namurian), NHMUK PI PG 122. (**2**) Paralectotype (original of Knight, 1941, pl. 44, fig. 6b), Glencart, Dalry, Ayrshire, Scotland; Upper Limestone Group (Namurian), NHMUK PI PG 123. (**3–5**) NHMUK PI PG 10258, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean). (**6–9**) NHMUK PI PG 10259, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean).

Description.—Shell high-spired, very small, cerithiform, with pleural angle of 40°. Early whorls including protoconch orthostrophic, smooth, convex, consisting of 1.5–2.0 whorls; initial whorl W: 0.24–0.28 mm; protoconch/teleoconch transition unclear, with spiral cords of teleoconch appearing on third whorl. Whorl face rounded, convex in profile. Teleoconch with five to six whorls; first teleoconch whorl with two spiral cords, later whorls ornamented with five spiral cords: one subsutural cord, two cords at selenizone borders that are situated above periphery, and two below selenizone; third and fourth cords are most prominent; lowermost cord (fifth) occasionally covered by subsequent whorl; third cord (abapical border of selenizone) representing the midwhorl of spire whorls. Base anomphalous (minutely phaneromphalous in early stages, see Knight, 1941), slightly convex, facing abapically. Inner lip straight to slightly convex. Aperture subovate, slightly higher than wide.

Other material.—Two specimens, PI PG 10258–10259, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—Knight (1941) gave an exhaustive description and discussion of this species. The protoconch/teleoconch transition is unclear due to preservation. The relatively large diameter of the first whorl indicates non-planktotrophic larval development for this species (compare with the better preserved *Stegocoelia* species reported by Bandel et al. [2002] from the Pennsylvanian Buckhorn Asphalt deposit from Oklahoma, USA).

Stegocoelia (*Stegocoelia*) sp. A
Figure 11

Description.—Shell high-spired, slender, small (~7 whorls, H: 2.7 mm, W:1.1 mm), with pleural angle of 20°. Protoconch orthostrophic, smooth, convex, consisting of one and one-half whorls, terminating abruptly; diameter of initial whorl 0.28 mm. Whorls convex in profile; teleoconch with six preserved whorls; first teleoconch whorl with two spiral cords, uppermost representing the abapical selenizone border in later ontogeny; whorl face ornamented with four distinct spiral cords from second whorl onward. Whorl face between adapical suture and selenizone short, slightly convex. Selenizone concave, situated between the uppermost two cords (first and second cords) high on whorl face; second and third cords most prominent, separated by concave interspace; third cord representing periphery; suture just below the fourth cord.

Material.—A single specimen, NHMUK PI PG 10260, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—*Stegocoelia* (*Stegocoelia*) sp. A resembles *Stegocoelia* (*Stegocoelia*) *compacta,* but it lacks the subsutural cord between suture and selenizone and is distinctly more slender. As in *Stegocoelia* (*Stegocoelia*) *compacta* discussed above, the paucispiral and the relatively large diameter of the first whorl indicate nonplanktotrophic larval development for this species, which we retain in open nomenclature pending discovery of further specimens. *Stegocoelia* sp. indet. reported by Peel (2016) from the Namurian of Cheshire has four closely spaced spiral cords below the selenizone, unlike *Stegocoelia* (*Stegocoelia*) sp. A, which has only two spiral cords below its selenizone. As already discussed by Peel (2016), the specimens assigned to *Stegocoelia* sp. indet. by him resembles *Donaldina* sp. indet. from the same assemblage.

Stegocoelia (*Stegocoelia*) cf. *Stegocoelia* (*Stegocoelia*) *cincta* (Donald, 1895)
Figure 12

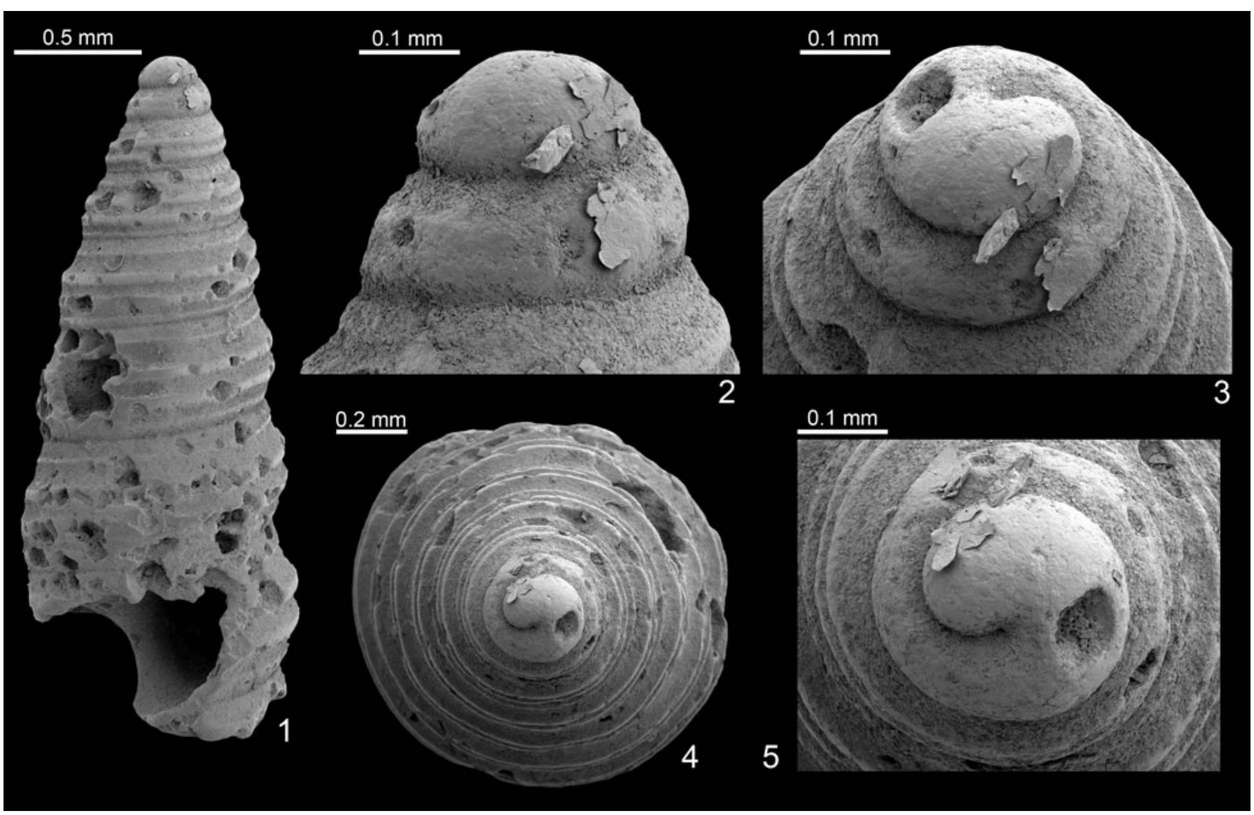

Figure 11. *Stegocoelia* (*Stegocoelia*) sp. A, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), NHMUK PI PG 10260.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

