Fossil Fishes of Great Britain

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Chapter 3

Late Silurian fossil fishes sites of the Welsh Borders

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INTRODUCTION: PALAEOGEOGRAPHY AND STRATIGRAPHY

During Late Silurian times the marine Welsh Basin gradually filled with a wedge of clastic sediments advancing from the north, producing a diachronous transition to non-marine beds. These continental clastic facies, the Old Red Sandstone, began to develop widely in the latest Silurian and Early Devonian. In the north of the area (Shropshire), the Old Red Sandstone facies comprised overbank deposits, mudflats and fluvial sands, whilst in the south (Dyfed) the facies is represented by more distal alluvial plain sedimentation.

The Old Red Sandstone sequence in the Welsh Borders extends over a large area (Figure 3.1) and may be divided into Lower Old Red Sandstone (late Silurian: Přídolí (Downtonian) Series and the early Devonian: Lochkovian, Pragian, and Emsian stages = Dittonian and Breconian) and Upper Old Red Sandstone (late Devonian: Frasnian and Famennian stages = Farlovian). Middle Devonian rocks are not represented. The Lower Old Red Sandstone succession is important internationally because it contains a great number of species of early fishes, especially in the Clee Hills area of Shropshire. The beds there, and in Wales, have been divided into the Downtonian, Dittonian and Breconian 'stages' (House *et al.*, 1977), but these terms are only of local application.

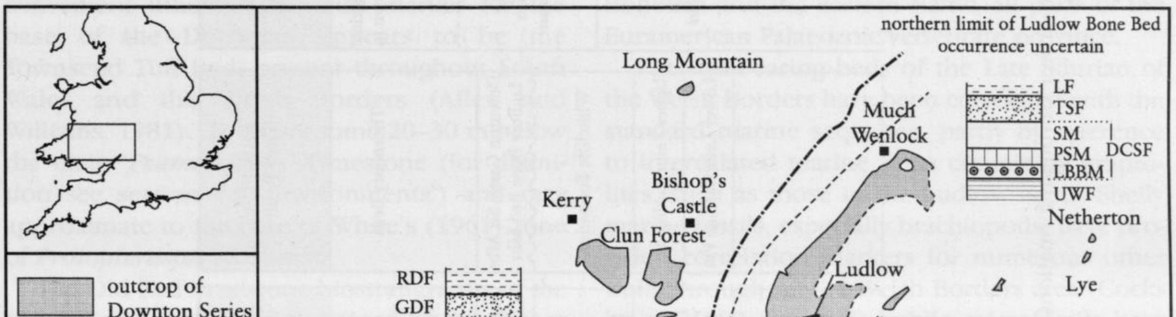


Figure 3.1 Map of the Downtown Series throughout the Welsh Borders, with schematic summaries of the stratigraphical successions and relationships with the Ludlow Series: UWF, Upper Whitcliffe Formation; DCSF, Downton Castle Sandstone Formation; LBBM, Ludlow Bone Bed Member; PSM, Platyschisma Shale Member; TSF, Temeside Shale Member; LF, Ledbury Formation; PPB, phosphatized pebble beds; PHF, *Platyschisma helicites* Formation; YDF, Yellow Downton Formation; GDF, Green Downton Formation; RDF, Red Downton Formation; Lud, undifferentiated Ludlow strata; SM, Sandstone Member; TF, Tilestones Formation; u/c, unconformity (after Bassett, Lawson and White, 1982).

Series	Stage	Radiometric age (Ma bp)	Graptolite biozones	Conodont biozones	Tortworth–Tites Point	Corvedale	Ludlow Anticline	Knighton and Old Radnor	Llandovery Llangadog
Přídolí	(not yet defined)	405	no younger Silurian graptolites known in Britain	no younger Silurian conodonts known in Britain	Thornbury Beds	Ledbury Formation	Ledbury Formation	Red Downton Group	Raglan Marl Group
						Temeside Shales Formation	Temeside Shales Formation	Green Downton Bed Yelloe Downton Bed *P. helicites* Bed	Long Quarry Formation
				Ozarkodina steinhornensis eosteinhornensis	Downton Castle Sst Mbr Ludlow Bone Bed Mbr	Downton Castle Sst Fm Ludlow Bone Bed Mbr	Downton Castle Sst Fm Ludlow Bone Bed Mbr	Lan-Wen Hill Bed	
Ludlow	Ludfordian		*Bohemograptus* proliferation		Whitcliffe Formation	Whitcliffe Group	Whitcliffe Group	Wern Quarry Beds	U. Roman Camp Formation
				Pelekysgnathus dubius				Knucklas Castle Beds	Lower Roman Camp Fm
			S. leintwardinensis		Upper Leintwardine Fm	Leintwardine Group	Leintwardine Group	Bailey Hill Formation	Upper Cwm Clŷd Formation
					Lower Leintwardine Fm				L. Cwm Clŷd Fm / Trichrûg Fm
	Gorstian	407 ± 14	*P. tumescens*/*S. incipiens*	? ?		Bringewood Group	Bringewood Group		Black Cock Formation
		419 ± 7 ± 18	*L. scanicus*			Elton Group	Elton Group	lower Ludlow graptolitic shales	Tresglen Formation
		420	*N. nilssoni*	? ?					

Figure 3.2 Correlation table of Late Silurian–Lower Devonian formations of the Anglo-Welsh province (after Siveter *et al.*, 1984; House *et al.*, 1977).

However, they have historical importance, and the Downtonian and Dittonian have been used to correlate stratigraphical sequences elsewhere in the world (e.g. Scotland, Spitsbergen, Canada and Podolia) by comparison with the (mainly vertebrate) faunas found in the Welsh Borders. The Downtonian was regarded as spanning the Silurian–Devonian boundary, while the Dittonian (Lochkovian–Pragian) and Breconian (Pragian–?Eifelian) are largely Early Devonian in age (House *et al.*, 1977, p. 43). Today, these units are subdivided, with various local names for the Downtonian, which is seen as entirely of Silurian age (Holland and Bassett, 1989; Cocks *et al.*, 1992). The term Ditton Group and St Maughans Group are retained for the earliest Devonian units in the Welsh Borders area. A convenient lithostratigraphical marker for the base of the Devonian appears to be the Townsend Tuff Bed, present throughout South Wales and the Welsh Borders (Allen and Williams, 1981). It occurs some 20–30 m below the main '*Psammosteus*' Limestone (for definition see section on 'Environments') and may approximate to the base of White's (1961) zone of *Protopteraspis leathensis*.

The Old Red Sandstone biostratigraphy of the Welsh Basin has been determined by fish faunas and by palynomorphs, although it is hard to match this with the thick marine sequences in Devon and Cornwall because their fossils are almost mutually exclusive. The international stratigraphical standard for dating of the Silurian is founded on marine sequences dated by graptolites and conodonts. These have provided a sequence of about 30 biozones for the 30 Ma or so of Silurian time (Cocks *et al.*, 1992; Figure 3.2).

The fish-bearing units to be described below all fall in the Upper Silurian sequences (Figure 3.2). The base of the Ludlow Series correlates with the base of the *Neodiversograptus nilssoni* Biozone, and the boundary stratotype is in the Ludlow area of the Welsh Borders (Pitch Coppice). The Ludlow Series is divided into two stages, the Gorstian Stage and the Ludford Stage. The base of the former coincides with the base of the Ludlow Series, and the base of the latter correlates with the base of the *Saetograptus leintwardinensis* Biozone, and the boundary stratotype is again in the Ludlow area (Sunnyhill Quarry). The Gorstian Stage combines the previously used Eltonian and Bringewoodian stages, and the Ludford Stage combines the Leintwardinian and Whitcliffian stages. The base of the Přídolí Series corresponds to the base of the *Monograptus parultimus* Biozone, and the boundary stratotype is located in the Prague Basin, Czech Republic. The base of the Devonian has been set at the base of the *Monograptus uniformis* Biozone, and the stratotype is also located in the Prague Basin of the Czech Republic. A recent extensive survey of the ostracod and conodont distributions across the Ludlow/Přídolí boundary of Wales and the Welsh Borderland by Miller (1995) contains references to the succession in the Ludlow (Ludford) area. The Ludlow Bone Bed Member of the Downton Castle Formation (see Ludford Lane report below) and its correlation are included; the correlation extends from eastern North America to Bohemia and the eastern Baltic, all parts of the Euramerican Palaeozoic vertebrate province.

The fish-bearing beds of the Late Silurian of the Welsh Borders have been correlated with the standard marine sequence, partly by reference to intercalated marine units containing graptolites, such as those in the Ludlow area. Shelly marine fossils, especially brachiopods, have provided correlation markers for numerous other units throughout the Welsh Borders area (Cocks *et al.*, 1992, pp. 4–5), while microfossils have been used to correlate some of the upper units of the Ludlow area sequence that appear to be Přídolí in age.

Biostratigraphical schemes for the Late Silurian based on fish remains have been attempted (Blieck *et al.*, 1988; Märss, 1989; Dineley and Loeffler, 1993; Janvier and Blieck, 1993). These divide the Ludlow and Přídolí series of the Baltic area into six or seven vertebrate 'zones' which are correlated by the brachiopod and graptolite zonal schemes. All fish groups are used in biostratigraphical correlation, but acanthodians have proved particularly useful since they occur abundantly in places and particular species may be found in several basins. Of increasing importance for the future will be vertebrate microfossils (scales, denticles, teeth), particularly thelodonts in the Late Silurian (Turner, 1970, 1971), and zonal schemes are currently being drawn up (e.g. Karatajute-Talimaa, 1978; Märss, 1989; Dineley and Loeffler, 1993; Janvier and Blieck, 1993). Turner, who initiated thelodont-based biostratigraphy in Britain (1973) is, with A.C. Young now developing one for the Silurian and Devonian successions of Australia.

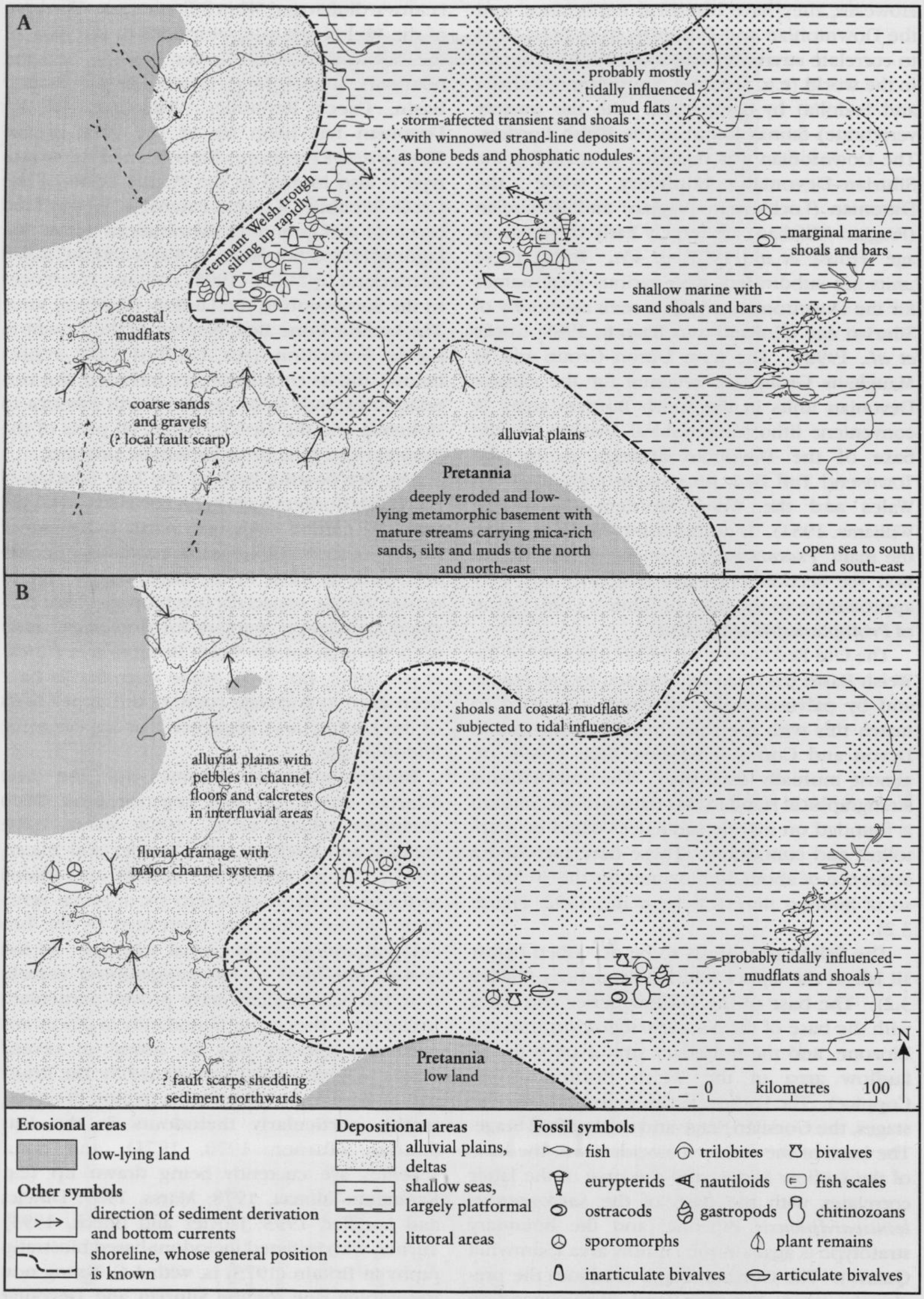


Figure 3.3 Přídolí (latest Silurian) palaeogeography of southern Britain (after Bassett *et al.*, 1992). (A) early Přídolí; (B) late Přídolí.

ENVIRONMENTS

The Late Silurian to Early Devonian vertebrates of the Euramerican province occur in both marine and non-marine sediments. As noted in Chapter 1, the earliest fishes, of Ordovician and Early Silurian age occur in marine strata together with unquestionably marine fossils (Boucot and Janis, 1983; Elliot *et al.*, 1991). Many earlier workers (e.g. Romer and Grove, 1935) believed that the early fishes lived in rivers, and that the occurrence of their remains in marine sediments was due to post-mortem transport. However, as more specimens were found in marine sequences, the belief that they lived in the sea became more widely held (e.g. Denison, 1956). Studies of the relationship between sedimentology and fish faunas in the Welsh Borderland (Ball and Dineley, 1961; Allen and Tarlo, 1963; Allen *et al.*, 1968) have suggested that, here at least, they originally occupied a fluvial habitat. For some time this has been the generally accepted view, although Goujet (1984), Blieck (1984) and Märss (1989) have again revived the argument that these animals were marine by demonstrating that some Old Red Sandstone fish-bearing sediments in mainland Europe are marine. For example, Märss (1989) suggested that much of the fish-bearing Old Red Sandstone of the eastern Baltic is a marine deposit, consisting of clastics washed off an upland raised by the late Caledonian orogeny. Allen (1985) thought that the Upper Downton Group (Ledbury Formation) was partly intertidal, but widespread sedimentological evidence confirms the earlier hypothesis that this unit, and the Lower Ditton Group, in the central Welsh Borders are entirely non-marine (Figure 3.3A, B).

The sedimentary history of the Anglo-Welsh Basin area was more complicated than a simple progression from marine-influenced to freshwater conditions. The habitat of the vertebrate faunas remains equivocal. Barclay *et al.* (1994) have suggested that brackish or marine incursions occurred throughout the Přídolí and into the Lochkovian (Dittonian, Early Devonian) time, reaching northwards as far as Ammons Hill, Worcestershire. A marine embayment may have existed in the vicinity of the Little Missenden (Buckinghamshire) borehole during this period. Many reports of molluscs, arthropods and ichnofossils have appeared since W.W. King (1934) produced these fossils from a number of Downtonian and Dittonian horizons in the Welsh Borderland. Throughout the area, the Přídolí faunas are dominated by *Traquairaspis (Phiaspis) symondsi* (Lankester), *Tesseraspis tesselata*, Thyestida and other osteostracans, cyathaspids (Wills, 1935) and acanthodians, both juveniles and adults. Most of the species in this fauna are unknown outside the Anglo-Welsh area. Few of the Přídolí fish species extend above the overlying '*Psammosteus*' Limestones, and those that occur in the Ditton Group are rare. The term *Psammosteus* Limestone, first used by W.W. King (1934), is based on a misidentification of a fragment of *Traquairaspis symondsi* from a nearby intraclast conglomerate. *Psammosteus* is a Mid–Late Devonian heterostracan with a stellate tubercle ornamentation on the outer surface of the dermal plates. It has not been found in the Anglo-Welsh Basin but is common in the eastern Baltic area. The Limestone is one of several pedocals and is a terrestrial deposit devoid of vertebrate remains. The name persists in the literature for pedocals for this level of strata. The main '*Psammosteus*' Limestone is interpreted as representing a significant phase of aridity (lasting for up to 10 000 years according to Allen, 1985, 1986), this may have caused the extinction of fish species. The only fishes to occur commonly both above and below the '*Psammosteus*' Limestone are thelodonts, known to have been adapted to brackish as well as freshwater conditions (Turner, 1973) so could escape from the locally hostile arid conditions. In contrast, the species found in the Ditton Group of Devil's Hole seem to have been adapted to both marine and freshwater environments, as they occur elsewhere in marine strata (Tarrant, 1991).

The Ditton Group seems to mark a return to a wetter climate, with extensive river systems reappearing across the Anglo-Welsh floodplain. The fluvial channels were colonized by new assemblages of fishes, few of which occur below the '*Psammosteus*' Limestone, and those that do are found there only extremely rarely. Furthermore, unlike the Downton Group faunas, most of these species are also found in marine or brackish sequences elsewhere (e.g. Spitsbergen). Fluvial deposition gained vigour as the Ditton Group accumulated, with repeated desiccation of the floodplain suggested by the abundance of the pedocal (concretionary) horizons. For a full discussion see Chaloner and Lawson (1985).

FISH FAUNAS

The Old Red Sandstone of the Welsh Borders has long been known as a rich source of fossil fishes, many of which are unique to the area. Reports as early as 1835 include mention of fish remains in Silurian rocks in the region (Lloyd and Lewis, 1835). Agassiz (1839) included descriptions of several in his work for Murchison. The Přídolían faunas seem impoverished in comparison to those of Canada, Vestspitsbergen and parts of Europe (Dineley and Williams, 1978), whereas numerous species apparently flourished in Ditton Group times. The obvious faunal division in the Welsh Borders occurs with the first appearance of *Protopteraspis* just a few metres below the *'Psammosteus'* Limestones, which lie at the base of the Ditton Group, and thus generally corresponds to the boundary between the Přídolí and the Lochkovian, and hence of the Silurian and Devonian.

The fossil fishes from the Silurian of the Welsh Borders (i.e. Lower Downton Group) are listed below, with the classification of agnathans based on Halstead (1993) and of acanthodians on Zidek (1993). The Devonian fish faunas are listed in Chapter 4.

AGNATHA

Heterostraci: Eriptychiformes: Tesseraspididae
- *Kallostrakon podura* Lankester, 1870
- *K. macanuffi* Tarlo, 1964
- *K. grindrodi* Tarlo, 1964
- *Tesseraspis tessellata* Wills, 1935

Heterostraci: Cyathaspidiformes: Tolypelepididae
- *Tolpelepis* sp.

