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, expe riencing 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 elastic infill lay in the rising Caledonides to the north. J.R.L. Allen (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 diachro-nously 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)

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 stensioi (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: Trematapidiformes: 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)

Stensiopelta 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: Thriniidae

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 P■ídolí 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 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 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 thanato-coenose preservation and few bioceonoses are indicated. Articulated specimens and squama-tion 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.

(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 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*	Lower Red Downton Group

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 P■ídolí–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 (Weston, 1979; Pan and Dineley, 1988). Those from the Lower Devonian of the Welsh Borders are found as rare fragments, mostly in 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 arc 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; (Figure 4.5) and (Figure 4.6). Six GCR sites are selected here, repre senting those locations

with the richest faunas. Most of these are within the essentially local point-bar fluvial conglomerates and contiguous sandy units (Figure 4.7)A-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 P■ídolí (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.

Devil's Hole, Shropshire [SO 672 929]. P■ídolí-Lochkovian/Downtonian-Dittonian.

Oak Dingle, Tugford, Shropshire [SO 5656 8712]. Lochkovian/Dittonian.

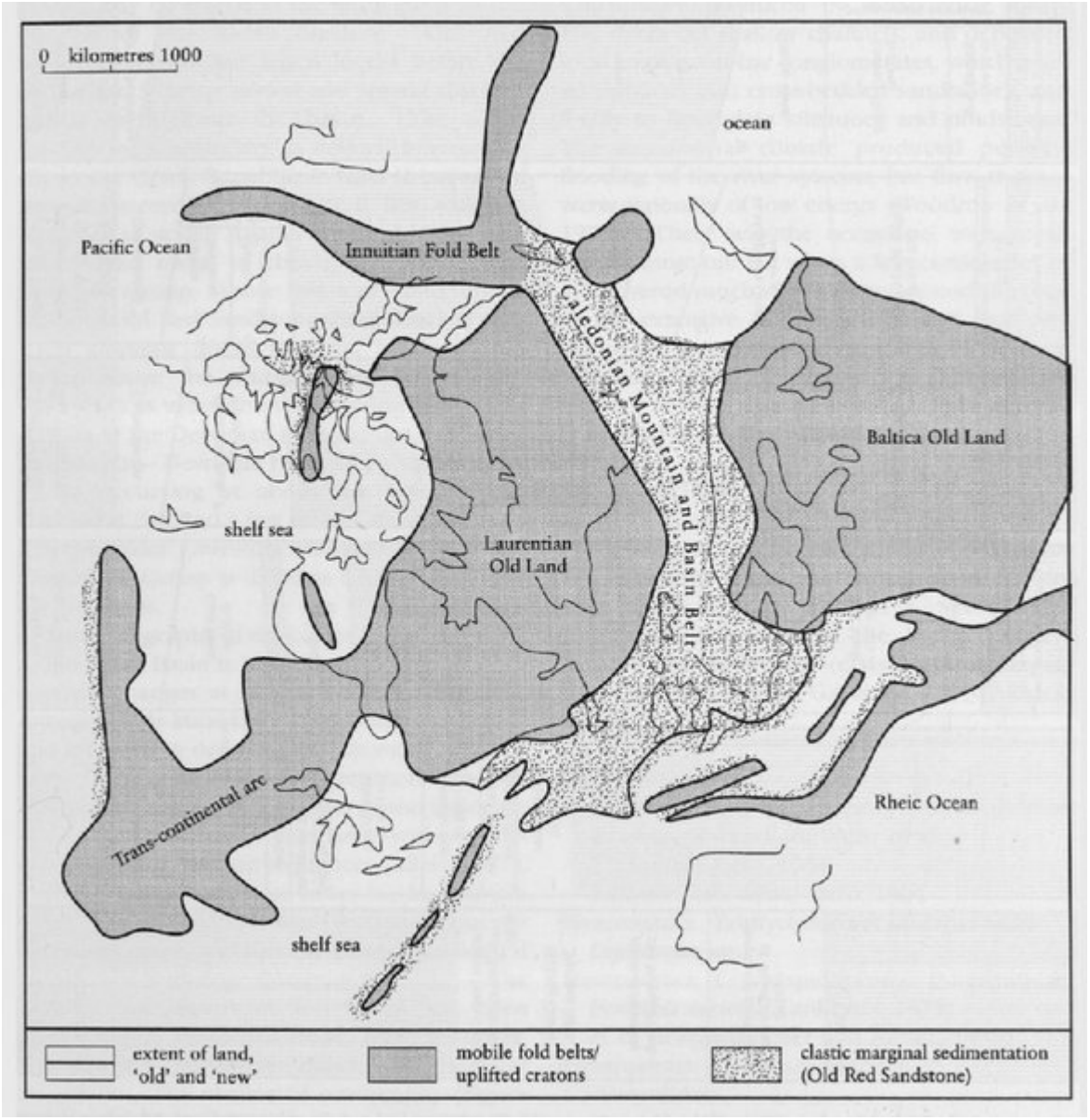
Cwm Mill, Gwent [SO 311 156]. Lochkovian/Dittonian.

