

GASTROPODS FROM THE CARBONIFEROUS (NAMURIAN) OF CONGLETON EDGE, CHESHIRE, UK

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Abstract: Gastropod assemblages of late Carboniferous age (Namurian; Chokierian–Alportian) from the Morridge Formation at Pot Bank Quarry, Congleton Edge, Cheshire, contain 27 species, the most diverse gastropod fauna known from the Silesian of the southern UK. Chokierian sandstones yield a sparse assemblage of mainly high-spired *Stegocoelia* and bivalves, but flooding associated with the *Hudsonoceras proteus* marine band (basal Alportian) introduced a diverse invertebrate fauna in which the gastropod fraction is dominated by the bellerophontoideans *Bellerophon*, *Retispira*, *Euphemites* and *Patellilabia*, and the eotomarioid *Angyomphalus*. A later, previously unrecognized marine

assemblage of probable Alportian age contains numerous small pleurotomariiform gastropods, but bellerophontoideans are less common and *Angyomphalus* is absent. In formal international usage the assemblages are of Pennsylvanian (Bashkirian Stage) age. One new genus *Liraloron cornoviorum* gen. et sp. nov. and the following new species are described: *Retispira mowensis*, *Patellilabia britannica*, *Angyomphalus congletonensis*, *Neilsonia coatesi*, *N. ganneyica*, *Eirlysia ceramicorum*, *Meekospira acrolopha*.

Key words: gastropods, taxonomy, late Carboniferous, Namurian, Pennsylvanian.

CONGLETON EDGE rises to more than 300 m above sea level as a bastion above the down-faulted Triassic rocks of the Cheshire Plain in north-west England, while its dip slope forms the up-turned margin of the North Staffordshire coalfield to the south-east (Fig. 1). The scarp contains a full succession of Namurian (late Carboniferous, Pennsylvanian) strata overlying an inlier of Carboniferous Limestone (Dinantian) at its foot and culminates with typical feldspathic Millstone Grits at its crest (Evans *et al.* 1968). Until the beginning of the last century the limestone, numerous quartzite beds (ganister, locally also called crowstone) within the mudstone-dominated succession, and the grits themselves, were quarried and mined, although these workings are now overgrown.

The largest ganister excavation occurs at Pot Bank Quarry where quartzites of the Lum Edge Sandstone (Cleal & Thomas 1996; Cheddleton Sandstone of Turner *et al.* 1994) were formerly worked at the surface and in adits down the 50° dip. The quartzites are still exposed, although exposures of the overlying mudstones yielding a rich marine fauna of Namurian (Chokierian–Alportian) age are now largely overgrown. Hind (1902; *in* Gibson 1905) listed 47 species from the fossil assemblages above the quartzite but this list was increased to more than 60 by Hind (1907, 1910). The fauna as a whole has not been

monographed, although Ramsbottom (*in* Evans *et al.* 1968, p. 81) reviewed descriptions of individual brachiopods, bivalves, gastropods and goniatites. An extensive palynoflora of more than 60 taxa was documented by Turner *et al.* (1994) following an earlier study by Neves (1961).

Gastropods form a conspicuous element of the fossil assemblages from Pot Bank Quarry and the present paper describes 27 species, about four times the number listed by previous authors, from a succession straddling the *Hudsonoceras proteus* marine band which forms the base of the Alportian Substage. Of these 27 taxa, 14 occur in a previously unrecognized assemblage from the stratigraphically youngest strata from the quarry, but they are probably also of Alportian age. One new genus *Liraloron cornoviorum* gen. et sp. nov. and the following new species are described: *Retispira mowensis*, *Patellilabia britannica*, *Angyomphalus congletonensis*, *Neilsonia coatesi*, *N. ganneyica*, *Eirlysia ceramicorum*, *Meekospira acrolopha*.

In terms of European usage, all the gastropods are of late Carboniferous (Silesian) age, from the Chokierian and Alportian substages of the Namurian Regional Stage (Figs 2, 3). This is the earliest part of the Pennsylvanian Subsystem (Bashkirian Stage) in formal international usage.

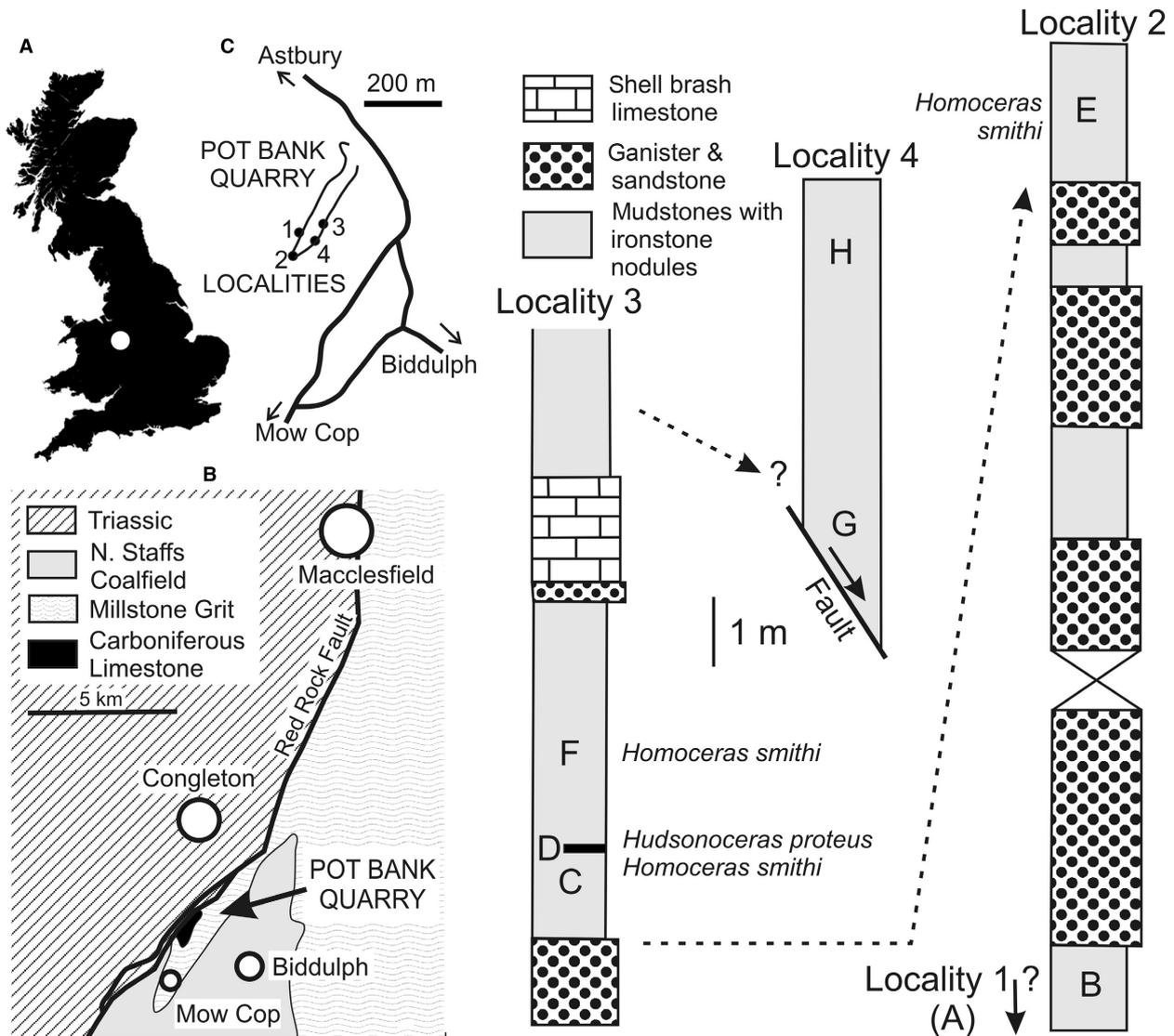


FIG. 1. Location (A–C) and stratigraphical sections of the Morridge Formation (Namurian, Chokierian–Alportian), Pot Bank Quarry (latitude 53° 7' 50" N; longitude 2° 11' 49" W), Congleton Edge, Cheshire. Gastropod assemblages A–H are discussed in Figure 3 and the text.

PREVIOUS WORK

The definitive faunal studies of early Carboniferous gastropods in western Europe are the extensive monographs of de Koninck (1842, 1881, 1883). Eastern European late Carboniferous gastropods were revised and described in a series of papers by Mazaev (1994–2011) based on material from the central Russian Plate. Both of the faunas are derived from marine carbonate facies.

In Britain, leading earlier works include Phillips (1836, 1841), Portlock (1843) and M'Coy (1844; *in* Sedgwick & M'Coy 1851–55). The comprehensive monograph of Batten (1965–66) described almost 100 species from the Carboniferous Limestone of Somerset, revising much

earlier work, and is the last significant description of British Carboniferous gastropods. A series of papers by Donald (1885–1898), continued as Longstaff (1912–1933), is complemented by important papers by Weir (1931) on bellerophontoideans and Thomas (1940) on pleurotomariiform gastropods. British gastropod faunas are mainly derived from marine carbonates of early Carboniferous (Dinantian) age, with little representation from the widespread fluvio-deltaic to coal-forming delta top deposits of the late Carboniferous (Silesian; Fig. 2). However, a diverse late Carboniferous gastropod fauna is known from the Upper Limestone Formation (Namurian; Pendleian–Arnsbergian) of the Midland Valley of Scotland, but it has not been described as an entity. Longstaff (1926,

CARBONIFEROUS	PENNSYLVANIAN	GLOBAL STAGES	North America Stages	Europe Stages		Yeadonian	Rosendale Fm
		GZHELIAN	Virgilian	SILESIAN	Stephanian	Marsdenian	Marsden Fm
		KASIMOVIAN	Missourian			Kinderscoutian	MORRIDGE FORMATION
		MOSCOVIAN	Desmoinesian		Alportian		
		BASHKIRIAN	Atokan		Chokierian		
	SERPUKHOVIAN	Chesterian	NAMURIAN		Arnsbergian	Bowland Sh. Fm	
	MISSISSIPPIAN	VISEAN	Meramecian	DINANTIAN	Visean	Pendleian	CONGLETON EDGE
			Osagean			NAMURIAN SUBSTAGES	
		TOURNAISIAN	Kinderhookian		Tournaisian		

FIG. 2. Stratigraphical nomenclature.

NAMURIAN:	CHOKIERIAN			ALPORTIAN				
	A	B	C	D	E	F	G	H
<i>Bellerophon cf. anthracophilus</i>			○	●	●	●		○
<i>Bellerophon sp. A</i>				●	●	●		
<i>Retispira concinna</i>				●	●	●		
<i>Retispira undata</i>				●	●	●		
<i>Retispira mowensis</i>				●	●	●		
<i>Patellilabia britannica</i>				●	●	●		
<i>Euphemites jacksoni</i>		○		●	●	●		
<i>Angyomphalus congletonensis</i>				●	●	●		
<i>Glabrocingulum armstrongi</i>						○		●
<i>Eirlysia ceramicorum</i>						●		
<i>Neilsonia coatesi</i>			●	●		○		
<i>Neilsonia ganneyica</i>								●
<i>Luciellina sp.</i>								●
<i>Liraloron cornoviorum</i>								●
<i>Amaurotoma sp.</i>								●
<i>Stegocoelia sp.</i>	●							
<i>Platyceras sp.</i>					?			
<i>Naticopsis sp.</i>						●		●
<i>Leptoptygma cf. virgatum</i>						●		●
<i>Leptoptygma sp. A</i>						●		
<i>Leptoptygma sp. B</i>						●		
<i>Girtyspira sp.</i>	●							
<i>Meekospira acrolopha</i>			○	○	○	●		○
<i>Palaeozygopleura roboystonensis</i>					●			●
<i>Platyconcha cf. hindi</i>						●		
<i>Microptychis sp.</i>	●							
<i>Donaldina sp.</i>								●

FIG. 3. Faunal list and distribution of gastropods from Pot Bank Quarry. The location of assemblages A–H is given in Figure 1. Open circles indicate tentative identifications of poorly preserved specimens.

1933) described more than 20 high-spired taxa, a significant point of difference from the Pot Bank Quarry assemblages. Weir (1931) described about 10 bellerophon-toidean species and Thomas (1940) a similar number of pleurotomariiform species distributed between a variety of horizons and localities from a formation attaining a maximum thickness of almost 600 m. Wilson (1967) published a comprehensive account of Namurian faunas from the Midland Valley and Dean (2001) provided extensive faunal lists including numerous gastropods.

In North America, major studies exist of rich gastropod faunas of both Mississippian and Pennsylvanian age (Fig. 2). Early work by authors such as Meek & Worthen (1861), Norwood & Pratten (1855), Whitfield (1882), Girty (1910, 1915) and Weller (1916) was followed by numerous extensive monographs concerned solely with gastropods. A series of papers by Knight (1930–1934b) described 144 species from the Pennsylvanian (Desmoinesian) of Missouri, although several gastropod groups, including the diverse pleurotomariiform gastropods, were not described. Thein & Nitecki (1974) described over 70 species from the late Mississippian (Chesterian) of the Illinois Basin. Gordon & Yochelson (1987) described 79 species from the Chainman Shale (late Mississippian) of Utah. Batten (1995) monographed more than 90 species from the Magdalena Formation (Pennsylvanian, Morrowan) of Texas, while Kues & Batten (2001) identified 157 species from the Flechado Formation (Desmoinesian) of New Mexico. Hoare *et al.* (1997) noted 227 recognizable gastropod taxa from the Pennsylvanian of the Appalachian Basin.

The meagre fauna described herein from the Namurian of Pot Bank Quarry (27 species; Figs 3–12) palls on comparison with the faunas from USA. However, viewed as a whole, the fauna from Pot Bank Quarry is the most diverse gastropod assemblage described from the numerous marine bands that characterize the Namurian and Westphalian in the UK. Gastropods are widely reported from many of the marine bands but taxonomic descriptions of the low diversity assemblages are few (e.g. Sowerby *in* Prestwich 1840; Stobbs & Hind 1905; Bolton 1907). Bellerophontoideans were described by Weir (1931) and some high-spined species by Longstaff (1926, 1933). One of the most diverse faunas is from the Clay Cross marine band (= Vanderbeckei marine band), marking the base of the Duckmantian substage within the Westphalian (Fig. 2), from which Edwards & Stubblefield (1947) listed 9 gastropod species in a marine fauna of about 50 species. Overviews of the marine bands with lists of faunas were given by Edwards & Stubblefield (1947), Calver (1968), Ramsbottom (1981) and Brand (2011); see also Cleal & Thomas (1996) and many Memoirs of the Geological Survey (e.g. Bromehead *et al.* 1933; Evans *et al.* 1968).

Elsewhere in Europe, Demanet (1941) described almost 20 species of gastropods in his comprehensive memoir of Belgium Namurian faunas, noting that gastropods are essentially restricted to the l'assise d'Andenne (Kinder-scoutian and younger age). However, specimens are crushed in shale and difficult to compare with the present material from Pot Bank Quarry. Demanet (1943) also described gastropods from the Aegiranum marine band (Westphalian, Bolsovian) of Belgium, equivalent to the fauna from the Gin Mine marine band of North Staffordshire (Stobbs & Hind 1905). Bojkowski (1967) listed about 25 gastropod species from the lower Namurian of Poland, and a few species were also described by Korejwo (1969). Namurian gastropods from Germany were reviewed by Amler (2005).

GEOLOGICAL BACKGROUND

Pot Bank Quarry (latitude 53° 7' 50" longitude N; 2° 11' 49" W; National Grid Reference SJ 869 593) is designated site number 322 in the Geological Conservation Review of the Joint Nature Conservation Committee, described by Cleal & Thomas (1996). Pot Bank quarry itself is a V-shaped cut about 300 m long and 15–20 m deep, excavated along the strike of the Lum Edge Sandstone, trending approximately north-east to south-west.

Evans *et al.* (1968) assigned the Pot Bank Quarry succession to the Churnet Shales while recognizing that the interbedded quartzites represented a southerly derived lithofacies distinct from the overlying, northerly derived,

feldspathic sandstones (Middle Grit and Rough Rock Groups) which crop out along the crest of Congleton Edge. This stratigraphic nomenclature has been superseded, however, with the Churnet Shales and underlying Minn Beds of Evans *et al.* (1968) replaced by Morridge Formation, and the overlying Middle Grit and Rough Rock Groups by the Marsden and Rossendale formations, respectively (Waters *et al.* 2009; Fig. 2). The Minn Beds of Evans *et al.* (1968) and the quartzite formerly worked in Pot Bank Quarry (referred to the Cheddleton Sandstone by Turner *et al.* 1994 and to the Lum Edge Sandstone Formation by Cleal & Thomas 1996) represent prominent sandstone units now placed within the Morridge Formation (Waters *et al.* 2009).

MATERIAL

Fossils reported by Evans *et al.* (1968) were collected for the British Geological Survey by C. G. Goodwin in May 1960 and selected BGS specimens are described herein. However, most of the material described herein is derived from my own collections made in 1964–67 from the south-east wall of the quarry, about 110 m north-east of the south-west end of the quarry (Fig. 1, locality 3). At this locality, the uppermost 1 m of the Lum Edge Sandstone and overlying fossiliferous strata (assemblages C, D, F) were exposed in the side of a subsidence hollow produced by collapse of the underlying workings of the sandstone. This hollow appears to be the site of the measured section given by Evans *et al.* (1968, p. 49, table 4, BGS locality 104) and by Turner *et al.* (1994, fig. 3, section 2).

Additional specimens were collected on the same side of the quarry on the southern (downthrow) side of a small fault that cuts east–west through the quarry at about 60 m from the crags at its south-western end (Fig. 1, locality 4, assemblages G and H). Lower strata exposed here may be equivalent in part to unfossiliferous mudstones forming the upper part of the section at locality 3, but assemblages G and H are stratigraphically younger than fossiliferous horizons previously described from the quarry. A few specimens were collected from mudstones at the south-western end of the quarry (Fig. 1, locality 2, assemblage E; locality 106b of Evans *et al.* 1968) above exposures of the Lum Edge Sandstone figured by Cleal & Thomas (1996, fig. 9.6) and comprising section 1 of Turner *et al.* (1994).

C. G. Goodwin collected bivalves and gastropods from alternating sandstones and mudstones about 12 m below the top of the Lum Edge Sandstone at the south-west end of the quarry (Fig. 1, locality 2, assemblage B). This is locality 105 noted by Evans *et al.* (1968) from mudstones about 12 m below its top, but I have not examined this horizon or its fauna.

Probably the stratigraphically oldest fossils described herein comprise an assemblage of mainly high-spired gastropods and bivalves which I collected in 1967 on the upper surface of a thin argillaceous sandstone bed with carbonaceous streaks at the lip of the north-western side of the quarry about 70 m from its south-western end (Fig. 1 locality 1, assemblage A); the stratigraphic relationship of this assemblage to assemblage B is uncertain but both assemblages are dominated by gastropods and bivalves. The sub-horizontal dip of this sandstone at this locality is anomalous in the context of the 40–50° dips evident both regionally and in the quarry itself, and probably reflects deformation associated with an approximately east-west fault passing through the quarry near this point.

GASTROPOD ASSEMBLAGES

Gastropod occurrences are grouped into a series of assemblages for purposes of discussion (Figs 1, 3).

Assemblage A. This is probably the oldest association described here, although its precise stratigraphical position is uncertain (Fig. 1, locality 1), as is its relationship to assemblage B. It contains mainly high-spired gastropods preserved as external moulds in sandstone and less frequent bivalves, some of which are in life position. The gastropods are usually preserved as external moulds which often show significant diagenetic deformation (compare Fig. 12B, C). The fauna is dominated by *Stegocoelia*, with rare *Girtyspira* and *Microptychis* (Figs 3, 12).

Assemblage B. Evans *et al.* (1968; locality 105) reported *Euphemites* sp. associated with abundant bivalves from a mudstone bed with coal streaks at its base (Fig. 1, locality 2; Fig. 3) but this unit has not been examined.

Assemblage C. Assemblage C (Fig. 1, locality 3) lies between the top of the Lum Edge Sandstone and the thin mudstone bed (15–20 cm) with *Hudsonoceras proteus* and *Homoceras smithi* (at about 1.25 m above the ganister) at which the base of the Alportian is placed. Collection 104b of Evans *et al.* (1968) from dark mudstones 0–60 cm below the *Hudsonoceras proteus* marine band includes the holotype and oldest known specimen of *Neilsonia coatesi* sp. nov. (Fig. 10A–D) and a specimen of *Bellerophon* cf. *anthracophilus* (Fig. 3). It is Chokierian in age.

