Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **116**, 185–197, 2025

Review Article

The Pentlandian: fact or fiction?

David A.T. HARPER[1,2]*, Yves CANDELA[2] and Emma E. GALLAGHER[3]

[1] Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK.
[2] Department of Natural Sciences, National Museums Scotland, National Museums Collection Centre, Edinburgh, EH5 1JA, UK.
[3] National Museums NI, Holywood, BT18 0EU, UK.
*Corresponding author. Email: david.harper@durham.ac.uk

ABSTRACT: The Silurian inliers of the Pentland Hills contain abundant and diverse fossil assemblages and have interested geologists for more than 150 years. However, the faunas are very different from those found in the classic Anglo-Welsh area or the Spanish El Pintado Global Boundary Stratotype Section and Point (GSSP) for the Telychian Stage in peri-Gondwana. Initial geological exploration of the hills found few fossils, with little meaningful interest shown in the area until Dr Archibald Lamont, a controversial Scottish geologist, began researching the inliers. Lamont was the first to suggest that the rocks might be upper Llandovery rather than Wenlock, and went on to propose that their unique fossil assemblages warranted a new division being erected between the Llandovery and Wenlock series, which he named the 'Pentlandian'. This new division was rejected by the international geological community. Euan Clarkson's arrival in Edinburgh and his introduction to the Pentland Hills began what would be a lifetime's fascination with the geology of the area. He instigated an extensive series of research projects and recruited researchers looking at the geology and a wide range of fossil groups, the most abundant of which is the Brachiopoda. The Telychian Wether Law Linn Formation in particular contains many shelly and graptolite faunas enabling correlation. The palaeocommunities identified suggest a deeper-water palaeoenvironment with finer-grained siliciclastic sediments set in a regressive marine sedimentary succession. Multivariate analyses show the mutual proximity of the Pentland associations and their distinctiveness from other Llandovery faunas. The Pentlandian is considered a regional term but the distinctive nature of the Pentlandian biotas, on a global scale, is confirmed and introduced here as the *Pentlandian Biotic Complex*.

KEY WORDS: Edinburgh, fossils, Llandovery, Pentland Hills, Silurian

Within the rolling hills of the Pentlands, south of Edinburgh, lie some of the most fossiliferous rocks of the Silurian System (Fig. 1a). The first fossils were discovered in the early 19th Century, but knowledge of the rocks and their rich biotas was generated by two geologists, the enigmatic Archibald (Archie) Lamont (1907–1985) and the charismatic and inspirational Euan Clarkson (1937–2024).

The inliers of the Pentland Hills are part of the Midland Valley Terrane, a rift valley developed on the margin of Laurentia during the Early Palaeozoic (Bluck 1985; Williams & Harper 1988, 1991). The steeply dipping tectonic structures of the Highland Boundary Fault to the northwest and the Southern Upland Fault to the southeast delimit the terrane (Fig. 1a). The Silurian rocks are succeeded to the northwest and southeast by the lower part of the Lanark Group (upper Silurian) within the Old Red Sandstone Supergroup, overlain by the lower Carboniferous (Clarkson & Harper 2016). A number of authors have discussed the Pentland Hills within the context of the chain of inliers stretching from south of Edinburgh to the west of Ireland (Doyle 1989; Doyle *et al.* 1990, 1991). There are also similarities with faunas in the Oslo Region (Cocks & Worsley 1993), whereas Cocks & Rong (2019) reviewed the biogeography and biodiversity of Telychian brachiopods globally, assigning the Pentlands assemblages to the southern margin of the Midland Valley of Scotland (*op. cit.*, fig. 1). The margin of the Midland Valley of Scotland during the Silurian was located just north of 30° S latitude, within the subtropics. Much of the globe was generally warm in contrast to the higher latitudes of the Anglo-Welsh area situated on the Avalonian Terrane. The position and setting of this terrane were thus quite different from those of the Anglo-Welsh area and their contrasting biotas is not unexpected.

We document here the biotas of the Silurian rocks of the Pentland Hills, their occurrence, setting and significance through the lens of Euan Clarkson's remarkable journey, navigating their fossils, and citing many colleagues he encouraged and met on the way (Clarkson 2000).

1. The type Llandovery series

The formative studies on the Silurian System were enmeshed within the Grauwacke debate, and are summarised in

 doi:10.1017/S1755691025100923

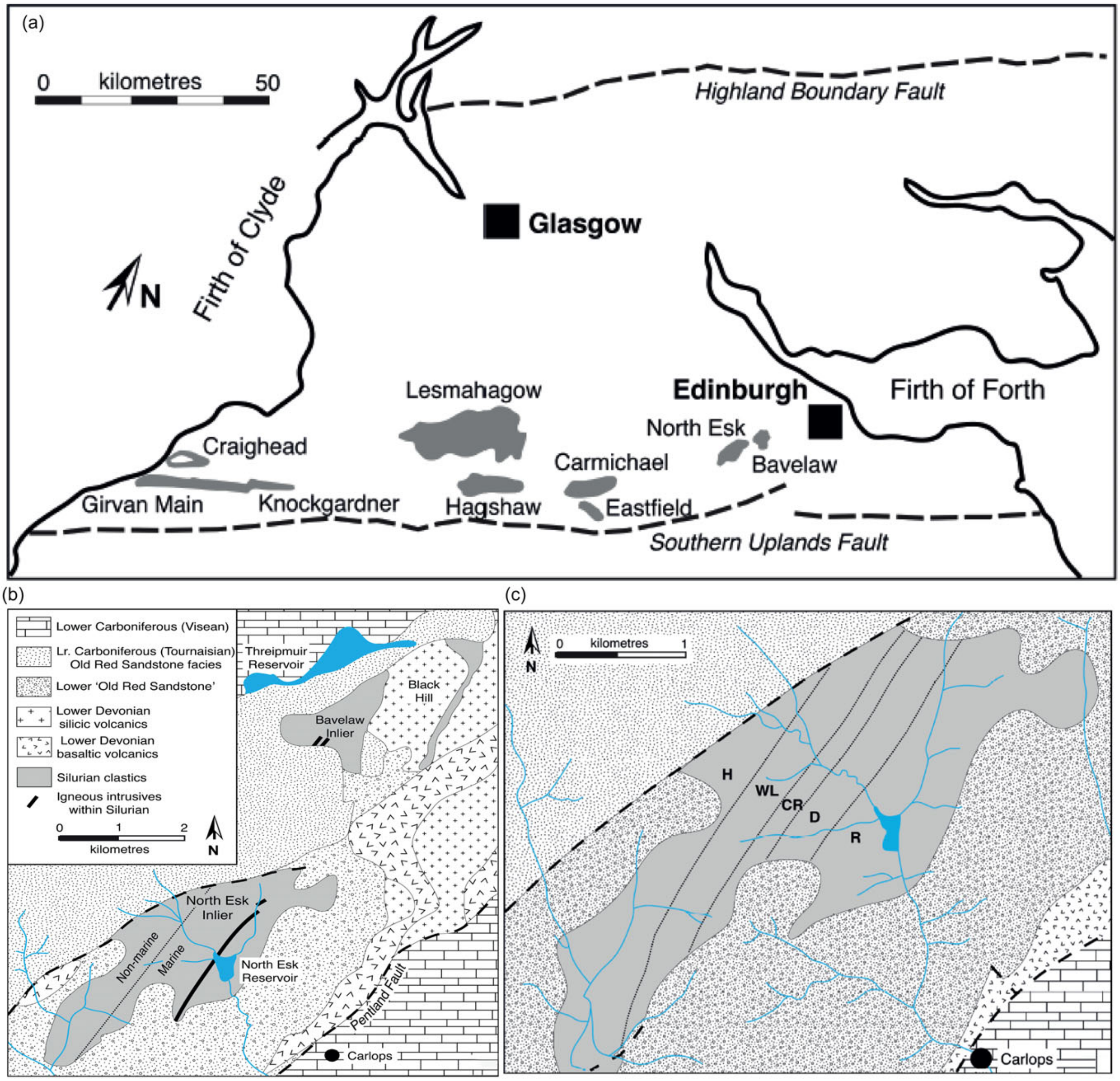

Figure 1 (a) Location of the Silurian inliers across the Midland Valley of Scotland. (b) Location of the inliers within the Pentland Hills. (c) Outcrop of the Silurian formations; in ascending order: the Reservoir (R), Deerhope (D), Cock Rig (CR), Wether Law Linn (WL) and Henshaw (H) formations. After Gallagher & Harper (2024).

Bassett (1985). By international agreement during the International Geological Congress in Oslo (1960) the so-called Transition Rocks were designated the Silurian System in keeping with Murchison's original concept described 150 years previously. Investigations were focused on the Anglo-Welsh area that became the historical type area for the system. Following the establishment of the International Commission on Stratigraphy (see Cohen *et al.* 2025) a much greater precision was required in both the definition and correlation of the bases of chronostratigraphic units. The bases of these units (e.g., systems, series and stages) must be defined by a Global Boundary Stratigraphic Section and Point (GSSP), fulfilling a set of criteria (Harper *et al.* 2022). The first GSSP was defined in 1972 for the base of the Devonian System, at Klonk in the Czech Republic.

