

LUDFORD LANE AND LUDFORD CORNER

OS Grid Reference: SO51167413

Highlights

The Ludlow Bone Bed and the overlying Downton Castle Sandstones at Ludford Corner in Shropshire are internationally famous for their rich fauna of up to 14 species of Late Silurian fishes. This is the type locality for five of these species, and it remains an excellent source of acanthodian spines and thelodont denticles.

Introduction

The uppermost part of the Upper Whitcliffe Beds (Ludlow Series) and the lowermost part of the Downton Castle Formation (Píldolí Series) are exposed along Ludford Lane (Whitcliffe Road) and its junction with the main road (A49) into Ludlow (Ludford Corner; Figure 3.9). The section includes two important fish-bearing horizons, the Ludlow Bone Bed (LBB) and the *Platyschisma* Shales. Fishes also occur sporadically and extremely rarely in the overlying Downton Castle Sandstone Formation.

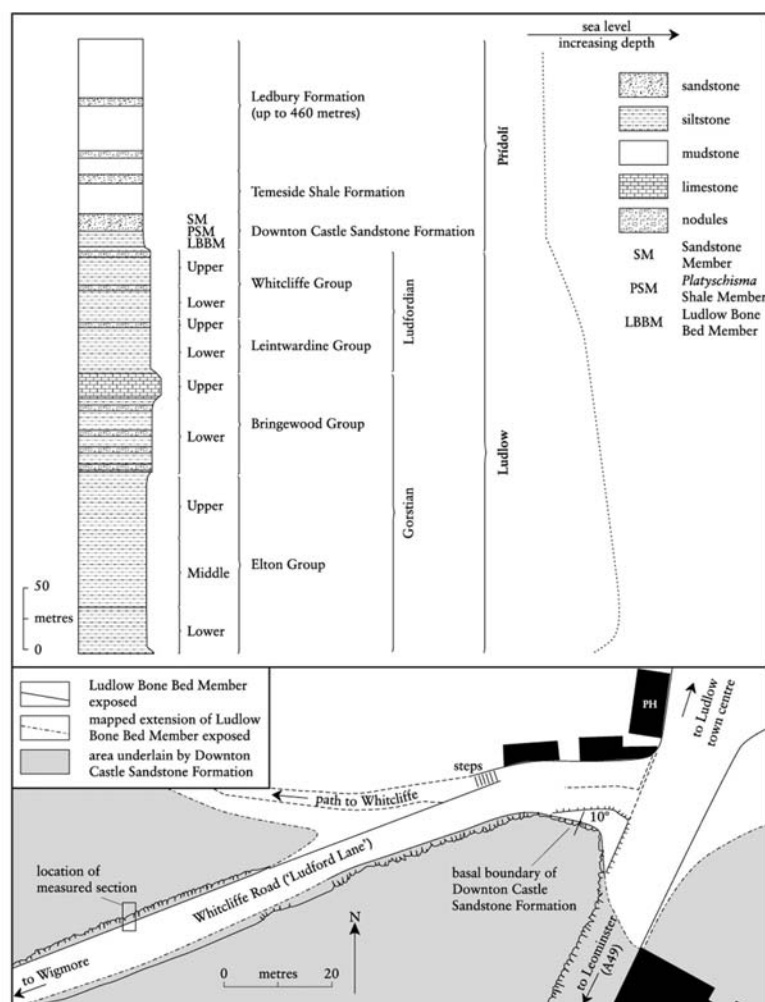


Figure 3.9: Sketch map and stratigraphical section of the site at Ludford Lane, Ludlow (after Bassett et al., 1982).

There is a transition from the marine brachiopod-dominated faunal assemblage of the Whitcliffe Beds to the restricted faunas of the overlying Downton Castle Sandstone Formation. The latter faunas are dominated by bivalves and ostracods, and contain vertebrates. The base of the Ludlow Bone Bed is taken as the boundary between the Ludlow and overlying Píldolí Series

(Siveter *et al.*, 1989), a boundary defined chronostratigraphically in marine sediments in the Prague Basin, Czech Republic.

The Ludlow Bone Bed was discovered by Dr J. Lloyd and the Reverend T.T. Lewis in 1835. Murchison (1839) recorded the Ludford Lane section, and traced the bone bed, which he described as having the appearance of gingerbread, along the cliffs opposite Ludlow; he also found bone beds near Richards Castle. The fishes discovered then were clearly some of the oldest then known. Acanthodian spines and ostracoderms from here were described by Agassiz (1839).

The Ludlow Bone Bed was long thought to mark the first appearance of fossil fishes, heralding the 'age of the vertebrates' (e.g. Symonds, 1872; Lapworth, 1879; Stamp, 1923), and was chosen as the base of the Devonian (White, 1950), or latterly as the base of the Downton Series (Holland *et al.*, 1963; Bassett *et al.*, 1982).