Wayne Herbert, Herefordshire [SO 335 320]. Lochkovian and Dittonian.

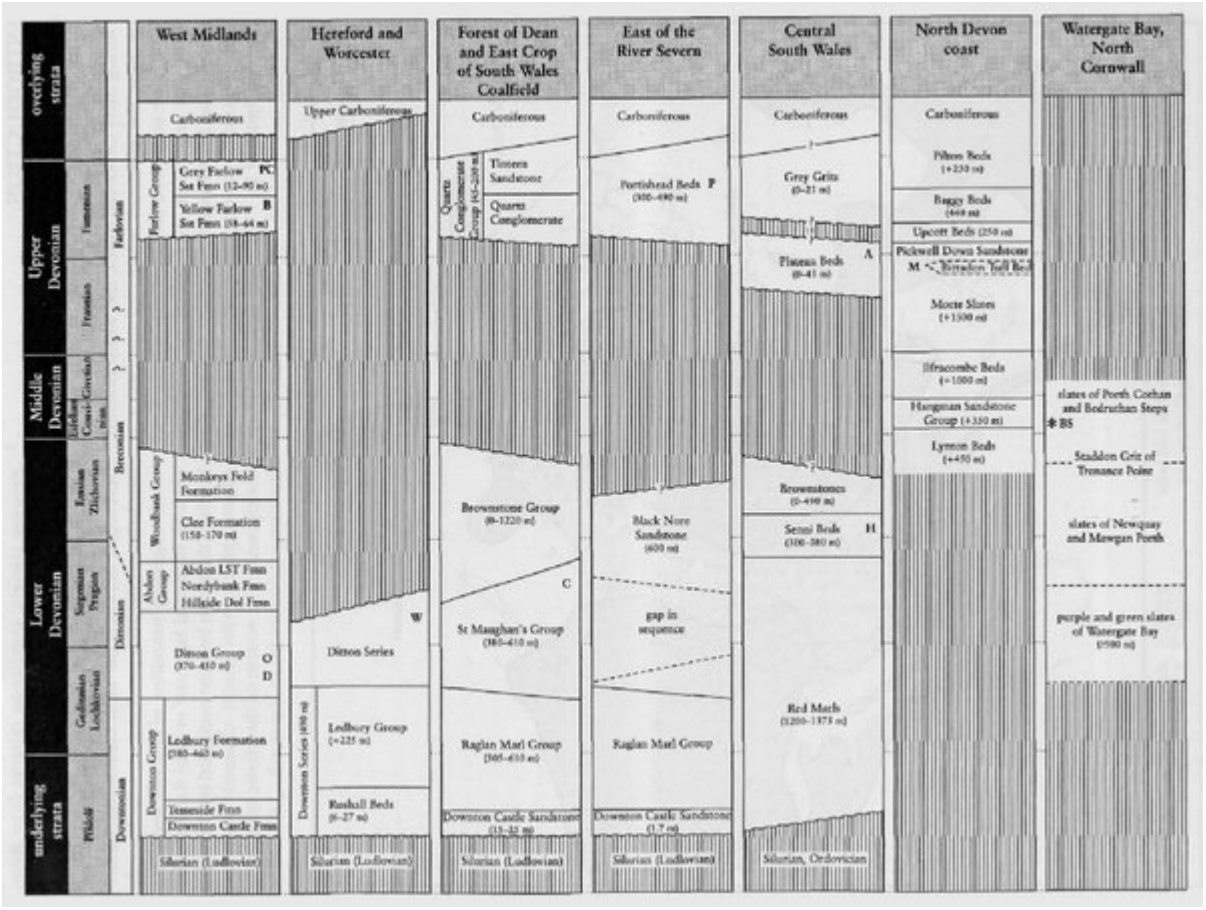
Besom Farm Quarry, Shropshire [SO 6076 8194]. Lochkovian/Dittonian.

