J.N.C.C.

Fossil Fishes of Great Britain

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GCR Editor: **D. Palmer**

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Chapter 4

Early Devonian fossil fishes sites of the Welsh Borders

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INTRODUCTION: PALAEOGEOGRAPHY AND STRATIGRAPHY

During early Devonian times, the Welsh Borders lay near the southern margin of the Old Red Sandstone continent (Euramerica), a large land mass that extended over much of northern Europe and North America, and marked the site of the recently closed and subducted Iapetus Ocean (Figure 4.1). The Old Red Sandstone continent straddled the Devonian equator, experiencing climatic conditions ranging from monsoonal to hot and arid (Ziegler, 1989).

The Welsh Borders area was then part of the Anglo-Welsh Basin of continental sedimentation developed between the local Caledonian mountain belt and the Hercynian ocean, with a southwards-migrating strandline of beaches and barriers with sheltered lagoonal or tidal-flat deposits. Much of the basin became occupied by extensive alluvial plains with fluvial channels and low floodplains. The source of the clastic infill lay in the rising Caledonides to the north. J.R.L. Allen

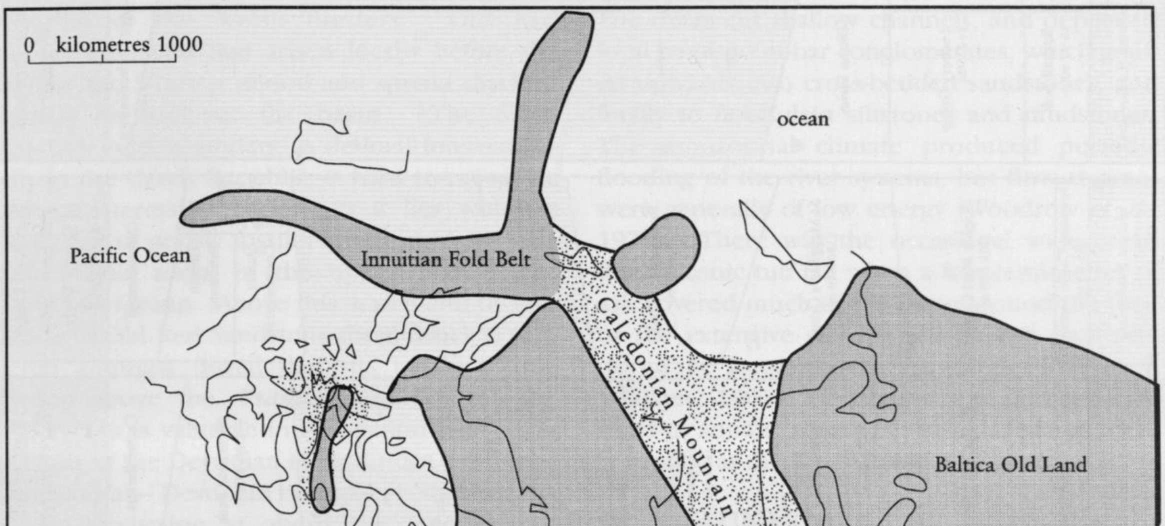


Figure 4.1 The Old Red Sandstone Continent (Euramerica or Laurussia); a general map, early Devonian to mid-Devonian times.

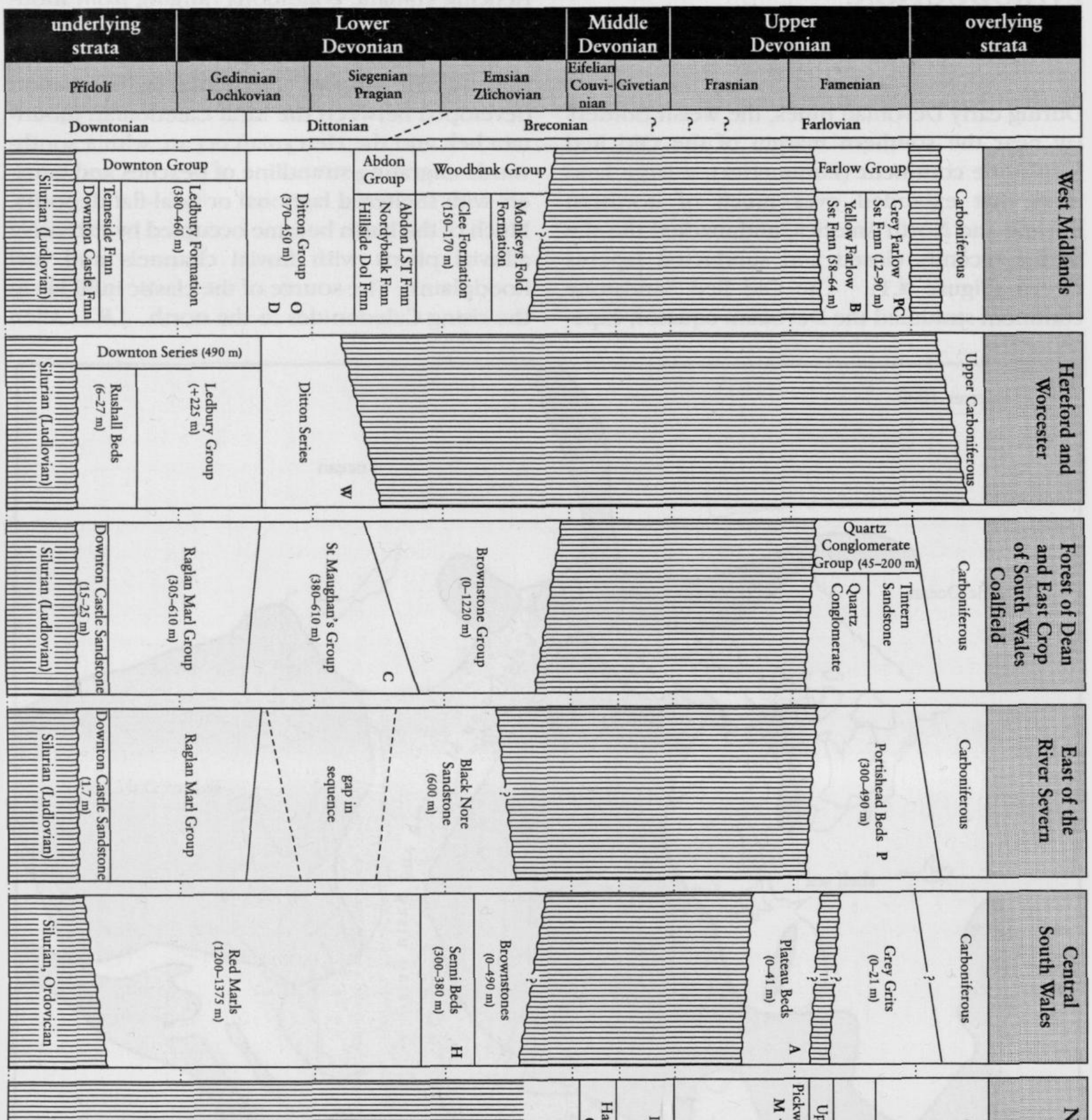


Figure 4.2 Stratigraphical sections of the Devonian in the Welsh Borderland–South-west England (after House *et al*., 1977) with GCR site horizons indicated: A, Afon y Waen; B, Besom Farm; BS, Bedruthan Steps; C, Cwm Mill; D, Devil's Hole; H, Heol Senni; M, Mill Rock; O, Oak Dingle; P, Portishead; PC, Prescott Corner; W, Wayne Herbert. Exact stratigraphical positions are not certain.

(1974) attributed the accumulation of the Old Red Sandstone of the Clee Hills (Welsh Borders) to the action of rivers at least 400 km long. By 1983 sufficient palaeocurrent data led him and S.F. Crowley (Allen and Crowley, 1983) to propose that the Dingle–Shannon and Anglo-Welsh basins were joined in Lochkovian time, but that ensuing uplift separated them. The Caledonian basin remained a separate feature throughout.

The beginnings of the transition from deep and marginal marine conditions in the British Silurian to continental Old Red Sandstone conditions may be traced in the latest parts of the Silurian of the Welsh Borders. Old Red Sandstone facies had arisen locally before the end of the Silurian period and spread diachronously throughout the basin. The Silurian–Devonian boundary, as defined internationally in the Czech Republic, is hard to recognize since in terms of rock units it lies within a sequence of poorly fossiliferous and highly variable clastic rocks in the upper part of the Downton Group. Above this, a rich and diverse fauna of Old Red Sandstone fossil fishes is scattered amongst fluvial deposits in the Ditton Group above the '*Psammosteus*' Limestones. This fauna is valuable in correlation with other regions of the Devonian Euramerican continent. The Silurian– Devonian boundary is now regarded as occurring at about the level of the Townsend Tuff Bed a few metres above the main '*Psammosteus*' Limestone throughout this basin. The Ditton Group is dated as Lochkovian, earliest Devonian.

The stratigraphy of the Lower Devonian of the Anglo-Welsh Basin is highly complex and reveals regional changes at several levels: many areas remain poorly known with only roughly mapped and incomplete definition of lithostratigraphical units. Moreover, older stratigraphical terminology is often confused; fossil plants and fishes are limited in distribution compared with invertebrate fossils in marine sequences (Allen, 1977). A succession of vertebrate zones has been established for parts of the Lower Devonian sequence within the basin, and there is some palynological evidence for dating (McGregor, 1979). The zonation by means of vertebrates has been extended to western Europe (Blieck, 1982a, 1982b, 1982c; Janvier and Blieck, 1993; Blieck *et al.*, 1995). The outline of stratigraphy (Figure 4.2) is based on Allen's summary (1977) and Allen and Williams (1978; see also Dineley, 1992).

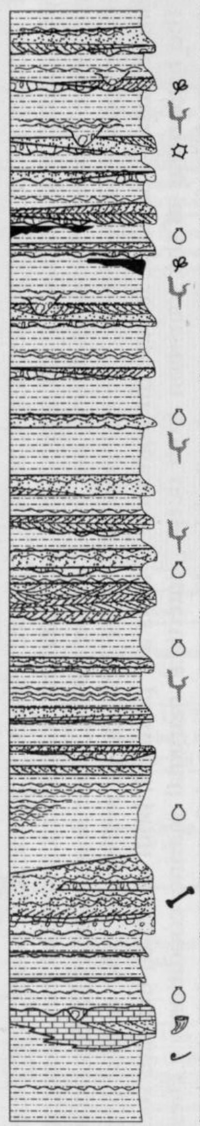
ENVIRONMENTS

The transitional beds between fully marine Silurian and continental Old Red Sandstone record a series of marine regressions, with facies of shallow subtidal to intertidal environments (Allen, 1974). Rare lingulid brachiopods occur in life position in mudstones, and vertical burrows are plentiful, both of which indicate such intertidal marginal marine conditions. These low-energy coastal facies are overlain by great thicknesses of repeated fining-upwards cycles, which were produced by meandering rivers. The rivers cut shallow channels, and deposited local basal point-bar conglomerates, which graded upwards into cross-bedded sandstones, and finally to floodplain siltstones and mudstones. The monsoonal climate produced periodic flooding of the river systems, but flow regimes were generally of low energy (Woodrow *et al.*, 1974). There was the occasional widespread fine volcanic tuff fall when a few centimetres of ash covered much of the basin around the time of the extensive caliche soil growth that produced the '*Psammosteus*' Limestones (Allen and Williams, 1981). Vegetation was perhaps confined to aquatic algae with vascular plants locally prolific at the water margins (Figure 4.3).

FISH FAUNAS

Acanthodians, heterostracans and cephalaspids are all common, and arthrodire placoderms are seen for the first time in this area. Species from the Lower Devonian of the Welsh Borders include the following (classifications largely from Halstead, 1993; Gardiner, 1993a; Zidek, 1993):

AGNATHA
Heterostraci: Eriptychiformes: Tesseraspididae
Tesseraspis tessellata Wills, 1936
T. toombsi Tarlo, 1964
Kallostrakon alleni Tarlo, 1964
Heterostraci: Eriptychiformes *incertae sedis*
Lepidaspis sp.
Heterostraci: Cyathaspidiformes: Poraspididae
Poraspis sericea (Lankester, 1873)
P. cf. *elongata* (Kiaer and Heintz, 1935)
Heterostraci: Cyathaspidiformes: Corvaspididae
Corvaspis kingi Woodward, 1934
Heterostraci: Pteraspidiformes: Pteraspididae
Pteraspis rostrata (Agassiz, 1835)



				Lithology	Vertebrates	Interpretation
Lower Devonian	Dittonian	Ditton Formation	Ditton Group	Thick red siltstones, sometimes with concretions. Thin green or red sandstones: cross-bedding, flat-bedding, current lineation, scour-and-fill, current ripples, rainprints. Thin intraformational conglomerates above erosional surfaces. Suncracks. Rare animal burrows. No molluscs. Drifted plants.	*Althaspis leachi*, *Pteraspis rostrata*, *Pteraspis crouchi*, *Weigeltaspis*, *Corvaspis*, *Protaspis*, *Benneviaspis*, *Securiaspis*, *Cephalaspis*	**Fluviatile:** fans of sand spread by strong distributary rivers after crevassing on floodplain with silty lakes and mudflats. Floods. Strong currents. Frequent desiccation. Pedocals forming.
		'Psammosteus' Limestones Member	Ditton Group	Thick red siltstones with concretionary limestones. Thin green or red sandstones: cross-bedding, current lineation, scour-and-fill, suncracks, current ripples, channels. Conglomerates on erosional surfaces. Animal burrows. Mollusc bands. Plants.	*Pteraspis leathensis*, *Traquairaspis symondsi*, *Traquairaspis pococki*, *Poraspis*, *Tesseraspis*, *Kallostrakon*, *Anglaspis*, *Corvaspis*, *Cephalaspis*, *Didymaspis*	**Chiefly fluviatile:** fans of sand spread by strong rivers after crevassing on floodplain with temporary silty lakes and mudflats. Brief marine invasions giving brackish silty and sandy lagoons. Floods. Frequent desiccation. Soils (pedocals) forming.
Silurian	Downtonian	Upper Red Downton Formation	Downton Group	Thick red siltstones with animal burrows. Thin micaceous red sandstones: cross-bedding, current ripples. Siltstone pebbles. Thin bands with molluscs.	*Didymaspis*, *Thyestes*	**Subtidal and intertidal:** sands of subtidal shoals and lower intertidal flats. Silts of upper intertidal flats. Turbid and brackish water.
		Holdgate Sandstones Formation	Downton Group	Thick micaceous coarse sandstones: festoon-bedding, current ripples, cross-bedding, flat-bedding. Erosional surfaces. Siltstone gravel. Thick red siltstones. Abundant animal burrows. Rare molluscs.	*Kallostrakon*, *Didymaspis*	**Fluviatile with tidal intercalae:** channels of strong rivers aggraded by fluviatile sands and tidal silts. Fresh to brackish turbid water.
		Lower Red Downton Formation/Temeside Shale Formation	Downton Group	Thick red or green siltstones, often laminated. Thin green or red micaceous sandstones: cross-bedding, flat-bedding, current ripples. Molluscs. Abundant animal burrows and *Lingula*.	*Hemicyclaspis*, *Didymaspis*, *Thyestes*, *Sclerodus*, *Kallostrakon*	**Subtidal and intertidal:** sands of subtidal shoals and lower intertidal flats. Silts of upper intertidal flats. Strong waves and currents. Brackish and turbid water.
		Downton Castle Sandstone Formation	Downton Group	Yellow sandstones above: scour-and-fill, cross-bedding, flat-bedding, current ripples. Bone beds: shells, phosphatic debris. Green siltstones below: current ripples, lamination. *Lingula* and abundant molluscs.	*Hemicyclaspis*, *Thyestes*, *Sclerodus*, *Cyathaspis*	**Nearshore to beach:** silts formed offshore within wavebase overlain by transgressive sand shoals and beaches. Strong waves. Turbid, often brackish, water.
		Ludlow Bone Bed Fm	Downton Group	Bone beds: sandstones, siltstones, current ripples, cross-bedding, shell and phosphatic debris. Discordant.	*Sclerodus*, *Cyathaspis*	**Advance of strand after retreat:** beach and littoral sands and silts.
	Ludlovian	Ludlow Series		Dominantly green siltstones and shales: current ripples, lamination. Thin sandstones: flat-bedding, current ripples. Occasional discordant bone beds. Limestones: shelly, some authochthonous, others detrital, conglomeratic, cross-bedded. Abundant corals, brachiopods and molluscs.	*Cyathaspis*, *Archegonaspis*	**Chiefly open sea:** clays, silts, sands and limestones formed offshore chiefly within wavebase. Clear sea, often turbid, sometimes brackish. Periodic strand retreat–advance.
					Thelodont denticles and acanthodian scales throughout	

Figure 4.3 The Silurian–Devonian succession in the Welsh Borders with faunas and suggested environments (after Allen and Tarlo, 1963).