Assemblage D. This assemblage occurs in the mudstone bed (15–25 cm) with *Hudsonoceras proteus* and *Homoceras smithi* which marks the base of the Alportian (Fig. 1, locality 3). It contains small specimens of *Neilsonia coatesi* sp. nov. (Fig. 10E, F) and poorly preserved subulitoideans (Fig. 3).

Assemblage E. Assemblage E is derived from grey shale beds with abundant ironstone nodules and bands which occur between 30 and 60 cm above the *Hudsonoceras proteus* marine band exposed above the small crags of Lum Edge Sandstone at the south-western end of the quarry (Fig. 1 locality 2; Cleal & Thomas 1996, fig. 9.6); this is locality 106b of Evans *et al.* (1968). *Angyomphalus congletonensis*, *Retispira undata*, *R. concinna*, *Euphemites jacksoni* and *Meekospira* (Fig. 3) occur in a richly fossiliferous assemblage dominated by brachiopods and containing *Homoceras smithi*. I examined this horizon only briefly, but *Palaeozygopleura robroytonensis* (Fig. 12G) can be added to this list. Assemblage E is considered to be equivalent to assemblage F from locality 3 (Fig. 1).

Assemblage F. Highly fossiliferous mudstones with bands of sideritic nodules occurring from about 15 cm to 2 m above the goniatite band have yielded assemblage F. In addition to my own collections, two collections listed by Evans *et al.* (1968) contribute to this assemblage. Collection 104f (15 cm–1 m) includes *Euphemites jacksoni*, *Retispira concinna* and *Angyomphalus congletonensis* (Fig. 3); it is considered to be equivalent to assemblage E from locality 2 (Fig. 1). Collection 104g is derived from the overlying, more shaly 1 m and contains *Homoceras smithi* but no gastropods. Most of my own collections from locality 3 are derived from this assemblage (i.e. equivalent to both collections 104f and 104g of Evans *et al.* 1968) where the diverse fauna is rich in specimens of *Bellerophon* cf. *anthracophilus*, *B.* sp., *Retispira concinna*, *R. undata*, *Euphemites jacksoni*, *A. congletonensis* and *Meekospira acrolopha* (Fig. 3).

At locality 3 (Fig. 1) the mudstones yielding assemblage F are overlain by a bed of ganister (30 cm) with a median seam yielding fragments of fish bones and juvenile gastropods. This in turn is overlain by a shell brash limestone (1.5 m) composed almost entirely of valves of schizophoriid brachiopods. Evans *et al.* (1968) noted 6.4 m of mudstones with sideritic nodules above this limestone but recorded only *Lingula* sp. (at 3.3 m above the limestone); I found no gastropods or other fauna. The precise relationship of these mudstones to the section exposed in locality 4 (Fig. 1) is not known since the underlying limestone lies at a lower level and is therefore not exposed at locality 4; there is also evidence of downfaulting to the south of locality 4 relative to locality 3. However, the lower part of the 6–7 m of mudstones exposed at locality 4 may overlap stratigraphically with the mudstones above the shell brash limestone at locality 3.

Assemblage G. Assemblage G is from the lowest 1 m of mudstone at locality 4 (Fig. 1) where two thin bands of partly decalcified buff-coloured nodules yield sharp

external and internal moulds of fossils. Brachiopods dominate but are associated with bivalves and the gastropods *Retispira concinna*, *R. undata* and *Euphemites jacksoni* (Fig. 3).

Assemblage H. This assemblage occurs at the top of the exposure at locality 4 (Figs 1, 3). Two thin bands of partly decalcified sideritic nodules separated by 45 cm of mudstone are followed by a similar band about 1 m higher that was exposed at the lip of the quarry about 7 m to the south-west. The nodules are highly fossiliferous, with sharp external moulds. Productid brachiopods dominate but small bivalves and gastropods are common. The most common gastropods are *Neilsonia ganneyica* and *Glabrocingulum armstrongi*, associated with *Bellerophon*, *Retispira undata*, *Euphemites jacksoni*, *Liraloron cornoviorum*, *Palaeozygopleura robroytonensis*, *Donaldina* sp., *Meekospira* sp., *Leptoptygma* cf. *virgatum*, *Naticopsis* sp., *Amaurotoma* sp. and *Luciellina* sp. (Fig. 3).

Remarks. The three principal assemblages (A, [E+F], H) differ in faunal composition, lithology and preservation. Assemblage A is overwhelmingly dominated by high-spired gastropods and occurs as external moulds in sandstone with carbonaceous streaks. Assemblages E and F yield diverse faunas dominated by bellerophonitoideans, in terms of both specimens and species, and *Angyomphalus congletonensis* from mudstones and ironstone nodules. *Angyomphalus congletonensis* is absent and bellerophonitoideans are uncommon in assemblage H, which is dominated by small gastropods, particularly *Neilsonia ganneyica* and *Glabrocingulum armstrongi*, occurring as external moulds in decalcified nodular horizons. It is evident, however, that this decalcification is conducive to the preservation and determination of small gastropods when compared to the muddy assemblages E and F.

Turner *et al.* (1994) related palynological assemblages from Pot Bank Quarry to changes in the transgressive system tract associated with the *Hudsonoceras proteus* marine band. Detailed sampling between the Lum Edge Sandstone (as Cheddleton Sandstone) and the shell brash limestone, apparently from locality 3 of the present study (Fig. 1C), indicated that the shales containing the diagnostic goniatite represented the maximum flooding surface and period of greatest water depth, following an initial transgressive surface at the top of the sandstone (Turner *et al.* 1994, fig. 6). Thus, gastropod assemblages D–F correspond to this period of maximum marine influence, as might be deduced from both the diversity and abundance of the invertebrate fossil fauna in assemblages E and F, in general. Turner *et al.* (1994) noted that abrasion and fragmentation of brachiopod shells in the shell brash limestone indicated a prolonged period of exposure on the sea floor but considered sequence

stratigraphic interpretation of the overlying, largely unfossiliferous mudstones and shales to be problematic. They suggested the incursion of brackish waters, perhaps associated with deltaic encroachment. Miospores were recorded from about 1 m and 4 m above the limestone, but the assemblages are less diverse than from those below.

This decrease in marine influence proposed by Turner *et al.* (1994) and the lack of fossils provides additional evidence that the section at locality 4 (Fig. 1) mainly lies above that exposed at locality 3. Both assemblages G and H at locality 4 contain abundant brachiopods, especially productids, and bivalves associated with the gastropods, while the larger sample from assemblage H also included nautiloids, scaphopods, bryozoans and a conulariid. Thus, assemblages G and H represent a second advance of open marine conditions after the return to brackish conditions which followed the initial flooding associated with the *Hudsonoceras proteus* marine band. Unfortunately, evidence from goniatites as to the age of this second marine advance is lacking.

AGE OF THE FAUNA

In terms of European subperiods, the gastropods described from Pot Bank Quarry are late Carboniferous (Silesian) in age, from the Chokierian and Alportian substages of the Namurian Regional Stage (Figs 2, 3). This is early Pennsylvanian (Bashkirian Stage) in formal international usage.

Bisat (1924) figured the zonal early Alportian goniatite *Hudsonoceras proteus* (Brown, 1841) characteristic of assemblage D, from just above the quartzites now referred to the Lum Edge Sandstone from Pot Bank Quarry (Fig. 1); it was originally described from the locality by Hind (1902, 1907, 1910, 1918) as *Glyphioceras spirale* (Phillips, 1841). Ramsbottom (1958; in Evans *et al.* 1968) subsequently recognized *Homoceras undulatum* (Brown, 1841) amongst goniatites identified by Hind (1918, p. 438) at Pot Bank Quarry. The latter species indicates a medial Alportian age but the precise point of collection in the quarry relative to the *Hudsonoceras proteus* band is not known. Most of the recorded invertebrate fauna is derived from mudstones with ironstone nodules just above the *Hudsonoceras proteus* marine band but below the prominent shell brash limestone (Fig. 1, assemblages E, F) and Hind's publications do not suggest that any of his collections came from above this limestone. However, the description herein of fossiliferous mudstones occurring some metres above the shell brash limestone (Fig. 1, locality 4, assemblages G, H) indicates that Alportian strata younger than the *Hudsonoceras proteus* Biozone may be present, although I have not collected goniatites

from locality 4. Medial Kinderscoutian goniatites (*Reticuloceras dubium* Biosubzone) were reported by Evans *et al.* (1968, p. 56; National Grid Reference SJ 8642 5843) about 1 km to the south-south-west of Pot Bank Quarry at an estimated 33 m above the *Hudsonoceras proteus* marine band.

Evans *et al.* (1968) suggested a possible correlation of their locality 105 (Fig. 1, locality 2, assemblage B herein) with fossiliferous mudstones (their locality 109) occurring at the top of a sandstone dominated section (National Grid Reference SJ 8640 5855) in a stream in Limekiln Wood, about 600 m to the south-west of Pot Bank Quarry. In this section the *Homoceras beyrichianum* marine band (Evans *et al.* 1968, locality 108) was reported at about 15 m below locality 109, suggesting that 27–30 m of strata separate this late Chokierian marine band from the basal Alportian *Hudsonoceras proteus* marine band exposed in Pot Bank Quarry. However, Bolton (1978) correlated locality 109 in Limekiln Wood with strata occurring above the sandstone in Pot Bank Quarry (Fig. 1, locality 2, assemblage E herein; Cleal & Thomas 1996, fig. 9.6) which suggests that only 15 m of strata (mainly Lum Edge Sandstone) separate the two marine bands.

The assignment by Evans *et al.* (1968) of the fauna from BGS locality 106b to the *Homoceras beyrichianum* marine band (Chokierian) is enigmatic since it is stated to occur in mudstone with abundant *Homoceras smithi* (Brown, 1841) in the accompanying section (Evans *et al.* 1968, p. 49). *Homoceras smithi* occurs together with *Hudsonoceras proteus* in the *Hudsonoceras proteus* marine band. However, in the caption to the table 4 localities 105 and 106 contain overlapping series of specimen numbers (locality 105, YPM 4511–4549; locality 106a, YPM 4530–4532, locality 106b, YPM 4533–87), although localities 105 and 106b are separated by more than 12 m of strata in the accompanying section (Evans *et al.* 1968, p. 49). The British Geological Survey hand written registry entry accompanying the collections made by C. G. Goodwin and identified by W. H. C. Ramsbottom indicates that BGS collections YPM 4533–4557 were derived from 0 to 60 cm above the top of the *Hudsonoceras proteus* marine band exposed at the south-west end of the quarry, while BGS collections YPM 4558–4587 were collected from 30 to 60 cm above the top of the band. Both of these number series were included within locality 106b by Evans *et al.* (1968) but were assigned to just 15 cm of mudstone with abundant *Homoceras smithi* (Brown, 1841) in the accompanying section (Evans *et al.* 1968, p. 49), although only a single fragment of *H. smithi* is recorded in Goodwin's collections. Following the registry entry, BGS collections YPM 4533–4587 (Evans *et al.* locality 106b) are considered herein to be derived from above the *Hudsonoceras proteus* marine band and to be

Alportian; they are referred to assemblage E (Fig. 1, locality 4).

In summary, assemblages A–C are derived from strata below the *Hudsonoceras proteus* marine band and are Chokierian in age. Assemblages D–F are collected within and just above the *Hudsonoceras proteus* marine band and are Alportian. Although appearing in an apparent resurgence of marine conditions later than the flooding event witnessed by the *Hudsonoceras proteus* marine band, assemblages G and H are also considered to be Alportian.

SYSTEMATIC PALAEOLOGY

Repositories. Most illustrated specimens are deposited in the Palaeontology Type Collection of the Museum of Evolution, Uppsala University, Uppsala, Sweden (PMU prefix). Additional material, including non-gastropod material, is deposited in the same museum under accession number 2016:028. Earlier, I deposited some non-gastropod material mainly from assemblage F (Fig. 1, locality 3) in the Sedgwick Museum, Cambridge, where it is stored under accession numbers E 20677–E 20856. The British Geological Survey, Keyworth, houses the extensive collections made by C. G. Goodwin from Pot Bank Quarry listed by Evans *et al.* (1968) and some older material; I have examined selected BGS specimens and a few are figured here (BGS prefix). Specimens of bellerophonitoidean gastropods collected by J. W. Jackson at Pot Bank Quarry and figured by Weir (1931) are deposited in the geological collection of Manchester Museum. I have previously examined this material but it is not re-figured herein.

Class GASTROPODA Cuvier, 1797

Remarks. The schemes proposed by Wenz (1938) and Knight *et al.* (1960) provided homogenous, practical, classifications of Palaeozoic gastropods but are outdated. Advances in the fields of genomics, soft part anatomy and protoconch morphology, the latter particularly relevant to older fossil materials, have brought considerable change in recent years to the picture of gastropod phylogeny, but the early history of the gastropods and the relationship of major taxa largely based on crown groups to many well established Palaeozoic groups (presumably their stem groups) remains unclear. An example is provided by the patellogastropods recognized by Ponder & Lindberg (1995, p. 145) as a group equivalent to the rest of the gastropods, but without a reliable Lower Palaeozoic record. Ponder & Lindberg (1995, 1997) proposed Eogastropoda to include patellogastropods and their undefined Palaeozoic ancestors, but the latter remain largely unidentified. A notable attempt at phylogenetic reorganization based on shell morphology from a Lower Palaeozoic perspective was

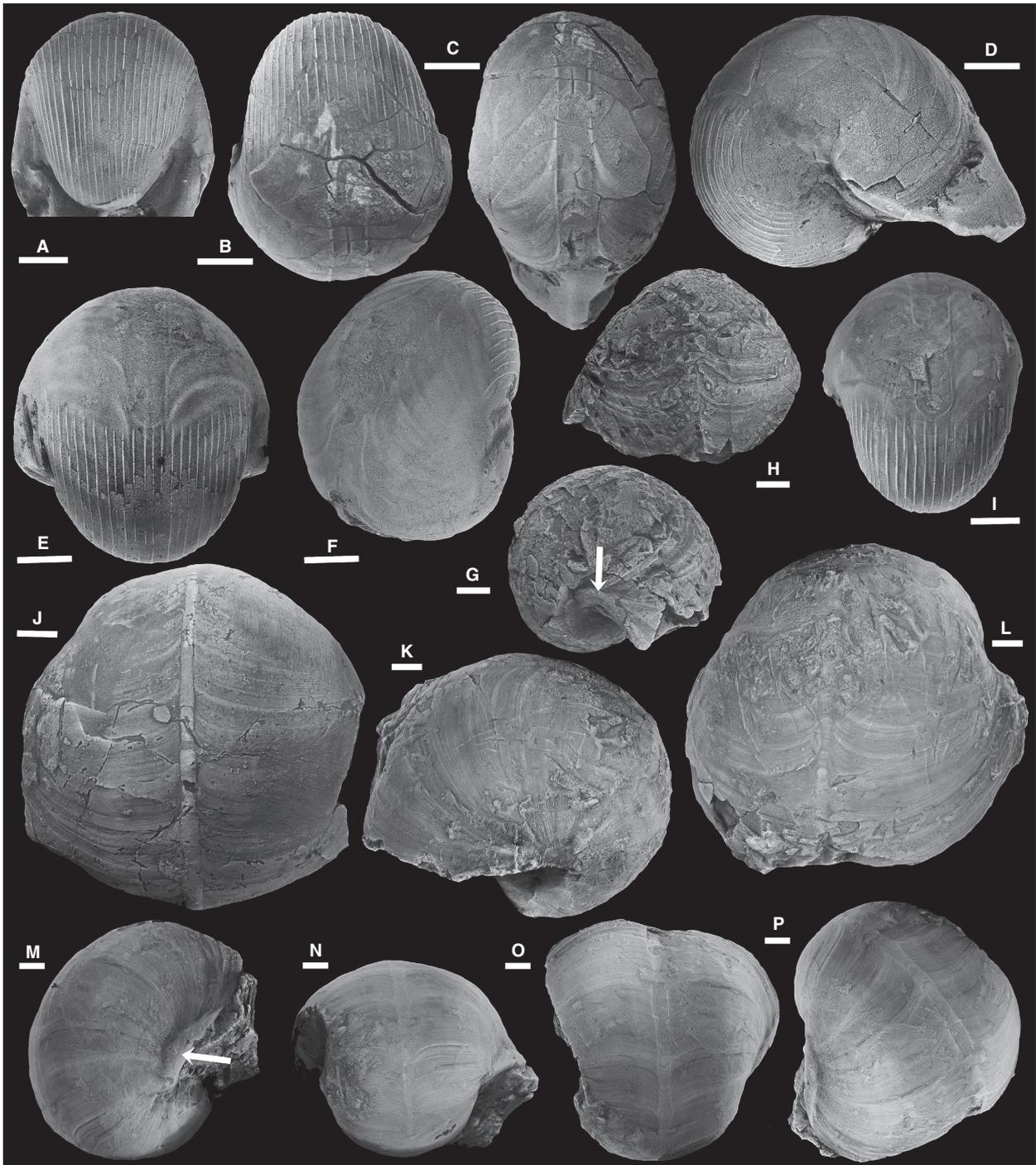


FIG. 4. Bellerophontoidean gastropods from the Morridge Formation, Carboniferous (Namurian, Alportian), Pot Bank Quarry, Congleton Edge, Cheshire. A–F, *Euphemites jacksoni* (Weir, 1931); A–D, PMU 29711, postero-dorsal (A), dorsal (B), antero-dorsal (C) and lateral (D) views; E, F, PMU 29712, dorsal (E) and oblique dorsal (F) views; I, PMU 29713, dorsal view. G, H, J–L, *Bellerophon* cf. *anthracophilus* Frech, 1906; G, H, PMU 29714, lateral view (G) showing the thickened adaxial apertural margin (arrow) and closed umbilicus, and antero-dorsal view (H); J, PMU 29715, dorsal view; K, L, PMU 29716, lateral (K) and slightly oblique dorsal (L) views. M–P, *Bellerophon* sp. A, PMU 29717; oblique lateral view (M) showing umbilicus closed by thickened axial lip (arrow) and postero-dorsal (N), dorsal (O) and oblique dorsal (P) views. All specimens from assemblage F (Fig. 1, locality 3). All scale bars represent 2 mm.

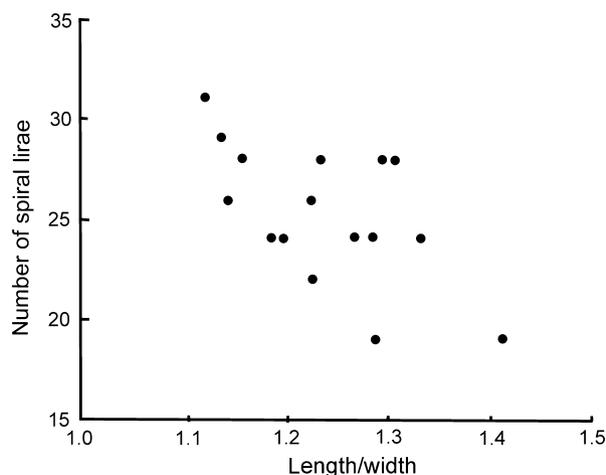


FIG. 5. Relationship between shell shape and number of spiral lirae in *Euphemites jacksoni* (Weir, 1931) from assemblage F (Fig. 1, locality 3), Pot Bank Quarry.

made by Wagner (2002), representing a radical revision of the scheme produced by Knight *et al.* (1960).

The embracive system presented by Bouchet & Rocroi (2005) is a milestone in gastropod classification, although its laudable objectivity as a working document serves to further emphasize the uncertainty surrounding many Palaeozoic gastropod groups. Many well known superfamilies (clisospiridae, loxonematidae, trochonematidae, etc.) and numerous families (anomphalids, holopeids, raphistomatids, sinuopeids, etc.) were accepted as Gastropoda but not assigned at a higher level (Bouchet & Rocroi 2005, p. 241). Euomphaloideans and macluritoideans were considered to be of 'uncertain position within Mollusca (Gastropoda?)' while others (bellerophontoideans, archinacelloideans, pelagielloideans, etc.) were 'uncertain position within Mollusca (Gastropoda or Monoplacophora)'.

A full review of the current status of gastropod phylogeny in the Palaeozoic was given by Frýda (2012) but a classification was not presented. In the present context, classification above superfamily is not given since such relationships generally are not discussed.