Heterostraci: Cyathaspidiformes: Cyathaspididae
- *Cyathaspis banksi* (Huxley and Salter, 1856)
- *Archaegonaspis ludensis* (Salter, 1859)
- *Anglaspis macculloughi* (Woodward, 1891a)

Heterostraci: Cyathaspidiformes: Corvaspididae
- *Corvaspis kingi* (Woodward, 1934)

Heterostraci: Phialaspidiformes: Traquairaspididae
- *Traquairaspis (Phialaspis) symondsi* (Lankester, 1866)
- *T. pococki* White, 1946 (= *Toombsaspis pococki* of Tarrant, 1991)

Thelodonti: Thelodontida: Coelolepidae
- *Thelodus costatus* (Pander, 1856)
- *T. parvidens* Agassiz, 1839
- *T. traquairi* Gross, 1947
- *T.* sp.
- *T. bicostatus* (Hoppe 1939)
- *T. pugniformis* Gross, 1947
- *T. trilobatus* (Hoppe 1939)
- *Goniporus alatus* (Gross, 1967)

Thelodonti: Thelodontida: Loganellidae
- *Loganellia cruciformis* Gross, 1967
- *L. cuneata* (Gross, 1947)
- *L. kummerowi* Gross, 1967
- *L. ludlowiensis* Gross, 1967
- *L. scotica* (Traquair, 1898)

Thelodonti: Phlebolepiformes: Phlebolepididae
- *Katoporodus grossi* Karatajute-Talimaa, 1970
- *K. tricavus* Gross, 1967

Osteostraci: Tremataspidiformes: Didymaspididae
- *Didymaspis grindrodi* Lankester, 1867

Osteostraci: Tremataspidiformes: Sclerodontidae
- *Sclerodus pustuliferus* Agassiz, 1839

Osteostraci: Ateleaspidiformes: Ateleaspididae
- *Hemicyclaspis murchisoni* (Egerton, 1857)
- *H. murchisoni* var. *ludlowensis* Stensiö, 1932
- *H. lightbodii* (Lankester, 1870)

Osteostraci: Cephalaspidiformes: Procephalaspididae
- *Auchenaspis salteri* Egerton, 1857
- *A. egertoni* Lankester, 1870

GNATHOSTOMATA

Acanthodii: Ischnacanthiformes: Ischnacanthidae
- *Ischnacanthus kingi* White, 1961
- *Gomphonchus hoppei* (Gross, 1947)
- *G. sandalensis* (Pander, 1856)
- *Gomphonchus* sp.
- *Plectrodus mirabilis* Agassiz, 1839

Acanthodii: Climatiiformes: Climatiidae
- *Climatius* sp.
- *Erriwacanthus manbrookensis* Miles, 1973
- *Nostolepsis striata* Pander, 1856
- *Nostolepis* sp.
- *Onchus murchisoni* Agassiz, 1837
- *O. tenuistriatus* Agassiz, 1837
- *O. decorus* Phillips, 1848

Acanthodii: *incertae sedis*
- *Onychodus anglicus* Woodward, 1888 (symphysial tooth-whorl)
- *'Plectrodus' pleiopristis* Agassiz, 1839 (inferognathal)

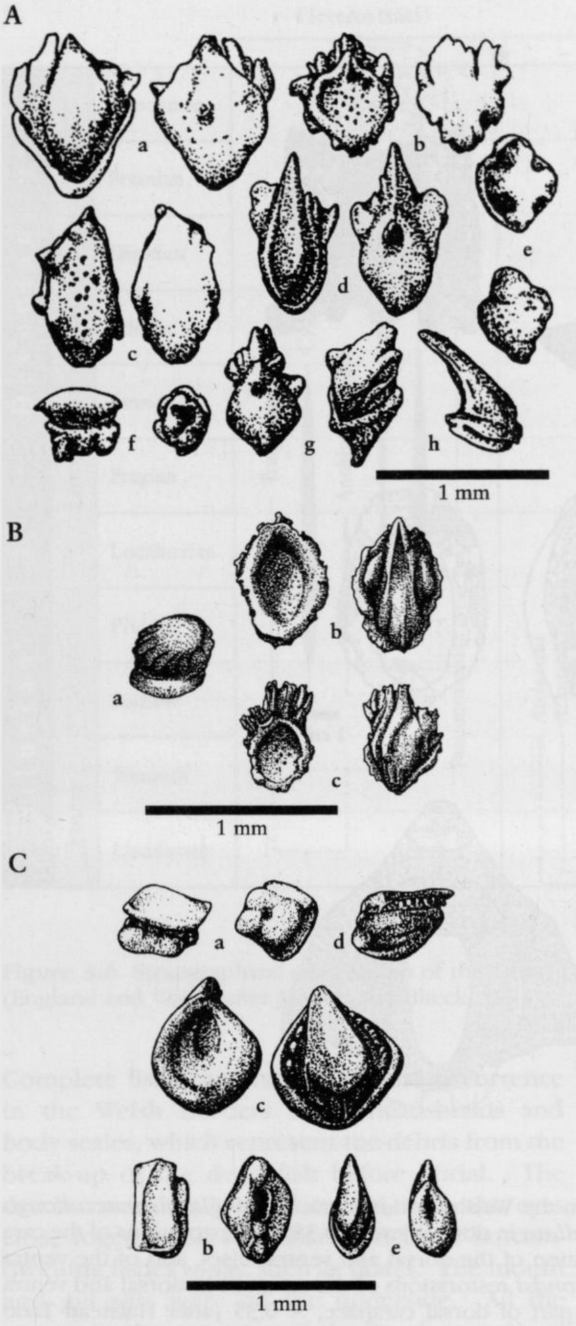


Figure 3.4 Silurian thelodont denticles from the Welsh Borderland (after Turner, 1973). (A) from the *T. pococki* zone of the Downtonian: a, b, *Goniporus alatus* (Gross), c, d, *Loganellia ludoviensis* (Gross); e, *Loanellia cuneata* (Gross); f, *L. cruciformis*; g, *Turinia pagei* (Powrie); h, *Loganellia* sp. indet. (B) (Lower) Downton Formation, a, *Thelodus costatus*, Pander; b, *Kataporodus tricavus* Gross; c, *Goniporus alatus* (Gross): (C) Woolhope Limestone, a–b, *Thelodus parvidens* Agassiz; c–d–e, *Loganellia ludoviensis* (Gross).

The heterostracans of the Late Silurian had heavily-scaled bodies and head shields made from numerous curved plates (Figure 3.5). The headshield extended back to about halfway along the length of the body, and it was circular in cross-section, or sometimes flattened in a horizontal plane. The headshield enclosed the head, including the eyes, nostrils and branchial (breathing) openings, as well as the trunk. In most forms there was a broad ornamented dorsal plate, one or more branchial plates along the side, and one or more ventral plates. In some forms all the plates, except the ventral disc, were fused into a single bony capsule. The mouth appears to have operated by movements of the small plates around it and, since there were no jaws, feeding must have occurred by suction. The posterior part of the body was covered with broad sheet-like bony scutes or smaller bony scales, depending on the species, and swimming must have been effected by sideways movements of the tail. There were no paired fins and the heterostracans are not thought of as rapid swimmers (Belles-Isles, 1987); they may have lived close to the bottom, feeding on organic litter and matter in the loose surface sediment.

The stratigraphical distribution of the heterostraci received sustained attention from E.I. White and H.A. Toombs at the Natural History Museum over three decades. They established the Late Downtonian zones of *Traquairaspis pococki* and *T. symondsi*. Ball and Dineley (1961) showed that *T. pococki* is a rare intruder into the overlying zone of *T. symondsi*. The earlier species was found in several localities (White, 1946), none of which is now accessible or productive, though fragments are widespread in the Welsh Borders (e.g. Clarke, 1950; Tarrant, 1991). Tarrant (1991) revised the taxonomy of these heterostraci and proposed a single biozone of *Phialaspis symondsi–Toombsaspis pococki*. The present authors have not adopted these revisions. *Traquairaspis pococki* is illustrated in Figure 3.5 since it had been referred to in the literature as a zonal fossil.

Thelodonts, as discussed in Chapter 2, are less well known since they are very rarely found intact. Indeed, most thelodont finds consist of isolated scales. Typical Late Silurian forms from the Welsh Borders are shown in Figure 3.4. One genus that can be reconstructed, *Phlebolepis* from the Late Silurian of the Baltic area (Bystrov, 1949), a relative of the Welsh Borders phlebolepid, was about 70 mm long, and had a cigar-

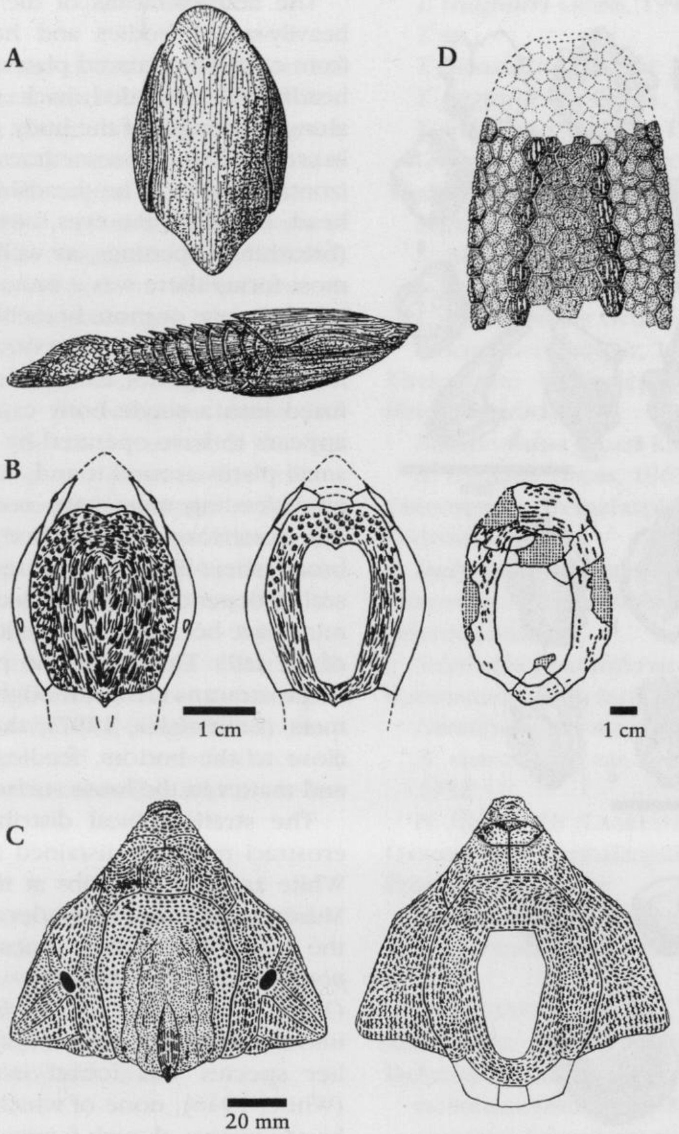


Figure 3.5 Late Silurian heterostracan vertebrates from the Welsh Borders area. (A) *Anglaspis macculloughi* in dorsal and lateral views, × 0.75, and, *Tesseraspis tessellata* in dorsal view, × 0.35; (B) restorations of the carapace of *Traquairaspis pococki* showing the ornamentation of the dorsal and ventral discs, and of the ventral disc of *T. symondsi*, dorsal view; (C) *Traquairaspis symondsi* restorations of the carapace in dorsal and ventral views (after Tarrant, 1991); (D) *Tesseraspis tessellata* part of dorsal carapace, × 0.35 (after Halstead Tarlo, 1964).

shaped body which was slightly flattened in the horizontal plane. (There was a wide jawless mouth at the front and an eye close to each corner of the mouth. The body was covered with small pointed scales. This thelodont swam by beating its tail from side to side, and steered using its pectoral fins which were triangular flaps on either side of the body just behind the head.) The scales are made from dentine, as in a tooth, and enclose a hollow pulp cavity. Scale shape and histology are used in identification.

Typically, osteostracans had a bony headshield which extended over the front part of the body, and rows of bony scales over the remainder of the body (see Figure 3.14). *Ateleaspis*, an early osteostracan from the Silurian of Scotland has already been described in Chapter 2. The tail and fins were covered with smaller, bony scales.

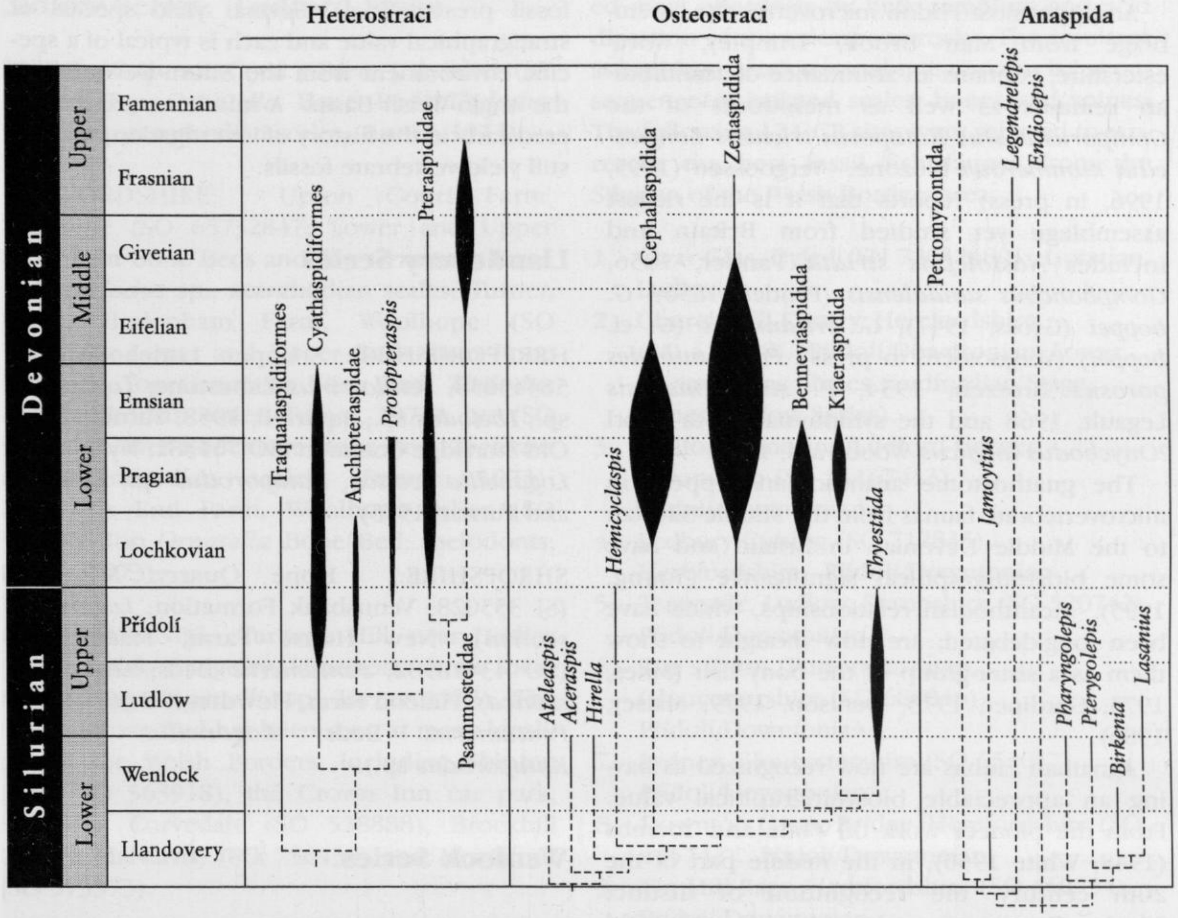


Figure 3.6 Stratigraphical distribution of the Siluro-Devonian agnathans of the Old Red Sandstone continent (England and Wales; after Janvier and Blieck, 1993).

Complete fishes are rare, the usual occurrence in the Welsh Borders being headshields and body scales, which represent the debris from the break-up of the dead fish before burial. The osteostracan head was flattened, with the eyes close together on top, characteristic of bottom-dwelling fishes today, such as skates. The mouth and gill slits were on the underside. All the spaces in the top part of the head were lined with bone, which therefore preserved the outlines of the brain, and the course of the nerves and veins of the head. There are three depressed areas on the headshield that are covered with small plates, one medially behind the eyes, and two lateral ones. They are connected to the brain by large canals, and they probably had a sensory function. The osteostracans, like the heterostracans, were probably largely bottom-dwellers that lived by sucking up organic-rich sediment and extracting food particles.

Acanthodians include some of the oldest known vertebrates with jaws. They were generally no longer than 6 cm in the Silurian, with large eyes and streamlined bodies covered by bony stud-like scales. Their most distinctive feature was a single row of dorsal fin spines and paired ventral fins, one row on each side, each fin being supported by a large 'cut-water' spine. In the Old Red Sandstone of the Welsh Borders, it is these spines that are preferentially preserved, and on which many of the species names are based. Details of the gross morphology are determined from complete specimens of similar species from sites where unusual taphonomic conditions have given rise to the preservation of complete carcasses, as in the Lower Devonian of Scotland (Chapter 5). The fusiform body and heterocercal tail are characteristic of active swimmers and most acanthodians must have been mid- to surface-water fishes.

An uppermost Přídolí microvertebrate assemblage from Man Brook, Trimpley, Worcestershire, contains an abundance of acanthodian remains as well as thelodonts of the *Goniporus alatus–Kataporus tricavus–Loganellia kummerowi* biozone. Vergoossen (1995, 1996, in press) reports that it is the richest assemblage yet studied from Britain and includes *Nostolepsis striata* Pander, 1856, *Gomphonchus sandalensis* (Pander, 1856), *G. hoppei* (Gross, 1947), *G. britannicus* (*G.* cf. *hoppei*) (Vergoossen, in press), *Paracanthodes porosus* Brotzen, 1934, *P. stonehousensis* Legault, 1968 and the symphysial tooth-whorl ?*Onychodus anglicus* Woodward, 1888.

The gnathostome acanthodians appear in microvertebrate faunas from the Middle Silurian to the Middle Devonian in Britain and have some biostratigraphical significance (Young, 1995). Acanthodian relationships, which have been long-debated, are now thought to show them as a sister-group of the bony fish (Miles, 1973; Gardiner, 1973; Denison, 1979; Maisey, 1986).

Agnathan faunas are now recognized as having an appreciable biostratigraphical value. From the pioneer work of White and Toombs (1948; White 1950), in the middle part of the 20th century, the recognition of distinct Silurian–Devonian vertebrate zones in the Old Red Sandstone facies of England and Wales has been extended to mainland Europe (Blieck, 1984; Janvier and Blieck, 1993), Spitsbergen (Blieck *et al.*, 1987) and Canada (Elliot, 1984; Dineley, 1990). This has largely been on the basis of the ranges of cyathaspidids and pteraspidids, but Turner (1973) has revealed the value of thelodonts in this field in Britain and in the eastern Baltic–Russian outcrops.

FISH SITES

Fossil fish remains have been found at numerous localities in the Silurian of the Welsh Borders. They include sporadic occurrences in Lower Silurian rocks, and much commoner finds in Upper Silurian sediments, particularly those of Ludlow and Přídolí Series age. In the following list, with localities arranged by stratigraphical stage, and then by county, the fossils are almost exclusively of microvertebrate remains, and new localities are discovered virtually every year. They have been selected on account of the particular taxa present and the quality of the fossil preservation. Several yield species of stratigraphical value and each is typical of a specific environment from the Siluro-Devonian of the Anglo-Welsh Basin. A number were discovered early in the history of investigation, yet may still yield vertebrate fossils.

Llandovery Series

HEREFORDSHIRE: Upper Littlehope (SO 58343658; *Petalocrinus* Limestone; *Loganellia* sp., *Thelodus* sp.; Squirrell, 1958; Turner, 1973; Old Storridge Common (SO 761381; Wych Beds; *Loganellia scotica*, *Kataporodus* sp., Aldridge and Turner, 1975).

SHROPSHIRE: Hope Quarry, Minsterly (SJ 355028; Venusbank Formation; *Loganellia scotica*); New House Farm, Marshbrook (SO 43418982; *Pentamerus* Beds; *Loganellia scotica*); Hillend Farm, Plowden (SO 39568769; *Pentamerus* Beds; *Loganellia scotica, Kataporodus* sp.).

