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: Ptido (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.

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 P■ídolí 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 strato-type is also located in the Prague Basin of the Czech Republic. A recent extensive survey of the ostracod and conodont distributions across the Ludlow/P■ídolí 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 grapto-lites, 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 P■ídolí in age.

Biostratigraphical schemes for the Late Silurian based on fish remains have been attempted (Blieck *et al.,* 1988; Marss, 1989; Dineley and Loeffler, 1993; Janvier and Blieck, 1993). These divide the Ludlow and P■ídolí 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 thclodonts in the Late Silurian (Turner, 1970, 1971), and zonal schemes are currently being drawn up (e.g. Karatajute–Talimaa, 1978; Marss, 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.

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 sed-imentology 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 Marss (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, Marss (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 3.3)A, 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 P■ídolí 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 WW. King (1934) produced these fossils from a number of Downtonian and Dittonian horizons in the Welsh Borderland. Throughout the area, the P■ídolí faunas are dominated by *Traquairaspis* (*Philiaspis*) *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 P■ídolí 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 Phidolian 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 P■ídolí 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: Phialaspidiformcs: 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

Gompbonchus hoppei (Gross, 1947)

G. sandalensis (Pander, 1856)

Gompbonchus 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)

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 bio-zone of *Phialaspis symondsi–Toombsaspis pococki.* The present authors have'not adopted these revisions. *Thiquairaspis 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-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.

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 P■ídolí microvertebrate assemblage from Man Brook, Trimpley, Worcestershire, contains an abundance of acanthodian remains as well as thelodonts of the *Goniporus alatus–Kataporus tricavus–Longanellia 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. boppei* (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 pteras-pidids, 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 P■ídolí 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 5834 3658]; *Petalocrinus* Limestone; *Loganellia* sp., *Thelodus* sp.; Squirrell, 1958; Turner, 1973; Old Storridge Common ([SO 761 381]; Wych Beds; *Loganellia scotica, Kataporodus* sp., Aldridge and Turner, 1975).

SHROPSHIRE: Hope Quarry, Minsterly ([SJ 355 028]; Venusbank Formation; *Loganellia scotica*)*;* New House Farm, Marshbrook (SO 4341 8982; *Pentamerus* Beds; *Loganellia scotica*)*;* Hillend Farm, Plowden ([SO 3956 8769]; *Pentamerus* Beds; *Loganellia scotica, Kataporodus* sp.).

Wenlock Series

GLOUCESTERSHIRE: Brinkmarsh Quarry, Tortworth inlier ([ST 6735 9132]; *Loganellia* sp., *Thelodus* sp.; Siveter and Turner, 1982).

HEREFORDSHIRE: Ledbury Council Quarry ([SO 717 384]; bone bed at base of Wenlock Limestone and Gorsley Limestone; *Thelodus* sp.; Squirrell, 1958; Turner, 1973); Linton Quarry ([SO 677 257]; bone bed at base of Wenlock Limestone and Gorsley Limestone; *Thelodus* sp.; Squirrell, 1958; Turner, 1973); Canwood ([SO 613 381]; bone bed at base of Wenlock Limestone and Gorsley Limestone; *Thelodus* sp.; Squirrell, 1958; Turner, 1973); Storridge ([SO 755 496]; Lower Woolhope Limestone; *Thelodus* sp., *Loganellia* sp., *Gomphonchus?* sp., acanthodian scales; Turner, 1973).

Ludlow Series: Gorstian Stage

SHROPSHIRE: Shelderton Rock, near Clungunford ([SO 419 779]; Aymestry Limestone Member; thelodont scales; Rhodes, 1953; Turner, 1973).

Ludlow Series: Ludford Stage

GWENT: Common Coed y Paen, Usk inlier ([ST 340 984]; Top *Ornatella* Bone Bed; *Thelodus parvidens,* acanthodian scales; Turner, 1973).

HEREFORDSHIRE: Upton Court Farm, Woolhope ([SO 6573 2847]; Lower and Upper Bodenham Bone Beds and Top *Ornatella* Bone Bed; *Thelodus* sp., acanthodian scales; Turner, 1973); Bodenham Farm, Woolhope ([SO 6524 3200]; Lower and Upper Bodenham Bone Beds and Top *Ornatella* Bone Bed; *Thelodus* sp., acanthodian scales; Turner, 1973); Lye ([SO 660 296]; Lower Bodenham Bone Bed; *Thelodus* sp., acanthodian scales; Turner, 1973); Whittocks End Farm, Woolhope inlier ([SO 660 296]; Top *Ornatella* Bone Bed; thelodonts; Turner, 1973).