P. rostrata var. *trimpleyensis* White, 1935
Protopteraspis gosseleti (Leriche, 1906)
Parapteraspis jackana (White, 1935)
Errivaspis waynensis (White, 1935)
Brachipteraspis monmouthensis (White, 1935)
Loricopteraspis dairydinglensis (White, 1961)
Larnovaspis stensiöi (White, 1935)
Althaspis leachi (White, 1938)
Rhinopteraspis dunensis (Roemer, 1855)
R. crouchi (Lankester, 1868)
Europrotaspis crenulata White, 1961
Heterostraci: Phialaspidiformes: Traquairaspididae
Traquairaspis symondsi (Lankester, 1868)
T. pococki (White, 1946)
T. sabrinae (White, 1946)
Weigeltaspis godmani Tarlo, 1964
Osteostraci: Tremataspidiformes: Thyestiidae
Didymaspis grindrodi Lankester, 1867
Osteostraci: Cephalaspidiformes
Pattenaspis whitei (Stensiö, 1932)
Osteostraci: Benneviaspidiformes
Benneviaspis lankesteri Stensiö, 1932
B. anglica Stensiö, 1932
B. salopiensis White, 1961
Osteostraci: Scolenaspidiformes
Zenaspis salweyi (Egerton, 1857)
Stensiöpelta woodwardi (Stensiö, 1932)
Osteostraci *incertae sedis*
'*Cephalaspis*' *heightingtonensis* Stensiö, 1932
'*C.*' *acutirostris* Stensiö, 1932
'*C.*' *lankesteri* Stensiö, 1932
Eucephalaspis agassizi (Lankester, 1870)
'*Cephalaspis*' *fletti* Stensiö, 1932
'*C.*' *cradleyensis* Stensiö, 1932
'*Cephalaspis*' *whitbachensis* Stensiö, 1932
'*C.*' *sollasi* Stensiö, 1932
'*C.*' *jacki* White, 1935
'*C.*' *bouldonensis* White, 1961
'*C.*' *cwmmillensis* White and Toombs, 1983
'*C.*' *abergavenniensis* White and Toombs, 1983
Cwmaspis billcrofti White and Toombs, 1983
Securiaspis kitchini Stensiö, 1932
S. kingi Stensiö, 1932
Thelodonti: Thelodontida: Turiniidae
Turinia pagei (Powrie, 1870)
T. oervigi Karatajute-Talimaa, 1968
T. sp. nov.
Thelodonti: Thelodontida: Apalolepididae
Apalolepis toombsi Turner, 1973
Thelodonti: Thelodontida: Nikoliviidae
Nikolivia sp.
Thelodonti: Phlebolepidiformes (syn. Katoporida): Phlebolepididae
Katoporodus grossi (Karatajute-Talimaa, 1970)
Logania kummerowi Gross, 1968
L. cuneata Gross, 1967
L. cruciformis Gross, 1968

GNATHOSTOMATA
Placodermi: Arthrodira: Actinolepidae
Ailuracantha dorsifelis White, 1969
Heightingtonaspis anglica (Traquair, 1890)
H. ?willsi (White, 1961)
Placodermi: Arthrodira *incertae sedis*
Overtonaspis billballi White, 1961
Prescottaspis dineleyi White, 1961
Wheathillaspis wickhamkingi White, 1961
Acanthodii: Ischnacanthiformes: Ischnacanthidae
Ischnacanthus ?anglicus White, 1961
I. wickhami White, 1961
Uraniacanthus spinosus Miles, 1973
Acanthodii: Climatiiformes: Climatiidae
Vernicomacanthus waynensis Miles, 1973
Acanthodii *incertae sedis*
Nodonchus bambusifer White, 1961
Onchus major Symonds, 1872
O. wheathillensis White, 1961
O. ?besomensis White, 1961

Whereas many Silurian vertebrates persist into the Devonian faunas, two groups appear for the first time in the lowest rocks of the Ditton Series – the heterostracan pterapsids and the placoderm arthodires. The Eriptychiformes are a poorly known group of tesselated heterostraci, the two genera of which are known from many localities within the Silurian Ledbury Formation and the Devonian (Lower) Ditton Series. They do not extend beyond the *Rhinopteraspis crouchi* Zone (Figure 4.4). Cyathaspidids are rare in the Dittonian rocks but the Phialaspidiformes are present mostly as fragments within the Dittonian. Few Dittonian localities yield complete carapaces, or even whole discs, whereas in the Přídolí they are relatively common. The pteraspids were a successful and wide-ranging group of heterostracans throughout the Euramerica province (Young, 1981; Blieck 1984). They seem to have originated from a group of cyathaspids (Elliott, 1983). Evidence for this appears in the Canadian Arctic

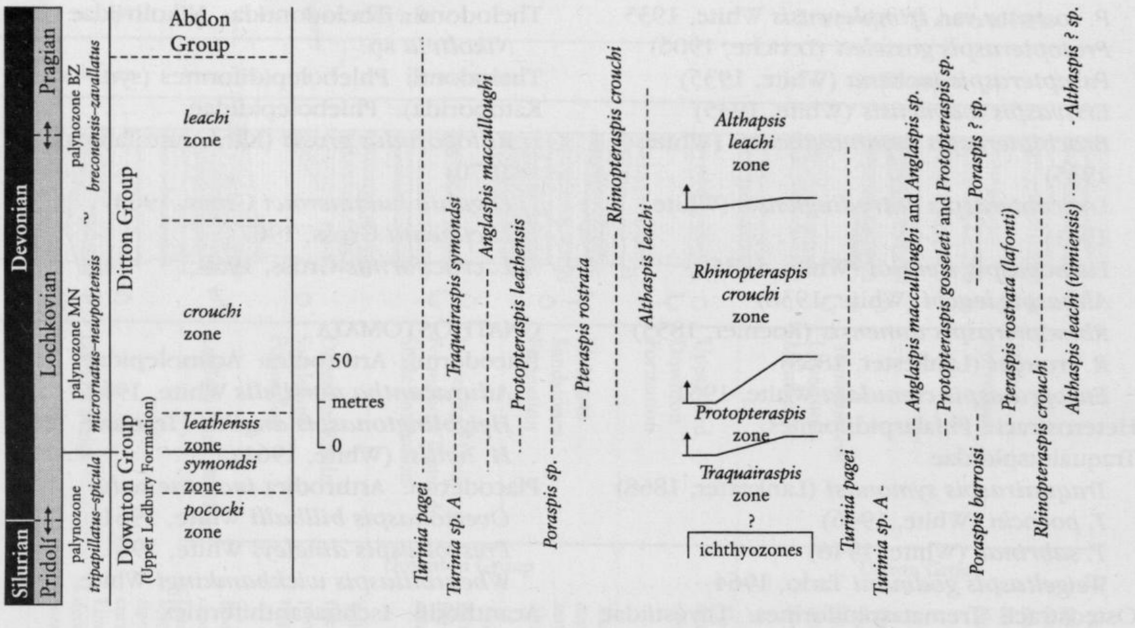


Figure 4.4 Fish zones in the Upper Downtonian and Dittonian of the Welsh Borderland and in the Lievin Group in northern France (after Blieck and Janvier, 1989). N.B. a narrow zone of *Pteraspis rostrata* between those of *Rh. crouchi* and *Protopteraspis* is postulated for northern France and may also be justified in Britain.

Islands, but the early Protopteraspidae occur widespread in North America, Spitsbergen, Europe (Elliott and Dineley, 1983; Blieck, 1985; Ilyes and Elliot, 1994) and northern Russia. Between earliest Lochkovian and Pragian times they gave rise to a large number of taxa. The distribution of these shows some provincialism with Great Britain falling into a probable western European province. See Blieck (1985, p. 150, fig. 78) for a cladogram of pteraspids and their corresponding geographical areas. Pteraspidid evolution seems to have led this group in adaptations for the exploitation of various bottom conditions and plant cover. The mode of life remains the subject of much active debate (Kermack, 1943; Belles-Isles, 1987). In Britain pteraspids occur in Cornwall and Devon, Wales, the Welsh Borderland (Figure 4.5) and in Scotland. *Pteraspis* had an armoured anterior carapace made up of several plates of bone, and a tail covered by overlapping rhomboid scales. The genus (s.l.) has an important range in Britain and appears to diversify rapidly throughout the Early Devonian here, in Spitsbergen, North America and mainland Europe. The record of the cephalaspids is similar. Turner's pioneer work (1973) on the thelodonts of this region of the Lower Old Red Sandstone distinguished four faunas (Table 4.1). The sequence differs from that in the Baltic area, but a *T. pagei* fauna is found in Scotland. No thelodonts are known above the higher Dittonian, as at Cwm Mill (q.v.).

Osteostracans possess a dermal headshield with a flattened ventral surface, bearing a simple terminal mouth and branchial pouches, and a convex dorsal surface bearing eyes, pineal and nasohypophysial openings and dorsal and lateral fields (see Figure 4.16). Those which are loosely termed '*Cephalaspis*' may more correctly be described as cornuate osteostracans (Janvier, 1985a) because they bear laterally pointed processes, cornua, in front of the paired fins. They are regarded as a monophyletic group because of the unique cornual processes, although these have been secondarily reduced or lost several times independently (Janvier, 1980, 1981, 1985a). Cornuate osteostracans appear first in the lowermost Devonian, become abundant in the Lower Devonian and are present, but rare, in the Middle Devonian and Frasnian.

Osteostracans make a strong showing in the Lower Devonian faunal lists in Britain, Europe and Spitsbergen, though, so far, not so much in North America. Seven families are present in the Pragian and of these, three are known in Scotland. Morphological differences between

Table 4.1 Thelodont faunas in the Upper Silurian–Lower Devonian Old Red Sandstone of the Anglo-Welsh Basin. They are based on scale species (largely after Turner, 1973): recent discoveries, as yet unpublished, show that other fish groups are also represented by scales and may be of similar stratigraphical value.

Thelodont fauna	Stratigraphical Formation
Turinia pagei	Ditton Group
T. pagei fauna with *Apalolepis*	'*Psammosteus*' Limestone
	Lower Ditton Group
Goniporus, *L. kummerowi*, *Katoporodus* sp. with *L. cuneata*	Upper Red Downton Group
Acanthodians only	(M. Downtonian) Holdgate Sandstone Group
Thelodus parvidens fauna, with *G. alatus* and *K. tricavus*	Lower Red Downton Group
T. parvidens fauna, including *L. ludlowiensis*, *T. bicostatus*, *T. trilobatus*, *T. pugniformis*, and *T. costatus*	
T. parvidens, *L. ludlowiensis* and *T. bicostatus*	
T. parvidens and *L. ludlowiensis*	

species of '*Cephalaspis*' *sensu lato* are small and several species are known from a single locality – as is the case in the Anglo-Welsh area. This may reflect restrictions to migrations between habitats so that local communities soon acquired local characteristics. Many occurrences of isolated or fragmentary headshields suggest thanatocoenose preservation and few bioceonoses are indicated. Articulated specimens and squamation are not common, and most of the fossils have been water-transported to some extent. It is possible that these animals could survive in very shallow water where other vertebrates were in difficulty.

Acanthodians are common throughout the Upper Silurian and Lower Devonian of the Welsh Borders as isolated derived scales and spines, plus occasional shoulder girdle material.

Thelodonts and other microvertebrate remains are currently under study as possible major biostratigraphical indices. Fresh information is making an impact; for example Turner *et al*. (1995) have reported the presence of *Lepidaspis* sp. in a *Turinia pagei* assemblage from South Wales. This genus has been recorded from the Delorme Formation of north-western Canada (Dineley and Loeffler, 1976), and *Lepidaspis sp.* was subsequently identified in the *vogti* horizon of the Ben Vevis Formation of Vestspitsbergen and in northern Russia. The Talgarth (S. Wales) locality is within the *T. symondsi* zone at the Přídolí–Lochkov boundary.

Chondrichthyan scales are also known from several localities within the Early Devonian of the Anglo-Welsh Basin (Vergoossen, in press). Biozones based upon acanthodians have been erected for marine and non-marine facies of the Devonian of northern Europe by Valiukevicius (1995, 1998), and there is little doubt that, as collections improve in Britain, similar biozonation of the Lower Old Red Sandstone will be possible. The records for the Middle and Upper Devonian are less useful so far.

The Arthrodira, the best known and most prolific order of the Placodermi, were locally wholly restricted to the Devonian (Denison, 1978; Gardiner, 1988, 1993a). They were typically benthic with a flattened venter and terminal mouth and heavy armour consisting of a bony cranial shield made from tuberculated dermal plates, articulating with a shoulder girdle or trunk shield. They were probably not powerful swimmers, though predatory or scavenging in habit. Early Devonian arthrodires occur globally in the world and in all the early Devonian vertebrate provinces. Thus they are also found abundantly in Australia and Antarctica, but are rare in China (Westoll, 1979; Pan and Dineley, 1988). Those from the Lower Devonian of the Welsh Borders are found as rare fragments, mostly in

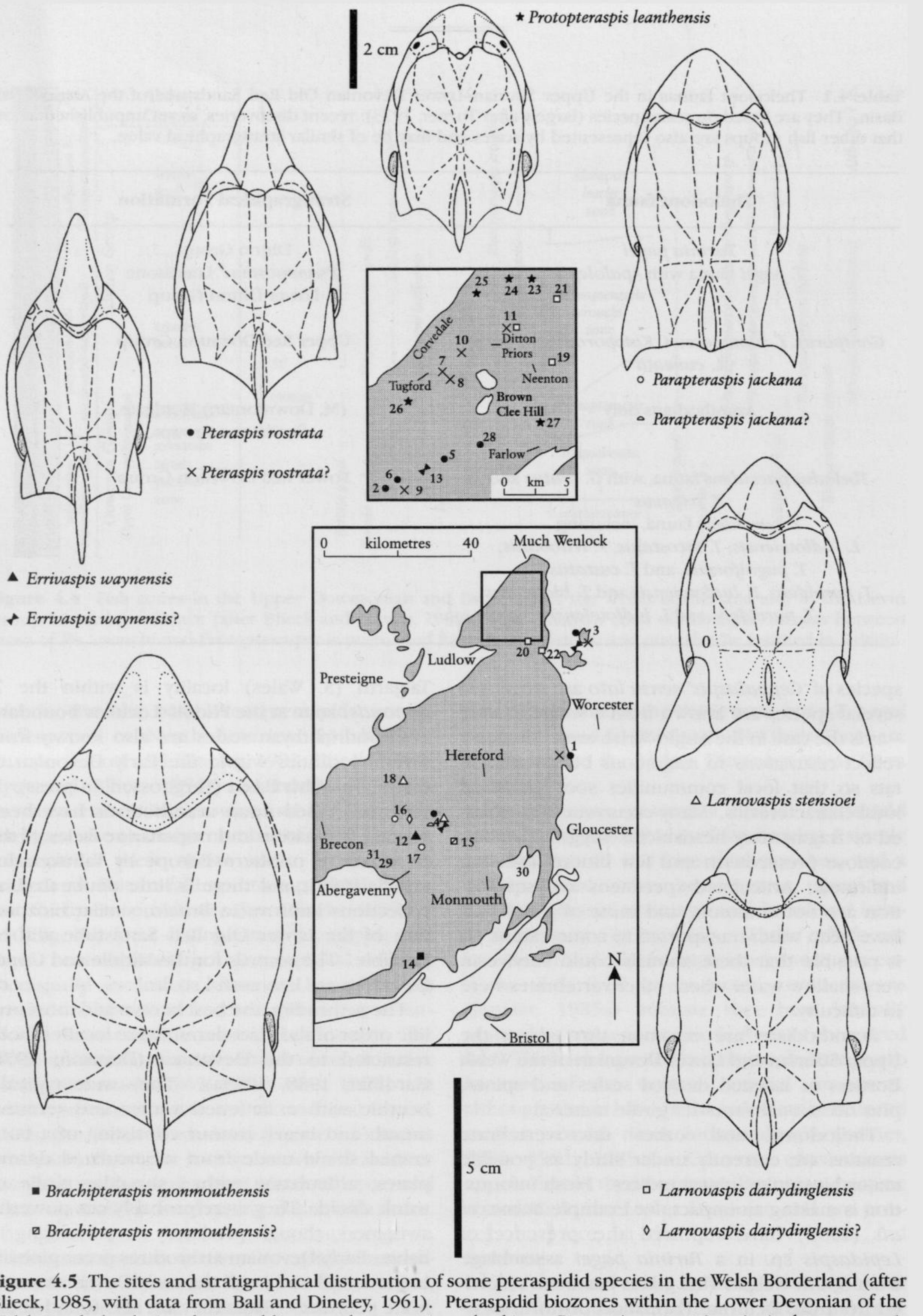


Figure 4.5 The sites and stratigraphical distribution of some pteraspidid species in the Welsh Borderland (after Blieck, 1985, with data from Ball and Dineley, 1961). Pteraspidid biozones within the Lower Devonian of the Welsh Borderland. Localities yielding zonal species (mostly akin to *Pteraspis rostrata*): principal map area: 1, Cradley, near Malvern; 3, Guildings Brook, Trimpley; 4, Wayne Herbert Quarry; 12, Pool Quarry, Walterstone; 14, Goldstop, Newport; 15, Kentchurch Hill, Hereford; 16, Castle Mattock; 17, Pandy, Monmouth; 18, Wern Gwenny, Dorstone; 20, Hopton Brook, Cleobury Mortimer; 22, Hazely Brook West, Cleobury; inset (Brown Clee Hill area): 2, Whitbatch Quarry, Ludlow; 5, Ledwyche Brook, Ludlow; 6, Targrove Quarry, Ludlow; 7, Oak Dingle, Bouldon; 8, Abdon Brook; 9, Targrove; 10, New Buildings, Holdgate; 11, Rea Bridge, Derrington; 13, Jubilee Brook, Hopton Cangeford; 21, Upton Cressett Quarry. *Protopteraspis* occurs at: 23, Meadowley Bank, Morville; 24, Monkhopton; 25, The Leath; 26, New Inn; 27, Besom Farm. *Rhinopteraspis* occurs at: 28, Rea Brook, Silvington; 29, Primrose Hill Quarry; 30, Wilderness Quarry, Mitcheldean; 31, Hoel Senni.