Since Murchison (1839, 1853, 1867), the geology of the site has been described many times, reflecting the importance of the succession here; see White (1950a), with more recent contributions by Holland *et al.* (1963), Turner (1973), Antia and Whitaker (1979), Antia (1979a, 1979b, 1980), Bassett *et al.* (1982), Siveter *et al.* (1989) and Smith and Ainsworth (1989). The vertebrates have been studied by Agassiz (1839), M'Coy (1853), Harley (1861), Marston (1882b), Lankester (1870), Woodward (1891a, 1904b), Woodward and Dixon (1904), Denison (1956, 1974, 1979), Gross (1967), Turner (1973, 1976) and Forey (1987).

Description

The sequence of major units in the Upper Silurian of the Ludlow area is as shown in Figure 3.12 (after Siveter *et al.*, 1989; the Ludford Lane section is shown in Figure 3.9).

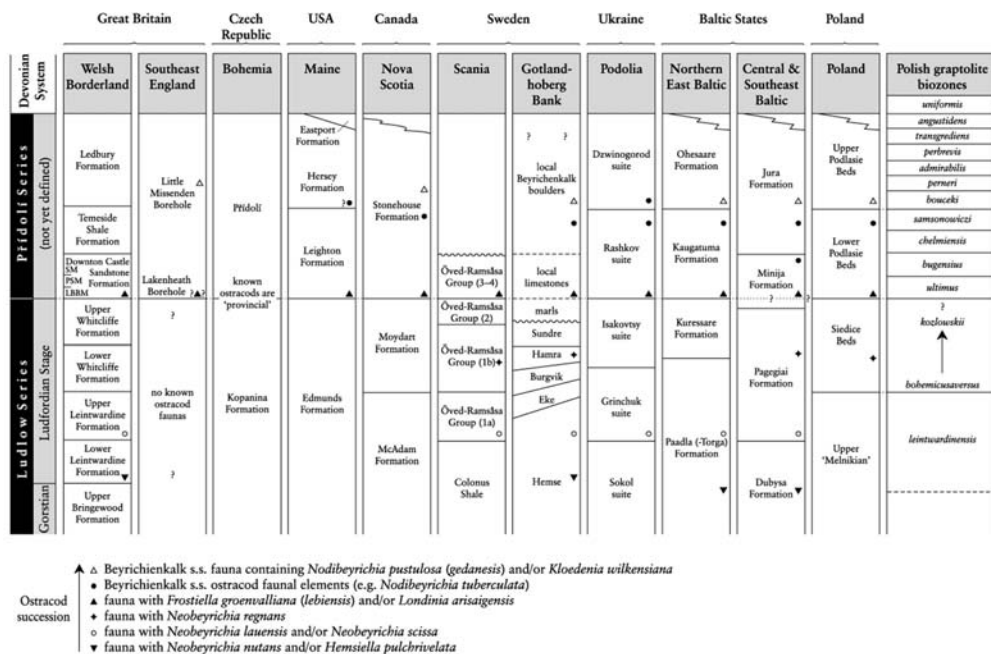


Figure 3.12: Ludlow–Přídolí correlation for Europe and North America. Vertical columns not drawn to scale (after Siveter *et al.*, 1989).

	Thickness (m)
Píldolí Series (= Downtonian in part)	
Ledbury Formation	< 460
Temeside Shales Formation	< 37
Downton Castle Sandstone Formation	< 173
Sandstone Member (SM)	
<i>Platyschisma</i> Shale Member (PSM)	
Ludlow Bone Bed Member (LBBM)	
Ludlow Series	
Ludfordian Stage	
Upper Whitcliffe Formation	30
Lower Whitcliffe Formation	24
Upper Leintwardine Formation	1.5–5.5
Lower Leintwardine Formation	30
Gorstian Stage	
Upper Bringewood Formation	12
Lower Bringewood Formation	41
Upper Elton Formation	46
Middle Elton Formation	46
Lower Elton Formation	20

The Ludlow Bone Bed Member lies at the base of the Downton Castle Sandstone Formation. At Ludford Lane all that can be seen of it is a deep, horizontal notch created by fossil collectors. It is a thin bed, about 0.2 m thick, of ripple-laminated lenticular-bedded siltstones with the Ludlow Bone Bed itself at the base, another bone bed 90 mm above the base, and a further three bone lenticles at the top of the member (Bassett *et al.*, 1982). Murchison (1839) reported a single thick bone-bed at Ludford Lane, but Antia (1979a, 1979b, 1980) argued that subsequent erosion has revealed that there are several thin, laterally impersistent bone-bed lenses. The widening of the Ludford road junction in the 1920s removed a large area of bone bed (Watts, 1925, pp. 395–6).