WEST MIDLANDS: Turner's Hill, near Dudley ([SO 915 908]; 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 563 918], the Crown Inn car park, Munslow, Corvedale [SO 528 888], Brockhill Quarry, Malverns, [SO 756 439] and Mordiford [SO 573 373].

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).

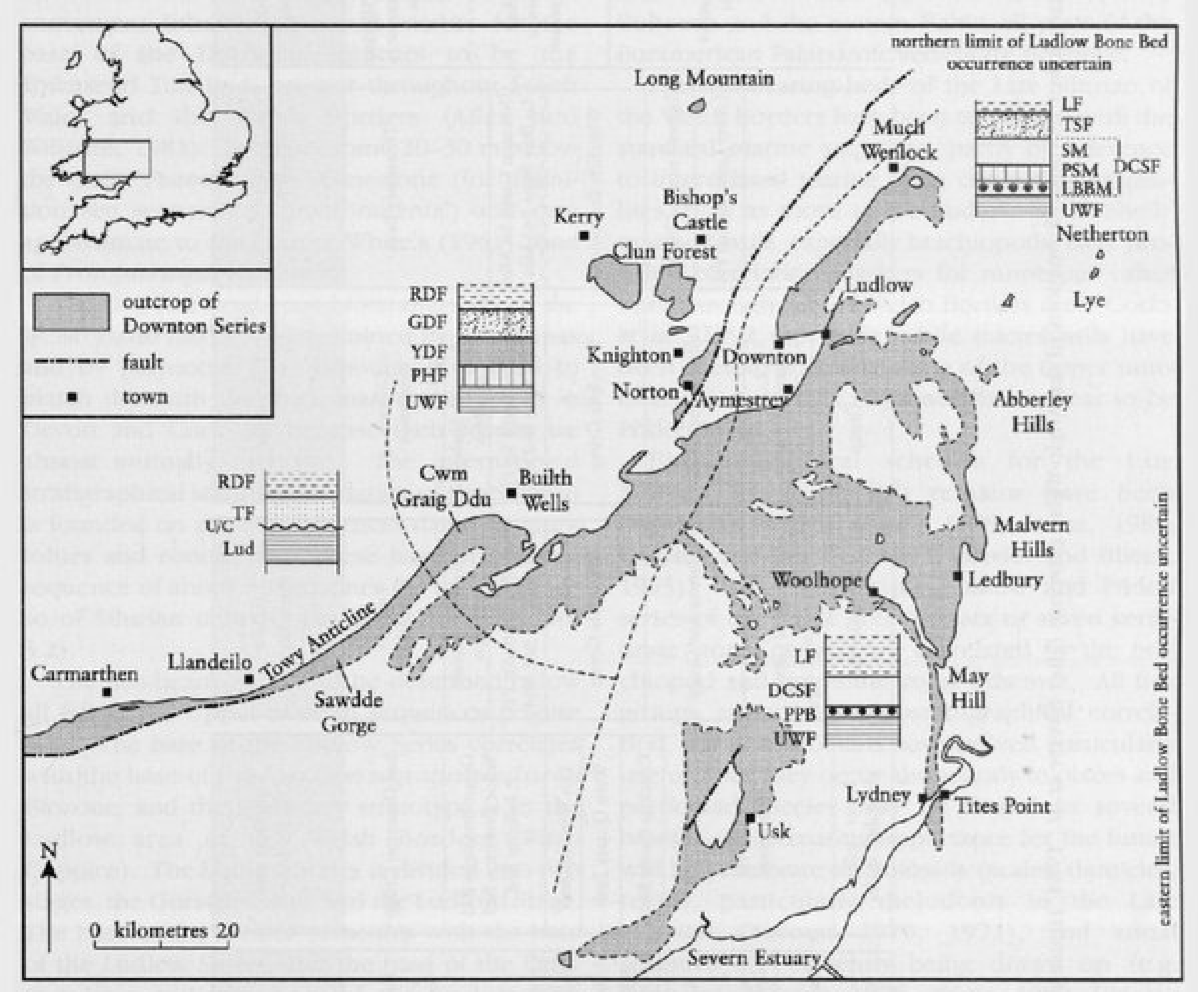
SHROPSHIRE: Beaconhill Brook, Monkhopton ([SO 6330 9426]; mid part of the Red Downton Formation *Kallostrakon* sp., acanthodian scales; Ball and Dineley, 1961); Foxhole Coppice, Monkhopton ([SO 6180 9308]; *Kallostrakon* sp., acanthodian scales, jaws, spines; Ball and Dineley, 1961).