Hoel Senni Quarry, Powys [SN 9145 2210]. Lochkovian–Pragian/Dittonian–Breconian.

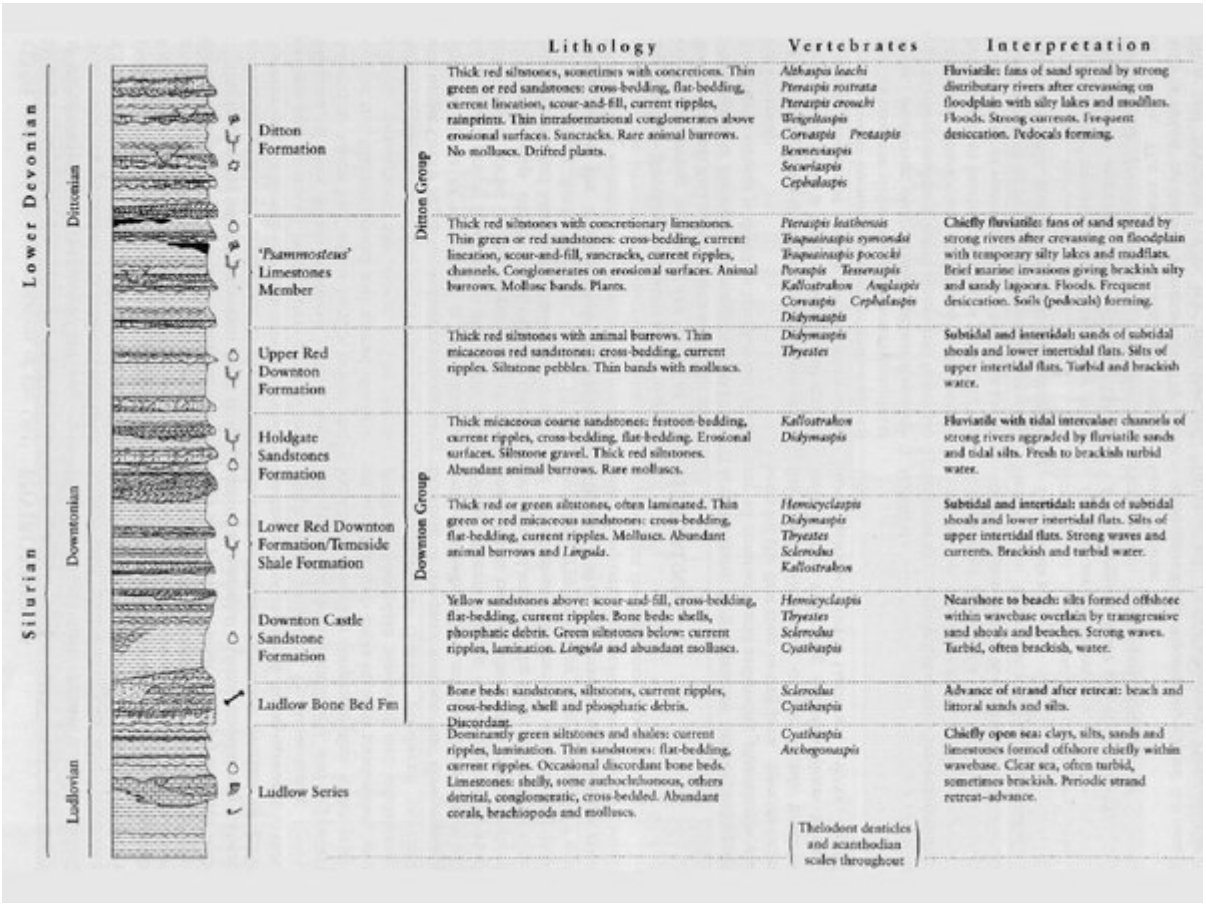
References