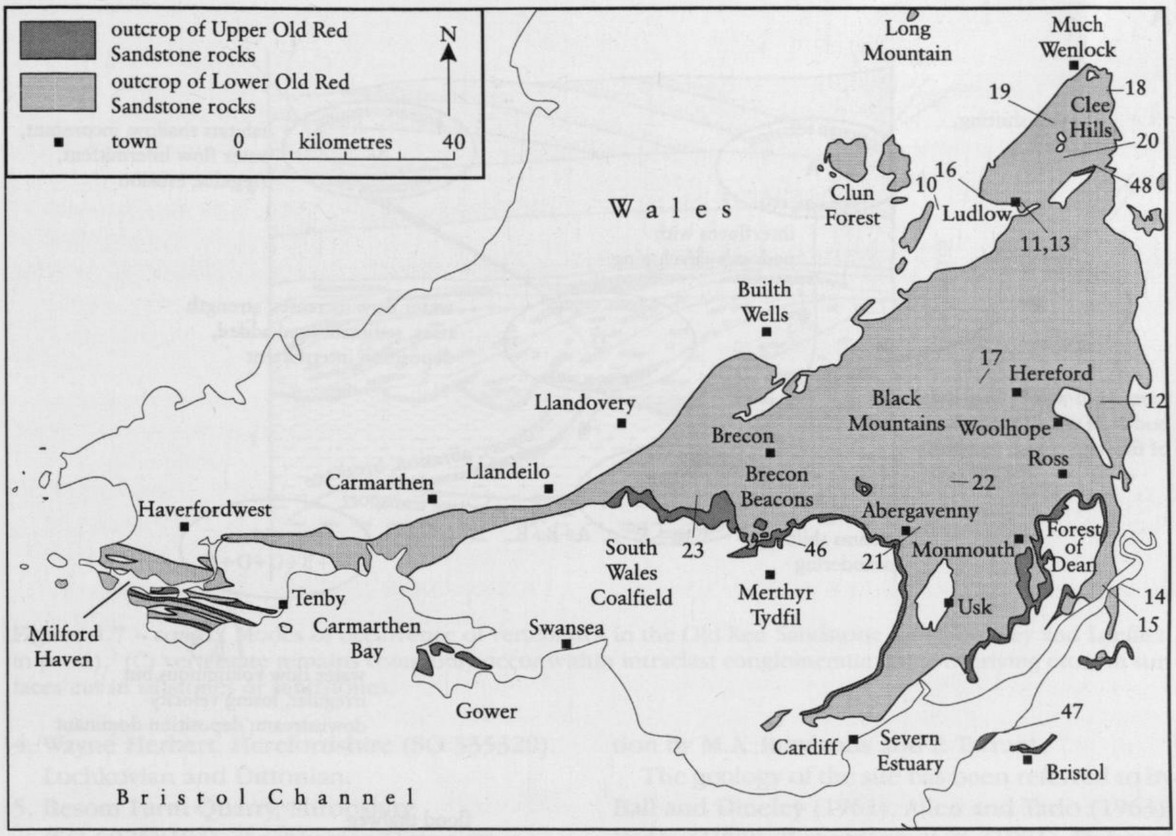


Figure 4.6 Map of the Lower and Upper Old Red Sandstone divisions in the Anglo-Welsh Basin with GCR sites indicated. Key to numbers is provided in Table 1.2.

rocks of the Ditton Series.

Turner's (1973) work on the thelodont faunas of this outcrop of the Lower Old Red Sandstone distinguished four faunas. The sequence differs from that in the Baltic area, but the *T. pagei* fauna is found in the Arbuttnott Group of central Scotland. No thelodonts occur above the Dittonian of the Anglo-Welsh area (Table 4.1).

FISH SITES

Numerous vertebrate-bearing sites have been reported in the Lower Devonian of the English Midlands, Welsh Borders and south-west Welsh region. Most of the older ones are now non-productive, worked out or obscured, but see the lists, for example in Ball and Dineley (1961) and Turner (1973). Horizons yielding vertebrates within the Downton and Ditton Groups are described in several Geological Survey Sheet memoirs. Twenty-two Anglo-Welsh sites yielding pteraspids are listed in Blieck (1984; Figures 4.5 and 4.6). Six GCR sites are selected here, representing those locations with the richest faunas. Most of these are within the essentially local point-bar fluvial conglomerates and contiguous sandy units (Figure 4.7A–C). The result is a fossil assemblage of laterally restricted extent, soon 'worked out' by collectors. The taphonomy of this type of occurrence is described in detail by Dineley and Loeffler (in press). These sites range stratigraphically from the lowest Dittonian into the early Breconian and illustrate especially a diversity of pteraspids (Figure 4.5).

Stratigraphically extended sections are uncommon, but the Devil's Hole exposes a sequence from Late Přídolí (Downtonian) to Early Lochkovian (Dittonian; see below). Other localities are of ages up to and including the ?Late Pragian. The GCR sites are as follows.

1. Devil's Hole, Shropshire (SO 672929). Přídolí–Lochkovian/Downtonian–Dittonian.
2. Oak Dingle, Tugford, Shropshire (SO 56568712). Lochkovian/Dittonian.
3. Cwm Mill, Gwent (SO 311156). Lochkovian/Dittonian.

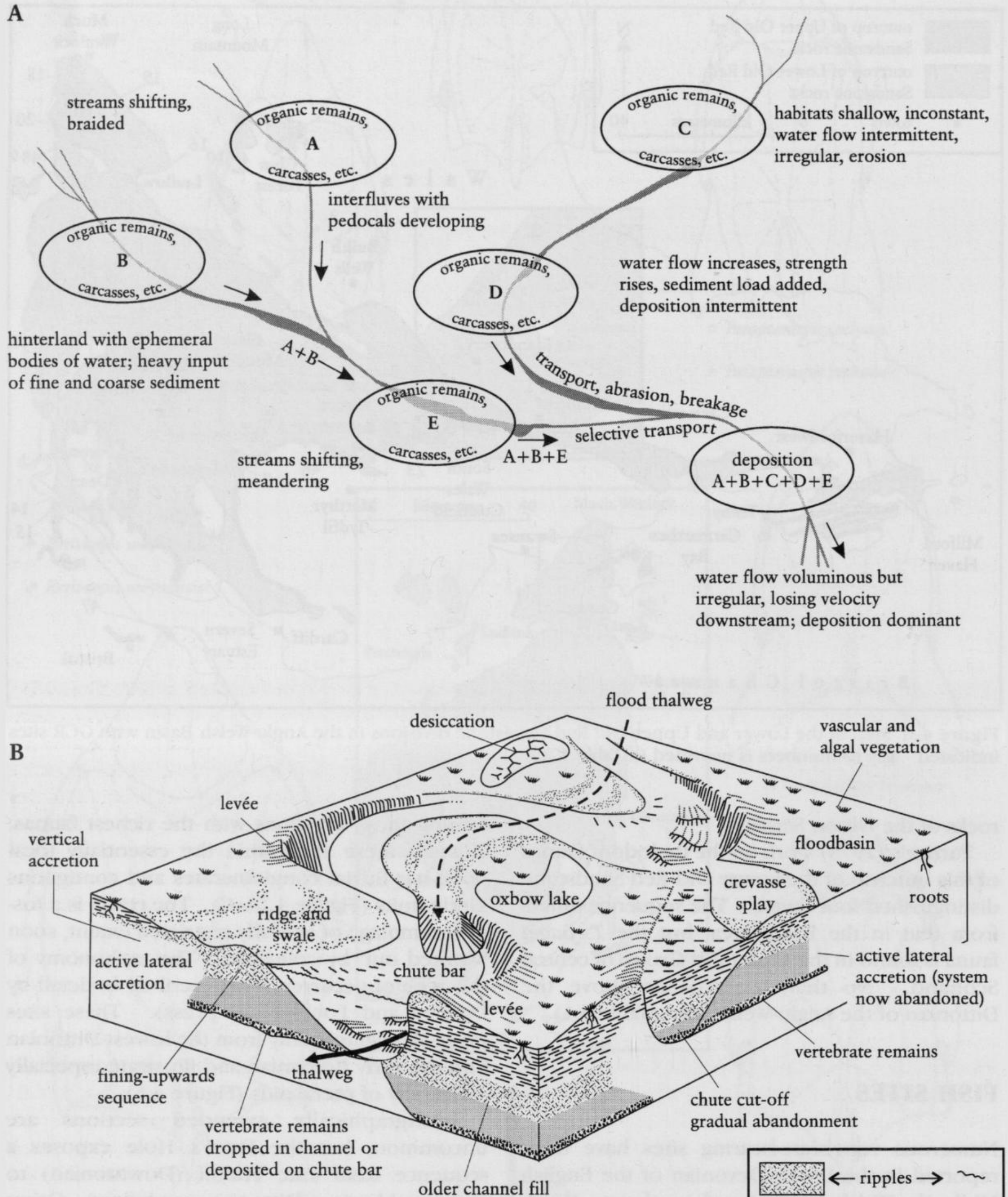


Figure 4.7 Modes of occurrence of vertebrates in the Old Red Sandstone (after Dineley and Loeffler, in press). (A) separate, perhaps different, communities within a fluvial basin yield materials that are swept together and mixed downstream; (B) deposition within a meandering river system where vertebrate remains accumulate in a variety of situations. (Continued on p. 119.)

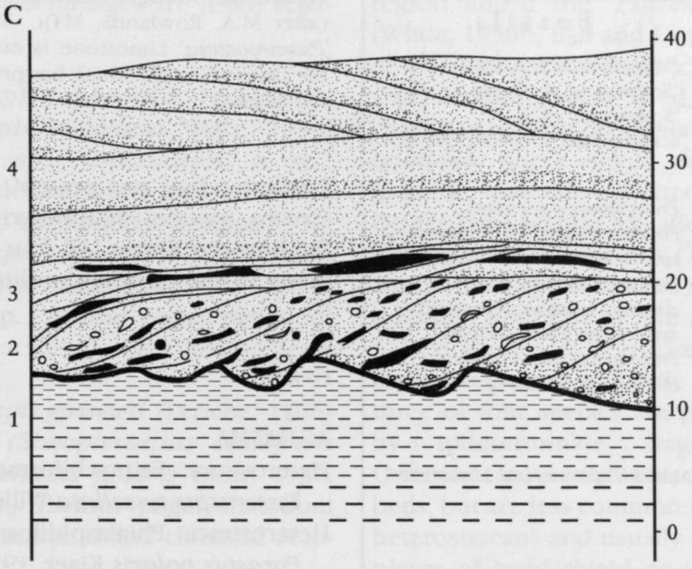


Figure 4.7 – *contd.* Modes of occurrence of vertebrates in the Old Red Sandstone (after Dineley and Loeffler, in press). (C) vertebrate remains commonly occur within intraclast conglomeratic layers overlying erosion surfaces cut in siltstones or sandstones.

4. Wayne Herbert, Herefordshire (SO 335320). Lochkovian and Dittonian.
5. Besom Farm Quarry, Shropshire (SO 60768194). Lochkovian/Dittonian.
6. Hoel Senni Quarry, Powys (SN 91452210). Lochkovian–Pragian/Dittonian–Breconian.

DEVIL'S HOLE (SO 672929)

Highlights

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

INTRODUCTION

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

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

Description

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

The four main fossil-bearing beds in Devil's Hole are called Lye Brook 1, Lye Brook 3 and Lye Brook 4, abbreviated to LB1, LB3 and LB4 (Ball and Dineley, 1961) and the *'Cephalaspis* Sandstone', a unit named by W.W. King (1934), who believed it to be a laterally continuous sandstone recognizable throughout the Welsh

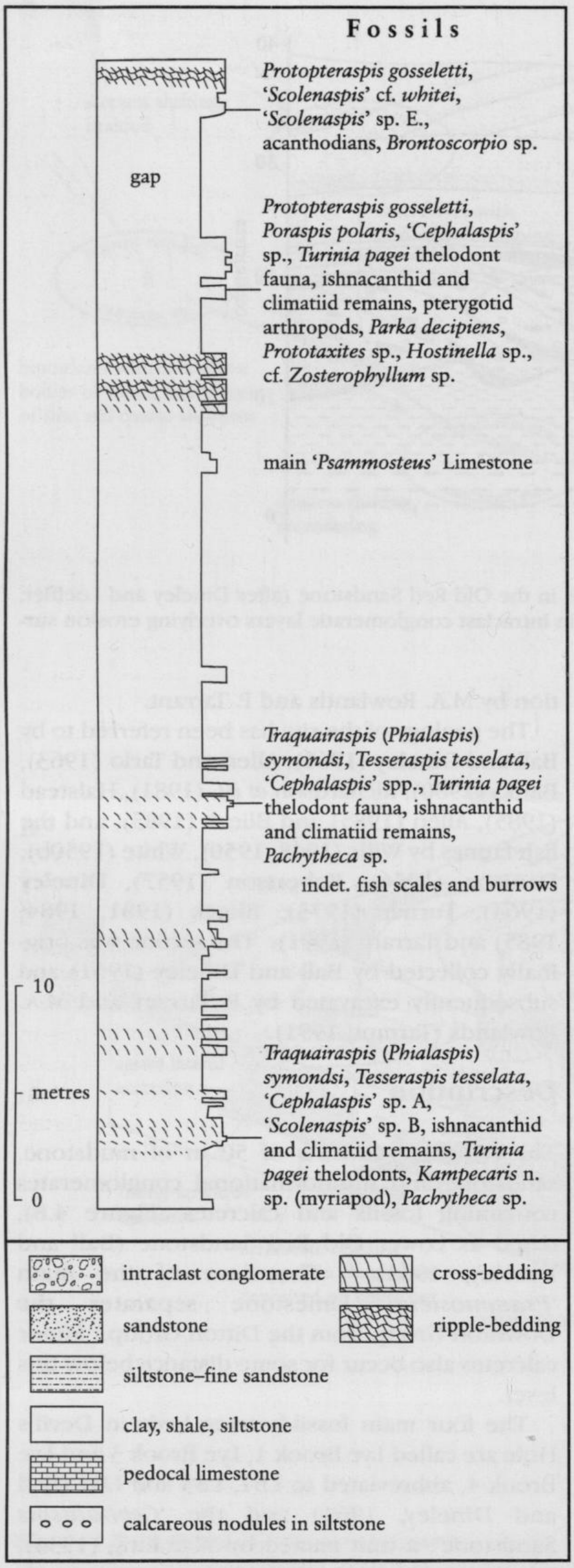


Figure 4.8 Stratigraphical section in The Devil's Hole (after M.A. Rowlands, MS). The base of the Main '*Psammosteus*' Limestone is mapped as the base of the Ditton Group, which has predominantly pteraspidid faunas.

Borders. It is not present at the Devil's Hole Stream section, but outcrops on Meadowley Bank to the north. All four beds can be recognized at several other localities locally.

Fauna

AGNATHA
Heterostraci: Eriptychiformes: Tesserapididae
Tesseraspis tessellata Wills, 1935
Heterostraci: Phialaspidiformes: Poraspididae
Poraspis polaris Kiaer, 1930
Heterostraci: Phialaspidiformes: Traquairaspididae
Traquairaspis symondsi (Lankester, 1868)
Heterostraci: Pteraspidiformes: Pteraspidae
Protopteraspis gosseleti (Leriche, 1906)
(= Pteraspis *leathensis* White, 1948)
Osteostraci: Scolenaspidiformes: Scolenaspididae
'*Scolenaspis*' n. sp.
Pattenaspis whitei (Stensiö, 1932)
Osteostraci *incertae sedis*
'*Cephalaspis*' sp.
Thelodonti: Thelodontida: Turiniidae
'*Turinia pagei* fauna' (see Table 4.1)

GNATHOSTOMATA
Acanthodii *incertae sedis*
'Ischnacanthid and climatiid spines'

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

There seem to be two quite distinct assemblages, one in the LB1 Bed and LB3 Bed, the other in the LB4 Bed and *Cephalaspis*

Sandstone. These assemblages are listed separately below.

