Contents lists available at ScienceDirect

Geobios

journal homepage: www.elsevier.com/locate/geobio

Original article

Middle Ordovician brachiopods from Tagoat, Co. Wexford, SE Ireland: Dapingian diversity drivers ☆

David A.T. Harper [a,*], Denis E.B. Bates [b]

[a] Department of Earth Sciences, Durham University, Durham DH1 3LE, UK
[b] Department of Geography & Earth Sciences, Aberystwyth University, Aberystwyth SY23 3DB, UK

A B S T R A C T

The Dapingian (Arenig) siltstones and sandstones of the Tagoat Group, County Wexford, SE Ireland, contain a well-preserved and diverse brachiopod fauna including a new genus of alimbellid, *Palaeotagoatia* (type species: *Orthis Bailyana* Davidson) together with the plectorthid *Ffynnonia costata* (Bates) *hibernica* nov. subsp. Of the 13 forms documented, at least six are conspecific with brachiopods from the upper Arenig (Dapingian-lowest Darriwilian) Treiorwerth Formation on Anglesey and a further two are identified with species occurring in the older Dapingian Carmel Formation. The faunal province affinities of the fauna are with those assemblages assigned to the peri-insular and marginal Celtic province and which occupied positions within the Middle Ordovician Iapetus Ocean between the Laurentian and Baltic platform provinces. More precise correlation of Middle Ordovician units suggests a significant species richness during the Dapingian-earliest Darriwilian and signalling also an early development of the Celtic province. But the shallow-water siliciclastic facies associated with these islands may also have influenced the distribution of some elements of the Celtic brachiopods and promoted the prevalence of coarse-ribbed orthides, such as *Paralenorthis*.

© 2023 The Authors. Published by Elsevier Masson SAS. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Ordovician brachiopods have been known for over a century from siliciclastic rocks occurring in the vicinity of Tagoat, County Wexford, SE Ireland (Baily *in* Kinahan, 1879) but it is only recently that their precise age and biogeographical significance have been appreciated (Bates *in* Brenchley et al., 1967; Williams, 1973; Neuman and Bates, 1978). The assemblage is one of a group of faunas that now occur along the axial part of the Appalachian-Caledonide mountain belt which during the Middle Ordovician inhabited the shelves of volcanic or microcontinental islands within the central parts of the Iapetus Ocean (Neuman, 1984; Neuman and Harper, 1992). The islands supported a distinctive type of fauna commonly quite different from those of the adjacent platform provinces, termed the Celtic province (Harper et al., 2013). The brachiopod fauna as a whole is most similar to that from the Treiorwerth Fm. on the North Wales island of Anglesey nearby; this correlation together with the occurrence of graptolites

of the *Didymograptus extensus* and *D. hirundo* biozones indicate a middle to late Arenig (Dapingian-earliest Darriwilian) age for the Tagoat Group. The Middle Ordovician brachiopods from both Tagoat and Anglesey contrast markedly with coeval assemblages in the Anglo-Welsh Borderlands. These faunal differences indicate support for the view that the Irish sea area may represent a suspect or allochthonous terrane within the Caledonides which moved into its present position near the end of the Devonian (Nutt and Smith, 1981). More recent research (Cocks and Popov, 2021) has included brachiopod faunas from south-west Wales, associated with the western edge of the Avalon terrane; farther west is Ramsey Island (Bates, 1969).

2. Stratigraphical background

The Tagoat Group (Lower Silurian, Caradoc-Bala of Kinahan (and Baily), 1879; Tagoat Beds of Baker, 1966 and Brenchley et al., 1967; Tagoat Fm. of Gardiner and Brenchley, 1970; Tagoat Group of Molyneux et al., 2023) is a heterogeneous succession of conglomerates, sandstones, siltstones and shales which apparently rests unconformably on the Precambrian Rosslare Complex. The group is poorly exposed and crops out in a WSE-ENE trending belt
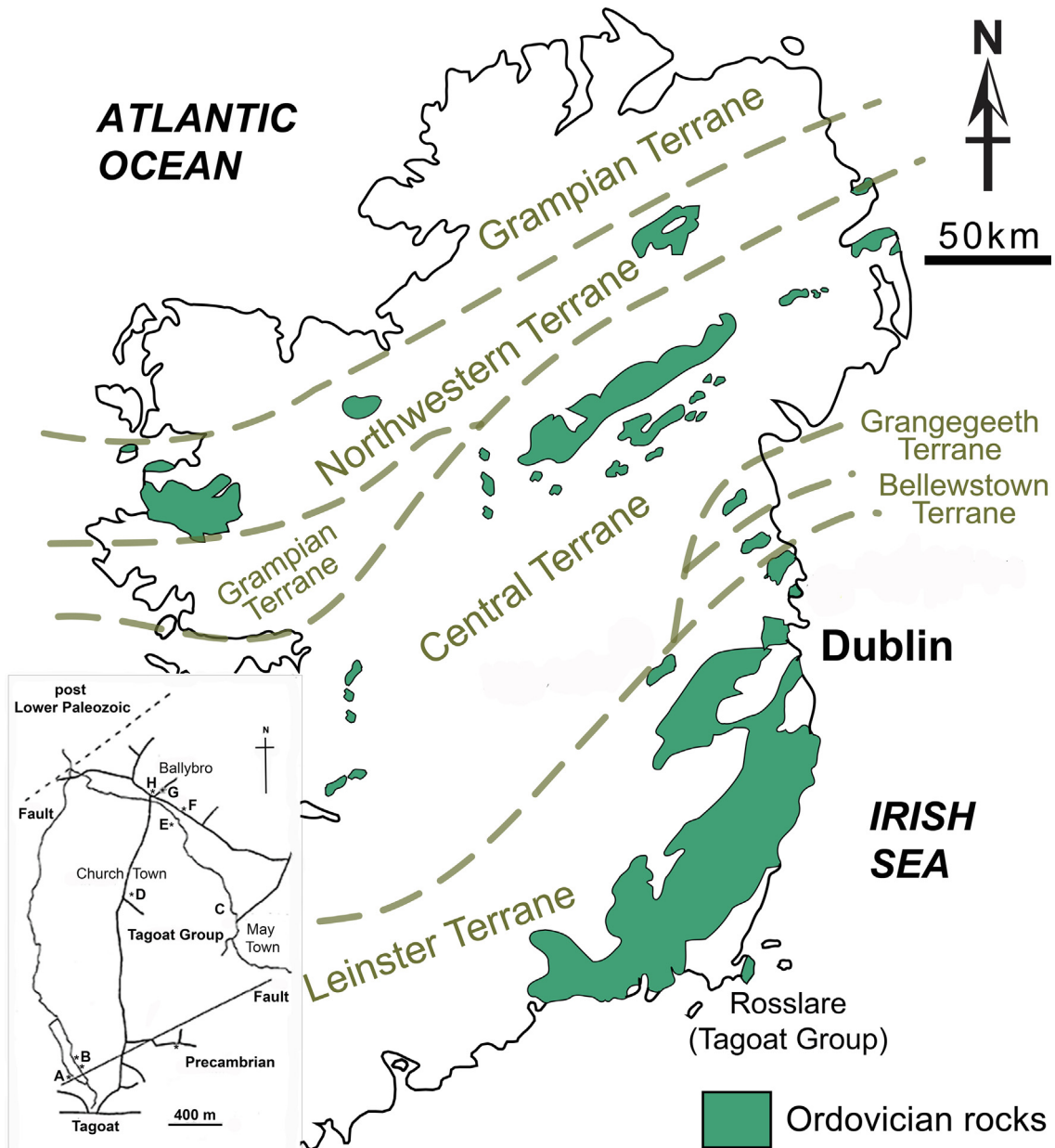
Fig. 1. Caledonian tectonic terrane map of Ireland, based on a figure provided by Annlise Ferretti, from various sources including Harper and Parkes (1989) and Murphy et al. (1991). Inset is a locality map for the exposures of the Tagoat Group: A, Conglomerates; B, Grey and purple conglomerates, sandstones and siltstones; C, Shales with sandy ribs in banks of stream; D, fossiliferous scree, bedrock not exposed; E-G, coarse-fine grained buff coloured sandstones and mudstones; H, fossiliferous locality, recorded by Geological Survey of Ireland. Based on Baker (1966) and field notes by DEBB.

between Ballybro and Tagoat (Fig. 1, inset). More or less along strike the Tagoat Group appear to pass laterally into the Silverspring Beds which Baker (1966: p. 4) considered to represent a different metamorphic facies of the Tagoat strata. There is no unequivocal evidence to suggest a direction of younging of the successions but some information from graded bedding at locality E indicates a possible younging to the south, implying the succession is inverted. The Tagoat Group is in excess of 120 m thick (Baker, op. cit.); the landscape over much of its outcrop is subdued and featureless.

Although due to the poor exposure the detailed relationships of the various constituent sedimentary facies cannot be determined with any accuracy, a fairly precise age for the group is available. In the vicinity of Ballybro (localities F, G and H; Fig. 1, inset) graptolite faunas have been collected indicative of the *Didymograptus*

extensus Biozone (Brenchley et al., 1967: p. 387); there is, however, the possiblity that the graptolites from locality G may be indicative of a *D. hirundo* Biozone fauna (loc. cit.). The co-occurring trilobites were also, on balance, assigned to an horizon within the *D. hirundo* Biozone (loc. cit.). Bates (*in* Brenchley et al., 1967: p. 388) considered that the rich brachiopod fauna from locality E indicates a comparison and correlation with similar faunas he had then recently documented from Anglesey (Bates, 1964). Significantly, graptolites obtained from loose blocks, presumably near locality E, were considered by Brenchley et al. (1967: p. 389) to represent the biozone of *D. hirundo* although the presence of the *D. extensus* biozone could not be excluded. The present study confirms this correlation; the brachiopods are most similar, at the specific level, to those of the Treiorwerth Fm. on Anglesey which is correlated with the upper Arenig (Bates, 1972; Molyneux et al., 2023). Of the 13

brachiopod taxa discussed below, at least six are considered to be conspecific with forms occurring in the Treiorwerth Fm. on Anglesey. Two, *Hesperonomiella carmelensis* and *Paralenorthis proava*, occur also in the underlying Carmel Fm. However, due to the discontinuous occurrence of the faunas, both on Anglesey and at Tagoat, details of the precise ranges of taxa from these areas are not available. Thus in the absence of such data a partial correlation of the fossiliferous Tagoat strata with the barren upper Carmel Fm. may be suggested.

3. Material and methods

The preparation, photographic and measurement techniques adopted are conventional, whereas the classification is that of the Treatise of Invertebrate Paleontology (part H revised). Citations to taxa including and above the level of genera are to be found in the revised brachiopod treatise and are not included here. Measurements are provided for some of the material in the tables included; many of the specimens are unsuitable for measurement. Approximate magnifications are indicated by scale bars on the figures. The following abbreviations are used: sagl, sagittal length; maxw, maximum width; hinwi, hinge width; sagl mf, sagittal length of muscle field; maxw mf, maximum width of muscle field; dh, depth; sagl npl, sagittal length of notothyrial platform; maxw npl, maximum width of nothyrial platform. Much of the present material was collected by DEBB from two key localities (E and F) and this is reposited in the National Museum of Ireland (NG:F); other material is in the Geological Survey of Ireland and Trinity College, Dublin (TCD).

4. Systematic palaeontology

Phylum Brachiopoda Duméril, 1806
Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Obolidae King, 1850
Genus *Palaeoglossa* Cockerell, 1911
Type species: By original designation: *Lingula attenuata* Sowerby *in* Murchison, 1839, from the Rorrington Fm. (Sandbian, Aurelucian) of Shropshire, England.

Palaeoglossa? sp.
Fig. 2(J)
?1879. *Lingula ovata* - Baily in Kinahan, p. 56.
Remarks: Two small incomplete and indeterminate valves from locality G are tentatively assigned to *Palaeoglossa*. Cocks and Popov (2019) described and illustrated *P. petalon* (Davidson, 1868) from Floian Ogof Hên Fm. of the Llangynog Inlier and the Blaencediw Fm. (Floian), together with occurrences in the Penmaen Dewi Fm. (Floian-Dapingian) and the Pontyfenni Fm. (Dapingian). The Tagoat shells are tentatively assigned to *Palaeoglossa* and are possibly conspecific with the broadly coeval material from south-west Wales.

Order Kutorgininida Kuhn, 1949
Kutorgininide superfam., fam., gen. et sp. indet.
1978. Superfamily, family, genus and species unknown - Neuman and Bates, p. 580, pl. 63, figs. 3, 4, text-fig. 2.
Material and locality: One broken and poorly preserved valve from locality E; not figured.
Remarks: The only valve of this form available for study from Tagoat is incomplete; the posterior part of the shell bearing the hinge region is missing. Nevertheless, the outline and profiles of the valve agree well with those reported for an indeterminate trimerellide from the Treiorwerth Fm. on Anglesey (Neuman and Bates 1978: p. 580); furthermore, the Irish specimen possesses lon-

gitudinal grooves and ridges, medially in the valve interior similar to those of the Welsh species. Both the Irish and Welsh material has been preserved in opaline silica possibly replacing an original calcareous shell. Neuman and Bates (1978) also suggested an alternative assignment to the Trimerellidae. The Tagoat material is incomplete and sparse and cannot advance any firm hypotheses on the affinities of this taxon.