Many of these localities have only poor exposures of the strata and the fossils may be collect ed 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.

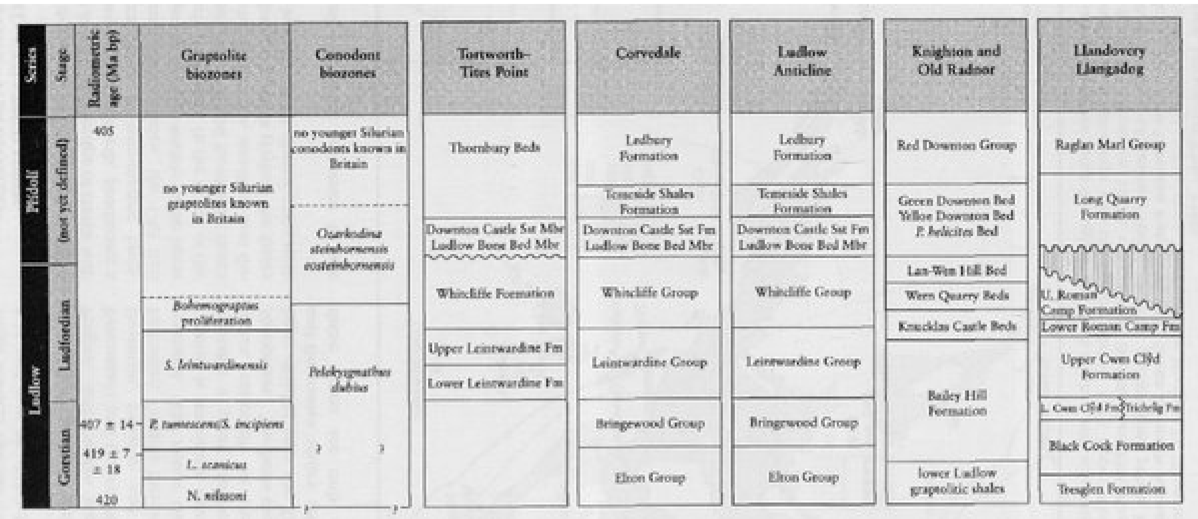
1. Cwar Glas, Dyfed [SN 7263 2480]. Gorstian, Ludlovian.
2. Church Hill Quarry, Herefordshire [SO 412 738]. P■ídolí/Downtonian, Lower Leintwardine Shales (Ludfordian Stage, upper Ludlow Series).
3. Ludford Lane and Ludford Corner, Shropshire [SO 5116 7413]. P■ídolí/Downtonian.
4. Ledbury Cutting [SO 712 835], Herefordshire. P■ídolí/Downtonian.
5. Temeside, Ludlow, Shropshire [SO 520 742]. P■ídolí/Downtonian.
6. Tite's Point (Purton Passage), Gloucestershire [SO 688 046]. P■ídolí/Downtonian.
7. Lydney, Gloucestershire [SO 652 017]. P■ídolí/Downtonian.
8. Downton Castle Bridge, Herefordshire [SO 445 742]. P■ídolí/Downtonian.
9. Tin Mill Race, Herefordshire [SO 460 754]. P■ídolí/Downtonian.
10. Forge Rough Weir, Herefordshire [SO 456 752]. P■ídolí/Downtonian.
11. Castle Bridge Mill Quarry, Herefordshire [SO 443 743]. P■ídolí/Downtonian.
12. Bradnor Hill, Herefordshire [SO 291 578]. P■ídolí/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.