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

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

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

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

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

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

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

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

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

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

Several good headshields of rare osteostracans have been recovered from the '*Cephalaspis*' Sandstone. A single specimen of a headshield of cf. *Pattenaspis whitei* Stensiö was found in the basal intraclast layers of sandstone near the head of Devil's Hole section, and several other specimens of headshield of a second kind were recovered from loose blocks of the overlying sandstones from Meadowley Bank. The second

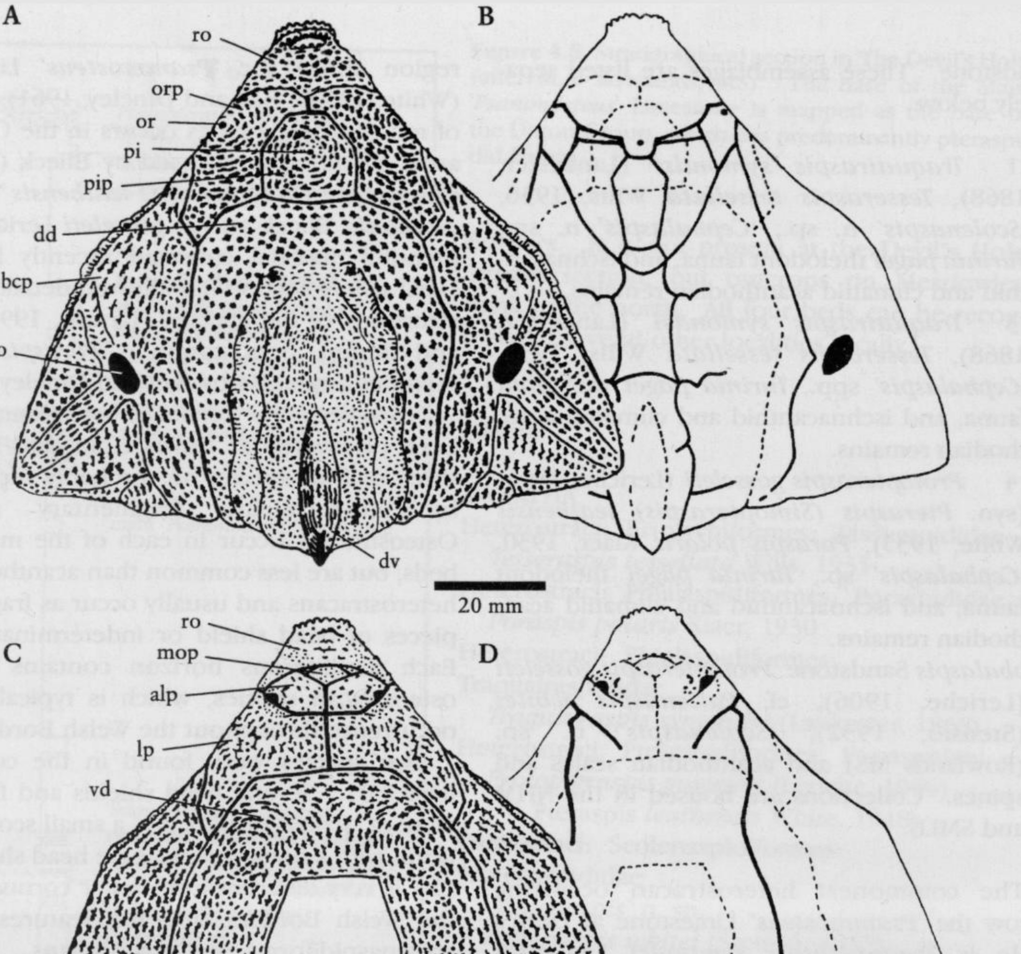


Figure 4.9 *Traquairaspis (Phialaspis) symondsi* (Lankester), restorations of the carapace on the basis of material from Devil's Hole by P.R. Tarrant (1991). (A) carapace in dorsal view, showing ornamentation of tubercles and branchial openings set near the middle of the dorsal surface of the branchial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

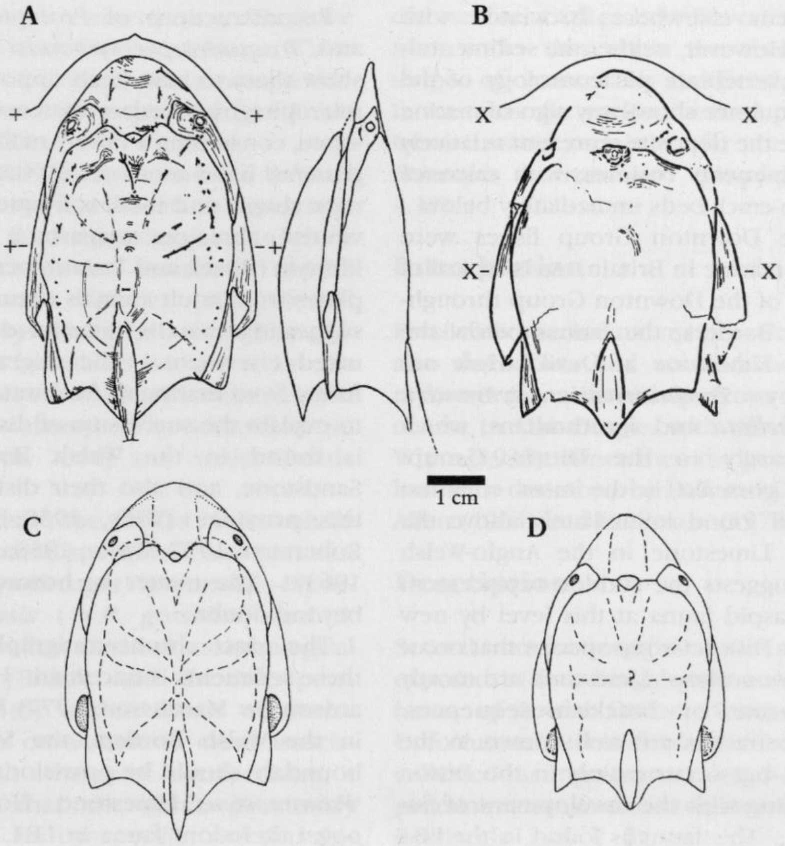


Figure 4.10 *Protopteraspis gosseleti* Leriche. White's (1950b) *Pteraspis (Simopteraspis) leathensis* (A)–(C), is now regarded as a junior synonym of this species (D). The lateral line canals are shown by broken lines in C and D. (A)–(B) from White (1950b); (C), (D) from Blieck (1985).

species, '*Scolenaspis*' n. sp., is a small cephalaspid with eyes well forward, and has similarities with *Eucephalaspis agassizi*. As in other instances throughout the Anglo-Welsh Lower Devonian, the osteostracans of this assemblage are rather uniform in size and composition, perhaps indicating that the osteostracans preferred habitat was separate from that of other fishes present.

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

Interpretation

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

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

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

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

Reconstructions of *Protopteraspis gosseleti* and *Traquairaspis symondsi* (Tarrant, 1991) show them to have been opportunistic perhaps microphagous feeders that rooted in the substrate, consuming a variety of food. However, *P. gosseleti* has a more evenly vaulted cephalothoracic shape, and the less frequent occurrence of ventral abrasion suggests a more nectonic lifestyle (Blieck and Tarrant, pers. comm.). Only plates from adult animals occur at Devil's Hole, suggesting that its juvenile development occurred elsewhere. The migration of juvenile forms from marine to freshwater has been used to explain the succession of distinct species that is found in the Welsh Borders Old Red Sandstone, and also their distribution outside this province (Wills, 1950; Denison, 1956; Robertson, 1957; White, 1958a; Allen and Tarlo, 1963). The matter is, however, not resolved beyond doubt.

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

Comparison with other localities

The site LB1 has a relatively similar relationship to the '*Psammosteus*' Limestone to those of other *Traquairaspis* localities in the Clee Hills area. Little Oxenbold and Earnstrey Brook localities (Ball and Dineley, 1961) bear a similar fauna. Other localities around the Clee Hills and at approximately the same level below the '*Psammosteus*' Limestone lack the distinctive

Phialaspis symondsi element (e.g. Targrove Dingle 6; *in* Ball and Dineley, 1961). White (1946) and Tarrant list other sites of comparable position and fauna throughout the Welsh Borderland and Wales.

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

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

Conclusion

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

OAK DINGLE, TUGFORD (SO 56568712)

Highlights

Oak Dingle in Shropshire has yielded a rich and diverse fauna of earliest Devonian fossil fishes from rocks that show the three-dimensional shapes of channel fills and floodplain deposits. It contains the earliest record of *Weigeltaspis* from Britain, and is so far the best site for *Pteraspis rostrata* var. *trimpleyensis* (Figure 4.12).

Introduction

Fossil fish specimens, mainly osteostracans but also thelodonts and acanthodians, have been reported from several horizons in the stream course in Oak Dingle, with the first reports by White (1935). Since then the geology of the site has been described by Ball and Dineley (1961), Allen (1964) and Collinson (1978).

Description

Several intraclast conglomerates and sandstones exposed in Oak Dingle yield a rich and diverse fauna of lower Ditton Group fossil fishes. Unfortunately, identifiable fossils have only been collected as transported fragments from the prominent sandstone–conglomerate unit (M.A. Rowlands and P. Tarrant collections, 1985–1991). Figure 4.11 gives the generalized succession as recorded by Allen (1964).

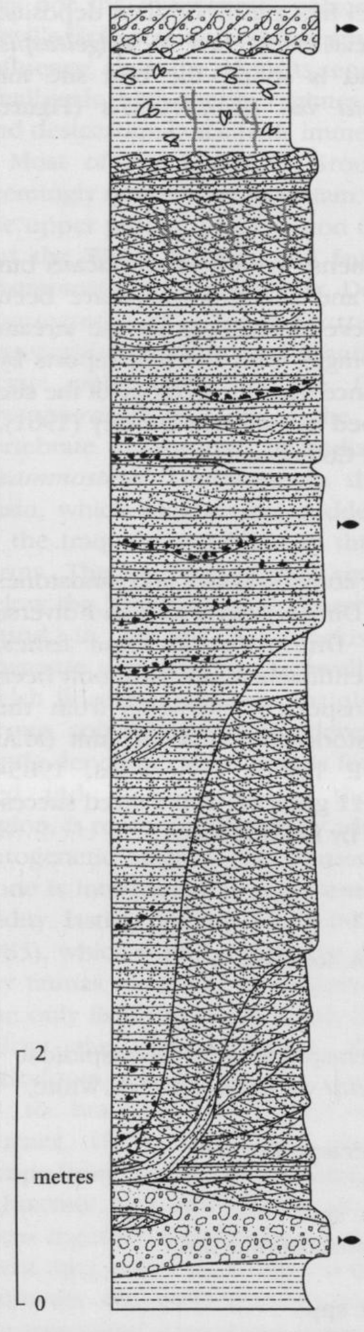
Fauna

(Recorded by M.A. Rowlands)

AGNATHA
Heterostraci: Pteraspidiformes: Pteraspididae
Pteraspis rosrata var. *trimpleyensis* White, 1935
Heterostraci: Pteraspidiformes: Wiegeltaspididae
Wiegeltaspis n. sp.
Osteostraci: Cephalaspidiformes: Cephalaspididae
Cephalaspis n. spp.
Stensiöpelta sp.

GNATHOSTOMATA
Acanthodii: Climatiiformes: Climatiidae
climatiid spines indet.
Acanthodii: Iscnacanthiformes
spines indet.

The lowermost bed SZ yielded abundant and



Main facts	Interpretation
Red coarse siltstones with invertebrate burrows and abundant calcium carbonate concretions, above red, very fine, ripple- or flat-bedded sandstones with invertebrate burrows.	Vertical accretion deposit from overbank floods. Levee overlain by backswamp deposits. Fluctuating groundwater table during times of exposure.
Fills and covers channel. Red, flat-bedded, fine sandstone with parting lineation, scour-and-fill and local scoured surfaces. Scattered siltstone clasts. Local cross-stratification. Lenticular sun-cracked siltstone.	Channel-fill and lateral accretion deposit. Sand transported as bed-load and reworked over shifting channel floor of flat-topped banks. Exposure of higher banks.
Cut on siltstone or very fine sandstone. In form of channel. Relief ~4.8 m.	Erosion at floor of wandering river channel. Extent of wandering possibly controlled by earlier channel plug.
Red, flat- or ripple-bedded, very fine sandstone passing up into red, coarse siltstone with carbonate concretions. Scattered siltstone clasts at base.	Channel-fill deposit. Overbank floods plug cut-off channel almost to top. Fluctuating groundwater table and periodic exposure.
Cut on very fine sandstones. In form of channel. Relief ~2.2 m.	Attempt to re-open plugged channel.
Repeated graded units overlying scoured surface with small-scale channels. Mostly ripple-bedded, very fine sandstone. Some siltstone.	Channel-fill deposit. Repeated intrusions of suspended sediment down a sloping surface, probably at times of higher stage.
Wedging intraformational conglomerate with sandstone lenticles.	Lag deposit formed at deepest parts of floor of wandering river channel.
Cut on siltstone. Low relief.	Erosion at floor of wandering river channel.

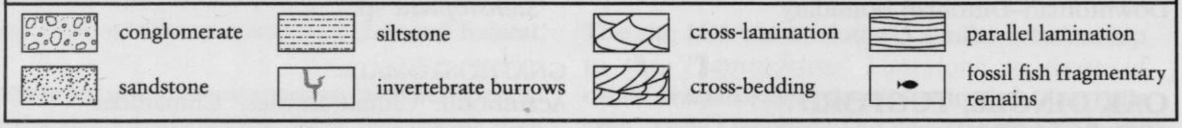


Figure 4.11 Section through the cyclothem in the Lower Ditton Group at Oak Dingle, Tugord (after Allen, 1964, and M.A. Rowlands MS).

large *Pteraspis rostrata* var. *trimpleyensis* (White, 1935) and '*Cephalaspis*' sp. (a scolenaspid) (Figure 4.12). The bottom channel S5 is described by Ball and Dineley (1961, p. 232) as their site 75, and it is the main fossil-bearing horizon in the section. Other taxa represented are *Weigeltaspis* n. sp., abundant fragments of '*Cephalaspis*' spp., *Stensiöpelta* sp., a climatiid, small ischnacanthid spines, and a *Turinia pagei* thelodont fauna.

The red intraclast-filled channels S8 and S9 have yielded *P. rostrata* var. *trimpleyensis*, *Weigeltaspis* n. sp. fragments, ?*Stensiöpelta* sp. fragments '*Cephalaspis*' sp., and climatiid spines.

Weigeltaspis n. sp. has previously been recorded from Oak Dingle as *Traquairaspis symondsi* and as *Tesseraspis* sp. (Ball and Dineley, 1961). The material represents a species of *Weigeltaspis* which has yet to be described. This is the earliest record of *Weigeltaspis* from Britain, although earlier specimens occur in Canada.

Stensiöpelta sp. is a genus of cephalaspid erected for *Cephalaspis woodwardi* Stensiö, 1932 by Denison (1951). The examples from Oak Dingle occur in the lower part of the Ditton Group, lower stratigraphically than at any other locality. This fish has a very distinctively shaped cephalic shield, which has long laterally directed cornua that delimit very wide and deep pectoral sinuses. The headshield is ornamented with clusters of rounded tubercles, and is superficially similar to *Mimetaspis* and *Pattenaspis* (Wängsjö, 1952) from Spitsbergen and *Hildenaspis* from Germany (Janvier, 1985a), but studies of *Stensiöpelta* material from Podolia show that it shares the type of ornamentation and shape of nasohypophysial opening with the scolenaspidiforms, but has no synapomorphy with *Pattenaspis* (Janvier, 1985b). *Stensiöpelta woodwardi* is recorded from the Ditton Group of Hereford and Worcester and Gwent, with the type locality being the Asylum Grounds, Abergavenny (Stensiö, 1932), now an inaccessible site. The other known species is the closely related *S. pustulata* Janvier, 1985 from the upper Lochkovian of Podolia.

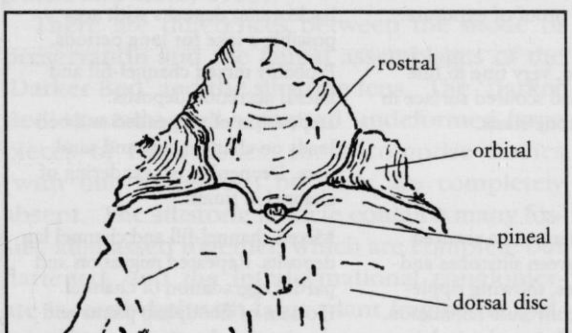


Figure 4.12 *Pteraspis rostrata* var. *trimpleyensis* White, common fragments occur in Oak Dingle, Bouldon, and the adjacent Bouldon ford. This specimen from Bouldon figured by White (1961).

Interpretation

The section from which fossils have been collected lies just beneath the cyclothem described by Allen (1964) as being produced by a meandering and aggrading river complex crossing a floodplain; this is the cyclothem described from the Anglo-Welsh Old Red Sandstone facies in Collinson (1978). Backswamp deposits, soils with caliches, and sandflats are all indicated in this sedimentary complex. As Allen (1964) noted, the cyclothem begins just above the lowest fossil-bearing bed SZ. The section then starts some 30 m above the '*Psammosteus*' Limestone, i.e. well within the lower part of the Ditton Group and in the zone of *P. rostrata–P. crouchi*.

Comparison with other localities

The Oak Dingle site shows many sedimentological features which are found throughout the outcrop of the Ditton Group of the Anglo-Welsh Basin and reveals similarities in the preservation and composition of its agnathan faunules. Similar features have also been recorded by Blieck and co-workers in northern France and Belgium (Blieck *et al.*, 1995).

Conclusion

The Oak Dingle exposure follows the strike that is uncommon for Old Red Sandstone fossil-bearing streams in the Welsh Borders. This provides the conservation value of the site because it shows the three-dimensional relationships between the sedimentary channels, lag deposits and overbank deposits. It has produced a varied fish fauna in recent excavations, and some of the taxa are the earliest instances of their groups, a result of the basal Devonian age of the site. It has considerable potential for further collecting.

CWM MILL (SO 311156)

Highlights

Cwm Mill in Gwent has yielded two exceptional specimens of *Rhinopteraspis crouchi*, as well as several cephalaspids, to provide important information about the body, tail, armour and mouth parts. Complete specimens of this age (earliest Devonian) are very rare, and the site has potential for more such excellent finds.