Order Billingsellida Schuchert, 1893
Suborder Clitambonitidina Öpik, 1934
Superfamily Polytoechioidae Öpik, 1934
Family Tritoechia Ulrich and Cooper, 1936
Genus *Tritoechia* Ulrich and Cooper, 1936
Type species: By original designation: *Deltatreta typica* Schuchert and Cooper, 1932, from the Middle Ordovician of Oklahoma, U.S.A.

Tritoechia pyramidalis (Bates, 1968)
Fig. 2(A-F, I)
1967. *Tritoechia* (?) sp. - Bates in Brenchley et al., p. 388.
1968. *Antigonambonites pyramidalis* Bates - p. 163, pl. 6, figs. 12–18.
1968. *Tritoechia* sp. - Bates, p. 161, pl. 6, figs. 1–3, 5.
1978. *Tritoechia* sp. - Cocks, p. 83.
1978. *Antigonambonites pyramidalis* Bates - Cocks, p. 84.
1978. *Tritoechia pyramidalis* (Bates) - Neuman and Bates, p. 599, pl. 64, figs. 39–49.
2008. *Tritoechia pyramidalis* (Bates) - Cocks, p. 11.
Holotype: By original designation, a dorsal valve, BB30561, from the Treiorwerth Fm. (upper Arenig), Anglesey.
Material and localities: Several ventral valves and a dorsal valve mainly from a spoil heap near locality F.
Description: Several ventral valves of a polytoechioid are considered to be conspecific with *Tritoechia pyramidalis* (Bates, 1968). The valves are pyramidal in shape with long, flat, cataclinal interareas. The ventral muscle scars comprise well-defined diductor scars and more deeply impressed adductors situated on a callus of secondary shell in the form of a crude pseudospondylium. The anterior edges of the muscle scars are not undercut whilst the dental plates descend almost vertically to the floor of the valve. One small valve has a convex pseudodeltidium but on the remaining specimens it is either broken or absent since only thin lateral plates are visible.
Remarks: Neuman and Bates (1978: p. 599) have redescribed this species on the basis of abundant and well-preserved material from the Treiorwerth Fm. on Anglesey and have discussed the affinities and diagnostic features of the species. In particular, the Anglesey material is characterised by a marked contrast between the development of strong and weak costellae whilst the number of weaker costellae, developed between accentuated ribs, is greater than that for other species of *Tritoechia*.

Tritoechia bolahaulensis Cocks and Popov, 2019 from the Bolahaul Mb., Ogof Hên Fm. (Floian) is older and differs from *Tritoechia pyramidalis* Bates, 1968, in having a multicostellate in contrast to parvicostellate radial ornament, a strongly elongate rather than transverse ventral muscle field bounded laterally by long, almost parallel dental plates, and depressed ventral adductor scars slightly longer than diductor scars.

Superfamily Clitambonitoidea Winchell and Schuchert, 1893
Family Clitambonitidae Winchell and Schuchert, 1893
Genus *Palaeoneumania* Hansen and Harper, 2005
Type species: By original designation, *Atelelasma atlanticus* Neuman, 1976, from the Summerford Group (upper Arenig), Newfoundland, Canada.
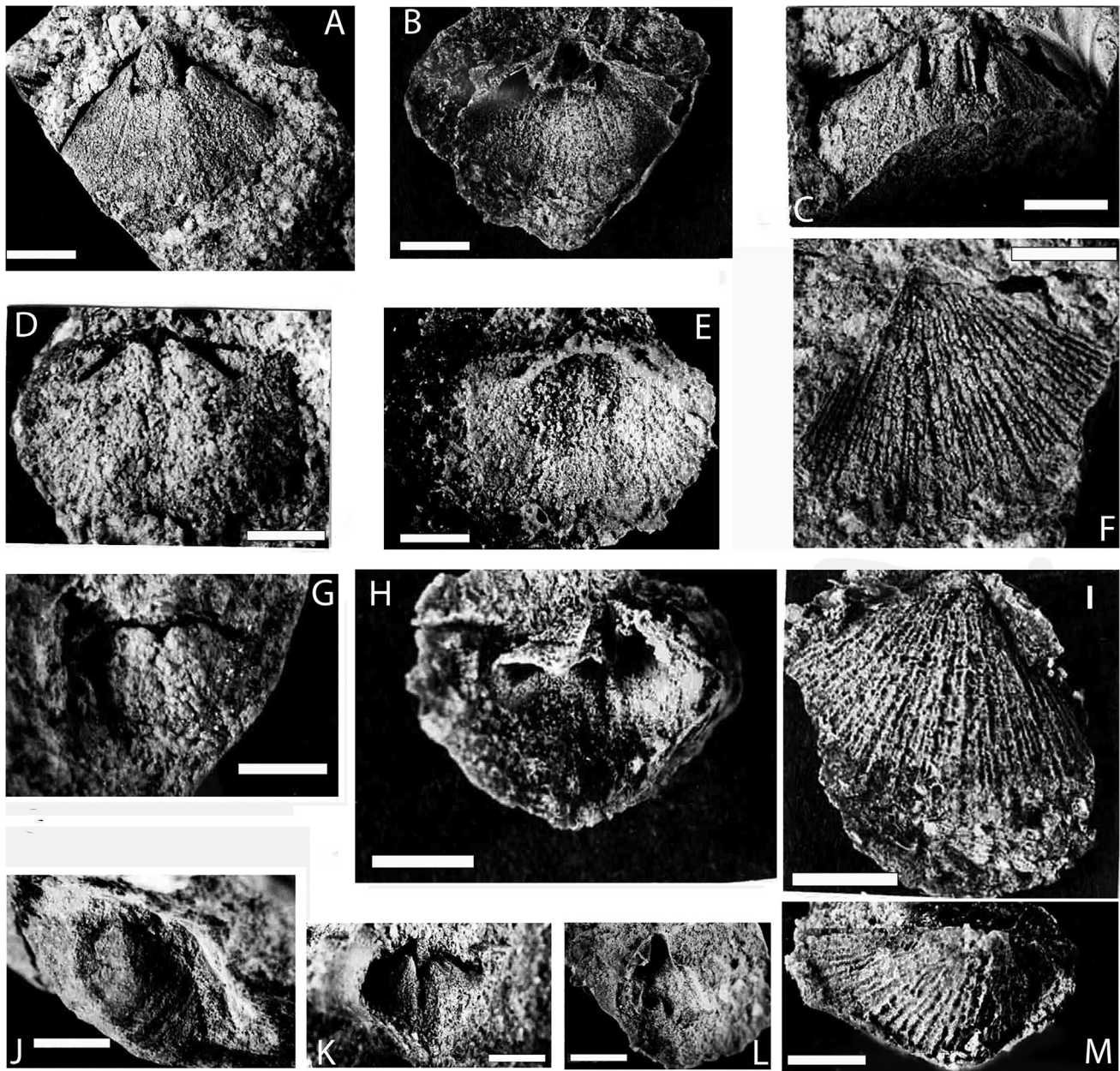
Fig. 2. A-F, I. *Tritoechia pyramidalis* (Bates). A, B: internal mould and latex cast of ventral valve, NG:F35328; C: internal mould of ventral valve, NG:F35329; D, E: internal mould and latex cast of dorsal valve, NG:F35330; F, I: external mould and latex cast of dorsal valve, NG:F35331. **G, K-M.** *Skenidioides* sp. G: internal mould of ventral valve, NG:F35332; K, L: internal mould and latex cast of ventral valve, NG:F35333; M: latex cast of ventral exterior, NG:F35334. **H.** *Palaeoneumania* sp., latex cast of ventral valve interior, NG:F35335. **J.** *Palaeoglossa*? sp., partial ventral valve, NG:F35336. Scale bars: 5 mm A-F, H and 2.5 mm for G, J-M.

Remarks: The clitambonitide brachiopod *Neumania* Harper, 1981 (*in* Bruton and Harper, 1981) was established for a distinctive atelelasmatid genus with a prominent imbricate ornament developed over the entire surface of the shell together with a pronounced dorsal sulcus and narrow plates bordering the delthyrium. The type species, *Atelelasma atlanticus* Neuman, 1976, occurs in the upper Arenig Summerford Group, central Newfoundland, Canada. The name *Neumania* was, however, already occupied for a group of pionatacinine water mites. Thus the brachiopod *Neumania* Harper is a junior homonym of the water mite genus *Neumania* Lerbert. Hansen and Harper (2005) proposed the new name *Palaeoneumania* as a replacement that would cause minimal confusion.

Palaeoneumania? sp.

Fig. 2(H)

1967. *Atelelasma* (?) sp. - Bates in Brenchley et al., p. 388.
2008. *Neumania* sp. - Wright in Cocks, p. 109.

Material and locality: One ventral valve from locality E.

Description: Only one internal mould of this form is available for study. The valve is of pyramidal shape, widest at hinge line and with a flat, cataline interarea, twice as wide as long; the delthyrium is open and is restricted laterally by thin plates extending inwards from the margins of the delthyrium. The spondylium simplex is supported by a thick median septum.

Remarks: The presence of the spondylium simplex and open delthyrium suggest attribution to the Atelelasmatinae whilst the

incipient development of lateral plates is characteristic of both *Atelelasma* itself and *Palaeoneumania*. Moreover, the valve would appear similar to ventral interiors of *Atelelasma* from the Bod Deiniol Fm. on Anglesey (Neuman and Bates, 1978: pl. 68, figs. 14, 15) which have been reassigned to *Palaeoneumania*, principally on account of its lamellose ornament (Harper *in* Bruton and Harper, 1981). Furthermore, both the Anglesey and Irish specimens are small.

Order Protorthida Schuchert and Cooper, 1931
Superfamily Skenidioidea Kozłowski, 1929
Family Skenidiidae Kozłowski, 1929
Genus *Skenidioides* Schuchert and Cooper, 1931
Type species: By original designation, *Skenidioides billingsi* Schuchert and Cooper, 1931, from the Rockland Fm. (Katian), Ottawa River, Quebec.

Skenidioides sp.
Fig. 2(K-M)
1967. *Skenidioides* sp. - Bates in Brenchley et al., p. 388.
1968. *Skenidioides* sp. (1) - Bates, p. 156, pl. 5, figs. 1, 2.
1978. *Skenidioides* sp. (1) - Cocks, p. 35.
1978. *Skenidioides* sp. (1) - Neuman and Bates, p. 597, pl. 64, figs. 12–23.
2008. *Skenidioides* sp. - Cocks, p. 113.
Material and locality: Two poorly preserved ventral valves from locality E.
Description: The two ventral valves which comprise the present material cannot be determined specifically. The valves are hemipyramidal, ca. two-thirds as deep as long and with a relatively long, almost catacline, flat interarea. The spondylium is shallow and supported by a very short, thin, receding septum. The external mould simple rounded costae; no intercalated or bifurcated costellae are present on the part of the valve preserved. Information is sparse but the ventral valves are broadly similar to those of *Skenidioides* sp. from the Treiorthwerth Fm. on Anglesey (Neuman and Bates, 1978).
Remarks: *Skenidioides pontyfennensis* Cocks and Popov, 2019 from the Pontyfenni Fm. (Dapingian), south-west Wales, has broad similarities regarding outline and shape, but it lacks an accentuated median rib and has fewer ribs. The Tagoat material is restricted to ventral valves, thus comparisons with the distinctive dorsal valves of *Protoskenioides revelata* Williams, 1974 from the Mytton Flags (Floian-Dapingian), Shelve inlier, Shropshire, is not possible.

Order Orthida Schuchert and Cooper, 1935
Suborder Orthidina Schuchert and Cooper, 1932
Superfamily Orthoidea Woodward, 1852
Family Hesperonomiidae Ulrich and Cooper, 1936
Genus *Hesperonomiella* Ulrich and Cooper, 1936
Type species: By original designation, *Hesperonomiella carmelensis* Bates, 1968, from the Carmel Fm. (lower Arenig), Anglesey.
Remarks: *H. carmelensis* has been described in considerable detail by Bates (1968) and compared with an unamed species from the Treiorwerth Fm. on Anglesey (Neuman and Bates, 1978). This latter taxon possesses many of the key features of the genus *Hesperonomiella* where it was originally placed; the present study confirms its generic affinity.

Hesperonomiella aff. *carmelensis* Bates, 1968
Fig. 3
?1879. *Strophomena expansa* J. de C. Sowerby - Baily in Kinahan, p. 56.