Wenlock Series

GLOUCESTERSHIRE: Brinkmarsh Quarry, Tortworth inlier (ST 67359132; *Loganellia* sp., *Thelodus* sp.; Siveter and Turner, 1982).

HEREFORDSHIRE: Ledbury Council Quarry (SO 717384; bone bed at base of Wenlock Limestone and Gorsley Limestone; *Thelodus* sp.; Squirrell, 1958; Turner, 1973); Linton Quarry (SO 677257; bone bed at base of Wenlock Limestone and Gorsley Limestone; *Thelodus* sp.; Squirrell, 1958; Turner, 1973); Canwood (SO 613381; bone bed at base of Wenlock Limestone and Gorsley Limestone; *Thelodus* sp.; Squirrell, 1958; Turner, 1973); Storridge (SO 755496; Lower Woolhope Limestone; *Thelodus* sp., *Loganellia* sp., *Gomphonchus?* sp., acanthodian scales; Turner, 1973).

Ludlow Series: Gorstian Stage

SHROPSHIRE: Shelderton Rock, near Clungunford (SO 419779; Aymestry Limestone Member; thelodont scales; Rhodes, 1953; Turner, 1973).

Ludlow Series: Ludford Stage

GWENT: Common Coed y Paen, Usk inlier (ST 340984; Top *Ornatella* Bone Bed; *Thelodus parvidens*, acanthodian scales; Turner, 1973).

HEREFORDSHIRE: Upton Court Farm, Woolhope (SO 65732847; Lower and Upper Bodenham Bone Beds and Top *Ornatella* Bone Bed; *Thelodus* sp., acanthodian scales; Turner, 1973); Bodenham Farm, Woolhope (SO 65243200; Lower and Upper Bodenham Bone Beds and Top *Ornatella* Bone Bed; *Thelodus* sp., acanthodian scales; Turner, 1973); Lye (SO 660296; Lower Bodenham Bone Bed; *Thelodus* sp., acanthodian scales; Turner, 1973); Whittocks End Farm, Woolhope inlier (SO 660296; Top *Ornatella* Bone Bed; thelodonts; Turner, 1973).

WEST MIDLANDS: Turner's Hill, near Dudley (SO 915908; Sedgeley Limestone bone bed; *Thelodus* sp., *Loganellia* sp.; Turner, 1973). The Ludlow Bone Bed has been seen at many localities in the Welsh Borders, including Shipton Lane (SO 563918), the Crown Inn car park, Munslow, Corvedale (SO 528888), Brockhill Quarry, Malverns, (SO 756439) and Mordiford (SO 573373).

Downton Series: Ledbury Formation

A widespread topographical feature, the so-called *'Psammosteus* Limestone escarpment' occurs throughout much of the Welsh Borders, marking the incoming sandstones of the uppermost Downtian and the Lower Dittonian. Many small stream sections expose fossiliferous horizons (Ball and Dineley, 1961; Dineley and Gossage, 1959; Clarke, 1950, 1951, 1954; Greig *et al.*, 1968).

SHROPSHIRE: Beaconhill Brook, Monkhopton (SO 63309426; mid part of the Red Downton Formation *Kallostrakon* sp., acanthodian scales; Ball and Dineley, 1961); Foxhole Coppice, Monkhopton (SO 61809308; *Kallostrakon* sp., acanthodian scales, jaws, spines; Ball and Dineley, 1961).

Many of these localities have only poor exposures of the strata and the fossils may be collected most effectively by bulk sampling and acid digestion of the calcareous rock. The resultant assemblage of microvertebrate remains is in consequence of isolated scales, bones and spines. The following 12 GCR sites were selected to represent the best fossil fish faunas from the Silurian of the Welsh Borders area.

1. Cwar Glas, Dyfed (SN 72632480). Gorstian, Ludlovian.
2. Church Hill Quarry, Herefordshire (SO 412738). Přídolí/Downtonian, Lower Leintwardine Shales (Ludfordian Stage, upper Ludlow Series).
3. Ludford Lane and Ludford Corner, Shropshire (SO 51167413). Přídolí/Downtonian.
4. Ledbury Cutting (SO 712835), Herefordshire. Přídolí/Downtonian.
5. Temeside, Ludlow, Shropshire (SO 520742). Přídolí/Downtonian.
6. Tite's Point (Purton Passage), Gloucestershire (SO 688046). Přídolí/Downtonian.
7. Lydney, Gloucestershire (SO 652017). Přídolí/Downtonian.
8. Downton Castle Bridge, Herefordshire (SO 445742). Přídolí/Downtonian.
9. Tin Mill Race, Herefordshire (SO 460754). Přídolí/Downtonian.
10. Forge Rough Weir, Herefordshire (SO 456752). Přídolí/Downtonian.
11. Castle Bridge Mill Quarry, Herefordshire (SO 443743). Přídolí/Downtonian.
12. Bradnor Hill, Herefordshire (SO 291578). Přídolí/Downtonian.

Four of the GCR sites, because of their geological and geographical proximity have been written up in one site report, the Downton Castle area.

CWAR GLAS (SN 72632480)

Highlights

This old but still-accessible quarry in Gorstian age strata of Dyfed has recently yielded the heterostracan *Archaegonaspis* sp., a much earlier occurrence than elsewhere in Britain.

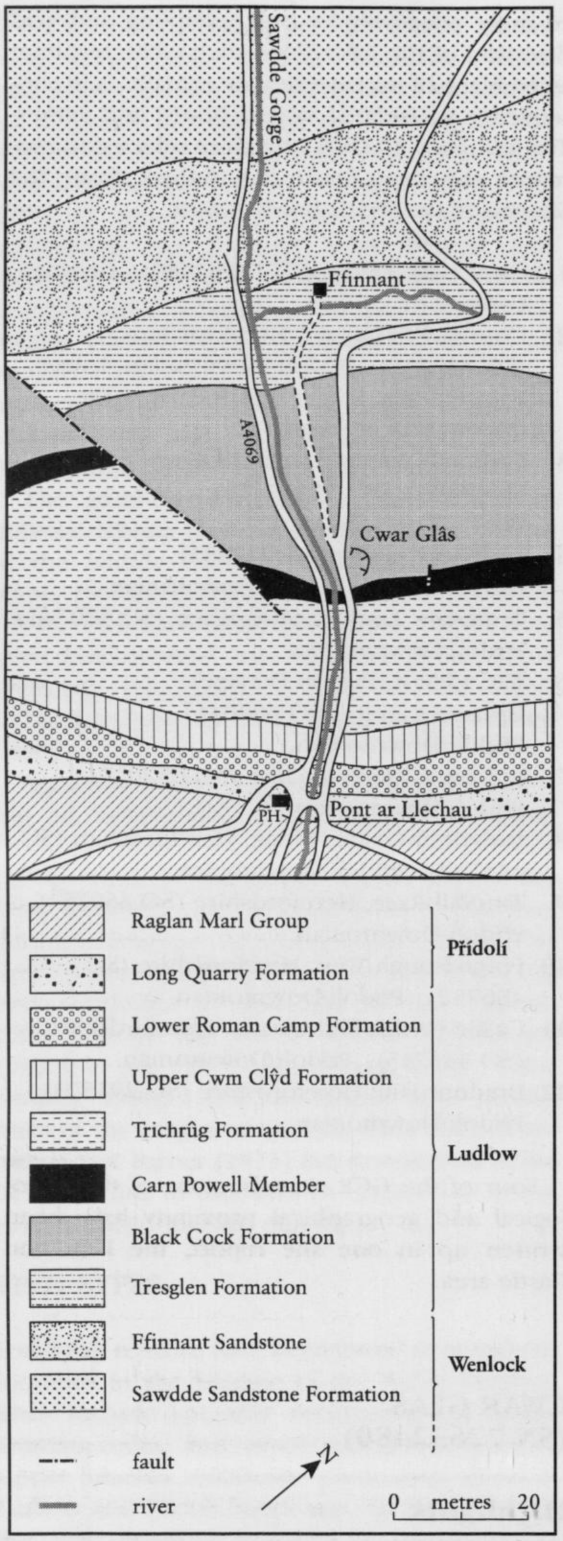


Figure 3.7 Geological sketch map and stratigraphical section of the Cwar Glas site in the Sawdde Gorge (after Bassett, 1982).

Introduction

The strata from this site in Dyfed have been well known for many years and have yielded a rich fauna of marine invertebrates. The fossil fishes are rare, but important because they are older than the Ludlow Bone Bed faunas from Welsh Border localities.

Description

The fishes were found in a thin calcareous broken-shell bed (coquina) in the upper part of the Black Cock Beds, which are dated as belonging to the Gorstian Stage of the Ludlow Series (Siveter *et al.*, 1989, pp 92–93; Cocks *et al.*, 1992, pp. 9–10; Figure 3.7).

Fauna

AGNATHA
Heterostraci: Cyathaspidiformes:
Cyathaspididae
Archaegonaspsis ludensis (Salter, 1859)

Archaegonaspis is a genus known from the late Silurian of Poland, Scotland, Sweden, Wales and the Welsh Borders. The type species, *A. integra*, comes from the glacial erratics of Germany, and several other species are known. *Archaegonaspis* sp. is said to occur in the middle Ludlow and ?early Devonian bone beds of Presteigne, Wales but remains one of the rarer heterostracan genera from the Welsh Borders.

Archaegonaspsis ludensis is the earliest known species of British heterostracan, and during early research in the 19th century, its discovery was of historical importance because it showed that 'true fishes' existed in beds underlying the Ludlow Bone Bed. In consequence, it was considered to be a forerunner for the 'Age of Fishes'. The genus is one of the more primitive members of the Family Cyathaspididae Kiaer, with few paired plates in the headshield. The earliest species is of Lower Wenlockian age; the latest is Upper Lochkovian. All members are marine.

Interpretation

The calcareous coquina occurs in several beds a few centimetres thick with a dominantly bivalve–gastropod fauna (Loeffler, pers. comm., 1990). Coquinas of this kind are known in littoral, tidal and subtidal environments; many

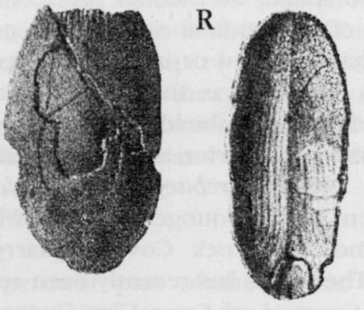


Figure 3.8 (L) Dorsal and (R) ventral discs of the cyathaspidid *Archaegonaspis ludensis* from the Ludlovian, × 0.8 (from Lankester, 1864).

have yielded vertebrate fragments. The fragments at Cwar Glas may have been introduced from freshwater or supratidal environments or more probably result from marine animals; they do not seem to have travelled any great distance as judged from their excellent preservation.

Conclusion

Specimens of the coquina are still easy to obtain, but require lengthy laboratory preparation. This site suggests that future examination of comparable localities in the lower Silurian of the Welsh Borders may yield early examples of fish fossils from palaeoenviroments that have previously not been considered worth searching because they represent the 'wrong' places to look for fishes. Thelodonts have now been recovered from many sites in the lower Silurian by maceration and sieving for microvertebrates (Turner, 1973). The conservation value lies in this being the earliest occurrence in Britain of larger, identifiable vertebrate remains and its potential for further investigation.

CHURCH HILL QUARRY (SO 412738)

Highlights

This famous quarry was the source of one of the earliest fossil fish from Herefordshire in the Welsh Borders, *Archaegonaspis ludensis* (Salter) (Figure 3.8). It was discovered in the middle of the 19th century, and was notable at the time because it proved that fishes occur below the Ludlow Bone Bed. The site is also important because it is in marine sediments.

Introduction

Many fine fossils were recovered from the Lower Leintwardine Shales (Ludfordian Stage, upper Ludlow Series) at the Church Hill quarries in the 19th century. Several different species of fossil starfish were found here, as well as several almost complete eurypterids and other invertebrates, recorded as 'a glorious list of fossils, all found in one quarry' by Marston (1882b). In the 1850s the site yielded what was then the earliest known fish (*Archaegonaspis*; Salter, 1859), which at that time was regarded as important because it showed that fishes occur in beds older than the Ludlow Bone Bed.

The site was visited by the Geologists' Association in 1904 (Dixon, 1904) when starfish were collected, and by Watson *et al.* (1948), but only the original few specimens found at the site are known. Recent collecting (in 1984) has concentrated at the upper levels because of current lack of exposure and has failed to produce fish material.

The geology of the site has been described by, amongst others, Woodward (1891a), Marston (1882b), la Touche (1894), Alexander (1936), Whitaker (1962), Goldring and Stevenson (1972) and Siveter *et al.* (1989). The small heterostracan *Archaegonaspis ludensis* was described and discussed by Salter (1859), Lankester (1868), Woodward (1891a), Kiaer (1932b), Watson *et al.* (1948) Denison (1956, 1964), and White (1958a).

Description

Alfred Marston, who discovered the 'Starfish Beds', described the site as consisting of several Lower Ludlow quarries close together near the summit of Church Hill, facing Leintwardine, the most prolific one being 'the uppermost, and nearest to the hedge from which starfish were first produced and also where they occur in the greatest abundance ... the starfish and other fossils lying in bands, very seldom with any intermixture of the species' (Marston,1882b). From the lower Leintwardine Shales (Ludfordian) of Church Hill quarry, Lightbody and Lee discovered the earliest known 'pteraspid' in the Welsh Borders, *Archaegonaspis ludensis*, together 'with shells, starfish and a large species of *Pterygotus*' (Salter, 1859), and therefore presumably roughly in the same horizon as the starfish. Marston (1882b) mentioned small graptolites in the upper beds of the quarry, possibly at the horizon that is exposed today as some 2–3 m of bluish green microlaminated siltstones in small, scattered exposures. The starfish beds are some way beneath this; although Marston (1882b) did not produce a section, Woodward (1891a, p. 94) gave a sketch of the 'Starfish Quarry'.

Hawkins (Hawkins and Hampton, 1927) re-excavated 'the southerly' of two remaining quarries, which he identified as the Starfish Quarry, and cut a new section 12 ft 6 in (3.7 m) deep through calcareous shales that contained *Monograptus leintwardinensis* throughout. There were frequent shell bands, and two starfish beds were traced, the higher 5 ft 3 in (1.6 m) below the surface, the lower 10 ft 6 in (3.0 m) below. The specimens of starfish, crinoids, etc. in these beds were nearly all perfect and fragments were extremely rare. They do not lie on bedding planes but are often oblique within the siltstone. No vertebrates were found. The Ludlow strata in the Leintwardine area are similar to those at Ludlow, but show evidence of slumps and submarine erosion. Six parallel channels trending NE–SW off the shelf over an area of 12 km^2 were postulated by Whitaker (1962). Of these, the Church Hill Channel had first been recognized by Alexander (1936). Some 580 ft (174 m) of strata below the higher Lower Leintwardine Beds are cut out by a channel with steep sides. The many fossil specimens do not lie parallel to the bedding planes but obliquely and specimens are often complete, although fragile.

Fauna

AGNATHA
Heterostraci: Cyathaspidiformes:
Cyathaspididae
Archaegonaspis ludensis (Salter, 1859)

Archaegonaspis ludensis (Salter, 1859) was described initially as *Pteraspis ludensis*, and as *Scaphaspis* by Lankester (1868). Woodward (1891a) redescribed it, and it is mentioned by Kiaer (1932b). Denison (1964) redescribed the species within his Family Cyathaspididae but concluded that its referral to the genus could not be firmly established. Its occurrence at Church Hill is mentioned by Woodward (1891a), Denison (1956) and White (1958a).

Archaegonaspis is a cyathaspid with a moderately broad shield, no median process, and an ornament of longitudinal ridges. The post-rostral field has a fanned or irregular pattern with the ridges occurring as short lengths or denticles. On the ventral shield the pattern is longitudinal, with an anterior area of fanned ridges (Denison, 1964). *Archaegonaspis ludensis* is also present in the younger rocks at Whitcliffe Quarry and Woodcock Covert Quarry, near Ludlow. The genus has recently been recorded from the Gorstian of Cwar Glas Quarry (q.v.), which is the oldest record of heterostracans in Britain. Four species of *Archaegonaspis* are known from the late Silurian of the eastern Baltic, Poland, Gotland, Sweden, the Welsh Borders and Wales.

Interpretation

The evidence of slumps and submarine erosion within the Ludlovian around Church Hill mark its position close to the palaeogeographical shelf edge. The parallel channels are interpreted as Ludlow-age submarine canyon heads that were infilled later in lower Leintwardine times. Whitaker (1962) thought that the fossil fauna was indigenous to the canyon heads, because it was not found outside them. However, Goldring and Stevenson (1972) showed that the specimens were suspended within the sediments, and they argued that the fauna had been introduced within fine-grained turbidite flows in the channels.

Conclusion

The main conservation value of the Church Hill quarries is important as the source of the oldest identifiable fish specimens in the Silurian of the Welsh Borders. *Archaegonaspis* is found also in other Welsh Borders localities, and farther afield, providing useful evidence for dating. Today there is little left of the quarries on Church Hill. All that can be seen is a large, irregular pitted area with few exposures of bluish green graptolitic siltstones, but the site could be re-excavated for further study.

LUDFORD LANE AND LUDFORD CORNER (SO 51167413)

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 (Přídolí 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.

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 Přídolí 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).

	Thickness (m)
Přídolí Series (= Downtonian in part)	
Ledbury Formation	< 460
Temeside Shales Formation	< 37
Downton Castle Sandstone Formation	< 173
Sandstone Member (SM)	
Platyschisma 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	12–46
Lower Bringewood Formation	41–69
Upper Elton Formation	46–76
Middle Elton Formation	46–107
Lower Elton Formation	20–46

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

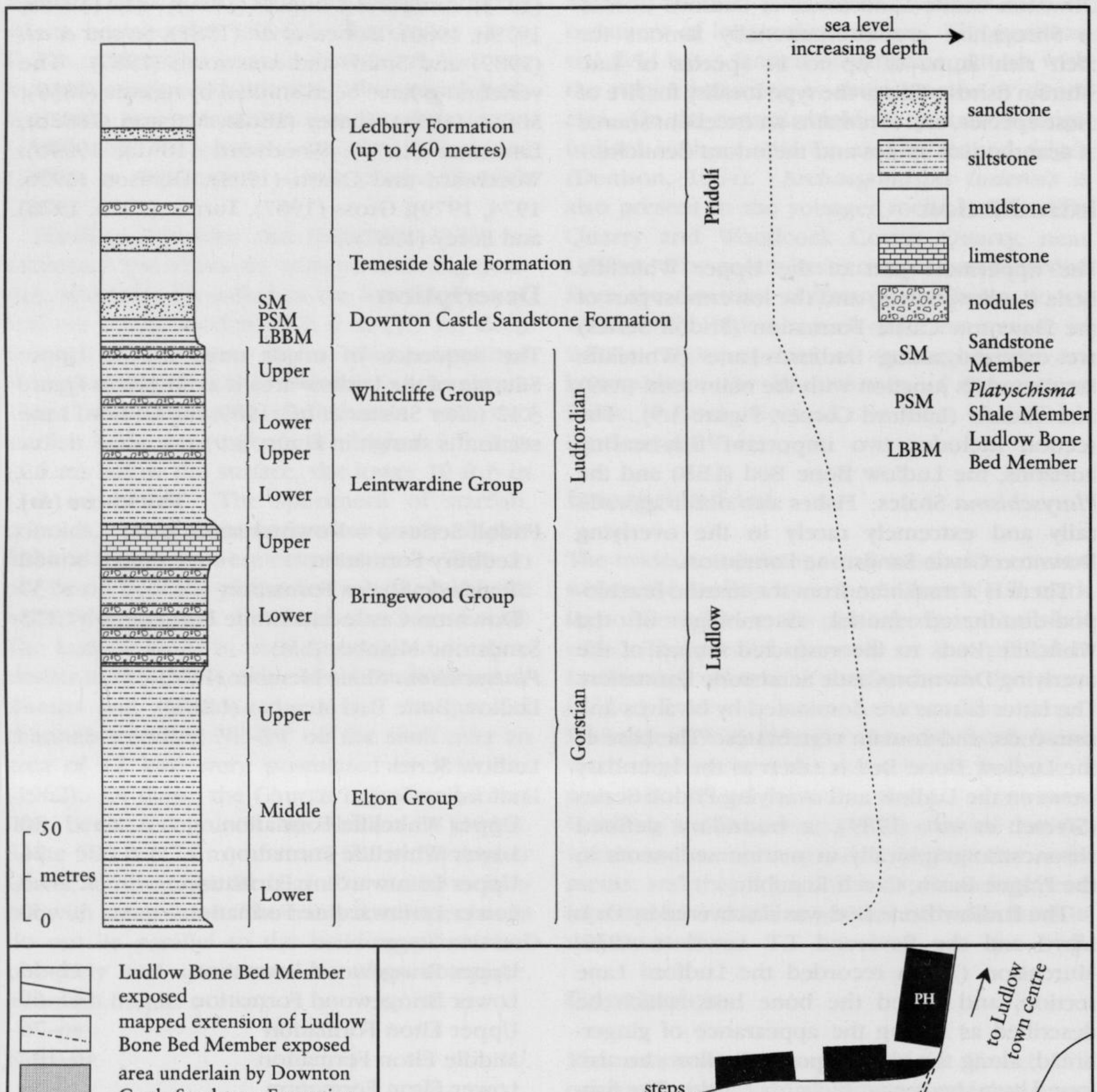


Figure 3.9 Sketch map and stratigraphical section of the site at Ludford Lane, Ludlow (after Bassett *et al.*, 1982).

