Chapter 5 Early Devonian fossil fishes sites of Scotland

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Introduction: palaeogeography and stratigraphy

Early Devonian rocks occur in and close to the Midland Valley of Scotland, where they accumulated as post-orogenic molasse on the uplift of the Caledonide mountains. The Valley itself is a complex major tectonic feature, largely defined by north-east-trending boundary faults with both vertical and transcurrent displacements. The Valley basin became filled with many thousands of metres of continental red-beds and contemporary volcanic deposits from local centres. It lay fairly close to the margin of the Old Red Sandstone continent (Laurussia) and within the Caledonide orogenic belt that marked the collision of Laurentia and Baltica (Bluck, 1983). Fault movement has probably continued spasmodically there ever since, but during Devonian times it was responsible for strong rift-valley topography. Coarse flanking screes and alluvial fans, together with scattered volcanic deposits, were laid down while finer debris settled in the medial parts of the valley (Bluck, 1978, 1983). The sedimentary regime was one of much lateral variation, in which clastic sediments dominated and with longitudinal and well as lateral sediment transport taking place. Water flow was highly spasmodic and locally turbulent. The position of a possible outflow to the coast and links to other lacustrine areas remain conjectural, but faunal migration between this and other sedimentary basins within Laurussia took place. Throughout Early Devonian times the Caledonian (Midland Valley) Basin nevertheless was entirely separated from the Anglo-Welsh Basin (Figure 5.1).

Events in Middle Devonian time here seem to have been largely erosional, as the Lower Devonian rocks are unconformably overlain by those of the Late Devonian (see Morton, 1979; Cameron and Stephenson, 1984). The rest of Scotland appears to have been upland throughout early Devonian time. See Craig (1983) and Cameron and Stephenson (1984) for general accounts of the geology and palaeogeography (Figure 5.2).

The Lower Old Red Sandstone rocks of the Forfarshire and Kincardineshire area are not only important stratigraphically, but also contain some key early fossil fish beds. The sequence is composed principally of sandstones, but coarse conglomerates are prominent in Kincardineshire and along the Highland Border. Thick volcanic units are also present, particularly in the Ochil and Sidlaw Hills, and there are also important shale and mudstone formations (Armstrong and Paterson, 1970). Thin laminites containing fishes and other fossils occur at intervals throughout the sequence. Two other lithologies contain osteostracans, grey flagstones (fine-grained grey sandstone) and also red micaceous sandstones overlying these flagstones, the Garvock Group sediments. Field guides to the geology of the Midland Valley have been provided by Mitchell and Mykura (1960) and Bluck (1973).

Armstrong and Paterson (1970), following Campbell (1913), divided the Lower Old Red Sandstone laminites into six groups, from the (Downtonian) Stonehaven Group (see Chapter 2) to the (Breconian) Strathmore Group. The fish beds of the Forfarshire area occur within the Arbuthnott Group, which outcrops along the NE–SW-trending Sidlaw Anticline. The Arb-uthnott Group is 2100 m of sandstone, shale, flagstone, conglomerate, lava and pyroclastic rocks of probable Dittonian age (Weston, 1951; Armstrong and Paterson, 1970), of Lochkovian and Pragian age, and hence coeval with the Early Devonian fish faunas of the Welsh Borders (see Chapter 4).

The name Arbuthnott Group (Figure 5.2), first applied by Campbell (1913) to the conglomeratic sequence in Kincardineshire, was correlated with the strata to the south by Armstrong and Paterson (1970). The Dundee Formation contains most of the notable Angus fish beds. The Arbuthnott Group interdigitates with most of the overlying Garvock Group, which presents problems for correlating the fish beds into any stratigraphical order. Miospores have led Richardson *et al.* (1984) to equate much of this Group (*c.* 1200 m) with the Lower Devonian *micrornatus–newportensis* Zone, equivalent to the lower part of the Ditton Group of Shropshire where it is only 20–30 m thick. The fish beds at Tillywhandland and Aberlemno appear to be near the top of the Arbuthnott Group in the Forfar area, but are shown to be some 700 m below the Canterland Den Fish Bed, which marks the top of the Arbuthnott Group in the north of the outcrop. The Canterland Den Fish Bed is therefore of the same age as strata within the Garvock Group to the south.

Armstrong and Paterson (1970) arranged the fossil fish beds in sequence, based on field evidence and published information, but not on a re-examination of the fossils themselves. Hickling (1912) had attempted the same thing earlier.

Wherever a fish bed is seen, the section is very similar, consisting of green shales and mudstones grading into dark grey laminated siltstones, then back again. This led the early discoverers of fossils to assume that a single continuous fish bed was present throughout the area (Powrie, 1864, 1870). However, Armstrong and Paterson (1970) showed that fish beds occur at many horizons, the exact relationships of which have yet to be determined.

Environments

The Early Devonian fish-bearing units of the Arbuthnott Group indicate a mix of continental environments of deposition, including river and floodplain deposits, with highly variable water flow (Bluck, 1978; Allen and Crowley, 1983). Local lava and pyroclastic beds derived from neighbouring volcanoes occur thoughout the Midland Valley. The fishes are all preserved in laminated finer-grained, probably lacustrine units. During this time the climate was warm and humid, and a primitive vascular plant flora occupied waterside environments. An invertebrate terrestrial fauna had begun to occupy these habitats.