1967. *Hesperonomiella* sp. nov. - Bates in Brenchley et al., p. 388.
aff. 1968. *Hesperonomiella carmelensis* Bates - p. 142, pl. 1, figs. 1–6.
ff. 1972. *Hesperonomiella carmelensis* Bates - Bates, p. 35.
1978. *Hesperonomiella* sp. - Neuman and Bates, p. 583, pl. 63, figs. 29–34.
aff. 1978. *Hesperonomiella carmelensis* Bates - Cocks, p. 36.
aff. 2008. *Hesperonomiella carmelensis* Bates - Cocks, p. 120.
Holotype: By original designation, a dorsal valve, BB30529, from the Carmel Fm. (lower Arenig), Anglesey.
Material and localities: Seven ventral valves and three dorsal valves. Majority of the well-preserved specimens are from Locality E. These specimens are congeneric and possibly conspecific with *Hesperonomiella* sp. (*in* Neuman and Bates, 1978) from coeval strata on Anglesey.
Measurements: See Table 1.
Remarks: The specimens assigned to this taxon are broadly similar to those of *H. carmelensis* from the Carmel Fm., on Anglesey; the outline and profiles of both valves together with their internal morphologies are similar. Unfortunately, the ornament of the Irish specimens is barely discernable since the average grain size of the enclosing sediments is commonly greater than the wavelength of the relatively fine ribs; however, one ventral valve exterior gave a density of six evenly rounded ribs per mm, 5 mm anteromedianly with both the first and the sixth ribs slightly accentuated. This compares well with data for the Anglesey species of 30 ribs per 5 mm at the same place on the shell (Bates 1968: p. 143). The available evidence thus suggests the two are closely related. Nevertheless, their closest relative is *Hesperonomiella* sp. from the Treiorwerth Fm. These younger specimens from both Ireland and Wales have more rounded outlines, obtuse cardinal extremities and with a well-developed notothyrial platform, a thickened cardinal process and deep sockets flanked by widely divergent brachiophores. Combined, these features may provide the basis for a new species but the material is currently inadeqaute.

Family Orthidae Woodward, 1852
Subfamily Orthinae Woodward, 1852
Genus *Paralenorthis* Havlíček and Branisa, 1980
Type species: By original designation *Paralenorthis immitatrix* Havlíček and Branisa, 1980; from the Middle Ordovician of San Lucas, Bolivia.

Paralenorthis proava (Salter, 1866)
Fig. 4
1866. *Orthis calligramma* var. *proava* Salter *in* Ramsay - p. 335, pl. 355, fig. 1.
1869. *Orthis Caurusii* Salter - Davidson, p. 229, pl. 33, figs. 1–7.
1879. *Orthis calligramma* Dalman - Baily in Kinahan, p. 56.
1883. *Orthis Caurusii* Salter - Davidson, p. 182, pl.14, figs. 21–26.
1912. *Orthis proava* Salter - Matley, pp. 78–79.
1967. *Lenorthis proava* (Salter) - Bates in Brenchley et al., p. 388
1968. *Lenorthis proava* (Salter) - Bates, p. 146, pl. 1, fig. 21, pl. 2, figs. 1–8.
1968. *Lenorthis* sp. - Bates, p. 146, pl. 2, figs. 11, 12.
1972. *Lenorthis proava* (Salter) - Bates, pp. 35, 36, 37.
1974. *Lenorthis* cf. *proava* (Salter) - Williams, p. 52, pl. 8, figs. 2–9.
1978. *Orthambonites proava* (Salter) - Cocks, p. 39.
1978. *Orthambonites* sp. - Neuman and Bates, p. 585, pl. 64, figs. 1–11.
1993. *Paralenorthis proava* (Salter) - Jaanusson and Bassett, p. 34, pl. 3, figs. 9–13, pl. 4, figs. 6–8.
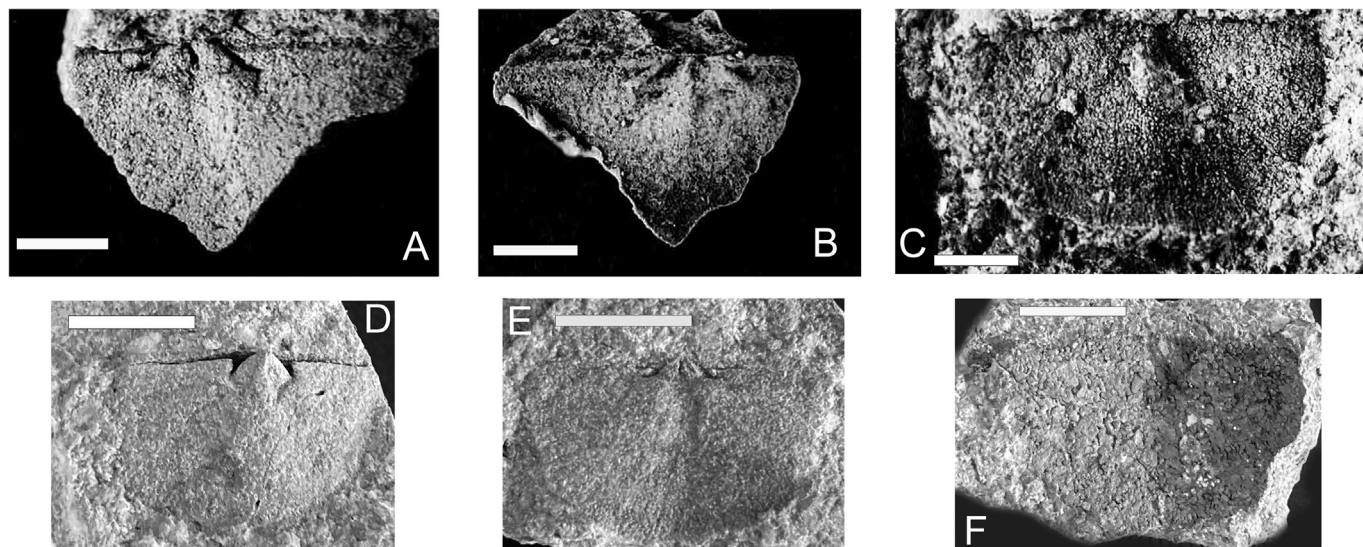2008. *Paralenorthis proava* (Salter) - Cocks, p. 114.

Fig. 3. *Hesperonomiella* aff. *carmellensis* (Bates). **A, B.** Internal mould and latex cast of dorsal valve, NG:F35337. **C.** External mould of dorsal valve, NG:F35338. **D.** Internal mould of ventral valve, NG:F35339. **E.** Internal mould of dorsal valve, NG:F35340. **F.** External mould of valve showing infestations, NG:F35341. Scale bars: 5 mm.

Table 1
Measurements (in mm) of *Hesperonomiella* specimens.

VV	sagl	maxw	sag1 mf	maxw mf	ante dpls	maxs dpls	dh				
	11.9	17.6	2.6	4.2	1.6	4.5	1.5				
	16.8	26.0	4.0	6.3	2.1	6.5	1.5				
	-	17.3	3.5	5.0	2.1	5.2	1.2				
DV	**sagl**	**maxw**	**sagl**	**maxw mf**	**sagl mf**	**maxw mf**	**sagl mf**	**maxw npl**	**ante npl**	**maxs sdg**	**maxw sdg**
	-	-		3.0	6.0	2.5	5.8	2.0	3.5	1.4	5.2
	9.0	~18.0		-	-	-	-	2.0	2.5	1.2	3.8

Lectotype: Selected by Cocks (1978: p. 39), a dorsal valve, GSM 104182A from the Carmel Fm. (lower Arenig), Anglesey.

Material and localities: Most the specimens are from a quarry on the south-west side of the stream (locality E) with others from loose debris on the north-east side of the stream.

Measurements: See Table 2.

Remarks: Neuman and Bates (1978) noted the common occurrence of coarse-ribbed orthids in early (sic.) Ordovician assemblages. Many are associated with shallow-water facies and commonly with coarse-grained sediments. Those authors also discussed some of taxonomic issues around the assignment of material to *Lenorthis*, within the context of *Lenorthis proava* (Salter) (see Bates, 1968), and assigned their material instead to *Orthambonites* a relatively rare Baltic genus based on *Orthis calligramma* Dalman, restricted to the Kundan Stage in Baltoscandia (Jaanusson and Bassett, 1993). The situation is now resolved by the abandonment of the genus name *Lenorthis* and the placement of its species and others within the genus *Paralenorthis* Havlíček rather than *Orthambonites* (Jaanusson and Bassett, 1993).

The genus *Paralenorthis* is one of the most widespread Ordovician brachiopod taxa, most common at high to intemediate latitudes. *Paralenorthis proava* (Salter, 1866) is the most common taxon in the Tagoat fauna. Preservation of the material is, however, far from perfect (the specimens are preserved in a coarse sandstone) and measurements, though possible, are not accurate due to fragmentation and some tectonic deformation. The shape and ornament is very similar to those of *P. proava* from the Carmel Fm. on Anglesey (Bates, 1968); costae are between 16 and 22,

and ventral valve bears a median costa. Six dorsal valves have a mean costal wavelength of 1 mm (range 0.8–1.3 mm) measured at 5 mm from the umbo. Measurements and some statistics are provided for both valves (Table 2).

Paralenorthis (*Orthambonites*) sp. from the younger Treiorwerth Fm. on Anglesey (Neuman and Bates, 1978) has a weaker median ridge in the dorsal valve and shorter dental plates in the ventral valve than those of *P. proava*. The Tagoat specimens have well-developed dorsal median ridges and relatively long dental plates, supporting their inclusion in the Carmel Fm. species.

Family Productorthidae Schuchert and Cooper, 1931
Subfamily Productorthinae Schuchert and Cooper, 1931
Genus **Productorthis** Kozłowski, 1927
Type species: By original designation, *Productus obtusus* Pander, 1830, from the Middle Ordovician (Dapingian) of the St. Petersburg region, Russia.

Productorthis lamellosa (Bates, 1968)
Fig. 5
1967. *Panderina* sp. nov. - Bates *in* Brenchley et al., p. 388.
1968. *Panderina lamellosa* Bates - p. 151, pl. 3, figs. 10–18.
1978. *Panderina lamellosa* Bates - Cocks, p. 42.
1978. *Productorthis* sp. - Neuman and Bates, p. 588, pl. 63, figs. 5–13, pl. 68, figs. 1–11.
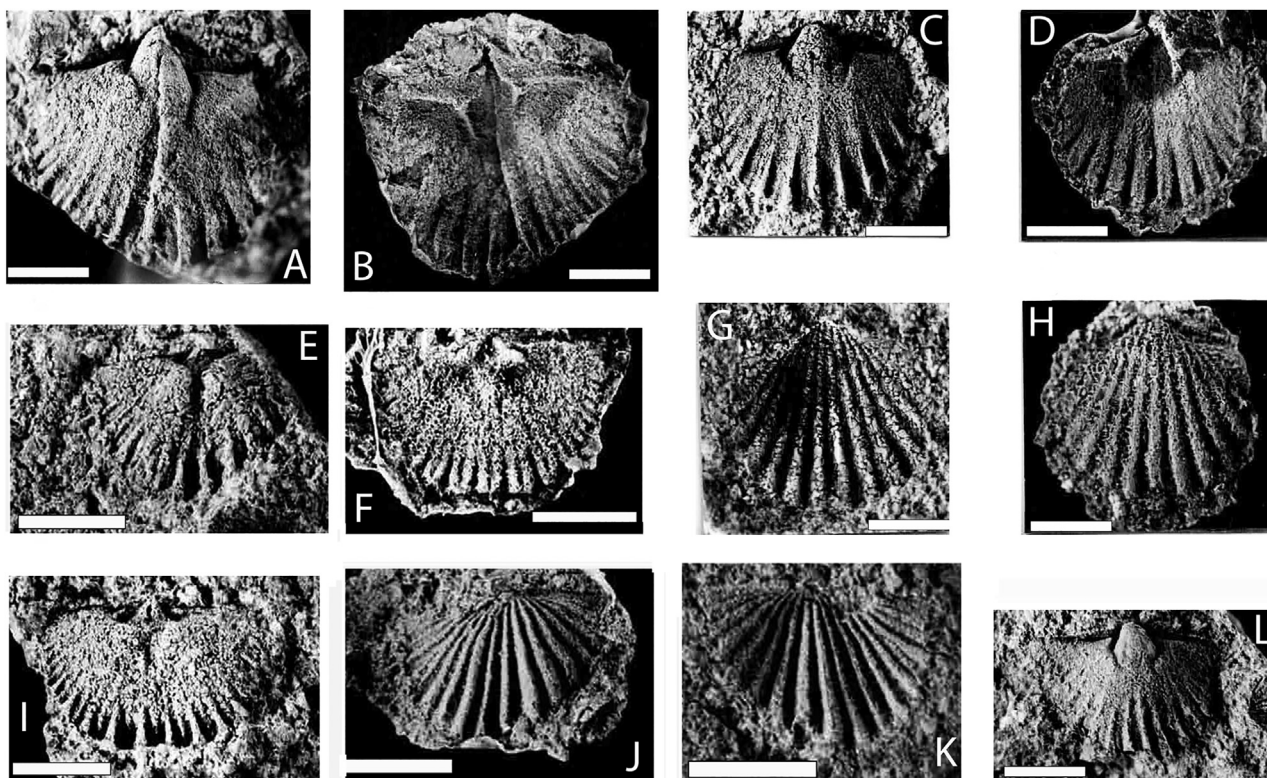2008. *Panderina lamellosa* Bates - Cocks, p. 133.