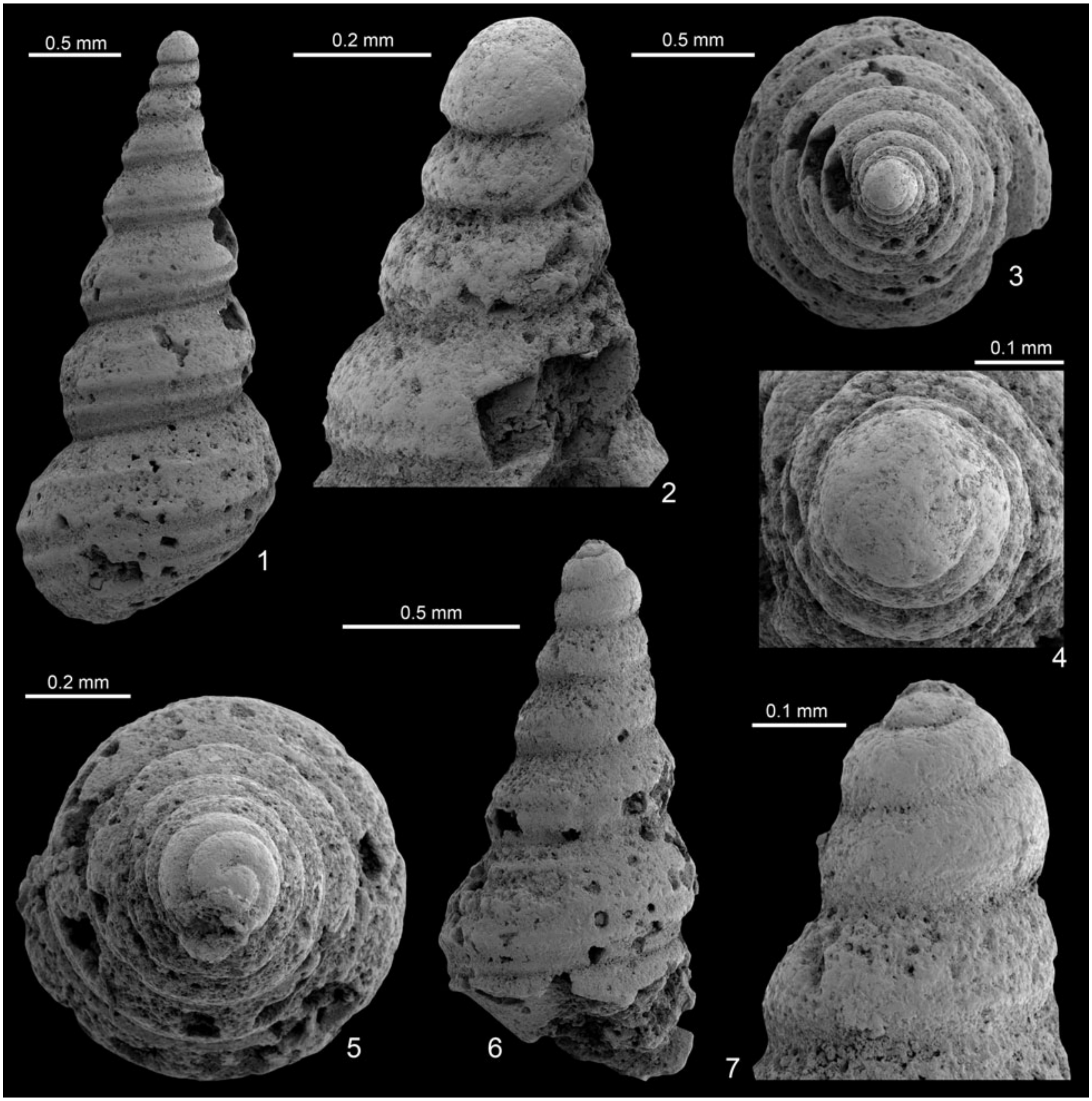

Figure 12. *Stegocoelia* (*Stegocoelia*) cf. *Stegocoelia* (*Stegocoelia*) *cincta* (Donald, 1895), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean). (**1–4**) NHMUK PI PG 10261. (**5–7**) NHMUK PI PG 10262.

cf. 1895 *Murchisonia* (*Stegocoelia*) *cincta* Donald, p. 219, pl. 8, figs. 1, 2.
1926 *Hypergonia cincta*; Longstaff, p. 542, pl. 36, fig. 2.

Lectotype.—Lectotype designated subsequently by Longstaff (1926) (original of Donald, 1895, fig. 1), which is from the Young Collection, and reposited in Kelvingrove Museum, Glasgow according to Longstaff (1926). Type locality, strata and age: Glencart, Dalry, Ayrshire, Scotland, Upper Limestone Formation (Namurian).

Material.—A total of five specimens, NHMUK PI PG 10261–2, 3 additional specimens, PI PG 10263(1–3), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—*Stegocoelia* (*Stegocoelia*) cf. *Stegocoelia* (*Stegocoelia*) *cincta* is identical in ornamentation to *Stegocoelia* (*Stegocoelia*) sp. A, but *Stegocoelia* (*Stegocoelia*) cf. *Stegocoelia* (*Stegocoelia*) *cincta* has a distinctly more rounded, convex whorl profile and seemingly has two protoconch whorls. Its protoconch is mamillated and heliciform and consists of slightly more than two whorls. Its first whorl has a diameter of 0.17 mm, much smaller than the other two *Stegocoelia* (*Stegocoelia*) spp. treated above. This protoconch reflects planktotrophic larval development. Pleural angle of *Stegocoelia* (*Stegocoelia*) cf. *Stegocoelia*

(*Stegocoelia*) *cincta* is 33°–37° and not so different from the other two *Stegocoelia* (*Stegocoelia*) spp. According to the original description by Longstaff (1895) and a drawing of a whorl given by Longstaff (1926), *Stegocoelia* (*Stegocoelia*) *cincta* bears a subsutural cord, which is not visible in the present specimens.

Subgenus *Hypergonia* Donald, 1892

Type species.—*Murchisonia quadricarinata* McCoy, 1844; by original designation.

Remarks.—*Hypergonia* was erected as a subgenus of *Murchisonia* d'Archiac and de Verneuil, 1841 by Donald (1892). According to Donald (1892), *Hypergonia* could be differentiated from *Stegocoelia* by lacking an umbilicus and not having a reflected inner lip. Longstaff (1926) elevated *Hypergonia* to generic rank and placed the type species of *Stegocoelia*—*Murchisonia* (*Stegocoelia*) *compacta*—in *Hypergonia* and stated the lack of an umbilicus in *Stegocoelia*. Subsequent authors regarded *Hypergonia* as a subgenus of *Stegocoelia* (e.g., Knight et al., 1960; Batten, 1966b, 1995; Thein and Nitecki, 1974; Kues and Batten, 2001). Knight et al. (1960) differentiated *Hypergonia* from *Stegocoelia* with the former being more slender and higher spired. Bandel (2002) regarded *Hypergonia* as a separate genus. According to Mazaev (2001, 2011), the distinction between *Hypergonia* and *Stegocoelia* is unclear and *Hypergonia* is a junior synonym of *Stegocoelia*. *Hypergonia* resembles *Stegocoelia* in having the same type of protoconch and the same early ontogenetic shell development. In both taxa, the selenizone is concave, without ornament and situated on the same position on the whorl. *Hypergonia* differs from *Stegocoelia* in developing an angulated profile during later ontogeny, which represents the lower border of the selenizone. Herein, we follow most previous authors and regard it as a subgenus of *Stegocoelia*. Longstaff (1926) provided drawings and photographs of the initial heliciform whorls but did not document the protoconch-teleoconch boundary. Thein and Nitecki (1974, p. 168) described the protoconch "seemingly composed of two smooth and rounded whorls" but did not provide photographs. Due to the lack of clear documentation of the protoconch, Nützel and Bandel (2000) did not include *Hypergonia* in Goniasmatidae. Herein, the caenogastropod-type protoconch is documented for the first time in *Hypergonia* and hence the taxon can be placed as a subgenus of *Stegocoelia* in the Goniasmatidae. *Stegocoelia* (*Hypergonia*) *tenuis* Yoo, 1988 (see also Yoo, 1994) and *Stegocoelia* (*Hypergonia*) *elongata* Yoo, 1988 also have this type of protoconch but lack carinated teleoconch whorls and therefore do not represent the subgenus *Hypergonia*.