The term Telychian was first introduced for the upper part of the upper Llandovery based on a section in the farm of Pen-lan-Telych within the type area of the Llandovery Series (Cocks *et al.* 1970). The base of the stage was defined at a point above the last occurrence of the brachiopod *Eocoelia intermedia* in a collection which also contains *Stricklandia lens progressa*. The stage was thus characterised by the total ranges of *E. curtisi* and *E. sulcata* together with the arrival of *S. laevis* and the lower range of *Costistricklandia lirata* within a *Pentamerus* community (Cocks *et al.* 1970). The Telychian as defined included the C4–C6 beds of previous usage (e.g., Williams 1951) obviating the need for a stage between it and the base of the Wenlock. In the absence of graptolites the base thus relied on brachiopods for correlation. In detail, the original definition of the boundary stratotype (GSSP) for the stage in the Cefn-cerig Road Section, Wales, UK (Cocks *et al.* 1984) within the Wormwood Formation [Grid reference: 51.9700°N, 3.7900°W] was ratified by the International Union of Geological Sciences (IUGS) in 1985. The boundary correlates with the base of the *Monograptus turriculatus* graptolite Biozone (Bassett 1985) but there is a lack of graptolites anywhere near the base of the stage (Cocks *et al.* 1984; Temple 1988). Moreover, mapping by the British Geological Survey subsequently demonstrated that the GSSP was positioned within a sedimentary melange and thus unsuitable for the definition and correlation of a stadial boundary (see Loydell *et al.* 2025 for summary).

Following a global search for a replacement, the Spanish El Pintado section 1 (Loydell *et al.* (2025) was recently ratified, unopposed, by the IUGS as replacement GSSP for the base of the Telychian Stage. The section has a continuous sedimentary record through upper Aeronian–lower Telychian strata, is graptolitic throughout, and the abundant and diverse faunas have been intensively studied, together with its $\delta^{13}C_{org}$ chemostratigraphy. The base of the Telychian is marked in the section by the first appearance datum (FAD) of helically spiral *Spirograptus* and the onset of diversification of *Streptograptus* (the FAD of *S. picarrai*). *Paradiversograptus runcinatus* appears 0.4–0.6 m above the base of the Telychian and the 'Rumba low' negative $\delta^{13}C_{org}$ excursion culminates 1.4–1.6 m above the base of the Telychian. The GSSP for the Telychian Stage had now moved from the classic type area in Wales (Avalonia) to peri-Gondwana. Both sections, one in a shelly facies and one in a graptolitic facies, hosted very different facies and faunas from those of the Pentlands on peri-Laurentia.

Little attention was paid to the diverse and highly fossiliferous Silurian rocks of the southern part of Scotland, particularly those cropping north and south of the Girvan Valley and in the Pentland Hills. Many of the major reviews of the early 20th Century (e.g., Jones 1938) paid scant attention to southern Scotland and especially the Pentland Hills. The region appeared beyond the pale for stratigraphers. Nevertheless, the rocks merited brief mentions in summaries of the Silurian of Britain and Ireland (e.g., Cocks *et al.* 1971, 1992; Clarkson & Taylor 2002a, 2002b). By the mid-late 20th Century there may have been an undue emphasis on the historically significant classic Silurian sections in Wales and the Welsh Borderlands at the expense of sections elsewhere in the search to address the modern criteria for a GSSP.

2. Stratigraphy

The stratigraphy of the Silurian rocks of the Pentlands has been summarised briefly in a number of publications (e.g., Cocks *et al.* 1971, 1992) and more recently in detail by Clarkson & Taylor (2007) together with Clarkson & Harper (2016). These rocks occur in two main inliers (Fig. 1b), currently assigned to five formations (Fig. 1c); in ascending order, the Reservoir, Deerhope, Cock Rig, Wether Law Linn and Henshaw formations (Robertson 1989; Clarkson *et al.* 2001). Each of the units, their lithologies and distribution were described in detail by Clarkson & Taylor (2007); their fossil content described and illustrated in Clarkson *et al.* (2007) and Gallagher & Harper (2024) for the abundant and diverse brachiopod fauna. The strata range from the Aeronian Stage (Reservoir Formation) into the lower Wenlock (Henshaw Formation) and represent a marine regression from distal turbidite facies in the Reservoir Formation to the continental deposits in the Henshaw Formation (Clarkson & Taylor 2007). This regression can be tracked along the Silurian belt exposed in the inliers stretching from the Pentland Hills to the mountains of counties Galway and Mayo in western Ireland (Williams & Harper 1988, 1991; Clarkson & Harper 2016) supported by a commonality of sedimentary facies across the inliers extending to the west of Ireland. The Telychian strata, specifically the Wether Law Linn Formation, are very fossiliferous, with shelly and graptolite faunas allowing its correlation.

3. Discovery

While the laser focus of Sir Roderick Murchison and others was on the Silurian rocks of the Anglo-Welsh area, much farther north the search for fossils in the Pentland Hills had already commenced in the early 1800s. Thomas Davidson (1868, p. 2), the eminent brachiopod monographer, resident in Edinburgh, noted: 'As early as 1813, the then young and zealous French geologist, M. Ami Boué, was diligently exploring the Pentland Hills, ...'. Unfortunately, the expatriate Monsieur Boué did not spot a single fossil, but his efforts were not wasted as he did report the 'nearly vertical transition beds' and the overlying unconformable Old Red Sandstone, thus recognising rocks older than the Devonian. Thomas Davidson and R. J. H. Cunningham explored the area in 1835 and also noted the absence of fossils (in Cunningham 1838). However, shortly after their excursion, Charles MacLaren, a one-time editor of *The Scotsman* and an energetic amateur collector, visited the Pentland Hills and discovered the orthide brachiopod *Orthis Maclareni* [*sic*] together with an orthocone cephalopod, which was then considered to resemble a Wenlock species. MacLaren included descriptions of this material together with his descriptions of Silurian and Old Red Sandstone rocks in his publication (MacLaren 1838).

By 1858 the Geological Survey had commenced mapping the area for the first time, and Geikie (in Howell & Geikie 1861) considered the Silurian rocks to be equivalent to the Ludlow strata of England, and the overlying, essentially red, strata to be of 'Lower Old Red Sandstone age'. The survey's palaeontologist John William Salter (*op. cit.*), in the appendix of the same memoir, included some 40 species of fossils. It was, however, David Brown, George Haswell and John Henderson from the Edinburgh Geological Society who completed the first detailed investigation of the North Esk Inlier. Haswell produced a modest publication, essentially a field guide, entitled 'On the Silurian Formation of the Pentland Hills' in 1865, where he described the geology and figured 55 species of fossils. Thomas Davidson later accompanied Haswell and Brown on an excursion to the Pentland Hills in 1866 and concurred with their findings. A few years later, Henderson & Brown (1867) published the first detailed map of the inlier and identified eight fossiliferous horizons, A to H, a number of which were described as highly fossiliferous. Horizons A to E were correlated with the Wenlock Series, and F to H the Ludlow Series. Robert Etheridge (1869) studied the rocks in more detail and constructed a stratigraphical column while making a substantial collection of fossil material.

Davidson (1867) published the first illustrated monograph of the brachiopods of the Pentland Hills, the most abundant taxon in the faunas. Davidson (*op. cit.*) figured and described in detail 26 species of brachiopod from the North Esk Inlier (1869) and commented that one or two additional species may be present in the many fragmented specimens also collected. Malcolm Laurie (1892, 1899), who excavated and collected material together with John Hardie of Bavelaw Castle, described and illustrated the eurypterids from the Gutterford Burn.

As part of their meticulous geological survey of the Southern Uplands of Scotland, Peach & Horne (1899) provided a very thorough description of the geology of the Pentland Hills and comprehensive faunal lists, but the brachiopod faunas were still considered to be of Wenlock and Ludlow age. In the early part of the 20th Century the starfish fauna was described (Spencer 1914–1940); otherwise the trail went cold.

4. Development

Despite these early studies, the Pentland faunas remained largely unknown until the researches of Dr Archibald (Archie) Lamont FRSE (Fig. 2). Lamont was a controversial Scottish geologist and palaeontologist, a poet and writer, and an ardent Scottish

https://doi.org/10.1017/S1755691025100923 Published online by Cambridge University Press

Figure 2 A party of colleagues from Lund University visit the Pentland Hills (22nd May 1977). From left to right, Archie Lamont, Louis Liljedahl, Euan Clarkson and Jan Bergström. Photo courtesy of Per Ahlberg.