Introduction

A small stream section in the Ditton Group at Cwm Mill, near Abergavenny, has yielded rare complete articulated specimens of cephalaspids, including the body and tail region, which is unusual since most finds in the Welsh Borders are headshields alone. These came from a lens of grey-green siltstone, which has yielded some 50 articulated specimens (White and Toombs,

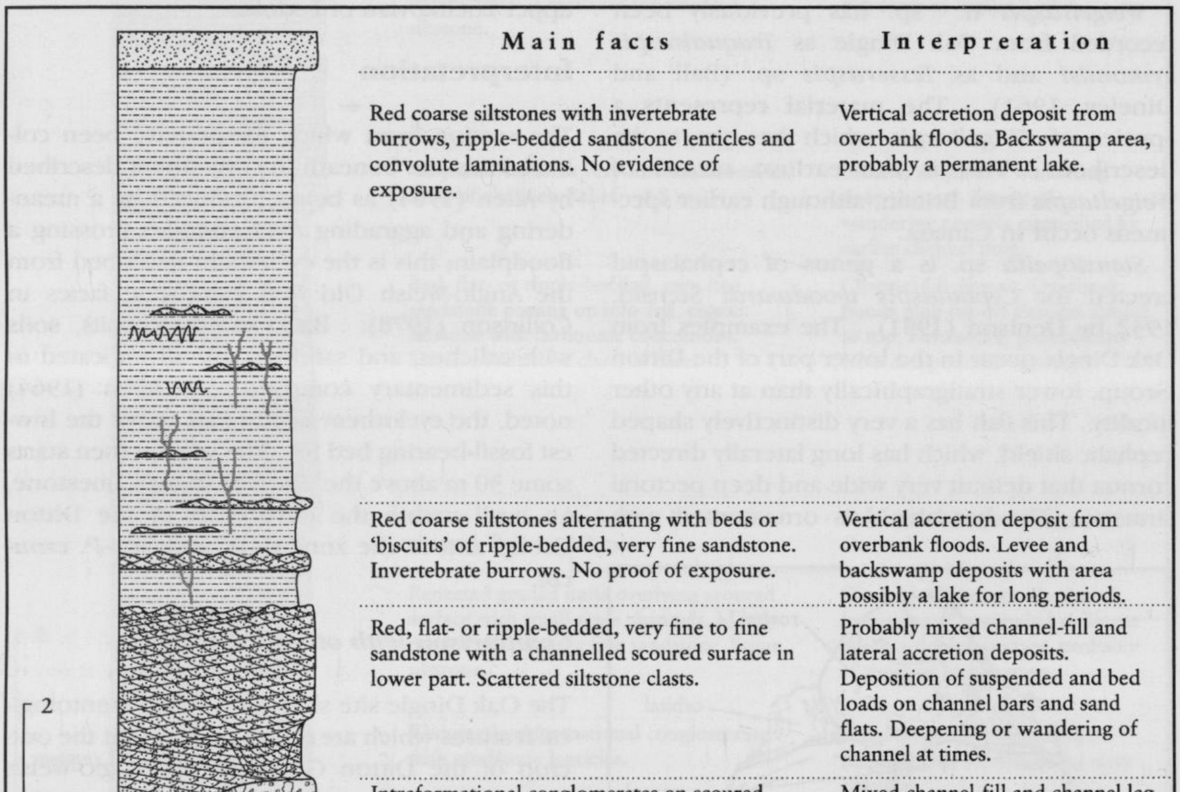


Figure 4.13 The succession at Cwm Mill, Abergavenny (after Allen, 1964).

1983). The geology of the site is mentioned in papers by Allen and Tarlo (1963), Allen (1964), White (1973) and White and Toombs (1983), and the fish fauna by White (1935, 1950b, 1958b, 1961), Westoll (1945, 1958), Denison (1951a, 1956, 1967b, 1970), Novitkskaya (1975), Goujet and Blieck (1979), Blieck (1980) and Janvier (1980, 1981, 1985a).

Description

Allen (1964) scrutinized the cyclothem (Figure 4.13) which contains the fossil fishes within a conglomerate unit and which rests on a scoured surface of siltstone. The horizon that yielded the complete articulated cephalaspid specimens lies 'a little below' a fossiliferous intraformational conglomerate. It is a lens of siltstone passing laterally into a coarser, vertebrate-bearing, grey-green sandstone (Allen and Tarlo, 1963). White and Toombs (1983) described the lens that yielded the cephalaspids as being part of the 'Darker Bed' (p. 166), which is found in Unit 2 or 3 of the cyclothem (Allen, 1964, fig. 11).

A mudstone layer near the base has yielded complete cephalaspids, but the only other specimens present within the whole section were 'half a dozen broken head shields here and there of similar animals' plus *Rhinopteraspis crouchi* plates, either alone or with plant and/or eurypterid remains. This *Rhinopteraspis* debris is from individuals of all sizes found together (Allen and Tarlo, 1963).

There are differences between the mode of preservation and the faunal assemblages of the 'Darker Bed' and the siltstone lens. The 'Darker Bed' contains well-separated undeformed large pieces of fossil fishes; these comprise bodies (with one exception) but tails are completely absent. The siltstone lenticle contains many fossils, all massed together, which are complete but flattened, and the intraformational conglomerate is 'crowded with large plant fragments, pellets of wood, *Pachytheca*, eurypterid skins, and pteraspid and cephalaspid scales, plates and discs.' (Allen, 1964, p. 186).

Fauna

AGNATHA
Osteostraci: Cephalaspidiformes: Cephalaspididae
Cephalaspis abergavenniensis White and Toombs, 1983
'C.' cwmmillensis White and Toombs, 1983
'C.' cradleyensis Stensiö, 1932
Cwmaspis billcrofti White and Toombs, 1983
Heterostraci: Pteraspidiformes: Pteraspididae
Rhinopteraspis crouchi (Lankester, 1868)
Thelodonti: Phlebolepidiformes: Phlebolepididae
Goniporus alatus (Gross, 1947)

Rhinopteraspis crouchi (Figure 4.15) was originally distinguished by Lankester as *Pteraspis crouchi*, and has been described subsequently by White (1935, 1950b, 1961, 1973), Denison (1967b, 1970), Novitskaya (1975), Goujet and Blieck (1979) and Blieck (1980). The majority of the plates of *Rhinopteraspis* from this site are from half-grown small animals, and include examples of the youngest state of development. The dorsal and ventral discs of *Rhinopteraspis* vary in length from 20 to 70 mm (large adult). This site has yielded two exceptional specimens of articulated pieces of almost the whole of the body armour including the mouth parts (White, 1973). However, it is unclear whether the specimens came from the siltstone lenticle or the 'Darker Bed'. These pteraspids show the configuration and relationship of the tooth plates, orbital plates and branchial plates, and allow the identification of isolated plates found elsewhere in the Welsh Borders. Using this material, White (1973) was able to define the body armour of this species for the first time, and Blieck (1980) gave a reconstruction based on White's (1973) description.

White and Toombs (1983) reported on the fifty articulated specimens of 'cephalaspid' material collected by Croft at this site in the mid-1930s, all but three of which are *'Cephalaspis' cradleyensis* (Figure 4.14). Each of the other three specimens represents a new species. The darker bed around the siltstone lens yielded further specimens of cephalic shields of *C. cradleyensis* plus fragments of other species. These provided greater detail than the complete specimens from the site, and form the basis of the reconstruction of the headshield of *C. cradleyensis* (White and Toombs, 1983, fig. 6).

The new material from Cwm Mill, consisting of 42 individuals, many with the squamation of the body and tail, allowed White and Toombs (1983) to produce a new description and diagnosis of this species. The total length is about 120 mm, with the median length of the head,

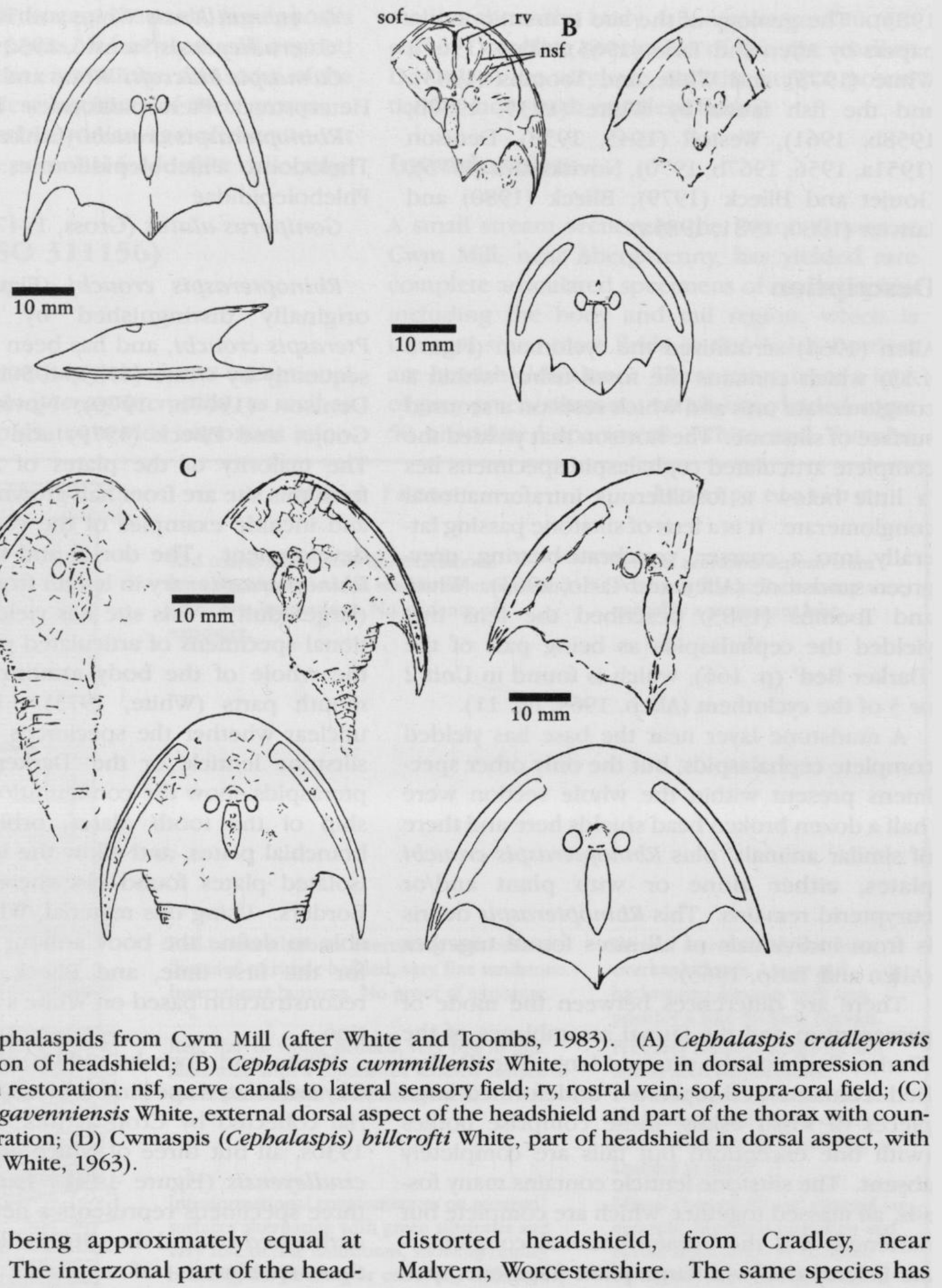


Figure 4.14 Cephalaspids from Cwm Mill (after White and Toombs, 1983). (A) *Cephalaspis cradleyensis* Stensiö, restoration of headshield; (B) *Cephalaspis cwmmillensis* White, holotype in dorsal impression and counterpart, with restoration: nsf, nerve canals to lateral sensory field; rv, rostral vein; sof, supra-oral field; (C) *Cephalaspis abergavenniensis* White, external dorsal aspect of the headshield and part of the thorax with counterpart and restoration; (D) Cwmaspis (*Cephalaspis*) *billcrofti* White, part of headshield in dorsal aspect, with restoration (after White, 1963).

body and tail being approximately equal at *c*. 40 mm each. The interzonal part of the headshield bears a low but distinct spine, and the species possessed shallow pectoral sinuses. The ventral surface of the headshield was similar to *Hemicyclaspis* in possessing a wide narrow mouth and an external surface covered by numerous small irregular scales. There were at least eight box-like branchial pouches on each side. The body was covered by scale rows. The pectoral fins were leaf-like in shape.

'*Cephalaspis*' *cradleyensis* was erected by Stensiö (1932) for a single small imperfect and distorted headshield, from Cradley, near Malvern, Worcestershire. The same species has been described from a single specimen from the Red Bay Series of Spitsbergen (Wängsjö, 1952), and it may have some palaeogeographical significance.

'*Cephalaspis*' *cwmmillensis* White and Toombs 1983 is based on a single small imperfect headshield from Cwm Mill, which has lost most of its associated body and tail. The outline of the head shield is distinctively oval (Figure 4.14), with no rostral angle. The upper surface was covered with small thorn-like denticles, and

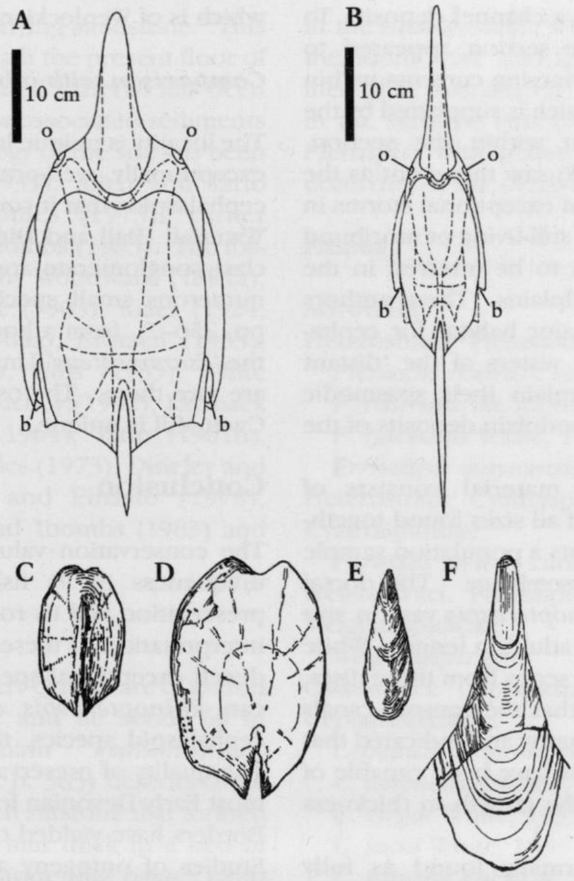


Figure 4.15 *Rhinopteraspis crouchi* (Lankester) from Cwm Mill (after White, 1973; Blieck, 1980). (A) *R. crouchi* carapace in dorsal view with sensory canal system shown by broken lines: b, branchial openings; o, orbits; (B) *R. dunensis* (Roemer) carapace in dorsal view, the extreme elongated form found in the higher Dittonian strata: (C), (D) dorsal discs; (E), (F) rostral plates.

the mucous canal system was enclosed in the exoskeleton.

Cephalaspis abergavenniensis White and Toombs, 1983 is based on a single small imperfect flattened cephalic shield with much of the body attached, which was complete when collected, but now lacks part of the body and tail (White and Toombs, 1983). The pectoral sinuses are narrow and deep. Ornamentation on the exoskeleton consists of numerous small well-separated stellate tubercles, which are larger and thorn-like towards the back of the shield.

Cwmaspis billcrofti White and Toombs, 1983 is another species based on a single small imperfect headshield. However, the great breadth and shortness of the headshield, together with very short cornua, and other proportions (Figure 4.14) suggested assignment to a new subgenus, *Cwmaspis*, by White and Toombs (1983), which is raised to the level of genus, because of the restriction of the genus *Cephalaspis* to *Cephalaspis lyelli* (Janvier 1980, 1981, 1985a). Although the shape of the cephalic shield is similar to *Benneviaspis*, unlike that genus, *Cwmaspis* retains the cephalaspidid sensory fields and position of orbits.

Interpretation

Allen (1964) interpreted the cyclothem as fluviatile in origin; the intraformational conglomerate containing disarticulated fossil material is interpreted as the 'flotsam of a waning flood' that was perhaps deposited at the head of a channel bar or in the entrance to a slough where gravel from the channel floor might also be found. The disarticulated fossil material is thought to have been derived from an earlier deposit, whereas the articulated specimens may represent fishes that died catastrophically in the river as the result of flood conditions (Allen, 1964, p. 187). Allen and Halstead (1968) explained this section as a channel deposit. To White (1973) the whole section appeared to have been deposited by varying currents within a short period of time, which is supported by the restricted fauna present within the section. White and Toombs (1983) saw this event as the result of floodwaters from exceptional storms in the uplands which swept still-living or moribund animals down the rivers to be interred in the drying pools of the floodplains. These authors suggested that, if the major habitat for cephalaspids was in the fresh waters of the 'distant uplands', this would explain their spasmodic occurrence within the floodplain deposits of the Anglo-Welsh Basin.

This *Rhinopteraspis* material consists of plates from individuals of all sizes found together and probably represents a population sample from the original life assemblage. The dorsal and ventral discs of *Rhinopteraspis* vary in size from 20 to 70 mm (large adult) in length. White (1973) produced growth series from these discs, which showed the way that the sensory canals developed as the animal grew and indicated that the basal bone layer must have been capable of resorption to allow for the growth in thickness of the plates.

Cephalaspids are normally found as fully grown adults (Westoll, 1945, 1958; Denison, 1951b, 1956; White 1958), which has led to the conclusion that they acquired their bony skeleton only when fully grown (Wängsjö, 1952): if they lived in marine or brackish waters, there would be no need for bony shields for salinity control. However, one specimen of *'Cephalaspis' cradleyensis* apparently shows incompletely formed hard parts. White and Toombs (1983) thought this was the result of post-mortem changes, because the complete individual is associated with, and on the same surface as, another that is perfectly normal. Moreover, the unusual specimen is merely a 'ghost', preserved as an impression only. It is also slightly smaller than the other specimens of the species. It was regarded by White and Toombs (1983) as possibly a young animal in the early stages of forming armour. Thus it would follow that the young animals may have been soft-bodied while within the fluvial environments, and that ossification took place evenly throughout the animal.