Stegocoelia (*Hypergonia*) *variabilis* (Donald, 1895)
Figures 13, 14

*1895 *Murchisonia* (*Stegocoelia*) *variabilis* Donald, p. 228, pl. 9, figs. 6, 7, 11.
1926 *Hypergonia variabilis*; Longstaff, p. 552.

Lectotype.—Lectotype designated subsequently by Longstaff (1926) (original of Donald, 1895, fig. 6), which is from the Smith Collection. The whereabouts of the lectotype is unknown. Type locality, strata and age: Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Description.—Shell high-spired, small (largest studied specimen H: 4.3 mm, W: 1.5 mm), with pleural angle of 23–29°. Protoconch orthostrophic, smooth, heliciform, mammilated, consisting of two whorls, terminating at sinusigera strengthened by varix; protoconch ~0.25 mm L and W; initial whorl W: 0.16 mm. Teleoconch whorls angulated; teleoconch with maximum of seven whorls; first teleoconch whorl with two spiral cords, uppermost representing the abapical selenizone border in later ontogeny and whorl angulation; subsutural cord and upper selenizone border appearing within second teleoconch whorl; late teleoconch whorls ornamented with one subsutural cord, two cords at selenizone borders, and two below selenizone; third and fourth cords are most prominent; lowermost cord (fifth) occasionally covered by subsequent whorl; third cord (abapical border of selenizone) representing the midwhorl of spire whorls. Selenizone wide, concave between second and third cords. Base anomphalous, slightly convex, facing abapically. Inner lip straight; aperture subovate, slightly higher than wide, with siphonal canal.

Material.—A total of 93 specimens; five specimens, NHMUK PI PG 10264–10268, 88 specimens, PI PG 264(1–88); Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—*Stegocoelia* (*Hypergonia*) *variabilis* resembles *Stegocoelia* (*Stegocoelia*) spp. studied herein but differs by developing a clear whorl angulation and possessing a wider selenizone. The protoconch is typical for that group and represents a larval shell of the planktotrophic type.

Genus *Donaldospira* Batten, 1966

Type species.—*Murchisonia pertusa* de Koninck, 1883; by original designation.

Remarks.—*Donaldospira* was initially erected as a subgenus of *Murchisonia* by Batten (1966b) for high-spired, slit-bearing taxa with a convex selenizone situated at a whorl angulation. It was treated as a subgenus of *Stegocoelia* by Batten (1995). Mazaev (2001) considered *Donaldospira* to be a separate genus. A protoconch belonging to a member of this genus was first documented by Bandel (2002), who assigned *Donaldospira* to Goniasmatidae (= Orthonemidae sensu Bandel, 2002).

Donaldospira plana? (Donald, 1892)
Figure 15

?1892 *Murchisonia* (*Hypergonia*) *plana* Donald, p. 571, pl. 16, figs. 14, 15.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

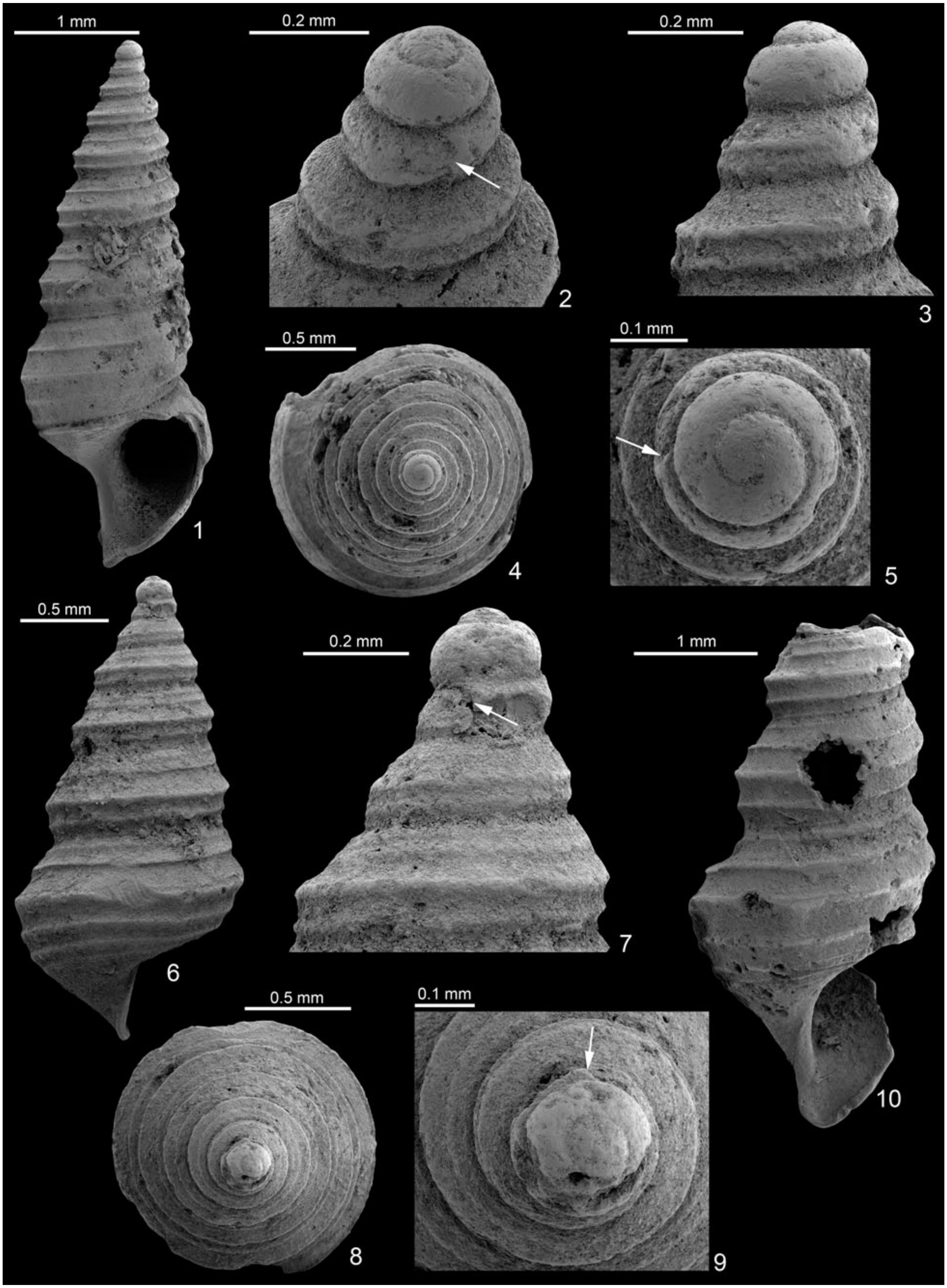

Figure 13. *Stegocoelia* (*Hypergonia*) *variabilis* (Donald, 1895), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean). (**1–5**) NHMUK PI PG 10265. (**6–9**) NHMUK PI PG 10266. (**10**) NHMUK PI PG 10267. Arrows = protoconch-teleoconch boundary.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