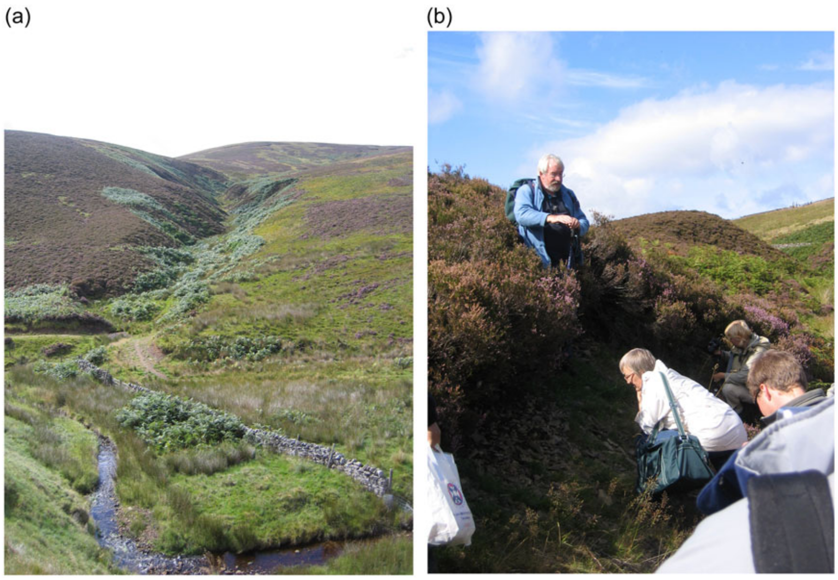

Figure 3 Pentland Hills: (a) The Wether Law Linn; the most fossiliferous sites are located on either side of the linn. (b) Euan Clarkson instructs a party of colleagues visiting the Pentlands during an IGCP excursion to southern Scotland in September 2006.

Nationalist, who retired after a short academic career to the village of Carlops where he spent some 50 years of his life in the shadow of the Pentland Hills (Clarkson 1986, 2007, 2000; Waterston 1986) and its fossiliferous strata (Fig. 3). Lamont worked for a short time at the University of Edinburgh as a Carnegie Research Fellow and University Research Fellow from 1945 to 1951. Owing to his deteriorating health (asthma) and also having disagreements with the then Professor, Arthur Holmes (Clarkson 2007), Lamont retired and remained in his cottage in Carlops, becoming increasingly more eccentric and isolated from the national and international palaeontological community. He disregarded engagement with referees, avoided scrutiny of his published work, and encountered problems with editors. The resulting papers flouted the rules of taxonomic nomenclature set by the International Commission on Zoological Nomenclature and many of his taxa were thus deemed invalid (Candela & Crighton 2019). From 1965 he edited, printed and was largely the only contributor to his *Scottish Journal of Science*, published from Jess Cottage in Carlops. Not surprisingly, his later scientific papers lacked the rigour and significance of his earlier publications. Many of his initial publications were of a good quality. He made contributions, for example, to the palaeoecology of the brachiopods (1934) and his investigation of the Drummuck Group, Girvan (1935) presented a new map, revised stratigraphy and faunal analysis (including the erection of the widespread brachiopod genus *Hirnantia*) for this critical area of Upper Ordovician geology (see also Harper 1981, 1982). He monographed Silurian brachiopods from England (Lamont & Gilbert 1945) and edited and published posthumously B. B. Bancroft's (1949) study on Welsh Valentian brachiopods (see also Cocks 2019).

Lamont, in a series of papers (e.g., 1947, 1952), was the first to suggest that the fossiliferous marine sedimentary successions of the North Esk Inlier were in fact correlated with the Llandovery and not Wenlock or Ludlow. He identified the graptolite *Monoclimacis crenulata* from the Gutterford Burn and assigned the brachiopod assemblages to the Upper Gala-Tarrannon, now known to correlate with the Llandovery Series. He used the

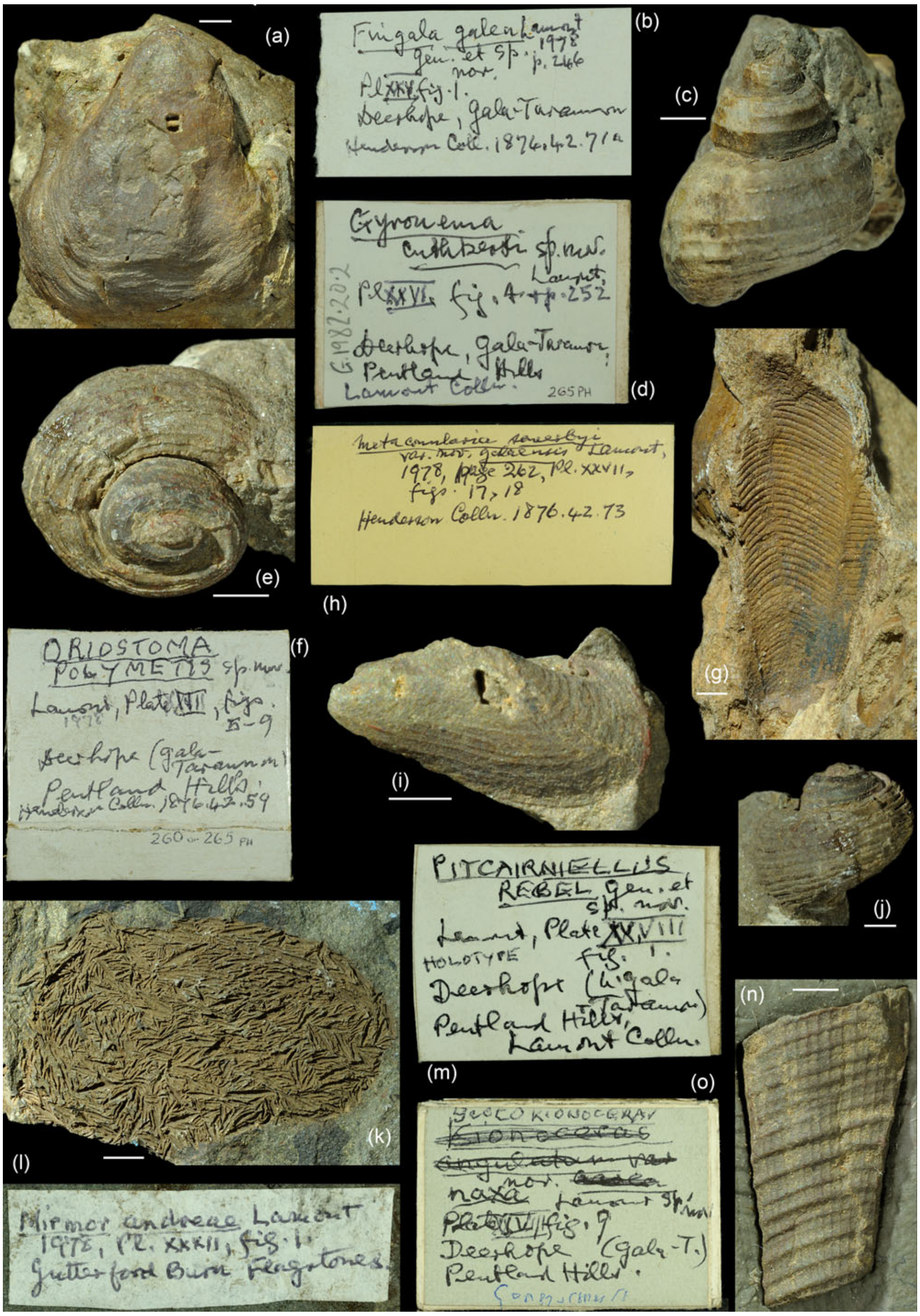

Figure 4 Selection of molluscs and cnidarians from the Pentland Hills, originally described in Lamont (1978), alongside their respective labels with Lamont's handwriting, in the collections of the National Museums of Scotland. (a–b) *Fingala galea* Lamont; (a) normal view of specimen NMS G.1876.42.71.1 and (b) label with locality, age and publication details. (c–d) *Gyronema cuthberti* Lamont; (c) lateral view of specimen NMS G.1982.20.2 and (d) label with locality, age and publication details. (e–f, j) *Oriostoma polymetis* Lamont; (e, j) apical and lateral views of the specimen NMS.G.1876.42.59 and (f) label with locality, age and publication details. (g–h) *Metaconularia sowerbyi* var. *galaensis* Lamont; (g) specimen NMS G.1876.42.73.2 and (h) label with publication details. (i, m) *Pitcairniellus rebel* Lamont; (i) normal view of specimen NMS G.1979.77.3 and (m) label with locality, age and publication details. (k–l) *Mirmor andreae* Lamont; (k) original external mould (latex cast is figured in Lamont 1978, pl. XXXII, fig. 1) of specimen NMS G.1979.45.1 and (l) label with horizon and publication details. (n–o) *Scotokionoceras naxa* Lamont; (n) specimen NMS G.1979.77.11 and (o) label with locality, age and publication details. Specimens (a) from the Wether Law Linn Formation; specimen (k) from the lower Deerhope Formation; all other specimens, horizon non-specified. Scale bars represent 1 mm (e, j); 2 mm (a, c, h–i, o); 5 mm (k).

brachiopod fauna to support this correlation, highlighting the presence of such index fossils for the upper Llandovery as *Dalejina pentlandica* (Davidson) and *Pentlandella pentlandica* (Haswell). Significantly, many taxa appeared endemic to the Pentland Hills. This is particularly true of the recently described fossil sponge fauna (Botting 2007; Botting *et al.* 2019).