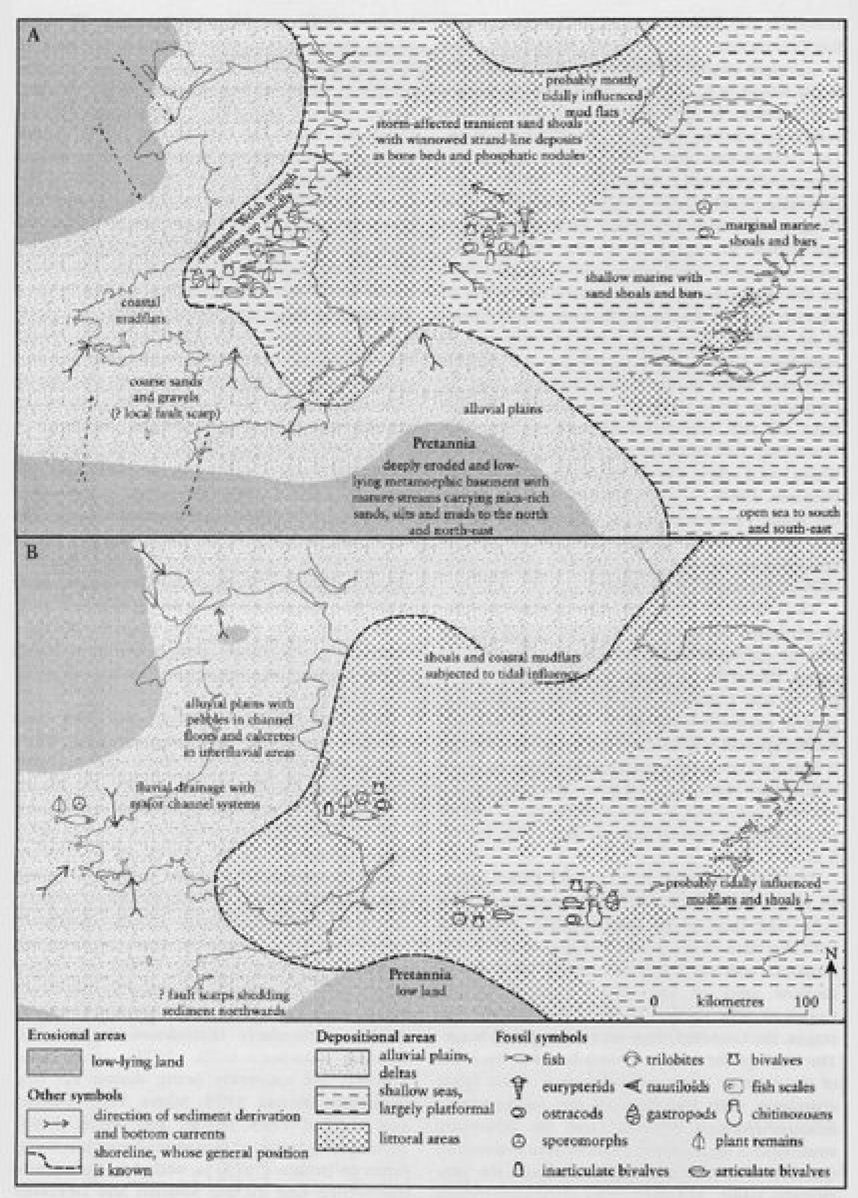
References



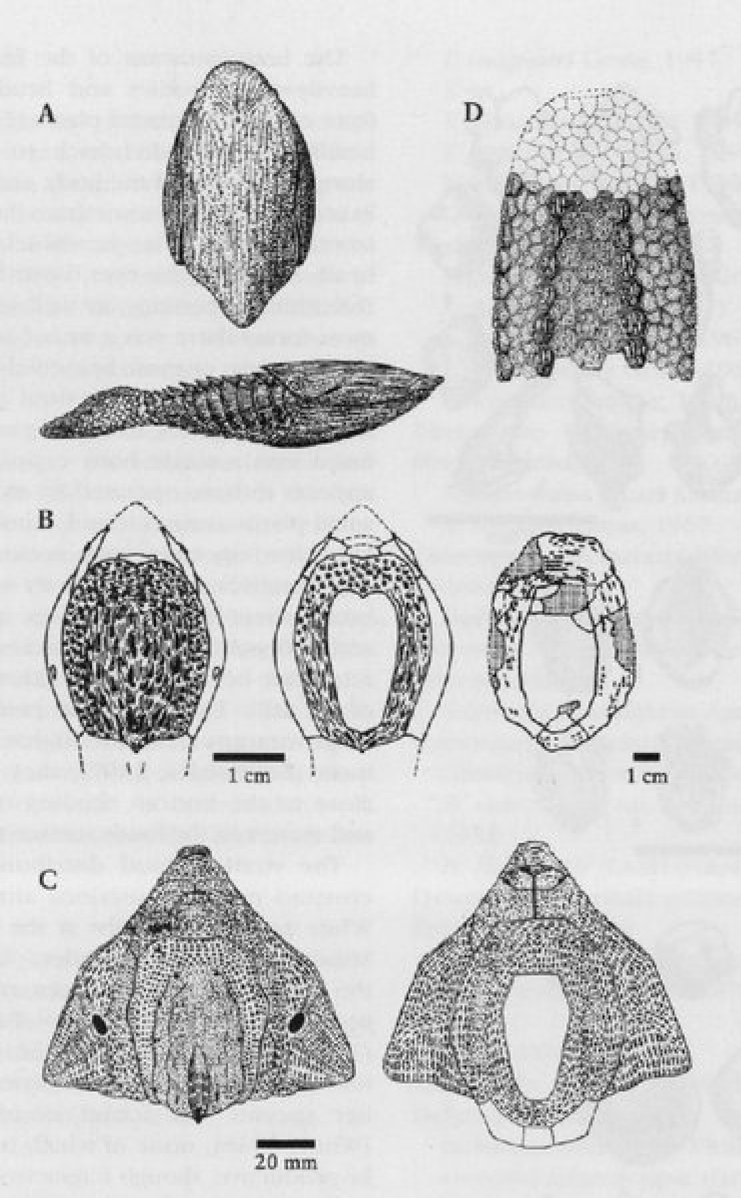
(Figure 3.1) Map of the Downtown Series throughout the Welsh Borders, with schematic summaries of the stratigraphical successions and relationships with the Ludlow Series: UWF, Upper Whitcliffe Formation; DCSF, Downton Castle