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).

AGNATHA
Thelodonti: Thelodontida: Ceololepididae
Thelodus parvidens Agassiz, 1839
T. bicostatus (Hoppe, 1939)
T. pugniformiis 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

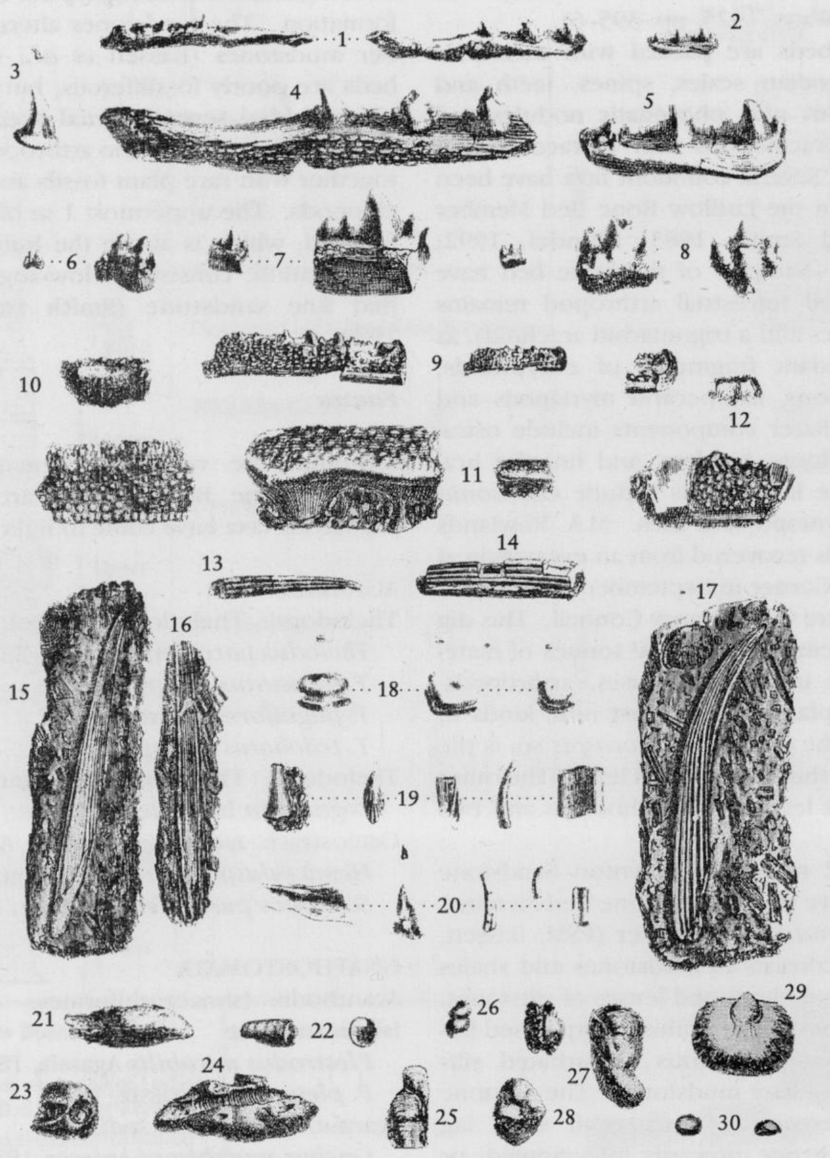


Figure 3.10 Fossils from the Ludlow Bone Bed illustrated in a plate from Murchison's Siluria (1872). 1–8, *Plectrodus mirabilis*, fragments of jaws; 9–12, *P. pustuliferus*, fragments of jaws; 13, 14, *Onchus murchisoni*, fin spines; 15–17, *O. trenuistriatus*, fin spines; 18, *Thelodus parvidens*, denticles;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

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 lenticles, 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

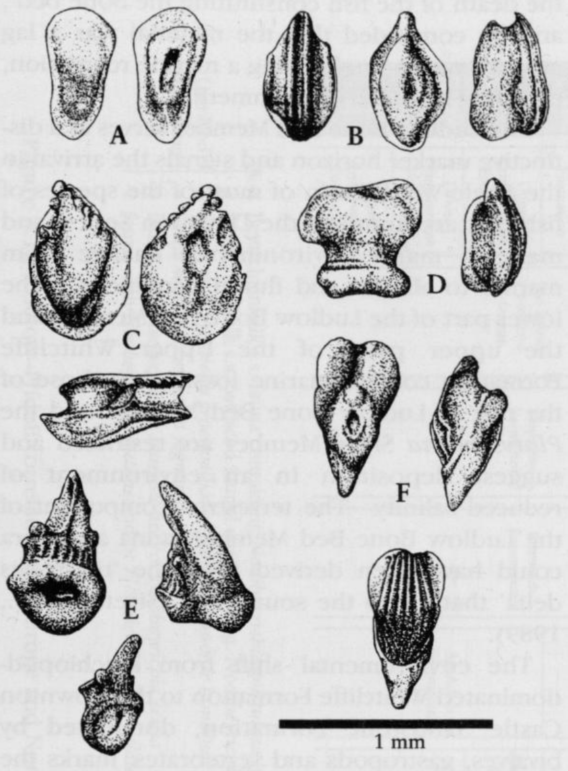


Figure 3.11 Thelodonts from the Ludlow Bone Bed (after Turner 1973). (A) *Thedolus parvidens*; (B) *Thelodus bicostatus*; (C) *Loganellia ludlowiensis* head scale; (D) *Thedolus pugniformis*; (E) *Thelodus parvidens*?; (F) *Thelodus trilobatus*.

Ludford had been lost, but Turner (1973) recovered a specimen recorded by the British Geological Survey as the type material.

Thelodus 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. *Thelodus 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 *Thelodus* 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 Temeside 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).

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 murchisoni 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. murchisoni* 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; Blieck *et al.*, 1988; Janvier and Blieck, 1993). The *Thelodus parvidens* fish fauna of the Ludlow Bone Bed Member marks a biozone spanning the Ludlow/ Přídolí 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).

Conclusion

The fish fauna from the Ludlow Bone Bed Member and the *Platyschisma* Shale Member is

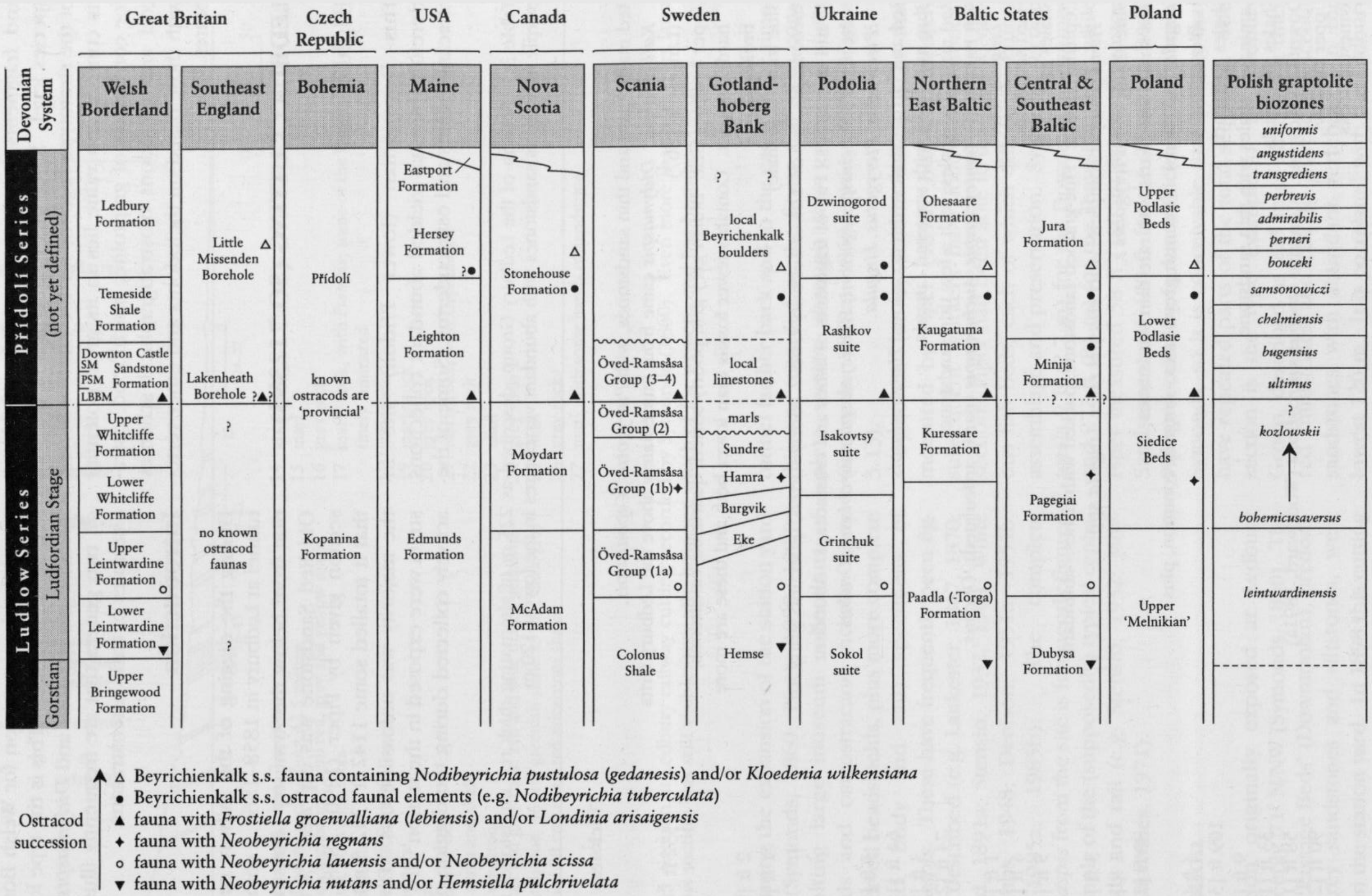


Figure 3.12 Ludlow–Přídolí correlation for Europe and North America. Vertical columns not drawn to scale (after Siveter *et al.*, 1989).

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.

LEDBURY CUTTING (SO 712385)

Highlights

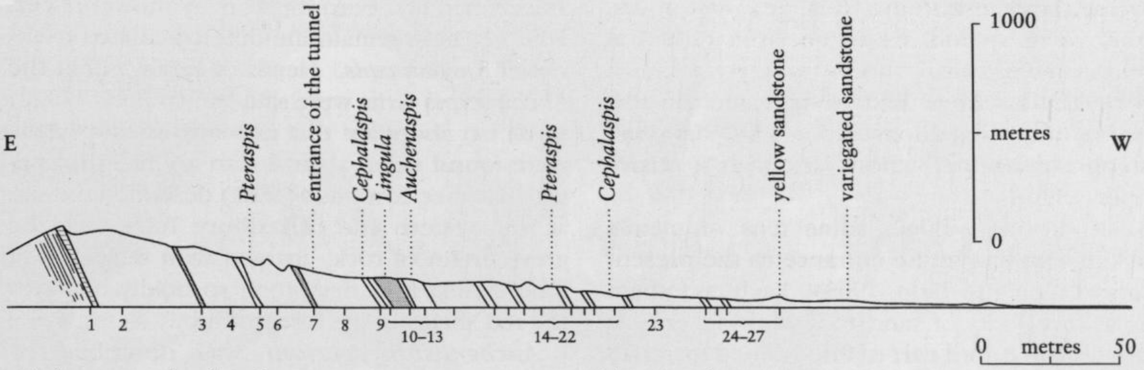
This Downtonian (lower Přídolí) site in Herefordshire has yielded abundant collections of acanthodians and ostracoderms. Some of the specimens are complete with the body and tail still attached, which is unusual and represents exceptional preservation for Welsh Borders Old Red Sandstone sites. This is the type locality for *Auchenaspis egertoni* and *Didymaspis grindrodi*, two genera that are frequently illustrated as examples of early osteostracans.

Introduction

During the digging of the railway cutting and tunnel at Ledbury in 1858–1860, a complete section from below the Aymestry Limestone to the Old Red Sandstone was exposed. A measured section given by Piper (1890, 1898) indicates that it totalled some 1142 ft (342.5 m) of which the majority was unfossiliferous. Downtonian strata were exposed in the station yard and were actively collected during the digging of the tun-

Table 3.1 Section of the Ledbury Group, described as 225 m of alternating thick red mudstones and red to purple micaceous sandstones with abundant vertebrates in the lowest 120 m

	Thickness ft [m]
Red marls, clays and thin sandstones, with *Pterygotus*, *Cephalaspis*, *Kallostrakon*. *Didymaspis* came from immediately above the Ledbury Grits (Lankester, 1867)	332 ft [101 m]
Upper Ledbury Grit. Bluish grey grit, poorly sorted, quartzitic, calcareous, hard, compact. Contains fewer fossils than lower bed, and these are more broken up	2 ft [0.6 m]
Blue mud (soft shale)	1 ft [0.3 m]
Auchenaspis Bed or 'Lower Ledbury Grits'. Poorly sorted, quartzitic, gritty and calcareous. Full of fragments of fishes and crustaceans. Abundant heads of *Auchenaspis egertoni*, *Hemicyclaspis murchisoni*, *Onchus*, ?*Plectrodus*, *Pterygotus*, *Lingula*.	3 ft [0.9 m]
Red and purple shales with occasional *Hemicyclaspis*	64 ft [19.5 m]
Blue mudstone with scattered *Lingula*	3 ft [0.9 m]
Red marls and shales, with a few thin sandstones	74 ft [22.6 m]
Soft band with *Hemicyclaspis*, *Auchenaspis* (partly articulated), *Onchus*, *Lingula*, etc.	1 ft [0.3 m]
Hard sandstone	4 ft [1.2 m]
Shales and marls	5 ft [1.5 m]
Cephalaspis Bed. Fine-grained sandstone, packed with fishes: abundant *Hemicyclaspis* complete, *Auchenaspis* rarer. *Lingula* spp.	3 ft [0.9 m]
Blue shales with *Pterygotus*	1 ft [0.3 m]
Red shales and marls with rare thin sandstones	80 ft [24.4 m]
Lingula Bed (?lens). Greenish grey shales. *Lingula* common, plus *Pterygotus*	4 ft [1.2 m]
Shales and marls	109 ft [33.2 m]
Laminated shales with thin sandstone	9 ft [2.7 m]
Shales and marls	33 ft [10.1 m]
Downton Sandstone. Contains *Onchus murchisoni* (Woodward, 1891a)	58 ft [17.7 m]
Upper Ludlow	90 ft [27.4 m]
Aymestry Rocks	



1 Aymestry rocks, about 3 metres
2 Upper Ludlow rocks, about 42.5 metres
3 Downton Sandstone. with red, grey and yellow marls
4 red marls, with grey spots
5 mottled marls
6 red marl with *Pteraspis*
7 red sandstone
8 red marl
9 grey shale
10 purple marls and shale
11 purple sandstone
12 grey marl and grey rock: red and blue marls; yellowish-grey sandstone, 46 cm; greenish shale 15 cm; dark-grey sandstone 20 cm; deep-red micaceous shale
13 marl
14 grey rock
15 marl
16 grey rock
17 marly rock, with *Pterspis*; some of the hard bands finely laminated
18 grey rock
19 marly rock
20 grey rock
21 marly rock, with *Cephalaspis*
22 grey rock
23 marl
24 grey rock
25 marl
26 grey rock
27 marl, with some bands of sandstone

Figure 3.13 Section at Ledbury railway cutting recorded by Symonds (1860). Even more than 100 years later much of this section was still visible; recently, however, much of the western end has become obscured.

nel and during the expansion of the station yard in 1898 (Symonds, 1860; Piper, 1890, 1898). The resulting large museum collections of eurypterids and osteostracans include many well-preserved headshields, plus more complete (i.e. head, body and tail) specimens of *Hemicyclaspis*. These have frequently been figured and described (e.g. Lankester, 1867, 1870; Woodward, 1891a; Stensiö, 1932, 1964; White and Toombs, 1948; Denison, 1951a, 1951b; Janvier, 1985a, 1985b). The complete *Hemicyclaspis* from the site is frequently figured as an example of the (supposedly) typical cephalaspid body and tail (e.g. Stensiö, 1932; Moy-Thomas and Miles, 1971).

Description

The section originally exposed at Ledbury dipped steeply, 71° N/NW (Symonds, 1860). The so-called 'Passage Beds' (Downtonian), predominantly grey sandstones and siltstones, were exposed in the station yard. In 1898 this cutting was dug back farther, putting the entrance to the tunnel farther back and to the east. At the time, this was regarded as the finest and most complete section through this group of rocks (Symonds, 1859a, 1860, 1861, 1872; Figure 3.13).

Symonds' (1872) section differs from that measured by Piper (1898), but unfortunately subsequent workers have followed Symonds' section. Piper had been able to delimit the various fish beds, each of which differed in faunal assemblage and preservation. Symonds' section totals 9 ft (2.7 m) for the Downton Sandstones and 272 ft (83 m) for the Temeside Beds, while Piper measured 58 ft (180 m) for the Downton Sandstones and 400 ft for the Temeside Beds. Piper's section is of greater thickness than that of Symonds, so it is conceivable that faulting may have repeated parts of the total sequence. This section is the type example of the Ledbury Group, described as 225 m of alternating thick red mudstones and red to purple micaceous sandstones with abundant vertebrates in the lowest 120 m. It is correlated with the Ledbury Formation of the Clee Hills area which overlies the Temeside Formation (Allen, *in* House *et al.*, 1977). The section, based on Piper (1898) is given in Table 3.1.

The Ludlow Bone Bed was not seen in this section, but it was discovered nearby, in a small cutting linking the station yard with a quarry (Piper, 1890).

The existing section, some tens of metres thick, is exposed at the entrance to the present tunnel (Allen and Tarlo, 1963). Each cyclothem has a lower part of sandstone with an erosive base, and an upper part of fine-grained material. A fine-grained well-sorted sandstone in the middle of the section shows cross-bedding and flat-bedding, and has basal siltstone clasts above a sharp erosional base that cuts into a burrowed siltstone. It is interpreted as a channel on a tidal flat and contains broken, well-sorted faunal remains, including fishes, thought to have been deposited in channels which were swept by the tide. Presumably this is the source of the fossils listed as 'small ostracoderm shields, fish spines and *Lingula cornea*' (Lawson, 1955), and of a *Thelodont parvidens* thelodont assemblage (S. Turner, pers. comm., 1982).

