

# DEVIL'S HOLE

OS Grid Reference: SO672929

## Highlights

The late Downton vertebrate faunas at this Shropshire site represent some of the earliest known freshwater vertebrates from Britain, and are locally succeeded by pteraspids of the Dittonian stage. The site's importance is in showing the strength of the late Downtonian–early Dittonian vertebrate communities.

## Introduction

Devil's Hole is a stream section at the northern edge of the Anglo-Welsh Old Red Sandstone outcrop, where it cuts the '*Psammosteus*' Limestone escarpment, and hence, the Downtonian–Dittonian junction. The GCR Unit undertook a series of excavations here between 1980 and 1982, enabling a detailed sedimentological and palaeontological analysis to be made of the section by M.A. Rowlands and P. Tarrant.

The geology of the site has been referred to by Ball and Dineley (1961), Allen and Tarlo (1963), Banks (1980), Richardson *et al.* (1981), Halstead (1985), Allen (1985) and Blicek (1985), and the fish faunas by Wills (1948, 1950), White (1950b), Denison (1956), Robertson (1957), Dineley (1964), Turner (1973), Blicek (1981, 1984, 1985) and Tarrant (1991). The section was originally collected by Ball and Dineley (1961) and subsequently excavated by P. Tarrant and M.A. Rowlands (Tarrant, 1991).

## Description

The sequence consists of 50 m of mudstone, sandstone and intraformational conglomerates containing fossils and calcretes (Figure 4.8), dated as Lower Old Red Sandstone (Ball and Dineley, 1961). The base of the main '*Psammosteus*' Limestone separates the Downton Group from the Ditton Group. Minor calcretes also occur for some distance below this level.

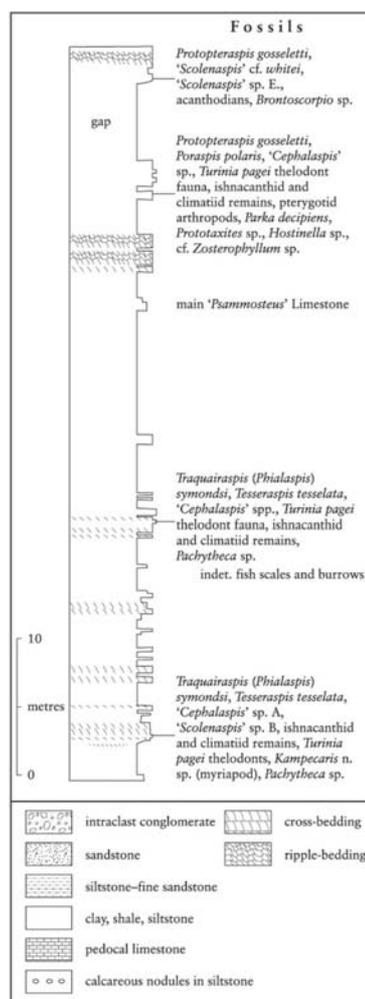


Figure 4.8: Stratigraphical section in The Devil's Hole (after M.A. Rowlands, MS). The base of the Main 'Psammosteus' Limestone is mapped as the base of the Ditton Group, which has predominantly pteraspidid faunas.

The four main fossil-bearing beds in Devil's Hole are called Lye Brook 1, Lye Brook 3 and Lye Brook 4, abbreviated to LB1, LB3 and LB4 (Ball and Dineley, 1961) and the 'Cephalaspis Sandstone', a unit named by W.W. King (1934), who believed it to be a laterally continuous sandstone recognizable throughout the Welsh Borders. It is not present at the Devil's Hole Stream section, but outcrops on Meadowley Bank to the north. All four beds can be recognized at several other localities locally.

### Fauna

AGNATHA Heterostraci: Eriptychiformes: Tesserapididae

*Tesseraspis tessellata* Wills, 1935

Heterostraci: Phialaspidiformes: Poraspididae

*Poraspis polaris* Kiaer, 1930

Heterostraci: Phialaspidiformes: Traquairaspididae

*Traquairaspis symondsii* (Lankester, 1868)

Heterostraci: Pteraspidiformes: Pteraspidae

*Protopteraspis gosseletti* (Leriche, 1906)

( = *Pteraspis leathensis* White, 1948)

---

Osteostraci: Scolenaspidiformes: Scolenaspidae

'*Scolenaspis*' n. sp.