The thelodont *Goniporus alatus* (Gross, 1947) is the last recorded member of the family Phlebolepididae, the first (oldest) genus of which is of Wenlockian age.

Comparison with other localities

The locality is unique in Britain in the number of exceptionally well-preserved pteraspidids and cephalaspids that it contains. Only at Silvington Waterfall (Ball and Dineley, 1961) has an intraclast conglomerate and sandstone yielded very numerous small specimens (see White, 1961, pp. 256–7), from a horizon about 150 m above the *'Psammosteus'* Limestone, but cephalaspids are rare there. The osteostracan assemblage at Cwm Mill is unique.

Conclusion

The conservation value of the site lies in the uniqueness of its fish fauna, the quality of preservation and its role in the palaeobiological interpretation of these fish. Cwm Mill has produced exceptional specimens of the heterostracan *Rhinopteraspis crouchi* and of several cephalaspid species, three unique to this site. The quality of preservation is uncommon, since most Early Devonian fossil fish sites in the Welsh Borders have yielded only fragmentary remains. Studies of ontogeny and growth of the fishes may be possible, based on Cwm Mill material, because of the range of specimen sizes preserved. This site is crucial for further palaeobiological study of heterostracans and osteostracans, but the potential for further discoveries is rather restricted without further excavation.

WAYNE HERBERT QUARRY (SO 335320)

Highlights

The Wayne Herbert site in Herefordshire has yielded a diverse fossil fauna including rare complete cephalaspids, pteraspids and the oldest known complete acanthodians. Its importance rests in the quality of these specimens and in their age.

Introduction

A small overgrown quarry to the south-west of Wayne Herbert (or Wainherbert) Farm yielded in the 1930s a rich and diverse fauna of complete fossil fishes and eurypterids from a green siltstone lenticle and its overlying sandstone. This original level is now beneath the present floor of the quarry, but disarticulated material has been obtained recently from the associated sediments above the lens. The geology of the site has been referred to by White (1935), Allen and Tarlo (1963), Allen (1964), Miles (1973), Turner (1982a) and White and Toombs (1983). The fossils have been described by Woodward (1891a), Traquair (1899a), Leriche (1903), Kiaer (1924, 1932b), Gross (1933, 1968a), Brotzen (1933), Kiaer and Heintz (1935), Wills (1935), White (1935), Berg (1940), Obruchev (1941), Kermack (1943), Denison (1956, 1964), Tarlo (1961b), Halstead Tarlo (1965), Miles (1973), Dineley and Loeffler (1976), Märss and Einasto (1978), Turner (1982a), White and Toombs (1983) and Blieck (1984).

Description

The strata in Wayne Herbert Quarry are of Ditton Group (Lochkovian) age and lie about 66 m above the (local) main *'Psammosteus'* Limestone. White (1935, p. 383) described the fish bed as a very fine green siltstone that formed a thin restricted lens 50 mm thick in a bed of normal coarse grey sandstone that passes laterally into a coarser unfossiliferous rock or thins out. It contains a *Turinia pagei* thelodont assemblage and lies within the *Rhinopteraspis crouchi* Zone; it is also placed in the *microratus–newportensis* spore Zone of Richardson and MacGregor (1986), i.e. Lochkovian. The first specimen was found in pieces among the debris on the floor of the quarry. White and Toombs (1983) recorded *P. rostrata* var. *waynensis*, *P. rostrata* var. *virgoi* and *P. ?jackana* as from above the siltstone lenticle, and *P. rostrata* var. *toombsi* from within it. In his study of the Pteraspidiformes, Blieck (1984) created the genus *Errivaspis* for *P. rostrata* var. *waynensis*. The rock overlying the lens also contains fossil material, although it is disarticulated, and mostly isolated dorsal and ventral pteraspid discs. A fragment of the arthropod *Prearcturus gigas* and broken plates of *Weigeltaspis* sp. were recorded from the 'uppermost beds at Wayne Herbert' (White, 1935, p. 385). There are differences between the species of heterostracans found in the siltstone lens and the associated 'sandstones', but all the cephalaspids (as yet undescribed species), together with *Cephalaspis jacki* and the acanthodians, are found complete in the siltstone lens, where articulated pieces of thelodont were also found. A complete specimen of *P. rostrata* var. *toombsi* has been found in the siltstone lens (the first known complete *Pteraspis*) with plates of the other pteraspids occurring in the overlying cornstone.

Fauna

AGNATHA
Heterostraci: Pteraspidiformes: Pteraspididae
Pteraspis rostrata sensu stricto Agassiz, 1835
P. rostrata var. *toombsi* White, 1935
P. ?jackana White, 1935
Errivaspis waynensis (White, 1935)
Heterostraci: Cyathaspidiformes: Cyathaspididae
Poraspis sericea Lankester, 1873
Heterostraci: Phialaspidiformes: Weigeltaspididae
Weigeltaspis sp.
Osteostraci: Cephalaspidiformes: Cephalaspididae
Cephalaspis toombsi White, 1935
C. waynensis White, 1935
C. virgoi White, 1935
C. jacki White, 1935
C. salweyi Egerton, 1857
Thelodonti: Thelodontida: Nikoliviidae
Nikolivia milesi Turner, 1982

GNATHOSTOMATA
Acanthodii: Climatiformes: Climatiidae
Ptomacanthus anglicus Miles, 1973
Vernicomacanthus waynensis Miles, 1973
Acanthodii: Ischnacanthiformes: Ischnacanthidae
Uraniacanthus spinosus Miles, 1973

The arthropods *Pterygotus anglicus*? and *Prearcturus gigas* are also found at Wayne Herbert.

Pteraspis rostrata was first described as *Cephalaspis rostratus* by Agassiz (1835), based on an internal cast from the Ditton Group of Whitbach Quarry (no longer extant), near Ludlow. This specimen is an immature form, and therefore atypical, which meant that when White (1935) described the species of *Pteraspis* known at the time, he gave five new varieties for all the newer material, while stating that eventually one of these could be shown to be the typical form (Figure 4.16). White's five varieties were: *P. rostrata* var. *waynensis*, *P. rostrata*

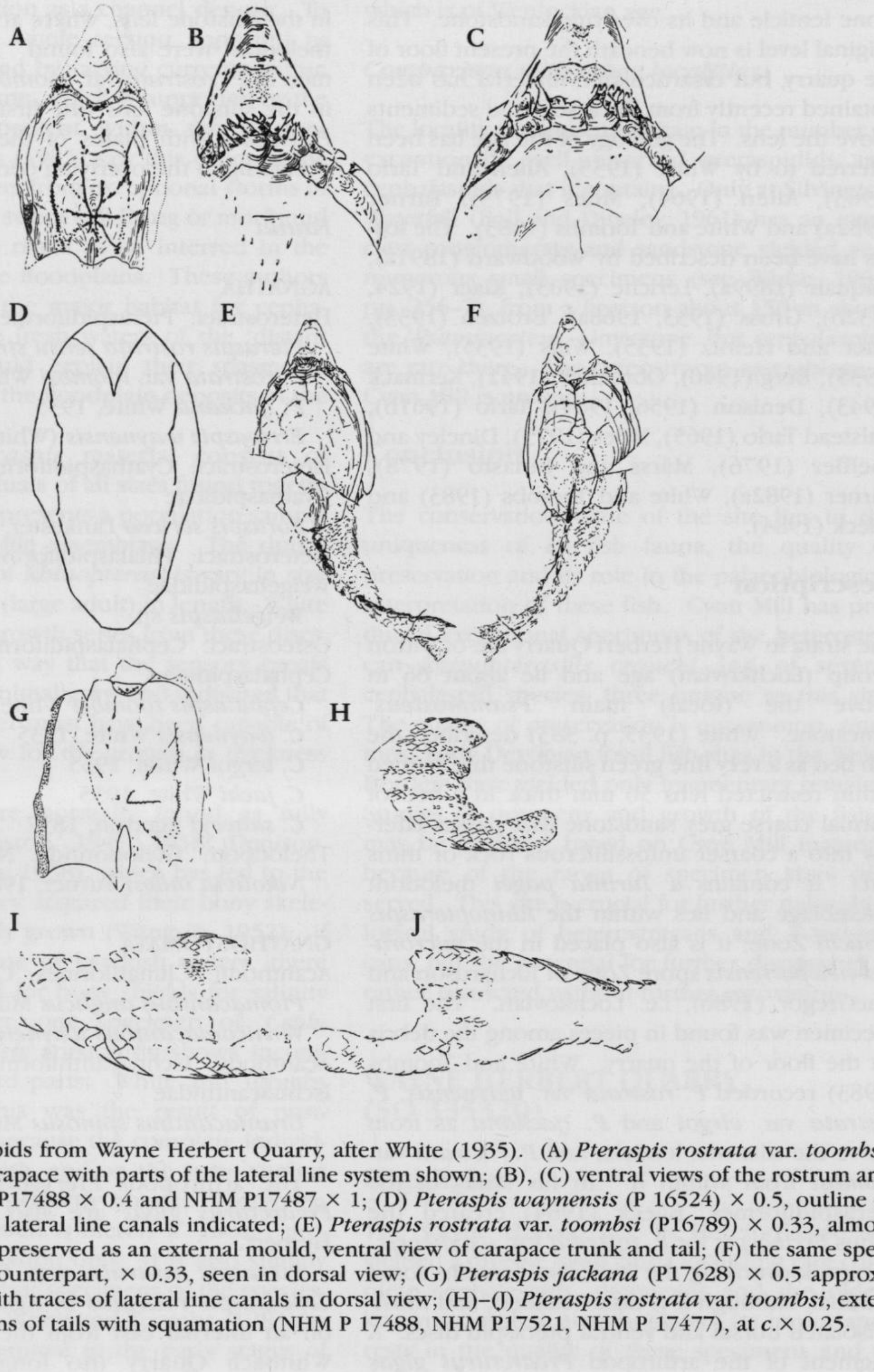


Figure 4.16 Pteraspids from Wayne Herbert Quarry, after White (1935). (A) ***Pteraspis rostrata*** **var.** ***toombsi***, dorsal view of the carapace with parts of the lateral line system shown; (B), (C) ventral views of the rostrum and oral appratus, NHM P17488 × 0.4 and NHM P17487 × 1; (D) ***Pteraspis waynensis*** (P 16524) × 0.5, outline of the ventral disc with lateral line canals indicated; (E) ***Pteraspis rostrata*** var. ***toombsi*** (P16789) × 0.33, almost complete individual preserved as an external mould, ventral view of carapace trunk and tail; (F) the same specimen preserved in counterpart, × 0.33, seen in dorsal view; (G) ***Pteraspis jackana*** (P17628) × 0.5 approximately, dorsal disc with traces of lateral line canals in dorsal view; (H)–(J) ***Pteraspis rostrata*** var. ***toombsi***, external lateral impressions of tails with squamation (NHM P 17488, NHM P17521, NHM P 17477), at *c.*× 0.25.

var. *toombsi*, and *P. rostrata* var. *virgoi*, all from Wayne Herbert, *P. rostrata* var. *trimpleyensis* from Trimpley, Worcestershire, and *P. rostrata* var. *monmouthensis* from Monmouth. Blieck (1984) redefined *Pteraspis rostrata*, removing *P. rostrata* var *virgoi*, and creating a new genus *Errivaspis* for *P. rostrata* var. *waynensis*, thus *Errivaspis waynensis*.

Six more or less complete, flattened specimens of *Pteraspis rostrata* var. *toombsi* were found in the siltstone lenticle at Wayne Herbert, together with some fragments of the caudal and tail region. *Pteraspis rostrata* also occurs in northern France and Belgium.

Pteraspis jackana was described by White (1935) from south-west Herefordshire, and north Monmouthshire, with a type specimen from Castle Mattock. An isolated dorsal disc showing growth stages was found above the siltstone lens at Wayne Herbert, and is referred tentatively to this species by White and listed as *P. ?jackana* in White and Toombs (1983).

Poraspis sericea, described (Lankester, 1873a, 1873b) from 'Abergavenny', occurs in the Middle Dittonian of the Welsh Borders (Denison 1964) and was recorded at Wayne Herbert by Turner (1982a). It is the type species of the cyathaspidid genus *Poraspis*, and is one of the last species of the Order Cyathaspidiformes to appear in the stratigraphical record. It is also the largest species of the genus, and may be related to *P. magna* from Spitsbergen. Denison (1964) listed 15 species of *Poraspis* from Spitsbergen, the Welsh Borders, Pas de Calais (France), and Podolia (Ukraine). He used length, width, and orbital ratios to distinguish species.

Weigeltaspis sp. is recorded from the beds overlying the siltstone lenticle. It has plates ornamented by elongate leaf-shaped tubercles, and when first discovered was thought to be an arthrodire (Brotzen, 1933). Halstead Tarlo (1965) redescribed the genus from new material, suggesting that *Weigeltaspis* is very similar to many of the advanced psammosteids. However, Blieck (pers. comm.) adduces evidence to place it within the Family Traquairaspidae. It occurs in the Upper Lochkovian of Podolia, Latvia, the Welsh Borders and Spitsbergen.

The first discovered specimen of the thelodont *Nikolivia milesi* Turner, 1982 was found at Wayne Herbert. It consisted of a large, 150 mm long fragment from the ventral surface of the cephalothorax. Articulated thelodonts are very rare; most of the 50–60 species described are based entirely on isolated scales. Only two articulated specimens, and several separate scales of this species, are known from the Lower Devonian of Britain (Turner, 1982a). The type species of the genus is *N. oervigi* Karatajute-Talimaa, 1968 from Podolia. Isolated scales in the Early Devonian of Europe and Australia, are associated with turiniid thelodonts, and in the Early Silurian to Early Devonian of north-west Canada (Turner, 1982a). *N. milesi* is a large thelodont, longer than 145 mm, with long cephalothorax and slim triangular pectoral flaps (Figure 4.17). It has thin lanceolate scales with leaf-like crowns, about 1.5 mm long. No isolated scales have yet come from Wayne Herbert (Turner, 1982a).

The acanthodians from Wayne Herbert are the oldest known intact British specimens of this group (Miles, 1973). The only other articulated Lower Old Red Sandstone acanthodian material occurs in the Angus fish beds of Scotland. As isolated scales and spines, with occasional shoulder girdle and jaw material, acanthodians are common throughout the Upper Silurian and Lower Devonian of the Welsh Borders. The Wayne Herbert specimens were found in the siltstone lenticle, which also yielded the complete fossils, *Pteraspis rostrata*, described by White (1935). *Ptomacanthus anglicus* Miles, 1973 is the type species of this primitive genus of climatiid (Figure 4.18). It reaches a length of at least 300 mm, and is closely related to *Nostolepis* and *Climatius*. *Vernicomacanthus waynensis* Miles, 1973 is closely related to the smaller *V. uncinatus* from the the Lower Old Red Sandstone of Turin Hill, Angus, which is the type and only other specimen of this climatiid genus. It has six pairs of intermediate fins, an unusually large number, and a correspondingly elongate body. *Uraniacanthus spinosus* Miles, 1973 is represented by this single species from Wayne Herbert, although it is possible that some of the isolated detached spines found elsewhere in the Dittonian of the Welsh Borders and usually labelled '*Ischnacanthus*' sp. represent this genus.