Fauna

AGNATHA
Osteostraci: Tremataspiformes: Didymaspididae
Didymaspis grindrodi Lankester, 1867
Osteostraci: Thyestiformes: Thyestiidae
Auchenaspis egertoni Lankester, 1870
Osteostraci: Ateleaspiformes: Ateleaspididae
Hemicyclaspis murchisoni (Egerton, 1857)
H. lightbodii (Lankester, 1870)
Heterostraci: Eriptychiformes: Tesseraspididae
Kallostrakon sp.

GNATHOSTOMATA
Acanthodii: Climatiiformes: Climatiidae
Onchus sp.
Acanthodii *incertae sedis*
Plectrodus sp.

Auchenaspis heads were first found here in 1858, at almost the same time as they were discovered at Ludlow. The body was unknown (Symonds, 1872) until March 1882, when Piper discovered the first articulated specimens in the Ledbury cutting, and subsequently found complete specimens in beds beneath the '*Auchenaspis*' Grits where *Auchenaspis* head-shields had first been found in profusion (Piper, 1890). These remain the only articulated material of *Auchenaspis*. Heads of fishes within the *Auchenaspis* Grits were said by Symonds (1872) to be 'so abundant that as many as four heads were found upon a small slab a foot in diameter'. Further, Symonds (1861) described the site at the western end of Ledbury Tunnel as 'the grey curtain of rock, charged with the relics of long extinct fish, that stood so boldly out with the red shales in the foreground ...'.

Auchenaspis egertoni was described by Lankester (1870) as a second species of the genus that had been described first from Ludlow Railway Cutting as *Auchenaspis salteri* Egerton, 1857. Woodward (1891a) synonymized *Auchenaspis* with *Thyestes*, a view followed by Stensiö (1932, 1964). Stensiö (1932) based his understanding of *Auchenaspis* on 40 specimens of *A. egertoni*, including articulated remains showing the trunk region, from Ledbury. Subsequent workers (e.g. Janvier, 1985a) have also based their assumptions about the genus on an examination of the better preserved and more numerous material from Ledbury, and ignored the rarer original material of *A. salteri* from Ludlow.

Stensiö (1932) noted that the trunk of *Auchenaspis* decreased in width rapidly backwards, so was probably short (Figure 3.14; reconstruction of *A. egertoni* in Stensiö, 1932). There is no anterior dorsal fin, or dorsal ridge scutes as in cephalaspids and *Hemicyclaspis*. *A. egertoni* is slightly larger than *A. salteri*, being at most 50 mm long (Stensiö, 1932), and it has longer cornua than *A. salteri*.

Janvier (1985a) accepted that *Auchenaspis* is distinct from *Thyestes*, but he found no shared characteristics between the two species. He (Janvier, 1985b) attributed all the material to a single species, *Auchenaspis salteri*, arguing that they were considered to be separate species largely because of the difference in size. However, re-examination of all the material may confirm that the size ranges of the two species do not overlap, that the cornua have different size and shape, and that *A. egertoni* has a longer abdominal region. The species of *Auchenaspis* are basal forms in a phylogenetic series of 'prothyestids', from *Procephalaspis oeselensis*, *A. salteri*, *A. egertoni*, *Witaaspis schrenki* to *Thyestes verrucosus* (Janvier, 1985a, fig. 65).

A single small specimen of *Didymaspis grindrodi* was found in beds immediately over-

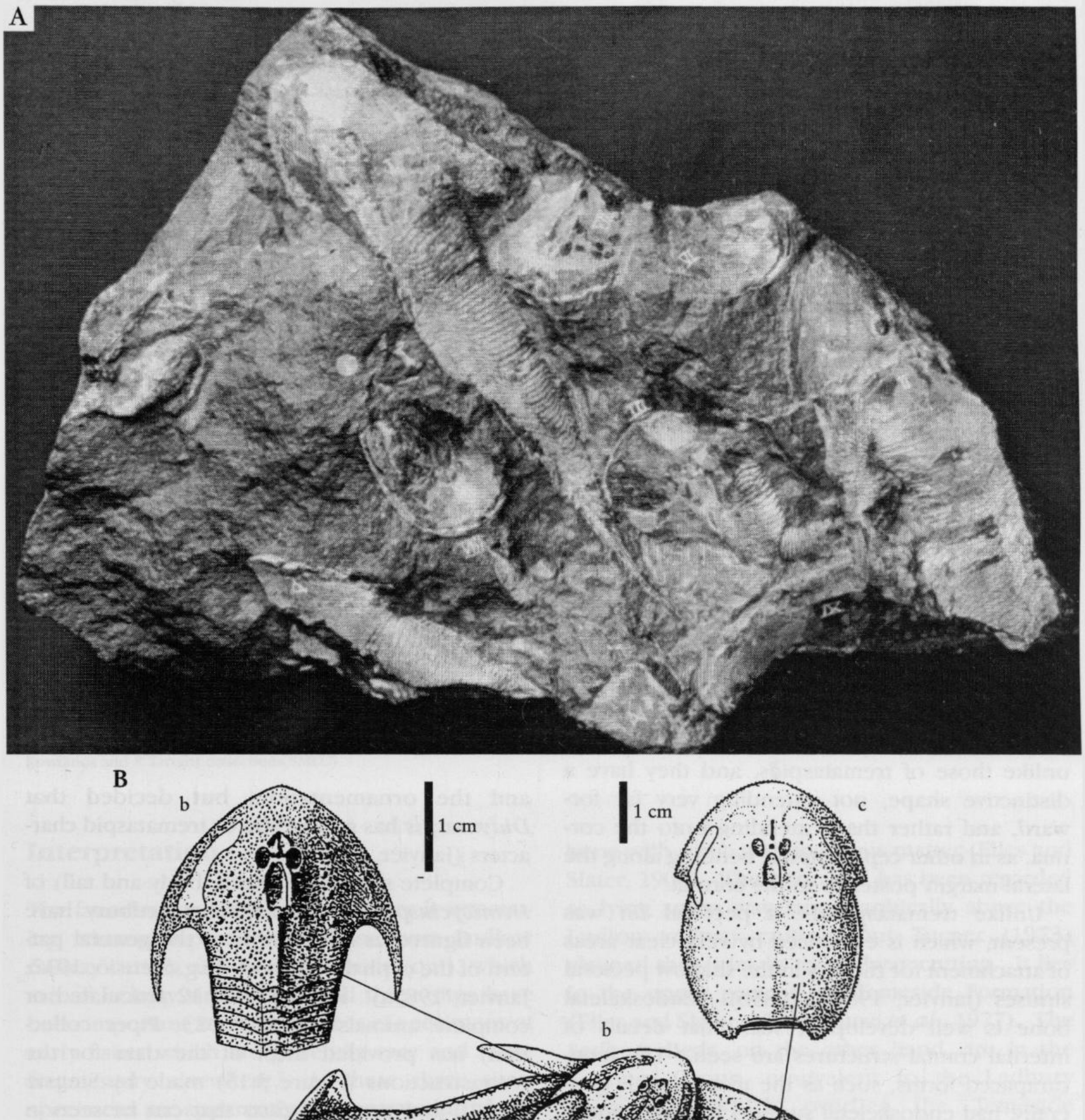


Figure 3.14 Osteostracans from the Ledbury cutting. (A) *Hemicyclaspis murchisoni* Egerton in rare preservation, one of many such slabs collected over 100 years ago, *c.* × 0.25, (photograph courtesy The Natural History Museum,London, T05398/A). (B) Restoration of vertebrates found at Ledbury: a, *Hemicyclaspis murchisoni*; b, *Auchenaspis egertoni* Lankester; c, *Didymaspis grindrodi* Lankester (from Blieck and Janvier, in press).

lying the *Auchenaspis* Grits by Dr J. Grindrod in the 1860s. This long-carapaced form was recognized as cephalaspid in character by Lankester (1867), who named and subsequently illustrated it (Lankester, 1870). Stensiö (1932) redescribed the species (Figure 3.14), having 16 specimens available to him, not only from Ledbury Cutting but also from Man Brook, Trimpley, and Bush Pitch, Ledbury. The Man Brook site yielded further specimens in the 1950s. *Didymaspis grindrodi* is the single representative of the genus, and has been found at several sites in the Downtonian of the Welsh Borders, and also (possibly) in Russia (Janvier, 1985b).

The shield is very long, and the cornua project laterally, but are short and indistinct, superficially resembling those of tremataspids. The headshield bears an obtuse dorsal median crest (Stensiö, 1932), whereas the ventral surface is flat. The rostral margin is rounded. The nasohypophysial opening is a long notch at the bottom of a hollow, which is unlike any comparable osteostracan. The dorsal field is short, and the external openings of the endolymphatic duct are situated within it. There is no independent pineal plate. The lateral fields are continuous, unlike those of tremataspids, and they have a distinctive shape, not extending very far forward, and rather than extending onto the cornua, as in other cephalaspids, bending along the lateral margin posterior to the cornua.

Unlike tremataspidids, a pectoral fin was present, which is evidenced by very clear areas of attachment for the fins in the shallow pectoral sinuses (Janvier, 1985a, 1985b). Endoskeletal bone is well developed, such that details of internal cranial structures are seen. The long-carapaced forms, such as the tremataspids generally, had endoskeletal support for the posterior part of the shield, which in Tremataspididae took the shape of a short ventro-lateral prolongation in the scapular region (Janvier, 1985a). *Didymaspis* had a greater development of this support which, unlike tremataspids, consisted of a relatively long blade of endoskeleton strengthening the ventro-lateral edge of the abdominal division (Janvier, 1985a).

The relationships of *Didymaspis* are unclear. Denison (1961) believed it was a tremataspidid since the long headshield resembled that of *Trematаspis* from Estonia. However, Janvier (1985a) suggested that *Didymaspis* may show affinities with kiaeraspids because of the absence of a pineal plate, the shape of the lateral fields

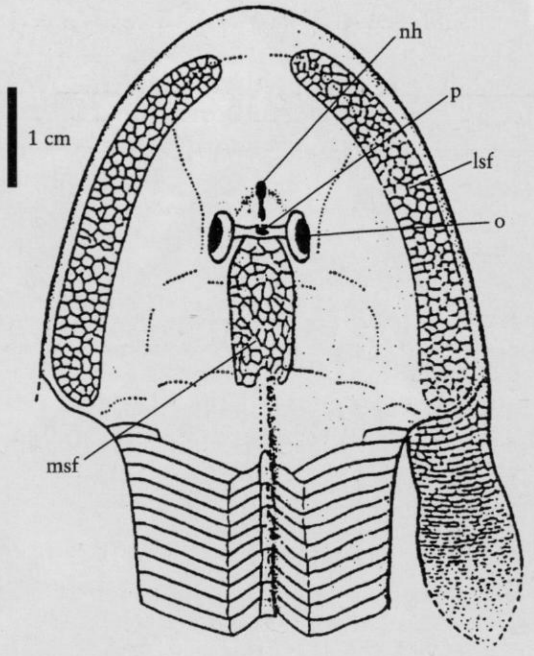


Figure 3.15 *Hemicyclaspis murchisoni* Lankester, detail of the dorsal surface of the headshield: p, pineal foramen; o, orbits; nh, nasal hypophysis; lsf, lateral sensory field; msf, median sensory field (after Stensiö, 1932).

and the ornamentation, but decided that *Didymaspis* has no thyestid or trematаspid characters (Janvier, 1985b).

Complete specimens (head, body and tail) of *Hemicyclaspis murchisoni* from Ledbury have been figured as an example of the general pattern of the cephalaspid body (e.g. Stensiö, 1932; Janvier, 1985a). A block with 12 articulated or complete animals (NHM P6023; Piper collection) has provided most of the data for the reconstructions (Figure 3.15) made by Stensiö (1932), and provided casts that can be seen in several museums. The pectoral fins were well developed, the anterior dorsal fin was reduced to a high dorsal crest made up of imbricating scutes, and situated well back on the body there was a small posterior dorsal fin, which was supported on its anterior edge by a thick spine. The tail was heterocercal, and the fin membrane was divided into three lobes. A full description is given in the Temeside report, the type locality of this species.

Specimens labelled *Pteraspis* n. sp. in OUM are all *Kallostrakon* (White and Toombs, 1948), an enigmatic heterostracan. Remains of the acanthodians *Onchus* sp. and *Plectrodus* sp. consist of isolated fin spines.

Table 3.2 Comparison of faunal assemblages at Ludlow railway cutting, Temeside and Ledbury.

Ludlow railway cutting		Temeside		Ledbury	
Hemicyclaspis lightbodii		*H. lightbodii*	R	*H. lightbodii*	R
H. (prob.) *murchisoni*	C	*H. murchisoni*	R	*H. murchisoni*	R
		?Hemicyclaspis sp.	R		
Auchenaspis salteri		*Au. ?salteri*	R	*Au. egertoni*	A
Onchus murchisoni		*Onchus* spp.	C	*Onchus* spp.	R
		Pl. mirabilis	C		
Plectrodus sp.		*Plectrodus* sp.	A	*Plectrodus* sp.	R
		climatiid sp.	C		
		ischnacanthid sp.	C		
Pterygotus anglicus		*Pt. banksii*	C		
Pt. ludensis	A	*Pterygotus* sp.	C		
Pt. gigas	R				
Pt. problematicus	C				
Stylonurus megalops					
Eurypterus pygmaeus	?R	*Eurypterus* spp.			
Eu. acuminatus	?R				
Lingula cornea	C	*L. cornea*	R	*Lingula* sp.	C
		plant material	A	plant material	?

A = abundant, C = common, and R = rare (compiled from Woodward, 1872; Elles and Slater, 1906; Piper, 1895; Stensiö, 1932; M.A. Rowlands and P. Tarrant collections,SMLU).

Interpretation

The faunal assemblage from Ledbury is interesting when compared with those from Ludlow railway cutting and from Temeside (q.v.), which are all of very similar age. All three sites have been important and rich sources of specimens of early fishes which are generally rare and more fragmentary elsewhere. At these three sites, specimens are apparently concentrated in abundance within 'fragment' bone beds. The material from these three sites is compared in Table 3.2.

The bone bed at Ludlow railway cutting has been described as 'dark micaceous shales' (Egerton, 1857, and as a 'grit band with fishes' (Murchison, unpublished sections in Ludlow Museum, *c.* 1852; see Antia, 1981, pp. 164–5). Two lithologies are represented by specimens in the NHM, one is a grey-green rippled siltstone packed with fragments of *Hemicyclaspis*, and arthropods plus *Lingula cornea*, the second is a buff to greenish grey grit with *L. cornea*. The Temeside Bone Bed has been described as a grey calcareous grit containing large fragments of bone with some carbonaceous matter (Elles and Slater, 1906). The bone bed has been regarded as lying some way stratigraphically above the Ludlow railway cutting, but Turner (1973) claimed that it lay in the railway cutting. It lies in the upper part of the Temeside Formation (Elles and Slater, 1906; House *et al.*, 1977). The Ledbury Beds, on the other hand, are in the Ledbury Group, equivalent to the Ledbury Formation, which overlies the Temeside Formation (Allen, *in* House *et al.*, 1977). However, the great similarity between the sites has been recognised (Salter, 1851; Roberts, 1861; Symonds, 1860, 1861). The Ledbury Grits of Piper's (1898) section are remarkably similar in lithology to the fragment beds near Ludlow, whereas all the lower fish beds of the Ledbury section have similar faunal assemblages to the Temeside Group fish beds of the Ludlow area. The exception is the upper part of the Ledbury section, described as red marls and sandstones, which bear *Kallostrakon* and *Didymaspis*. Similarly, in the Clee Hills area, higher Downtonian beds within the Ledbury Formation yield these two genera, together with

Hemicyclaspis murchisoni and *Auchenaspis* (Allen, *in* House *et al.*, 1977). However, the two do not occur in the Temeside Bone Beds, which may conform to a facies change (Allen and Tarlo, 1963) from intertidal and subtidal sediments that contain brackish-water *Hemicyclaspis* and acanthodians, to fluviatile and intercalated tidal sediments which hold probably freshwater *Kallostrakon* and *Didymaspis* (Allen and Tarlo, 1963), together with the brackish-water forms. Differences between the assemblages, in particular the similar species (e.g. *Auchenaspis salteri* from Ludlow, which is very similar to *A. egertoni* from Ledbury) may represent different environments or time horizons.

Conclusion

The Ledbury site is of particular palaeontological importance and conservation value because two of the fish-bearing horizons yielded complete specimens of *Auchenaspis* and *Hemicyclaspis*. This is the only site for complete *Auchenaspis*, whereas complete *Hemicyclaspis* has also been found in the Downton Castle Sandstone Formation at Gornal in the West Midlands (Wills, 1948; Ball, 1951; Allen and Tarlo, 1963). Articulated and whole specimens of cephalaspids are extremely rare in the Welsh Borders, and complete cephalaspids elsewhere in Britain are only known from later Old Red Sandstone sites. Ledbury is also the type locality of the only known species of the enigmatic osteostracan *Didymaspis*. The total fossil assemblages from Ledbury and two other coeval sites suggest different habitats.

Nowadays only a few metres of rock are seen at the entrance to the railway tunnel at Ledbury. Fishes may still be collected from red marls and siltstones here which yield 'small ostracoderm shields, fish spines and *Lingula cornea*' (Lawson, 1955), and a *Thelodus parvidens* thelodont fauna (S. Turner, pers. comm., 1982).

TEMESIDE, LUDLOW (SO 520742)

Highlights

This Shropshire site has yielded a rich fauna of hemicyclaspids and acanthodians from an early example of a typical Old Red Sandstone fish-bearing channel. *Hemicyclaspis murchisoni* is well represented in collections from here, which is probably the type locality.

Introduction

On the right bank of the Teme, opposite the site of the Old Paper Mill in Ludlow, is found the earliest known typical fish-bearing channel fill in the Welsh Borders. This type of bed-form occurs commonly in the upper part of the Downtonian and Dittonian, but this is the only example known in the lower Přídolí and therefore the faunal assemblage contained within it is important. The specimens are thought to represent species that inhabited tidal areas, as the earliest channels were probably swept by erosive currents or tides. Many new specimens have been discovered here during recent excavations. Fossils occurred throughout the channel infill and were mainly hemicyclaspids and acanthodians, plus fragments of plant and arthropod.

The local geology was described several times prior to Elles and Slater (1906), Lightbody (1869) and Antia (1981). The site has been known to palaeontologists for 140 years, and reference to the fish fauna has been made by Egerton (1857), Murchison (1853), Roberts (1865), Lankester (1870), Woodward (1891a), Kiaer (1931), Stensiö (1932), White (1950a), Allen and Tarlo (1963), and Janvier (1985b).

Description

The Temeside Shale Formation succeeds the Downton Castle Sandstone Formation at Ludlow, but the junction is not seen there. The section along the River Teme shows the Lower Temeside Shale Formation, then a gap, probably representing a considerable thickness of shales (Elles and Slater, 1906), followed by the section described below. It exposes about 6 m of the upper part of the Temeside Shales within which are several 'beds' containing fish remains, in particular the fish-bearing channel that has recently been fully repeated by rockfalls, which was previously thought to be a planar bed, and named the 'Temeside Bone-Bed' (Elles and Slater, 1906; Figure 3.16).