It was not surprising that Lamont (1952) erected the Pentlandian as a new division between the Llandovery and the Wenlock to explain why some of the fossils found appeared to be unique to the North Esk Inlier while others were too cosmopolitan and long-ranging to be of any use in further refining the stratigraphy and its detailed correlation; this interval appeared to fill a gap between the Llandovery and Wenlock series. This new division was not embraced by the geological community and is now accepted as a bioregional and facies variant of the Telychian Stage of the Llandovery Series; the Pentlandian is no longer in common usage as a chronostratigraphic term, regionally or globally.

Figure 5 Selection of trilobites from the Pentland Hills, described or redescribed in Lamont (1978), alongside their respective labels with Lamont's handwriting in the collections of the National Museums of Scotland. (a–b) *Scotoharpes domina* Lamont; (a) close-up of cephalon of specimen NMS G.1978.61.547 and (b) label with locality details. (c–d) *Youngia douglasii* (Lamont); (c) dorsal view of glabella of specimen NMS G.1979.77.39 and (d) label with locality, age and publication details. (e–f) *Eskaspis phylax* Lamont; (e) cephalon of specimen NMS G.1979.77.36 and label with locality and publication details. (g–h) *Aytounella scotica* Lamont; (g) glabella of specimen NMS G.1979.77.37 and (h) label with locality, age and publication details. (i–j) *Cuchulainn lugi* Lamont; (i) complete mould of specimen NMS G.1979.77.34 and (j) label with locality, age and publication details. (k–m) *Acidaspis (Bruxaspis) dealgach* Lamont; (k–l) partial cephalon and pygidium of specimen NMS G.1979.77.45.1 and (m) label with locality and publication details. Specimen (i) from the Deerhope Formation; specimens (k–l) horizon not specified; all other specimens from the Wether Law Linn Formation. Scale bars represent 1 mm (c, e, g–h); 2 mm (i, k); 5 mm (a).

Lamont's *magnus opus* (1978), which coincided with the initial work on the Pentlands trilobites by Clarkson and associates, presented a phenomenal number of new genera, 40 in all, many emphasising the inimitable character of the Pentlandian biota, and building on his earlier hypothesis of the individuality of this Scottish assemblage. Many of Lamont's specimens have been now located in the palaeontological collections of the Department of Natural Sciences, National Museums Collection Centre, by the second author (Fig. 4: molluscs and cnidarians; Fig. 5: trilobites; Fig. 6: brachiopods, machaeridians and a sponge). This was Lamont's last hurrah published against the background of a new wave of research and researchers led by a newly appointed lecturer in the Edinburgh department, Dr Euan Clarkson.

5. Revival

Two years prior to Euan Clarkson's arrival in Edinburgh, Mitchell *et al.* (1962) published their Survey Memoir on the geology of Edinburgh and the surrounding area, and within it Mykura & Smith provided further evidence of the strata in the inlier being of pre-Wenlock age. Euan commenced a vigorous research programme that would continue until his death in parallel with his investigation of vision in trilobites, the ecology and evolution of Cambrian trilobites from southern Scandinavia, the Carboniferous of the Midland Valley and much more. His research in the Pentlands attracted and inspired both undergraduate and graduate students, colleagues and friends (including ourselves) together with a cast of international experts (Fig. 6).

John Tipper, Euan's first PhD student, was recruited in 1970 and was encouraged to investigate the faunal assemblages of the Pentlands; his interest was in numerical methodologies and these he applied to their study. Although it was clear the rocks were pre-Wenlock in age, a precise correlation with global chronostratigraphy was lacking. The presence of *Eoplectodonta penkillensis* Reed was cited as an indication of a late Llandovery age, and R. B. Rickards (in Tipper 1976) observed that the available Pentland Hills graptolites are 'most likely to be of pre-

Figure 6 Selection of brachiopods, machaeridians and sponge described by Lamont (1978) or redescribed (Candela & Crighton 2015; Candela *et al.* 2017) or newly described (Botting *et al.* 2019) in the collections of the National Museums of Scotland. (a–c) *Leptaena mauseae* Lamont; (a) internal mould of ventral valve of specimen NMS G.1885.24.86.1; (b–c) labels with locality, age, publication details, and etymology of Lamont's new species. (d–e) *Coolinia applanate augusta* Lamont; (d) internal mould of dorsal valve of specimen NMS G.2016.4.1 and (e) associated label. (f–g) *Eoghanospongia carlinslowpensis* Botting *et al.*; specimen NMS G.2010.38.1 and counterpart NMS G.2010.38.2. (h–k) *Plumulites ruskini* Lamont; (h–i, k) internal mould of various shell plates and (j) label with publication details. Specimen (a) from the Deerhope Formation; all other specimens from the Wether Law Linn Formation. Scale bars represent 1 mm (h–i, k); 2 mm (d); 5 mm (a); 10 mm (f–g).

Wenlock age'; a correlation with the *crenulata* Biozone was noted by Robertson (1989); graptolite evidence was further discussed by Bull (1987) together with Bull & Loydell (1995). Tipper (1976) redefined the stratigraphy, establishing four formations: in ascending order, the Reservoir, Deerhope, Wether Law Linn and Henshaw formations. He was the first to recognise the presence of a volcanic ash band within the Wether Law Linn Formation, reaching up to 265 m thick at its maximum development and marking a distinct faunal change in the formation. Batchelor & Clarkson (1993) formally identified the ash band as a metabentonite, probably of rhyodacitic composition, and discussed the change from a highly diverse brachiopod-dominated fauna stratigraphically below the bentonite to a sparse low-diversity fauna stratigraphically above.

Gary Robertson (1989), following Tipper's work, mapped in detail the three inliers of the Pentland Hills, constructing sedimentary logs and adding a fifth formation stratigraphically above the Deerhope and below the Wether Law Linn formations, which he named the Cock Rig Formation. He extended the work of Tipper (1975) on the development of palaeocommunities (Robertson 1999), expanding the scope of the work higher into the Wether Law Linn Formation. He referred the marine strata to the Telychian Stage of the Upper Llandovery Series and the *Monoclimacis crenulata* Biozone, with the possibility of the lowermost Henshaw Formation being of *griestoniensis* Biozone (early Wenlock) age. Moreover Robertson (1999) graphically illustrated the majority of the palaeocommunities, many brachiopod-dominated, through the succession. The graptolite succession was examined by Elizabeth Bull who published on the dendroids (1987, 1996a, 1996b) and the graptoloids (Bull & Loydell 1995). The work continued across a range of fossil groups, gradually confirming the uniqueness of the succession and its biotas.

Many studies have been published on the biotas, the majority of them in the Palaeontological Association's *Field Guide to Fossils 11* (Clarkson *et al.* 2007). In 18 chapters all aspects of the

Table 1 Overview of the contents of 'Silurian Fossils of the Pentland Hills' (Clarkson *et al*. 2007).

Author(s)	Topic
E. N. K. Clarkson and C. M. Taylor	Rocks and fossils in the Pentland Hills
J. P. Botting	Algae, receptaculitids and sponges
E. N. K. Clarkson and C. Taylor	Corals
S. J. Stephen and E. N. K. Clarkson	Bryozoans
E. E. Gallagher and D. A. T. Harper	Brachiopods
E. Geldart, E. N. K. Clarkson and S. E. Stewart	Bivalves
C .H. Holland	Cephalopods
J. O. R. Ebbestad	Gastropods
E. N. K. Clarkson and C. Taylor	Trilobites
L. I. Anderson	Unmineralised arthropods
D. J. Siveter	Ostracods
D. K. Loydell	Graptolites
S. K. Donovan, F. E. Fearnhead and D. N. Lewis	Crinoids
C. H. Jeffry-Abt	Echinoids
D .J. Gladwell	Stelleroids
S. E. Stewart, L. I Anderson and E. N. K. Clarkson	Miscellanea