*Pattenaspis whitei* (Stensiö, 1932)

Osteostraci *incertae sedis*

'*Cephalaspis*' sp.

Thelodonti: Thelodontida: Turiniidae

'*Turinia pagei* fauna' (see Table 4.1)

GNATHOSTOMATA

Acanthodii *incertae sedis*

'Ischnacanthid and climatiid spines'

The largest accumulations of fossils, particularly the fish plates, occur near the base of the intraformational conglomerates, together with clasts of reworked mudstone and calcrete. The remains are disarticulated and have been water-sorted. Taken as a whole, acanthodian spines form the major percentage of fossils, followed by heterostracans. The material in LB4 is poorly preserved and often completely demineralized, even though some specimens are associated with well-preserved fragments of *Protopteraspis*. It is possible, therefore, that this material is derived.

There seem to be two quite distinct assemblages, one in the LB1 Bed and LB3 Bed, the other in the LB4 Bed and *Cephalaspis* Sandstone. These assemblages are listed separately below.

LB 1 *Traquairaspis symondsi* (Lankester, 1868), *Tesseraspis tessellata* Wills, 1936, '*Scolenaspis*' n. sp., '*Cephalaspis*' n. sp., *Turinia pagei* thelodont fauna, and ischnacanthid and climatiid acanthodian remains.

LB 3 *Traquairaspis symondsi* (Lankester, 1868), *Tesseraspis tessellata* Wills, 1936, '*Cephalaspis*' spp., *Turinia pagei* thelodont fauna, and ischnacanthid and climatiid acanthodian remains.

LB 4 *Protopteraspis gosseleti* (Leriche, 1906) (syn. *Pteraspis (Simopteraspis) leathensis* White, 1935), *Poraspis polaris* Kiaer, 1930, '*Cephalaspis*' sp., *Turinia pagei* thelodont fauna, and ischnacanthid and climatiid acanthodian remains.

*Cephalaspis* Sandstone *Protopteraspis gosseleti* (Leriche, 1906), cf. *Pattenaspis whitei* (Stensiö, 1932), '*Scolenaspis*' n. sp. (Rowlands MS) and acanthodian scales and spines. Collections are housed in the NHM and SMLU.

The commonest heterostracan occurring below the '*Psammosteus*' Limestone at Devil's Hole is *Traquairaspis symondsi* Lankester (Figure 4.9). Most publications dealing with this species have placed it in the genus *Traquairaspis* (e.g. Ball and Dineley, 1961; White, 1961), but new material from Devil's Hole suggested to Tarrant (1991) that it is sufficiently different from the type species (*T. campbelli* (Traquair)) to merit its own genus, *Phialaspis*. The only record of *T. symondsi* from outside the Welsh Borders is from the Knoydart Formation of Canada (Dineley, 1964) which should probably be referred to as *T. cf. symondsi*.