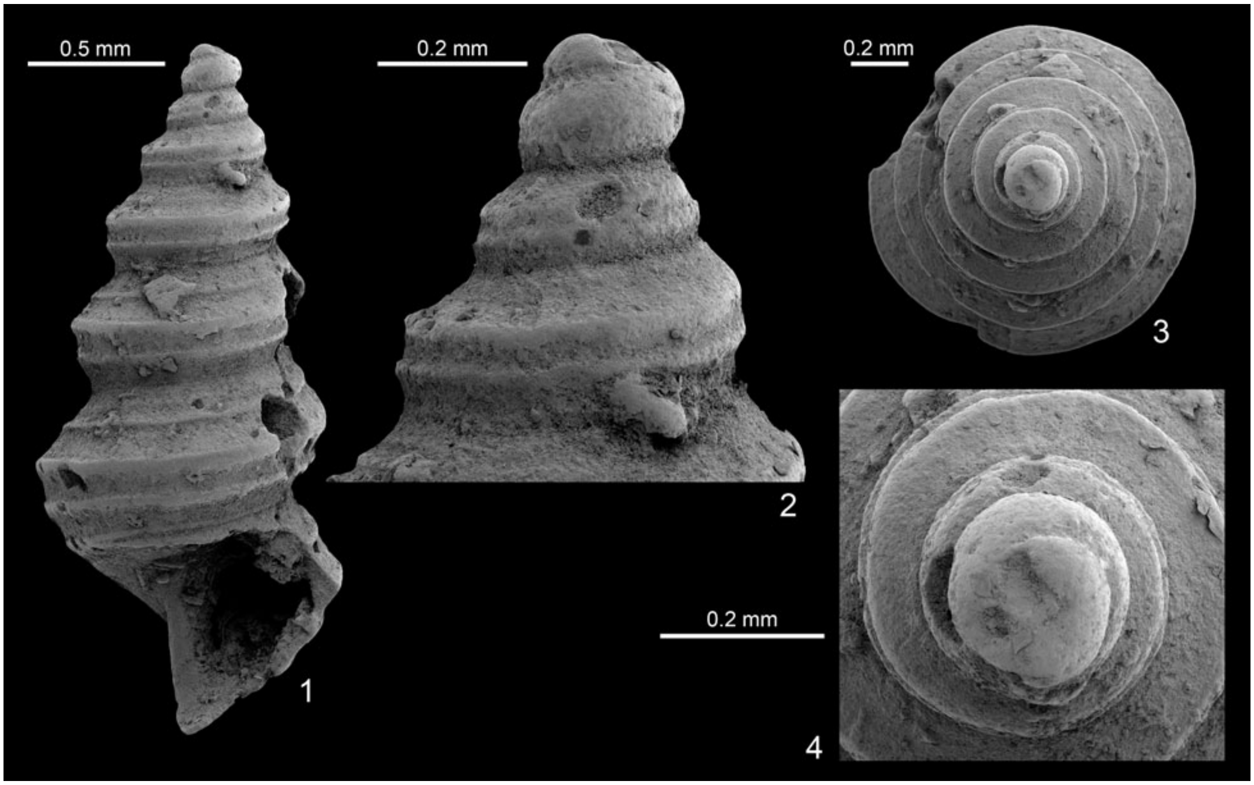

Figure 14. *Stegocoelia* (*Hypergonia*) *variabilis* (Donald, 1895), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), NHMUK PI PG 10268.

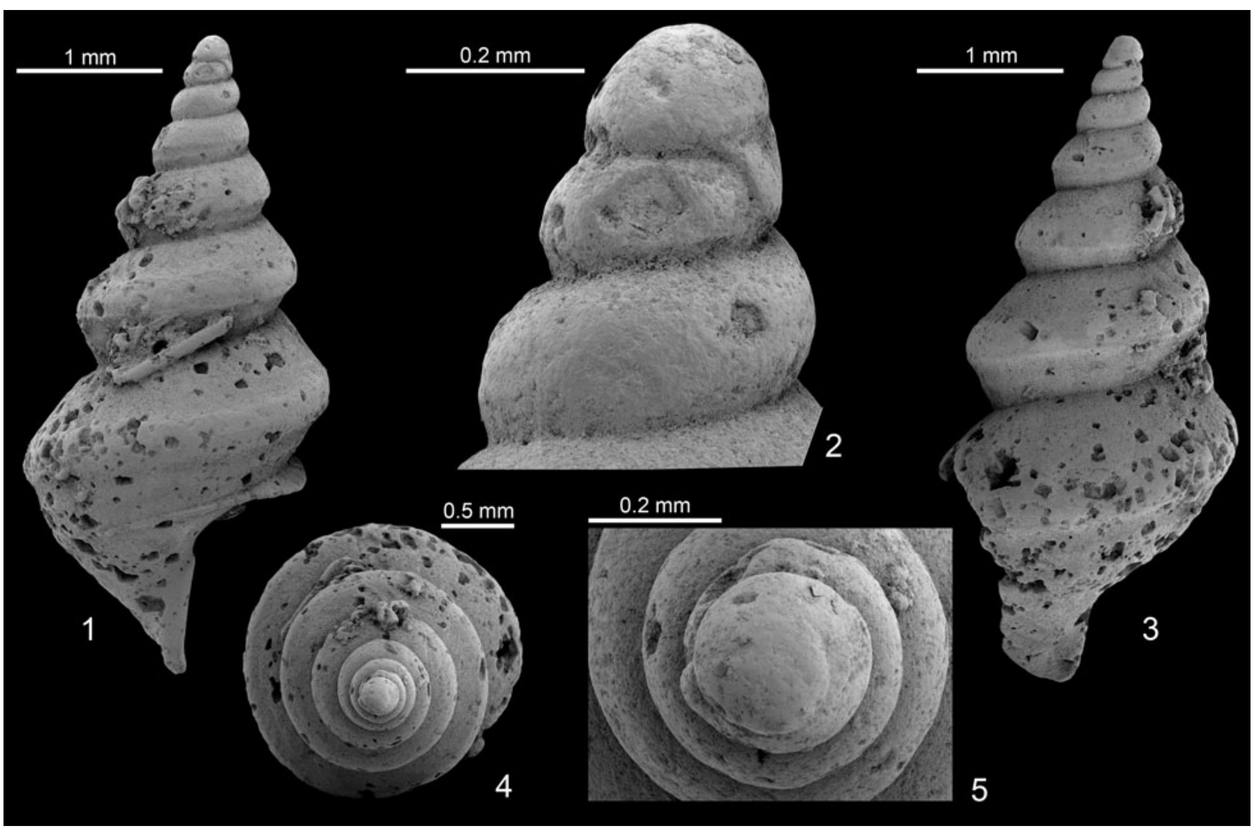

Figure 15. *Donaldospira plana*? (Donald, 1892), Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), NHMUK PI PG 10270.

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

Type specimens.—Donald (1892) reported specimens from shales within the Lower Limestone Formation (Visean) at two different localities: Law Quarry, Dalry and Craigenglen, Campsie, Scotland. The whereabouts of the syntypes is unknown, and types have not been subsequently designated.

Description.—Shell high-spired, small (H: 4.3 mm, W: 2.1 mm), murchisoniform, with pleural angle of 43°; protoconch coarsely recrystallized, orthostrophic, mammilated, smooth, heliciform, consisting of 1.5–2 whorls, terminating in opisthocyrt sinusigera. Teleoconch with six whorls; first two teleoconch whorls rounded; whorl face becoming acutely angulated from third teleoconch onward. Ramp slightly convex, smooth, slightly wider than lower whorl face. Selenizone convex, situated at median angulation representing periphery, bordered by faint spiral cords; selenizone borders slightly protruding. Lower whorl face slightly convex, smooth except from spiral cord between selenizone and abapical suture. Base anomphalous, convex. Aperture higher than wide, with siphonal canal; inner lip straight.