Sandstone Formation; LBBM, Ludlow Bone Bed Member; PSM, Platyschisma Shale 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).



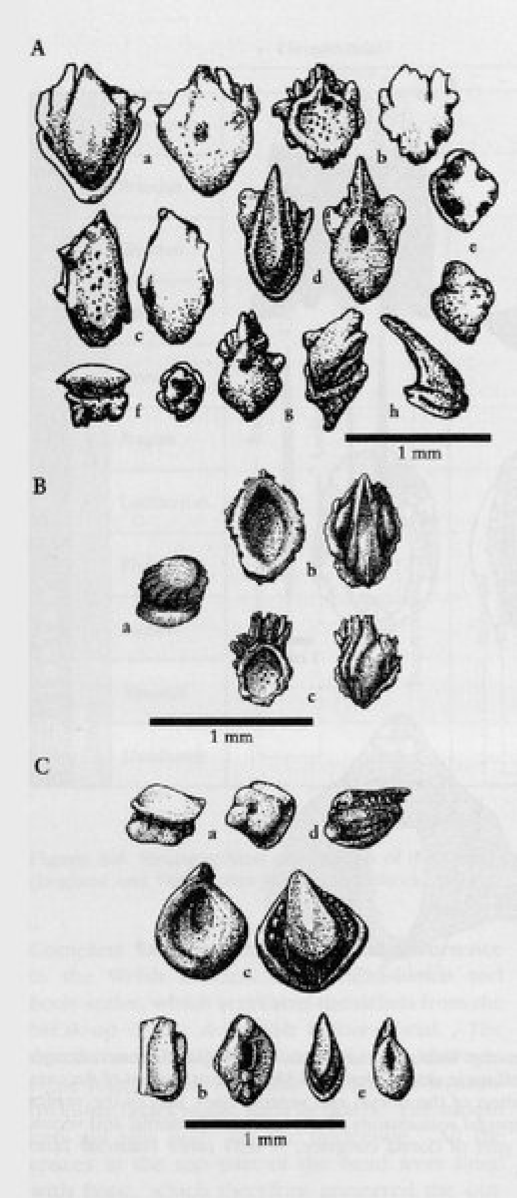
(Figure 3.2) Correlation table of Late Silurian-Lower Devonian formations of the Anglo-Welsh province (after Siveter et al., 1984; House et al., 1977).