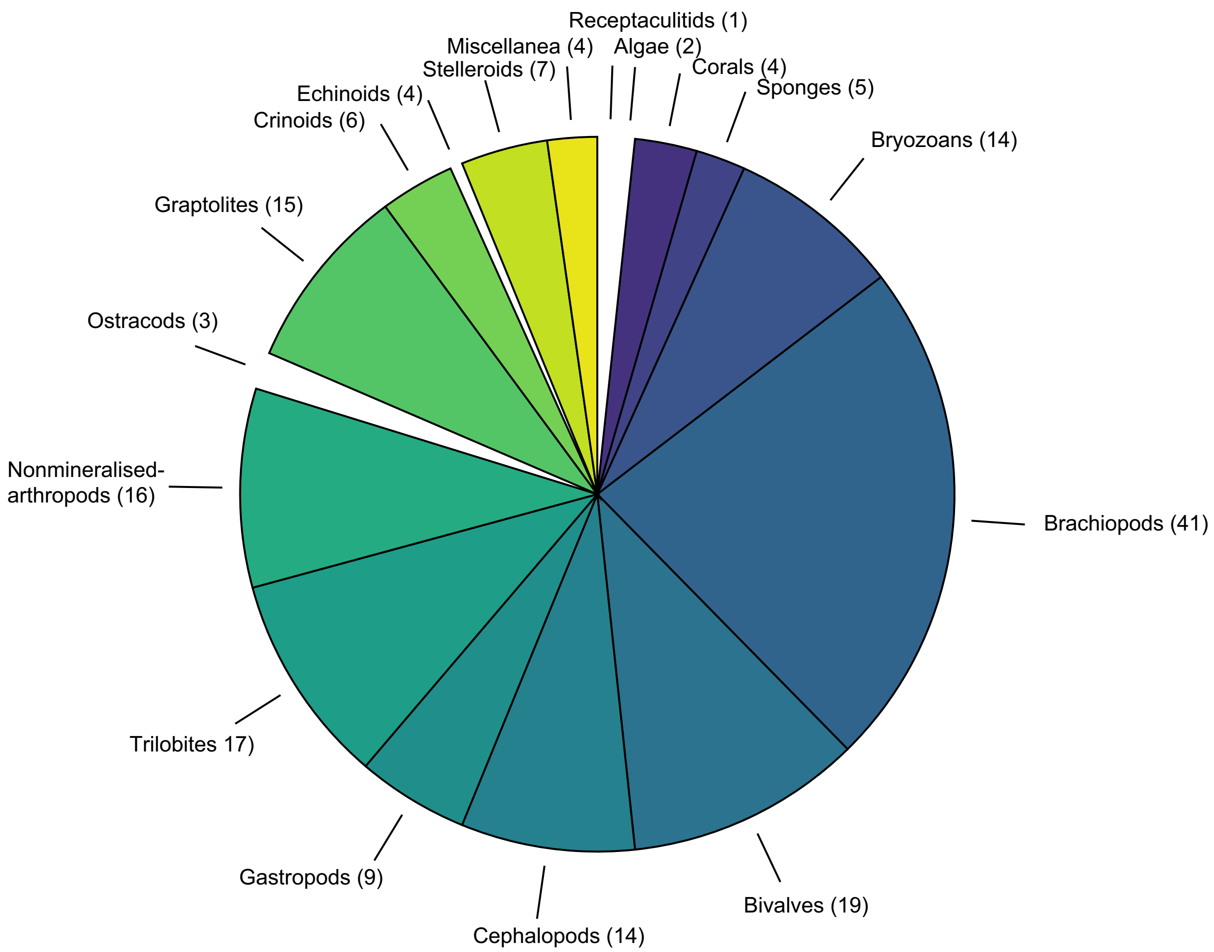

Figure 7 Pie chart displaying the numbers of taxa from the Silurian of the Pentland Hills identified in Clarkson *et al*. (2007).

North Esk Inlier were considered (see Table 1); Euan Clarkson participated in seven of the chapters and led the editorial team. Following the publication of this remarkable compendium of the Pentlands fossil biota, new discoveries continue to be made. These complement the body of work already published. Candela & Crighton (2015, 2017) reviewed and updated the machaeridian fauna, erecting a new species in honour of Dr Lamont (*Plumulites lamonti* Candela & Crighton 2017). Candela *et al.* (2017) dealt with the brachiopods, previously overlooked or designated *nomina dubia*, and described by Lamont (1978) in a separate chapter entitled 'Length to breadth proportions in brachiopod palaeoecology'. Candela & Crighton (2019) revised, discussed and properly illustrated all the taxa described in Lamont (1978). Finally Botting *et al.* (2019) described an endemic new hexactinellid sponge discovered recently, emphasising again the uniqueness of the Pentland Hills faunas.

Figure 8 Selection of the most common brachiopod taxa in the Pentland Hills from the collections of the National Museums of Scotland. (a–b) *Pentlandina tartana* (Bancroft); (a) internal mould of ventral valve, NMS G.2006.40.2; (b) internal mould of dorsal valve, NMS G.2015.35.5. (c–d) *Leptaena eska* Gallagher & Harper; (c) external mould of dorsal valve, NMS G.2006.40.6.1; (d) internal mould of ventral valve, NMS G.1876.42.91.3. (e) *Skenidioides lewisii* (Davidson), internal moulds of ventral and dorsal valves, NMS G.2006.40.17. (f–g) *Eoplectodonta* (*Eoplectodonta*) *penkillensis* (Reed); (f) internal mould of ventral valve, NMS G.2006.40.9; (g) internal mould of dorsal valve, NMS G.1876.42.97.1. (h, k) *Isorthis* (*Ovalella*) *clarksoni* Gallagher & Harper; (h) internal mould of ventral valve, NMS G.2006.40.19; (k) internal mould of dorsal valve, holotype, NMS G.2006.40.18. (i–j) *Coolinia pecten* (Linnæus); (i) internal mould of ventral valve, NMS G.2015.35.27; (j) internal mould of dorsal valve, NMS G.2015.35.28. (l–m) *Visbyella visbyensis* (Lindström); (l) internal mould of ventral valve, NMS G.1876.42.89; (m) internal mould of dorsal mould, NMS G.2015.35.42. (n–o) *Dicoelosia paratenua* Gallagher & Harper; (n) internal mould of ventral valve, NMS G.1876.42.88.1; (o) internal mould of dorsal valve, NMS G.1876.42.88.2. Specimens on (a–g, i–j, l–o) from the Wether Law Linn Formation; specimens on (h, k) from the Deerhope Coral Bed, Deerhope Formation. Scale bars represent 1 mm (e, o); 2 mm (a–b, f–n); 5 mm (c–d).

The most abundant element of the faunas is the Brachiopoda (Figs 7, 8). To date, the most comprehensive and up-to-date study since Davidson (1868) is that of Gallagher (2003), which formed the basis for Gallagher & Harper (2007) who briefly described and illustrated the 20 most common and distinctive taxa in the field guide to the fossils of the Pentland Hills (Clarkson *et al.* 2007). Cocks (1978, 2019; see also 2008) noted many of the Pentland's taxa in his reviews of British and Irish Lower Palaeozoic brachiopods and in his description of Llandovery brachiopods from England and Wales. Currently over 50 brachiopod species are now known from the Silurian rocks in the Pentland Hills, with the most recent descriptions and illustrations in Gallagher & Harper's Palaeontographical Society Monograph (2024).

6. The biotic succession

Life in the Silurian sea inhabited by the Pentland Hills fauna was summarised by Clarkson & Harper (2007). The Pentland Hills fauna is distinctive, being dominated by orthide and strophomenide brachiopods, whereas the more typical Silurian elements, for example the atrypides, athyridides and spiriferides, are generally less common, although some are locally abundant; they are more characteristic of Anglo-Welsh assemblages. There are very few representatives of the brachiopod lineages commonly used for correlation with the Llandovery shelly facies (Cocks *et al.* 1984) requiring other means to effect correlation. As a whole, the faunas are most similar to the deeper-water *Dicoelosia* palaeocommunities

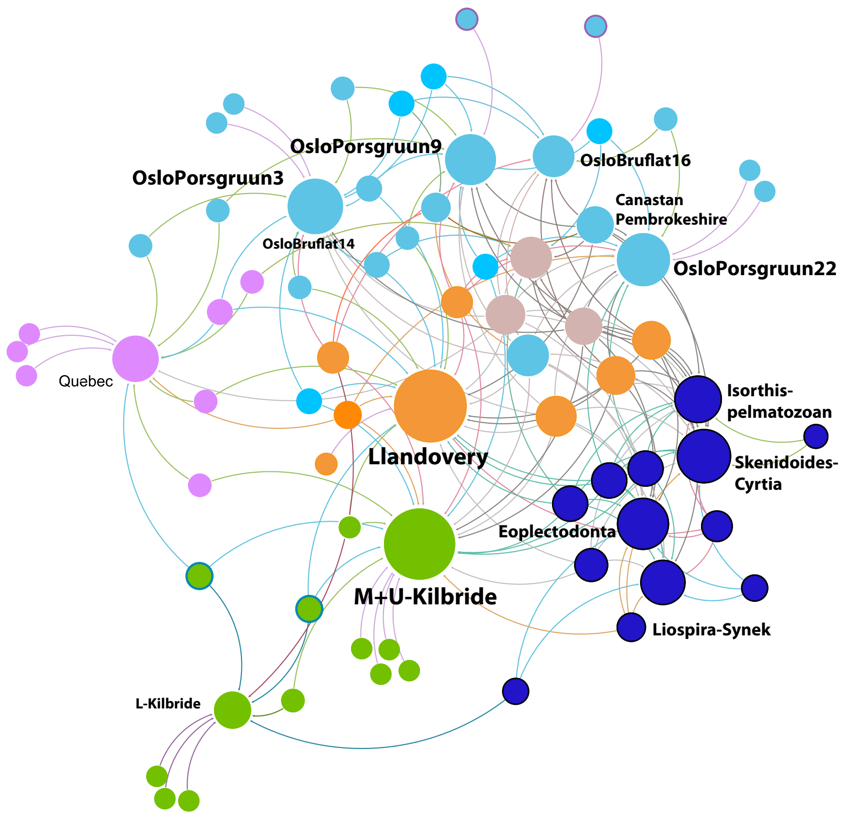

Figure 9 Network analysis, using Gephi software, of a selection of later Llandovery brachiopod faunas from adjacent sites. Graph modified from Gallagher & Harper (2024), text-fig. 6. Data sources: the following sites with sources are displayed: *Isorthis*-Pelmatozoan, *Skenidioides-Cyrtia*, *Eoplectodonta*, *Liospira*?-*Synek*, associations from the North Esk inlier (Robertson 1985, 1989, 1999; Gallagher & Harper 2024), OsloPorsgruun3, Oslo Porsgruun9, OsloPorsgruun22, OsloBruflat14 and OsloBruflat16 from named formations in the Oslo Region, southern Norway (Cocks & Worsley 1993), Canastan from Canastan, Pembrokeshire (Watkins & Boucot 1978), Llandovery (Cocks *et al.* 1984), L-Kilbride and M + U-Kilbride from the Kilbride Formation in western Ireland (Doyle 1989 and pers. obs.) and Quebec (Watkins & Boucot 1978). The plot indicates the coherence of the Pentlands deeper-water marine faunas.