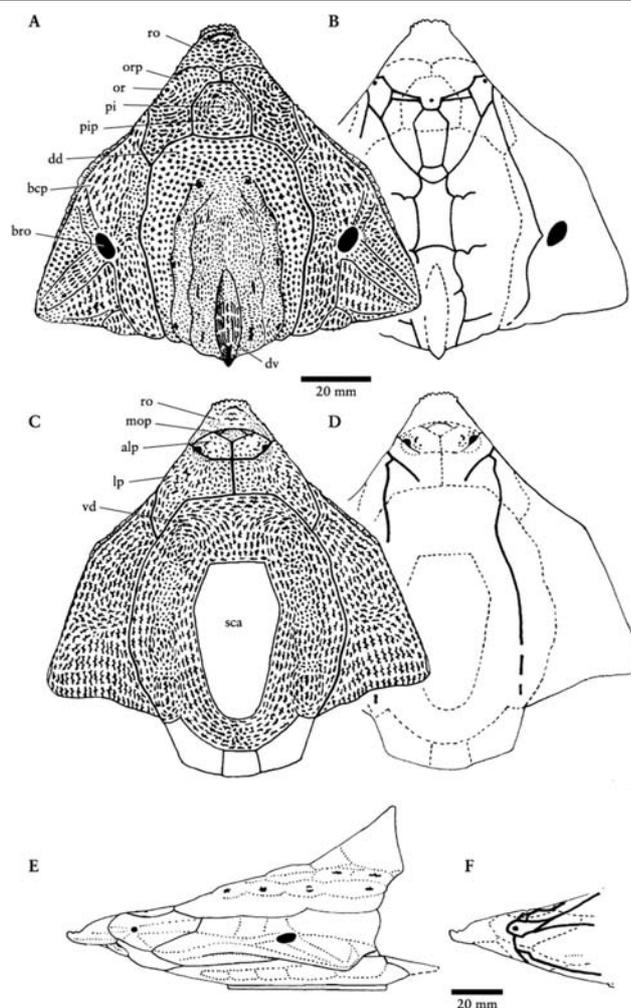


Figure 4.9: *Traquairaspis (Phialaspis) symondsii* (Lankester), restorations of the carapace on the basis of material from Devil's Hole by P.R. Tarrant (1991). (A) carapace in dorsal view, showing ornamentation of tubercles and branchial openings set near the middle of the dorsal surface of the branchial plates; (B) the sensory canal pattern of the dorsal carapace; (C) the carapace in ventral view with characteristic smooth central area; (D) pattern of sensory canals on the ventral side of the carapace; (E) and (F) lateral view of the carapace with sensory canals shown: alp, anterior lateral plate; bcp, branchio-cornual plate; bro, branchial opening; dd, dorsal disc; vd, ventral disc; lp, lateral plate; mop, median oral plate; or, orbit; orp, orbital plate; pi, pineal opening; pip, pineal plate; ro, rostrum; sca, smooth central area; dv, dorsal vane (or spine).

Isolated tesseræ of *Tesseraspis tessellata* are commonly found associated with *T. symondsii* in the Downtonian beds, where there appears to be a range of sizes of individuals at different stages of exoskeletal development. There are no records of *T. tessellata* from outside the Anglo-Welsh Old Red Sandstone.

*Protopteraspis gosseleti* is a common vertebrate macrofossil above the 'Psammosteus' Limestone in many Welsh Border localities (Figure 4.10). It is found in the upper Downton Group of Little Oxenbold (Ball *et al.*, 1961) but only becomes widespread in the Anglo-Welsh region above the 'Psammosteus' Limestone (White, 1950b; Ball and Dineley, 1961). A range of morphological types occurs in the Cleve Hills area, including those used by Blicek (1981) to characterize *Protopteraspis leathensis* White, *P. aquilonia* Blicek and *P. gosseleti* Leriche. The plentiful material collected recently from the Devil's Hole section has allowed detailed reconstructions of the species (Tarrant, 1991; Blicek and Tarrant, pers. comm.). *Poraspis* sp. was recorded from LB4 by Ball and Dineley (1961).