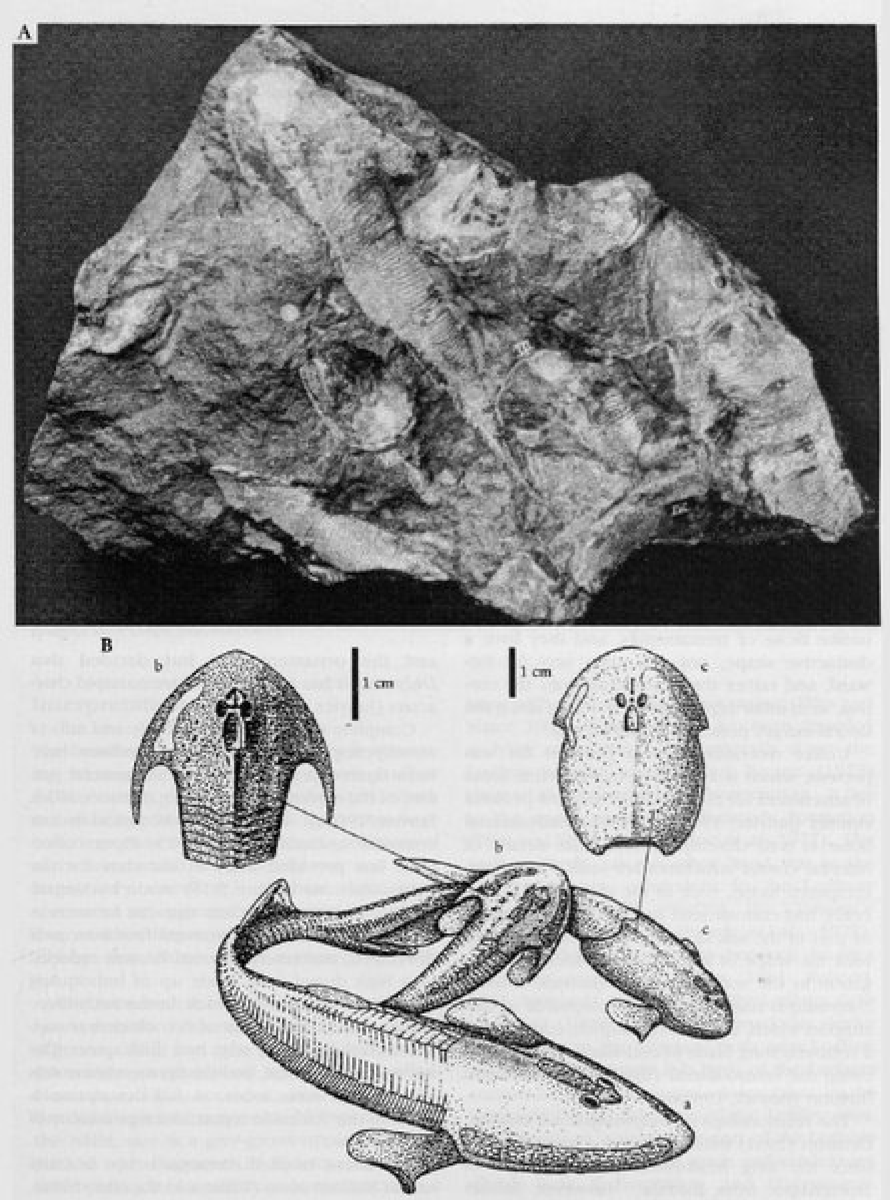
(Figure 3.3) P■ídolí (latest Silurian) palaeogeography of southern Britain (after Bassett et al., 1992). (A) early P■ídolí; (B) late P■ídolí.



(Figure 3.5) Late Silurian heterostracan vertebrates from the Welsh Borders area. (A) Anglaspis macculloughi in dorsal and lateral views, x 0.75, and, Tesseraspis tessellata in dorsal view, x 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, x 0.35 (after Halstead Tarlo, 1964).



(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).



(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. x 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).