Material.—Two specimens, NHMUK PI PG 10269–10270, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—*Murchisonia subtilistriata* Donald, 1889 from the Upper Limestone Formation at Dalry has a similar whorl profile but its selenizone is situated on the upper whorl face. The lower border of the selenizone represents the periphery, and it has multiple spiral cords on the lower whorl face. *Murchisonia* (*Hypergonia*) *plana* from the same locality and horizon (Law Quarry, Dalry, Lower Limestone Formation) and the studied specimens have the same whorl profile and a single spiral cord on the lower whorl face. Donald (1892) stated that in *Donaldospira plana,* the angulation forms the lower boundary of the selenizone, and it has a subsutural spiral cord. In the present specimens, the selenizone represents the whorl angulation and subsutural spiral cord is not visible. Therefore, the studied specimens are assigned to this species only tentatively.

Genus *Platyzona* Knight, 1945

Type species.—*Pleurotomaria trilineata* Hall, 1858; by original designation.

Platyzona sp. indet.
Figure 16

Material.—A single specimen, NHMUK PI PG 10257, Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Formation (Visean, Brigantian).

Remarks.—A single shell fragment, likely belonging to a juvenile, shows the characteristic features of *Platyzona* with its rounded whorls and very wide selenizone. With its relatively high spire (pleural angle of 55°), it resembles *Platyzona tornatilis* Phillips, 1836 (see Batten, 1966a, pl. 5, fig. 11 for a figure of the holotype), which has prominent spiral cords on the ramp above the selenizone. The present specimen shows faint, prosocyrt growth lines above the ramp but lacks distinct spiral ornament on the ramp.

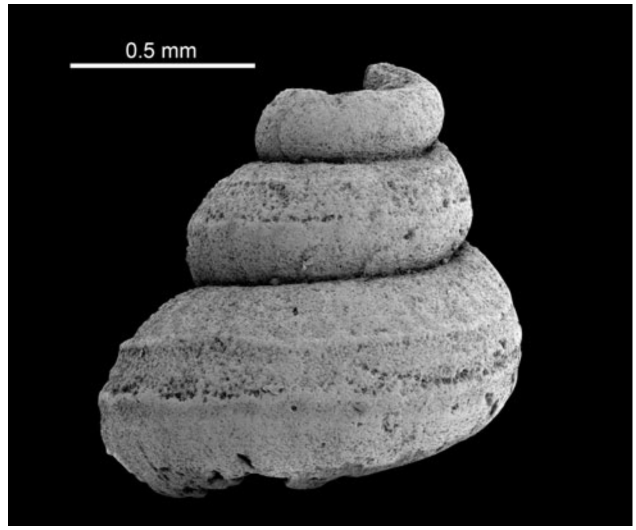

Figure 16. *Platyzona* sp., Law [Quarry], Dalry, Ayrshire, Scotland; Lower Limestone Group (Visean), NHMUK PI PG 10257.

Conclusions

The slit-bearing gastropod fauna of early Carboniferous (Visean) specimens from Dalry, Ayrshire is composed of the cosmopolitan Carboniferous genera: *Biarmeaspira*, *Neilsonia*, *Tapinotomaria*, *Borestus*, *Stegocoelia* (*Stegocoelia*), *Stegocoelia* (*Hypergonia*), *Donaldospira*, and *Platyzona* (e.g., Belgium: de Koninck, 1883; Poland: Gromczakiewicz-Łomnicka, 1973; Russia: Mazaev, 2001, 2002, 2011; Germany: Amler, 2006; Australia: Yoo, 1988, 1994; Morocco: Heidelberger et al., 2009; United States: Thein and Nitecki, 1974; Batten, 1995; Hoare et al., 1997; Kues and Batten, 2001; Karapunar et al., 2022; Japan: Kase, 1988). The studied fauna shares two common species with the contemporaneous (Visean) Hotwells Limestone of Somerset, England (Batten, 1966a, b): *Stegocoelia* (*Stegocoelia*) *compacta* (Donald, 1889) and *Borestus similis*. However, there are no shared species between the studied fauna and slightly younger (Namurian) fauna from Cheshire, England, suggesting a high turnover rate through time and/or high endemism. It should also be noted that studies on Visean gastropods from regions other than the UK are scarce (e.g., Poland: Gromczakiewicz-Łomnicka, 1973; Japan: Kase, 1988; Morocco: Heidelberger et al., 2009) and the foundational work on the Carboniferous gastropods of Belgium by de Koninck (1842–1844, 1883) still needs modern taxonomic revision, which complicates understanding the relationship of the Dalry fauna to other Visean faunas.

The study of well-preserved specimens from Dalry, Ayrshire, Scotland from the Longstaff collection reveals new features about the early ontogeny of *Neilsonia* and *Tapinotomaria*. These features corroborate their placement in the vetigastropod order Pleurotomariida. *Biarmeaspira* was previously known only from the Permian of the USA, Russia (Mazaev, 2006, 2015, 2016, 2017), and Thailand (Ketwetsuriya

https://doi.org/10.1017/jpa.2024.1 Published online by Cambridge University Press

et al., 2020). *Biarmeaspira heidelbergerae* n. sp. from the Visean represents the first Carboniferous record and suggests a possible repeated evolution of *Biarmeaspira* spp. from different *Baylea* spp. (iterative evolution). In the evolutionary history of Pleurotomariida, an angulated selenizone evolved several times (e.g., in the late Paleozoic: *Worthenia* de Koninck, 1883, *Biarmeaspira*; Triassic: *Sisenna*, *Wortheniella* Schwardt, 1992, *Nodocingulum* Karapunar and Nützel, 2021, *Schizogonium* Koken, 1889; Jurassic: *Ptychomphalus* Agassiz, 1837, *Trochotomaria* Conti and Fischer, 1981, *Bathrotomaria* Cox, 1956). Slit-band gastropods with angulated shells (wortheniform taxa) evolved more frequently than the other forms, e.g., conical forms (late Paleozoic: *Glyptotomaria* Knight, 1945, *Neilsonia*; Triassic: *Stuorella* Kittl, 1891, *Codinella* Kittl, 1899; Jurassic: *Pyrgotrochus* Fischer, 1885). The increasing proportion of certain forms can be due to (i) high origination rates in certain clades, (ii) more frequent evolution of some forms than others (e.g., Wagner and Erwin, 2006), and (iii) selective extinction of certain clades or certain forms (e.g., Vermeij, 1987; Erwin, 1990). Wagner and Erwin (2006) found that certain shell forms (e.g., pleurotomariiform, euomphaliform) evolved more frequently in the early Paleozoic due to their higher origination rates, and they explained this with ecomorphology. The extinction of the bellerophontid form at the end-Permian and higher origination of trochiform taxa in the Triassic (Erwin, 1990) is an example of the selective origination/extinction of a shell form. One hypothesis to explain morphological trends in gastropod shells over Phanerozoic is the elimination of some shell forms (openly umbilicate or high-spired shells) by selective agents (Vermeij, 1987). Previous studies (Schindel et al., 1982; Lindström, 2003) showed that *Worthenia* has higher shell-repair frequency than other pleurotomariid taxa, indicating that wortheniform shell morphology has higher resistance to predation (assuming a similar life span among taxa). Repaired shell fractures are also present in the studied pleurotomariid taxa (*Biarmeaspira heidelbergerae* n. sp., Fig. 3.2.; *Neilsonia seussae* n. sp., Fig. 6.5; *Tapinotomaria longstaffae* n. sp., Figs. 7.6, 8.1). Obviously durophagous predation was an important selective agent in the Paleozoic (e.g., Ebbestad and Peel, 1997; Ebbestad, 1998; Brett and Walker, 2002; Lindström and Peel, 2005; Karapunar et al., 2022) and might have favored more resistant shell forms. Answers to the questions whether wortheniform shells (e.g., *Biarmeaspira*) appeared repeatedly and independently, if the frequency of their appearance changed through time (more wortheniform taxa in the Mesozoic), and if wortheniform taxa appeared more frequently in certain clades will require detailed phylogenetic hypotheses. The differential origination/extinction rates among clades and their impact on frequency of certain shell forms have yet to be investigated.