The bone beds are packed with thelodont scales, acanthodian scales, spines, teeth and bone fragments, plus phosphatic nodules and fragmentary brachiopods and ostracods in a sandy matrix. Several conodont taxa have been recovered from the Ludlow Bone Bed Member (Aldridge and Smith, 1985; Blondel, 1992; Miller, 1995). Samples of the bone bed have recently yielded terrestrial arthropod remains (two centipedes and a trigontarbid arachnid), as well as abundant fragments of eurypterids, aquatic scorpions, kampecarid myriapods and land plants. Rarer components include ostracods, scolecodonts, bivalves, and lingulid brachiopods. The land plants include *Cooksonia* and sterile rhyniophytoid axes. M.A. Rowlands recorded fossils recovered from an excavation at Ludford Lane Corner in September, 1988, funded by the Nature Conservancy Council. This dig involved the removal of several tonnes of material. The list includes molluscs, arthropods, annelids and plants and at least nine kinds of vertebrates. The presence of *Poraspis* sp. is the only record of this genus at this level. The other taxa include at least five acanthodians and two thelodonts.

The basal 2 m of the Downton Sandstone Formation above the Ludlow Bone Bed Member, the *Platyschisma* Shale Member (PSM; Bassett, *et al.*, 1982), consists of mudstones and shales with subordinate bands and lenses of siltstones. The lower is a sequence of thin, sharp-based fining-upwards, unfossiliferous bioturbated siltstones and subsidiary mudstones. The siltstone lenses have erosional bases with shell lag deposits, which fine upwards into rippled, or cross-bedded units (Bassett *et al.*, 1982; Smith and Ainsworth, 1989). The upper half of the *Platyschisma* Shale Member is fairly fossiliferous, with several ostracod bands and impersistent bone sand beds including the *Platyschisma* band. This contains the gastropod '*Platyschisma*' *helicites* within a bone sand from which Marston (1882b) described collecting several shields of 'either *Pteraspis* or *Cephalaspis*' (possibly *Sclerodus*?). Hummocky cross-stratification extends

from the middle of the PSM into the lower part of the overlying sandstones.

The Sandstone Member (SM), forming the bulk of the Downton Castle Sandstone Formation (Bassett *et al.*, 1982) consists of thick fine-grained yellow sandstones that show cross-bedding and channelling, typical of aeolian dune formation. The sandstones alternate with thinner mudstones (Bassett *et al.*, 1982). These beds are poorly fossiliferous, but have over the years yielded several partial specimens of fish and large portions of the arthropod *Pterygotus*, together with rare plant fossils and lingulid brachiopods. The uppermost 1 m of the section at Ludford, which is above the hummocky cross-stratification, consists of low-angle cross-stratified fine sandstone (Smith and Ainsworth, 1989).

Fauna

Although the vertebrate remains from the Ludlow Bone Bed Member are fragmentary, numerous taxa have come to light (Figure 3.10).