Superfamily BELLEROPHONTOIDEA M'Coy in Sedgwick & M'Coy, 1852

Remarks. The systematic position of bellerophontiform molluscs was reviewed by Peel (1991a), Wahlman (1992), Geyer (1994), Harper & Rollins (2000) and Frýda & Rohr (2004). Members of the group are variously considered to be gastropods, untorted molluscs or a mixture of both groups. Bellerophontiform molluscs have often been placed within Amphigastropoda Simroth, 1906, but this term has been employed at class, sub-class and order

levels for various constellations of genera. Frýda *et al.* (2008) and Frýda (2012) developed earlier suggestions (e.g. Peel 1991a) that bellerophontiform molluscs are polyphyletic. This point of view is supported herein and bellerophontoideans are considered to be gastropods.

The starting point for the description of bellerophontoidean gastropods from Pot Bank Quarry is the monograph of Weir (1931) which describes 77 species from the Carboniferous of Britain and Belgium. Most of these are of early Carboniferous age (Dinantian; Tournaisian and Viséan) reflecting the fully marine carbonate-dominated successions. The Namurian record is much reduced, but Weir (1931) described three species which are common at Pot Bank Quarry: *Retispira concinna* (Weir, 1931), *R. undata* (Etheridge, 1876) and *Euphemites jacksoni* (Weir, 1931). Given the extent and uniformity of Weir's (1931) study, little attempt is made to revise his systematic concept. Additionally, his illustrations are often small and insufficient, making comparisons with other described taxa difficult; in Weir's (1931) account the three named species are each represented from Pot Bank Quarry by only a single specimen in dorsal view. Nevertheless, discrimination of the species at Pot Bank Quarry is unequivocal. Specimens figured by Weir (1931) from Pot Bank Quarry in the J. W. Jackson collection, geological collections of Manchester Museum, have been examined but are not figured here. Surprisingly, Weir (1931) did not record *Bellerophon* Montfort, 1808 from Pot Bank Quarry; two species are described herein, together with specimens of the less common *Patellilabia britannica* sp. nov. and a single specimen of *Retispira mowensis* sp. nov.

Family BELLEROPHONTIDAE M'Coy in Sedgwick & M'Coy, 1852

Genus BELLEROPHON Montfort, 1808
Bellerophon cf. *anthracophilus* Frech, 1906
Figure 4G, H, J-L

Figured material. PMU 29714–29716, all from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. More than 30 specimens, mainly from assemblage F (Fig. 3).

Remarks. This species is referred to Weir's (1931, p. 782) 'group of *Bellerophon hiulcus*' on account of its globular form, closed umbilici and narrow, simple, selenizone. Comparison is made to *Bellerophon anthracophilus* Frech, 1906, a form frequently preserving comarginal undulations on the dorsum, although Weir (1931) noted that specimens with a smooth dorsum often occur together with undulose

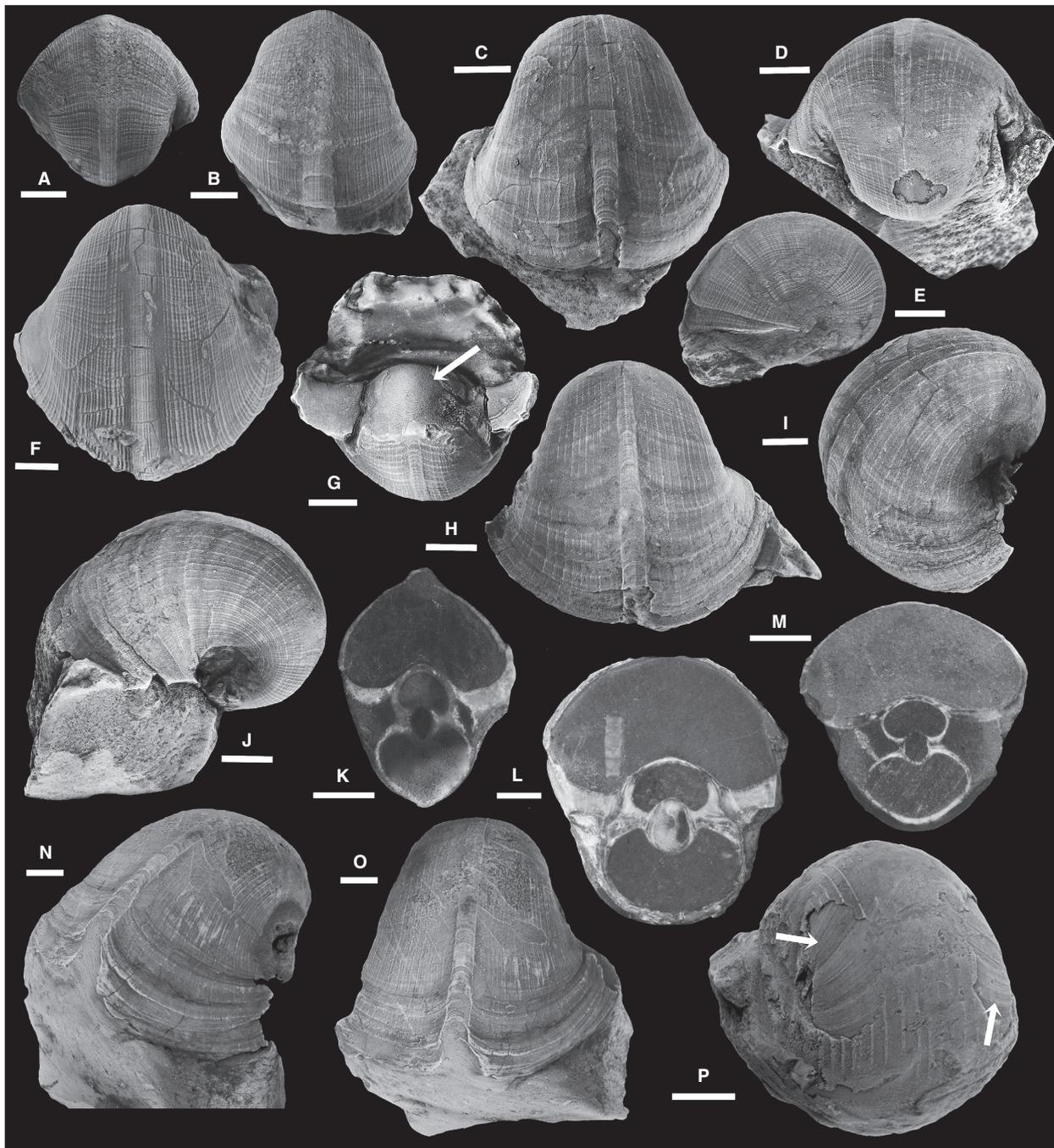


FIG. 6. Bellerophontoidean gastropods from the Morridge Formation, Carboniferous (Namurian, Alportian), Pot Bank Quarry, Congleton Edge, Cheshire. A, B, E, F, K, *Retispira concinna* (Weir, 1931); A, B, E, PMU 29718 in dorsal (A), antero-dorsal (B) and lateral (E) views; F, PMU 229719 in antero-dorsal view; K, PMU 29720, slightly off-centre cross-section showing open umbilici. C, D, G–J, M–O, *Retispira undata* (Etheridge, 1876); C, I, PMU 29721, antero-dorsal (C) and oblique dorsal (I) views; D, H, J, PMU 29722, postero-dorsal (D), antero-dorsal view (H) and lateral view showing the open umbilicus (J); G, PMU 29723, apical view with apertural margins broken away, showing industrial pad (arrow); M, PMU 29724, slightly off-centre cross-section showing open umbilici; N, O, PMU 29725, oblique (N) and antero-dorsal (O) views showing comarginal undulations. L, *Bellerophon* sp. A, PMU 29726, slightly off-centre cross-section showing filled umbilici. P, *Euphemites jacksoni* (Weir, 1931); PMU 29727, oblique view showing dorsal shell surface with growth lines (arrows) exposed below exfoliated industrial later with spiral lirae. All specimens from assemblage F (Fig. 1, locality 3). All scale bars represent 2 mm.

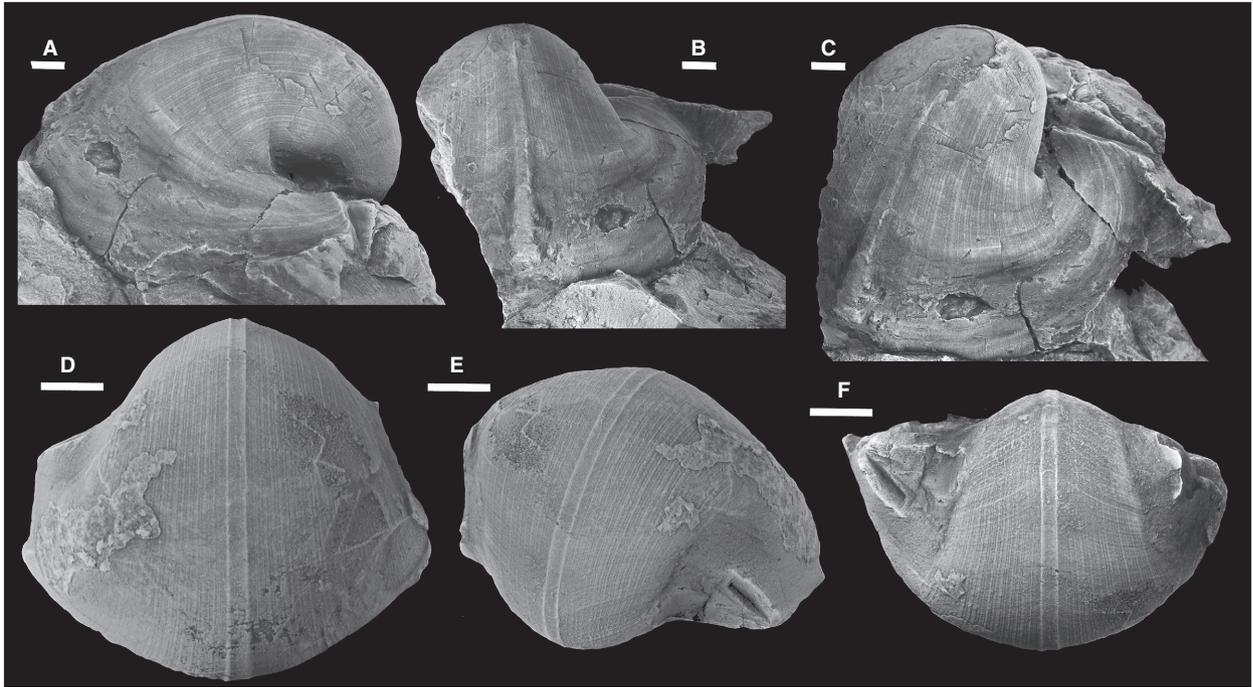


FIG. 7. *Patellilabia britannica* sp. nov. from the Morridge Formation, Carboniferous (Namurian, Alportian), Pot Bank Quarry, Congleton Edge, Cheshire. A–C, PMU 29728, holotype, in lateral (A), antero-dorsal (B) and oblique antero-dorsal (C) views. D–F, PMU 29729, paratype, in dorsal (D), oblique postero-dorsal (E) and postero-dorsal (F) showing the concave selenizone between bounding cords. All specimens from assemblage F (Fig. 1, locality 3). All scale bars represent 2 mm.

specimens. While some specimens show a periodicity in the degree of expression of the growth lines producing a fasciculate appearance (Fig. 4G, H), it is the smooth form which occurs at Pot Bank Quarry (Fig. 4J–L).

Specimens of *B. cf. anthracophilus* often occur partially crushed in mudstones of assemblage F (Fig. 1, locality 3) but attain a length of up to 20 mm. Specimens are easily damaged on extraction from the mudstones, resulting in loss of the lateral extremities and apertural margin (Fig. 4J, right side). However, the greater rate of whorl expansion in Figure 4G, H compared to Figure 4J–L causes the thickened adaxial margins in the former (arrowed in G) to diverge strongly antero-laterally from their junction with the earlier whorl. The umbilici are closed. The growing edge of the aperture is slightly reflexed in the axial region, such that close stacking of successive growth increments produces a thickened apertural margin which may be bounded by a narrow channel on its dorsal side on both sides of the shell (arrow in Fig. 4G). The upper surface of the narrow selenizone is shallowly convex or flattened, bounded by fine grooves (Fig. 4J) or threads (Fig. 4H) and ornamented by numerous fine lunulae.

Due to its smooth dorsum, the *B. cf. anthracophilus* resembles a specimen referred to *Bellerophon hiulcus* Sowerby, 1824 by Weir (1931, pl. 1, fig. 6). The reliability of the comarginal undulations as a taxonomic character

can be questioned since large specimens of *Retispira undata* (Etheridge, 1876) and *Patellilabia britannica* sp. nov. from Pot Bank Quarry also display the character (Figs 6N, O; 7A–C). Growth lines in the Pot Bank Quarry material have less apertural convexity than most of the specimens of *B. anthracophilus* illustrated by Weir (1931). Weir (1931) based his description of *B. anthracophilus* on Scottish material, mainly from the Upper Limestone Formation (Namurian, Pendleian–Arnsbergian) where the species attains its maximum development. However, his description emphasized the high degree of variation described by Frech (1906) and Klebelsberg (1912) in specimens from the Silesian (Namurian) of central Europe, and by Delépine *in* Dordolot & Delépine (1930) from the Namurian of Belgium. Indeed, Weir (1931) also included material assigned to *Bellerophon tenuifascia* (Sowerby 1823–25) by Klebelsberg (1912) and Delépine *in* Dordolot & Delépine (1930) in his concept of the species. Specimens illustrated by Demanet (1941) from the Namurian of Belgium as *Bellerophon anthracophilus* are crushed in shale and difficult to compare with Weir's (1931) illustrations, but also seem to lack comarginal undulations. Schwarzbach (1937) described a stratigraphic sequence of mutations of *B. anthracophilus* and his closely related species *B. eoanthracophilus* from the Ostrava Formation

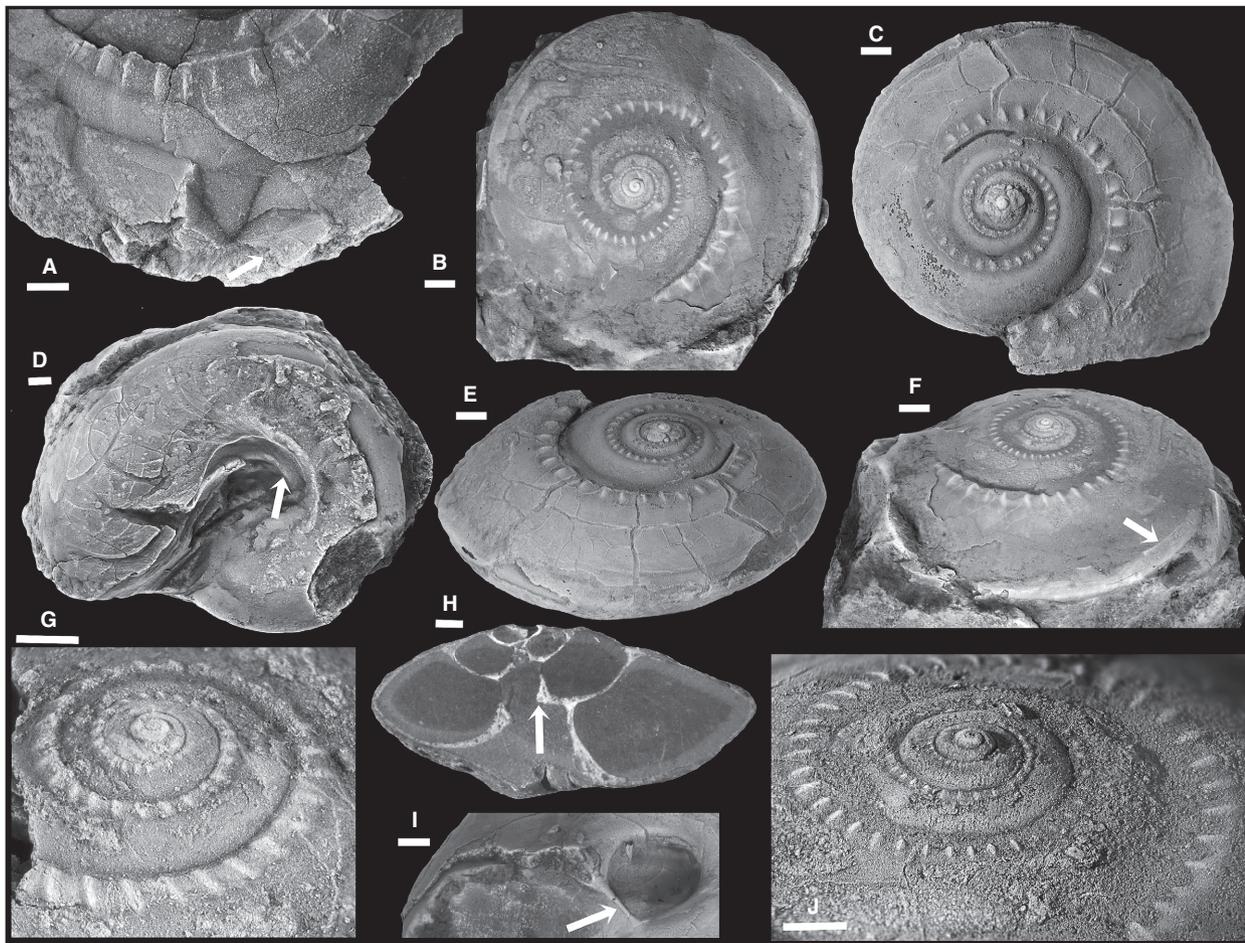


FIG. 8. *Angyomphalus congletonensis* sp. nov. from the Morridge Formation, Carboniferous (Namurian, Alportian), Pot Bank Quarry, Congleton Edge, Cheshire. A, PMU 29730, paratype, detail of apertural margin on upper whorl surface showing selenizone (arrow). B, F, J, PMU 29731, holotype, in apical (B) and oblique apical (F) views, with detail of early whorls (J); arrow indicates upper margin of selenizone. C, E, PMU 29732, paratype, in apical (C) and oblique apical (E) views. D, PMU 29733, paratype, basal view showing growth ornamentation, funicle (arrow) and circumbilical ridge around open umbilicus. G, PMU 29734, paratype, oblique apical view of early whorls. H, PMU 29735, paratype, transverse polished section showing open umbilicus and circumbilical funicle (arrow). I, PMU 29736, paratype, oblique basal view showing umbilicus, and thin inner lip (arrow) passing into thickened funicle and basal lip. All specimens from assemblage F (Fig. 1, locality 3). All scale bars represent 1 mm.

(Ostrauer Schichten; early Namurian) of the Upper Silesian coal basin, but these appear to be based on specimens strongly affected by compaction or deformation. *Bellerophon anthracophilus* was also reported from similar sections in Poland by Bojkowski (1967) and from Belgium by Demanet (1943). Wilson & Thompson (1959) listed *B. anthracophilus* from the Colsterdale marine band (Namurian, Arnsbergian) of Yorkshire. De Stefani (1917) assigned material from the Carboniferous of Elba to Frech's (1906) species, placing it within *Pharkidonotus* Girty, 1912, but the species assignment is rejected herein.

Xi (1994) described the new species *Bellerophon huashibanensis* from the Weining Formation (Namurian) of Guizhou, China, stating that it resembled *B. anthracophilus* except in the absence of irregularly fasciculate or

wrinkled comarginal ornamentation. It compares closely with specimens illustrated here as Figure 4J–L. However, the greater rate of whorl expansion in Figure 4G, H causes the thickened adaxial margins (arrowed in G) to diverge more strongly antero-laterally from their junction with the earlier whorl.

Bellerophon sp. A
Figures 4M–P, 6L

Figured material. PMU 29717 and 29726 (Fig. 6L) from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.