Paleozoic gastropods with preserved protoconchs and fine morphological details of the teleoconch are rare. The gastropods from Dalry (*Stegocoelia*, *Hypergonia*, *Donaldospira*) confirm that the majority of late Paleozoic murchisoniform (high-spired with slit) gastropods have heliciform, caenogastropod-type protoconchs including some species with planktotrophic larval development (see also Yoo, 1988, 1994; Nützel, 1998; Bandel, 2002; Bandel et al., 2002; Mazaev, 2002, 2011, 2015, 2020; Nützel and Pan, 2005; Karapunar et al., 2022). The lack of nacre (Bandel et al., 2002) and tendency to have a siphonal canal suggest a closer relationship with Caenogastropoda, near Cerithioidea, and a more distant relationship with very high-spired Pleurotomariida (Nützel, 1998; Nützel and Pan, 2005). As to the status of these characters in the Devonian genus *Murchisonia*, more research is warranted—it is possible that *Murchisonia* belongs to Pleurotomariida.

Good shell preservation is crucial for improving our knowledge of gastropod shell morphology, which is the main source to infer evolution and phylogeny of extinct gastropods. Given the fine-scaled silicification of the studied material from Dalry, it is desirable to study other taxa from Longstaff's collection at NHMUK and to prospect for new material from extant localities exposing the same horizon.

Acknowledgments

K. Collins (NHMUK) is greatly acknowledged for their help in returning loaned material, providing archived material of Jane Longstaff, and providing inventory numbers. Deutsche Forschungsgemeinschaft (DFG) is acknowledged for financial support (project NU 96/14-1, NU 96/14-2). We are thankful to the reviewers M. Amler (University of Cologne), A. Mazaev (Russian Academy of Sciences), and J.O. Ebbestad (Uppsala University) for their critical comments. S. Zamora, J. Kastigar, and P.M. Mikkelsen are acknowledged for editorial comments. Open access funding enabled and organized by DFG.

Declaration of competing interest

Authors have no conflicts of interest to declare.

References

Agassiz, L., 1837, Großbritanniens Mineral-Conchologie oder ausgemahlte Abbildungen und Beschreibungen der Schaltier-Überreste, welche zu verschiedenen Zeiten und in verschiedenen Tiefen der Erde erhalten worden sind; von James Sowerby: Neuchâtel, Switzerland, H. Nicolet, 689 p.

Amler, M.R.W., 2006, Gastropoden und Bellerophontiden: Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, v. 41, p. 106–120.

Bandel, K., 2002, Reevaluation and classification of Carboniferous and Permian Gastropoda belonging to the Caenogastropoda and their relation: Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, v. 86, p. 81–188.

Bandel, K., Nützel, A., and Yancey, T.E., 2002, Larval shells and shell microstructures of exceptionally well-preserved late Carboniferous gastropods from the Buckhorn Asphalt deposit (Oklahoma, USA): Senckenbergiana Letheae, v. 82, p. 639–690, https://doi.org/10.1007/BF03042954.

Batten, R.L., 1956, Some new pleurotomarian gastropods from the Permian of West Texas: Journal of the Washington Academy of Sciences, v. 46, p. 42–46.

Batten, R.L., 1958, Permian Gastropoda of the southwestern United States: 2, Pleurotomariacea: Portlockiellidae, Phymatopleuridae, and Eotomariidae: Bulletin of the American Museum of Natural History, v. 114, p. 153–246.

Batten, R.L., 1966a, The lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset, Part 1: Palaeontographical Society Monographs, v. 119, no. 509, p. 1–52.

Batten, R.L., 1966b, The lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset, Part 2: Palaeontographical Society Monographs, v. 120, no. 513, p. 53–109.

Batten, R.L., 1995, Pennsylvanian (Morrowan) gastropods from the Magdalena Formation of the Hueco Mountains, Texas: American Museum Novitates, v. 3122, p. 1–46.

Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M., and Strong, E.E., 2017, Revised classification, nomenclator and typification of gastropod and monoplacophoran families: Malacologia, v. 61, nos. 1/2, p. 1–526, https://doi.org/10.4002/040.061.0201.

Brett, C.E., and Walker, S.E., 2002, Predators and predation in Paleozoic marine environments: The Paleontological Society Papers, v. 8, p. 93–118, https://doi.org/10.1017/S1089332600001078.

Brown, S.S., 1977, Petrogenesis and depositional environment of the Dockra Limestone (Upper Visean), North Ayrshire [Ph.D. thesis]: Glasgow, Scotland, University of Glasgow, 146 p.

Chronic, B.J., 1949, Invertebrate paleontology (excepting fusulinids and corals), *in* Newell, N.D., Chronic, J., and Roberts, T.G., eds., Upper Paleozoic of Perú: New York, Columbia University Press, p. 46–173.

Cleevely, R.J., Tripp, R.P., and Howells, Y., 1989, Mrs Elizabeth Gray (1831–1924): a passion for fossils: Bulletin of the British Museum of Natural History (Historical Series), v. 17, no. 2, p. 167–258.

Conrad, T.A., 1835, Description of five new species of fossil shells in the collection presented by Mr. Edward Miller to the Geological Society: Transactions of the Geological Society of Pennsylvania, v. 1, p. 267–270.

Conti, M.A., and Fischer, J.C., 1981, Preliminary notes on the Aalenian gastropods of Case Canepine (Umbria, Italy), *in* Farinacci, A., and Elmi, S., eds., Rosso Ammonitico Symposium Proceedings: Rome, Edizioni Tecnoscienza, p. 137–145.

Cox, L.R., 1936, Mrs. Mary Jane Longstaff (née Donald): Proceedings of the Geologists' Association, v. 47, p. 97.

Cox, L., 1956, A new genus of Mesozoic Pleurotomariidae: Journal of Molluscan Studies, v. 32, nos. 1/2, p. 79.

Cox, L.R., 1960a, Gastropoda: general characteristics of Gastropoda, *in* R.C. Moore, ed., Treatise on Invertebrate Paleontology, Part 1, Mollusca 1: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. I84–I169.

Cox, L.R., 1960b, Thoughts on the classification of the Gastropoda: Proceedings of the Malacological Society of London, v. 33, p. 239–261.

Cox, L.R., and Knight, J.B., 1960, Suborders of Archaeogastropoda: Proceedings of the Malcological Society, v. 33, p. 262–264.

Creese, M.R., and Creese, T.M., 1994, British women who contributed to research in the geological sciences in the nineteenth century: The British Journal for the History of Science, v. 27, no. 1, p. 23–54.

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, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an 3: Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts, v. 2, p. 433–449.

d'Archiac, E.J.A., and de Verneuil, E.P., 1841, Note sur le genre *Murchisonia*: Bulletin de la Société Géologique de France, v. 12, no. 1, p. 154–164.

de Koninck, L.G., 1842–1844, Description des Animaux Fossiles qui se Trouvent dans le Terrain Carbonifère de Belgique: Liège, Belgium, H. Dessain, 636 p.

de Koninck, L.G., 1883, Faune du calcaire carbonifère de la Belgique, quatrième partie, Gastéropodes (suite et fin): Annales du Musée Royal d'Histoire Naturelle de Belgique, v. 8, p. 1–240.

Donald, J., 1885, Notes on some Carboniferous Gasteropoda from Penton and elsewhere: Transactions of the Cumberland Association, v. 11, p. 150–151.