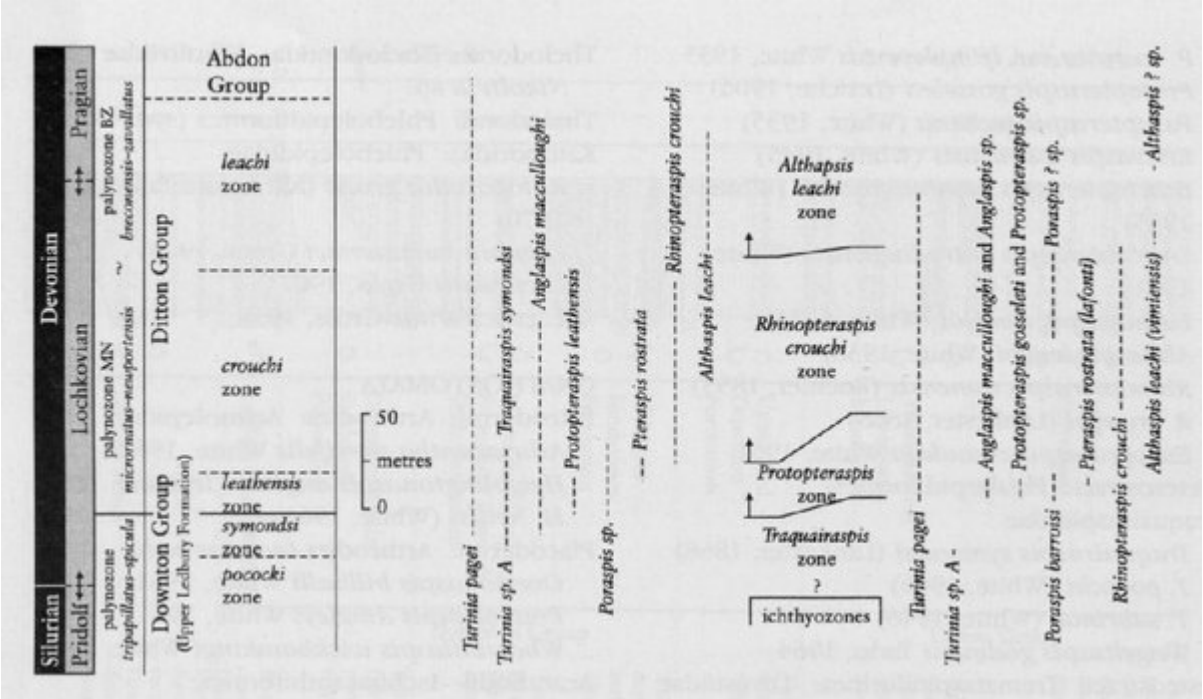
(Figure 4.1) The Old Red Sandstone Continent (Euramerica or Laurussia); a general map, early Devonian to mid-Devonian times.