Fig. 4. *Paralenorthis proava* (Salter). **A, B.** Internal mould and latex cast of ventral valve, NG:F35342. **C, D.** Internal mould and latex cast of ventral valve, NG:F35343. **E, F.** Internal mould and latex cast of dorsal valve, NG:F35344. **G, H.** External mould and latex cast of ventral valve, NG:F35345. **I.** Internal mould of dorsal valve, NG:F35346. **J, K.** External mould and latex cast of dorsal valve, NG:F35347. **L.** Internal mould of ventral valve, NG:F35348. Scale bars: 5 mm.

Table 2
Measurements (in mm) and statistics for *Paralenorthis* specimens.

VV	sagl	maxw	hinw	sag1 mf	maxw mf	Dh	
	17.2	17.8	16.6	6.0	4.0	2.5	
	12.4	14.2	12.8	5.0	4.2	1.8	
	10.5	12.7	11.7	3.2	2.5	2.0	
DV	**sagl**	**maxw**	**hinw**	**sagl mf**	**maxw mf**	**sag1 npl**	**maxw npl**
	8.4	12.3	11.0	-	-	4.2	3.2
Ventral valves: N = 9	**sag1**	**maxw**	**Dh**				
Vector means	10.4	12.9	3.4				
Variance	6.1	5.5	0.4				
Dorsal valves: N = 6	**sag1**	**maxw**	**Dh**				
Vector means	7.2	9.5	1.1				
Variance	3.7	5.8	0.05				

Holotype: By original designation, a dorsal valve, BB30525, from the Treiorwerth Fm. (Dapingian), Anglesey.

Material and localities: Majority of specimens are from locality E.

Measurements: See Table 3.

Remarks: The Tagoat specimens are conspecific with *Productorthis lamellosa* (Bates, 1968) from the Treiorwerth and Bod Deiniol formations on Anglesey. Although Neuman and Bates (1978) suppressed the specific name *lamellosa* since, in fact, all species assigned to *Productorthis* possess lamellae; the name, however, remains valid, despite its inapplicability, unless, of course, the species is eventually synonymized with an existing named species of *Productorthis* (Harper *in* Bruton and Harper, 1985).

Family Alimbellidae Andreeva, 1960
Genus ***Palaeotagoatia*** nov. gen.

Derivation of the name: After the hamlet of Tagoat, County Wexford, Ireland.

Type and only known species: By original designation, *Orthis Bailyana* Davidson, 1869, from the Tagoat Group (Middle Ordovician), Tagoat, County Wexford, Ireland.
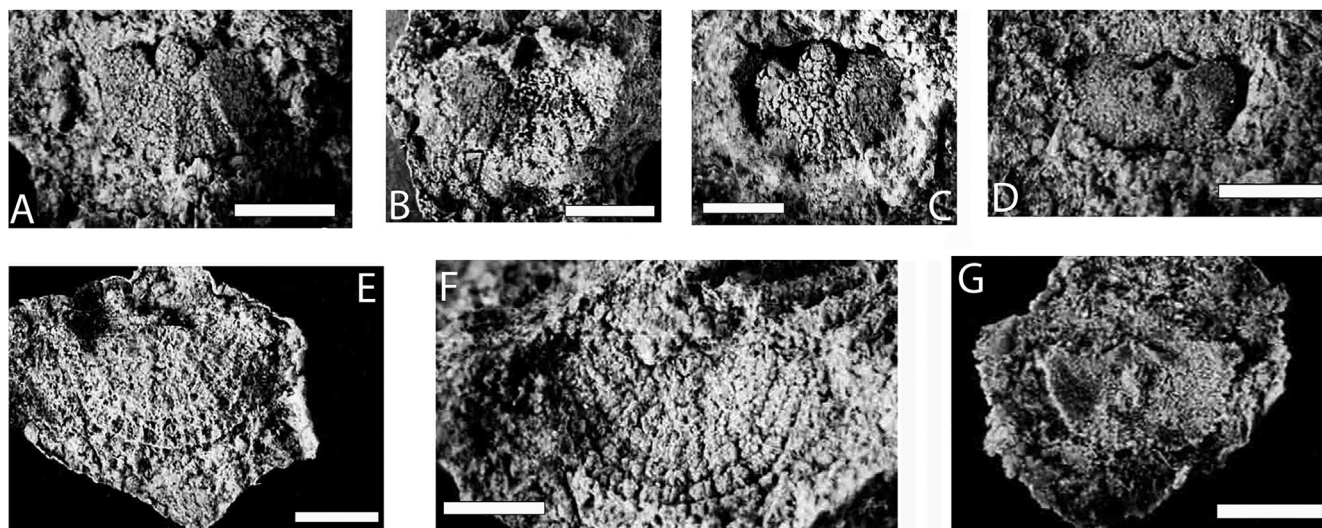
Fig. 5. *Productorthis lamellosa* (Bates). **A, B.** Internal mould and cast of ventral valve, NG:F35349. **C.** Internal mould of ventral valve, NG:F35350. **D, G.** Internal mould and latex cast of dorsal valve, NG:F35351. **E, F.** External mould and latex cast of dorsal valve, NG:F35352. Scale bars: 2.5 mm.

Table 3
Measurements (in mm) of *Productorthis* specimens.

VV	sagl	maxw	hinw	sag1 mf	maxw mf	dh	
	5.4	6.4	6.2	2.2	1.8	1.4	
	5.9	7.5	7.5	2.0	1.9	1.6	
	5.0	6.3	6.3	1.2	1.5	1.2	
DV	sagl	maxw	hinw	sag1 npl	maxw npl	ante sdg	maxs sdg
	4.1	7.3	7.3	1.7	1.8	0.9	2.0

Diagnosis: Large subequally biconvex alimbellid genus of subcircular outline, rectimarginate; delthyrium and notothyrium both wide and open. Ventral interior with short, strong teeth supported by receding dental plates ankylosed to posterior part of tongue-like pseudospondylium. Dorsal interior with linear cardinal process flanked by short, blunt socket ridges; adductor scars quadripartite with anterior pair the larger and more deeply impressed. Ornament of very fine ribs.

Remarks: Davidson (1869: p. 224) noted a number of unusual features in his new species *Orthis Bailyana*, in particular, the distinctive shape of the dorsal muscle scars, the absence of a prominent cardinal process and the smallness of the "brachial processes" (brachiophores). His description of the species was based only on internal moulds; a larger sample is now available which includes fragments of valve exteriors. The morphology of *Palaeotagoatia* nov. gen. is that of the Alimbellidae Andreeva, 1960; although both Andreeva (1960: p. 292) and Biernat (1965: p. H530) considered the family as aberrant porambonitoids, Williams (1974: p. 68) recognised the overwhelming orthide characters of the group and transferred it to the Orthacea (sic.). The new genus *Palaeotagoatia* differs from *Alimbella*, *Medesia* and *Astraborthis* in lacking a fold and sulcus; moreover, the exteriors of *Alimbella* and *Astraborthis* are respectively smooth and coarsely costate.

Palaeotagoatia bailyana (Davidson, 1869), nov. comb.
Fig. 6
1869. *Orthis Bailyana* Davidson - p. 233, pl. 29, figs. 19, 20.
1879. *Orthis Bailyana* Davidson - Baily *in* Kinahan, p. 56.

1967. '*Orthis*' *bailyana* Davidson - Bates *in* Brenchley et al., p. 388.
1978. *Platystrophia bailyana* (Davidson) - Cocks, p. 55.
1982. *Platystrophia bailyana* (Davidson) - Nudds, p. 67.
2008. *Platystrophia bailyana* (Davidson) - Cocks, p. 141.

Type specimens: The type specimens of *Orthis bailyana* Davidson, 1869 lie on two slabs, TCD 14739 and TCD 14740, now housed in the Geology Department of Trinity College, University of Dublin (Nudds, 1982). Slab TCD 14740, which holds the lectotype selected by Cocks (1978: p. 55), has on its top side a well-preserved internal mould of the ventral valve of *Ffynnonia costata* (Bates) *hibernica* nov. subsp., herein, relatively well-preserved internal moulds of both ventral and dorsal valves of *Orthis bailyana* and an internal mould of *Paralenorthis proava* (Salter). In addition, there are fragments of at least two external moulds of *P. proava*. In establishing *O. bailyana*, Davidson (1869) figured the moulds of both the ventral and dorsal valves (op. cit.: pl. 29, figs. 19, 20) together with reconstructions of the interiors of these valves (op. cit.: pl. 29, figs. 19a, 20a). It, therefore, seems probable that Cocks (1978: p. 55; see also Cocks 2008: p. 141) in his assignment of that species to *Platystrophia* mistakenly identified the ventral valve of the plectorthid *Ffynnonia* on the same slab as Davidson's type specimen of *O. bailyana*. The underside of the slab has an external mould of the ventral valve of *Productorthis lamellosa* (Bates) together with various fragments of external moulds of *P. proava*. The second slab, TCD 14739, displays on its top side internal moulds of the dorsal valves of each of *O. bailyana*, *F. c. hibernicus* and *P. proava*; whereas on the underside there are various external moulds of *P. proava*.
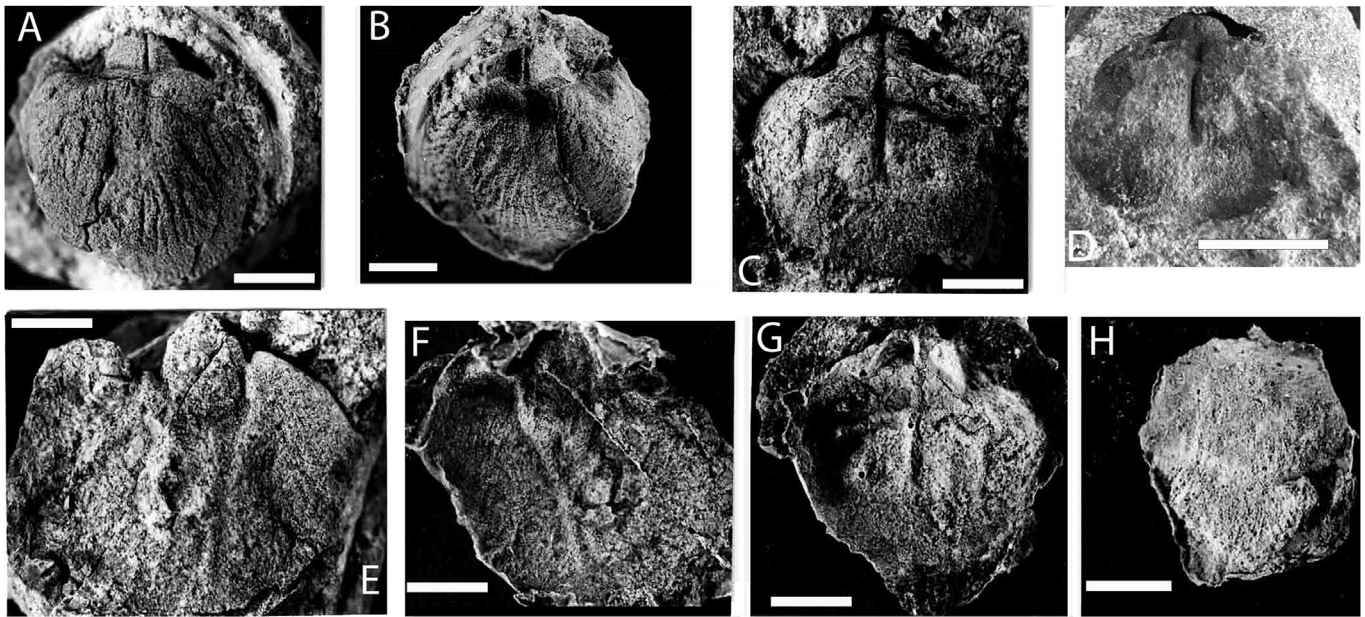
Fig. 6. *Palaeotagoatia bailyana* (Davidson) nov. comb. **A, B.** Internal mould and latex cast of dorsal interior, NG:F35353. **C, G.** Internal mould and latex cast of dorsal interior, NG:F35354. **D.** Internal mould of dorsal interior, NG:F35355. **E, F.** Internal mould and latex cast of ventral valve, NG:F35356. **H.** Latex cast of partial dorsal exterior, NG: F35357. Scale bars: 10 mm.