Donald, J., 1887, Notes upon some Carboniferous species of *Murchisonia* in our public museums: Quarterly Journal of the Geological Society, v. 43, nos. 1–4, p. 617–631.

Donald, J., 1889, Descriptions of some new species of Carboniferous Gasteropoda: Quarterly Journal of the Geological Society, v. 45, nos. 1–4, p. 619–625.

Donald, J., 1892, Notes on some new and little-known species of Carboniferous *Murchisonia*: Quarterly Journal of the Geological Society, v. 48, p. 562–575.

Donald, J., 1895, Notes on the genus *Murchisonia* and its allies; with a revision of the British Carboniferous species, and descriptions of some new forms: Quarterly Journal of the Geological Society, v. 51, nos. 1–4, p. 210–234.

Donald, J., 1898, Observations on the genus *Aclisina*, de Koninck, with descriptions of British species and of some other Carboniferous Gasteropoda: Quarterly Journal of the Geological Society, v. 54, nos. 1–4, p. 45–72.

Donald, J., 1899, Remarks on the genera *Ectomaria*, Koken, and *Hormotoma*, Salter, with descriptions of British species: Quarterly Journal of the Geological Society, v. 55, nos. 1–4, p. 251–272.

Donald, J., 1902, On some of the Proterozoic Gasteropoda which have been referred to *Murchisonia* and *Pleurotomaria*, with descriptions of new subgenera and species: Quarterly Journal of the Geological Society, v. 58, nos. 1–4, p. 313–339.

Donald, J., 1905a, Observations on some of the Loxonematidae, with descriptions of two new species: Quarterly Journal of the Geological Society, v. 61, nos. 1–4, p. 564–566.

Donald, J., 1905b, On some Gasteropoda from the Silurian rocks of Llangadock (Caermarthenshire): Quarterly Journal of the Geological Society, v. 61, nos. 1–4, p. 567–578.

Donald, J., 1906, Notes on the genera *Omospira*, *Lophospira*, and *Turritoma*; with descriptions of new Proterozoic species: Quarterly Journal of the Geological Society, v. 62, nos. 1–4, p. 552–572.

Ebbestad, J.O.R., 1998, Multiple attempted predation in the Middle Ordovician gastropod *Bucania gracillima*: GFF, v. 120, no. 1, p. 27–33.

Ebbestad, J.O.R., and Peel, J.S., 1997, Attempted predation and shell repair in Middle and Upper Ordovician gastropods from Sweden: Journal of Paleontology, v. 71, no. 6, p. 1007–1019.

Erwin, D.H., 1990, Carboniferous–Triassic gastropod diversity patterns and the Permo-Triassic mass extinction: Paleobiology, v. 16, p. 187–203.

Etheridge, R., 1881, Descriptions of certain peculiar bodies which may be the opercula of small Gasteropoda, discovered by Mr. James Bennie in the Carboniferous limestone of law quarry, near Dalry, Ayrshire, with notes on some Silurian opercula: Annals and Magazine of Natural History, v. 7, no. 37, p. 25–31.

Fischer, P., 1880–1887, Manuel de Conchyliologie et de Paléontologie Conchyliologique, ou Histoire Naturelle des Molluscques Vivants et Fossiles: Paris, F. Savy, Paris, (1), p. 1–112 (1880); (2), p. 113–192 (1881); (3), p. 193–304 (1881); (4), p. 305–416 (1882); (5), p. 417–512 (1885); (6), p. 513–608 (1883); (7), p. 609–688 (1884); (8), p. 689–784 (1885); (9), p. 785–896 (1885); (10), p. 897–1008 (1886); (11), p. 1009–1369 (1887).

Gromczakiewicz-Łomnicka, A., 1973, Visean gastropods from Gałęzice (Holy Cross Mts., Poland) and their stratigraphical value: Studia Geologica Polonica, v. 41, p. 7–53.

Hall, J., 1858, Description of new species of fossils from the Carboniferous limestones of Indiana and Illinois: Transactions of the Albany Institute, v. 4, p. 1–37.

Heidelberger, D., Korn, D., and Ebbighausen, V., 2009, Late Viséan (Carboniferous) gastropods from the Gara El Itima (eastern Anti-Atlas, Morocco): Fossil Record, v. 12, no. 2, p. 183–196, https://doi.org/10.5194/fr-12-183-2009.

Hoare, R.D., Sturgeon, M.T., and Anderson, J.R.J., 1997, Pennsylvanian marine gastropods from the Appalachian Basin: Journal of Paleontology, v. 71, p. 1019–1039.

Karapunar, B., and Nützel, A., 2021, Slit-band gastropods (Pleurotomariida) from the upper Triassic St. Cassian Formation and their diversity dynamics in the Triassic: Zootaxa, v. 5042, no. 1, p. 1–165, https://doi.org/10.11646/zootaxa.5042.1.1.

Karapunar, B., Nützel, A., Seuss, B., and Mapes, R.H., 2022, Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA: Papers in Palaeontology, v. 8, no. 2, p. 1–95 (n. e1417), https://doi.org/10.1002/spp2.1417.

Kase, T., 1988, Early Carboniferous (Visean) gastropods from the Hikoroichi Formation of the Kitakami Mountains, northeast Japan: Transactions and Proceedings of the Paleontological Society of Japan, n. ser., v. 149, p. 361–370.

Ketwetsuriya, C., Karapunar, B., Charoentitirat, T., and Nützel, A., 2020, Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. Zootaxa, v. 4766(1), p. 1–47, https://doi.org/10.11646/zootaxa.4766.1.1.

Kittl, E., 1891, Die Gastropoden der Schichten von St. Cassian der südalpinen Trias, I Theil: Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums, v. 6, p. 166–262.

Kittl, E., 1899, Die Gastropoden der Esinokalke, nebst einer Revision der Gastropoden der Marmolatakalke: Annalen des Kaiserlich Königlichen Naturhistorischen Hofmuseums, v. 14, p. 1–237.

Knight, J.B., 1941, Palaeozoic gastropod genotypes: Geological Society of America Special Papers, v. 32, p. 1–510.

Knight, J.B., 1945, Some new genera of Paleozoic Gastropoda: Journal of Paleontology, v. 19, p. 573–587.

Knight, J.B., 1956, New families of Gastropoda: Journal of the Washington Academy of Sciences, v. 46, no. 2, p. 41–42.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L., and Robertson, R., 1960, Systematic descriptions, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part 1, Mollusca 1: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. I169–I310.

Koken, E., 1889, Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband, v. 6, p. 440–463.

Koken, E., 1896, Die Gastropoden der Trias um Hallstatt: Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, v. 46, p. 37–126.

Kues, B.S., and Batten, R.L., 2001, Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico: Journal of Paleontology, v. 75, supplement to no. 1, p. 1–95.

Lindström, A., 2003, Shell breakage in two pleurotomarioid gastropods from the upper Carboniferous of Texas, and its relation to shell morphology: GFF, v. 125, no. 1, p. 39–46, https://doi.org/10.1080/11035890301251039.

Lindström, A., and Peel, J.S., 2005, Repaired injuries and shell form in some Palaeozoic pleurotomarioid gastropods: Acta Palaeontologica Polonica, v. 50, no. 4, p. 697–704.

Longstaff, J., 1909, On the genus *Loxonema*, with descriptions of new Proterozoic species: Quarterly Journal of the Geological Society, v. 65, nos. 1–4, p. 210–228.

Longstaff, J., 1912, Some new lower Carboniferous Gasteropoda: Quarterly Journal of the Geological Society, v. 68, nos. 1–4, p. 295–309.