Murchison (1854) first drew attention to a fish-bearing locality on the river Teme at Ludlow. Egerton (1857) reported the discovery of 'scanty' fossil fish material by Lightbody at the Ludlow railway cutting and from 'a grit bed below the Paper Mills on the Teme at Ludlow' (i.e. Temeside) which together yielded fossils he described as acanthodian spines and jaws, and *Hemicyclaspis murchisoni* Egerton. Symonds

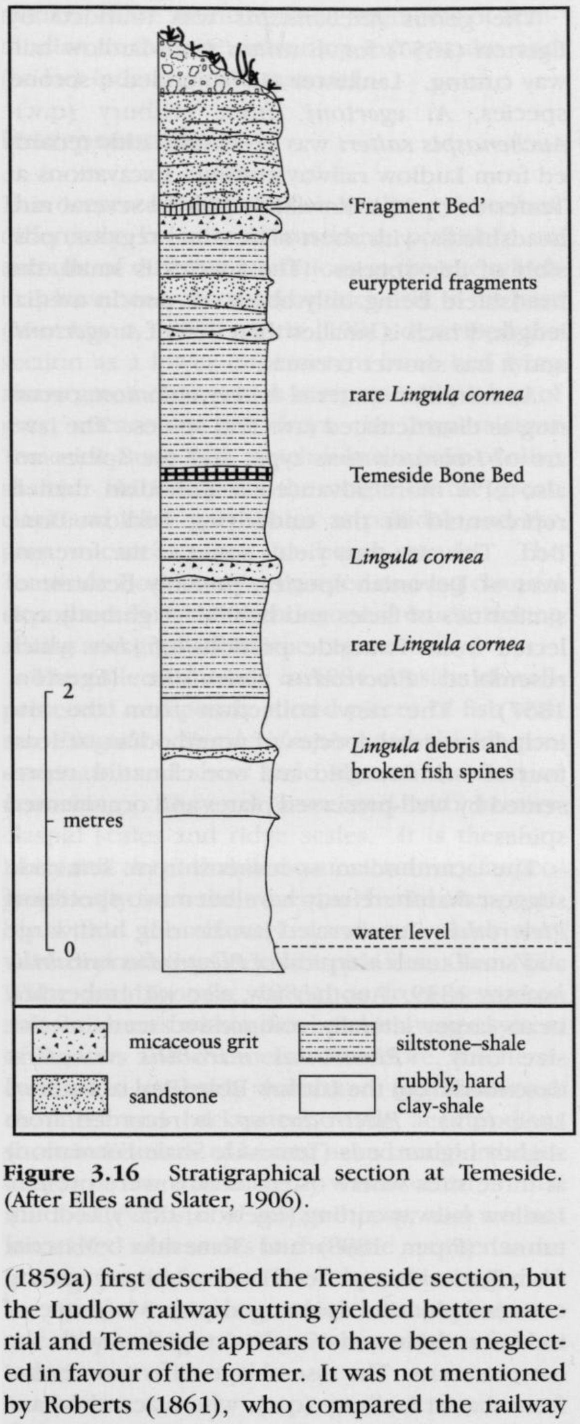


Figure 3.16 Stratigraphical section at Temeside. (After Elles and Slater, 1906).

(1859a) first described the Temeside section, but the Ludlow railway cutting yielded better material and Temeside appears to have been neglected in favour of the former. It was not mentioned by Roberts (1861), who compared the railway cutting at Ludlow to the newly discovered cutting at Ledbury.

In a long footnote on these new sites Murchison (1853), regarded the Temeside fish bed as being above the Ludlow railway cutting fish bed, but not yielding *'Trochus helicites'* as does the railway cutting bed. Interestingly, Murchison also described the section here on the right bank of the River Teme as having a heavy cover of drift and gravel, so perhaps the exposure was much poorer in the past and thus received little attention from collectors.

Elles and Slater (1906) gave a vertical section (Figure 3.16), but denoted the channel as a grit bed, with an overlying 'Temeside-Bone-Bed' containing large fragments of bone and fish spines. They did not describe the palaeontology. Recent examination showed that the fishes were not contained in a planar bed, such as is seen at similar horizons in the Downton Gorge area, but that the source is an infilled channel cut into the underlying silts. Antia (1981) measured the section and sampled the fauna throughout. He drew the Temeside Bone Bed as a laterally impersistent bed (= a 'shoestring').

Fauna

AGNATHA
Osteostraci: Thyestiformes: Thyestiidae
Auchenaspis ?salteri Egerton, 1857
Osteostraci: Ateleaspidiformes: Ateleaspididae
Hemicyclaspis murchisoni Egerton, 1857
H. lightbodii (Lankester, 1870)

GNATHOSTOMATA
Acanthodii: Ischnacanthiformes: Ischacanthidae
Plectrodus mirabilis Agassiz (in Murchison, 1839)
Plectrodus sp.
Acanthodii: Acanthodiformes: Acanthodidae
Onchus spp.
Onchus murchisoni Agassiz, 1837
Ischnacanthids indet.

Based on collections made in 1984 by M.A. Rowlands, the faunal assemblage consists mainly of vertebrate fragments and whole shields of *Hemicyclaspis* sp., together with acanthodian spines and scales, and rarer jaws. Also occurring are *Lingula cornea* (not *in situ*), occasional large pieces of *Prototaxites*, and some large plates of *Pterygotus* sp.. *Auchenaspis ?salteri* is much rarer with only a few fragments found. Acanthodian spines and jaws are common here, indicating several species of ischnacanthid and one climatiid. The taxa recorded include the osteostracans *Hemicyclaspis murchisoni*, *Hemicyclaspis lightbodii*, *?Hemicyclaspis* sp., *Auchenaspis ?salteri*, *Plectrodus mirabilis* Agassiz, 1839 and *Plectrodus* sp., together with acanthodians including two or three species of ischnacanthid jaws, *Onchus* spp., climatiid spines and pectoral plates. For comparison, the railway cutting yielded *Plectrodus* sp., *Onchus murchisoni*, *Lingula cornea*, *Beyrichia kloedeni* (these four also found in the lower bone bed), plus *Hemicyclaspis (Cephalaspis ornatus) Hemicyclaspis murchisoni* var. *ludlowiensis*, *Auchenaspis salteri*, *Pterygotus anglicus* and *Eurypterus pygmaeus*.

Hemicyclaspis murchisoni has a distinct cornual angle and rounded rostral angle. The sclerotic ring consists of a continuous circular piece of bone. It had a continuous superficial layer, and the mucous canal system (except posteriorly) is enclosed. Egerton (1857) named the species from a specimen collected opposite the Paper Mill, Temeside. He erected two species, *Cephalaspis murchisoni* from the Paper Mill, and *C. ornatus* from Ludlow railway cutting. Lankester (1870) showed that they were both *C. ornatus*, being preserved differently, and showing an ornament of 'denticles', whilst those from Temeside were preserved as thin decalcified films within the sandstone. Recently collected material from Temeside contains both forms, both being jumbled together within the poorly sorted channel deposits. It appears that the ventral rims and ventral surface of the cornua were thick and heavily ornamented, whereas the dorsal surface was probably of thinner bone, and was likely to be crushed and demineralized during preservation. *H. murchisoni* is recorded from several lower Downtonian sites in the Welsh Borders, and is also found in Norway (Kiaer, 1931) and Somerset Island, Arctic Canada (Dineley, 1968). The genus *Hemicyclaspis* ranges from Lower Ludlow to the Downton Group, and is regarded as an index fossil for the lowest part of the Downton Group (White, 1950a).

Hemicyclaspis lightbodii was established on a fragmentary ventral rim by Lankester (1870), who found it impossible to decide to which subgenus of *Cephalaspis* it belonged. It has a more pronounced rostral angle than *H. murchisoni*. The superficial layer is present only in the tubercles which form the ornamentation. Some of those tubercles are hooked. The mucous canal system forms an open network on the surface of the shield. The type locality is Ludlow railway cutting (in a grey-green mudstone with *Lingula cornea* and arthropod cuticle), and the species is also known from the Paper Mill, Temeside (NHM specimen).

The genus *Auchenaspis* was founded by Egerton (1857) for *A. salteri* from Ludlow railway cutting. Lankester (1870) added a second species, *A. egertoni*, from Ledbury (q.v.). *Auchenaspis salteri* was previously only recorded from Ludlow railway cutting. Excavations at Temeside by M.A. Rowlands yielded several rare headshields with short abdominal regions, possibly of this species. The species is small, the headshield being only about 12 mm in medial length, which is smaller than that of *A. egertoni*, and it has shorter cornua.

Acanthodian material is very common, occurring as disarticulated jaws and spines. The jaws are of *Ischnacanthus* type, and the spines are also of a more advanced acanthodian than is represented in the underlying Ludlow Bone Bed. This site thus yields some of the forerunners of Devonian species, possibly because of similarities of facies and habitat. Lightbody collected from Temeside portions of jaws which resembled *Plectrodus mirabilis* (Egerton, 1857). The new collection from the site includes several species of acanthodian, at least four of ischnacanthid and one climatiid, represented by well-preserved plates and ornamented spines.

The acanthodian specimens from Temeside suggest that there may have been two species of *Plectrodus*. A tubercled jaw bearing both large and small teeth is typical of *Plectrodus mirabilis* Agassiz, 1839. Another jaw, also with tubercles, bears larger laterally compressed teeth of one size only. *Plectrodus mirabilis* was first described from the Ludlow Bone Bed of Ludford Lane (q.v.). *Plectrodus* sp. is recorded from slightly higher beds (Temeside Shale Formation) at three sites where osteostracans were prolific, Ludlow railway cutting (Egerton, 1857), Ledbury tunnel (Piper, 1898) and Temeside. Material from Temeside and from Ludlow railway cutting contains plentiful spines and pieces of bone of ischnacanthids and '*Onchus*' together with the osteostracans. The assemblage differs somewhat from that at Ledbury (q.v.), where acanthodians seem to have been rarer.

Other much larger ischnacanthid jaws, up to 60 mm long, abound and represent at least three types. Slender ischnacanthid spines are the most common form of spine and also several different forms of '*Onchus*' spine occur. Climatiids are represented by ornamented spines and shoulder girdles. The ornament is similar in all this material, so it is from a single species of climatiid. There are many small fragments of acanthodian at this site, including many scales and (so far) indeterminate material.

Interpretation

This occurrence of fossil fish has been described differently by several workers, probably on account of differing conditions at the site which may have been obscured by thick drift in the past (Murchison, 1853). Antia (1981) described the section as a lower impersistent bone bed lying above green clays, which is separated by a bed of grey micaceous grit from the impersistent Temeside Bone Bed, which is at the base of olive shales. He interprets the origin of the green clays and olive grey-shales as paludal, and the grey micaceous grit as beach sands. The Temeside Bone Bed is regarded as a lag channel deposited in back-beach lagoonal muds, during a long and gradual marine regression.

The collection made in 1984 consists of well-preserved and poorly sorted pieces of fish with rare *Lingula*. *Hemicyclaspis* head shields predominate, and show little sign of abrasion or reworking. They are associated with hemicyclaspid scales and ridge scales. It is therefore likely that they inhabited waters not very far geographically from their eventual burial site, possibly within the channel system in which they were deposited (cf. cephalaspids from Cwm Mill; White and Toombs, 1983), or from reworked soft sediments within this brackish-water system of lagoons and channels. Therefore, the hemicyclaspids probably inhabited brackish-water channels and backwaters. The acanthodians show indications of having been transported for longer or more thoroughly water-sorted, in that the fossils consist of isolated jaws, and are not associated with scales in the same manner as the hemicyclaspid fossils. They represent large fishes, up to 30 cm long, which occupied marine waters, possibly entering river systems to feed or breed.

Conclusion

The Temeside site has experienced recent improvement in exposure and its conservation value results from the production of an important early Přídolí fauna of fishes, particularly of acanthodians and osteostracan agnathans. The osteostracan *Hemicyclaspis* is particularly well represented: this site is the type locality for one species, and is a source of other varieties and species of the genus. Recent collecting indicates the continuing potential of the site.

TITE'S POINT (PURTON PASSAGE; SO 688046)

Highlights

This Gloucestershire site has produced a *Thelodus parvidens* fish fauna, evidence that its age matches that of the Ludlow Bone Bed. It is particularly important as an early source of specimens of the heterostracan fish *Cyathaspis*, and it is also notable as the most southerly of the Welsh Borders late Silurian fish sites, possibly lying close to the coast of that time.

Introduction

At low tide, Leintwardine (Ludlow) and Downton Castle Sandstone Formation beds are exposed on the eastern shore of the River Severn to the west of Tite's Point, Gloucestershire. The outcrop consists of the core of an anticline, plunging north-north-west, dipping 30° towards the north-west and 5° towards the north-east (Cave and White, 1971, p. 241). To the west and north-west, the Lower Old Red Sandstone is in depositional contact with the underlying Ludlow beds, but the exposure is extensively faulted, with faults becoming more numerous to the east close to a large north–south trending pre-Triassic fault. The Downton Castle Sandstone Formation in the east has a faulted contact with the Ludlow rocks (Figure 3.17).

The geology of the site has been described by Murchison (1839), Phillips (1848), and Holland *et al.* (1963), and the fish fauna by Murchison (1839), Phillips (1848), Huxley and Salter (1856), Cave and White (1971) and Turner (1973). The locality figures in the Geologists' Association Guide to the Silurian inliers of the Welsh Borders (Lawson *et al.*, 1982).

Description

The succession at Tite's Point (Curtis, 1972; Cave, 1977; Cocks *et al.*, 1992) is:

	Thickness (m)
Upper Old Red Sandstone	?
(unconformity)	

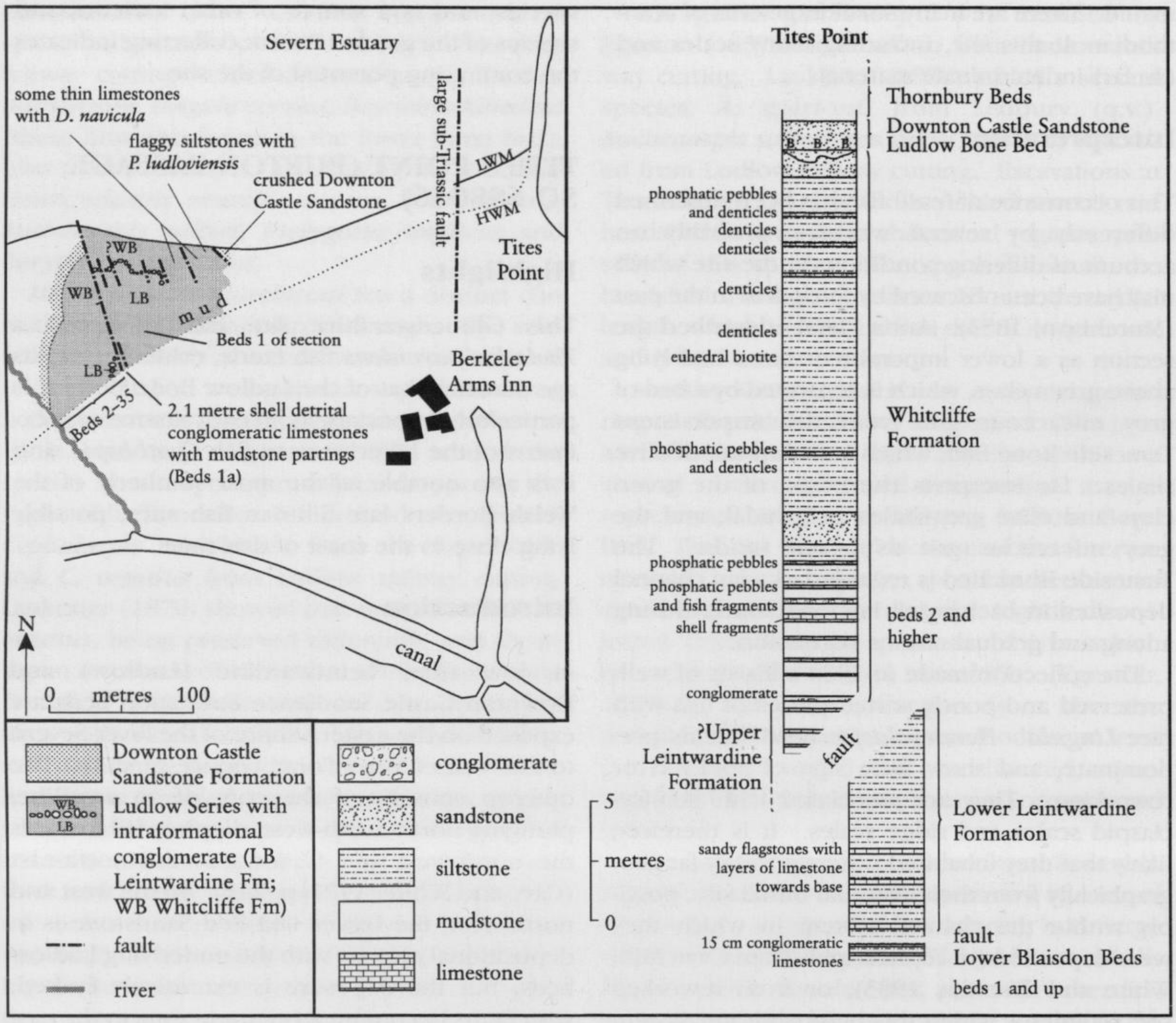


Figure 3.17 Sketch map of the GCR site at Tite's Point, and stratigraphical section (after Cave and White, 1971).

Přídolí Series		
	Thornbury Beds	?
Ludlow Series		
Ludfordian Stage		
	Whitcliffe Formation	21.8
	Leintwardine Formation	13.5
Gorstian Stage		
	Bringewood Formation	25+

The Whitcliffe Formation is a succession of silty mudstones, siltstones and thin limestone layers. The last mentioned occur particularly in the upper part of the sequence, and commonly contain a concentration of brachiopods, worm tubes, various other organic debris, including small phosphatic pebbles, and fish denticles (Cave and White, 1971). These are the bone beds recorded by Phillips (1848, p. 191): 'at Tites Point are several beds in which white sand drift is mixed with shales and calcareous matter, and each yields scales and teeth', and on p. 226, 'in the the Tortworth country, I discovered several bands of fish remains in the uppermost Ludlow strata on the shore at Pyrton Passage exposed to an unusual degree in 1843; but the full exploration of the bed was prevented by the redeposition of the sediments of the Severn'. In his map and section, Phillips (1848, pl. 3) noted five bone beds in all, while Cave and White (1971) showed seven horizons containing fish fragments or denticles, plus the 'Ludlow Bone Bed', within the overlying sandstones which have channels cut into sandstones at the top of the Whitcliffe Formation below.

The Whitcliffe Formation is overlain by 1.7 m of Thornbury Sandstone (?equivalent to the Downton Castle Sandstone Formation and Clifford's Mesne Sandstone of May Hill). The contact is seen in the west of the section and shows the sandstone channels cutting into the underlying fine-grained sandstone at the the top of the Whitcliffe Formation. This contact cannot always be seen because all but the tops of one or two harder bands are hidden under thick glutinous estuarine mud, and the rock can only be examined after exceptional conditions have swept away this mud. This is not a recent phenomenon: Phillips (1848, p. 191) wrote 'The fish beds ... have been as yet incompletely explored; they are so commonly covered with sediment of the river as to have several times eluded the most anxious search of our indefatigable collectors. In fact the few species which have been extracted were taken by the author of this memoir while engaged in measuring the Palaeozoic Beds and, in several subsequent visits, the fish beds were invisible'.

Murchison (1839), on the other hand, had described exposures of Lias at Purton Passage nearby, which had previously yielded vertebrate fossils, but which were then completely buried under reclaimed land. He described the process by which mud accumulated on lines of piles and osiers, but stressed that the Silurian exposures had not been similarly affected. He figured (p. 446) a sketch of the Silurian rocks showing a fairly complete exposure substantially domed out of the waters of the Severn. He must have viewed the site at a time when the mud had been well scoured away from the section; such a clear exposure cannot be seen today (1994).