Table 4
Measurement (in mm) of *Palaeotagoatia* nov. gen. specimens. Maximum widths are estimates.

VV	sagl	maxw
	20.7	23.2
DV	**sagl**	**maxw**
	25.7	26.8
	20.5	25.6
	26.0	24.4

Material and localities: Excluding material in the Geological Survey of Ireland and Trinity College, Dublin (TCD), six dorsal valves and two ventral valves from loose blocks (locality F). Majority of specimens are from locality E.

Measurements: See Table 4.

Diagnosis: Large, subequally biconvex, subquadrate *Palaeotagoatia* species with very fine radial ornament.

Description: Exterior. Large, dorsibiconvex valves of rounded subquadrate outline with maximum width at or near mid-valve length; cardinal extremities rounded and obtuse, anterior commissure rectimarginate. Ventral valve about as long as wide and ca. one-third as deep as long; anterior and lateral profiles evenly convex. Ventral interarea relatively long, ca. one-quarter as deep as wide, curved and apsacline. Delthyrium open and where widest distally at teeth ca. one-third of hinge line. Dorsal valve about as long as wide and ca. one-third as deep as long; both profiles evenly convex. Dorsal interarea anacline to virtually orthocline with open notothyrium. External ornament of fine ribs with evenly rounded profiles and wavelengths of ca. one-third mm.

Ventral interior. Teeth strong, transversely directed and split into two ridges by an oblique groove; supported by receding dental plates which converge slightly onto floor of valve and diverge anteriorly at ca. 45°. Ventral muscle field of elongate subquadrate outline, ca. three-quarters as long as wide and extending anteriorly to ca. one-half valve length.

Dorsal interior. Cardinal process simple, developed on high notothyrial platform and consisting of relatively long, thin, linear ridge partitioning pair of oval adductor scars sited on pads of secondary shell in gerontic individuals. Anterior to platform, cardinal process continuous with low ridge bisecting compound muscle scars.

Remarks: The genus is currently represented by only the type species, however a small sample of conspecific material has now been recognised in collections from the Treiorwerth Fm. on Anglesey, including some silicified specimens. The umbones of both valves are not well preserved due either to postmortem abrasion or possible resorption during growth; thus both the delthyrium and notothyrium appear truncated posteriorly. Within the dorsal valve the short brachiophores are of a similar size to the teeth; the development of a crude denticulation of the tooth and socket system, in gerontic individuals, may have aided control of the opening of the valves. Davidson (1869: p. 224) commented on the unusual configuration of the dorsal musculature which is particularly distinctive. Whereas the diductor scars were situated on the notothyrial platform, bisected by the cardinal process, the quadripartite adductor scar occupied almost one-half of the valve floor anterior to the notothyrial platform. The anterior margins of the smaller posterior pair are concave anteriorly but have curved lateral margins forming an arc, convex outwards, which links the anterior margin of the scar to an area beneath each brachiophore. The margin of the scar is undercut laterally and provides for an extension of the muscle bases laterally over the gonocoels.

The specimens ascribed to articulate brachiopod indet. from the Bjørnskalle Fm. (upper Arenig) on the Hardangervidda, Norway (Bruton et al., 1984) have similarities with the alimbellids and is possibly related to *Palaeotagoatia* nov. gen. This fauna in the southwest part of the Norwegian mountain belt occurs near the edge of the Baltic craton.

Superfamily Plectorthoidea Schuchert, 1929
Family Platystrophiidae Schuchert, 1929
Genus *Ffynnonia* Neuman and Bates, 1978
Type species: By original designation, *Pleurorthis costatus* Bates, 1968, from the Treiorwerth Fm. (Dapingian), Anglesey.
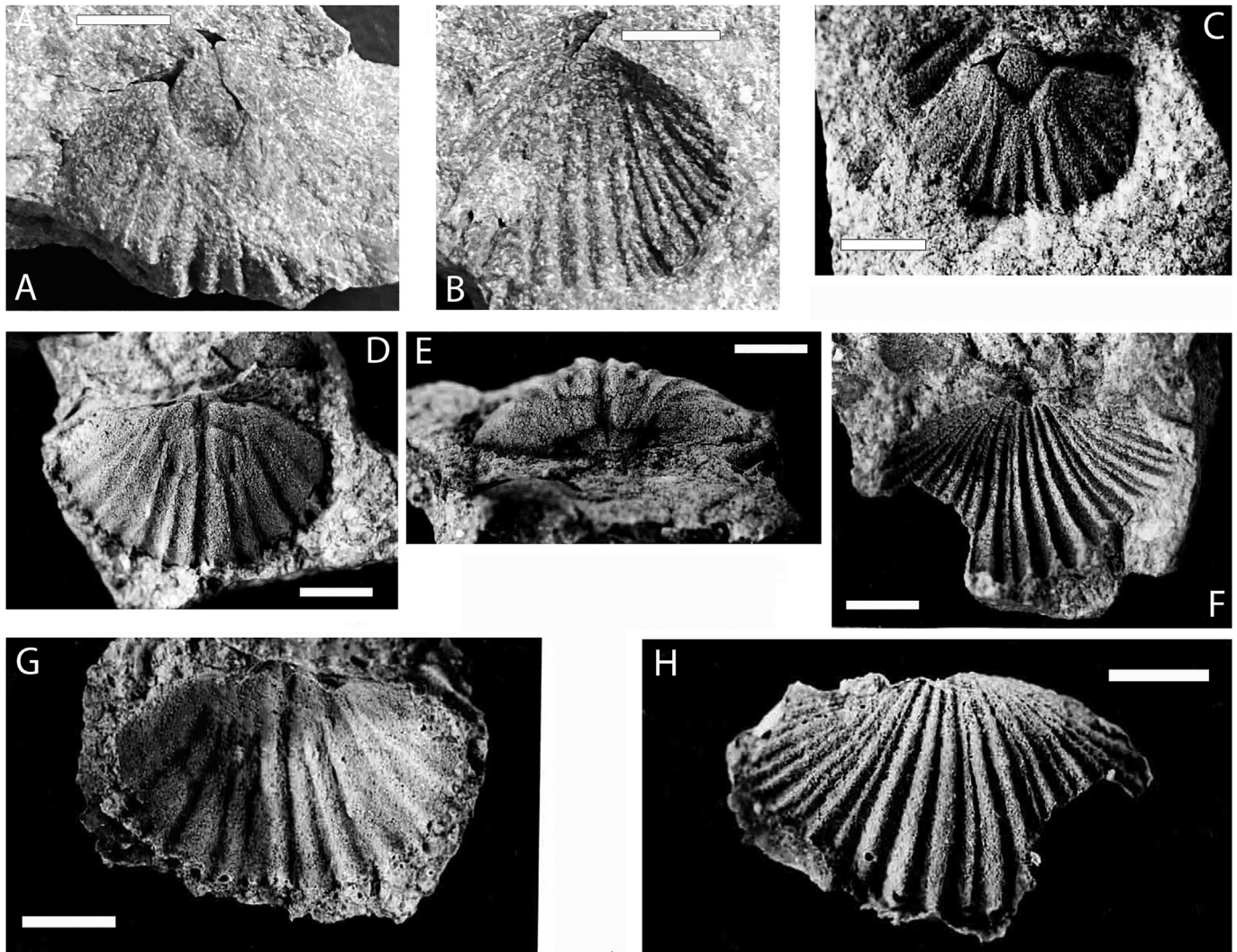*Ffynnonia costata* (Bates, 1968) *hibernica* nov. subsp.

Fig. 7. *Ffynonnia costata* (Bates) *hibernica* nov. subsp. **A, B.** Internal and external moulds of ventral valve, NG:F35358. **C.** Internal mould of ventral valve, NG:F35359. **D, E, G.** Holotype, internal mould, posterior view and latex cast of dorsal valve, NG:F35360. **F, H.** Counterpart of holotype, external mould and latex cast of dorsal valve, NG:F35360. Scale bars: 5 mm for A-F and 3 mm for G,H.

Figs. 7, 8(D, E)
1879. *Orthis biforata* Schlotheim - Baily in Kinahan, p. 56.
1967. *Pleurorthis* (?) sp. - Bates in Brenchley et al., p. 338.
Derivation of the name: For Ireland.
Holotype: A dorsal valve, NG:F35360 (part and counterpart), from the Tagoat Group (Dapingian), Tagoat, County Wexford.
Material and localities: Six dorsal valves and 12 ventral valves. Majority of specimens are from locality E.
Measurements: See Table 5.
Diagnosis: *Ffynnonia costata* with a coarse ornament and having first order costellae only on the flanks of the fold and sulcus; both the fold and sulcus are less pronounced that those of the nominate subspecies.

Description: Exterior. Subequally convex to dorsibiconvex valves of transversely subquadrate outline. Anterior commissure uniplicate. Maximum width just anterior to hinge line and ca. three-quarters hinge width; cardinal extremities obtuse and rounded. Ventral valve ca. two-thirds as long as wide and less than one-third as deep as long. Anterior and lateral profiles initially convex, shallow sulcus originating at ca. 6 mm from ventral umbo with evenly curved floor and sides. Ventral interarea slightly concave, ca. one-fifth valve length and apsacline; delthyrium open or occasionally partly modified by incipient deltidial plates. Dorsal

valve ca. three-quarters as long as wide and ca. one-third as deep as long. Anterior and lateral profiles initially evenly convex but gently convex fold with curved sides and crest developing anteriorly Dorsal interarea about half length of ventral interarea, anacline and with open notothyrium. Ornament of costae and costellae, initially subangular but develop subrounded profiles anteriorly; arrangement fascicostellate. Four costae are present in sulcus whilst five ornament the fold; costellae on fold and in sulcus are rare; they are more common on flanks. Each flank has at least five costae with costellae appearing by internal branching on dorsal valve and external branching on ventral valve.

Ventral interior. Short, broad, simple teeth supported by short, thin dental plates converge towards valve floor defining posterolateral edges of pseudodeltidium. Muscle scars sited on pseudospondylium, about as wide as long and extending anteriorly to ca. two-fifths valve length. Centrally situated adductor scars elongately rectangular and flanked by triangular diductor scars. Pair of vascular media, subparallel, extending anteriorly from edge of muscle field.

Dorsal interior. Cardinal process simple linear ridge situated on well-defined but small notothyrial platform. Thin, blade-like brachiophores diverge anteriorly at right angles – defining, together with crural plates and the hinge line, shallow concave sockets.
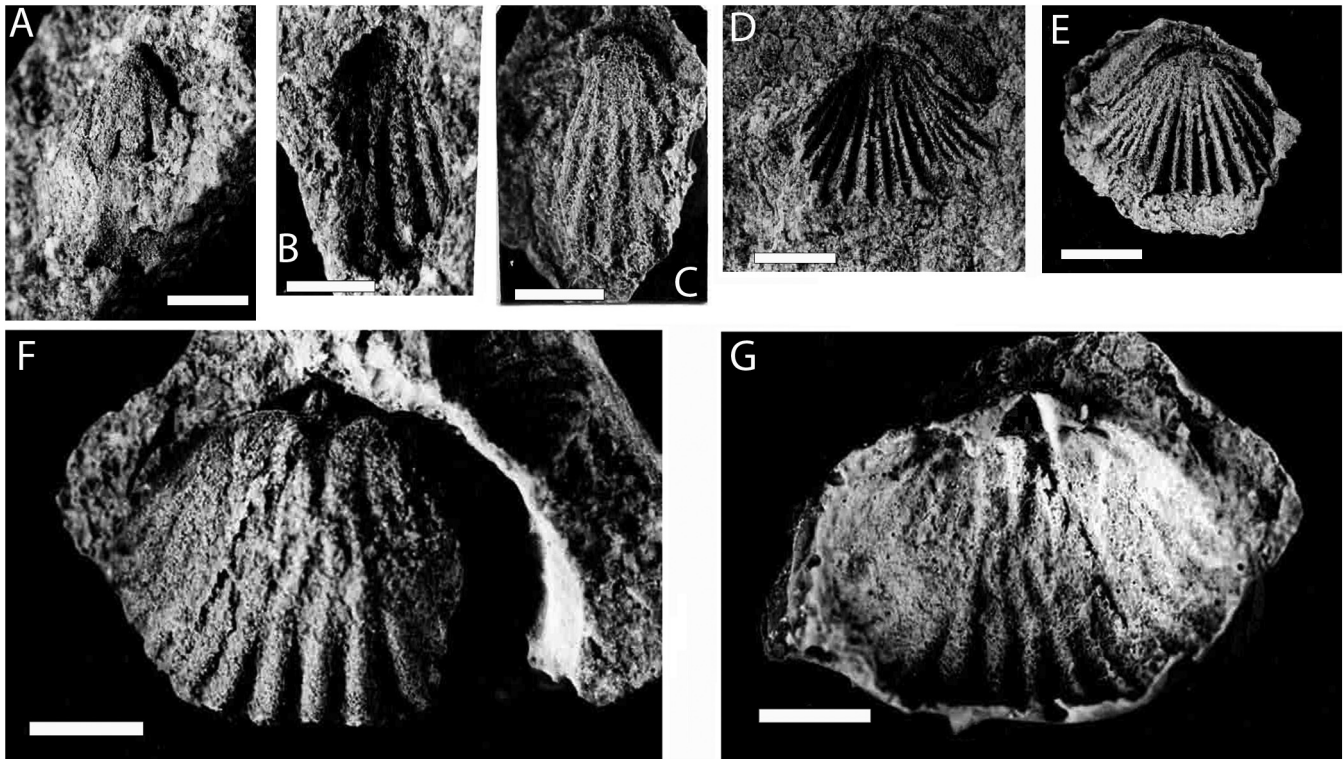
Fig. 8. A-C, F, G. *Rhynchorthis rotunda* Bates. A: internal mould of ventral valve, NG:F35361; B, C: external mould and latex cast of ventral valve, NG:F35362; F, G: internal mould and latex cast of dorsal valve, NG:F35363. **D, E.** *Ffynonnia costata* (Bates) *hibernica* nov. subsp., external mould and latex cast of ventral valve, NG:F35364. Scale bars: 5 mm for A-E and 3 mm for F,G.