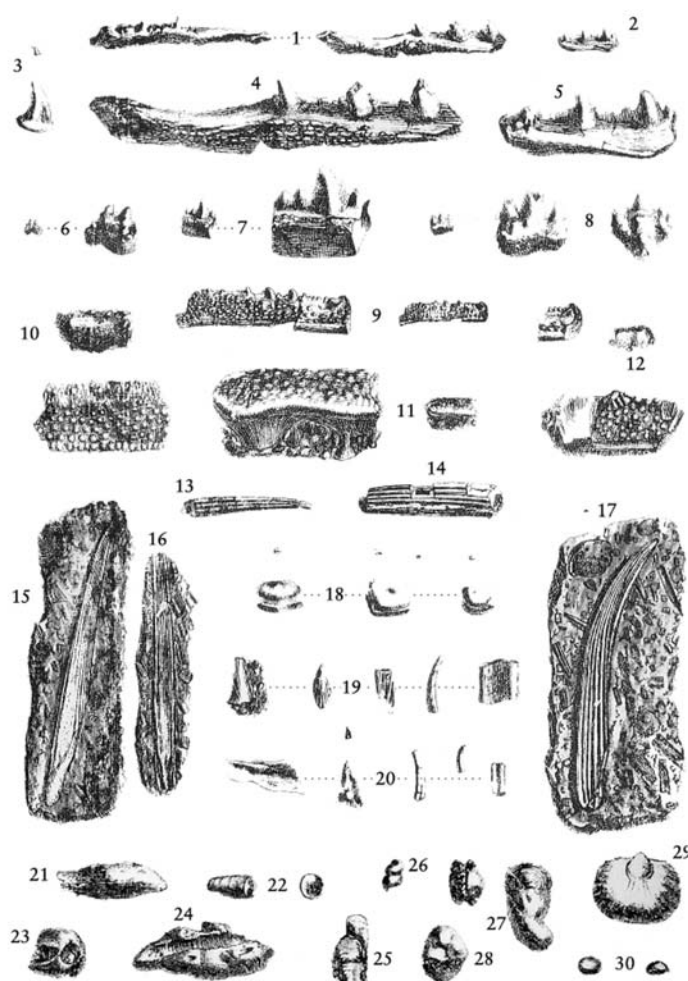


Figure 3.10: Fossils from the Ludlow Bone Bed illustrated in a plate from Murchison's *Siluria* (1872). 1–8, *Plectrodus mirabilis*, fragments of jaws; 9–12, *P. pustuliferus*, fragments of jaws; 13, 14, *Onchus murchisoni*, fin spines; 15–17, *O. trenuistriatus*, fin spines; 18, *Thelodus parvidens*, denticles; 19–20, indeterminate fragments; 21–28, coprolites containing invertebrate fragments; 29, *Orthis lunata* Sowerby; 30, *Pachtheca sphaerica*. All approximately natural size.

AGNATHA Thelodonti: Thelodontida: Ceololepididae

Thelodus parvidens Agassiz, 1839

T. bicostatus (Hoppe, 1939)

T. pugniformis Gross, 1967

T. trilobatus (Hoppe, 1939)

Thelodonti: Thelodontida: Loganellidae

Loganellia ludloviensis Gross, 1967

Osteostraci: Ateleaspidiformes: Ateleaspididae

Hemicyclaspis murchisoni (Egerton, 1857)

Sclerodus pustuliferus Agassiz, 1839

GNATHOSTOMATA

Acanthodii: Ishnacanthiformes: Ishnacanthidae

Plectrodus mirabilis Agassiz, 1839

P. pleiopristis Agassiz, 1839

Acanthodii: *incertae sedis*:

Onchus murchisoni Agassiz, 1837

O. tenuistriatus Agassiz, 1837

Gomphochus sp.

Acanthodian spines are commonly found in the Welsh Borders but little articulated material is known. Rare small fragments of *Sclerodus* occur at this level and a few plates of the cyathaspidid *Poraspis* sp. have been found at Ludford Lane, which is the lowest record for this genus.

The thelodonts are represented only by isolated denticles. These bear ornamentation patterns that permit the identification of the species. Such isolated remains are typical of the Welsh Borders, whereas occasional complete thelodonts have been found elsewhere, as in the Silurian of Scotland. The material from Ludford Corner includes the first thelodonts ever described (Agassiz, 1839).

Thelodus parvidens Agassiz, 1839 is by far the most common element in the Ludlow Bone Bed, being particularly abundant in the lower bone-bed lentils, and rarer higher up, where *Loganellia ludlowensis* takes its place (Antia and Whitaker, 1979; Antia, 1980; Figure 3.11). This variation in species abundance could be the result of sorting (Antia, 1980), but may be a real faunal change. *Thelodus parvidens* is the type species of the genus, and is widespread, having been reported from the Downtonian of England, Germany, eastern Canada, eastern Baltic, Timan and Ramsåsa (Turner, 1976). Murchison (1853) believed that the original specimens from Ludford had been lost, but Turner (1973) recovered a specimen recorded by the British Geological Survey as the type material.

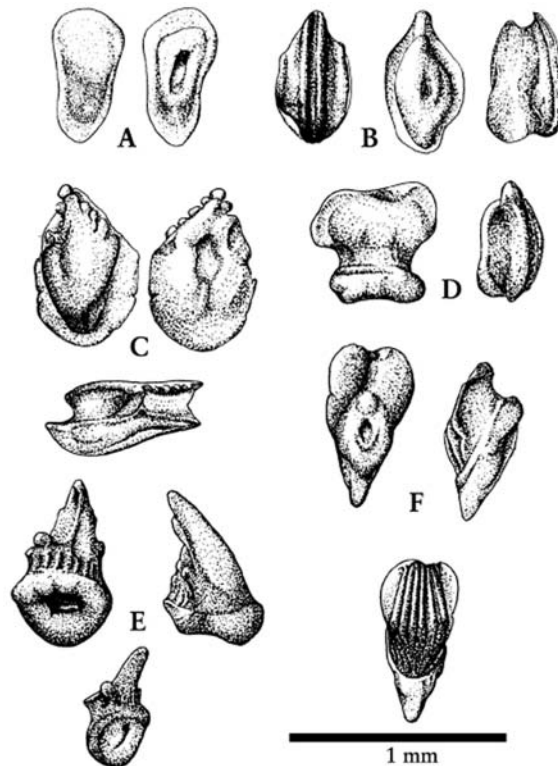


Figure 3.11: *Thelodonts from the Ludlow Bone Bed (after Turner 1973)*. (A) *Thelodolus parvidens*; (B) *Thelodolus bicostatus*; (C) *Loganellia ludlowiensis* head scale; (D) *Thelodolus pugniformis*; (E) *Thelodolus parvidens*?; (F) *Thelodolus trilobatus*.