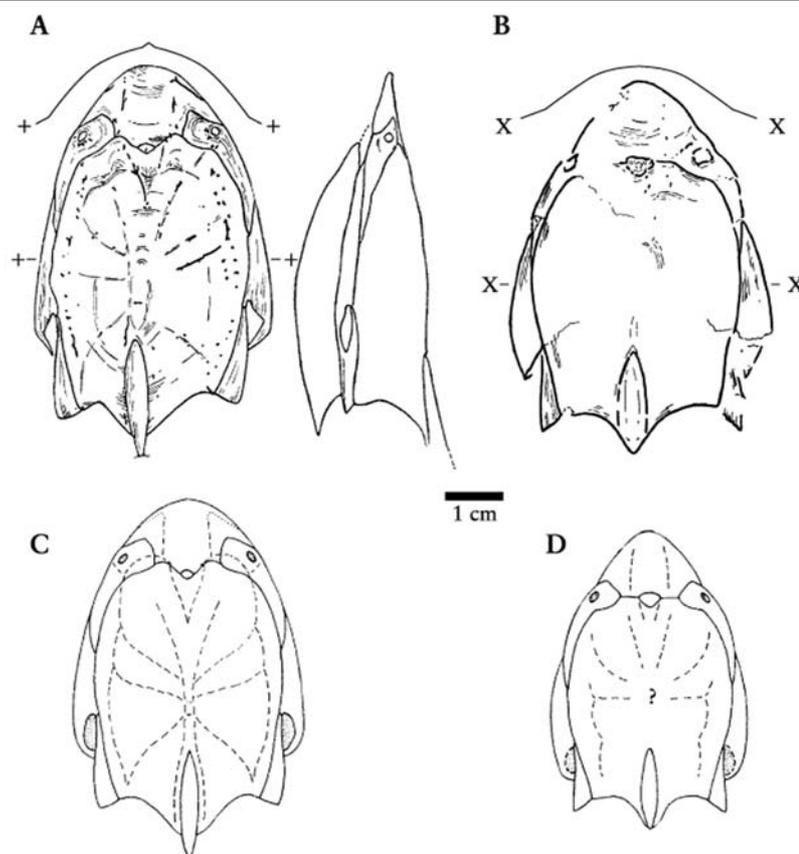


Figure 4.10: *Protopteraspis gosseleti* Leriche. White's (1950b) *Pteraspis* (*Simopteraspis*) *leathensis* (A)–(C), is now regarded as a junior synonym of this species (D). The lateral line canals are shown by broken lines in C and D. (A)–(B) from White (1950b); (C), (D) from Blicek (1985).

Five species of cornuate osteostracans have been discovered at Devils Hole, and a further three or four species are probably represented by indeterminate fragmentary material. Osteostracans occur in each of the main fossil beds, but are less common than acanthodians or heterostracans and usually occur as fragmentary pieces of head shield or indeterminate scales. Each fossiliferous horizon contains different osteostracan species, which is typical of their occurrence throughout the Welsh Borders.

Two species were found in the collections from LB1. Several head shields and fragments were of '*Scolenaspis*' n. sp., a small scolenaspidiform with a dorsal spine. One head shield from LB1 is very different from other cornuates from the Welsh Borders, and has features of both scolenaspidiforms and thyestidians. The two species recovered from LB1 represent two of the earliest known cornuate cephalaspids in the Welsh Borders: most osteostracans from the Downtonian are non-cornuate, and cornuate forms become common only in the Dittonian.

Cornuate osteostracan material dominates in the collections from LB3, consisting of fragments, including many portions of robust tuberculated cornua, and pieces of thick tuberculated ventral rim. LB4 is a highly fossiliferous bed, containing many discs of *Protopteraspis* and acanthodian spines, but species diversity is lower than in LB1 or LB3. Osteostracan material is rare, and identifiable material probably represents only one species of a medium-sized cornuate.

Several good headshields of rare osteostracans have been recovered from the *Cephalaspis* Sandstone. A single specimen of a headshield of cf. *Pattenaspis whitei* Stensiö was found in the basal intraclast layers of sandstone near the head of Devil's Hole section, and several other specimens of headshield of a second kind were recovered from loose blocks of the overlying sandstones from Meadowley Bank. The second species, '*Scolenaspis*' n. sp., is a small cephalaspid with eyes well forward, and has similarities with *Eucephalaspis agassizi*. As in other instances throughout the Anglo-Welsh Lower Devonian, the osteostracans of this assemblage are rather uniform in size and composition, perhaps indicating that the

---

osteostracans preferred habitat was separate from that of other fishes present.

Turner (1973) recorded denticles of *Turinia pagei* from the LB1 and LB3 Beds, and similar material has now been discovered in the LB4 Bed. Acanthodian specimens from Devil's Hole consist mainly of isolated fin spines representing a variety of species; some individuals reach 7 cm in length, indicating relatively large acanthodians.

## Interpretation

The sequence at Devil's Hole represents interdistributary bay and ephemeral channel deposits formed in an alluvial plain. Below the '*Psammosteus*' Limestone, the Downton sequence is dominated by overbank deposits with mud-cracks and calcretes. The overlying Ditton Group beds show the return of abundant fluvial sandstones, perhaps marking a wetter climate, with extensive river systems reappearing across the Anglo-Welsh floodplain. The fluvial channels were colonized by assemblages of fishes different from those that had been present during Downton Group time.