Table 5
Measurements (in mm) of *Ffynonnia* specimens.

VV	sagl	maxw
	10.9	15.0
	14.5	21.1
	11.6	16.0
DV	**sagl**	**maxw**
	13.8	17.6
	12.7	21.6

Adductor scars quadripartite, anterior pair larger than posterior ones. Low median ridge dividing the adductor scar.

Remarks: The Tagoat material is similar to *Ffynnonia costata* (Bates, 1968) from the Treiorwerth Fm. on Anglesey but differs in details of the radial ornament. The radial ornament is coarser, with first order bifurcations confined to the flanks; in addition, the fold and sulcus in adults are less pronounced, and the fold and sulcus are less pronounced in younger specimens.

Family Cyclocoeliidae Schuchert and Cooper, 1931
Genus ***Rhynchorthis*** Bates, 1968

Type species: By original designation, *Rhynchorthis rotundus* Bates, 1968, from the Treiowerth Fm. (Arenig), near Trefor, Anglesey.

Rhynchorthis rotunda Bates, 1968
Fig. 8(A-C, F, G)
1967. Angusticardiniidae gen. nov. - Bates *in* Brenchley et al., p. 388.
1968. *Rhynchorthis rotundus* Bates, p. 160, pl. 5, figs. 19–26.
1978. *Rhynchorthis rotundus* Bates - Cocks, p. 38.
1978. *Rhynchorthis rotundus* Bates - Neuman and Bates, p. 591, pl. 66, figs. 1–26.
1978. *Rhynchorthis rotundus* Bates - Cocks, p. 83.
2008. *Rhynchorthis rotundus* Bates - Cocks, p. 137.
2019. *Rhynchorthis rotunda* Bates - Cocks and Popov, p. 687, fig. 6A–G.

Holotype: By original designation, a dorsal valve, BB30551, from the Treiorwerth Fm. (Dapingian), Anglesey.

Material and localities: Two ventral valves and one dorsal valve from locality E.

Remarks: The material is included within the type species, *R. rotunda* Bates, 1968, from the Treiorwerth Fm. on Anglesey. Specimens from the Ogof Hên Fm., south-west Wales are closely comparable with the types from the Treiorwerth Fm. of Anglesey and the material from Tagoat; all three taxa are considered conspecific.

Rhynchorthis has been revised in detail by Neuman and Bates (1978) and on this basis, the genus was transferred from the rhynchonellids to the plectorthids. The taxon is in fact unique within Early-Middle Ordovician Orthidina (Cocks and Popov, 2019). *Rhynchorthis* is an enigmatic taxon having a functioning astrophic shell with a vestigial dorsal interarea, while possessing orthide cardinalia. Whereas the cardinalia of *Rhynchorthis* retain major orthide characters, there are similarities with those of early rhynchonellides such as the Ancistrorhynchidae indicating a possible source for that family within the Orthida. The role of *Rhynchorthis* as a possible progenitor for the Rhynchonellida has been suggested previously by Neuman (1984) and more recently by Cocks and Popov (2019), who confirmed its transfer to the Cycloceolidae.

Suborder Dalmanellidina Schuchert, 1913
Superfamily Dalmanelloidea Schuchert, 1913

Family Paurorthidae Öpik, 1933
Genus **Paurorthis** Schuchert and Cooper, 1931
Type species: By original designation, *Orthambonites parva* Pander, 1830, from the Volkov Fm. (Dapingian), near St Petersburg, Russia.

Paurorthis? sp.
Fig. 9(A, B)
1978. *Paurorthis*? sp. - Neuman and Bates, p. 598, pl. 64, figs. 24–38.
2008. *Paurorthis*? sp. - Cocks, p. 163.
?2019. *Paurorthis*? *llangynogensis* - Cocks and Popov, p. 687, fig. 5A–G, I-L.

Remarks: The material recovered from locality E of the Tagoat Group, two dorsal valves, is considered conspecific with *Paurorthis*? sp. from the Treiorwerth Fm. which has recently been assigned by Cocks and Popov (2019) to their new species *Paurorthis*? *llangynogensis* from the Llangynog Inlier in southwest Wales. Neuman and Bates (1978) described this species in detail, provided illustrations and measurements on the dorsal and ventral valves. Despite the adequacy of the material the presence of punctae typical of that genus were not identified in either the Welsh or the current Irish material. The generic assignment remains tentative. The Tagoat material available, lacks exteriors and ventral valves and cannot been confidently assigned to a species. It also has a more circular outline (see Fig. 9(B) for comparison) than the taxon from the Treiorwerth Fm. on Anglesey. It, nevertheless, remains under open nomenclature.

Order Syntrophiidina Ulrich and Cooper, 1936.
Superfamily Porambonitoidea Ulrich and Cooper, 1936.
Family Porambonitidae Davidson, 1853
Genus **Rugostrophia** Neuman, 1971
Type species: By original designation, *Rugostrophia sylvestris* Neuman, 1971, from the Middle Ordovician (Dapingian) of New Brunswick, USA.

Rugostrophia sp.
Fig. 9(C, D)
1968. *Porambonites* (s.s.) sp. - Bates, p. 177, pl. 11, figs. 3–6, 8, non figs. 1, 2.
1978. *Rugostrophia* sp. - Neuman and Bates, pl. 76, figs. 9, 10, 12, 15–18.
2008. *Rugostrophia* sp. (pars) - Cocks, p. 173.

Material and locality: One poorly preserved internal mould and several broken external moulds from locality E.
Remarks: This sparse material is assigned to *Rugostrophia*. It is insufficient for specific comparisons, nevertheless the ventral inte-

rior and reticulate ornament are sufficient to place the specimens within *Rugostrophia*. Similar specimens described from Anglesey are less convex and have a less pronounced sulcus.

5. Discussion

5.1. Taphonomy of the fauna

The brachiopod fauna of the Tagoat Group is overwhelmingly dominated by the disarticulated valves of *Paralenorthis proava*; the other species are markedly less common (Table 6). Approximately equal numbers of ventral and dorsal valves of *P. proava* are present in the samples studied; the more limited data for the less common species similarly indicate the near equality of numbers of both valves. Most of the valves were clearly complete prior to collection and preparation, however, since they are preserved as moulds in a coarse siliciclastic matrix the degree of abrasion of the more delicate internal structures and the external ribbing is hard to assess but appears minimal. With the exceptions of *Palaeoglossa*? and possibly the indeterminate kutorginide, the species described were all probably pedunculate epifaunal benthos. The majority of the forms are relatively large and robust and thus may have preferentially required a hard substrate, in high-energy environments, perhaps provided by the rocky coasts of an island or archipelago and to a certain degree the shells themselves. Rapid burial adjacent to their site of origin is envisaged to account for the nature of the available data (Table 6) and thus the fossil assemblage probably represents a fairly unbiased sample of the living brachiopod population.

5.2. Biogeography and biodiversity of the fauna

The Dapingian brachiopods of the Tagoat Group are, as a whole, not directly comparable with any coeval fauna from the Baltic, Mediterranean or Laurentian platform provinces which flanked the Iapetus Ocean during the early part of the Ordovician. As noted previously, the Tagoat assemblage is most similar to that from the Carmel and Treiorwerth formations on the island of Anglesey. The Anglesey brachiopods together with their Irish counterparts formed the basis of Williams's Celtic Province (1973). Williams (op. cit.) emphasised the strong links of this province with that of the Baltic but considered only *Rhynchorthis* to be endemic. In recent years the concept of this biogeographical unit has undergone considerable modification but, nevertheless, there is still a need to separate the Celtic assemblages from those quite different faunas which inhabited areas within the adjacent platform provinces and filled the apparently sterile oceans (Cocks and Fortey, 1982). Currently the Celtic province is interpreted as a peri-insular biogeographic unit characterised by a high proportion of
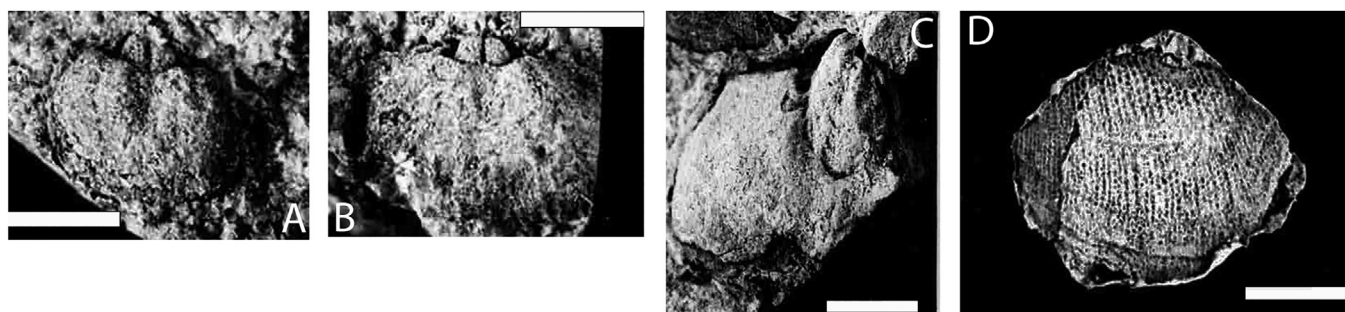

Fig. 9. A, B. *Paurorthis*? sp. A: internal mould of dorsal valve, NG:F35365; B: internal mould of dorsal valve, from the Treiorwerth Formation, Anglesey, NG:F35366. **C, D.** *Rugostrophia* sp. C: latex cast of valve exterior, NG:F35367; D: internal mould of ventral valve, NG:F35368. Scale bars: 5 mm for A,B and 10 mm for C,D.

Table 6

Brachiopod occurrences in the key fossiliferous localities of the Tagoat Group, mainly based on collections by DEBB. Abbreviations: VV, ventral valve; DV, dorsal valve.

	Lane (G)	Quarry (E)	Spoil heap (F)
Palaeoglossa? sp.	1 indet.		
Tritoechia pyramidalis		2 (VV)	3 (VV); 2 (DV)
Palaeoneumania sp.		1 (VV)	
Skenidioides sp.		2 (VV)	
Hesperonomiella aff. *carmellensis*		3 (VV); 2 (DV)	4 (VV); 1 (DV)
Paralenorthis proava		24 (VV); 23 (DV)	28 (VV); 16 (DV)
Productorthis lamellosa		3 (VV); 1 (DV)	4 (VV); 2 (DV)
Palaeotagotia bailyana		3 (DV)	3 (DV); 2 (VV)
Ffynnonia costata hibernica		6 (VV); 3 (DV)	6 (VV); 2 (DV)
Rhynchorthis rotunda		2 (VV); 4 (DV)	1 (VV); 1 (DV)
Paurorthis? sp.		2 (DV)	
Rugostrophia sp.		1 indet.	

endemic genera at both individual sites and in the province as a whole, together with forms which are better known from rocks of different ages elsewhere (Neuman, 1972, 1976, 1984; Neuman and Bates, 1978). Additionally, Neuman and Bates (1978: p. 571) considered the association of *Paralenorthis*, *Productorthis*, *Tritoechia* and *Rugostrophia* to be the hallmark of the Celtic province. These factors associate faunas from upper Arenig rocks in Maine, New Brunswick and Newfoundland with those from Anglesey and Tagoat (Neuman, 1976; Neuman and Bates, 1978). A comparable 'Celtic' fauna from probably upper Arenig rocks in the northern

Gander terrain of Newfoundland (Wonderly and Neuman, 1984) confirmed the existence of many such island complexes within the early Middle Ordovician Iapetus Ocean. More recent detailed analyses of both brachiopod genera and species from these and other related localities has confirmed their strong mutual affinities (Bruton and Harper, 1981; Bruton and Harper, 1985; Neuman, 1984; Neuman and Harper, 1992; Harper et al., 2008, 2009). The associated lithofacies, geological setting and distinctive faunal character of these assemblages favour the view that they represent the remains of animal communities which inhabited the shelves of islands or archipelagos within the Iapetus Ocean during the earlier part of the Ordovician.