FIG. 9. Pleurotomariiform gastropods from the Morridge Formation, Carboniferous (Namurian, Alportian), Pot Bank Quarry, Congleton Edge, Cheshire. A–C, E, J, *Liraloron cornoviorum* gen. et sp. nov.; A–C, E, PMU 29737, holotype, latex cast, lateral (A), oblique apical (B), apical (C), oblique lateral (E) views showing spiral ornamentation and selenizone high on whorl profile; J, PMU 29738, paratype, latex cast, lateral view of axially crushed specimen; both specimens from assemblage H (Fig. 1, locality 4). D, G, H, K, O, R, *Eirlysia ceramicorum* sp. nov.; D, H, R, BGS T4959A, holotype, apical view (D) with initiation of selenizone arrowed, lateral view (H), oblique lateral view (R); G, PMU 29739, paratype, oblique lateral view; K, O, PMU 29740, paratype, oblique lateral views with detail of spirally ornamented early whorl (O, arrow); paratypes from assemblage F (Fig. 1, locality 3), holotype likely so. F, I, *Amaurotoma* sp., PMU 29741, latex mould, in lateral view (F) and detail of broad sinus on outer whorl (I, arrow); assemblage H (Fig. 1, locality 4). L, M, P, Q, *Glabrocingulum armstrongi* Thomas, 1940; L, Q, PMU 29742, latex cast, in apical view (L) showing the initiation of the selenizone (arrow) and in oblique lateral view (Q) with arrow indicating suture between spirally ornamented juvenile and tuberculate, selenizone-bearing teleoconch; M, PMU 29743, latex cast showing transition from spirally ornamented juvenile shell to tuberculate and selenizone-bearing teleoconch; P, PMU 29744, latex cast, oblique lateral view showing transition from juvenile shell to teleoconch; assemblage H (Fig. 1, locality 4). N, *Luciellina* sp., PMU 29745, latex cast, oblique lateral view showing peripheral selenizone (arrow); assemblage H (Fig. 1, locality 4). All scale bars represent 1 mm.

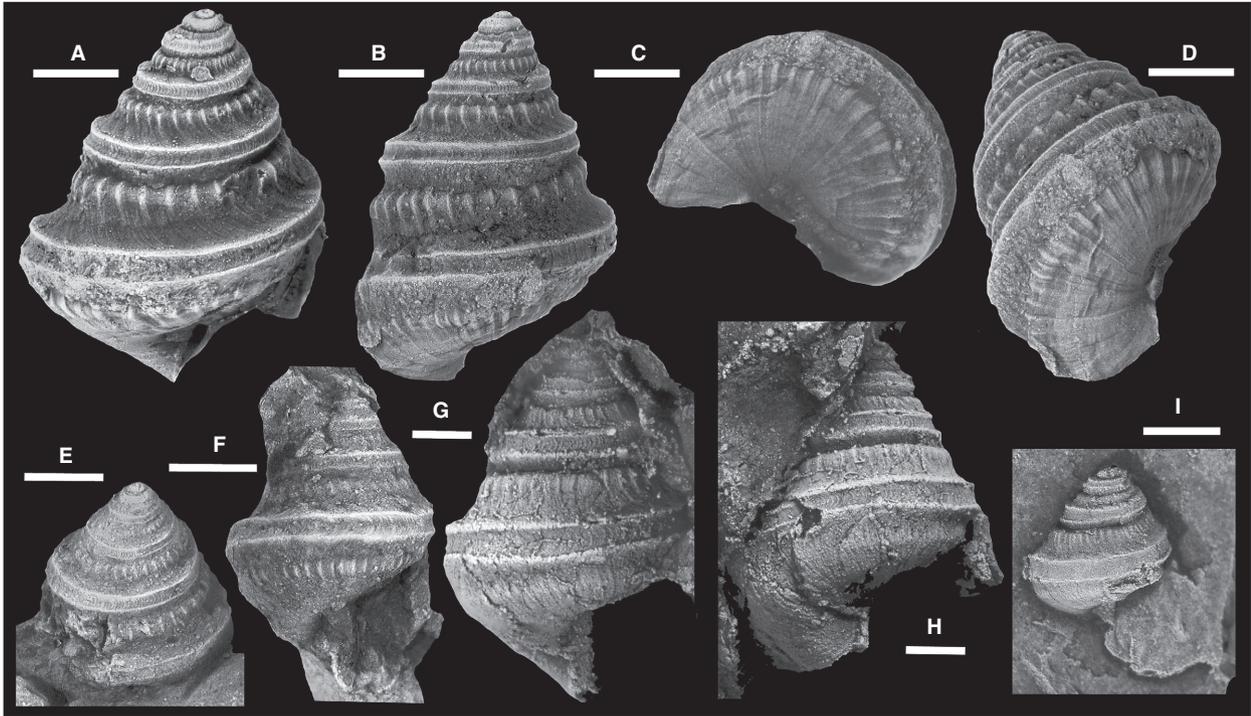


FIG. 10. *Neilsonia* from the Morridge Formation, Carboniferous (Namurian, Chokierian–Alportian), Pot Bank Quarry, Congleton Edge, Cheshire. A–F, *Neilsonia coatesi* sp. nov.; A–D, BGS YPF 4664a, holotype, in oblique lateral (A), lateral (B), basal (C) and baso-lateral (D) views; assemblage C (Chokierian), probably from locality 3 (Fig. 1); E, PMU 29746, paratype, oblique lateral view of spire; F, PMU 29747, paratype, lateral view; E, F from assemblage D (Alportian), locality 3 (Fig. 1). G–I, *Neilsonia ganneyica* sp. nov., latex casts from assemblage H (Fig. 1, locality 4); G, H, PMU 28748, holotype, lateral view (G) and oblique lateral view showing prominent repaired injury traversing final whorl (H); I, PMU 28749, paratype. All scale bars represent 1 mm.

Remarks. *Bellerophon* sp. A is similar to *Bellerophon* cf. *anthracophilus* and poorly preserved specimens of the two species are difficult to separate. It differs from the latter in having a lower rate of whorl expansion, producing a narrower shell, and a wider selenizone bounded by fine threads (Fig. 4N–P). The umbilici are closed in both species

(Fig. 4G, M) and growth lines show a similar degree of adapertural convexity. As in *B. cf. anthracophilus*, the apertural margin is thickened in the axial region (arrow in Fig. 4M). *Bellerophon* sp. A has a wider selenizone than *B. huashibanensis* described by Xi (1994) from the Weining Formation (Namurian) of Guizhou, China.

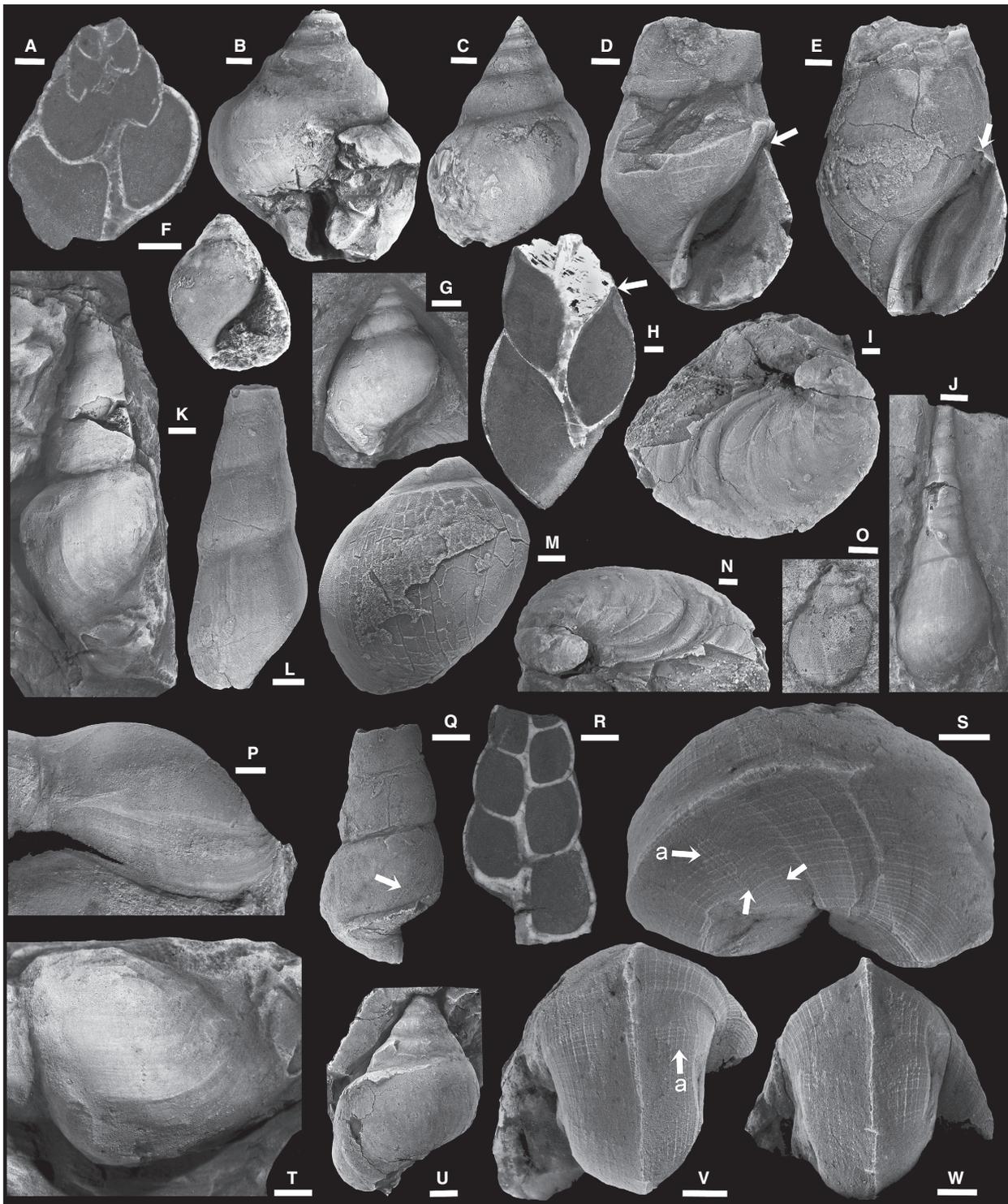
FIG. 11. Gastropods from the Morridge Formation, Carboniferous (Namurian), Pot Bank Quarry, Congleton Edge, Cheshire. A, C, U, *Leptotygyma* cf. *virgatum* (Knight, 1931b); A, PMU 29750, slightly off-centre, transverse cross-section with crushed early whorls showing smooth columella; C, PMU 29751, lateral view; U, PMU 29752, lateral view of slightly crushed specimen. B, *Leptotygyma* sp. A. PMU 29753, apertural view with damaged aperture. D, E, H, J–L, P, T, *Meekospira acrolopha* sp. nov.; D, PMU 29754, paratype, apertural view of broken specimen showing reflexed columellar lip and sub-sutural notch (arrow); E, PMU 29755, paratype, broken specimen in apertural view showing reflexed columellar lip and sub-sutural notch (arrow); H, PMU 29756, paratype, transverse cross-section showing smooth columella and sub-sutural notch (arrow); J, PMU 29757, paratype, lateral view; K, T, PMU 29758, holotype, in lateral view showing expanded final whorl (K) and detail of final whorl showing growth lines (T); L, PMU 29759, paratype, lateral view showing pendant whorl profile; P, PMU 29760, paratype, lateral view of final whorl showing slightly sinuoidal growth lines. F, G, *Leptotygyma* sp. B; F, PMU 29761, apertural view; G, PMU 29762, lateral view. I, N, *Platyceras* sp. BGS T 4979A, in apical (I) and oblique lateral views (N); probably assemblage F. M, *Naticopsis* sp. PMU 29763, lateral view. O, *Girtyspira* sp., PMU 29774; latex cast in lateral view from assemblage A (Fig. 1, locality 1). Q, R, *Platyconcha* cf. *hindi* Longstaff, 1933; PMU 29764, lateral view (Q) showing growth lines (arrow) and polished transverse cross-section (R). S, V, W, *Retispira mowensis* sp. nov., PMU 29765, holotype, in dorso-lateral (S), dorsal (V) and postero-dorsal (W) views; arrows indicate repaired shell injuries discussed in the text, with arrow a identifying the same fracture; assemblage F (Fig. 1, locality 3), except O. Scale bars represent 1 mm, except K which is 2 mm.

Genus RETISPIRA Knight, 1945a

Type species. Retispira bellireticulata Knight, 1945a.

Remarks. Retispira was considered to be a subgenus of *Knightites* Moore, 1941 by Knight *et al.* (1960).

Subsequent authors have been divided in accepting this placement (e.g. Yoo 1988, 1994) or maintaining full generic status (e.g. Batten 1972; Gordon & Yochelson 1987; Kues & Batten 2001). Weir (1931) assigned Carboniferous bellerophontoideans with reticulate ornamentation to *Bucaniopsis*, an unjustified spelling emendation of



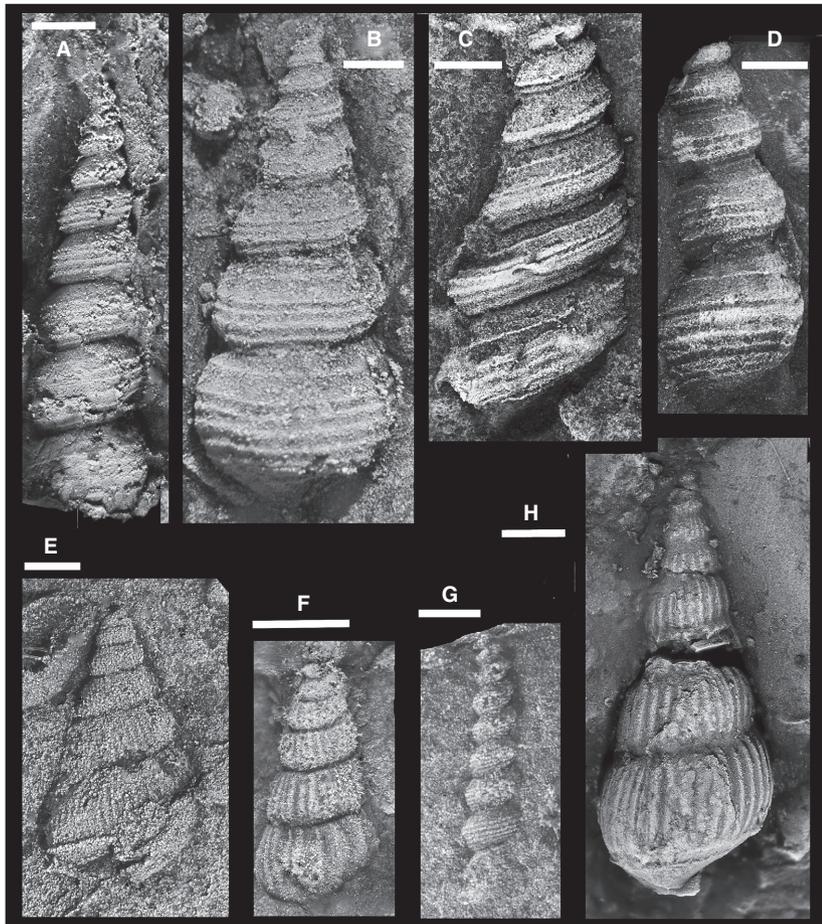


FIG. 12. Gastropods from the Morridge Formation, Carboniferous (Namurian), Pot Bank Quarry, Congleton Edge, Cheshire. A, G, *Donaldina* sp.; A, PMU 29766, lateral view; G, PMU 29767, lateral view; assemblage F (Fig. 1, locality 4). B–D, *Stegocoelia* sp.; B, PMU 29768; C, PMU 29769; D, PMU 29770; latex casts in lateral view from assemblage A (Fig. 1, locality 1). E, *Microptychis* sp., PMU 29771, latex cast, lateral view of crushed specimen from assemblage A (Fig. 1, locality 1). F, H, *Palaeozygopleura roboystonensis* (Longstaff, 1933); F, PMU 29772, latex cast in lateral view from assemblage H (Fig. 1, locality 4); H, PMU 29773, lateral view of fractured specimen, assemblage E (Fig. 1, locality 2). All scale bars represent 1 mm.

Bucanopsis Ulrich in Ulrich & Scofield, 1897 employed by Cossmann (1904, p. 109) and Reed (1921, p. 58).

Weir (1931, p. 817) recognized two principal groups of species within *Bucaniopsis* (= *Retispira*). A 'group of *Bucaniopsis decussatus*' contained species without notable expansion of the aperture and its members are readily assigned to *Retispira*. In contrast, a 'group of *Bucaniopsis striatus*' included species with expanded apertures and, in some cases, a prominent industrial plug within the aperture. Both these characters are features of *Patellilabia* Knight, 1945a and it is likely that with revision some of the four species he placed in the group should be assigned to that genus.

Retispira concinna (Weir, 1931)

Figure 6A, B, E, F, K

1931 *Bucaniopsis concinnus* Weir, p. 824, pl. 9, figs 24, 25.

Figured material. PMU 29718–29720, all from assemblage F (Fig. 1, locality 3). Paratype, specimen LL 250 in the geological

collection of Manchester Museum figured by Weir (1931, pl. 9, fig. 25). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. More than 70 specimens from assemblage F (Fig. 3); rare specimens from assemblages E and G.

Description. Species of *Retispira* with convex dorsum arched at raised median selenizone; rate of whorl expansion, measured as the ratio of the width of consecutive whorls (Fig. 6K), of about three, with maximum whorl width low on the whorl cross-section, near the open umbilici (Fig. 6K). Whorl width increasing to equal length in mature specimens. Aperture sub-planar with straight or even shallowly concave dorso-lateral margins (Fig. 6F) passing via shallow sinus into short, broad, median slit which generates a raised, convex, selenizone ornamented with numerous spiral cords crossed by shallow growth lines (Fig. 6A, B, E). Ornamentation dominated by spiral cords of several size orders, crossed by growth lines to form a fine reticulation which is finely nodose at intersections. Additional spiral cords introduced as fine threads between pre-existing spiral elements. Growth lines may be periodically thicker and accompanied by slight comarginal folding on the dorsum (Fig. 6B), but only weakly expressed in the latest growth stages of larger specimens (Fig. 6E).

Remarks. The holotype of *Retispira concinna* figured by Weir (1931, pl. 9, fig. 24) is from the Lower Limestone Formation (Dinantian, late Visean) of northern England, but Weir (1931, p. 824) reported the species also from the Upper Limestone Formation (Namurian, Arnsbergian), as well as from Pot Bank Quarry (Namurian). In his introductory discussion, Weir (1931, p. 776) inadvertently referred the Pot Bank Quarry occurrence of *R. concinna* to *R. densistriata* (Weir, 1931). *Retispira concinna* closely resembles *R. decussata* (Fleming, 1828 of Weir, 1931) which is widely distributed in the Lower Limestone and Upper Limestone formations of Scotland. Weir (1931, p. 824) considered the ornamentation of *R. concinna* to be much finer than that of *R. decussata* and the band to be less conspicuous, but the available sample from Pot Bank Quarry suggests that these characters are quite variable. The largest available specimen (Fig. 6F) shows the dominance of spiral ornamentation over comarginal ornamentation also seen in large specimens of the contemporaneous *R. undata* (Fig. 6N, O).

Retispira undata (Etheridge, 1876)

Figure 6C, D, G–J, M–O

- 1876 *Bellerophon decussatus* var. *undatus* Etheridge, p. 155, pl. 6, figs 9, 10.
 1878 *Bellerophon decussatus* var. *undatus*; Etheridge, p. 19, pl. 2, fig. 30.
 1931 *Bucaniopsis undatus*; Weir, pp. 826–828, pl. 4, figs 13–16.

Figured material. PMU 29721–29725, all assemblage F (Fig. 1, locality 3). Specimen LL 249, figured by Weir (1931, pl. 4, fig. 16), is in the geological collection of Manchester Museum. Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. About 50 specimens from assemblage F (Fig. 3) and rare specimens from assemblages E, G and H.

Description. Species of *Retispira* with uniformly convex dorsum and a rate of whorl expansion of about 3.5, measured from the width of successive whorls (Fig. 6M). Aperture reniform in cross-section (Fig. 6M), its margin periodically slightly flared in latest growth stage to produce dorsal undulations in larger specimens (Fig. 6N, O). A low median pad of inductura is deposited on the floor of the whorl covering the dorsum of the previous whorl (Fig. 6G). Dorso-lateral apertural margins almost straight near the umbilici (Fig. 6J) but becoming increasingly convex, adaperturally (Fig. 6C, H–J, N, O), prior to passage into a broad but shallow median sinus and a short slit which generates a flat-topped

selenizone bounded by spiral cords (Fig. 6N, O). Selenizone varies between slightly depressed to raised, but becomes raised in the final growth stage (Fig. 6C, O). Selenizone ornamented by a single median cord (Fig. 6D, H) which becomes inconspicuous in the latest growth stage (Fig. 6N, O), crossed by numerous concave lunulae. Ornamentation dominated by spiral cords, usually of two size orders, crossed by growth lines and forming small nodes at the intersections; additional spiral elements introduced as fine threads between pre-existing cords. Growth lines becoming more pronounced and lamellar in later growth stages (Fig. 6J, N, O), accompanied by comarginal undulations.