Thelodolus bicostatus (Hoppe, 1931) and *T. pugniformis* Gross, 1967 may be special scale types of *T. parvidens* (Turner, 1976). The first form is known also from Oesel, its type locality, and Germany, while the second is reported from the Beyrichienkalk erratics (type locality) of Germany, as well as Ramsåsa, Scania, Oesel and Timan. *Thelodolus trilobatus* (Hoppe, 1931) is known from the lower Ludlow to Lower Downtonian of Oesel (type locality), Ramsåsa, Beyrich, Ringerike, and the Welsh Borders (Turner, 1976).

Loganellia ludlowiensis Gross, 1967 is the second most common thelodont in the Ludlow Bone Bed. The genus *Loganellia* was distinguished from *Thelodolus* by Gross (1967), with *L. scotica* from the early Silurian of Birk Knowes (q.v.) in southern Scotland as the type species. Gross (1967) distinguished seven species of *Loganellia* from the Downtonian of England, Beyrich, the eastern Baltic and North Timan. He named the denticles from the Ludlow and Teme-side bone beds as *L. ludlowiensis*, but did not localize the holotype, which is merely listed as coming from the Ludlow Bone Bed (LBB; Gross, 1967, p. 66), presumably from Ludford Lane.

The acanthodians are represented almost exclusively by spines and scales that identify the group, but are less diagnostic at the generic and specific levels. This is typical of most Welsh Borders sites, although acanthodian jaws are also reported from Ludford Lane and a few other localities. The jaws, scales and spines indicate the presence of four, or perhaps five, species. *Plectrodus mirabilis* Agassiz, 1839 is a form species restricted to the type specimen (Denison, 1979) from the Ludlow Bone Bed (Figure 3.10). It is an ischnacanthid, based on jaws that bear large cusped teeth. The species is known from the LBB, the Temeside Shales Formation of Ludlow (q.v.), and has also been recorded from the Upper Silurian of Portugal (Priem, 1911). Originally Agassiz (1839) described two forms from the Ludlow Bone Bed, *Sclerodus* and *Plectrodus*, believing they were both fish jaws, but *Sclerodus* has proved to be an osteostracan (see Downton Castle area report below).

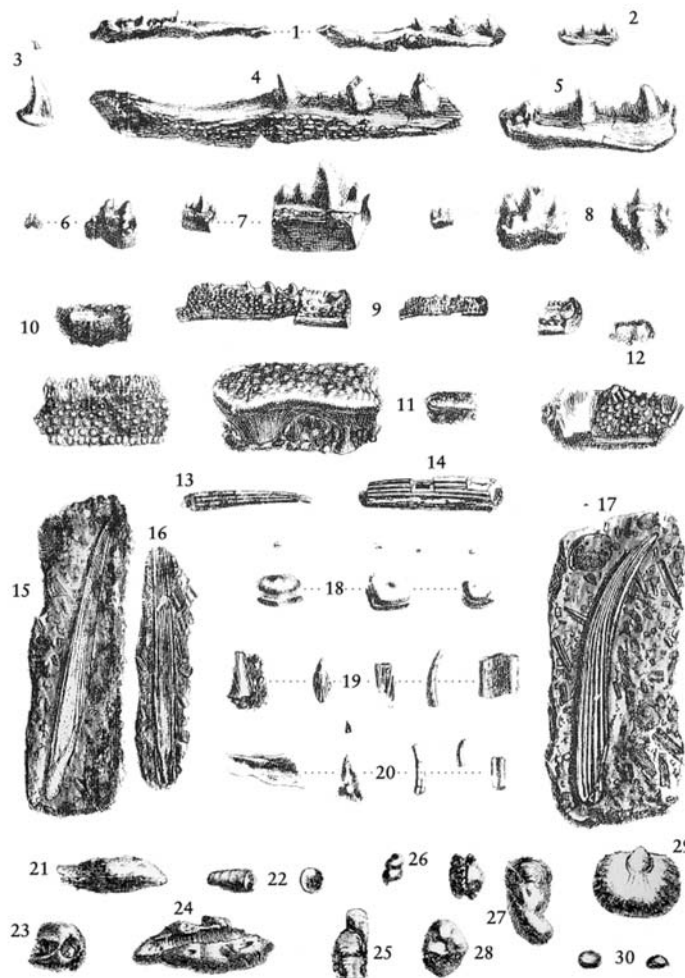


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Plectrodus pleiopristis Agassiz, 1839 is listed as an indeterminate genus by Denison (1979). The species is based on cusped acanthodian tooth plates (Figure 3.10) similar to those doubtfully referred to *Gomphonchus* (*Gomphodus*) by Gross (1957). *Gomphodus* sp. is recorded by Denison (1959) from the LBB, based possibly on a similar acanthodian tooth.