Significantly these islands were emergent during a period of global regression (Fortey, 1984) and are characterised by associations of shallow water lithofacies. Thus, despite the distinctive properties of the Celtic assemblages, the presence of more ubiquitous elements reflecting the shallow water and coarse siliclastic facies is to be expected. For example, *Paralenorthis* has been reported from many settings outside the Celtic province; however, since that genus at presently understood contains many heterogeneous forms its use in biogeographical assessment is currently limited.

More recent detailed numerical analyses have since confirmed the distinctiveness and identity of the Celtic province (Harper et al., 2013; Cocks and Popov, 2021). Earlier studies (Harper et al., 2009, 2013) conflated Dapingian and Darriwilian localities due to difficulties of precise correlation across many Middle Ordovician stratigraphies. Building on the availability of more refined correlations (Harper et al., 2023; Servais et al., 2023) bra-
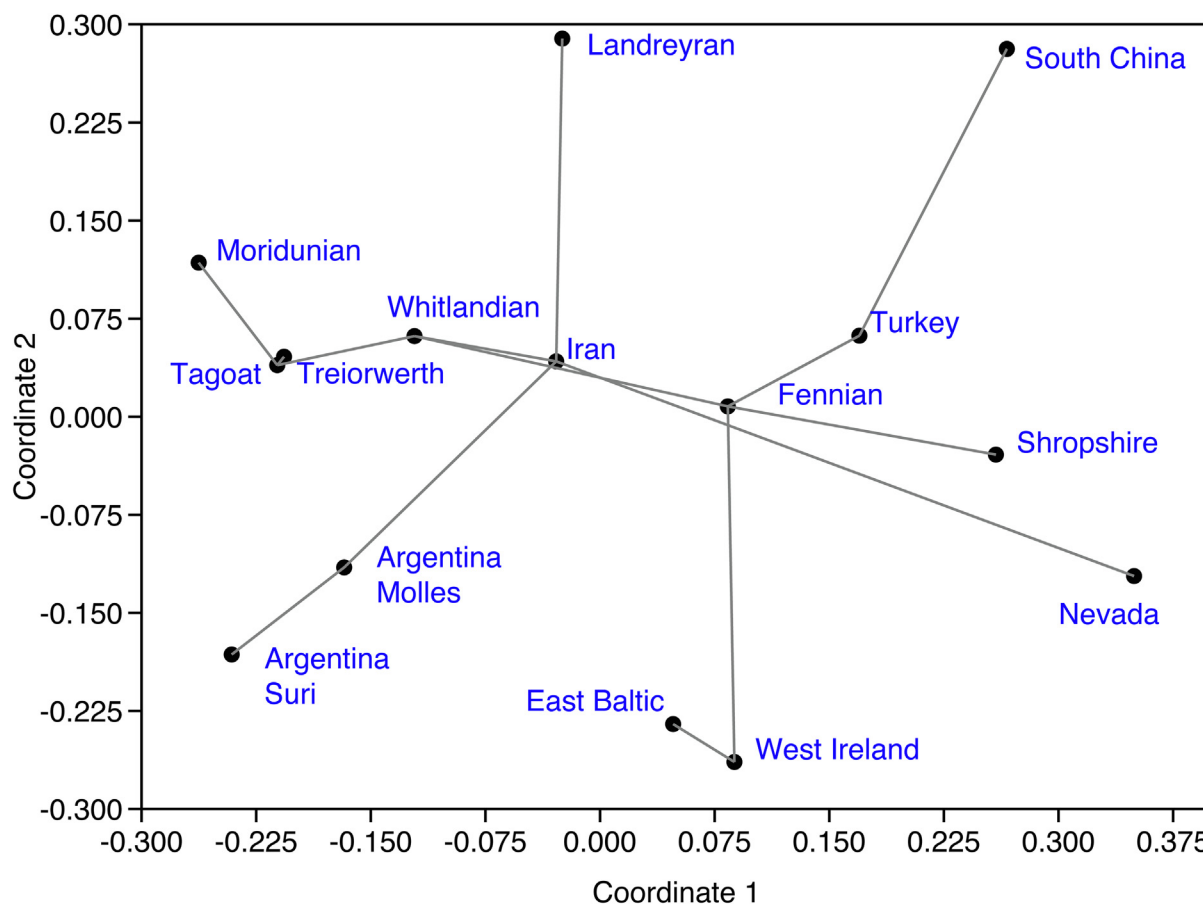

Fig. 10. Non-metric multidimensional scaling using PAST (Hammer et al., 2001; Hammer and Harper, 2006), indicating the close links of the Treiorwerth (Anglesey) and Tagoat (Wexford) faunas in terms of their placement on the scatter plot and their linkage with a minimum spanning tree. The sites are also linked to the Moridundian faunas which include those from SW Wales. The Raup-Crick similarity measure was used.
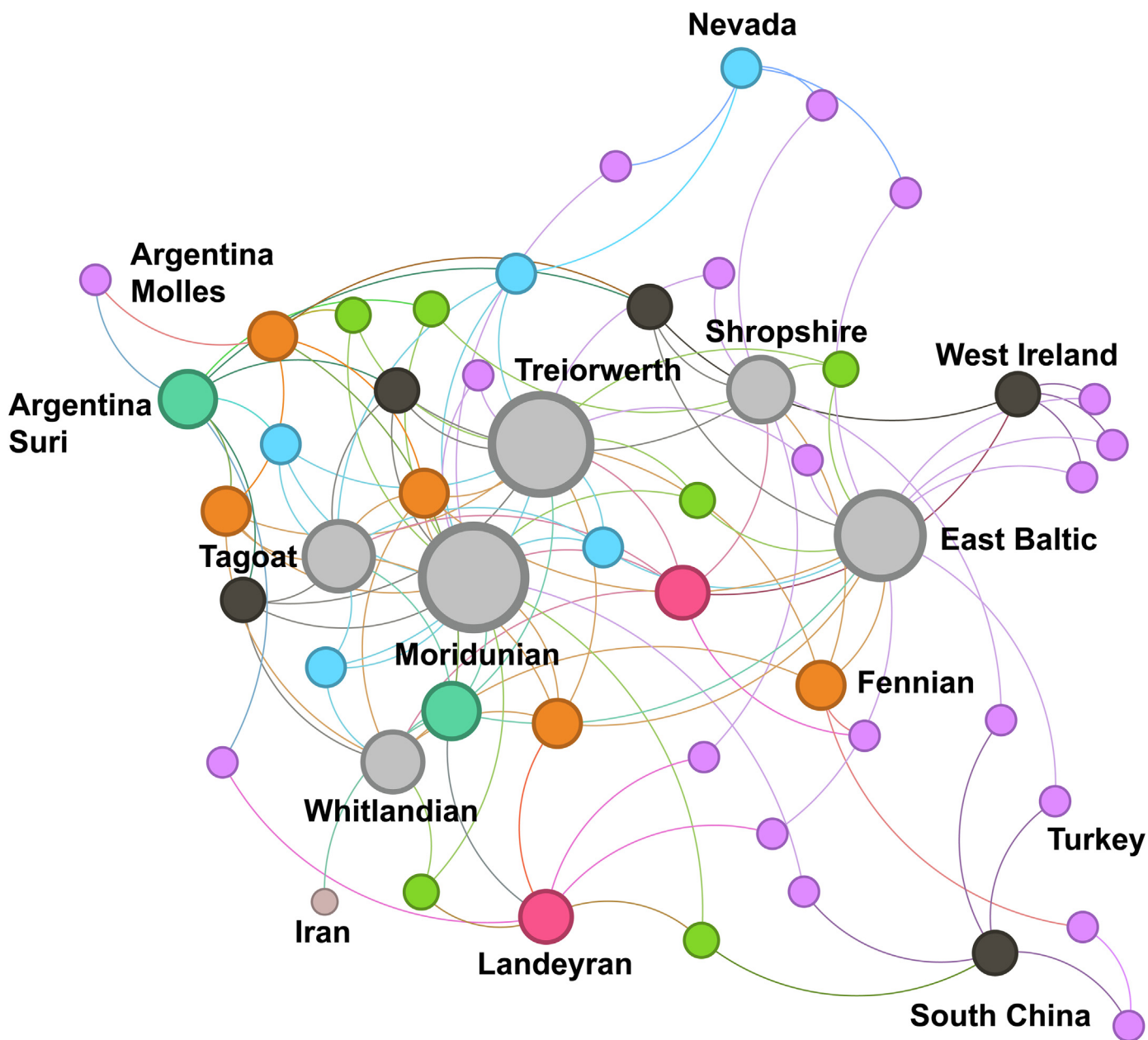
Fig. 11. Network analysis using GEPHI (Grandjean, 2015) linking the Treiorwerth, Tagoat and Moridunian faunas. The diameter of circles relates to the relative diversity of the faunas.

chiopods from Tagoat are compared herein with those from a number of key Dapingian-lowest Darriwilian (middle and upper Arenig) localities. Data for the Moridunian, Whitlandian, Fennian units in Wales, Argentina, Iran, Landeyran (Montagne Noire), and Turkey, are extracted from Cocks and Popov (2021); Shropshire (Shelve inlier) from Williams (1974), West of Ireland (Tourmakeady) from Williams and Curry (1985), South China from Zhan and Jin (2014), Nevada from Candela (2014), and East Baltic from Hints and Harper (2003). Single species occurrences were removed from the data matrix as were micromorphic brachiopods generally only recovered by acid etching from limestones. Analyses using NMDS (Hammer et al., 2001; Hammer and Harper, 2006; Fig. 10) and network analysis (Grandjean, 2015; Fig. 11), emphasise the close proximity of sites assigned to the Celtic Province, specifically Anglesey and Tagoat. Both analyses, although only assessing taxa at two or more sites, indicate a marked diversity in brachiopod fau-

nas already present during the Dapingian. This, however, masks those high-diversity faunas such as Tourmakeady with nearly 100 species, with large numbers of endemics and micromorphics. More data, however, are required from confacies within the platform to identify the presence of true cosmopolitan but facies restricted elements in the Celtic faunas (Lockley, 1983: p. 116).

The brachiopod faunas of both Tagoat and Anglesey differ considerably from coeval assemblages now located in adjacent areas of the British Isles. Neuman and Bates (1978: p. 578) commented in detail on the dissimilarity of the Middle Ordovician brachiopods to the south-east in the Shelve district of the Anglo-Welsh Borderlands (Williams, 1974) and those to the north-west from the Mweelrea Grits and Tourmakeady Limestone of County Mayo, western Ireland (Williams, 1972, 1973; Williams and Curry, 1985) when compared with the assemblages from Anglesey. Although origins in three distinct faunal provinces was suggested

to account for these differences the role of more local environmental factors was not excluded (Neuman and Bates, 1978: p. 579).

5.3. Palaeogeography

There has been a number of scenarios regarding the relative positions of Anglesey and mainland Wales. Nutt and Smith (1981) suggested that Anglesey did not arrive at its present position with respect to the rest of Wales until the Late Devonian. Apart from the contrasts in Ordovician faunas and facies between the two areas, differences in the Precambrian basements, the Mona Complex of Anglesey versus the Arvonian of the mainland, the Silurian successions of the two areas and the presence of the Old Red Sandstone on Anglesey but not in North Wales are evidential of dextral movement in excess of 100 km along a transcurrent fault separating the mainland and Anglesey (Nutt and Smith, 1981). Although the details of this model are not without opponents (Gibbons and Gayer, 1981; Tegerdine et al., 1981) there is geophysical data in support of the existence of such a fault (Kohnstamm and Mann, 1981). Confirmatory evidence for a position of the Irish Sea area removed from the classic Anglo-Welsh region was provided by geochemical and palaeomagnetic studies of the Precambrian basement complexes of England and Wales (Thorpe et al., 1984). These data suggest that in contrast to the Precambrian rocks of Scotland which developed as part of the Laurentian Shield, those of southern Britain were related to island arc complexes and accretionary prisms within the Iapetus Ocean. More recent research, however, indicates that movement along the fault was pre-Floian (Schofield et al., 2016), implying that this part of the Monian terrane had docked with the Cymry Terrane prior to the invasion of the region by the Celtic faunas during the Dapingian (Molyneux et al., 2023).