Remarks. Specimens of *R. undata* from Pot Bank Quarry are usually larger than the contemporaneous *R. concinna* and differ in that the selenizone is flat-topped, usually with a single median spiral thread and sharp bounding threads (Fig. 6C, I, N). In contrast, the selenizone in *R. concinna* is convex with numerous spiral threads (Fig. 6A, B, F). *Retispira concinna* also has a lower rate of whorl expansion and more vaulted cross-section than *R. undata* (compare Fig. 6K, M).

Weir (1931) illustrated *Retispira undata* from the Dinantian Calciferous Sandstone Measures of Scotland, the late Dinantian of northern England, the Namurian of Pot Bank Quarry and the early Westphalian of the Bristol Coalfield. Brand (2011) listed Namurian occurrences in the Stainmore Formation of northern England.

Retispira mowensis sp. nov.

Figure 11S, V, W

LSID. urn:lsid:zoobank.org:act:8F6F9C75-639C-4B3A-B241-0B4F637544F6

Derivation of name. From the nearby community of Mow Cop, at the south-western termination of Congleton Edge.

Holotype. PMU 29765 from assemblage F (Fig. 1 locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Diagnosis. Species of *Retispira* with prominent, acute, median dorsal keel bearing a narrow selenizone.

Description. Species of *Retispira* with an acute median keel on final whorl (Fig. 11W). Dorsal profile arched medially, passing rapidly around dorso-lateral extremities into open umbilici. Adaperturally convex growth lines indicate aperture with broad, shallow, dorsal emargination culminating in a median slit of unknown depth. At the earliest observed growth stage, about one whorl prior to the aperture, the selenizone is flat-topped and flush with the upper surface of the dorsum (Fig. 11W, lower edge). Subsequently, the keel rises with concave sides above the surface of the dorsum, with the narrow selenizone forming its

acute upper edge. Apertural margins with slight constrictions in rate of expansion producing undulose and periodically rugose growth lines (Fig. 11S). Ornamentation dominated by spiral cords of two or three size orders crossed by growth lines.

Remarks. In contrast to co-occurring specimens of *Retispira concinna* and *R. undata*, this species has a strongly keeled dorsum. The single specimen has been subject to compaction such that the latest growth stage is bent in towards the axis of coiling but this deformation has not affected the bilateral symmetry around the median dorsal, selenizone, plane (Fig. 11V, W). The specimen clearly shows shell repair following non-lethal predatory attacks during its life time, but these have not affected its symmetry significantly.

Retispira mowensis compares most closely with *R. nodulifera* Hoare, 1961 from the Pennsylvanian (Desmoinesian) of Missouri, in which the prominent median keel is topped by a series of nodes, apparently representing periodically developed rugose lunulae which may be equivalent to similarly spaced prominent comarginal ribs on the dorsal areas. Similar prominent comarginal ribs, growth lines produced by slight flaring of the apertural margin, are visible in the latest growth stage of *R. mowensis* (Fig. 11S) but also in *R. undata* (Fig. 6N, O). The development of a keel which rises with concave sides above the surface of the dorsum and carries the narrow selenizone at its acute upper edge has been described by Peel (1991b, p. 84) and is often seen in bucaniiform bellerophontoideans.

After about a third of a whorl, a distinct transverse dislocation in ornamentation (arrow a in Fig. 11S, V) indicates a repaired fracture on the dorsal surface extending from an impacted area on the umbilico-lateral shoulder; it is quickly followed by two similar fractures (arrowed in S). The three repaired injuries are restricted to the right side of the shell (as viewed in Fig. 11V) and no equivalent dislocations have been discerned on the left side. The shell resumes normal regular growth after (adapertural) the final repaired fracture, although slight comarginal undulations and periodic rugosities occur in later growth stages (Fig. 11S).

Numerous examples of failed predation on bellerophontiform molluscs have been described (summary in Ebbestad *et al.* 2009) where the distribution of repaired injuries usually indicates attack strategies focused on breakage of the aperture.

Genus PATELLILABIA Knight, 1945a

Type species. *Patellilabia tentoriolum* Knight, 1945a, Pennsylvanian of Missouri, USA.

Remarks. Knight (1945a) erected two new bellerophontoid genera with characteristic spiral ornamentation

crossed by comarginal growth elements: *Retispira* and *Patellilabia*. He distinguished the latter from the former mainly by its anteriorly expanded aperture which becomes explanate, with margins extending back beyond the earlier coiled portion of the shell (Knight 1945a, pl. 49, figs 3a–f). While the type species of the genera lie at opposing ends of a morphological spectrum, as regards the degree of expansion of the aperture, subsequent authors have assigned to *Patellilabia* species in which the expansion of the apertural margins is not so extensive as in the type species; this is also the case for *Patellilabia britannica* sp. nov., described herein. However, other characteristic features of *Patellilabia* include a prominent inductural boss within the aperture and ornamentation dominated by flat-topped, broad spiral cords. The tendency to develop an expanded late growth stage is seen in a number of bellerophontoidean gastropods and Peel (1975, 1977, 1978, 1984) suggested it was an adaptation to life on a soft bottom, the snow shoe effect also discussed by Gubanov *et al.* (1995). An explanate aperture and apertural boss are developed in *Anapetopsis* Peel, 1975 but in this bell-shaped late Silurian genus comarginal growth lines dominate the later growth stages in contrast to the spiral ornamentation of *Patellilabia*. Pan & Erwin (2002) recognized an *Extendilabrum* assemblage from deeper water sediments of the upper Permian Dalong Formation, Guizhou, China, characterized by a series of genera (*Extendilabrum*, *Aiptospira*, *Singulitubulus*, *Tetratubispira* all of Wang in Wang & Xi, 1980) which may prove to be synonyms of *Patellilabia*.

Patellilabia britannica sp. nov.

Figure 7

LSID. urn:lsid:zoobank.org:act:4812CB51-7A0C-47AC-A54B-B74F186A414A

Derivation of name. From *Britannia* (Latin), for Britain.

Holotype. PMU 29728. Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire (Fig. 1, locality 3, assemblage F).

Figured paratype. PMU 29729. Same locality and assemblage as holotype.

Other material. 12 specimens from the same locality and assemblage as the holotype.

Diagnosis. Species of *Patellilabia* in which the narrow selenizone is concave between bounding spiral cords, becoming flat and raised above the dorsum in the final growth stage.

Description. Species of *Patellilabia* with dorsal profile varying from uniformly convex to slightly arched at the selenizone, which is concave between spiral cords and traversed by fine lunulae (Fig. 7D–F). Rate of whorl expansion, measured as the ratio of internal height in two consecutive whorls, is 4.4 half a whorl prior to the aperture but increases to more than 6 in the latest half whorl, as the shell expands markedly forwards. Latest growth stage with apertural margins slightly wider than length, the posterior margin extending back beyond open umbilici (Fig. 7A); selenizone at this stage becoming flat-topped and raised (Fig. 7B, C), culminating in a short slit at the anterior margin. Low, pad-like inductura developed medially on the floor of the whorl within the aperture about one-quarter of a whorl back from the finally preserved apertural margin. Ornamentation of final whorl dominated by closely spaced spiral cords of several size orders, with cords becoming increasingly broad and flat-topped; spiral ornamentation only weakly expressed on lateral apertural margins. Comarginal growth lines most conspicuous in earlier growth stages, where they delimit a broad shallow sinus (Fig. 7F), and at apertural margins where slight periodicity in the rate of growth produces comarginal folds.

Remarks. With a maximum observed length of 23 mm, *Patellilabia britannica* is less than half the size of the largest illustrated specimen of *P. tentoriolum* Knight, 1945a (length 50 mm) from the Pennsylvanian of Missouri. In that species the margin of the explanate final growth stage extend back well beyond the coiled earlier whorls. In the holotype of *P. britannica* the coil is not fully encompassed by the expanded margin (Fig. 7A–C), although this may well be achieved in later growth stages than those currently available.

Demagnet (1943) referred crushed specimens of an explanate bellerophonitoidean from the Aegiranum marine band (Westphalian, Bolsovian) of Belgium to *Patellostium* aff. *montfortianum*. *Bellerophon montfortianum* Norwood & Pratten, 1855 is the type species of *Cymatospira* Knight, 1942 but Demagnet's (1943, pl. 4, figs 15, 16) illustrations indicate a shell similar to *Patellilabia britannica*, although with greater expansion of the apertural margins.

The illustrated holotype of *Patellilabia aplanata* Gromczakiewicz-Łomnicka, 1972 from the Visean of Orle, Poland, is crushed and poorly preserved but is distinguished from *P. britannica* by having the selenizone flanked by more strongly emphasized spiral depressions and an ornamentation of spiral threads. *Patellilabia scriptifera* (White, 1862), as illustrated by Weller (1900) from the Devonian of Burlington, Iowa, is a large, explanate, species (width 42 mm, length 33 mm) with the selenizone raised above the dorsum in the latest quarter whorl. Weller (1900) reported only three or four spiral threads on each dorso-lateral area in contrast to the abundant spiral elements seen in *P. britannica*. Both species develop comarginal wrinkles near the apertural margin.

Patellilabia chesterensis Thein & Nitecki, 1974 from the late Mississippian (Chesterian) of the Illinois Basin is

narrower than *P. britannica* prior to the late stage apertural expansion and its obscure ornamentation is dominated by growth lines, in contrast to the dominant spiral ornamentation of the latter. Yochelson & Saunders (1967) referred *Patellostium (Patellilabia) montfortianum* var. *intermedia* Elias, 1958 from the Redoak Hollow Formation (late Mississippian, Chesterian) of Oklahoma to *Cymatospira*. However, the illustrations of Elias (1958, pl. 1, figs 1, 2) suggest that his placement of the new variety within *Patellilabia* was correct, even if its assignment to *montfortianum* was not. The prominent dorso-lateral comarginal undulations located on each side of the selenizone in *Cymatospira* are not present in the illustrated specimens which show weak comarginal ornamentation near the aperture, as in *P. britannica* and other *Patellilabia* species. The raised selenizone of the Oklahoma specimen (Elias 1958, pl. 1, fig. 2) carries a prominent median thread not present in *P. britannica*. Hoare (1961, pl. 19, fig. 18) tentatively assigned to *P. tentoriolum* a specimen from the Pennsylvanian (Desmoinesian) which resembles *P. intermedia* Elias, 1958.

Brown & Hoare (1991) followed Yochelson (1969) in assigning *Patellostium laevigatum* Girty, 1910 from the Fayetteville Shale (late Mississippian, Chesterian) of Arkansas to *Patellilabia*. The type material is poorly preserved (Yochelson 1969, pl. 5, figs 44–48) but the specimen illustrated by Brown & Hoare (1991, fig. 1) preserves the characteristic spiral ornamentation of *Patellilabia* and a flat-topped selenizone. The single specimen has a lower, more rapidly expanding shell than the holotype of *P. britannica* which is about 20% larger, although the latero-posterior apertural margins in the Arkansas specimen are broken. At one whorl prior to the expanded apertural margin, the selenizone in *P. laevigata* is raised and flat, whereas in *P. britannica* it is concave between bounding spiral cords (Fig. 7D–F). Ornamentation is more strongly expressed in *P. britannica* where the spiral ornamentation persists to the dorsal apertural margin but becomes obsolete about a quarter of a whorl earlier in *P. laevigata*.

Patellilabia sulcata Jeffery *et al.*, 1994 from the Imo Formation (late Mississippian, Chesterian) of Arkansas has a greater rate of anterior whorl expansion than *P. britannica* and a prominent inductural plug within the aperture not known in the Pot Bank Quarry material where only a low inductural pad is preserved. Its flat-topped selenizone lies within a pronounced median spiral depression and is ornamented with fine transverse growth lines and infrequent spiral threads. A paratype illustrated by Jeffery *et al.* (1994, fig. 5.19) shows just a single median selenizone spiral thread, as in *Retispira undata* (Fig. 6H). In contrast, the selenizone in earlier growth stages of *P. britannica* is flush with the dorsal surface and concave between bordering threads, but without spiral ornamentation (Fig. 7D–F). However, in the latest growth stage of

the holotype of the latter species, the selenizone is raised and ornamented with fine spiral striations (Fig. 7B, C). The selenizone in *P. rhombadella* Jeffery *et al.*, 1994, also from the Imo Formation, is much wider than that in *P. britannica* and carries up to five spiral threads.

Patellilabia junior Yochelson, 1960 from the Leuders Formation (Permian, Kungurian) of Texas is known from fragmentary specimens of similar size to the type species, but reported to lack the extension of the aperture back beyond the coiled earlier whorls (Yochelson 1960). It differs from *P. britannica* in having more prominent spiral ornamentation and the central dorsal area being slightly trilobed, with the raised, convex, selenizone separated from weak flanking spiral lobes by shallow spiral depressions. The two species are similar in that the elevation of the selenizone increases during the last half whorl.

Co-occurring specimens of *Retispira undata* differ from earlier growth stages of *P. britannica*, where the selenizone is concave, in having a broader, flat-topped, selenizone with a prominent medial cord.

The four species placed by Weir (1931, p. 829) within his 'group of *Bucaniopsis* [= *Retispira*] *striatus*' display expanded apertures and, in some cases, a prominent inductural plug within the aperture; both characters are features of *Patellilabia*. However, none of the illustrated specimens of the *striatus* group preserve the widely expanded aperture typical of *Patellilabia*, although to some extent this reflects breakage of the apertural margins. Most have a flat-topped selenizone carrying three or more spiral ribs, a feature of *Retispira undata* from Pot Bank Quarry but unlike the concave, smooth, selenizone of *P. britannica*. At the present time, all four species are placed within *Retispira*, although they clearly differ from the type species *R. bellireticulata* in the expansion of the late growth stage.

Family EUPHEMITIDAE Knight, 1956

Genus EUPHEMITES Warthin, 1930

Type species. *Bellerophon urii* Fleming, 1828 from the Carboniferous of Scotland.

Euphemites jacksoni (Weir, 1931)

Figures 4A–F, I, 5, 6P

1931 *Euphemus jacksoni* Weir, p. 853, pl. 9, fig. 18.

Holotype. LL 248 in the geological collection of Manchester Museum, collected by J. W. Jackson, and illustrated by Weir (1931, pl. 9, fig. 18). Morridge Formation, Carboniferous, Namurian, Pot Bank Quarry, Congleton Edge, Cheshire.

Figured material. PMU 29711–29713, PMU 29727, all from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. About 70 specimens from assemblage F, and rare specimens from assemblages E, G and H (Fig. 3). Evans *et al.* (1968) reported *Euphemites* sp. from assemblage B but the specimen has not been examined.

Description. Species of *Euphemites* with length:width ratio of about 1.25 and a maximum observed length of 12 mm. Dorsum uniformly convex, with greatest whorl width adjacent to the sudden curvature into the pseudo-umbilici; rate of whorl expansion about 2.4; umbilici closed, pseudo-umbilici usually shallow. Spirally lirata inductura extending from the aperture and covering posterior areas of the shell up to half a whorl prior to the apertural margin (Fig. 4D); breakage of the inductura reveals growth lines and the selenizone of the underlying, normal, shell surface (Fig. 6P, arrows). Lirae sharply defined, varying in number between 19 and 31, average 25 ($n = 16$), with highest number in the broadest shells (Fig. 5). Lirae continuous but often slightly displaced during growth, with frequent introduction of short ephemeral lirae; new lirae usually introduced at the umbilical margins. Anterior half whorl without lirae, crossed by comarginal growth lines which vary from obscure to slightly rugose (Fig. 4E) and increase in curvature as the median slit and selenizone are approached. Slit broad and short, its margins and those of the selenizone often delimited by raised cords (Fig. 4C, F, I).

Remarks. Weir (1931) illustrated only a single dorsal view of the holotype of *Euphemites jacksoni* but this is similar in size and shape to the specimen figured here as Figure 4A–D. The largest available specimen has a length of 12 mm, a width of 9.5 mm and 24 spiral lirae. Weir (1931) and Batten (1966) commented that there is no relationship between the number of lirae and shell length or width in specimens of *Euphemites*, although it is evident from Figure 5 that wider shells (length:width 1.1) have more lirae than narrower shells (length:width 1.4) in *E. jacksoni* from Pot Bank Quarry. Peel (1974) described allometric increase in shell width during ontogeny in bellerophontoideans that might explain the variation seen here, with width increasing relative to length with growth, but all sampled shells in Figure 5 are of similar size (length *c.* 10 mm).

Weir (1931) also tentatively assigned specimens from the Namurian of Glamorgan, Yorkshire and possibly Nottingham to *E. jacksoni*, while Moseley (1953) reported *E. jacksoni* from the Namurian (Kinderscoutian) of the Lancaster Fells. *Euphemites jacksoni* was described from Belgium by Demanet (1941, p. 264, pl. 16, figs 8, 9) from the late Namurian (Kinderscoutian and younger) but the illustrated specimens are crushed in shale and cannot be assigned with conviction. Another Belgian occurrence of similar age was listed by Leckwijk (1968).

Euphemites jacksoni was also reported from the early Namurian of the Upper Silesia coal basin of Poland by Bojkowski (1967).

Euphemites anthracinus (Weir, 1931) from the Westphalian of Britain and Belgium (Demanet 1943) was distinguished from *E. jacksoni* by Weir (1931) by its fewer (about 20) more widely spaced lirae, although similar specimens occur within the collection from assemblage F (Fig. 1, locality 3) from Pot Bank Quarry (Fig. 5).

Euphemites whirligigi Jeffery *et al.*, 1994 from the Imo Formation (late Mississippian, Chesterian) of Arkansas has a similar profile but has fewer spiral lirae (22–24) than typical *E. jacksoni*.

Superfamily EOTOMARIOIDEA Wenz, 1938

Family EOTOMARIIDAE Wenz, 1938

Genus ANGYOMPHALUS Cossmann, 1915

Type species. *Euomphalus radians* de Koninck, 1843 from the early Carboniferous (Tournasian) of Belgium.

Remarks. Batten (1995) referred to *Angyomphalus* an unnamed species from the Magdalena Formation (Pennsylvanian, Morrowan) of Texas in which the selenizone lies just below the periphery, a character which he considered to be characteristic of the genus. Knight (1941) clearly stated that the selenizone in the type specimens of *A. radians*, the type species of *Angyomphalus*, lies above the whorl periphery, as is also the case in *A. congletonensis* sp. nov., described below. The Texan species also lacks sub-sutural nodes, a feature which prompted Blodgett & Johnson (1992) to propose *Eoangyomphalus* as a subgenus of *Angyomphalus*, on the basis of three middle Devonian species from North America. Subsequently, Blodgett *et al.* (1999) described an additional new species, *Angyomphalus (Eoangyomphalus) weyanti*, from the Devonian (Givetian) of France. *Angyomphalus* was regarded as a sub-genus of the anomphalous *Trepospira* Ulrich & Scofield, 1897 by Knight *et al.* (1960) but various authors, including Shikama & Nishida (1968) and Blodgett & Johnson (1992) have refuted this placement.

Angyomphalus congletonensis sp. nov.

Figure 8

? 1905 *Raphistoma radians*, Hind in Stobbs & Hind, p. 532, pl. 35, fig. 8a, b.

LSID. urn:lsid:zoobank.org:act:2A3975B1-7CC3-4B19-8B49-3ACD53734BFF

Derivation of name. From the type locality, Congleton Edge, Cheshire.

Holotype. PMU 29731, Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire (Fig. 1, locality 3, assemblage F).

Figured paratypes. PMU 29730–29736, all from the same locality and assemblage as the holotype.

Other material. More than 20 specimens from assemblage F (Fig. 3). Present in assemblage E (Evans *et al.* 1968 collection 106b).

Diagnosis. Species of *Angyomphalus* morphologically close to the type species but differing in that the sub-sutural comarginal nodes are more widely spaced and shorter, extending radially across 10–15% of the upper whorl surface of the final whorl when compared to 25% in the type species.

Description. Species of *Angyomphalus* with about seven whorls and height about 45% of maximum width. Lenticular, with open umbilicus about one-fifth of width (Fig. 8H). Initial whorls protuberant, consisting of about two smooth whorls with convex upper whorl surface, thereafter with decreasing convexity until only shallowly convex, shouldered below incised sutures when sub-sutural comarginal nodes appear at about three and a half whorls (Fig. 8G, J). In later growth stages the upper whorl surface may be shallowly concave just above the selenizone. Outer lip prosocline, as indicated by growth lines that are steeply inclined, almost perpendicular to the suture, before sweeping regularly backwards into the short slit which generates an obscure selenizone bounded only by fine threads (Fig. 8A, F, arrows). Lower margin of selenizone lying at whorl periphery, its surface ornamented by fine, concave, lunulae (Fig. 8A). Apertural margin strongly prosoclyt below peripheral selenizone, curving strongly backwards to the angulation forming the junction between the base and the umbilical wall; umbilical wall thin (Fig. 8I, arrow). A short funicle developed on the umbilical shoulder slightly restricts the open umbilicus and may generate a circumbilical fasciole in some specimens (Fig. 8D, funicle arrowed). Ornamentation of fine growth lines and a prominent sub-sutural band of comarginal tubercles. The tubercles extend for 10–15% of the width of the upper whorl surface (Fig. 8B, C) and are separated by interspaces which are almost as wide as the radial length of the tubercles themselves.