Onchus munchisoni Agassiz, 1837 is the type species of a common genus, based on ribbed acanthodian spines, which is known from the Lower Silurian of Pennsylvania, USA, the Lower or Middle Silurian of Bohemia, the Upper Silurian of the Welsh Borders, Sweden, Bohemia, Oesel, ?Portugal, Pennsylvania and Nova Scotia, the Lower Devonian of Wales, England, Germany, Bohemia, Spitsbergen, Podolia, Timan, Siberia, Lithuania, Wyoming and Ohio, USA, the Middle or Upper Devonian of Leningrad, and the Upper Devonian of Belgium. The type locality of the species *O. munchisoni* is Ludford Lane, and the species is known also from the Upper Silurian of Oesel. *O. tenuistriatus* Agassiz, 1837 is also known from the Upper Silurian of Oesel, Sweden and possibly Portugal (Denison, 1979).

The osteostracan *Sclerodus* is also represented by incomplete remains, mostly fragments of cornua with characteristic ornamentation and cusped margin. Agassiz (1839) mistakenly described a variety of small, cusped fragments from the Ludlow Bone Bed Member of Ludford Corner as fish jaws. He erected two genera for this material, *Sclerodus* and *Plectrodus*, but the identity of the material was debated. M'Coy (1853) thought they were crustaceans, while Murchison (1853, 1867) and Egerton (1857) described them as fish jaws. Harley (in Murchison, 1867, p. 241) sectioned a specimen and recognized this material as parts of cephalaspid

headshields, and not jaws. New material collected by Grindrod and Lightbody from the Downton Castle Sandstone at Ludford Lane enabled Lankester (1870) to describe the complete headshield for the first time, and he united *Sclerodus* and *Plectrodus* as *Eukeraspis pustuliferus* (details are given in the Downton Castle site report, q.v.). *Sclerodus pustuliferus* Agassiz, 1839 is the sole species of the genus, and it is one of the oldest cephalaspids known. The original material consisted of four specimens, of which the only survivor was chosen as lectotype by Stensiö (1932).

Stensiö (1932) gave a complete redescription, and Forey (1987) has reassessed the animal using new and old material. He listed 55 specimens that give details of the headshield: the sole relatively complete one is from the Downton Castle Sandstone Formation at Ludford Corner. A second specimen described by Stensiö (1932) is now lost.

Interpretation

The bone beds in the Ludlow Bone Bed Member represent lag deposits of drifted debris formed in a very shallow subtidal to low intertidal environment, possibly deposited during storm events (Smith and Ainsworth, 1989). Dineley (1951) described the bone bed as a condensed layer of winnowed fragments, and a product of slow sedimentation. This is the interpretation also of the overlying *Platyschisma* Shale Member, which shows erosively based lenses of siltstone and basal shell lags. Antia (1980, p. 305) suggested that the individual bone bed lenses of the Ludlow Bone Bed Member formed over short periods of time, 'within 10 years of the death of the fish constituting the bone bed', and he concluded that the material was a lag concentrate formed during a marine regression, probably in a tidal environment.

The Ludlow Bone Bed Member serves as a distinctive marker horizon and signals the arrival in the Anglo-Welsh Basin of most of the species of fish that are found in the Downton Series, and marks a major environmental change from marine to alluvial and fluvial conditions. The lower part of the Ludlow Bone Bed Member and the upper parts of the Upper Whitcliffe Formation contain marine fossils, but those of the rest of Ludlow Bone Bed Member and the *Platyschisma* Shale Member are restricted and suggest deposition in an environment of reduced salinity. The terrestrial component of the Ludlow Bone Bed Member fauna and flora could have been derived from the 'tilestones delta' that lay to the south-west (Siveter *et al.*, 1989).

The environmental shift from brachiopod-dominated Whitcliffe Formation to the Downton Castle Sandstone Formation, dominated by bivalves, gastropods and vertebrates, marks the onset of continental Old Red Sandstone facies in Britain. This section has been regarded as a transition from marine to brackish-marine conditions (Murchison, 1853; Stamp, 1923), marine to deltaic (Allen and Tarlo, 1963), or shallow marine to intertidal mudflats and beach sands (Allen, 1974, 1979; Antia, 1979, 1980). The horizon is also correlated with equivalents in mainland Europe and North America on the basis of the ostracod succession to which vertebrate-bearing horizons are also related (Figure 3.12).