(Watkins *et al.* 2000) that inhabited the more amphicratonic habitats of the Silurian palaeocontinents, commonly associated with more siliciclastic, fine-grained facies. Robertson (1985, 1989, 1999) expanded the palaeocommunity description and interpretation of the succession, first established by Tipper (1975), defining four main associations, outlined below, in ascending order. These are quite different from the assemblages in the Anglo-Welsh area where more typical Silurian faunas dominated by *Eocoelia* and *Stricklandia* lineages are prevalent. The term *Isorthis mackenziei* – pelmatozoan Association has been changed to the *Isorthis clarksoni* – pelmatozoan Association to take account of the revised taxonomic status of the dalmanelloid taxon (Gallagher & Harper 2024).

***Isorthis clarksoni* – pelmatozoan Association** is dominated by the dalmanelloid brachiopods *Isorthis (Ovalella) clarksoni* Gallagher & Harper, *Visbyella visbyensis* (Lindström) and *Pentlandella pentlandica* (Haswell) together with species of *Dictyocaris* and *Ptilodictya*; the most dominant element is the ostracode *Craspedobolbina* (*Mitrobeyrichia*) *impendens* (Haswell) together with cystoporate bryozoans and the trilobite *Encrinurus expansus* Haswell. Tipper (1974, 1975) named this assemblage the Isorthid – *Glassia* Community, based on the misidentification of *Pentlandella* as *Glassia*. The association occurs within the upper Cock Rig Formation and uppermost part of the Lower Member of the Wether Law Linn Formation.

***Skenidioides lewisii* – *Cyrtia exporrecta* Association** is synonymous with Tipper's (1974, 1975) *Skenidioides* – *Dicoelosia* Community. In terms of brachiopods the association is dominated by *Skenidioides lewisii* (Davidson) and *Cyrtia exporrecta* (Wahlenberg) together with *Coolinia applanata* (Salter) and *Eoplectodonta penkillensis* (Reed) accompanied by a species of *Oglupes*.

***Eoplectodonta penkillensis* Association** is overwhelmingly dominated by two brachiopod taxa, *Eoplectodonta penkillenis* (Reed) and *Visbyella visbyensis* (Lindström).

***Liospira*? *simulans* – *Synek* Association**. In terms of brachiopods the association is dominated by *Coolinia pecten* (Linnæus) and *Eoplectodonta penkillensis* (Reed) but much of the diversity is represented by molluscs such as the abundant *Liospira*? *simulans* (Salter) and a species of *Synek*? together with the ostracode *Craspedobolbina* (*Mitrobeyrichia*) *impendens* (Haswell).

The first three associations are associated with relatively deep water evolving against a background of regression, culminating in the shallowest-water *Liospira*? *simulans* – *Synek* Association. All four are strongly linked by the common occurrence of orthide and strophomenide taxa. In contrast to the faunas with more typical Silurian elements in the Anglo-Welsh area (Copper 2004), with the exception of *Eocoelia sulcata* (Prouty), members of the key *Eocoelia*, *Pentameroides* and *Stricklandia*-*Costistricklandia* lineages (Rong & Bassett 2002) have never been reported; neither have any of the eponymous elements of the *Eocoelia*, *Pentamerus*, *Costistricklandia* and *Clorinda* communities (Ziegler *et al.* 1968).

7. Palaeobiogeography

During the Telychian a range of different brachiopod communities evolved, associated with the varied sedimentary

https://doi.org/10.1017/S1755691025100923 Published online by Cambridge University Press

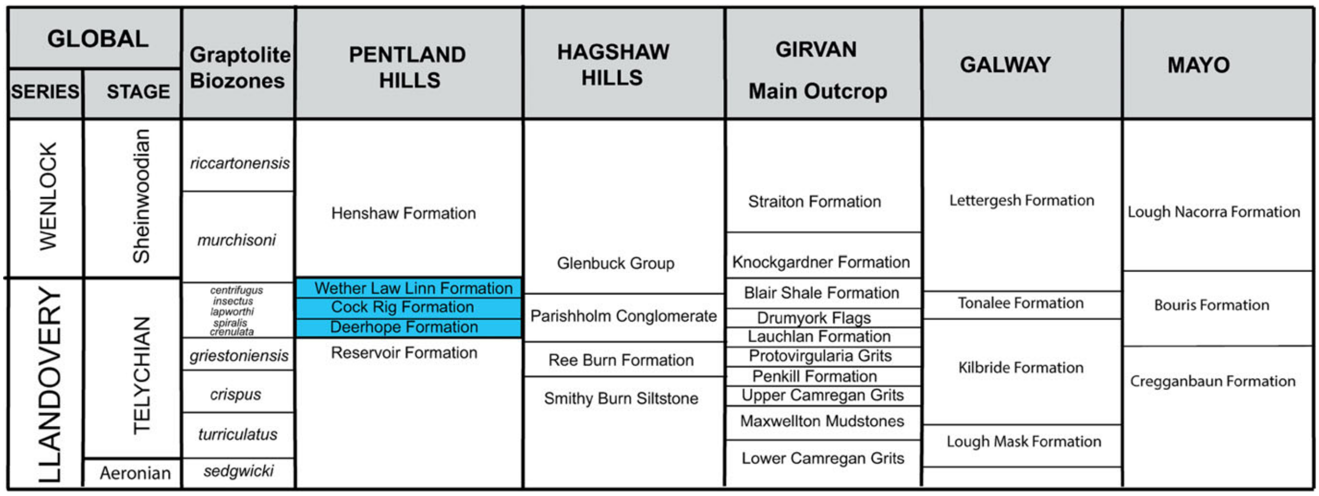

Figure 10 The Pentlandian Biotic Complex (indicated in blue) based on text-fig. 4 in Gallagher & Harper (2024).

environments and the separations of the main continents; many genera were widespread, forming a substantial faunal province that was virtually 'cosmopolitan' (e.g., Rong & Bassett 2002; Cocks & Rong 2019). Across the highest palaeolatitudes, associated with southern-hemisphere Gondwana, the *Clarkeia* Fauna, the precursor of the late Silurian and Devonian Malvinoxhosan Realm (Penn-Clarke & Harper 2021, 2023) developed. In the northern hemisphere, there was the origin of the *Tuvaella* Faunal Province in the northernmost part of Siberia at that time. Both bioregions continued beyond the end of the Silurian and into the Devonian.

Brachiopods are the most abundant taxon within the biota and as noted above have been recently described and illustrated in detail (Gallagher & Harper 2024). These authors presented multivariate analyses, using non-metric multidimensional scaling (NMDS) and network analysis, that indicated, not unexpectedly, the mutual closeness of the Pentlands associations. The NMDS plot presents a cluster of the three deep-water associations from the North Esk Inlier separated from those elsewhere including the type Llandovery, giving some credence to their inclusion within a distinctive Pentlandian assemblage (Lamont 1947, 1952). The stress value of 0.16 indicated on the Shepard plot is adequate for this analysis. Network analysis (using Gephi) of groups is revised and presented here (Fig. 9); the sites are placed according to interactions between common taxa with the diameter of each node proportional to the diversity at that locality. A similar clustering is apparent for the same three faunas with the addition of the shallower-water *Liospira*?-*Synek* association.

8. The Pentlandian: a key Llandovery biotic complex

The Pentlandian is a regional term and although proposed by Lamont (1952) as a chronostratigraphic unit between the Llandovery and Wenlock it never gained traction. Subsequent research has shown that the Pentlandian is equivalent and correlatable with part of the Telychian. Potentially it has the status of a regional chronostratigraphic stage but the unit and its faunas have not been readily identified elsewhere and thus the Pentlandian was never adopted by the national or international community. Nevertheless, its distinctive biotas deserve recognition for evolving in a deep shelf ecosystem to include the evolving ecosystems of the Deerhope, Cock Rig and Wether Law Linn formations. In palaeontology, a 'biotic complex' refers to the interconnected network of living organisms (both plants and animals) and their interactions within a specific environment or ecosystem, as represented in the fossil record. The term has been widely used particularly for Devonian assemblages (e.g., Penn-Clarke and Harper 2021, 2023). The term Pentlandian Biotic Complex (Fig. 10) seems an appropriate term, capturing too the researches of both Archie Lamont and, especially, Euan Clarkson.

Acknowledgements

We extend our sincere thanks to Annalisa Ferretti and Jin Jisuo for thoughtful reviews, together with Alan Owen for his careful editorial work. All three improved our manuscript. We also thank Euan for his encouragement and inspiration, supporting the many researchers, including ourselves, who he attracted to the Pentland Hills.