The excavations at Devil's Hole reinforced the earlier hypothesis (Ball and Dineley, 1961; Allen and Tarlo, 1963; Halstead, 1985) that the upper Downton Group and lower Ditton Group in the central Welsh Borders are entirely non-marine, although Allen (1985) and Barclay *et al.* (1994) have shown that the upper Downton Group was partly intertidal to the south. Blicek (1985) interpreted the Anglo-Welsh Old Red Sandstone faunas as occurring in marine intercalations in otherwise non-marine sequences, because similar faunas occur elsewhere associated with marine strata. However, neither the sedimentology nor the invertebrate palaeontology of the Devil's Hole sequence shows any sign of marine influence, since the deposits represent relatively small-scale high-energy regimes, with calcretes and desiccation-crack beds immediately below.

Most of the Downton Group fishes were seemingly non-marine in Britain. As is typical of the upper part of the Downton Group throughout the Welsh Borders, the faunas below the '*Psammosteus*' Limestone at Devil's Hole are dominated by *Traquairaspis symondsi*, *Tesseraspis tessellata* and acanthodians, which occur only rarely in the Ditton Group. *Protopteraspis gosseleti* is the most common vertebrate fossil found immediately above the '*Psammosteus*' Limestone in the Anglo-Welsh basin, which suggests the sudden replacement of the traquairaspid fauna at this level by new forms. The few Ditton Group species that occur below the '*Psammosteus*' Limestone are mostly found in marine or brackish sequences. Cornuate osteostracans are well known in the Welsh Borders, but occur mainly in the Ditton Group, coinciding with the development of fluvial deposits. This fauna is found in the LB4 Bed and, as elsewhere in the Anglo-Welsh region, is represented only by adults of a simple ontogenetic stage. The '*Psammosteus*' Limestone is interpreted as representing a period of aridity lasting for up to 10 000 years (Allen, 1985), which would have had a drastic effect on any faunas restricted to freshwater conditions. The only fishes to occur locally both above and below the '*Psammosteus*' Limestone are thelodonts, a group known to have been adapted to brackish and freshwater conditions (Turner, 1973), and would thus be able to escape from hostile arid climates.

Juvenile and adult forms of heterostracans occur together, which suggests that these fishes spent their entire life-history in freshwater environments. The extinction of some species at the '*Psammosteus*' Limestone event suggests that they were unable to adapt to a changed habitat. On the other hand, the Ditton Group species appear to have been adapted to both marine and freshwater environments since they occur elsewhere in marine strata. Such adaptability to both marine and fresh water habitats at different stages in their life cycle is seen in modern fishes (Wills, 1950).

Reconstructions of *Protopteraspis gosseleti* and *Traquairaspis symondsi* (Tarrant, 1991) show them to have been opportunistic perhaps microphagous feeders that rooted in the substrate, consuming a variety of food. However, *P. gosseleti* has a more evenly vaulted cephalothoracic shape, and the less frequent occurrence of ventral abrasion suggests a more nectonic lifestyle (Blicek and Tarrant, pers. comm.). Only plates from adult animals occur at Devil's Hole, suggesting that its juvenile development occurred elsewhere. The migration of juvenile forms from marine to freshwater has been used to explain the succession of distinct species that is

found in the Welsh Borders Old Red Sandstone, and also their distribution outside this province (Wills, 1950; Denison, 1956; Robertson, 1957; White, 1958a; Allen and Tarlo, 1963). The matter is, however, not resolved beyond doubt.

The exact chronostratigraphical position of these sediments is uncertain. Holland and Richardson (*in* Martinsson, 1977) have argued that, in the Welsh Borders, the Silurian–Devonian boundary should be provisionally placed at the '*Psammosteus*' Limestone. However, a *Turinia pagei* thelodont fauna in LB1, the lowest fossil bed, might indicate that this section is entirely within the Lower Devonian (Karatajute-Talimaa, 1978), and that the boundary between the Píidolí Series and the Lochkovian Series must lie within the Downton Group in the Welsh Borders. A spore assemblage from the *Proto-pteraspis* Bed, just above the '*Psammosteus*' Limestone, indicates an early Lochkovian age (Banks, 1980; Richardson *et al.*, 1981). Current opinion, which places the boundary at the base of the lowest bed with the protopteraspid *P.*

*gosseleti*, needs to be substantiated by a detailed account of a stratotype section for the base of the Devonian in this facies. The Devil's Hole section appears to be a strong candidate.