Thelodonts have good biostratigraphical potential (Turner, 1973, in press; Blicek *et al.*, 1988; Janvier and Blicek, 1993). The *Thelodus parvidens* fish fauna of the Ludlow Bone Bed Member marks a biozone spanning the Ludlow/ Píldolí series boundary, and may be correlated throughout northwest Europe, as well as in New Brunswick and Nova Scotia (Turner, 1973). The thelodont species in the Baltic area, however, are different (Märss, 1986), and direct correlation between that area and the British Isles is not possible on the basis of these vertebrates alone (Figure 3.12).

Conclusions

The fish fauna from the Ludlow Bone Bed Member and the *Platyschisma* Shale Member is diverse, and especially rich in thelodonts. Although the fossils are mainly isolated scales and fragments, many are now identifiable at species level. Since this locality lies in the area of the stratotype sections for the Ludlow Series, its conservation value lies in its great potential for correlation of graptolite, brachiopod, ostracod and conodont biostratigraphical schemes with those based on thelodonts and other vertebrates.

Reference list

- Agassiz, J.L.R. (1839) Fishes of the Upper Ludlow Rock. In *The Silurian System*, R.I. Murchison (ed.), Vol.2, 605–7, John Murray, London.
- Aldridge, R.J. and Smith, M.P. (1985) Lower Palaeozoic succession of the Welsh Borderland. *Fourth European Conodont Symposium (ECOS IV) Field Excursion B, Guidebook*, 39 pp.
- Allen, J.R.L. (1974) Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills area, Shropshire, England. *Sedimentary Geology*, **12**, 73–167.
- Allen, J.R.L. (1979) Old Red Sandstone facies in external basins, with particular reference to southern Britain. In *The Devonian System* (eds M.R. House, C.T. Scrutton and M.G. Bassett), *Special Papers in Palaeontology*, **23**, pp. 65–80.
- Allen, J.R.L. and Tarlo, L.B.H. (1963) The Downtonian and Dittonian facies of the Welsh Borderland. *Geological Magazine*, **100**, 129–55.
- Antia, D.D.J. (1979a) Comments on the environment and faunas across the Ludlovian–Downtonian boundary (Upper Silurian) at Siefert, Salop. *Geological Journal*, **14**, 127–34.
- Antia, D.D.J. (1979b) Bone-beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbios. *Mercian Geologist*, **7**, 93–174.
- Antia, D.D.J. (1980) The sedimentology of the type section of the Upper Silurian Ludlow–Downton series boundary at Ludlow, Salop, England. *Mercian Geologist*, **7**, 291–321.
- Antia, D.D.J. and Whitaker, J.H. McD. (1979) A scanning electron microscope study of the fishes of the Upper Silurian Ludlow bone bed. In *Scanning Electron Microscopy in the Study of Sediments* (ed. W.B. Whalley), Geo-Abstracts, Elsevier Science Publishers, Norwich, 119–36.
- Bassett, M.G., Lawson, J.D. and White, D.E. (1982) The Downtonian Series as the fourth series of the Silurian System. *Lethaia*, **15**, 1–24.
- Blieck, A., Mark-Kurik, E. and Märss, T. (1988) Biostratigraphic correlations between Siluro-Devonian invertebrate-dominated and vertebrate-dominated sequences: the East Baltic example. In *Devonian of the World* (eds N.J. McMillan, A.F. Embry and D.L. Glass), *Canadian Society of Petroleum Geologists Memoir* 14, II, 179–587.
- Blondel, C. (1992) Initiation à la micropalaeo-ichthyologie des micro-restes des vertébrés du Ludlow Bone Bed (Silurian supérieur, Angleterre). *Memoire de Maitrise de Géologie Fondamentale et Appliquée*. Université des Sciences et Technologies de Lille, Flandres, Artois.
- Denison, R.H. (1956) A review of the habitat of the earliest vertebrates. *Fieldiana: Geology*, **11**, 359–457.
- Denison, R.H. (1974) The structure and evolution of teeth in lungfishes. *Fieldiana: Geology*, **33**, 31–58.
- Denison, R.H. (1979) Acanthodii. In *Handbook of Paleoichthyology*, Vol. 5 (ed. H.-P. Schultze), Gustav Fischer Verlag, Stuttgart, New York, 62 pp.
- Dineley, D.L. (1951) The northern part of the Lower Old Red Sandstone outcrop of the Welsh Borders. *Transactions of the Woolhope Naturalists' Field Club*, **33**, 127–47.
- Egerton, P. de M.G. (1857) Palaeoichthyological notes: on some fish remains from the neighbourhood of Ludlow. *Quarterly Journal of the Geological Society of London*, **13**, 282–91.
- Forey, P.L. (1987) The Downtonian ostracoderm *Scelerodus* Agassiz (Osteostraci: Tremataspidae). *Bulletin of the British Museum (Natural History), Geology*, **41**, 1–30.
- Gross, W. (1957) Mundzähne und Hautzähne der Acanthodier und Arthrodiren. *Palaeontographica, Abteilung A*, **109**, 1–40.
- Gross, W. (1967) über Thelodontiers Schuppen. *Palaeontographica Abteilung A*, **127**, 1–67.
- Harley, J. (1861) On the Ludlow Bone Bed and its crustacean remains. *Quarterly Journal of the Geological Society, London*, **17**, 542–52.
- Holland, C.H., Lawson, J.D. and Walmsley, V.G. (1963) The Silurian rocks of the Ludlow District, Shropshire. *Bulletin of the British Museum Natural History (Geology)*, **8**, 93–171.
- Janvier, P. and Blieck, A. (1993) The Silurian–Devonian agnathan biostratigraphy of the Old Red Continent. In *Palaeozoic Vertebrate Biostratigraphy and Biogeography* (ed. J.A. Long), Belhaven Press, London, 67–86 pp.
- Lankester, E.R. (1870) The Cephalaspidae. In *A monograph of the fishes of the Old Red Sandstone of Great Britain* (eds J. Powrie and E.R. Lankester), *Palaeontographical Society (Monograph)*, pp.33–62.
- Lapworth, C. (1879) On the tripartite classification of the Lower Palaeozoic rocks. *Geological Magazine*, (2), **6**, 1–15.