Fauna

AGNATHA
Heterostraci: Cyathaspidiformes:
Cyathaspididae
Cyathaspis banksi (Huxley and Salter, 1856)
Cyathaspis sp.
Thelodonti: Thelodontida: Coelolepididae
Thelodus parvidens Agassiz, 1839
T. bicostatus (Hoppe, 1939)
T. pugniformis Gross, 1967
T. trilobatus (Hoppe, 1939)

GNATHOSTOMATA
Acanthodii *incertae sedis*
Onchus sp.
indeterminate jaw fragments and scales

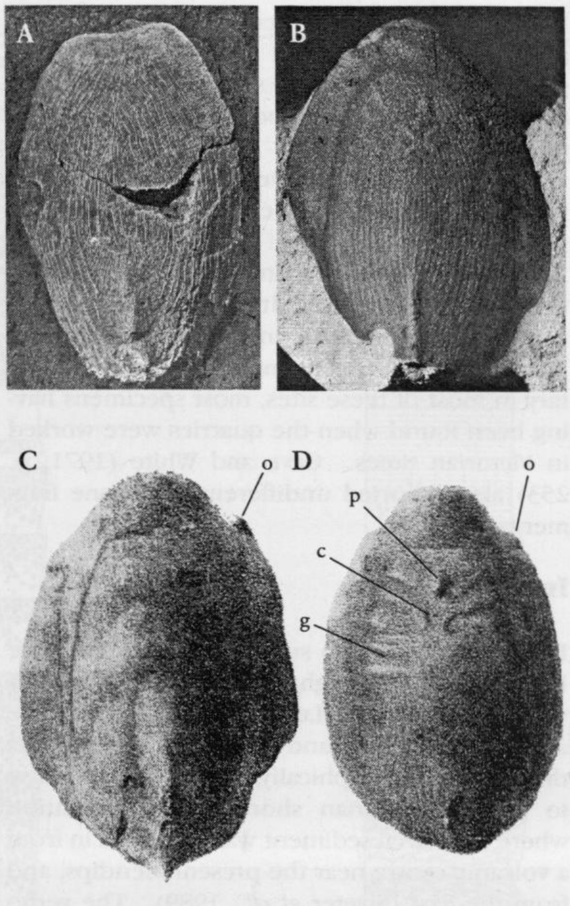


Figure 3.18 *Cyathaspis banksi* Lankester, × 1.25; a primitive heterostracan, relatively common in Ludlow–Přídolí sites in this region. (A) external surface of ventral disc; (B) internal surface of the ventral disc; (C) cast of the internal surface of dorsal disc; (D) impression of the internal surface of the dorsal disc showing position of the gill pouches (g), semi-circular canals (c), orbits (o) and pineal foramen (p). Specimens from Kington, in the Museum of Practical Geology when figured by Lankester (1868).

Tite's Point was sampled by Turner (1973) for thelodonts which are abundant in the upper Whitcliffe Formation bone beds; they constitute a typical *Thelodus parvidens* fauna (see Ludford Lane report). Acanthodian scales and a jaw are also recorded.

The bone bed at the base of the Thornbury Beds, associated with the channelling, contains a concentration of fish fragments, including *Cyathaspis banksi* scales and *Onchus* sp. spines (Huxley and Salter, 1856), which Cave and White (1971) suggest are indicative of the Ludlow Bone Bed horizon (Figure 3.17). *Cyathaspis* is relatively common, a scale having been found by Cave and White (1971), and an old record of a 'swarm of shields on a bedding plane, exposed after a storm had swept away all the mud' is given. Tite's Point is one site where *Cyathaspis* can be found when the rocks are exposed above the mud (Figure 3.18).

Cyathaspis is a primitive heterostracan, found in the Welsh Borders, New Brunswick, Siberia and the southern Urals. Its type locality is 'Kington', probably Bradnor Hill Quarry or Ivy Chimney Quarry (q.v.). It is recorded throughout the Late Ludlovian and Early Přídolí of the Welsh Borders. Specimens are rare or fragmentary in most of these sites, most specimens having been found when the quarries were worked in Victorian times. Cave and White (1971, p. 253) also reported undifferentiated bone fragments.

Interpretation

Holland *et al.* (1963) suggest that the Whitcliffe Formation here might represent a brackish-water phase in late Ludlovian times, but Cave and White (1971) found no evidence to support this. Palaeogeographically, Tite's Point lay close to the Late Silurian shoreline, at a location where terrestrial sediment was being fed in from a volcanic centre near the present Mendips, and from the east (Siveter *et al.*, 1989). The vertebrate remains are consistent with a basal Přídolí date.

Conclusion

The conservation value of this site lies in its fish fauna, which contains *Thelodus parvidens* and correlates the succession with the stratotype succession in the Ludlow area, 75 km to the north. In addition, the early heterostracan *Cyathaspis* is reasonably abundant at this site, and there is more potential for collecting. The location of the site is crucial, since it is the farthest south of the Welsh Borders fish sites, apparently close to the late Ludlovian–Přídolí shoreline.

LYDNEY (SO 652017)

Highlights

The cliffs and foreshore at this Gloucestershire site expose a section from Upper Přídolí (Upper Silurian) to Lower Devonian. Late Silurian (Raglan Marl Formation) vertebrates occur at several horizons. Two important Lower Devonian fish beds occur in a section along the foreshore of the River Severn, together with several other fish-bearing horizons. The section includes the type locality of *Sabrinacanthus* Miles (1973).

Introduction

As seen along the foreshore and low cliffs immediately north of the entrance to Lydney Docks, the sequence passes from the intertidal Downtonian Raglan Marl Group (Přídolí) strata to mainly fluviatile (Lower Ditton) St. Maughan's Group sediments. The fishes contained within the successive fish beds differ, and show a change from one faunal assemblage in the Downton sediments to another in the higher horizons. The geology of the section has been described by Welch and Trotter (1961), Allen and Tarlo (1963), Allen (1964, 1973, 1974), and fishes from this site have been considered by Miles (1973) and Denison (1979; Figure 3.19).

Description

The section exposed along the shore at Lydney passes from the mainly intertidal Raglan Marl Group (equivalent to the Ledbury Formation farther north) to the mainly fluviatile St Maughan's Group. The top of the Raglan Marl Group extends at about clifftop level from Cliff Farm north-eastwards along the river, and is well exposed, but to the south of Cliff Farm faulting lowers this horizon to the foreshore (Welch and Trotter, 1961), and St Maughan's Group is seen above in the cliff and inner foreshore. The lowest fish bed is the Fish Conglomerate (= Intraclast conglomerate on Figure 3.19), which is at the base of the exposed section (Welch and Trotter, 1961). Above this, in the upper part of the Raglan Marls, fish remains occur together with bivalve molluscs in the red marls (Allen, 1973).

The boundary between the Raglan Marl Group to St Maughan's Group is marked by the development of pedogenic carbonates, equivalent of the main *'Psammosteus'* Limestones of the Clee Hills area. The top of the Raglan Marl Group was taken as the base of this band of calcrete (Welch and Trotter, 1961), but the top of this bed forms a more consistent, regular plane and may be a better marker horizon (see Figure 3.19). It is rather a sharp transition, and the development of the major and persistent facies

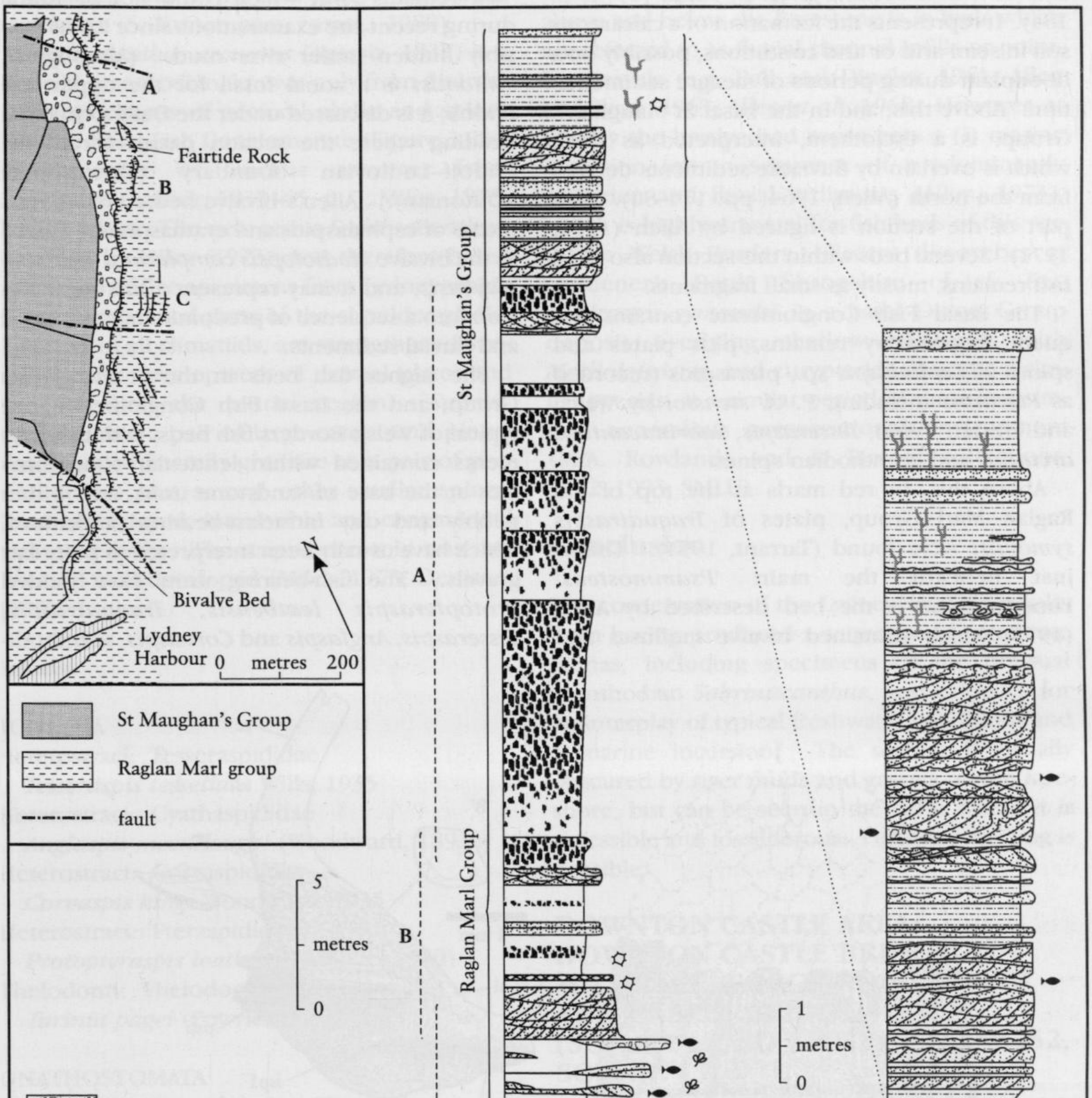


Figure 3.19 Sketch map and section of the outcrop at the cliffs and foreshore at Lydney (after Allen, 1978).

is shown in a section given by Allen (1974, p. 184). It represents the formation of a calcareous soil in semi-arid or arid conditions, possibly on a floodplain during periods of meagre sedimentation. Above this, and in the basal St Maughan's Group, is a cyclothem, interpreted as tidal, which is overlain by fluviatile sediments derived from the north (Allen, 1964, pp. 174–80). This part of the section is figured by Allen (1964, 1971). Several beds within this section also yield fish remains, mostly as small fragments.

The Basal Fish Conglomerate contains frequent fragmentary remains, plus plates and spines of *Cephalaspis* sp., pteraspids (recorded as *Pteraspis* including *P.* cf. *stensioi* by Welch and Trotter, 1961), *Tesseraspis*, *Sabrinacanthus arcuatus* and acanthodian spines.

Above this, in red marls at the top of the Raglan Marl Group, plates of *Traquairaspis symondsi* were found (Tarrant, 1991). This is just beneath the main *'Psammosteus'* Limestone, as is the bed described by Allen (1973) which contained bivalve molluscs and 'fish remains', but which could not be found during recent site examinations since it was possibly hidden under river mud. (Although *T. symondsi* is a zonal fossil for the uppermost Přídolí, it is discussed under the Devil's Hole site heading where the section passes across the Přídolí–Ludlovian boundary (Downtonian –Dittonian).) Allen's bivalve bed contains fragments of cephalaspids and cyathaspidids, as well as the bivalve *Modiolopsis complanata* var. *trimpleyensis*, and it may represent a marine incursion into a sequence of predominantly estuarine and fluvial sediments.

The higher fish beds in the St Maughan's Group, and the Basal Fish Conglomerate, are typical of Welsh Borders fish beds, with fish fragments contained within lenticular conglomerates at the base of sandstone units, and within pebbly and clay intraclast-bearing sandstones, which have usually been interpreted as point-bar gravels. The fish-bearing units have yielded *Protopteraspis leathensis*, *Traquairaspis*, *Tesseraspis*, *Anglaspis* and *Corvaspis*, acanthodi-

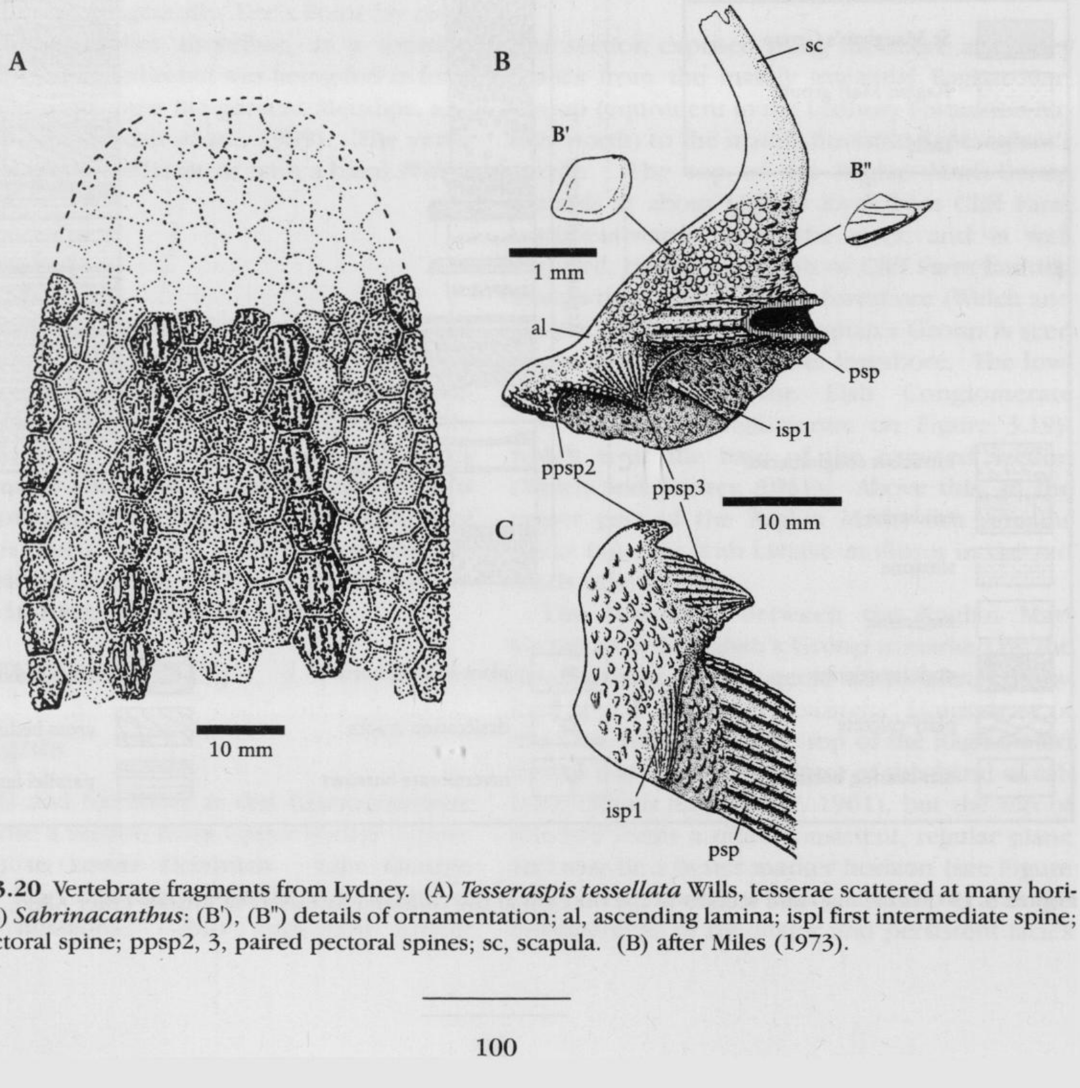


Figure 3.20 Vertebrate fragments from Lydney. (A) *Tesseraspis tessellata* Wills, tesserae scattered at many horizons; (B) *Sabrinacanthus*: (B'), (B") details of ornamentation; al, ascending lamina; ispl first intermediate spine; psp, pectoral spine; ppsp2, 3, paired pectoral spines; sc, scapula. (B) after Miles (1973).

an remains and a *Turinia pagei* thelodont assemblage (S. Turner, pers. comm., 1980).

Sabrinacanthus arcuatus (Agassiz, 1837) is a climatiid acanthodian, known only from disarticulated specimens of pectoral girdle and spines from the Basal Fish Conglomerate (Figure 3.20). The holotype of *Onchus arcuatus* from 'Bromyard' (Agassiz, 1833–45, p. 7; Miles, 1973, p. 170) is lost. The new genus *Sabrinacanthus*, described by Miles (1973), was therefore based on a series of five specimens from Lydney which showed articulated parts of the shoulder girdle. These, as in all climatiids, are strengthened ventrally by the development of dermal plates and spines, called the pinnal region. *Sabrinacanthus* has a pair of large compound pinnal plates, which laterally give rise to a pair of pectoral spines plus several other smaller spines. These were fused, immovable and ornamented with noded ribs. The scapulocoracoid was narrow and well developed (Miles, 1973; Denison, 1979).

Fauna

AGNATHA
Heterostraci: Tesseraspididae
Tesseraspis tessellata Wills, 1935
Heterostraci: Cyathaspididae
Anglaspis mcculloughi (Woodward, 1891a)
Heterostraci: Corvaspididae
Corvaspis kingi Woodward, 1935
Heterostraci: Pteraspididae
Protopteraspis leathensis (White, 1950)
Thelodonti: Thelodonta: Turiniidae
Turinia pagei (Powrie, 1870)

GNATHOSTOMATA
Acanthodii: Climatiformes: Climatiidae
Sabrinacanthus arcuatus Miles, 1973
Acanthodii *incertae sedis*
?*Onchus murchisoni* Agassiz, 1837

Interpretation

The sequence of fish-bearing rocks and associated strata in the cliffs of the River Severn at Lydney documents the faunal changes that took place in response to environmental changes around the time of deposition of the main '*Psammosteus*' Limestone. This major development of impersistent limestone generally accompanies a change in fauna everywhere across the Welsh Borders, and forms a good marker horizon. For the most part the fossil fish debris above and below the limestone is in beds which are referred to as fluvial channel infills or point-bar gravels (e.g. Ball and Dineley, 1961; Allen and Tarlo, 1963; Allen *et al*., 1968. However, at Lydney the bivalve bed represents a (?) marine incursion into a sequence of predominantly estuarine and fluvial sediments (Allen, 1973), which is highly unusual for fish beds of this age in the Welsh Borders. Recent discoveries at Gardener's Bank, Shropshire of cf. *Traquairaspis symondsi* in a basal Ditton Group deposit overlying shallow siltstones with *Modiolopsis* sp. and eurypterids illustrate a similar species, at a similar period of time, in a similar, anomalous preservational environment (M.A. Rowlands and P. Tarrant collections, 1992–1993, SMLU).