Interpretation

By comparison with the sedimentology of Cwm Mill, the Wayne Herbert siltstone lens records an exceptional preservation event resulting from a flood, which rapidly carried still-living or moribund animals down-river to be buried immediately in pools on the floodplains (Miles, 1973; White and Toombs, 1983). Allen and Tarlo (1963) described it as a cut-off channel that has dried out, but Turner (1982a) pointed out that no sedimentary desiccation structures have been described, and the fishes are not contorted, although they are partly disarticulated. Turner (1982a) described a rare articulated piece of thelodont as being folded as though pressed down into soft bottom sediment, which may indicate that the fish was trapped in wet mud. She suggested that, by comparison with similar

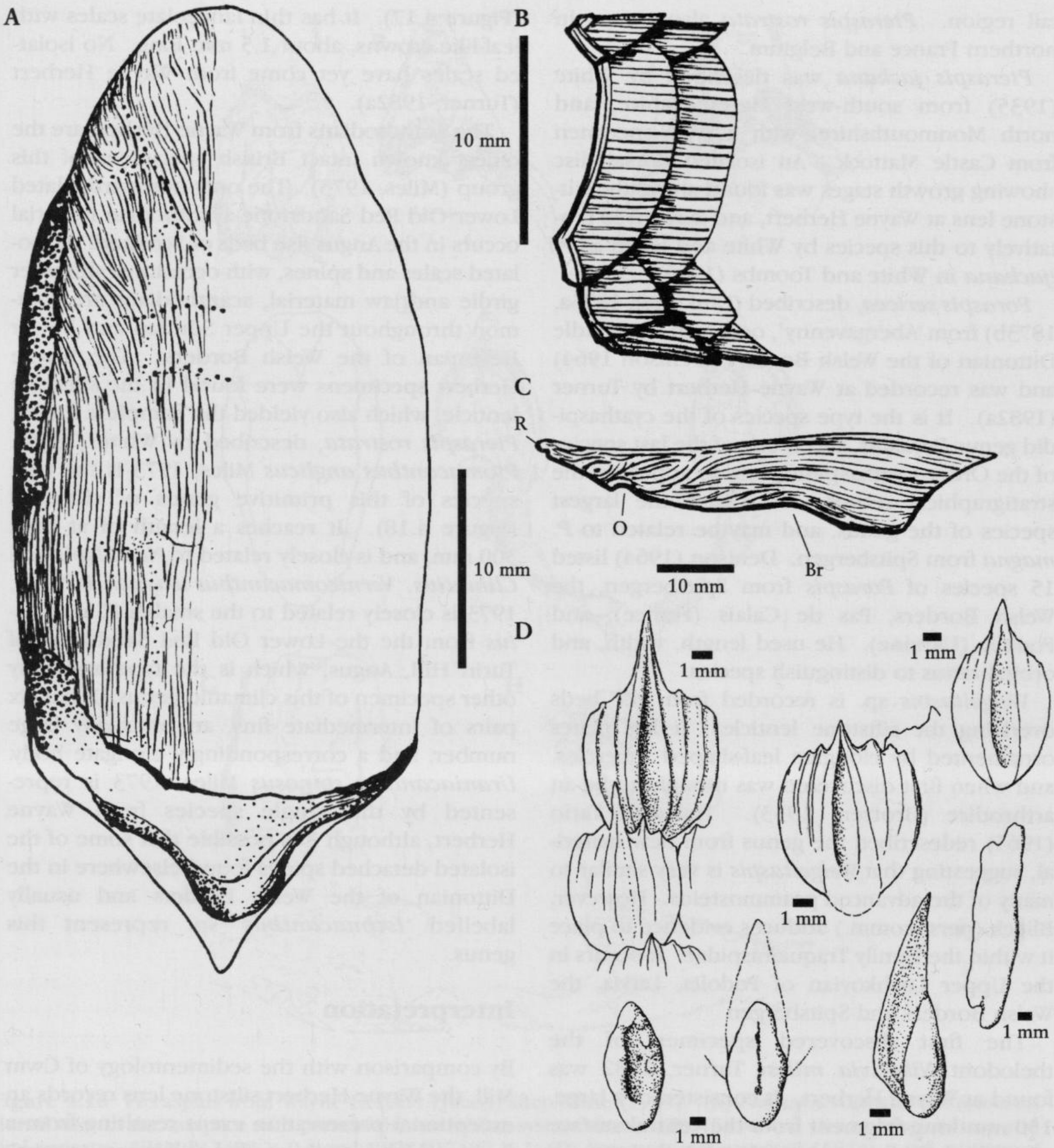


Figure 4.17 (A) *Poraspis sericea* Lankester from Wayne Herbert Quarry: a dorsal aspect of the dorsal disc of the holotype (NHM P.4117); (B) median dorsal, lateral, ventro-lateral and median ventral scales of *Poraspis*; (C) lateral profile of the dorsal disc of *Poraspis*; Br, position of the branchial opening between margins on the disc and the branchial plate; O, position of the orbit; R, rostrum; (D) *Nikolivia milesi*, denticles from the trunk showing overlap (NHM P. 53902). (From Turner, 1982a).

forms from Russia and Canada, this thelodont, *Nikolivia milesi*, lived in quiet waters, such as the ephemeral ponds and lakes of the Early Devonian flood plain of the Anglo-Welsh Basin or in the Caledonian lake.

This Ditton Group assemblage probably represents animals killed during a (local) catastrophe that rapidly buried and preserved the whole sample as mainly intact specimens. Their predator–prey relationships may be illustrated by the holotype of *Ptomacanthus anglicus*, which contains a cephalaspid headshield within its visceral cavity. This headshield was probably part of a fish that was swallowed whole, head first, similar

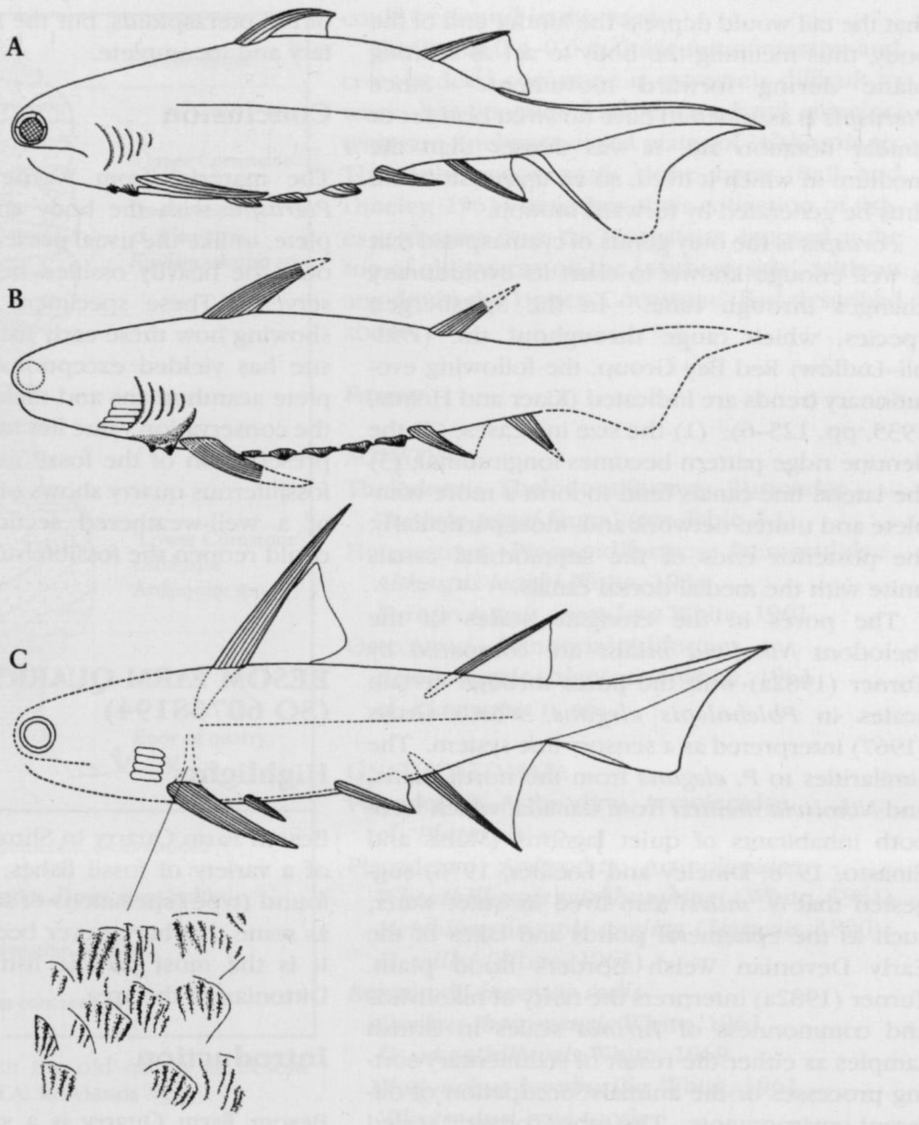


Figure 4.18 Acanthodians from Wayne Herbert Quarry (after Miles, 1973; Young, 1995). (A) *Ptomacanthus anglicus* Miles × 0.25; (B) *Vernicomacanthus waynensis* Miles, × 0.45; (C) *Uraniacanthus spinosus* Miles, × 0.66, with detail (× 2) of scale type in vicinity of the pectoral spine.

to modern fish, as it is the only small non-articulated specimen of this genus in the lenticle, and the poor preservation of its surface suggests that it has been damaged by digestive acids.

The Wayne Herbert specimens of *Pteraspis* were crucial in solving the biomechanical problem of how pteraspids swam. Previously, the shapes of the body and tail were hypothetical, and the tail had been assumed to be heterocercal (Woodward, 1891a; Traquair, 1899b; Leriche, 1903; Gross, 1933). As White (1935) pointed out, this would have thrust the head downward, making it extremely difficult for the fish to raise itself from the bottom sediments. The material discovered at Wayne Herbert showed that heterostracans had a hypocercal tail. This had already been suggested by Kiaer (1932b) for *Anglaspis*, following his important discovery of a hypocercal tail in the Anaspidida (Kiaer, 1924). The reconstruction of *P. rostrata* var. *toombsi* (White, 1935) became the basis of interpretations of the scaled trunk and tail of several heterostracans. This variety, and the six specimens of complete individuals from Wayne Herbert, are therefore extremely important. Kermack (1943) built a scale model of *P. rostrata* var. *toombsi* from White's reconstruction to test the functional significance of the hypocercal tail. He showed that the tail would depress the hinder end of the body, thus inclining the body to act as a lifting plane during forward movement. Since *Pteraspis* is assumed to have no swim bladder or similar flotation aid, it was denser than the medium in which it lived, so an upthrust would thus be generated by forward motion.

Poraspis is the only genus of cyathaspidid that is well enough known to chart its evolutionary changes through time. In the Spitsbergen species, which range throughout the (Přídolí–Ludlow) Red Bay Group, the following evolutionary trends are indicated (Kiaer and Heintz, 1935, pp. 125–6): (1) the size increases; (2) the dentine ridge pattern becomes longitudinal; (3) the lateral line canals tend to form a more complete and united network and, most particularly, the posterior ends of the supraorbital canals unite with the medial dorsal canals.

The pores in the elongate scales of the thelodont *Nikolivia milesi* are compared by Turner (1982a) with the pores through certain scales in *Phlebolepis elegans*, which Gross (1967) interpreted as a sensory-line system. The similarities to *P. elegans* from the north Baltic, and *Nikolivia ?heintzi* from Canada, which were both inhabitants of quiet lagoons (Märss and Einasto, 1978; Dineley and Loeffler, 1976) suggested that *N. milesi* also lived in quiet water, such as the ephemeral ponds and lakes of the Early Devonian Welsh Borders flood plain. Turner (1982a) interprets the rarity of nikoliviids and commonness of *Turinia* scales in British samples as either the result of sedimentary sorting processes or the animals' occupation of different environments. The more robustly scaled *Turinia* was adapted to bottom living in faster-flowing rivers and streams, common in the Welsh Borders Old Red Sandstone, whereas *Nikolivia* required the quieter lagoonal conditions that were prevalent in Podolia at the same time.

The acanthodians present were large, robust predators at the top of the local ecological pyramid, the thelodonts and cephalaspids being amongst the prey (Miles, 1973).

Comparison with other localities

Wayne Herbert remains unique in the extent and exceptional preservation of its fauna. There are many localities in the Anglo-Welsh Basin and in northern France–Belgium yielding one or other of the pteraspidids, but the material is fragmentary and incomplete.

Conclusion

The material from Wayne Herbert includes *Pteraspis* with the body and tail region complete, unlike the usual preservation mode where only the heavily ossified head shields are preserved. These specimens are important for showing how these early fishes swam. Also, the site has yielded exceptionally preserved complete acanthodians and thelodont fish. Overall, the conservation value lies in the unusually good preservation of the fossil material. This small, fossiliferous quarry shows only a small exposure of a well-weathered section, but excavation could reopen the fossiliferous horizons.

BESOM FARM QUARRY (SO 60768194)

Highlights

Besom Farm Quarry in Shropshire is the source of a variety of fossil fishes, including the first-found (type) specimens of some species, as well as some that have never been found elsewhere. It is the most prolific fish site in the Upper Dittonian of the area.

Introduction

Besom Farm Quarry is a small quarry east of Besom Farm that yields from the upper part of the Ditton Series (Ball and Dineley, 1961) a diverse fauna, including the type specimens of many species. There are remnants of small quarries on the south-east-facing slopes to the east of Besom Farm. The fish have been described by White (1956, 1960, 1961, 1969) and referred to by Whittard (1953), Denison (1956, 1970, 1978), Ball and Dineley (1961), Dineley and Loeffler (1976), Westoll (1979), Blieck and Jahnke (1980) and Blieck (1980, 1982b, 1984).

Description

There are two intraclast conglomerate ('cornstone') bands in Besom Farm Quarry (Figure 4.19). The upper unit is a concretionary cornstone overlain by a layer of conglomeratic

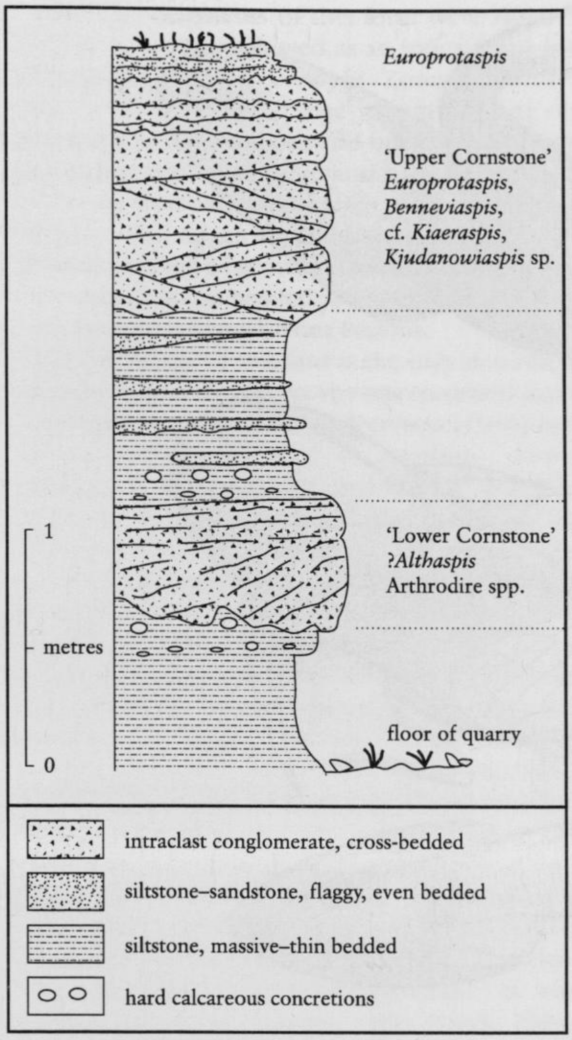


Figure 4.19 Section in the old quarry at Besom Farm, Wheathill (after M.A. Rowlands MS).

reworked nodules, which are rich in plates and large fragments of vertebrates. This unit is weathered and stratified, easily worked and is probably the band that yielded most material in the past. It is separated by just over 1 m of unfossiliferous sandstone and siltstone from the lower 0.4–0.6 m thick unit of massive intraclast conglomerate, which is extremely hard and difficult to work.

To the south of Besom Farm Quarry, a band of hard concretionary conglomerate can be traced down the slope to the stream. It contains many small bone fragments. This may be the lateral continuation of the lower 'cornstone' bed. Other thin bands outcrop in the stream at SO 60758160 and SO 60978162, but no outcrop of rock resembling the upper 'cornstone' bed could be found in this area.

The lower 0.4–0.6 m thick unit of massive and cross-bedded cornstone is extremely difficult to work, but contains fragmentary fossil remains, with rare finely preserved plates of ?*Althaspis* sp. The only major work done here (Ball and Dineley, 1961) describes their collection of fishes as coming from the 'cornstone exposed at the top of old quarry, on the southern side', without any doubt the Upper 'Cornstone' Bed described above.

Fauna

AGNATHA
Thelodonti: Thelodontiformes: Turiniidae
  '*Turinia pagei* fauna' (see Table 4.1)
Heterostraci: Pteraspidiformes: Pteraspididae
  Althaspis leachi White, 1934
  Europrotapsis crenulata White, 1961
Osteostraci: Benneviaspidiformes
  Benneviaspis salopiensis White, 1961
  cf. *Kiaeraspis* n. sp.

GNATHOSTOMATA
Placodermi: Arthrodira: Arctolepidae
  cf. '*Plataspis*' sp.
Placodermi: Arthrodira: Actinolepidae
  Wheathillaspis wickhamkingi (White, 1961)
  Heightingtonaspis anglica (Traquair, 1890)
  H. willsi (White, 1961)
Acanthodii *incertae sedis*
  Onchus ?besomensis White, 1961
  O. wheathillensis White, 1969
  Nodonchus bambusifer White, 1961
  '*Plectrodus*' type tooth
  climatiid shoulder girdle

Besom Farm Quarry is the type locality for the pteraspid species, *Europrotaspis crenulata* (White, 1961; Figure 4.20). This is a well-known species, founded on plentiful material, mainly from this site. White (1961) based *Protaspis (Europrotaspis) crenulata* on specimens from Besom Farm Quarry, Prescott Reaside, Farlow Brook Bridge and Upper Overton Quarry. The lectotype is an imperfect eroded dorsal shield with a fractured rostrum, and most of the right orbital plates were lost before fossilization, during which time *Spirorbis* shells colonized the under surface of the shield. The specimen is preserved in the round, but present-day weathering had removed the whole of the dorsal disc, and the dorsal side of the right branchial.