Remarks. *Angyomphalus congletonensis* sp. nov. is a common and conspicuous element in the Pot Bank Quarry fauna and specimens may attain a diameter of 25 mm. However, specimens are usually poorly preserved and details of the selenizone, growth lines and aperture are only rarely discerned. Knight (1941, p. 36, pl. 31, fig. 3a–d) described the holotype of *Angyomphalus radians* (de Koninck 1842–44) and a metatype illustrated by de Koninck

(1881) from the Early Carboniferous of Belgium, revealing a species which is closely similar to *A. congletonensis*. Armstrong *et al.* (1876) and Etheridge (1882) reported that de Koninck's (1842–44, 1881, 1883) type species occurred in the Carboniferous (late Visean and Namurian) of Scotland, while Wilson (1966) listed *A. cf. radians* (as *Angynomphalus*) from the Neilson Shell Bed from the Lower Limestone Formation (latest Visean) of the Glasgow area, commenting that this rare species was almost wholly restricted to this horizon in Scotland. Specimens were first described from England by Hind *in* Stobbs & Hind (1905) from the Gin Mine Marine Band (the local name for the Aegiranum Marine Band) in the Pennine Middle Coal Measures Formation (late Westphalian, Bolsovian) of the North Staffordshire Coalfield as *Raphistoma radians*; it was listed subsequently as *Trepostira radians* by Rees & Wilson (1998, p. 44). However, Hind also noted its occurrence in the Millstone Grit of Congleton Edge (= Pot Bank Quarry) but without comment (Hind *in* Stobbs & Hind 1905). The Gin Mine Marine Band specimen illustrated by Stobbs & Hind (1905, pl. 35, fig. 8a, b) has not been examined but its general morphology and the short radial extent of the sub-sutural comarginal tubercles suggest that it may be referable to *A. congletonensis*.

As *Trepostira cf. radians*, de Koninck's (1842–44, 1881, 1883) species was reported, but neither illustrated nor described, from the latest Namurian (Yeadonian) of west Yorkshire by Bromehead *et al.* (1933). Bolton (1907) reported, but did not illustrate, an occurrence of *Raphistoma radians* from the basement beds (basal Westphalian) of the Bristol Coalfield. Bolton (1907) also described as *Raphistoma? acuta* sp. nov. a species seemingly belonging within *Angyomphalus* in which the radial nodes are coarser and extend for a greater distance across the upper whorl surface from the suture than in *A. radians*. In a faunal list, Hind (1907) recorded *Raphistoma junior* from Pot Bank Quarry, a species described by de Koninck (1881) from the Visean of Belgium which he had previously considered to be a junior synonym of *R. radians* (Hind *in* Stobbs & Hind 1905). *Angyomphalus junior* has a lower spire and longer sub-sutural comarginal nodes than *A. congletonensis*. It is almost certain that Hind's (1907) record concerns *A. congletonensis*.

Kleblsberg (1912) illustrated specimens from the early Namurian Ostrava Formation (Ostrauer Schichten) of central Europe as *Raphistoma radians* but these are too poorly preserved to compare with either the type species or the present material.

Angyomphalus kentuckiensis Thein & Nitecki, 1974 from the late Mississippian (Chesterian) of the Illinois Basin, USA, is known from a single specimen with more inflated whorls than the type species and *A. congletonensis*; it also has a broad, raised, selenizone forming the vertical outer whorl surface, instead of flush with the outer margin of the

upper whorl surface as in the latter two species. *Angyomphalus kentuckiensis* was transferred to *Mourlonia* by Gordon & Yochelson (1987). *Angyomphalus penelenticulata* Rollins, 1975 from the earliest Mississippian (Kinderhookian) of Iowa lacks sub-sutural comarginal nodes and shows a higher degree of embracement of earlier whorls than *A. congletonensis*; it may be better placed in *Eoangyomphalus*.

Angyomphalus regularis Gordon & Yochelson, 1987 from the Mississippian of Utah is more inflated than *A. congletonensis* and is reported to have radial riblets around the umbilicus; the radial extent of the sub-sutural comarginal nodes is similar in both species. *Angyomphalus desultoria* Jeffery *et al.*, 1994 from the Imo Formation (late Mississippian, Chesterian) is lower spired than *A. congletonensis* and sub-sutural comarginal nodes are weakly developed or absent. It resembles *A. congletonensis* in that Jeffery *et al.* (1994) reported that the earliest whorls lack sub-sutural comarginal nodes.

Yoo (1994) distinguished his new species *A. radianodosa* from the Dangarfield Formation (early Carboniferous, Tournaisian) of New South Wales from the type species largely on account of its much smaller size (width 3–4 mm) compared to the holotype of *A. radians* figured by Knight (1941, width 11–15 mm). *Angyomphalus radians* and *A. congletonensis* are also less inflated, with a more angular periphery, and a tendency for the radiating nodes to form a raised sub-sutural band. Two species of *Angyomphalus* illustrated by Pan (1997) from the early Namurian of Ningxia, China, are distinguished by the prominence and radial extent (more than 40% of the width of the upper whorl surface) of the sub-sutural comarginal nodes. Two species described by Shikama & Nishida (1968) from the Carboniferous of Japan have extremely fine sub-sutural comarginal nodes in contrast to the prominent nodes of *A. radians* and *A. congletonensis*.

Angyomphalus junius Amler & Heidelberg (2003) from the latest Devonian of south-west England has more convex upper whorl surfaces, especially in the earlier whorls, than *A. congletonensis* and attains about only half its diameter.

Genus LUCIELLINA Kittl, 1912

Type species. *Luciellina contracta* Kittl, 1912 from the Triassic of Hungary.

Luciellina sp.

Figure 9N

Figured material. PMU 29745 from assemblage H (Fig. 1, locality 4). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. Batten (1965) noted that numerous undescribed species of *Luciellina* Kittl, 1912 exist in the British Carboniferous, thus extending its range down from the Triassic into the early Carboniferous (Visean). The single fragment illustrated herein shows the shallow trochiform spire in which the upper whorl surface is shouldered immediately below the suture with the preceding whorl prior to becoming concave as the periphery is approached. A narrow vertical peripheral band bounded by spiral threads and crossed by fine concave lunulae is interpreted as the selenizone (arrow in Fig. 9N); it is also visible in the spire immediately above the suture. The outer edge of the sub-sutural shoulder is marked by a prominent spiral cord, with about 11 cords between this and the upper margin of the selenizone on the latest preserved whorl traversed by fine prosocline growth ornamentation.

Luciellina poolvashensis Batten, 1965 from the Visean of the Isle of Man has a more gradate profile and relatively coarser spiral ornamentation. The selenizone is not visible in the spire in *L. poolvashensis* or in specimens from the Hotwells Limestone (Visean) of Somerset tentatively assigned to *L. helicinoïdes* M'Coy, 1844 by Batten (1965). It is visible in the spire, however, in a specimen assigned to the latter species by Batten (1965) from the late Visean (Brigantian) of Scotland, although this specimen differs in having nodose reticulate ornamentation just below the suture. Sowerby (*in* Prestwich 1840, pl. 40, fig. 1) proposed *Trochus? usocona* for a very large (width 6 cm) trochiform species from the Westphalian of Shropshire which seemingly has not attracted subsequent description or comment. The strong spiral ornamentation promotes comparison with the Pot Bank Quarry specimen and other species assigned to *Luciellina*, but it is distinguished by its broad peripheral selenizone (visible in the spire) carrying a prominent median spiral cord. *Luciellina oculatbanda* Kues & Batten, 2001, from the Pennsylvanian (Desmoinesian) differs in having a more perfectly conical whorl profile without the sub-sutural shoulders present in *Luciellina* sp. Additionally, its selenizone is located below the whorl periphery and ornamentation is dominated by comarginal growth lines rather than the very fine spiral threads.

Genus GLABROCIINGULUM Thomas, 1940

Type species. *Glabrocingulum beggi* Thomas, 1940 from the Carboniferous (Visean) of the Midland Valley of Scotland.

Remarks. The evolution and distribution of *Glabrocingulum* Thomas, 1940 was discussed by Batten (1972) who noted that representatives of the Devonian–Permian genus are often common in Upper Carboniferous collections. According to Knight *et al.* (1960), *Glabrocingulum* contains the subgenera *Glabrocingulum s.s.* and *Ananias*

Knight, 1945*b*, to which Batten (1972) added the new subgenus *Stenozone*, but these are accorded full generic status here.

Glabrocingulum armstrongi Thomas, 1940

Figure 9L, M, P, Q

1940 *Glabrocingulum armstrongi* Thomas, p. 42–3, pl. 2, fig. 3a–b.

Figured material. PMU 29742–29744, all from assemblage H (Fig. 1, locality 4). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Common in assemblage H (Fig. 3); rare poorly preserved specimens from assemblage F may belong here.

Remarks. Thomas (1940, p. 43) described *Glabrocingulum armstrongi* from the Upper Limestone and Passage formations of the Midland Valley (Namurian). It is the broadest of the species she assigned to *Glabrocingulum*, with an apical angle of 90° (measured from her pl. 2, fig. 3a illustration of the holotype). This is similar to the measured value in small specimens from Pot Bank Quarry (Fig. 9M) but in larger specimens the angle is clearly obtuse (Fig. 9Q), in which feature the Pot Bank Quarry specimens resemble *Glabrocingulum binodosum* Sadlick & Nielsen, 1963, described from the latest Mississippian (Chesterian) of the upper Chainman Formation of Utah. Neither Sadlick & Nielsen (1963) nor Gordon & Yochelson (1987) made comparison of *G. binodosum* with *G. armstrongi*, or with any other non-American material. The two species are closely similar in terms of ornamentation, notably the two rows of sub-sutural nodes and tendency for spiral ornamentation on the upper whorl surface to become less prominent as the selenizone is approached. Differences exist, however, in the nature of the protoconch, although Sadlick & Nielsen (1963) stressed that their material is incomplete, and it is this which mainly promotes reference of the present material to *G. armstrongi*. Ferguson (1962) reported *G. armstrongi* from the Lower Limestone Formation (latest Dinantian) of Fife. In northern England, Brand (2011) noted that the youngest record of *Glabrocingulum armstrongi* was from the Dipton Foot Shell Beds (Namurian, Kinderscoutian), slightly younger than the Pot Bank Quarry occurrence, but Owen (1988) reported it from the Yeadonian of South Wales.

Glabrocingulum ostraviensis (Klebelberg, 1912) from the Ostrava Formation (Ostrauer Schichten) of central Europe differs from specimens of *G. armstrongi* from Pot Bank Quarry in having more pronounced spiral cords on the base and a third row of sub-sutural nodes on the upper whorl surface.

Thomas (1940) recognized the characteristic early growth stages of *Glabrocingulum* with a smooth initial whorl followed by about two whorls with prominent spiral threads, after which the selenizone appears relatively suddenly at midwhorl between two not adjacent spiral ribs. Sadlick & Nielsen (1963) estimated that about three well-rounded smooth whorls were followed by one less well-rounded smooth whorl before a single row of nodes appears below the suture. They did not describe the place of the first appearance of the selenizone nor did they describe spiral threads on the early whorls, as reported by Thomas (1940) in the type species, *G. beggi*, and the other two species she described: *G. armstrongi* and *G. atomarium* (Phillips, 1836). The illustrations of Sadlick & Nielsen (1963) indicate a clearly delimited and seemingly well-preserved protoconch in *G. binodosum* but surface detail is not discernible.

The early whorls in specimens from Pot Bank Quarry compare closely with the descriptions of Thomas (1940). The initial part of the shell appears to be smooth, with five or six spiral threads appearing abruptly after about one and a half whorls (Fig. 9L, P). After an additional one and a half whorls, the number of spiral threads visible on the upper whorl surface has increased to nine. The selenizone appears abruptly at a point interpreted as the start of the teleoconch (Fig. 9L, arrow). Its slightly coarser bounding cords develop from the outer two of three earlier spiral threads located just above the periphery, with the lost intervening spiral thread corresponding to the medial line of the selenizone. Just prior to the appearance of the selenizone, regularly spaced comarginal ridges appear on the upper whorl surface below the suture with the previous whorl, while most of the previously clearly expressed spiral threads lose much of their expression. Half a whorl later, these comarginal ridges have become nodose at their intersections with the two uppermost spiral elements, which gradually attain greater prominence (cords). The upper whorl surface of the teleoconch is covered with fine growth lines, five or six in number, between the regularly spaced, nodose comarginal ridges which form a fine reticulation with numerous very fine spiral striations (Fig. 9L, P).

Genus EIRLYSIA Batten, 1956

Type species. *Eirlysia exquisita* Batten, 1956 from the Permian of the south-west USA.

Remarks. *Eirlysia* is typically a Permian genus with several species described by Batten (1958) from south-west USA and by Mazaev (2015) from European Russia. However, Batten (1995) described a single specimen from the earliest Pennsylvanian (Morrowan) of Texas which is of similar age and morphology to the Pot Bank Quarry occurrence.

Eirlysia ceramicorum sp. nov.

Figure 9D, G, H, K, O, R

LSID. urn:lsid:zoobank.org:act:F0E34D5D-A0B0-428F-9E54-A942FB2979E1

Derivation of name. From *ceramici* (Latinisation of Greek *keramikos*), the potters, alluding to the Potteries (Stoke-on-Trent), immediately south of the collection area.

Holotype. BGS T4959A (Fig. 9D, H, R), collected by D. Tait in 1904 from 'bed above a ganister in Silica Works [= Pot Bank Quarry] – SW of Willcocks [= Willocks] Wood' (my comments added to BGS catalogue entry). Morridge Formation, Carboniferous, Namurian, Pot Bank Quarry, Congleton Edge, Cheshire. Probably assemblage F or laterally equivalent assemblage E.

Figured paratypes. PMU 29739–29740, from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Rare, poorly preserved specimens from assemblage F (Fig. 3).

Diagnosis. Globose species of *Eirlysia* with inflated, uniformly convex base, well developed reticulate ornamentation and concave selenizone, the lower edge of which forms the whorl periphery.

Description. Species of *Eirlysia* in which the height of the dextral, turbiniform shell is about 75% of its width. There are about six whorls, with about three initial whorls occurring prior to the sudden development of the selenizone between bounding cords (Fig. 9D, arrow). Earliest stages of protoconch poorly known, but followed by about two whorls in which spiral ornamentation dominates (Fig. 9O, arrow). Upper whorl surface shallowly convex, embracing the previous whorl at just below the selenizone, becoming shallowly convex just prior to the upper edge of the selenizone. Selenizone flat or shallowly concave, slightly depressed between bounding cords, the lower of which forms the whorl periphery; selenizone ornamented by obscure fine lunulae. Base uniformly convex; width of umbilicus and form of inner lip not known. Below the selenizone, growth lines indicate that the apertural margin is initially shallowly prosocyrte before passing into a broad, shallow, sinus on the base. Following the appearance of the selenizone, ornamentation is dominated by spiral and comarginal cords of equal emphasis. Initially three spiral cords are present on the upper whorl surface (Fig. 9D) but this number has increased to ten in the latest observed growth stage (Fig. 9R). Intersections of spiral and comarginal cords are slightly nodose on the upper whorl surface, with both spiral and comarginal elements becoming thinner and less pronounced as the selenizone is approached; numerous fine growth lines are seen between the comarginal cords (Fig. 9R). Below the selenizone ornamentation is dominated by spiral cords of variable thickness; comarginal ornamentation consists of growth lines although a slight periodicity reflects the comarginal cords of the upper whorl surface.

Remarks. Permian species of *Eirlysia* were described by Batten (1958) and Mazaev (2015). *Eirlysia ceramicorum* sp. nov. most closely resembles *E. reticulata* Batten, 1958 from the Permian of south-west USA from which it differs in having a more inflated base and slightly taller shell. The selenizone of the latter species has prominent lunulae crossed by a median thread whereas fine lunulae are only sporadically visible on the selenizone of *E. ceramicorum* and the thread is lacking. Both species have well-developed reticulate ornamentation, with increased emphasis of the comarginal ribs on the sub-sutural part of the upper whorl surface. However, comarginal ornamentation in *E. ceramicorum* sweeps obliquely back from the suture (Fig. 9H, K) whereas in *E. reticulata* it is initially perpendicular to the suture for a short distance before curving backwards with greater forwards convexity to the selenizone.

Batten (1995) assigned to *Eirlysia* cf. *reticulata* a single specimen from the Magdalena Formation (earliest Pennsylvanian, Morrowan) of Texas, and thus of similar age to the Pot Bank Quarry occurrence. The specimen has a height of only 1.3 mm, compared with 6–8 mm for the illustrated specimens *E. ceramicorum* (Fig. 9D, G, H, K, O, R). Batten's (1995, p. 12, fig. 10) description of the specimen agrees well with *E. ceramicorum*, but the single illustration is insufficient for closer comparison.

Eirlysia lens Mazaev, 2015 from the middle Permian of the Volga–Urals region of Russia has a similar whorl profile to *E. ceramicorum*, although the base is less inflated and the selenizone is ornamented with prominent lunulae and a median groove. *Eirlysia nodata* Mazaev, 2015, from the middle Permian of the Volga–Urals region, has more shouldered whorls and the transition from outer whorl surface to the base is angular.

Batten (1958) described the early whorls of the type species *Eirlysia exquisita* Batten, 1956 as being simple and unornamented. In exceptionally well-preserved specimens of *Eirlysia lens* Mazaev, 2015, from the middle Permian of the Kirov region, a swollen initial stage is followed by one or two smooth whorls, and then a whorl where spiral ornamentation dominates before the selenizone appears abruptly between bounding cords (Mazaev 2015, pl. 8, fig. 2b). Material from Pot Bank Quarry is less well preserved but the spirally ornamented stage followed by the sudden appearance of the selenizone is clearly seen (Fig. 9D, O, arrows). For comparison, Thomas (1940) noted that an initial smooth whorl in *Glabrocingulum* was followed by two to two and a half whorls carrying five or six spiral ridges prior to the development of the selenizone, and this development is confirmed herein in specimens of *Glabrocingulum armstrongi* from Pot Bank Quarry (Fig. 9L, M, P, Q).

Genus NEILSONIA Thomas, 1940

Type species. *Neilsonia roscobiensis* Thomas, 1940, Lower Limestone Formation (Carboniferous, Visean), Fife, Scotland.

Remarks. *Austroneilsonia* Sabbatini, 1975 from the Upper Palaeozoic of Argentina differs from *Neilsonia* in having prominent lunulae on the broad selenizone and a lack of comarginal tubercles on the upper whorl surface, below the suture.

Neilsonia coatesi sp. nov.

Figure 10A–F

LSID. urn:lsid:zoobank.org:act:9AB60249-6F2C-4178-A832-F524C942798C

Derivation of name. For the Coates family (Peter, John, Denise) in recognition of their contributions to the economic, social and sporting well-being of the Stoke-on-Trent area.

Holotype. BGS YPF 4664a collected by C. G. Godwin, May 1960, in 'section exposed on East side of [Pot Bank] Quarry' (my comment added to BGS catalogue entry). Probably, locality 3 (Fig. 1). Morridge Formation, Carboniferous, Namurian (Chokierian), Pot Bank Quarry, Congleton Edge, Cheshire. Assemblage C.

Figured paratypes. PMU 29746–29747, from assemblage D (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Five additional specimens from assemblage D (Fig. 1, locality 3). Rare, poorly preserved specimens occur in assemblage F at locality 3 (Fig. 3). A partial external mould on BGS T4975A, associated with *Palaeozygopleura roboystonensis* (Longstaff, 1933) and *Angyomphalus congletonensis* sp. nov. collected by D. Tait in 1904 is probably from assemblage F or equivalent.

Diagnosis. Species of *Neilsonia* with a row of comarginally elongate tubercles below the selenizone, at the junction between the outer whorl face and the base; tubercles not visible in the spire.