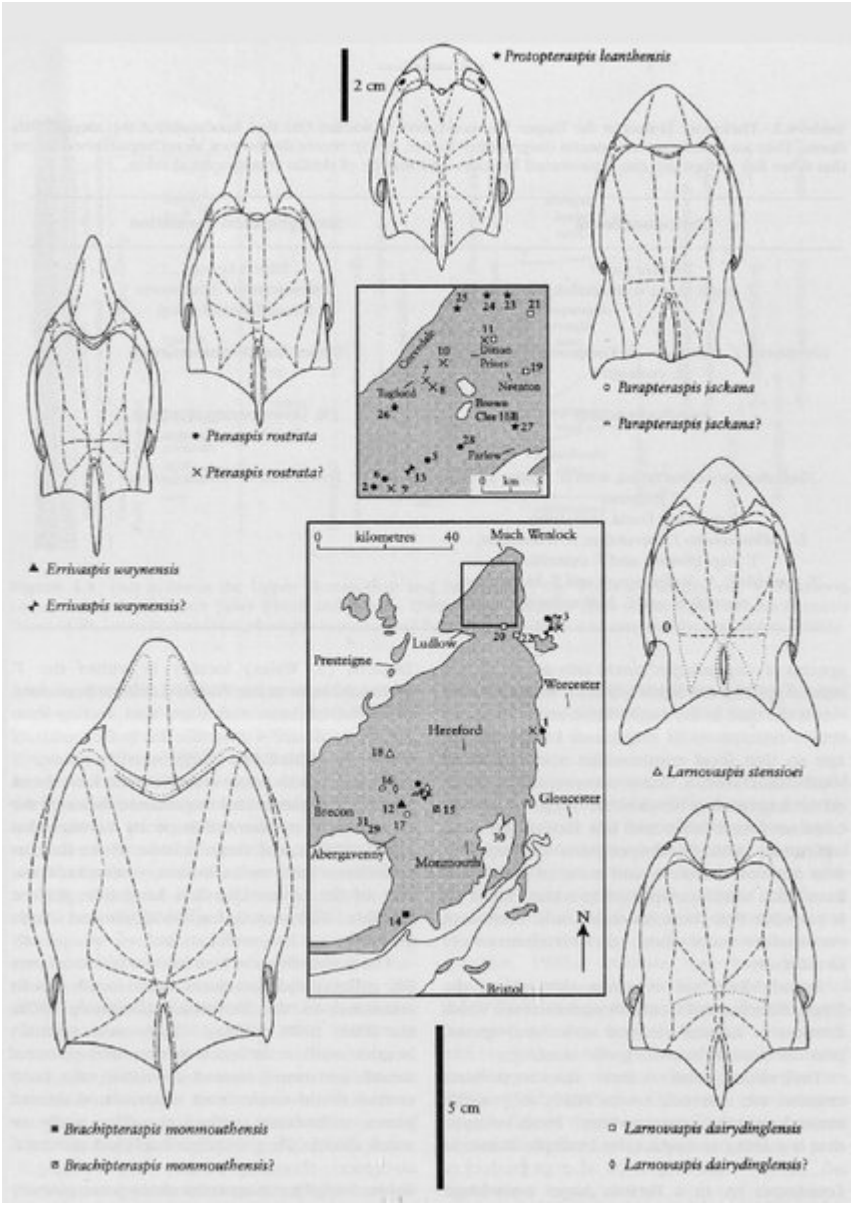
(Figure 4.2) Stratigraphical sections of the Devonian in the Welsh Borderland–South-west England (after House et al., 1977) with GCR site horizons indicated: A, Afon y Waen; B, Besom Farm; BS, Bedruthan Steps; C, Cwm Mill; D, Devil's Hole; H, Heol Senni; M, Mill Rock; O, Oak Dingle; P, Portishead; PC,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



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



(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.



(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.