### Comparison with other localities

The site LB1 has a relatively similar relationship to the '*Psammosteus*' Limestone to those of other *Traquairaspis* localities in the Clee Hills area. Little Oxenbold and Earnstrey Brook localities (Ball and Dineley, 1961) bear a similar fauna. Other localities around the Clee Hills and at approximately the same level below the '*Psammosteus*' Limestone lack the distinctive *Phialaspis symondsi* element (e.g. Targrove Dingle 6; *in* Ball and Dineley, 1961). White (1946) and Tarrant list other sites of comparable position and fauna throughout the Welsh Borderland and Wales.

Blieck *et al.* (1995) have issued a revised Upper Silurian–Lower Devonian ichthyostratigraphy of northern France and Belgium, in which they list localities to be correlated to the '*Traquairaspis* Zone'. Dineley (1964) found *Traquairaspis* cf. *symondsi* in a Canadian red-bed sequence that lacked any horizon to be correlated with the '*Psammosteus*' Limestone, but the zone was subsequently identified in Spitsbergen (Blieck, 1984) and Arctic Canada (Dineley, 1990).

The recent finds in the Devil's Hole include enigmatic osteostracan specimens, and plentiful material of *Traquairaspis symondsi*, *Proto-pteraspis leathensis* (= *P. gosseleti*) and *P. aquilonia*, which allow detailed morphological reconstructions (Blieck and Tarrant, pers. comm.). Since the varied forms of *Proto-pteraspis gosseleti* occur here in close association, together with a range of intermediates, it may be shown that the three previously described species are conspecific, and that this also occurs in the Psammites de Lievin of France and the Fraenkelryggen 'Division' (Red Bay Group) of Spitsbergen (Blieck, 1984). In Nova Scotia *P. whitei* occupies a similar stratigraphical position and is very like *P. gosseleti* (Denison, 1955).

## Conclusions

The conservation value of this site arises from the importance of its late Downtonian to early Dittonian fish faunas. Furthermore, from the viewpoint of interregional correlation this important site has much potential for new discoveries, being an accessible and extensive stream section and adjacent scarp face. Also, the site is an unbroken section across the important Downtonian–Dittonian boundary.

## Reference list

- Allen, J.R.L. (1985) Marine to fresh water: the sedimentology of the interrupted environmental transition (Ludlow–Siegenian) in the Anglo-Welsh region. *Philosophical Transactions of the Royal Society, London*, **B309**, 85–104.
- Allen, J.R.L. and Tarlo, L.B.H. (1963) The Downtonian and Dittonian facies of the Welsh Borderland. *Geological Magazine*, **100**, 129–55.
- Ball, H.W. and Dineley, D.L. (1961) The Old Red Sandstone of Brown Clee Hill and the adjacent area. I: Stratigraphy. *Bulletin of the British Museum (Natural History), Geology*, **5**, 178–242.