Longstaff, J., 1917, Supplementary notes on *Aclisina* de Koninck and *Aclisoides* Donald, with descriptions of new species: Quarterly Journal of the Geological Society, v. 73, nos. 1–4, p. 59–83.
Longstaff, J., 1924, Descriptions of Gasteropoda, chiefly in Mrs. Robert Gray's Collection, from the Ordovician and lower Silurian of Girvan: Quarterly Journal of the Geological Society, v. 80, nos. 1–4, p. 408–446.
Longstaff, J., 1926, A revision of the British Carboniferous Murchisoniidae, with notes on their distribution and descriptions of some new species: Quarterly Journal of the Geological Society, v. 82, nos. 1–4, p. 526–555.
Longstaff, J., 1933, A revision of the British Carboniferous members of the family Loxonematidae, with descriptions of new forms: Quaterly Journal of the Geological Society, v. 89, p. 87–125.
Mazaev, A.V., 2001, The gastropod genus *Stegocoelia* Donald, 1889 (Murchisoniidae) from middle and upper Carboniferous of the central part of Russian Plate: Ruthenica, v. 11, no. 2, p. 137–151.
Mazaev, A.V., 2002, Some murchisoniid gastropods from the middle and upper Carboniferous part of Russian Plate: Ruthenica, v. 12, no. 2, p. 89–106.
Mazaev, A.V., 2006, Permian gastropods from Kulogory Formation of northern Moscow Syneclise: Paleontological Journal, v. 40, p. 391–403, https://doi.org/10.1134/S0031030106040046.
Mazaev, A.V., 2011, Pennsylvanian gastropods of the suborders Murchisoniina Cox et Knight, 1960 and Sinuspirina Mazaev subordo nov. from the central regions of the Russian Platform: morphology, taxonomy, and phylogeny: Paleontological Journal, v. 45, p. 1533–1599, https://doi.org/10.1134/S003103011112001X.
Mazaev, A.V., 2015, Upper Kazanian (middle Permian) gastropods of the Volga-Urals region: Paleontological Journal, v. 49, p. 869–986, https://doi.org/10.1134/S0031030115080018.
Mazaev, A.V., 2016, Evolution of the genus *Baylea* (Gastropoda) in the Kazan Paleobasin (middle Permian, Volga-Ural region): Paleontological Journal, v. 50, p. 585–600, https://doi.org/10.1134/S0031030116060101.
Mazaev, A.V., 2017, The development of the genus *Biarmeaspira* (Gastropoda) in the Kazanian paleobasin (middle Permian, Volga-Urals region): Paleontological Journal, v. 51, p. 223–232, https://doi.org/10.1134/S0031030117020095.
Mazaev, A.V., 2020, Sakmarian gastropods from the Samarskaya Luka (lower Permian, Volga-Urals): Paleontological Journal, v. 54, no. 10, p. 1152–1177, https://doi.org/10.1134/S0031030120100056.
McCoy, F., 1844, A synopsis of the characters of the Carboniferous limestone fossils of Ireland: Dublin, M.H. Gill, 207 p.
McCoy, F., 1849, On some new genera and species of Palaeozoic corals and Foraminifera: Annals and Magazine of Natural History, v. 3, no. 13, p. 1–20.
Monro, S.K., 1999, Geology of the Irvine District: Memoir for 1: 50 000 Geological Sheet 22W and Part of Sheet 21E (Scotland): London, Stationery Office, 140 p.
Newell, N.D., 1935, Some Mid-Pennsylvanian invertebrates from Kansas and Oklahoma: 2, Stromaporoidea, Anthozoa, and Gastropoda: Journal of Paleontology, v. 9, p. 341–355.
Nützel, A., 1998, Über die Stammesgeschichte der Ptenoglossa (Gastropoda): Berliner Geowissenschaftliche Abhandlungen, Reihe E, v. 26, p. 1–229.
Nützel, A., and Bandel, K., 2000, Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda): Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 9, p. 557–569, https://doi.org/10.1127/njgpm/2000/2000/557.
Nützel, A., and Pan, H.-Z., 2005, Late Paleozoic evolution of the Caenogastropoda: larval shell morphology and implications for the Permian/Triassic mass extinction event: Journal of Paleontology, v. 79, p. 1175–1188, https://doi.org/10.1666/0022-3360(2005)079[1175:LPEOTC]2.0.CO;2.
Peel, J.S., 2016, Gastropods from the Carboniferous (Namurian) of Congleton Edge, Cheshire, UK: Papers in Palaeontology, v. 2, p. 399–438, https://doi.org/10.1002/spp2.1047.
Phillips, J., 1836, Illustrations of the Geology of Yorkshire: or a Description of the Strata and Organic Remains; Accompanied by a Geological Map, Sections, and Diagrams, and Figures of the Fossils, Part 2, The Mountain Limestone District: London, John Murray, 253 p.
Phillips, J., 1841, Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon and West Somerset: London, Longman Brown, 231 p.
Richey, J., 1947, Pene-contemporaneous structures in the Hurlet Limestone, near Kilbirnie, North Ayrshire: Transactions of the Geological Society of Glasgow, v. 21, no. 1, p. 61–73.
Salvini-Plawen, L. von, 1980, A reconsideration of systematics in the Mollusca: Malacologia, v. 19, p. 249–278.
Schindel, D.E., Vermeij, G.J., and Zisper, E., 1982, Frequencies of repaired shell fractures among the Pennsylvanian gastropods of north-central Texas: Journal of Paleontology, v. 56, p. 729–740.
Schwardt, A., 1992, Revision der *Wortheniella*-Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten): Annalen des Naturhistorischen Museums Wien, ser. A, v. 94, p. 23–57.
Thein, M.L., and Nitecki, M.H., 1974, Chesterian (Upper Mississippian) Gastropoda of the Illinois Basin: Fieldiana Geology, v. 34, p. 1–238.
Thomas, E.G., 1940, Revision of the Scottish Carboniferous Pleurotomariidae: Transactions of the Geological Society of Glasgow, v. 20, p. 30–72.
Vermeij, G.J., 1987, Evolution and escalation: an ecological history of life: Princeton, New Jersey, Princeton University Press, 527 p.
Wagner, P.J., and Erwin, D.H., 2006, Patterns of convergence in general shell form among Paleozoic gastropods: Paleobiology, v. 32, p. 316–337, https://doi.org/10.1666/04092.1.
Waters, C., Browne, M., Dean, M., and Powell, J., 2007, Lithostratigraphical framework for Carboniferous successions of Great Britain (onshore): British Geological Survey, Research Report RR/07/01, 60 p.
Weir, J., 1931, The British and Belgian Carboniferous Bellerophontidae: Transactions of the Royal Society of Edinburgh, v. 56, no. 3, p. 767–861.
Wenz, W., 1938–1944, Gastropoda, Teil I: Allgemeiner Teil und Prosobranchia, *in* O.H. Schindewolf, ed., Handbuch der Paläozoologie: Berlin, Gebrüder Borntraeger, xii + 1639 p.
Wyse Jackson, P.N., and Spencer Jones, M.E., 2007, The quiet workforce: the various roles of women in geological and natural history museums during the early to mid-1900s: Geological Society of London Special Publications, v. 281, no. 1, p. 97–113, https://doi.org/10.1144/SP281.6.
Yoo, E.K., 1988, Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales: Records of the Australian Museum, v. 40, nos. 3/4, p. 233–264.
Yoo, E.K., 1994, Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia: Records of the Australian Museum, v. 46, p. 63–110.
Young, J., 1884, Notes on the fossils found in a thin bed of impure Carboniferous at Glencart, near Dalry, Ayrshire: Proceedings of the Natural History Society of Glasgow, v. 5, p. 234–240.

Accepted: 21 December 2023