Thelodont fauna	Stratigraphical Formation
Turinia pagei *T. pagei* fauna with *Apalolepis*	Ditton Group '*Psammosteus*' Limestone Lower Ditton Group
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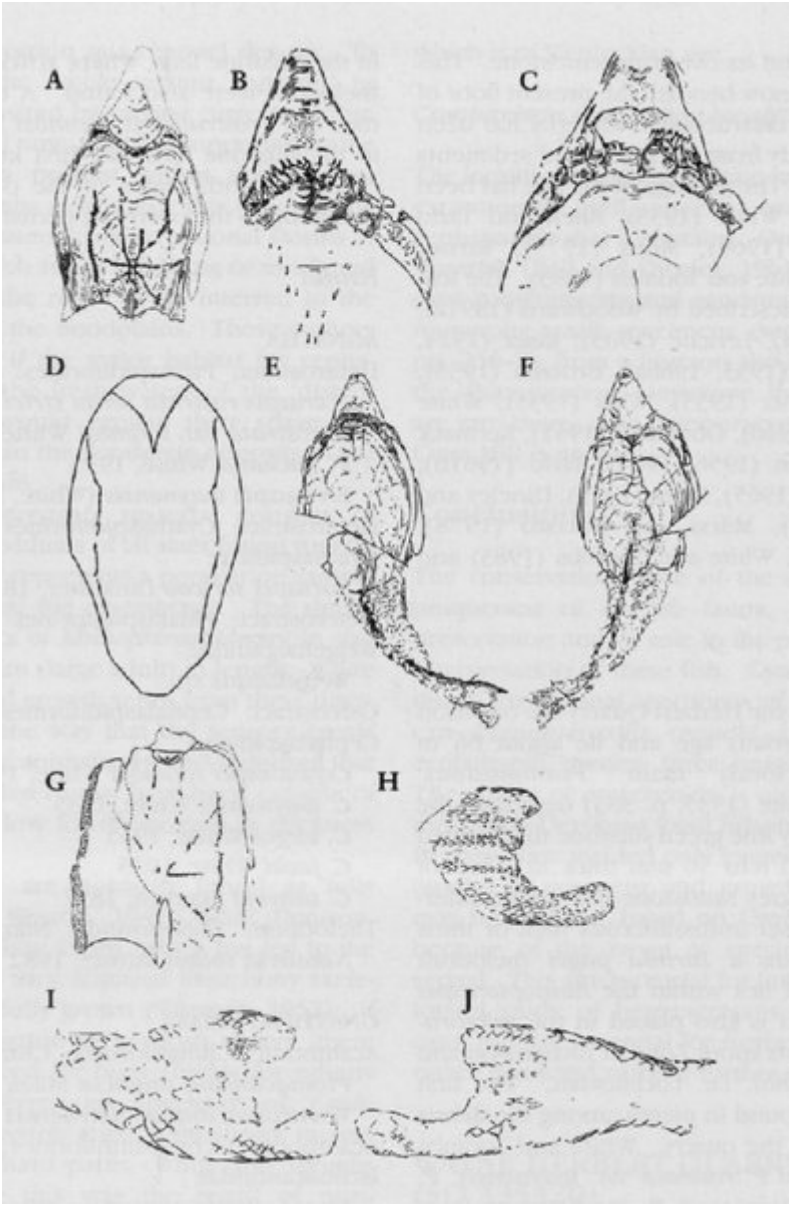
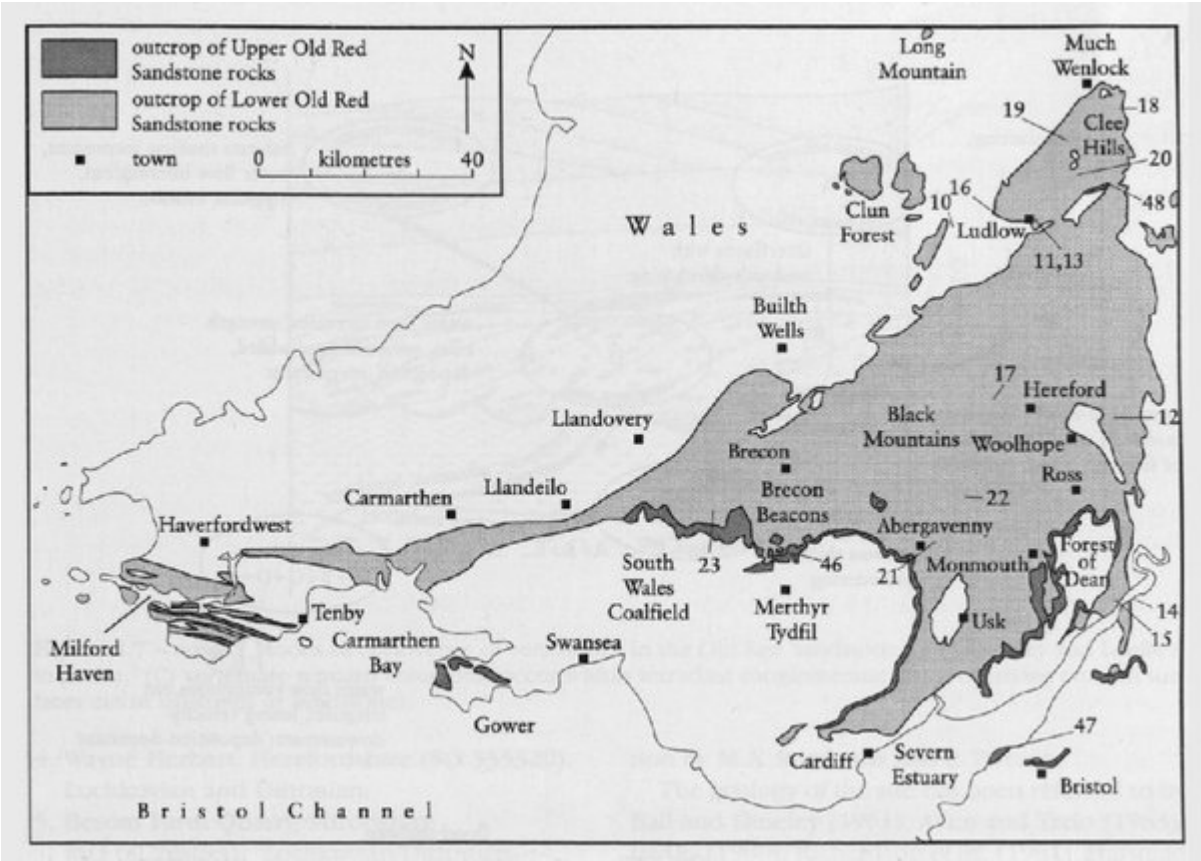
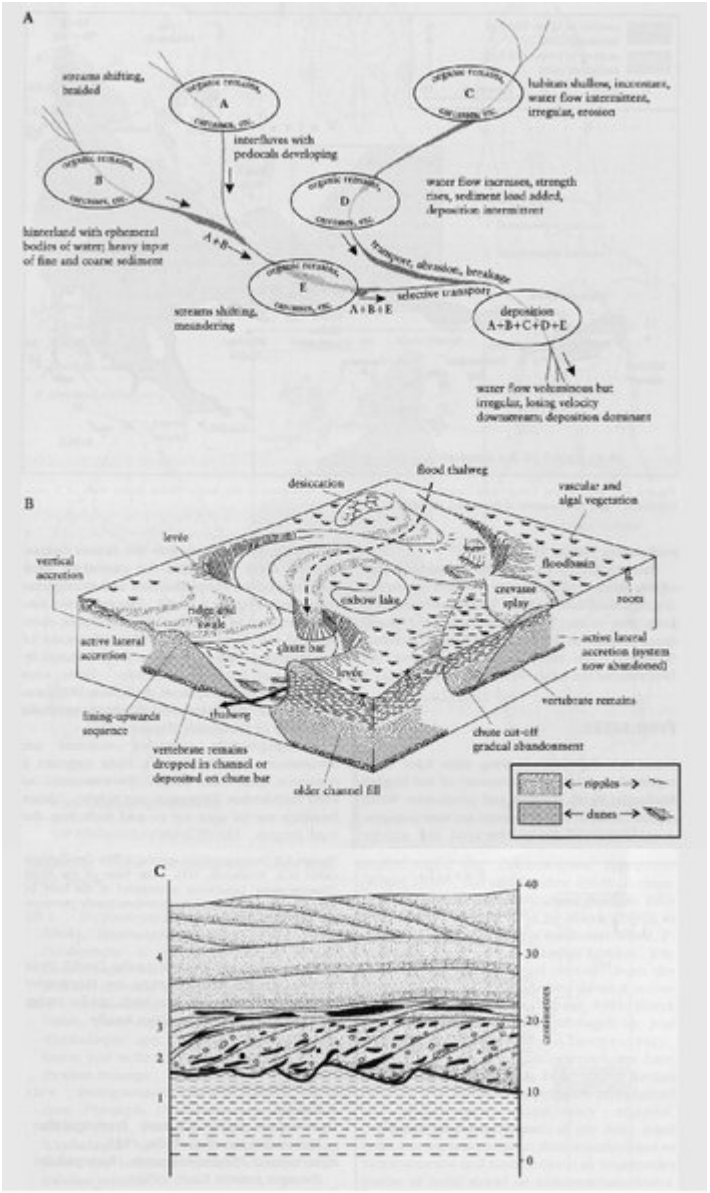
(Table 4.1) Thelodont faunas in the Upper Silurian-Lower Devonian Old Red Sandstone of the Anglo-Welsh Basin. They are based on scale species (largely after Turner, 1973): recent discoveries, as yet unpublished, show that other fish groups are also represented by scales and may be of similar stratigraphical value.



(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 x 0.4 and NHM P17487 x 1; (D) Pteraspis waynensis (P 16524) x 0.5, outline of the ventral disc with lateral line canals indicated; (E) Pteraspis rostrata var. toombsi (P16789) x 0.33, almost complete individual preserved as an external mould, ventral view of carapace trunk and tail; (F) the same specimen preserved in counterpart, x 0.33, seen in dorsal view; (G) Pteraspis jackana (P17628) x 0.5 approximately, dorsal disc with traces of lateral line canals in dorsal view; (H)—(1) Pteraspis rostrata var. toombsi, external lateral impressions of tails with squamation (NHM P 17488, NHM P17521, NHM P 17477), at c.x 0.25.



(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.



(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. (C) vertebrate remains commonly occur within intraclast conglomeratic layers overlying erosion surfaces cut in siltstones or sandstones.