Conclusion

The conservation of the Lydney sections results from having produced a sequence of vertebrate faunas, including specimens of the unusual acanthodian *Sabrinacanthus*, and evidence for an interplay of typical freshwater conditions and a marine incursion. The section is usually obscured by river muds and gravels on the foreshore, but can be seen in the cliffs, where it is accessible and fossiliferous. Further collecting is possible.

DOWNTON CASTLE AREA: DOWNTON CASTLE BRIDGE, TIN MILL RACE, FORGE ROUGH WEIR AND CASTLE BRIDGE MILL (SO 445742, SO 460754, SO 456752, SO 443743)

Highlights

Quarries and small exposures in the Downton Castle area in Herefordshire have for some time yielded vertebrate remains, including acanthodian fragments and the osteostracan *Hemicyclaspis*. The most important recent discoveries have been substantial specimens of the unusual osteostracan *Sclerodus*.

Introduction

Several exposures in the Downton Castle Estate have yielded early fossil fishes. A network of four of these sites has been selected as good sources of fossils, and as representatives of the stratigraphical range of fishes that may be found in this small area: New Forge Rough Weir, Castle Bridge Mill Quarry, Downton Castle Bridge and the Tin Mill Race. The geology of these localities has been described by, amongst others, Elles and Slater (1906), Whitaker (1962), Holland *et al.* (1963), Allen (1974), Antia (1981), Lawson (1982), Bassett *et al.* (1982), and Siveter *et al.* (1989). Fossil vertebrates from this area have been studied by Turner (1973), Antia (1981) and Forey (1987).

Description

Elles and Slater (1906) divided the Upper Silurian of the Downton Castle area into the Aymestry Group, the Upper Ludlow Group (with the Ludlow Bone Bed at the top), and the Temeside Group. The Temeside Group was subdivided into the Downton Castle or Yellow Sandstones and the overlying Temeside or Eurypterid Shales. This corresponds to the Upper Gorstian (Stage) Bringewood Group, through Ludfordian (Stage) Leintwardine and Whitcliffe Groups to the lower part of the Přídolí, Downton Castle Sandstone Formation and Temeside Shales Formation (Siveter *et al.*, 1989, p. 62). The Ludlow Bone Bed Member is taken as the basal unit of the Přídolí.

Fauna

The fossil vertebrate remains from these several localities listed include much material that is too poor to be identified even at generic level.

AGNATHA
Osteostraci: Sclerodontiformes: Sclerodontidae
Sclerodus pustulliferus Agassiz, 1839
Osteostraci: Ateleaspidiformes: Ateleaspididae
Hemicyclaspis murchisoni (Egerton, 1857)
Hemicyclaspis sp.
Thelodonti: Thelodontida: Coelolepididae
Thelodus parvidens Agassiz, 1839
T. costatus (Pander, 1856)
T. bicostatus (Hoppe, 1939)
Thelodonti: Thelodontida: Loganellidae
Loganellia ludlowiensis Gross, 1967

GNATHOSTOMATA: Acanthodii
acanthodians indet.

New Forge Rough Weir (SO 456752) shows a fine exposure of the Ludlow Bone Bed, the Downton Castle Sandstone Formation and a discrete Downton Bone Bed. Both bone beds are thick consistent units, unlike those at Ludford Corner (q.v.). Both bone beds contain quantities of thelodont denticles and acanthodian spines, and *Hemicyclaspis* sp. has also recently been found here. This site has also yielded important arthropod specimens (Manning, 1992). The section as a whole illustrates the environmental transition from marine to estuarine conditions which is also seen at Ludford Corner.

Castle Mill Quarry (SO 443743) has recently provided a relatively abundant collection of *Sclerodus pustuliferus* material (Figure 3.21). The quarry, exposing the Downton Castle Sandstone Member of the Downton Castle Sandstone Formation (Bassett *et al.*, 1982), exhibits a massive, parallel-laminated pale yellow to pale olive, coarse micaceous siltstone showing channelling and uneven scoured surfaces. Two small, laterally impersistent bone beds with abundant *Platyschisma helicites*, separated by 0.7 m of siltstone, in the base of this section have yielded specimens of *Sclerodus*.

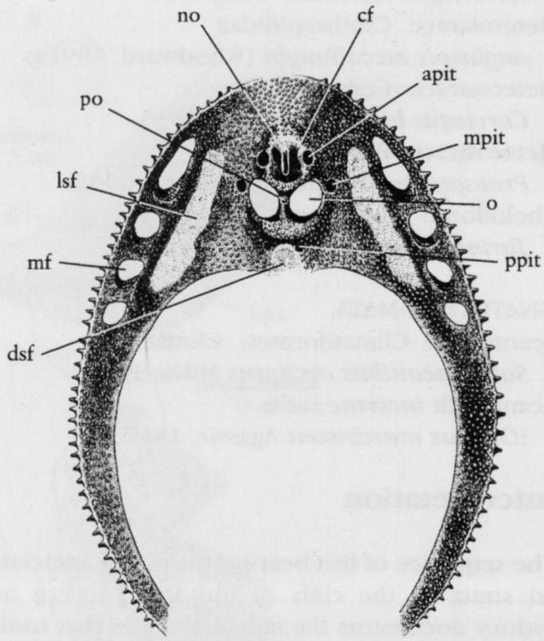


Figure 3.21 *Sclerodus pustuliferus*, cephalic shield in dorsal view; apit, anterior pit; cf, central field; dsf, dorsal sensory field; lsf, lateral sensory field; mf, marginal foramen; mpit, median pit; no, nasal opening; o, orbit; po, pineal opening; ppit, posterior pit; approximately natural size (after Forey, 1987, © The Natural History Museum, London).

The southern river bank at Downton Castle Bridge (SO 445742) shows two fish-bearing exposures. One on the west side of the path that goes south to Hunstay Cottage, exposes the Ludlow Bone Bed and the Downton Bone Bed. Elles and Slater (1906, pp. 208–9) and Holland *et al*. (1963, p. 135) describe this site. An old quarry and disturbed ground show the Ludlow Bone Bed 4 ft (1.2 m) above the level of the road with the Downton Bone Bed about 2 ft (60 cm) higher. This has been known as a fossil site for many years, having been visited by the Woolhope Naturalists Field Club in 1854. Close by, and separated by a fault from the first (Siveter *et al*., 1989, p. 62), at the west end of the track, which branches off to follow the south side of the river, are exposures of the Temeside Shale Formation. One such small exposure has yielded well-preserved headshields of *Hemicyclaspis* sp. from the basal Temeside Beds. The site has been known to yield fishes for many years. Banks (1893) reproduced a letter from Lightbody in 1860, who compared the cephalaspids from Oakley Park and Tin Mill with those from a new drive that had just been cut opposite Downton Castle in which he found 'cephalaspid' heads.

Tin Mill Race (SO 460754) is a historically important site that has yielded fossil fishes together with abundant eurypterid remains to collectors for many years. The section exposed here in the old mill race (Figure 3.22) was first described by Lightbody (1870); he named the beds the 'Tin Mill Shales' and correlated them with the Ledbury Shales (basal Ledbury Formation). Marston (1870) provided a list of the fossils collected from the 'upper bone bed' at this site. This is the bone bed equated with the Temeside Bone Bed at Temeside (q.v.) by Elles and Slater (1906, p. 213). The lower bone bed lies near the base of the section and contains generally smaller fragments of acanthodian spines.

At all Downton Castle sites, acanthodian remains predominate, together with *Pterygotus* fragments. Turner (1973) listed the very phosphatized thelodont scales from the bone bed at Tin Mill Race. The faunal list, compiled from Elles and Slater (1906), Whitaker (1962) and Turner (1973), includes acanthodians, an anaspid scale and thelodonts. Most of these fishes are described in the Ledbury, Ludlow and Temeside reports (q.v.), and only *Sclerodus* is discussed in part here.

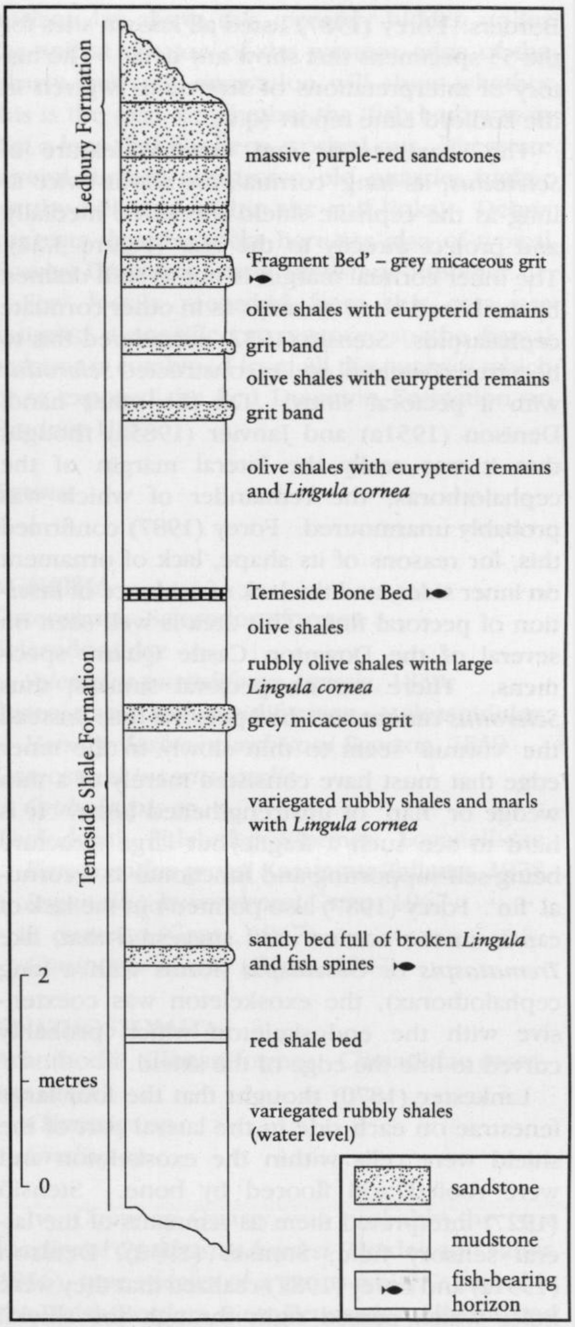


Figure 3.22 The stratigraphical section at Tin Mill Race (after Elles and Slater, 1906).

Sclerodus pustuliferus Agassiz, 1839 is an extremely rare and poorly known osteostracan which is usually found as small fragments. Very few specimens have been collected, and recent finds of well-preserved large fragments in the Downton Castle area are important. *Sclerodus pustuliferus*, the sole representative of the aberrant Family Sclerodontidae Fowler, 1947, is known only from the Downtonian of the Welsh

Borders. Forey (1987) listed all known sites for the 55 specimens that show any detail. The history of interpretations of *Sclerodus* is given in the Ludford Lane report (q.v.).

The characteristic and unusual feature of *Sclerodus*, its long 'cornua', are about twice as long as the cephalic shield measured medially, and project directly to the rear (Figure 3.21). The inner cornual margin is not as well defined by thickened bone or cusps as in other cornuate cephalaspids. Stensiö (1932) considered this to be a true cornuum, and reconstructed *Sclerodus* with a pectoral sinus. On the other hand, Denison (1951a) and Janvier (1985a) thought that it was really the lateral margin of the cephalothorax, the remainder of which was probably unarmoured. Forey (1987) confirmed this, for reasons of its shape, lack of ornament on inner sides, and the lack of evidence of insertion of pectoral fins. This area is well seen on several of the Downton Castle Quarry specimens. There are no pectoral sinuses, thus *Sclerodus* cannot have had pectoral fins. Instead the 'cornua' seem to thin slowly to the inner edge that must have consisted merely of a thin wedge or 'flap' of unstrengthened bone. It is hard to see such a fragile but large structure being self-supporting and functional as a cornual 'fin'. Forey (1987) also pointed out the lack of canals in the cornua, and suggested that, like *Tremataspis* or *Oeselaspis* (forms with a long cephalothorax), the exoskeleton was coextensive with the endoskeleton which probably curved to line the edge of the shield.

Lankester (1870) thought that the four large fenestrae on each side in the lateral part of the shield were cells within the exoskeleton and were roofed and floored by bone. Stensiö (1927) interpreted them as remnants of the lateral sensory field; Stensiö (1932), Denison (1951a) and Forey (1987) realized that they were holes which passed right through the shield. These marginal perforations have thick vertical inner walls, which are ornamented by tubercles in the same way as the rest of the dorsal surface of the cephalic shield. This feature is not seen in other osteostracans. The only obvious analogue is with the lunules of modern-day clypeasteroid echinoids (sand-dollars), in which they improve stability in currents and during burial in shallow water environments. Forey (1987) suggested that if *Sclerodus* were subject to varying water speeds, the fenestrae would provide stabilization to compensate for overall body shape.

Interpretation

The Downton Castle Bridge fish beds are probably at a slightly lower horizon than those at Temeside (q.v.), and the lithology also differs. The headshields of the hemicyclaspids were slightly smaller (Ludlow Museum specimens) and variations in form possibly related to slightly different environments. *Sclerodus* may have inhabited areas with soft sandy substrates subject to vigorous currents.

Conclusion

Together, the sites in the Downton Castle area give information on the environments and fish faunas of the latest Silurian, hence their importance and conservation value. The area as a whole has good exposure and the relationships between the groups of rocks can be well seen, unlike the situation which occurs in other, better-known sites that have yielded fish fossils of this type and age (e.g. Temeside, Ludlow and Ledbury railway cutting).

Recent finds of well-preserved large pieces of the head shield from the quarry at Downton Castle have enhanced our knowledge of the enigmatic osteostracan *Sclerodus*.

BRADNOR HILL QUARRY (SO 291578)

Highlights

The quarries on Bradnor Hill, near Kington, Herefordshire, have produced fish faunas from the latest Silurian, younger than those from the Ludlow Bone Bed Member and its equivalents elsewhere in the Welsh Borders region. The faunas are rich, including heterostracans, thelodonts, osteostracans and acanthodians.

Introduction

At Bradnor Hill, various exposures of the upper Ludlow to upper Přídolí succession can be seen. Once there were many highly fossiliferous quarries here, but today only Bradnor Hill and a lane section remain. When Symonds (1856) visited the quarries with Melville, Banks and Lightbody, they collected fish plates described as being abundant, though poorly preserved. The geology of the site has been described by Banks (1856), Symonds (1859a), Richardson (1905) and Stamp (1923) and the fish fauna by Banks (1856), Huxley and Salter (1856), Symonds (1859a), Denison (1964), and Turner (1973).

Description

Banks' (1856) work was summarized by Stamp (1923). (Symonds (1859a) described several quarries showing upper Ludlow Bone Beds, overlain by *Chonetes* beds, which are in turn overlain by sandstones containing fish remains.) More recent accounts of the stratigraphy of the Late Silurian of the Presteigne–Knighton area of Wales (Kirk, 1951; Holland, 1959, 1962; Bassett *et al.*, 1982; White and Lawson, 1989; Cocks *et al.*, 1992) indicate the following general succession for the upper part of the Ludlow Series and the Přídolí Series:

	Thickness (m)
Přídolí Series	
Red Downton Formation	> 610
Green Downton Formation	15–91
Yellow Downton Formation	8–11
Platyschisma helicites Formation	6–10
Ludlow Series	
Ludford Stage	
Llan-Wen Hill Formation	152
Wern Quarry Formation	37–52
Knucklas Castle Formation	457

The quarries on Bradnor Hill expose the lower parts of the yellow Downton Formation. The quarries of Bradnor Hill (SO 291578) and at Ivy Chimney (SO 293572), now obscured by farm buildings and the 'Iron Foundry Quarry', which can no longer be located, have provided most of the specimens found in collections of eurypterids and fishes from the Přídolí (Downton) of 'Bradnor' or 'Kington'. The 'Iron Foundry Quarry' was described by Richardson (1905) as being slightly lower down the hill than Ivy Chimney Quarry, but on old maps of the area, the Iron Foundry is situated by the river in the town of Kington. Ivy Chimney Quarry is now only a 3–4 m exposure behind a group of farm buildings. Access is no longer feasible (1995). All that is exposed in Bradnor Hill Quarry is 1.5 m of flaggy sandstones overlying 5 m of cross-bedded yellow sandstone dipping 20° to the south-east. By reference to the Banks (1856) section, it appears that the most fossiliferous horizon lay above this, possibly hidden under the soil at the top of the western edge of the quarry, but only excavation will show whether this is the case, or whether the 'fish bed' was in fact a lens that has been worked out. There are several further overgrown old quarries higher up the hill (and within the golf links). Debris suggests that the rocks here are also of typical (lower) Downton Castle Sandstone lithology.

Few fossils recorded from this area are assigned a specific provenance, so the faunal account is combined from all the quarries which once exposed the Red Downton Formation on Bradnor Hill.

Fauna

AGNATHA
Osteostraci: Sclerodontiformes: Sclerodontidae
Sclerodus pustuliferus Agassiz, 1839
Osteostraci: Ateleaspidiformes: Ateleaspididae
Hemicyclaspis murchisoni Egerton, 1859
Osteostraci *incertae sedis*
Cephalaspis sp.
Thelodonti: Phlebolepidiformes: Loganellidae
Katoporodus grossi Karatajute-Talimaa, 1978
Loganellia kummerowi Gross, 1967
L. cuneata (Gross, 1947)
Goniporus alatus (Gross, 1947)

GNATHOSTOMATA
Acanthodii: Climatiiformes: Climatiidae *incertae sedis*
Climatius sp.
Onchus sp.

Ivy Chimney Quarry was probably the type locality of *Cyathaspis banksi* (Huxley and Salter, 1856), type species of a genus which is found in the Welsh Borders, New Brunswick, Siberia, and the southern Urals. It is a primitive heterostracan, with a broad dorsal shield and a central arched epitegum. On the central part of the ventral shield there are a few coarse longitudinal dentine ridges separated by one to five finer ridges (Denison, 1964). *Cyathaspis banksi* occurs in the late Ludlow to early Přídolí of Shropshire, Herefordshire, Worcestershire, Gwent, and Gloucestershire, where it is found only rarely. The type locality is given as 'Kington' but the type specimen is not designated. The original specimens came either from

Bradnor Hill Quarry or more probably from Ivy Chimney Quarry.

Osteostracans from Bradnor Hill include *Sclerodus pustuliferus* Agassiz, 1839, *Cephalaspis* sp. and *Hemicyclaspis murchisoni* Egerton, 1857.

Turner (1973) recorded the thelodont taxa *Goniporus alatus*, ?*Katoporodus grossi*, *Loganellia kummerowi* and *L. cuneata*, and acanthodian scales from Bradnor Hill Quarry. The acanthodians *Climatius* sp. and *Onchus* sp. have been identified.

Interpretation

The thelodont fauna from the Upper Downtonian of Bradnor Hill (Turner, 1973) is characteristic of the upper Přídolí, and typical of various sites in the Welsh Borderland. It is also found in whole or in part association in some Beyrichienkalk erratics of north Germany and Poland, and can also be correlated with that of the Jura Beds of Lithuania and the Downtonian beds below the Eptarma horizon of North Timan (Turner, 1973). This is puzzling as the main Bradnor Hill Quarry is clearly very low in the Downtonian and yields no trace today of any bed from which thelodonts may be expected. The quarry and the disturbed hill slopes above on Bradnor Hill could be cleared and re-excavated relatively easily. However, they all appear on present field evidence to be low in the Downtonian succession. This makes Turner's record of an Upper Přídolí (Downtonian) Devonian fauna surprising.

Conclusion

The conservation value of the Bradnor Hill localities lies in their having characteristic late Přídolí faunas, including the *Katoporodus–Loganellia kummerowi* thelodont assemblage. This provides a useful biostratigraphical marker for the final part of Silurian time, and the Bradnor Hill localities have potential for further finds of fish faunas. Confirmation of the age of the site would be valuable.