Data availability

No additional data was used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Andreeva, O.N., 1960. New species of Ordovician brachiopods of the Urals and Mugodzhar. In: Markovskii, B.P. (Ed.), New Species of Ancient Plants and Invertebrates of the USSR, Part 1. Moscow, Gosudarstvennoe nauchno-tekhnicheskoe izdatelstvo literatury po geologii i okhrane nedr, pp. 286–298 (in Russian).

Baker, J.W., 1966. The Ordovician and other post-Rosslare series rocks in Southeast Co. Wexford. Geological Journal 5, 1–6.

Bates, D.E.B., 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. Bulletin British Museum Natural History (Geology) 16, 127–199.

Bates, D.E.B., 1969. Some early Arenig brachiopods and trilobites from Wales. Bulletin British Museum Natural History (Geology) 18, 1–28.

Bates, D.E.B., 1972. The stratigraphy of the Ordovician rocks of Anglesey. Geological Journal 8, 29–58.

Bates, D.E.B., 1964. The Lower Palaeozoic Rocks of Anglesey. Ph.D. Thesis, Queen's University of Belfast (unpubl.).

Biernat, G., 1965. Suborder Syntrophiidina. In: Moore, R.C. (Ed.), Treatise on invertebrate paleontology. Part H. Brachiopoda, vol. 2. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, pp. 523–536.

Brenchley, P.J., Harper, J.C., Skevington, D., 1967. Lower Ordovician shelly and graptolite faunas from southeastern Ireland. Proceedings of the Royal Irish Academy B 65, 385–390.

Bruton, D.L., Harper, D.A.T., 1981. Brachiopods and trilobites of the early Ordovician serpentine Otta Conglomerate, south central Norway. Norsk Geologisk Tidsskrift 61, 151–181.

Bruton, D.L., Harper, D.A.T., 1985. Early Ordovician (Arenig-Llanvirn) faunas from oceanic islands in the Appalachian-Caledonide orogen. In: Gee, D.G., Sturt, B.A. (Eds.), The Caledonide orogen - Scandinavia and Related Areas. John Wiley and Sons, Chichester, pp. 359–368.

Bruton, D.L., Harper, D.A.T., Gunby, I., Naterstad, J., 1984. Cambrian and Ordovician fossils from the Hardangervidda Group, Haukelifjell, southern Norway. Norsk Geologisk Tidsskrift 64, 313–324.

Candela, Y., 2014. Evolution of Laurentian brachiopod faunas during the Ordovician Phanerozoic sea level maximum. Earth-Science Reviews 141, 27–44.

Cocks, L.R.M., 1978. A review of British Lower Palaeozoic brachiopods. Monograph of the Palaeontographical Society, London 131, 1–256.

Cocks, L.R.M., 2008. A revised review of British Lower Palaeozoic brachiopods. Monograph of the Palaeontographical Society, London 161, 1–276.

Cocks, L.R.M., Fortey, R.A., 1982. Faunal evidence for oceanic separation in the Palaeozoic of Britain. Journal of the Geological Society, London 139, 465–478.

Cocks, L.R.M., Popov, L.E., 2019. Early Ordovician brachiopods from south-west Wales. Proceedings of the Geologists' Association 130, 677–690.

Cocks, L.R.M., Popov, L.E., 2021. The identity and significance of the high-latitude Early Ordovician Mediterranean brachiopod Province. Geological Magazine 158, 2187–2208.

Davidson, T., 1868. On the earliest forms of Brachiopoda hitherto discovered in the British Palaeozoic rocks. Geological Magazine 5, 303–316.

Davidson, T., 1869. A monograph of the British Brachiopoda, part VII. No. III. The Silurian Brachiopoda. Monograph of the Palaeontographical Society, 169–248.

Davidson, T., 1883. A Monograph of the British Fossil Brachiopoda, Vol. V. Silurian Supplement, Part 2, 135–242. Palaeontographical Society Monographs, London.

Sowerby, J. de C., 1839. Mollusca and Conchifers. In: Murchison, R.I. (Ed.), The Silurian System, Part 2. Organic Remains, pp. 577–768.

Fortey, R.A., 1984. Global earlier Ordovician transgressions and regressions and their biological implications. In: Bruton, D. L (Ed.), Aspects of the Ordovician System. Palaeontological Contributions from the University of Oslo 295, pp. 37–50.

Gardiner, P.R.R., Brenchley, P.J., 1970. The Pre-Cambrian and Lower Palaeozoic geology of Co. Wexford. Irish Naturalists' Journal 16, 370–379.

Gibbons, W., Gayer, R.A., 1981. Transcurrent faulting and pre-Carboniferous Anglesey. Discussion and reply. Nature 290, 760–761.

Grandjean, M., 2015. GEPHI – Introduction to network analysis and visualization, http://www.martingrandjean.ch/gephi-introduction.

Hammer, Ø., Harper, D.A.T., 2006. Paleontological Data Analysis. Blackwell, Oxford. 351 p.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST - Paleontological Statistics software: Package for Education and data Analysis. Palaeontologia Electronica 4, 9 p.

Hansen, J., Harper, D.A.T., 2005. *Palaeoneumania*, a new name for the genus *Neumania* Harper, 1981 (Brachiopoda), preoccupied by *Neumania* Lebert, 1879 (Arthropoda). Norwegian Journal of Geology 85, 223.

Harper, D.A.T., Bruton, D.L., Rasmussen, C.M.Ø., 2008. The Otta brachiopod and trilobite fauna: palaeogeography of Early Palaeozoic terranes and biotas across Baltoscandia. In: Harper, D.A.T., Long S.L., Nielsen, C. (Eds.), Brachiopoda: Fossil and Recent. Fossils and Strata 54, pp. 31–40.

Harper, D.A.T., Lefebvre, B., Percival, I.G., Servais, T. (Eds.), 2023. A Global Synthesis of the Ordovician System: Part 1. Geological Society, London, Special Publications 532.

Harper, D.A.T., Parkes, M.A., 1989. Palaeontological constraints on the definition and development of Irish Caledonide terranes. Journal of the Geological Society, London 146, 413–415.

Harper, D.A.T., Owen, A.W., Bruton, D.L., 2009. Ordovician life around the Celtic fringes: diversifications, extinctions and migrations of brachiopod and trilobite faunas at middle latitudes. Geological Society, London, Special Publications 325, 155–168.

Harper, D.A.T., Rasmussen, C.M.Ø., Liljeroth, M., Blodgett, R.B., Candela, Y., Jisuo, J., Percival, I.G., Jiayu, R., Villas, E., Zhan, R., 2013. Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. Memoir Geological Society, London 38, 127–144.

Havlíček, V., Branisa, L., 1980. Ordovician brachiopods of Bolivia (Succession of assemblages, climate control affinity to Anglo-French and Bohemian provinces). Rozpravy Československe Akademie Ved, Praha 90, 1–54.

Hints, L., Harper, D.A.T., 2003. Review of the Ordovician rhynchonelliformean Brachiopoda of the east Baltic: their biostratigraphy and biofacies. In: Harper, D.

A.T., Stouge, S. (Eds.), Studies in Ordovician geology: the Baltoscandian region. Bulletin of the Geological Society of Denmark 50, pp. 29–43.

Jaanusson, V., Bassett, M.G., 1993. *Orthambonites* and related Ordovician brachiopod genera. Palaeontology 36, 21–63.

Kinahan, G.H., 1879. Explanatory memoir to accompany sheets 169, 170, 180 and 181 of the Geological Survey of Ireland.

Kohnstamm, M.A., Mann, A., 1981. Transcurrent faulting and pre-Carboniferous Anglesey. Discussion and reply. Nature 290, 762.

Kozłowski, R., 1929. Les brachiopodes gotlandiens de la Podolie polonaise. Palaeontologia Polonica 1, 1–254.

Lockley, M.G., 1983. A review of brachiopod dominated palaeocommunities from the type Ordovician. Palaeontology 26, 111–145.

Matley, C.A., 1912. Notes on the *Orthis carausii* (Salter MS) Davidson and *O. calligramma* var. *proava* Salter. Memoir of the Geological Survey GB. Summary of Progress for 1911. Appendix 3, 78–79.

Molyneux, S.G., Harper, D.A.T., Cooper, M.R., Hollis, S.P., Raine, R.J., Rushton, A.W.A., Smith, M.P., Stone, P., Williams, M., Woodcock, N.H., Zalasiewicz, J.A., 2023. A synopsis of the Ordovician System in its birthplace – Britain and Ireland. Geological Society, London, Special Publications 532, 191–266.

Murphy, F.C., Anderson, T.B., Daly, J.S., Gallagher, V., Graham, J.R., Harper, D.A.T., Johnson, J.D., Kennan, P.S., Kennedy, M.J., Long, C.B., Morris, J.H., O'Keeffe, W.G., Parkes, M.A., Ryan, P.D., Sloan, R.J., Stillman, C.J., Tietzsch-Tyler, D., Todd, S.P., Wrafter, J.P., 1991. An appraisal of Caledonian suspect terranes in Ireland. Irish Journal of Earth Sciences 11, 11–41.

Neuman, R.B., 1976. Early Ordovician (late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. Geological Survey of Canada Bulletin 261, 11–61.

Neuman, R.B., 1984. Geology and paleobiology of islands in the Ordovician Iapetus Ocean. Geological Society of America Bulletin 95, 1188–1201.

Neuman, R.B., Bates, D.E.B., 1978. Reassessment of Arenig and Llanvirn age (Early Ordovician) brachiopods from Anglesey, north-west Wales. Palaeontology 21, 63–68.

Neuman, R.B., Harper, D.A.T., 1992. Paleogeographic significance of Arenig-Llanvirn Toquima-Table Head and Celtic brachiopod assemblages. In: Webby, B.D., Laurie, J.R. (Eds.), Global Perspectives on Ordovician Geology. Balkema, Rotterdam, pp. 242–254.

Neuman, R.B., 1972. Brachiopods of early Ordovician islands. In: Proceedings of the 24th International Geological Congress, Montreal 7, pp. 297–302.

Nudds, J.R., 1982. Catalogue of Type, Figured and Referred Fossils in the Geological Museum of Trinity College, Dublin: Part 2 (Brachiopoda, Mollusca). Irish Journal of Earth Sciences 5, 61–89.

Nutt, M.J.C., Smith, E.G., 1981. Transcurrent faulting and the anomalous position of pre-Carboniferous Anglesey. Nature 290, 492–493.

Pander, C.H., 1830. Beiträge zur Geognosie des Russischen Reiches. K. Kray, St. Petersburg, 165 p.

Salter, J.W., 1866. On the Fossils of North Wales. Appendix *in* Ramsey, A.C., 1866. The Geology of North Wales. Memoir of the Geological Survey GB 3, 381 p.

Schofield, D.I., Potter, J., Barr, S.M., Horák, J.M., Millar, I.L., Longstaffe, F.J., 2016. Reappraising the Neoproterozoic 'East Avalonian' terranes of southern Great Britain. Gondwana Research 35, 257–271.

Schuchert, C., Cooper, G.A., 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. Memoirs of the Peabody Museum of Natural History 4, 1–270.

Servais, T., Harper, D.A.T., Lefebvre, B., Percival, I.G. (Eds), 2023. A Global Synthesis of the Ordovician System: Part 2. Geological Society, London, Special Publications 533.

Tegerdine, G.D., Campbell, S.D.G., Woodcock, N.H., 1981. Transcurrent faulting and pre-Carboniferous Anglesey. Discussion and reply. Nature 290, 760.

Thorpe, R.S., Beckinsale, R.D., Patchett, P.J., Piper, J.D.A., Davies, G.R., Evans, J.A., 1984. Crustal growth and late Precambrian-early Palaeozoic plate tectonic evolution of England and Wales. Journal of the Geological Society 141, 521–536.

Ulrich, E.O., Cooper, G.A., 1936. New genera and species of Ozarkian and Canadian brachiopods. Journal of Paleontology 10, 616–631.

Williams, A., 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. Bulletin of the British Museum Natural History (Geology) Suppl. 11, 1–163.

Williams, A., Curry, G.B., 1985. Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co., Mayo, Ireland. Bulletin British Museum Natural History (Geology) 38, 183–269.

Williams, A., 1972. An Ordovician Whiterock fauna in western Ireland: Royal Irish Academy Proceedings 72 B12, 209–219.

Williams, A., 1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. In: Hughes, N.F. (Ed.), Organisms and continents through time. Palaeontological Association Special Papers in Palaeontology 12, pp. 241–269.

Wonderly, P.F., Neuman, R.B., 1984. The Indian Bay Formation; fossiliferous Early Ordovician volcanigenic rocks in the northern Gander Terrane, Newfoundland and their regional significance. Canadian Journal of Earth Sciences 21, 525–532.

Zhan, R., Jin, J., 2014. Early-Middle Ordovician brachiopod dispersal patterns in South China. Integrative Zoology 9, 121–140.