Description. Species of *Neilsonia* with about seven whorls. Protoconch seemingly smooth and of about two whorls (Fig. 10A). Teleoconch sub-trochiform, with an incremental angle of almost 60° and spire about one-third of total height (Fig. 10G). Upper whorl surface shouldered immediately below the deep suture, becoming concave and almost horizontal as the prominent cord forming the upper edge of the selenizone is approached. A similar cord forming the shell periphery marks the lower edge of selenizone. A concave alveozone lies between the selenizone and an angulation marking the junction of the outer whorl surface and the base, the latter curving uniformly into the miniscule

umbilicus. Outer lip sinuate, with prosocline growth lines on the upper whorl surface and shallow prosocyrct growth lines on the base; depth of slit unknown. Selenizone concave between bordering cords and ornamented with numerous concave lunulae. A row of comarginal, radially elongate, tubercles on the sub-sutural shoulder reflects periodic thickening of the growing margin. Similar tubercles occur on the angulation between the alveozone and the base. Whorl embracement is well below the selenizone but the lower row of tubercles is not visible in the spire.

Remarks. The holotype was collected from just below the *Hudsonoceras proteus* marine band (assemblage C; Chokierian), but the two paratypes are from the shale with *Hudsonoceras proteus* itself (assemblage D; Alportian).

The type species, *Neilsonia roscobiensis* Thomas, 1940, from the Lower Limestone Formation (Visean, Brigantian) and *N. acuminata* Thomas, 1940 from the Strathclyde Group (former Calciferous Sandstone Series) of the Midland Valley of Scotland lack the stepwise, gradate, profile produced by the concavity of the upper whorl surface immediately above the selenizone seen in *N. coatesi*. The latter also has more deeply incised sutures and the diagnostic row of comarginal tubercles below the selenizone. *Neilsonia invisitata* Hoare *et al.*, 1997 from the Pennsylvanian of the Appalachian Basin and *N. laticincta* Batten, 1989 from the Permian of the south-west USA differ from *N. coatesi* in lacking the comarginal, elongate, tubercles on the upper whorl surface below the suture and below the selenizone. In this respect they resemble *N. nuda* Mazaev, 2015 from the middle Permian of the Volga–Urals region.

Neilsonia welleri Thein & Nitecki, 1974 from the late Mississippian (Chesterian) of the Illinois Basin, USA, is more high spired than *N. coatesi*, with a prominent spiral cord at the junction between the outer whorl face and the base, although this may show a tendency to become tuberculate in some specimens when crossed by growth lines. *Neilsonia insculpta* (Hall, 1856), as figured by Whitfield (1882) from the Mississippian of Indiana, is also higher spired than *N. coatesi* and with more closely spaced, more comarginally elongate tubercles on the upper whorl surface; a narrow spiral cord is present below the selenizone.

Neilsonia ispharensis Licharev, 1967 from the late Carboniferous and early Permian of Fergana, Uzbekistan, has less prominent sub-sutural comarginal tubercles and a wider, coeloconoid, conical spire than *N. coatesi*. It also lacks the prominent band of comarginal tubercles below the selenizone which characterize *N. coatesi*.

Neilsonia ganneyica sp. nov.

Figure 10G–I

LSID. urn:lsid:zoobank.org:act:53DB31FC-4802-400D-8C18-85FFBDB5547F

Derivation of name. From Ganney (Ganny) Bank, the local name for the steep section of Mow Lane, connecting Astbury to Pot Bank Quarry, also known as the old Ganister Quarry on Congleton Edge.

Holotype. PMU 29748, from assemblage H (Fig. 1, locality 4). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Paratype. PMU 29749 from the same assemblage and locality as the holotype.

Other material. Common in assemblage H (Fig. 1, locality 4).

Diagnosis. Species of *Neilsonia* similar to *Neilsonia coatesi* sp. nov. but distinguished by the wider selenizone and obsolete row of comarginal tubercles on the base below the selenizone.

Description. Species of *Neilsonia* in which the earliest whorls and protoconch are not known. Teleoconch sub-trochiform, with an incremental angle of almost 60° and spire about one-half of total height (Fig. 10G). Upper whorl surface shouldered immediately below the deeply incised suture, becoming concave and almost horizontal as the prominent cord forming the upper edge of the selenizone is approached. A similar cord forming the shell periphery marks the lower edge of the selenizone. A concave alveozone lies between the selenizone and a spiral angulation marks the junction of the outer whorl surface and the base, the latter curving uniformly into the tiny umbilicus. Outer lip sinuate, with prosocline growth lines on the upper whorl surface and shallowly prosocyrct growth lines on the base; depth of slit unknown. Selenizone concave between bordering cords and ornamented with numerous concave lunulae. A row of comarginal, radially elongate, tubercles on the sub-sutural shoulder reflects periodic thickening of the growing margin. Growth lines crossing the spiral angulation at the junction between the alveozone and base may show weak tuberculation. Whorl embracement is well below the selenizone.

Remarks. The holotype (Fig. 10G, H) and other specimens of *Neilsonia ganneyica* from assemblage H are external moulds which attain a height of about 7 mm, almost twice the height of the holotype of *N. coatesi* from assemblage C. The selenizone is relatively wider in *N. ganneyica* than in *N. coatesi* from assemblages C (Chokierian) and D (Alportian). In the former it is almost the same height as the upper whorl surface, above it, in the spire measured along the shell axis (Fig. 10G, H), although slightly less so in the final whorl. In *N. coatesi* the selenizone is only about half of the upper whorl surface (Fig. 10B). Additionally, the comarginal tubercles below the selenizone, at the junction between the outer whorl surface and the base, are obscure, although the angulation between the alveozone and the base persists.

The gradate profile and deeply incised sutures of *N. ganneyica* are not seen in *N. roscobiensis* and *N. acuminata* from the Visean of the Midland Valley of Scotland (Thomas 1940). *Neilsonia invisitata* Hoare *et al.*, 1997 from the Pennsylvanian of the Appalachian Basin, *N. laticincta* Batten, 1989 from the Permian of the south-west USA and *N. nuda* Mazaev, 2015 from the middle Permian of the Volga–Urals region all lack the comarginal, elongate, tubercles on the upper whorl surface below the suture of *N. ganneyica* and have less shouldered whorls. *Neilsonia welleri* Thein & Nitecki, 1974 from the late Mississippian (Chesterian) of the Illinois Basin, USA, is higher spired than *N. coatesi*, with a more prominent spiral cord below the alveozone. *Neilsonia insculpta* (Hall, 1856), as figured by Whitfield (1882) from the Mississippian of Indiana, is also higher spired, with less emphasis of the peripheral selenizone and a narrower alveozone. The spire in *N. ispharensis* Licharev, 1967, from the late Palaeozoic of Uzbekistan, has a coeloconoid form and wider incremental angle and lacks angulation below the selenizone.

The holotype of *N. ganneyica* displays a repaired fracture in the apertural margin resulting from a non-lethal predatory attack (Fig. 10H). Similar repaired injuries in Carboniferous pleurotomariiform gastropods are well known (e.g. Lindström 2003; Lindström & Peel 2005) and show a similar tendency to focus on the slit and selenizone.

Family GOSSELETINIDAE Wenz, 1938

Genus LIRALORON nov.

LSID. urn:lsid:zoobank.org:act:3DB03409-97DA-4969-A6C4-39E120E2CB85

Type species. *Liraloron cornoviorum* gen. et sp. nov.

Derivation of name. From *lira* (Latin), ridge, combined to reflect the similarity of the spirally ornamented shell with *Stenoloron* Oehlert, 1888.

Diagnosis. Low turbiniform, phaneromphalous, with the narrow selenizone located high on the whorl. Ornamentation of numerous spiral threads crossed by growth lines which are prosocline above the selenizone and prosocyrct below it.

Remarks. *Liraloron* closely resembles *Stenoloron* Oehlert, 1888 in terms of shell shape, location of the narrow selenizone and the form of the emargination. It is distinguished by its ornamentation of numerous spiral threads, with only growth lines present in *Stenoloron*. *Paffratholon* Frýda, 2000, from the late Middle Devonian of Germany was proposed by Frýda (2000) as a subgenus of

Stenoloron and is distinguished by its lack of spiral ornamentation and the low rate of whorl expansion of about 1.2 compared with almost 2 in *Liraloron* and the type species of *Stenoloron*, *S. viennayi* Oehlert, 1888, as illustrated by Knight (1941, pl. 27, fig. 1a–c).

The selenizone in *Shansiella* Yin, 1932 is broad and often flush with the shell surface and usually lacks marginal cords that can differentiate it from the spiral ornamentation. Furthermore, it is usually located at or below the shell periphery (e.g. Kues & Batten 2001, figs 7.7–7.10), whereas that in *Liraloron* and *Stenoloron* is located high on the whorl. Many Carboniferous species assigned to *Gosseletina* Fischer, 1885 have prominent spiral ornamentation and a selenizone located high on the whorl face. The latter, however, is broad and unlike the narrow raised selenizone of *Liraloron*.

Liraloron differs from *Neoplatelyteichum* Maxwell, 1964 in possessing a narrow selenizone located high on the outer whorl surface. Although originally described as slit-bearing, Batten (1972, p. 20) concluded that no selenizone was present in the type species of Maxwell's (1964) genus from Queensland and re-interpreted it as a holopeid gastropod.

Liraloron appears closely similar to *Juvenispira* Mazaev, 2015 from the middle Permian of the Kirov region in terms of its turbiniform form and multispiral ornamentation. The latter, however, has a broad selenizone compared to the narrow selenizone of *Liraloron*, although its upper margin forms a raised band reminiscent in proportions of the entire selenizone of *Liraloron*.

Liraloron cornoviorum sp. nov.

Figure 9A–C, E, J

LSID. urn:lsid:zoobank.org:act:2C9376AF-F0DB-4A61-9388-34E9395A1A9D

Derivation of name. From the Celtic tribe Cornovii, former inhabitants of the Cheshire–Staffordshire area.

Holotype. PMU 29737 from assemblage H (Fig. 1, locality 4). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Paratype. PMU 29738 from the same assemblage, horizon and locality as the holotype.

Other material. Several fragmentary external moulds from assemblage H.

Description. Type species of *Liraloron* with about five whorls; low turbiniform with incremental angle about 95°; seemingly anomphalous or narrowly phaneromphalous. Upper whorl surface shallowly convex, shouldered below sutures which are

incised and embracing the previous whorl at its periphery. Outer whorl passing with uniform convexity onto base. Outer lip sinuate, with a narrow slit generating a slightly raised selenizone at about 75% of the whorl height (Fig. 9A), about mid-height of exposed whorl face. Ornamentation of numerous fine spiral threads crossed by fine growth lines which are shallowly convex above selenizone (Fig. 9E), more strongly prosocyrct below.

Remarks. The paratype (Fig. 9J) is partly crushed such that it appears more trochiform than the holotype (Fig. 9A–C, D). These and other fragmentary specimens are preserved as external moulds.

Stenoloron is typically a Devonian genus although *Eotomaria umbilicata* Yoo, 1994 from the Early Carboniferous of New South Wales was referred to the genus by P. J. Wagner (pers. comm. 2013). It is lower spired than *Liraloron cornoviorum*, has a broader selenizone bordered by spiral cords, lacks spiral ornamentation throughout growth and has a prominent sinus in the outer lip at the umbilical shoulder. *Pleurotomaria swallovana* Hall, 1856, as illustrated by Whitfield (1882, pl. 9, figs 1, 2) from the lower Carboniferous of Spergen Hill, Indiana, was also assigned to *Stenoloron* by P. J. Wagner (pers. comm. 2013). It is lower spired than *Liraloron cornoviorum* with more shouldered whorls; it lacks spiral ornamentation and differs in the selenizone being located at the whorl periphery, not well above it as in *L. cornoviorum* (Fig. 9A), and being bounded by distinct spiral cords.

The prominent spiral ornamentation in *Liraloron cornoviorum* is finer than in *Shansiella globosa* (Thomas, 1940) from the Visean to Namurian of Scotland, which has a more inflated, more shouldered shell with a broader selenizone. With a width of 15 mm, it is also much larger than the Pot Bank Quarry specimens (3–3.2 mm). Amler & Heidelberger (2003, text-fig. 11E, F) assigned a specimen from the Piltown Formation (latest Devonian) of south-west England to *Shansiella* cf. *globosa* (Thomas, 1940) which shows similar spiral ornamentation but more inflated whorls; it is reported to have a well developed selenizone. The holotype figured by Thomas (1940, pl. 4, fig. 1a–c) from the Lower Limestone Formation of southern Scotland shows a higher rate of whorl expansion than the Devonian specimen.

Superfamily TROCHONEMATOIDEA Zittel, 1895

Family TROCHONEMATIDAE Zittel, 1895

Genus AMAUROTOMA Knight, 1945b

Type species. *Pleurotomaria subsinuata* Meek & Worthen, 1861.

Remarks. P. J. Wagner (pers. comm. 2013) placed *Amaurotoma* in the Family Microdomatidae Wenz, 1938 of the

Superfamily Euomphaloidea de Koninck, 1881, although Bouchet & Rocroi (2005) considered microdomatids to be trochoideans.

Amaurotoma sp.

Figure 9F, I

Figured material. PMU 29741 from assemblage H (Fig. 1, locality 4). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. This relatively tall turbiniform species is known from a single fragmentary external mould preserving four whorls. The whorl profile is sharply shouldered just below the suture with the angulation accentuated by a spiral cord. The upper whorl surface is flattened in the spire, but in the last whorl is seen to increase uniformly in curvature towards the base. The upper whorl surface is occupied by a broad shallow sinus (arrow in Fig. 9I), the culmination of which lies about half way between the suture and the whorl periphery. Ornamentation consists of cords separated by slightly wider concave interspaces. On the upper whorl surface the cord at the edge of the shoulder angulation below the suture is followed by a spiral smooth area equivalent to about twice the width of each pair of cord and interspace preserved lower on the profile; there are six such pairs visible. Spiral cords are only weakly developed on the upper surface of the final whorl below the shoulder cord, but about 11 cords can be discerned below the whorl periphery (Fig. 9F).

On account of its fragmentary preservation *Amaurotoma* sp. appears similar to *Luciellina* sp. (Fig. 9N) but the upper whorl surface in the latter becomes shallowly concave near the periphery and is ornamented by about ten spiral ribs on the outer whorl surface. A narrow selenizone band not present in *Amaurotoma* sp. forms the periphery in *Luciellina* sp. (Fig. 9N, arrow).

Amaurotoma humerosa (Meek & Hayden, 1858) illustrated by Knight (1945b) from the Pennsylvanian of Texas, the type species of *Knightinella* Licharev, 1975, has a more gradate spire with the culmination of the shallow sinus lying above a peripheral angulation at about half the height of the exposed whorl surface in the spire. Two or three fine spiral ridges occur above this angulation whereas two coarse spiral ridges separated by concave interspaces occur between the peripheral angulation and the suture with the following whorl. *Amaurotoma zappa* Plas, 1972 from the Permian of Nevada has more convex whorls than *Amaurotoma* sp. with coarse spiral ornamentation and wide concave interspaces. The sinus is shallower and located higher on the outer whorl surface than in *Amaurotoma* sp.

Sabattini & Noirot (1969) referred a turbiniform species from the Carboniferous–Permian of Argentina with numerous fine spiral cords to *Neoplatyteichum* Maxwell, 1964. Although originally described as slit-bearing, Batten (1972, p. 20) concluded that no selenizone was present in the type species *Neoplatyteichum dickinsi* Maxwell, 1964 from the Carboniferous of Queensland. With the exception of a discounted internal mould, Batten (1972) concluded that the material from Argentina also lacked a selenizone (Sabattini & Noirot 1969, pl. 2, fig. 8). Both species differ from *Amaurotoma* sp. in having more convex whorls, finer spiral ornamentation, and prosocline growth lines on the upper whorl surface rather than a broad emargination.

Superfamily MURCHISONIOIDEA Koken, 1896
Family ORTHONEMATIDAE Nützel & Bandel, 2000

Remarks. Bouchet & Rocroi (2005) placed murchisonioideans within the Clade Vetigastropoda, but the difficulty of assigning many Palaeozoic gastropod groups to clades based on the morphology of modern taxa has resulted in persistence of archaeogastropods as an informal grouping (Frýda 2012). Following a detailed review, Mazaev (2011) proposed a Suborder Murchisoniina Cox & Knight, 1960 placed within the Order Pleurotomariida Cox & Knight, 1960, but did not recognize a superfamily.

Genus STEGOCOELIA Donald, 1889

Type species. *Stegocoelia compacta* Donald, 1889 from the Upper Limestone Formation (Namurian) of southern Scotland.

Stegocoelia sp.
Figure 12B–D

Figured material. PMU 29768–29770, all from assemblage A (Fig. 1, locality 1). Morridge Formation, Carboniferous, Namurian (Chokierian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Several external moulds from assemblage A.

Remarks. These external moulds from assemblage A (Fig. 1, locality 1) lack protoconchs and growth lines, such that the nature of the aperture, slit and selenizone are not known. Several have been diagenetically deformed prior to consolidation of the sediment (Fig. 12C), giving the effect of strong translation along the axis of coiling. Reference to *Stegocoelia* relies on the distribution of spiral ornamentation but this is also similar to *Donaldina*

robusta (Stevens, 1858) of Batten (1995) from the Magdalena Formation (Pennsylvanian, Morrowan) of Texas. At least eight whorls are present in a specimen about 8 mm tall (Fig. 12B) but the largest specimen is about twice this size. The whorl profile is convex with deep sutures emphasised by a prominent sub-sutural cord at the whorl shoulder; a narrow cord may be preserved adjacent to the suture (Fig. 12D). Four additional spiral cords separated by concave interspaces occur on the lower part of the outer whorl face, but seven are present on the base of the final whorl (Fig. 12B). The uppermost cord is placed midway between the suture and the second cord, the interspace between these two cords thus being about twice as wide as that between the lower cords. The incremental angle is about 23°.

The Pot Bank Quarry specimens are similar in profile and size to *Stegocoelia laschmanensis* Mazaev, 2001 from the Pennsylvanian (Moscovian) of the Ryazan region of the Russian Platform, although the spiral ridges below the periphery on the outer whorl face are closer together. Illustrations of the types of the type species, *Stegocoelia compacta*, given by Donald (1889, pl. 20, figs 9–13) suggest a similar form to the specimens from Pot Bank Quarry, although specimens illustrated by Knight (1941, pl. 44, fig. 6) indicate that the incremental angle decreases with growth, producing a narrower shell. *Stegocoelia compacta* has fewer, coarser, spiral ridges on the outer whorl face. *Stegocoelia kentuckyensis* Thein & Nitecki, 1974 from the Mississippian (Chesterian) of the Illinois Basin has fewer, coarser, spiral ridges and a wider incremental angle.

Superfamily PLATYCERATOIDEA Hall, 1859
Family PLATYCERATIDAE Hall, 1859

Genus PLATYCERAS Conrad, 1840

Type species. *Pileopsis vetusta* Sowerby, 1829 from the Lower Carboniferous of Ireland.

Platyceras sp.
Figure 11I, N

Figured material. BGS T 4979A, collected by D. Tait in 1904 from ‘Congleton Edge – bed above a ganister in Silica Works [= Pot Bank Quarry] – SW of Willcocks [= Willocks] Wood’ (my comments added to BGS catalogue entry). Probably from assemblage F (Fig. 1, locality 3) or equivalent. Morridge Formation, Carboniferous, Namurian, Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. This single well-preserved specimen has an almost flat, rapidly expanding shell coiled through about one whorl; the aperture is not visible. The upper surface is

marked by prosocyr growth lines which become undulose near the aperture; they curve strongly backwards into a broad irregular invagination at the whorl periphery. A similar shell form is seen in *Platyceras neverovoensis* Mazaev, 1996 from the Pennsylvanian (Kasimovian, Khamnovikian regional substage) of the central Russian Plate.

Superfamily NERITOPSIDOIDEA Gray, 1847
Family NATICOPSIDAE Waagen, 1880

Genus NATICOPSIS M'Coy, 1844

Type species. *Naticopsis phillipsi* M'Coy, 1844 from the Dinan-tian of Ireland.

Naticopsis sp.
Figure 11M

Figured material. PMU 29763 from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Fragments from assemblage H (Fig. 1, locality 4).