- M'Coy, F. (1853) On the supposed fish remains figures on plate 4 of the 'Silurian System'. *Proceedings of the Geological Society of London*, **9**, 12–15.
- Märss, T. (1986) Pozvonochniye Siluria Estonii: Zapondnoi Latvii (Silurian vertebrates of Estonia and west Latvia). *Fossilia Baltica*, **1**, Valgus, Tallinn, 104 pp.
- Marston, A. (1882b) *Guide to the Geology of Ludlow*. Privately published, Ludlow.
- Miller, C.G. (1995) Ostracodes and conodont distribution across the Ludlow/Pírdolí boundary of Wales and the Welsh Borderland. *Palaeontology*, **38**, 341–84.
- Murchison, R.I. (1839) *The Silurian System*, 2 vols, John Murray, London, 768 pp.
- Murchison, R.I. (1853) On some of the remains in the bone-bed of the Upper Ludlow Rock. *Quarterly Journal of the Geological Society of London*, **9**, 16–17.
- Murchison, R.I. (1867) *Siluria*, 4th edn, John Murray, London, 566 pp.
- Priem, F. (1911) Sur des Poissons et autres fossiles du Silurien Supérieur du Portugal. *Comunicações Serviços Geológicos do Portugal*, **8**, 1–10.
- Siveter, D.J., Owens, R.M. and Thomas, A.J. (1989) *Silurian Field Excursions. A Geotraverse across Wales and the Welsh Borderland*. National Museum Wales Geological Series **10**, Cardiff, 133 pp.
- Smith, R.D.A. and Ainsworth, R.B. (1989) Hummocky cross-stratification in the Downton of the Welsh Borderland. *Journal of the Geological Society, London*, **146**, 897–900.
- Stamp, L.D. (1923) The base of the Devonian, with special reference to the Welsh Borderland. *Geological Magazine*, **60**, 276–82, 331–6, 367–72, 385–410.
- Stensiö, E.A. (1932) *The Cephalaspids of Great Britain*. British Museum (Natural History), London, 220 pp.
- Symonds, W.S. (1872) *Records of the rocks; or, notes on the geology, natural history, and antiquities of north and south Wales, Devon, and Cornwall*, John Murray, London, 433 pp.
- Turner, S. (1973) Siluro-Devonian thelodonts from the Welsh Borderland. *Quarterly Journal of the Geological Society, London*, **129**, 557–84.
- Turner, S. (1976) *Fossilium Catalogus I: Animalia*. Part 122: *Thelodonti (Agnatha)*. Dr W. Junk B.V., 's – Gravenhage, 1–35.
- Watts, W.W. (1925) Excursion to south Shropshire. *Proceedings of the Geologists' Association*, **36**, 394–405.
- White, E.I. (1950a) The vertebrate faunas of the Lower Old Red Sandstone of the Welsh borders. *Bulletin of the British Museum (Natural History) Geology*, **3**, 1–67.
- Woodward, A.S. (1891a) *Catalogue of fossil fishes in the British Museum. Part II. Containing the Elasmobranchi (Acanthodii), Holo-cephali, Ichthyodermalites, Ostracodermi, Dipnoi and Teleostini (Crossopterygii), and Chondrosteian Actinopterygii*, British Museum (Natural History), London, 567 pp.
- Woodward, A.S. (1904b) Notes on the geology and fossils of the Ludlow district. *Proceedings of the Geologists' Association*, **18**, 429–42.
- Woodward, A.S. and Dixon, E.E.L. (1904) Long excursion to the Ludlow district. *Proceedings of the Geologists' Association*, **18**, 487–91.