Competing interests

The authors declare no competing interests.

References

Bancroft, B. B. 1949. Welsh Valentian brachiopods and *Strophomena antiqua* group of fossil brachiopods (edited by A. Lamont). Privately printed, 16 pp, 3 pls. Mexborough.

Bassett, M. G. 1985. 'Transition rocks and Grauwacké' – the Silurian and Cambrian systems through 150 years. *Episodes* **8**, 231–35. https://doi.org/10.18814/epiiugs/1985/v8i4/002.

Bassett, M. G. & Rong, J. Y. 2002. Brachiopods. *National Museum of Wales Geological Series* **21**, 163–65.

Batchelor, R. A. & Clarkson, E. N. K. 1993. Geochemistry of a Silurian metabentonite and associated apatite from the North Esk Inlier, Pentland Hills. *Scottish Journal of Geology* **29**, 123–30. https://doi.org/10.1144/sjg29020123.

Bluck, B. J. 1985. The Scottish paratectonic Caledonides. *Scottish Journal of Geology* **21**, 437–64. https://doi.org/10.1144/sjg21040437.

Botting, J. P. 2007. Algae, receptaculitids and sponges. *Palaeontological Association Field Guides to Fossils* **11**, 36–49.

Botting, J. P., Candela, Y., Crighton, W. R. B. 2019. A new hexactinellid sponge from the Silurian of the Pentland Hills (Scotland) with similarities to extant rossellids. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **111**, 17–25. https://doi.org/10.1017/S1755691019000045.

Bull, E. E. 1987. Upper Llandovery dendroid graptolites from the Pentland Hills, Scotland. *Palaeontology* **30**, 117–40.

Bull, E. E. 1996a. Implications of normal and abnormal growth structures in a Scottish Silurian dendroid graptolite. *Palaeontology* **39**, 219–40.

Bull, E. E. 1996b. *Geology and palaeontology of the Telychian (Silurian), reservoir formation of the North Esk Inlier, near Edinburgh, Scotland.* Unpublished PhD thesis, University of Edinburgh.

Bull, E. E. & Loydell, D. K. 1995. Uppermost Telychian graptolites from the North Esk Inlier. *Scottish Journal of Geology* **31**, 163–70. https://doi.org/10.1144/sjg31020163.

Candela, Y. & Crighton, W. R. B. 2015. Revision of *Plumulites ruskini* Lamont, and new data from the Silurian of the Pentland Hills, Scotland. *Scottish Journal of Geology* **51**, 31–42. https://doi.org/10.1144/sjg2014-053.

Candela, Y. & Crighton, W. R. B. 2017. Addenda to the record of machaeridian shell plates in the Wether Law Linn Formation (Late Llandovery), Pentland Hills, Scotland. *Scottish Journal of Geology* **53**, 35–39. https://doi.org/10.1144/sjg2016-006.

Candela, Y. & Crighton, W. R. B. 2019. Synoptic revision of the Silurian fauna from the Pentland Hills, Scotland described by Lamont (1978). *Palaeontologia Electronica*, 22.2.19A. https://doi.org/10.26879/868.

Candela, Y., Harper, D. A. T. & Crighton, W. R. B. 2017. Notes on the brachiopod species from the Silurian of the Pentland Hills described by Lamont (1978). *Scottish Journal of Geology* **53**, 29–33. https://doi.org/10.1144/sjg2016-003.

Clarkson, E. N. K. 1986. Archie Lamont MA, PhD, FRSE (1907–1985). Proceedings of the Edinburgh Geological Society December 1986, 3–5 (reprinted with amendments in 1991, The Trilobite Papers 3, 16–18).

Clarkson, E. N. K. 2000. Pentland Odyssey. *Scottish Journal of Geology* **36**, 8–16. https://doi.org/10.1144/sjg36010008

Clarkson, E. N. K. 2007. Archie Lamont (1907–1985), geologist and poet. *Proceedings of the Geological Society of Glasgow 150th Anniversary Special Edition* **150**, 35–38.

Clarkson, E. N. K. & Harper, D. A. T. 2007. Life in the Pentlands sea. *Palaeontological Association Field Guides to Fossils* **11**, 30–35.

Clarkson, E. N. K. & Harper, D. A. T. 2016. Classic localities explained: Silurian of the Midland Valley of Scotland and Ireland. *Geology Today* **32**, 195–200. https://doi.org/10.1111/gto.12152.

Clarkson, E. N. K., Harper, D. A. T. & Taylor, C. M. 2001. Scottish Silurian shorelines. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **91**, 479–87. https://doi.org/10.1017/s0263593300008324.

Clarkson, E. N. K., Harper, D. A. T., Taylor, C. M. & Anderson, L. I. (eds) 2007. *Silurian fossils of the Pentland Hills, Scotland* **11**, 218 pp. Palaeontological Association Field Guides to Fossils.

Clarkson, E. N. K. & Taylor, C. M. 2002a. The Deerhope formation in the North Esk Inlier, Pentland Hills, Scotland. In Wyse Jackson, P., Parkes, M. A. & Wood, R. (eds), *Studies in Palaeozoic palaeontology and biostratigraphy in honour of Charles Hepworth Holland* **67**, 29–44. *Special Papers in Palaeontology*.

Clarkson, E. N. K. & Taylor, C. 2002b. Telychian rocks of the British Isles. In Aldridge, R. J. *et al.* (eds) *National Museum of Wales Geological Series* **21**, 43–72.

Clarkson, E. N. K. & Taylor, C. M. 2007. Silurian rocks and fossils in the Pentland Hills. *Palaeontological Association Field Guides to Fossils* **11**, 8–29.

Cocks, L. R. M. 1978. A review of British Lower Palaeozoic brachiopods including a synoptic revision of Davidson's monograph. *Monographs of the Palaeontographical Society* **131**, 1–256. https://doi.org/10.1080/25761900.2022.12131735.

Cocks, L. R. M. 2008. A revised review of British Lower Palaeozoic brachiopods. *Monographs of the Palaeontographical Society* **161**, 1–276, pls 1–10. https://doi.org/10.1080/25761900.2022.12131809.

Cocks, L. R. M. 2019. Llandovery brachiopods from England and Wales. *Monographs of the Palaeontographical Society* **172**, 1–262. pls 1–41. https://doi.org/10.1080/02693445.2018.1537165.

Cocks, L. R. M., Holland, C. H. & Rickards, R. B. 1992. A revised correlation of Silurian rocks in the British Isles. *Geological Society of London, Special Reports* **21**, 1–32. https://doi.org/10.1144/sr21.1.

Cocks, L. R. M., Holland, C. H., Rickards, R. B. & Strachan, I. 1971. A correlation of Silurian rocks in the British Isles. *Journal of the Geological Society* **127**, 103–36. https://doi.org/10.1144/gsjgs.127.2.0103.

Cocks, L. R. M. & Rong J.-Y. 2019. A global analysis of distribution and endemism within Late Llandovery (Telychian) brachiopods. *Alcheringa: An Australasian Journal of Palaeontology* **43**, 406–22. https://doi.org/10.1080/03115518.2019.1616111.

Cocks, L. R. M., Toghill, P., Ziegler, A. M. 1970. Stage names within the Llandovery Series. *Geological Magazine* **107**, 79–87. https://10.1017/S0016756800054728.

Cocks, L. R. M., Woodcock, N. H., Rickards, R. B., Temple, J. T. & Lane, P. D. 1984. The Llandovery Series of the type area. *Bulletin of the British Museum (Natural History) Geology* **38**, 131–82.

Cocks, L. R. M. & Worsley, D. 1993. Late Llandovery and Early Wenlock stratigraphy and ecology in the Oslo Region. *Bulletin of the British Museum Natural History (Geology)* **49**, 31–46. https://doi.org/10.5962/p.313804.

Cohen, K., Harper, D. A. T., Gibbard, P. & Car, N. 2025. The ICS chronostratigraphic chart this decade. *Episodes* **48**, 105–15. https://doi.org/10.18814/epiiugs/2025/025001.

Copper, P. 2004. *Silurian (Late Llandovery-Ludlow) atrypid brachiopods from Gotland, Sweden and the Welsh Borderlands, Great Britain*, 215 pp. Ottawa: NRC Research Press. https://doi.org/10.1139/9780660190112.

Cunningham, R. J. H. 1838. On the geology of the Lothians. *Memoirs of the Wernerian Society of Edinburgh* **VII**, 3–160.

Davidson, T. 1867. A monograph of the British fossil Brachiopoda. Part VII. No. II. The Silurian Brachiopoda. *Monographs of the Palaeontographical Society* **20**, 89–168. https://doi.org/10.1080/02693445.1867.12113223.

Davidson, T. 1868. On the Upper Silurian Brachiopoda of the Pentland Hills and of Lesmahagow, in Lanarkshire. *Geological Society of Glasgow, Transactions* **1**, 1–24, pls 21–23.

Davidson, T. 1869. A monograph of the British fossil Brachiopoda. Part VII. No. III. The Silurian Brachiopoda. *Monographs of the Palaeontographical Society* **22**, 169–248. https://doi.org/10.1080/02693445.1869.12113231.