- Banks, H. (1980) Floral assemblages in the Siluro-Devonian. In *Biostratigraphy of Fossil Plants* (eds D.L. Dilcher and T.N. Taylor), Dowden, Hutchinson and Ross, Stroudsburg, pp. 1–24.
- Barclay, W.L., Rathbone, P.A., White, D.E. and Richardson, J.B. (1994) Brackish water faunas from the St. Maughans Formation: the Old Red Sandstone section at Ammons Hill, Hereford and Worcester, UK, re-examined. *Geological Journal*, **29**, 369–79.
- Blieck, A. (1981) Le genre *Protopteraspis* Leriche (Vertébrés, Hétérostracés) du Dévonien inférieur nord Atlantique. *Palaeontographica, Abteilung A*, **173**, 141–59.
- Blieck, A. (1984) Les Hétérostracés Pteraspidi-formes, Agnathans du Silurien Dévonien du Continent nord-atlantique et des blocs avoisines: revision systematique, phylogenie, biostratigraphie, biogéographie. *Cahiers de Paléontologie*, CNRS, Paris, 200 pp.
- Blieck, A. (1985) Paléoenvironnements des Hétérostracés Vertébrés agnathes Ordoviciens à Dévoniens. *Bulletin du Muséum national d'Histoire naturelle, Paris: Science de la Terre* **7**, 143–155.
- Blieck, A., Goujet, D. Janvier, P. and Meilliez, F. (1995) Revised Upper Silurian–Lower Devonian ichthyostratigraphy of northern France and southern Belgium (Artois, Ardenne). *Bulletin du Muséum national d'Histoire naturelle, Paris* **17**, (4) 447–59.
- Denison, R.H. (1955) Early Devonian vertebrates from the Knoydart Formation of Nova Scotia. *Fieldiana: Zoology*, **37**, 449–64.
- Denison, R.H. (1956) A review of the habitat of the earliest vertebrates. *Fieldiana: Geology*, **11**, 359–457.
- Dineley, D.L. (1964) New specimens of *Traquairaspis* from Canada. *Palaeontology*, **7**, 210–19.
- Dineley, D.L. (1990) Palaeozoic fishing – The Franklinian Grounds. In *Canada's Missing Dimension: Science and History in the Canadian Arctic Islands* (ed. C.R. Harington), Canadian Museum of Nature, Ottawa, **1**, pp. 55–80.
- Halstead, L.B. (1985) The vertebrate invasion of fresh water. *Philosophical Transactions of the Royal Society*, **B309**, 243–58.
- Karatajute-Talimaa, V.N. (1978) *Telodonty Silura i Devona SSSR: Spicebergena (Silurian–Devonian Thelodonts of the USSR and Spitsbergen)*. Mosklas, Vilnius. 334 pp. [In Russian.]
- King, W.W. (1934) The Downtonian and Dittonian strata of Great Britain and North-Western Europe. *Quarterly Journal of the Geological Society of London*, **90**, 526–70.
- Martinsson, A. (1977) Baltoscandia. In *The Silurian–Devonian Boundary* (ed. A. Martins-son), *International Union of Geological Sciences, Series A*, Stuttgart, **5**, 45–51.
- Richardson, J.B., Rashul, S.M. and Al-Ameri, T. (1981) Acritarchs, miospores and correlation of the Ludlovian–Downtonian and Silurian–Devonian boundaries. *Revue of Palaeo-botany and Palynology*, **34**, 209–24.
- Robertson, J.D. (1957) The habitat of the early vertebrates. *Biological Reviews, Cambridge*, **32**, 256–87.
- Stensiö, E.A. (1932) *The Cephalaspids of Great Britain*. British Museum (Natural History), London, 220 pp.
- Tarrant, P.R. (1991) The ostracoderm *Phialaspis* from the Lower Devonian of the Welsh Borderland and South Wales. *Palaeontology*, **34**, 399–438.
- Turner, S. (1973) Siluro-Devonian thelodonts from the Welsh Borderland. *Quarterly Journal of the Geological Society, London*, **129**, 557–84.
- White, E.I. (1935) The Ostracoderm *Pteraspis* Kner and the relationships of the Agnathous Vertebrates. *Philosophical Transactions of the Royal Society, London* **B225**, 381–457.
- White, E.I. (1946) The genus *Phialaspis* and the 'Psammosteus Limestones'. *Quarterly Journal of the Geological Society, London*, **101**, 207–42.
- White, E.I. (1950b) *Pteraspis leathensis* White, a Dittonian zone-fossil. *Bulletin of the British Museum (Natural History) Geology*, **3**, 69–89.
- White, E.I. (1958a) Original environment of the craniates. In *Studies on Fossil Vertebrates* (ed. T.S. Westoll), University of London, Athlone Press, pp. 212–34.
- White, E.I. (1961) The Old Red Sandstone of Brown Clee Hill and the adjacent area. II. *Palaeontology. Bulletin of the British Museum (Natural History) Geology*, **5**, 245–310.
- Wills, L.J. (1935) Rare and new ostracoderm fishes from the Downtonian of Shropshire. *Transactions of the Royal Society of Edinburgh*, **58**, 427–47.
- Wills, L.J. (1948) *The Palaeogeography of the Midlands*, 1st edn, University Press of Liverpool, 147 pp.
- Wills, L.J. (1950) *The Palaeogeography of the Midlands*, 2nd edn, University Press of Liverpool, 143 pp.