Remarks. The figured specimen is broken at the apex and the aperture but it is less globose, with a much lower incremental angle (about 95°), than the type species described by Knight (1941). In this respect it resembles *Naticopsis clinovata* Gordon & Yochelson, 1987 from the Chainman Shale (late Mississippian, Chesterian) of Utah, see also Jeffery *et al.* (1994) from the Imo Formation (Chesterian) of Arkansas, *N. waterloensis* Weller, 1916 of Thein & Nitecki (1974) from the Chesterian of the Illinois Basin, and *N. judithae* Knight, 1933b from the Pennsylvanian (Desmoinesian) of Missouri, and Pennsylvanian (Morrowan) of Texas (Batten 1995). The Pot Bank Quarry specimen is slightly more inflated than *Ianthinopsis gouldiana* described by Girty (1915) from the Wewoka Formation (Desmoinesian) of Oklahoma, although the single specimen of the latter is also distinguished by weak spiral threads on the upper whorl surface.

Hind *in* Stobbs & Hind (1905, pl. 35, fig. 10) assigned a similar shell from the Gin Mine Marine Band (Aegiranum Marine Band) in the Pennine Middle Coal Measures Formation (late Westphalian, Bolsovian) of the North Staffordshire Coalfield to *Naticopsis brevispira* (de Ryckholt, 1847), although it bears little similarity to that species from Belgium (Knight 1941, pl. 83, fig. 2). Hind (1908) recognized the same species in the Limestone Coal Formation (Namurian, Pendleian) of Scotland, but Wilson (1961) considered it to be poorly preserved and

assigned it just to *Naticopsis*? Demanet (1941, p. 267, pl. 16, fig. 20) described Hind *in* Stobbs & Hind's (1905) form from the Namurian of Belgium but the illustrated crushed specimen is too poorly preserved for comparison with the Pot Bank Quarry example.

Superfamily SUBULITOIDEA Lindström, 1884
Family SUBULITIDAE Lindström, 1884

Genus LEPTOPTYGMA Knight, 1936

Type species. *Auripygma virgatum* Knight, 1931b from the Pennsylvanian of Missouri.

Leptoptygma cf. *virgatum* (Knight, 1931b)
Figure 11A, C, U

Figured specimens. PMU 29750–29752, all from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Two external moulds and fragments from assemblage H (Fig. 1, locality 4).

Remarks. In terms of the incremental angle (60°) and relative height of the spire this species resembles Knight's (1931b) species from the Labette Shale (Pennsylvanian, Desmoinesian) of Missouri; it was also recorded from the Flechado Formation of similar age in New Mexico (Kues & Batten 2001). Knight (1931b, pl. 25, fig. 2b; 1941, pl. 94, fig. 6) illustrated a low columellar fold, visible also in cross-section (Knight 1931b, pl. 27, fig. 3), but this has not been detected here (Fig. 11A). Ornamentation consists of fine comarginal striations.

Leptoptygma sp. A
Figure 11B

Figured specimen. PMU 29753 from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. In addition to the presence or absence of a columellar fold, Nützel *et al.* (2000) demonstrated that the nature of the protoconch and early whorls is critical to distinguishing between several late Palaeozoic genera with similar globose shells. The apex and the aperture of the single Pot Bank Quarry specimen placed here are damaged, but the lack of a columellar fold argues against assignment to *Strobeus* de Koninck, 1881 despite the

general similarity of shell form; inductural deposits are not preserved. Sutures are partly obscured by sediment fill but the shell is ornamented with fine comarginal growth lines. The specimen has a similar whorl profile with an inflated final whorl to *Auripygma primitia* Elias, 1958 from the late Mississippian Redoak Hollow Formation of Oklahoma, which was transferred to *Leptotygyma* by Yochelson & Saunders (1967). It was illustrated by Elias (1958, pl. 2, fig. 11) from an external mould, and therefore appears to be sinistrally coiled.

Strobeus brevis (White, 1881), as illustrated by Kues & Batten (2001, fig. 16.13–15) from the Flechado Formation of New Mexico (Pennsylvanian, Desmoinesian), has a shorter spire and more globose final whorl. Specimens from the Carboniferous of Northumberland described by M'Coy in Sedgwick & M'Coy (1851–55) as *Macrochilus? spiratus* have a spire with a similar profile, although the final whorl is more globose. Bolton (1907) and Demanet (1941, pl. 16, fig. 21) illustrated similar specimens from the basal Westphalian of the Bristol Coalfield and the Namurian of Belgium, respectively.

Leptotygyma sp. B
Figure 11F, G

Figured specimen. PMU 29761 and 29762 from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. In the apparent absence of a columellar fold this species is referred to *Leptotygyma* rather than *Strobeus*. Gordon & Yochelson (1987, pl. 9, figs 26, 27) illustrated a similar specimen from the Chainman Shale (late Mississippian, Chesterian) of Utah. The shell is smooth apart from fine, almost orthocone, comarginal growth lines. It differs from *L. cf. virgatum* by its lower spire and from *L. sp. A* by having less globose whorls.

Family MEEKOSPIRIDAE Knight, 1956

Genus GIRTYSPIRA Knight, 1936

Type species. *Bulimella canaliculata* Hall, 1858 from the Mississippian of Indiana.

Girtyspira sp.
Figure 11O

Figured material. PMU 29774 from assemblage A (Fig. 1, locality 1). Morridge Formation, Carboniferous, Namurian (Chokierian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. A single poorly preserved external mould shows the narrow, flat-topped shoulder to the whorl characteristic of *Girtyspira*. The spire is about 35% of the total height, somewhat shorter than in *Girtyspira fusiformis* (de Koninck, 1881) as illustrated by Batten (1966) from the Hotwells Limestone (Visean) of England and the type species illustrated by Knight (1941), and significantly shorter than in *Girtyspira microspirula* Jeffery *et al.* 1994 (about 60%) from the Imo Formation of Arkansas. Details of the aperture are not known; growth lines on the final whorl are shallowly convex, almost orthocone.

Genus MEEKOSPIRA Ulrich in Ulrich & Scofield, 1897

Type species. *Eulima? peracuta* Meek & Worthen, 1861, from the Pennsylvanian of Illinois.

Meekospira acrolopha sp. nov.
Figure 11D, E, H, J–L, P, T

LSID. urn:lsid:zoobank.org:act:ABDEDF16-5079-44B8-8CBE-D391362CAFAA

Derivation of name. From *akrolophos* (Greek), crest of a hill, reflecting the collection locality on Congleton Edge.

Holotype. PMU 29758 from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other figured material. PMU 29754–29757, 29759, 29760. Same assemblage and locality as the holotype.

Other material. Poorly preserved, tentatively assigned specimens in assemblages D, E and H (Fig. 3).

Diagnosis. Species of *Meekospira* with a narrow sub-sutural notch in the outer lip and in which the final whorl in large specimens is expanded in width relative to earlier whorls.

Description. A species of *Meekospira* in which the final whorl is expanded, wider, and shouldered, relative to the whorls of the spire. Protoconch not known. Whorl profile varying from flattened, through uniformly convex to slightly pendant, passing with uniform convexity or slight angularity onto the base. Anomphalous, inner lip slightly reflexed on the smooth columella; aperture lenticular in cross-section, angulated abapically but without an anterior canal; apertural margin with a minute sub-sutural notch. Outer lip varying from straight to shallowly sinusoidal, with slight adapertual convexity below a shallow sinus on the upper whorl surface; convexity enhanced in the more tumid late growth stages of larger specimens. Ornamentation of fine comarginal growth lines only.

Remarks. The absence of an anterior notch in the aperture and lack of a columellar fold place this species in *Meekospira* Ulrich in Ulrich & Scofield, 1897, although the sub-sutural notch is reminiscent of *Girtyspira*. Most of the available specimens are not well preserved, with the spire somewhat crushed and its shell degraded. The whorl profile varies from flattened (Fig. 11D, E), through shallowly, but uniformly convex (Fig. 11P), to pendant, with the periphery near the suture with the following whorl (Fig. 11L). The transition from outer whorl to base may be slightly angular (Fig. 11D), as is commonly the case in *Meekospira*, or uniformly convex as in species often assigned to *Soleniscus* Meek & Worthen, 1861 (Fig. 1H, P), although a columellar fold characteristic of the latter genus is not present. Both the angular and uniformly convex forms show the small sub-sutural notch in the apertural margin (Fig. 11D, H). The sides of the spire may be slightly concave, although in Figure 11J this effect is increased somewhat by crushing. In the holotype, the largest available specimen, the final whorl is shouldered below the suture with the previous whorl, reflecting its increased tumidity (Fig. 11K, T). This coelocoid form is often seen in *Strobeus* and other globose subulitids (e.g. Jeffery *et al.* 1994, fig. 10.1–10; Kues & Batten 2001, fig. 17.3–6) but not in the higher spired *Meekospira*.

Specimens assigned to *Meekospira minuta* Weller, 1916 from the Imo Formation (Mississippian, Chesterian) of Arkansas by Jeffery *et al.* (1994) have a slightly wider incremental angle, but are of similar size and show the same variation in outer whorl profile as seen in *M. acrolopha*. *Meekospira batteni* Thein & Nitecki, 1974 and *M. evansvillensis* Thein & Nitecki, 1974 from the late Mississippian (Chesterian) of Illinois have wider incremental angles and more uniformly convex outer whorl face; the latter also has a flattened base with circumbilical spiral ridges. *Meekospira bamboiformis* Thein & Nitecki, 1974 is narrower than *M. acrolopha*. *Meekospira peracuta* (Meek & Worthen, 1861) and *M. choctawensis* Girty, 1912, as figured by Kues & Batten (2001) from the Flechado Formation (Pennsylvanian, Desmoinesian) of New Mexico, are larger species (height up to 20 mm and 35 mm respectively) with almost flat sides to the whorl profile, but the latter displays the flattened columellar lip seen in *M. acrolopha* (Fig. 11D, E) *Meekospira delgada* Kues & Batten, 2001 is a very slender, fusiform, species differing from *M. acrolopha* in that the shallowness of the sutures produces almost straight sides to the spire.

Superfamily LOXONEMATOIDEA Koken, 1889
Family PALAEOZYGOLEURIDAE Horný, 1955

Remarks. The importance of protoconch morphology in distinguishing between zygopleuriform gastropods and

the practical difficulties of discrimination of incompletely preserved specimens between otherwise homeomorphic taxa have been discussed at length by Kues & Batten (2001). As a result, they considered the Palaeozygopleuridae Horný, 1955 to be a junior synonym of Pseudozygopleuridae Knight, 1930, grouping them as zygopleuroideans. However, Bouchet & Rocroi (2005) maintained the separation of the two families, placing Palaeozygopleuridae within Loxonematoidea and regarding pseudozygopleurids as caenogastropods, as did Frýda *et al.* (2013). The absence of preserved protoconchs in any of the specimens discussed below inevitably qualifies all taxonomic assignments.

Genus PALAEOZYGOLEURA Horný, 1955

Type species. *Zygopleura alinae* Perner, 1907 from Dvorce-Prokop Limestone, Devonian (Pragian) of Czech Republic (Horný 1955; Frýda *et al.* 2013).

Palaeozygopleura roboystonensis (Longstaff, 1933)

Figure 12F, H

1933 *Zygopleura roboystonensis* Longstaff, p. 100, pl. 8, figs 1, 2, 5.

Figured material. PMU 29772 from assemblage H (Fig. 1, locality 4), PMU 29773 from assemblage E, (Fig. 1, locality 2). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Three external moulds in assemblage H (Fig. 1, locality 4). A partial external mould on BGS T4975A, collected by D. Tait in 1904, and associated with *Neilsonia coatesi* sp. nov. and *Angyomphalus congletonensis* sp. nov., is probably from assemblage F or equivalent.

Remarks. The most complete specimen has a height of about 7.5 mm and preserves parts of eight whorls. The whorl profile is uniformly convex with an incremental angle of 30°; sutures are deep in detail. Ornamentation consists of coarse comarginal ribs which slope slightly forward from the suture and terminate at the transition to the base; other apertural features unknown.

Longstaff (1933) described this species from the Lower and Upper Limestone formations of Scotland (latest Visean – Namurian, Arnsbergian), but tentatively recorded it also from the basal Westphalian of the Bristol Coalfield where it had been described as *Loxonema scalaroideum* Phillips, 1836 by Bolton (1907). The incremental angle of 25° is slightly less than in the Pot Bank Quarry specimens but almost twice that of *Palaeozygopleura*

benniana (Longstaff, 1933) which Longstaff (1933, p. 103) reported, but did not illustrate, from Congleton Edge, on the basis of a specimen in the Wheelton Hind Collection in the Natural History Museum (London). I have not seen the latter specimen or any other from Pot Bank Quarry with the slender spire of *P. benniana*. The record was referred to *Pseudozygopleura beaniana* by Ramsbottom in Evans *et al.* (1968, p. 81) but to *Palaeozygopleura benniana* by Batten (1966, p. 84).

Superfamily PALAEOSTYLOIDEA Wenz, 1938

Family PALAEOSTYLIDAE Wenz, 1938

Genus PLATYCONCHA Longstaff, 1933

Type species. *Platyconcha dunlopiana* Longstaff, 1933, Lower Limestone Formation (Viséan, Brigantian) of Scotland.

Platyconcha cf. hindi Longstaff, 1933

Figure 11Q, R

Figured material. PMU 29764 from assemblage F (Fig. 1, locality 3). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. A few broken specimens with a flattened outer whorls surface and a sub-quadratic whorl cross-section (Fig. 11R) from assemblage F (Fig. 1, locality 3) can be compared with *Platyconcha* Longstaff, 1933, or less certainly with *Streptacis* Meek, 1872, on the basis of traces of a broad sinus indicated by growth lines in the outer lip (Fig. 11Q, arrow); no indications of spiral ornamentation or a selenizional band are preserved. However, in the absence of diagnostic protoconchs any assignment is speculative. Knight *et al.* (1960) placed the two genera in the Family Streptacidae Knight, 1931a, although their protoconchs are quite different, disregarding the transfer by Horný (1955) of *Platyconcha* to the Palaeozygopleuridae Horný, 1955. Bandel (2002a) transferred *Platyconcha* to the Palaeostylidae, discussing the relationships and protoconch morphology of the heterostroph allogastropod *Streptacis* Meek, 1872 elsewhere (Bandel 2002b).

Platyconcha dunlopiana Longstaff, 1933, the type species of *Platyconcha* from the Lower Limestone Formation (Viséan, Brigantian) of Scotland, has a similar flattened whorl profile but its incremental angle is greater. The sinus is of similar shape to *Platyconcha* sp. but comarginal ornamentation is periodically rugose whereas only fine growth lines are present in *Platyconcha* sp. *Platyconcha hindi* Longstaff, 1933 from the Gin Mine Marine Band (= Aegiranum Marine Band) of North Staffordshire, first described by Hind in Stobbs & Hind (1905), is of similar shape and the

sinus is also only expressed by fine growth lines. *Platyconcha tenuilineata* Longstaff, 1933 from the Upper Limestone Formation (Namurian) of southern Scotland has a similar incremental angle but a shallower sinus.

Streptacis whitfieldi Meek, 1872, the type species of *Streptacis* from the Pennsylvanian of Illinois, as figured by Knight (1941), has a more slender spire and greater number of whorls. The closely related *Mapesella meeki* (Knight, 1931a), illustrated by Knight (1931a; as *Streptacis*) and Bandel (2002b) from the Pennsylvanian (Desmoinesian) of Missouri, also differs in the greater convexity of its whorls; its well developed sinus culminates higher on the whorl outer surface than in *Platyconcha* sp. Hoare *et al.* (1997) tentatively assigned two species from the Pennsylvanian of the Appalachian Basin to *Streptacis* but these are several times larger than *Platyconcha* sp. and have a wider incremental angle. *Streptacis gundyensis* Yoo, 1994 from the Early Carboniferous of New South Wales has slightly more convex whorls and lacks the sinus of the Pot Bank Quarry specimen.

Superfamily ZYGOPLEUROIDEA Wenz, 1938

Family PSEUDOZYGOPLEURIDAE Knight, 1930

Remarks. As noted above, Kues & Batten (2001) considered Palaeozygopleuridae Horný, 1955 to be a junior synonym of Pseudozygopleuridae Knight, 1930, grouping them as zygopleuroideans. Bouchet & Rocroi (2005) maintained Palaeozygopleuridae within Loxonematoidea and regarded pseudozygopleurids as caenogastropods, as did Frýda *et al.* (2013). Although this placement is followed here, the absence of a preserved protoconch in the specimen discussed below inevitably qualifies taxonomic assignment of the material from Pot Bank Quarry.

Genus MICROPTYCHIS Longstaff, 1912

Type species. *Microptychis wrighti* Longstaff, 1912, Dinantian, County Cork, Island.

Microptychis sp.

Figure 12E

Figured material. PMU 29771 from assemblage A (Fig. 1, locality 1). Morridge Formation, Carboniferous, Namurian (Chokierian), Pot Bank Quarry, Congleton Edge, Cheshire.

Remarks. This species is known from a single external mould of a partially flattened specimen. Thus, the incremental angle of the flat-sided spire is larger than in species figured by Longstaff (1933), including those she attributed

to its junior subjective synonym *Eoptychia* Longstaff, 1933 (Batten 1966). The comarginal ornamentation is coarser than in Longstaff's (1933) illustrated specimens, although equally coarse comarginal ornamentation is present in specimens from the Pennsylvanian of Ohio illustrated by Hoare & Sturgeon (1981). Additionally, the comarginal ribs persist onto the final whorl whereas they usually fade in the latest growth stages in other described species of *Microptychis* (Longstaff 1933; Batten 1966; Hoare & Sturgeon 1981). In terms of both the persistence of the comarginal ornamentation and its expression, *Microptychis* sp. resembles some species assigned to *Palaeozygopleura* Horný, 1955, such as *P. sculariodea* (Phillips, 1836) of Longstaff (1933, pl. 9, fig. 11) and Batten (1966, pl. 9, fig. 3), but these are usually more slender and with a shallowly convex profile to the whorl. *Helminthozyga larga* Kues & Batten, 2001 from the Flechado Formation of New Mexico has both similar ornamentation and a flat-sided spire as *Microptychis* sp. but its incremental angle (20°) is only half that of *Microptychis* sp., as preserved.

Superfamily STREPTACIDOIDEA Knight, 1931a
Family DONALDINIDAE Bandel, 2002b

Genus DONALDINA Knight, 1933a

Type species. *Aclisina grantonensis* Donald, 1898 from the Visean of Scotland.

Remarks. Details of the protoconch and aperture (as comarginal growth lines) of key importance for the correct determination were described in numerous British species by Donald (1898) and Longstaff (1917) under the name *Aclisina* de Koninck, 1881. All currently available specimens from Pot Bank Quarry lack protoconchs and growth lines, so assignment to *Donaldina* relies on the general morphology of these spirally ornamented, high-spired gastropods. Batten (1966) reappraised Longstaff's (1917) concept, recognizing the high degree of variation within species. In a major study of heterostrophan gastropods, Bandel (2002b) described several new genera mainly based on the structure of their protoconchs. Since such information is lacking here, the Pot Bank Quarry specimens are conservatively referred to *Donaldina*.

Donaldina sp.
Figure 12A, G

Figured material. PMU 29766 and 29767 from assemblage H (Fig. 1, locality 4). Morridge Formation, Carboniferous, Namurian (Alportian), Pot Bank Quarry, Congleton Edge, Cheshire.

Other material. Five additional external moulds from assemblage H.

Remarks. The specimens are preserved as external moulds from assemblage H (Fig. 1, locality 4) and lack protoconchs and growth lines. The spire is slender, with an incremental angle of about 12°; at least ten whorls are present in a specimen 7 mm tall (Fig. 12A). The whorl profile is convex, slightly angulated at the periphery in the early whorls where the upper whorl surface above the spiral cords is flattened (Fig. 12G). About five spiral cords are visible, with the next highest cord forming the whorl periphery. In the largest preserved whorls a fine cord is present on the upper whorl surface mid way between the lower cords and the suture.

In terms of its high spire and prominent spiral ornamentation *Donaldina* sp. resembles *Stegocoelia* sp. (Fig. 12B–D) from Pot Bank Quarry but it is readily distinguished by its much narrower spire. It is similar to slender examples of *Donaldina stevensana* (Meek & Worthen, 1866), described by Kues & Batten (2001) from the Flechado Formation (Pennsylvanian, Desmoinesian) of New Mexico. Kues & Batten (2001) noted that this is a variable species, with the incremental angle varying from 12 to 22°, and illustrated more slender specimens than those figured by Knight (1931a) from the Desmoinesian of Missouri. The protoconch is described in detail by Bandel (2002b) who assigned similar shells with a different protoconch morphology to a new genus *Royalella* based on two species from the Pennsylvanian (Desmoinesian–Missourian) of Texas.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/1AF5FA2A-2CC0-410F-989B-327921384BB9>.

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