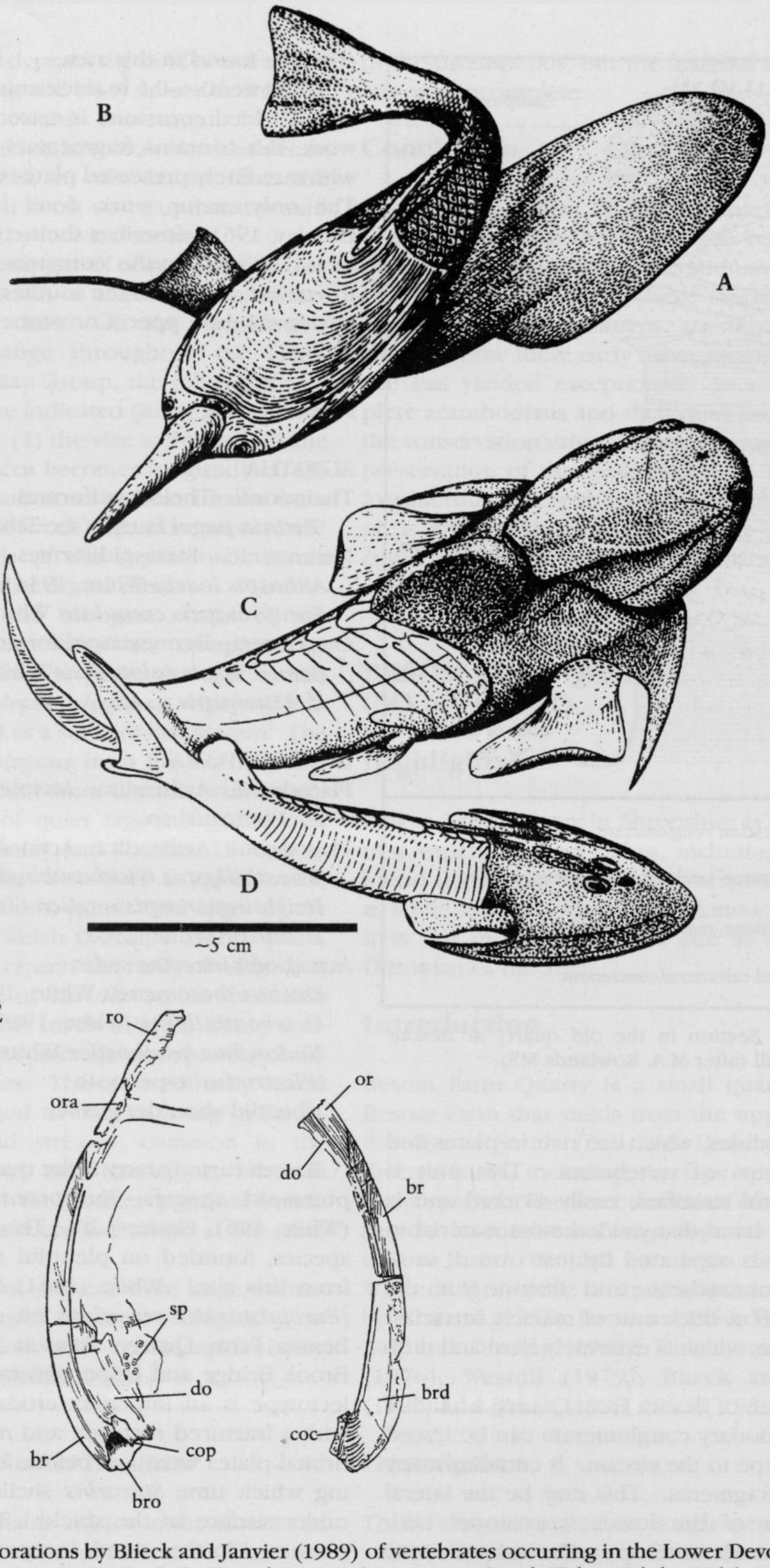


Figure 4.20 Restorations by Blieck and Janvier (1989) of vertebrates occurring in the Lower Devonian at Artois, France. The same species (A, B, C, D, E) and *Pattenaspis* occur in South Wales and the Welsh Borderland. (A) *Turinia pagei* (Powrie); (B) *Rhinopteraspis crouchi* (Lankester); (C) *Kujdanowiaspis* sp.; (D) *Pattenaspis artesensis* (Agassiz); (E) *Protaspis* (*Europrotaspis*) *cremulata* White, the holotype (NHM P28801) an imperfect dorsal shield *c*. × 0.66. br, Branchial plate; bro, branchial opening; brd, branchial duct; coc, cornual contact surface on branchial plate; cop, cornual plate; do, dorsal disc; or, orbital plate; ora, orbit; ro, rostrum; sp, shells of *spirorbis* attached to undersurface of dorsal disc (after White, 1961).

The first fragments of this form were discovered by L.J. Wills and used as an index fossil for post-*Rhinopteraspis crouchi* Zone Dittonian strata (White, 1950a). The ornamentation on the plates of the carapace and on the scales is of the typical pteraspid ridge and furrow type, but is coarser than most and unlike any other British species. The ridges are arranged approximately parallel to lines of growth (Denison, 1970), and they appear to be beaded, a feature also seen in *Europrotaspis arnelli* from Podolia.

Europrotaspis crenulata is the only described British species. *Protaspis* sp. was recorded from Watergate Bay, Newquay, by Denison (1956) but the material is in need of revision. *Europrotaspis* also occurs in Podolia (*E. arnelli*), Belgium (*E. wiheriesiensis*) and Germany (*E. rotunda*). These last two species remain poorly defined and their generic attribution is not certain (Blieck and Jahnke, 1980; Blieck, 1984).

White (1961) erected the subgenus *Europrotaspis* for *Protaspis crenulata* and *P. arnelli* from Podolia, and separated them from the American protaspids because of the differing position of the branchial opening and the form of the cornual plate. Denison (1970) concluded that *Europrotaspis* and *Protaspis* differed only slightly, but he retained both in his revised classification of the Pteraspididae. *Europrotaspis* was raised to the level of genus by Blieck and Jahnke (1980) and Blieck (1984), with *E. crenulata* designated as the type species. It was defined (Blieck and Jahnke, 1980; Blieck, 1984) as a medium-sized pteraspid with a large dorsal shield. Blieck (1984) listed *Europrotaspis* in the Family Pteraspididae, with closest similarity to *Rodenaspis* from the Lower Devonian of Wyoming, and he erected a new subfamily, the Protaspidinae, for *Protaspis*. *Europrotaspis* remains in the Pteraspidinae as it retains the cornual plate, a feature lost in protaspidines.

Althaspis leachi White, 1938 is the only other pteraspid from Besom Farm Quarry. Its type locality is Swanlake Bay, Dyfed, but it also occurs at Mitcheldean Quarry, various sites in the Clee Hill area and in France and Belgium. Thus it provides a useful means of correlation with continental strata of Pragian age, partially filling a stratigraphical gap between the '*crouchi–rostrata*' Zone of the Dittonian and the '*dunensis*' Zone of the Breconian (White, 1956, 1960). *Althaspis* is defined by the presence of an extensive subrostal surface covered with dentine ridges, and lacking a preoral field (Denison, 1970; Dineley and Loeffler, 1976). It was redescribed by White (1961), based mainly on material from Besom Farm Quarry. The other British species of *Althaspis* is *A. senniensis* Loeffler and Thomas, 1980 from the Senni beds of Powys (Figure 4.21).

The osteostracan species *Benneviaspis salopiensis* White, 1961 is based on a single specimen discovered in 1952 in the Upper Cornstone band (Whittard, 1953). This is a distorted, badly preserved cephalic shield of moderate size lacking cornua, but showing eyes and sensory fields (White, 1961). *Benneviaspis* is also known from Spitsbergen. White suggests a closer relationship between *B. salopiensis* and the Wood Bay Series Spitsbergen benneviaspids than with the other English species, since the former taxa have a distinctive, wide median dorsal sensory field, whereas the other English species have a narrow dorsal field, as do the benneviaspids from the earlier Red Bay Series of Spitsbergen.

Rare arthrodire fragments from Besom Farm Quarry are important since they represent some of the earliest British material of this group. Three species, and other unspecified fragments, have been found at this quarry, which is the type locality for *Heightingtonaspis ?willsi* and *Wheathillaspis wickhamkingi*. These have been reported from the higher (cornstone) level only, but two forms of arthrodire fragments occur in the two beds associated with *Althaspis leachi* and *Europrotaspis crenulata* (White, 1961), and those from the lower unit may be new species.

Heightingtonaspis White, 1969 is probably the oldest, and one of the most primitive, British arthrodires (Denison, 1978). There are two species, occurring at Besom Farm Quarry, and one species from the Upper Lochkovian of Maine, USA. *Heightingtonaspis anglica* (Traquair, 1890), the genotype, is from Cradley, Worcestershire. White (1961) reassigned this form to *Kujdanowiaspis anglica*, but later separated the English species from the Podolian *Kujdanowiaspis* (White, 1969, p. 305). *Heightingtonaspis anglica* occurs rarely but widely in the Welsh Borders and at Longhope, Gloucestershire. In the Clee Hills it is the only vertebrate species common in both the '*crouchi*' and '*leachi*' beds (White, 1969). *Heightingtonaspis ?willsi* White, 1961 was established as a new species *Kujdanowiaspis willsi*, based on several fragments from Besom Farm Quarry, the holotype being a small spinal plate (25 mm long). A single specimen from Goldtops, Gwent, is referred to this species or subspecies by White (1969). The status of *H. ?willsi* is hard to resolve with so little material.

White (1961) based *Wheathillaspis wickhamkingi* on a small specimen consisting of an anterior ventro-lateral plate with part of the spinal plate attached. This is the only known locality for *W. wickhamkingi*, with the exception of an anterior ventro-lateral plate from Upper Overton Quarry, Clee Hills, (now overgrown). The only distinguishing feature is the large oblique pectoral fenestra that is preserved in the holotype.

Besom Farm Quarry is the type and only locality for three species of acanthodian, based on three different types of spine. *Ischnacanthus* (?) *anglicus* White, 1961 was erected for an isolated fin spine and a small, finely ribbed spine showing the inserted part. *Ischnacanthus* occurs in the Upper Silurian and Lower Devonian of Canada, Scotland and the Welsh Borders, and ischnacanthids occur in the Early Devonian of Australia (Long, 1986). *Onchus wheathillensis* (White, 1961) was based on a single symmetrical and slightly arched median fin spine, ornamented by narrow, sharp, smooth ribs separated by deep and wide grooves, from Besom Farm Quarry. *Onchus ?besomensis* White, 1961 was also based on a single fragment of a large spine with long narrow ribbing.

Interpretation

Investigations into the fish fauna of this and other high Dittonian sites has shown geographical differences. Specimens of *Althaspis* from the Clee Hills area have finer ornamentation than those from Swanlake Bay, while those from Belgium have coarser ornamentation. White (1961) thought that this series represents a coarsening of ornamentation through slightly younger forms, but Blieck (1982b) credited the difference between the British and the French *A. leachi* to the differing local ecological conditions, as with *Rhinopteraspis crouchi* and *Pteraspis rostrata* (Blieck, 1980; Blieck and Jahnke, 1980). The fauna, comprising pteraspids, cephalaspids, arthrodires and acanthodians, maintains the level of diversity of older Dittonian levels, and a similarity of vertebrate community structure probably existed.

Comparison with other localities

At high levels within the Ditton Group and its equivalents in Wales there are relatively few highly fossiliferous sites with *Althaspis (Pteraspis) leachi*. Mention is made above of the occurrence of the species in South Wales and Belgium. In Shropshire the species occurs also at Bockleton Brook (Ball and Dineley, 1961). Localities with *Europrotaspis crenulata* in the Clee Hills area are at Upper Oventon Quarry, Prescott Reaside and Farlow Brook Bridge (Ball and Dineley, 1961). In none of these localities is the fauna so extensive as at Besom Farm.

Conclusion

Besom Farm Quarry has yielded a diverse and rich fish fauna, and it is the location for seven type specimens of heterostracan, osteostracan and acanthodian fishes; it is the sole locality for five of them. This site yields the most prolific fish fauna in the Dittonian of the area, hence its conservation value. The productive level is virtually worked out in Besom Farm Quarry, occurring as a well-weathered bed at the top of the southern side of the quarry, but there is potential for further collecting.

HOEL SENNI QUARRY (SN 91452210)

Highlights

Hoel Senni Quarry in Powys has produced specimens of the fossil fish *Althaspis senniensis*, which is known only from this site. Fossil fishes of uppermost Dittonian are very rare elsewhere, and the specimens enhance the importance of the site, which has also produced important fossil plants.

Introduction

Vertebrates are extremely rare in the Senni Beds and they are known from only two other sites at this stratigraphical horizon, Primrose Hill Quarry near Crickhowell and Ferryside in Carmarthenshire. The geology and fish fauna of the site have been described by Edwards *et al.* (1978) and by Loeffler and Thomas (1980), who ascribed a Lochkovian–Pragian age to these rocks.

A

B

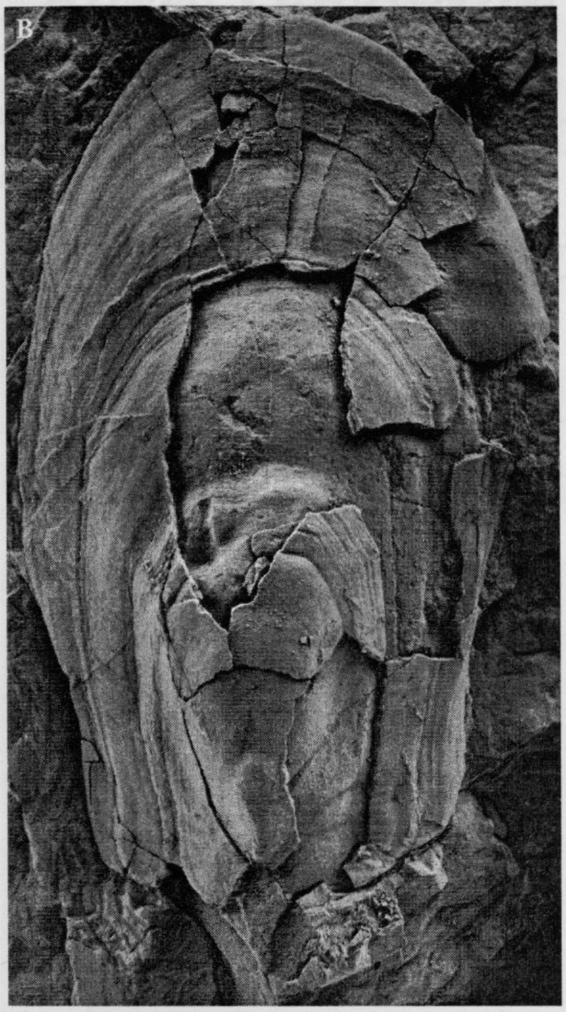


Figure 4.21 *Althaspis senniensis*: (A) rostral plate from Hoel Senni Quarry; (B) a ventral disc from Hoel Senni Quarry (after Loeffler and Thomas, 1980), both approximately natural size.

Description

Hoel Senni Quarry on the northeastern face of the Fan Bwlch Clwyth, Powys, exposes the Senni Beds, largely green sandstones with subordinate red or green mudstones, nodular mudstones, and intraformational conglomerates. Plant remains, which are abundant at this site, include *Drepanophycus*, *Gosslingia*, and *Zosterophyllum* (Edwards, 1968, 1969, 1970; Loeffler and Thomas, 1980). A well-preserved and distinctive miospore assemblage found in association with the fossil fish specimen is of great stratigraphical significance (Loeffler and Thomas, 1980). *Emphanisporites* and *Apiculiretispora* and over 50 taxa of miospores suggest correlation with the Cosheston Group of south-west Wales. Spores higher in the Senni Beds suggest a Pragian–Emsian age, the latter half of the Early Devonian (White, 1956; Allen, *in* House *et al.*, 1977).

Hoel Senni Quarry is the type and only locality of *Althaspis senniensis* Loeffler and Thomas, 1980 (Figure 4.21), the only vertebrate species found here, which is a typical pteraspid of the Ditton Group and is very similar, and possibly conspecific with *Althaspis leachi*, which occurs throughout north-west Europe at the top of the Lochkovian stage. The type specimen was found in a large fallen block of unlaminated blue-grey mudstone on the floor of the quarry in 1978. *Althaspis senniensis* is based on several plates from one individual found together, and is the best preserved and most complete recovered from the Senni beds. It shows similarities both to forms from Podolia and France, as well as Britain, and it can be considered to be a pteraspid of Dittonian aspect. Its presence in the Senni Beds indicates a level between the Dittonian and Breconian stages.

Fauna

AGNATHA
Heterostraci: Pteraspidiformes: Pteraspididae
Althaspis senniensis Loeffler and Thomas, 1980

Interpretation

The strata at Hoel Senni Quarry have been deposited rapidly under high water-table conditions, and a braided-meandering stream environment. Stream flow was high but periods of desiccation were frequent. Vascular plants were locally common around the water bodies. From this locality palynomorphs indicate a late Lochkovian to Pragian age and *Althaspis senniensis* is a late Dittonian to Breconian form of pteraspidid. Primrose Hill Quarry, near Crickhowell, Powys (SO 207200), yields

Rhinopteraspis dunensis (= cornubica) which occurs in the type area for the Siegenian (Pragian) stage. The evidence of the fossil fishes from Hoel Senni and Primrose Hill quarries show that the Lochkovian–Pragian boundary lies within the Senni Beds between these two fossil-bearing horizons.

At this level throughout the Anglo-Welsh Basin and adjacent mainland Europe there is a noticeable impoverishment of the vertebrate faunas (i.e. within the *leachi* and *dunensis* zones). Blieck *et al.* (1995) suggested that this may coincide with what is perceived as a lowering of sea level in late Lochkovian to Pragian time with some climatic change and concomitant earth movements. While the fishes of this interval are larger in size, the number of species, communities and sites are much reduced.

Comparison with other localities

Intraclast conglomerates, mudstones and sandstones of the types found at Hoel Senni Quarry are widespread in the Senni Beds of South Wales. None, however, has yet produced a comparable pteraspid.

Conclusion

Hoel Senni Quarry has produced only one fish specimen, but it is of great significance as one of the youngest fishes from the Early Devonian of the Anglo-Welsh Basin. The fish, and associated miospores from the site give unique evidence for the dating of the Senni Beds and form the basis of its conservation value.