Doyle, E. N. 1989. The biostratigraphy and sedimentology of the Lower Silurian (Llandovery) rocks of North Galway. PhD thesis, University College Galway.

Doyle, E. N., Harper, D. A. T. & Parkes, M. A. 1990. The Tonalee fauna: a deep-water shelly assemblage from the Llandovery rocks of the West of Ireland. *Irish Journal of Earth Sciences* **10**, 127–43.

Doyle, E. N., Höey, A. N. & Harper, D. A. T. 1991. The rhynchonellide brachiopod *Eocoelia* from the Upper Llandovery of Ireland and Scotland. *Palaeontology* **34**, 439–54.

Etheridge, R. 1869. Notice on additional fossils from the Upper Silurian series of the Pentland Hills. *Transactions of the Edinburgh Geological Society* **2**, 309–14.

Gallagher, E. E. 2003. Silurian brachiopods from the Pentlands Hills, Scotland: taxonomy, diversity and disparity. Unpublished PhD thesis, Department of Earth and Ocean Sciences, National University of Ireland, Galway.

Gallagher, E. E. & Harper, D. A. T. 2007. Brachiopods. *Palaeontological Association Field Guide to Fossils* **11**, 65–85.

Gallagher, E. E. & Harper, D. A. T. 2024. Silurian brachiopods from the Pentland Hills, Scotland. *Monographs of the Palaeontographical Society* **177**, 1–69, 13 pls. https://doi.org/10.1080/02693445.2023.2307703.

Harper, D. A. T., 1981. The stratigraphy and faunas of the Upper Ordovician High Mains Formation of the Girvan District. *Scottish Journal of Geology* **17**, 247–55.

Harper, D. A. T. 1982. The stratigraphy of the Drummuck Group (Ashgill), Girvan. *Geological Journal* **17**, 251–57. https://doi.org/10.1002/gj.3350170402.

Harper, D. A. T., Bown, P. R. & Coe, A. L. 2022. Chronostratigraphy: understanding rocks and time. In Coe, A. L. (ed.) *Deciphering Earth's history: the practice of stratigraphy*, 227–43. London: Geological Society.

Haswell, G. C. 1865. *On the Silurian Formation in the Pentland Hills*, 47 pp, 4 pls. Edinburgh: W. P. Nimmo.

Henderson, J. & Brown, D. J. 1867. On the Silurian rocks of the Pentland Hills, Part 1. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **1**, 23–33.

Howell, H. H. & Geikie, A. 1861. *The Geology of the Neighbourhood of Edinburgh. Memoirs of the Geological Survey* 58 pp. Printed by George E. Eyre & William Spottiswoode.

Jones, O. T. 1938. On the evolution of a geosyncline. *Quarterly Journal of the Geological Society of London* **94**, 60–110.

Lamont, A. 1934. Brachiopod morphology in relation to environment. *Cement, Lime and Gravel* **8**, 216–19.

Lamont, A. 1935. The Drummuck Group, Girvan; a stratigraphical revision, with descriptions of new fossils from the lower part of the group. *Transactions of the Geological Society of Glasgow* **19**, 288–334, pls VII–IX. https://doi.org/10.1144/transglas.19.2.288

Lamont, A. 1947. Gala-Tarannon beds in the Pentland Hills, near Edinburgh. *Geological Magazine* **84**, 193–208, 289–330. https://doi.org/10.1017/s0016756800082649.

Lamont, A. 1952. Ecology and correlation of the Pentlandian – a new division of the Silurian System in Scotland. *Report of the 18th International Geological Congress, London* **10**, 27–32.

Lamont, A. 1978. Pentlandian miscellany: Mollusca, Trilobita, etc. *Scottish Journal of Science* **1**, 245–302.

Lamont, A. & Gilbert, D. L. F. 1945. Upper Llandovery Brachiopoda from Coneygore Coppice and Old Storridge Common, near

Alfrick, Worcestershire. *Annals and Magazine Natural History. Series 11* **xii**, 641–82. pls III–VII. https://doi.org/10.1080/00222934508654774.
Laurie, M. 1892. On some eurypterid remains from the Upper Silurian rocks of the Pentland Hills. *Transactions of the Royal Society of Edinburgh.* **37**, 151–162.
Laurie, M. 1899. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. *Transactions of the Royal Society of Edinburgh* **39**, 575–89. https://doi.org/10.1017/S0080456800035109.
Loydell, D. K., Gutiérrez-Marco, J. C., Štorch, P. & Frýda, J. 2025. The replacement Global Stratotype Section and Point (GSSP) of the Telychian Stage of the Llandovery Series, Silurian System, at El Pintado (Spain). *Episodes* **48**, 199–211. https://doi.org/10.18814/epiiugs/2025/025009.
MacLaren, C. 1838. *A sketch of the geology of Fife and the Lothians including detailed descriptions of Arthur's Seat and Pentland Hills*. Edinburgh: Adam & Charles Black.
Mitchell, G. H., Tulloch, W. & Wilson, R. B. 1962. *The geology of the neighbourhood of Edinburgh*, 1–159. Scotland: Memoirs of the Geological Survey of Scotland.
Peach, B. N. & Horne, J. 1899. *The Silurian rocks of Britain* 1, 1–749. Scotland: Memoirs of the Geological Society of the United Kingdom.
Penn-Clarke, C. R. & Harper, D. A. T. 2021. Early-Middle Devonian brachiopod bioregionalization at high latitudes: a case study from southwestern Gondwana. *GSA Bulletin* **133**, 819–36. https://doi.org/10.1130/b35670.1.
Penn-Clarke, C. R. & Harper, D. A. T. 2023. The rise and fall of the Malvinoxhosan (Malvinokaffric) bioregion in South Africa: evidence for Early-Middle Devonian biocrises at the South Pole. *Earth-Science Reviews* **246**, 104595.
Robertson, G. 1985. Palaeoenvironmental interpretation of the Silurian rocks of the Pentland Hills. Unpublished PhD thesis, University of Edinburgh.
Robertson, G. 1989. A palaeoenvironmental interpretation of the Silurian rocks in the Pentland Hills, near Edinburgh, Scotland. Transactions of the Royal Society of Edinburgh: Earth Sciences **80**, 127–41. https://doi.org/10.1017/s0263593300014425.
Robertson, G. 1999. Upper Llandovery fossil associations in the Pentland Hills, Scotland. In Boucot, A. J. & Lawson, J. D. (eds) *Paleocommunities – a case study from the Silurian and Lower Devonian*, 408–18. Cambridge: Cambridge University Press.
Rong, J. Y. & Bassett, M. G. 2002. Palaeobiogeography. *National Museum of Wales Geological Series* **21**, 163–65.
Temple, J. T. 1988. Biostratigraphical correlation and the stages of the Llandovery. *Journal of the Geological Society* **145**, 875–79. https://doi.org/10.1144/gsjgs.145.5.0875.
Tipper, J. C. 1974. The marine Silurian of the North Esk Inlier, Midlothian, Scotland. Unpublished PhD thesis, University of Edinburgh.
Tipper, J. C. 1975. Lower Silurian animal communities – three case histories. *Lethaia* **8**, 287–301. https://doi.org/10.1111/j.1502-3931.1975.tb00933.x.
Tipper, J. C. 1976. The stratigraphy of the North Esk Inlier, Midlothian. *Scottish Journal of Geology* **12**, 15–22. https://doi.org/10.1144/sjg12010015.
Waterston, C. 1986. Archie Lamont MA, BSc, PhD. *Year Book of the Royal Society of Edinburgh 1986 (Session 1984-85)*, 190–91.
Watkins, R. & Boucot, A. J. 1978. Temporal pattern of diversity among some Siluro-Devonian brachiopods. *Evolutionary Biology* **11**, 636–55.
Watkins, R., Coorough, P. J. & Mayer, P. S. 2000. The Silurian *Dicoelosia* communities: temporal stability within an ecologic evolutionary unit. *Palaeogeography, Palaeoclimatology, Palaeoecology* **162**, 22–237. https://doi.org/10.1016/S0031-0182(00)00129-2.
Williams, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery District. *Quarterly Journal of the Geological Society* **107**, 85–136. https://doi.org/10.1144/Gsl. Jgs.1951.107.01-04.05.
Williams, D. M. & Harper, D. A. T. 1988. A basin model for the Silurian of the Midland Valley of Scotland and Ireland. *Journal of the Geological Society, London* **145**, 741–48. https://doi.org/10.1144/gsjgs.145.5.0741.
Williams, D. M. & Harper, D. A. T. 1991. End-Silurian modifications of Ordovician terranes in western Ireland. *Journal of the Geological Society, London* **148**, 165–71. https://doi.org/10.1144/gsjgs.148.1.0165.
Ziegler, A. M., Cocks, L. R. M. & Bambach, R. K. 1968. The composition and structure of Lower Silurian marine communities. *Lethaia* **1**, 1–27. https://doi.org/10.1111/j.1502-3931.1968.tb01724.x.

MS received 31 August 2025. Revised 01 November 2025. Accepted for publication 04 November 2025