Fish faunas

Almost all occurrences of early Devonian fish in Scotland are confined to relatively fine-grained sediments. A few are present in arenites, commonly cross-bedded and representing strongly flowing currents. Two groups of fishes, osteostracans and acanthodians, are commonly found in the Scottish Lower Old Red Sandstone. Usually they occur separately, although rare acanthodian spines have been found with '*Cephalaspis*' headshields, as at Canterland Den (Mitchell, 1860) and both occur together in laminites at Tillywhandland. The fish fauna for all localities consists of the following.

AGNATHA

Osteostraci: Cephalaspidiformes:

Cephalaspididae

Cephalaspis lyelli Agassiz, 1835 Type, and only, locality Glamis; doubtful record from Brechin

'*C.*' *pagei* (Lankester, 1870) Type locality Turin Hill; other sources Aberlemno, Kelly Den, Tealing, Reswallie, Carmylie, Pitairlie, Leysmill

'*C.*' cf. *pagei* Recorded from Aberlemno, Turin Hill

'*C.*' *powriei* (Lankester, 1870). Type locality Reisk Quarry, Brechin; other sources Craig nr Montrose, Crombie Burn, Brechin, ?Middleton, Leysmill, Turin Hill

'*Cephalaspis*' *powriei* var. *asper* (Lankester, 1870) Type locality Turin Hill; other source Reswallie

'*C.*' *powriei* var. *brevicornis*, 1932 Type locality Turin Hill; other sources Rossie Priory, Kinblythmont

'*C.*' cf. *powriei* (Lankester, 1870) Recorded from Turin Hill

'*C.*' *spinifer* Stensiö, 1932 Type locality Turin Hill

'*C.*' *traquairi* Stensiö, 1932 Type and only locality Tulloch Quarry, Galston Moor

'*C.*' *websteri* Stensiö, 1932 Type locality ?Brechin

'*C.*' *watsoni* Stensiö, 1932 Type (?only) locality Rossie Priory

'*C.*' *scotica* White, 1963 Type and only locality Wolf's Hole

'*C.*' sp. Recorded from Wolf's Hole (White, 1963)

'*Cephalaspis*' sp. Recorded by Stensiö (1932) from Glamis, Turin Hill, Aberlemno, Leysmill

Securiaspis caledonica White, 1963 Type and only locality Wolf's Hole

Securiaspis waterstoni White, 1963 Type and only locality Wolf's Hole

Heterostraci: Pteraspidiformes: Pteraspididae

Pteraspis mitchelli White, 1963 Type and only locality Wolfe's Hole

Thelodonti: Thelodonta: Turinididae

Turinia pagei (Powrie, 1870) Type locality Turin Hill

GNATHOSTOMATA

Acanthodii: Climatiiformes: Climatiidae

Brachyacanthus scutiger Egerton, 1860

Climatius reticulatus Agassiz, 1845

Euthacanthus macnicoli Powrie, 1870

E. grandis Powrie, 1870

E. curtus Powrie, 1870

Parexus recurvus Agassiz, 1845

P. falcatus Powrie, 1870

Vernicomacanthus uncinatus Powrie, 1864

Acanthodii: Ischnacanthiformes:

Ischnacanthidae

Ischnacanthus gracilis Egerton, 1861

Acanthodii: Acanthiformes: Acanthodidae

Mesacanthus mitchelli Egerton, 1860

?Uraniacanthus sp.

It is probable that not all these are valid taxa, and the several groups need further close study to establish their true content.

Assiduous collecting by early Victorian enthusiasts led to rare osteostracans being found in the 'Arbroath pavement' associated with *Pterygotus* and in the Garvock Group sediments, where they occurred as isolated shields not associated

with any other fauna. Only very occasionally have complete cephalaspids been found (Powrie, 1861). Nearly all the osteostracans were found in the 19th century by quarrymen working the sandstones and flagstones. Even 100 years after their first discovery, Stensiö (1932) could only find 141 good specimens, 77 from Scotland and 64 from England (White and Toombs, 1983), on which he based 20 species.

Those osteostracans which are loosely termed '*Cephalaspis*' may more correctly be described as cornuate. They have been regarded as a monophyletic group on account of the unique cornual processes, although these have been secondarily reduced or lost several times independently (Janvier, 1980, 1981, 1985a). Cornuate osteostracans appeared first in the lowermost Devonian, became abundant in the Lower Devonian, and are present, but rare, in the Middle Devonian and Frasnian.

The genus *Cephalaspis* was described by Agassiz (1835), with four species, three of which have now been removed from the osteostracans, leaving *C. lyelli* as the type species, founded on a NHM specimen from 'Glammis'. Lankester (1870) redescribed Agassiz's four figured species, and renamed three of these *C. powriei* and C. *agassizi.* Stensiö (1932) redescribed *C. lyelli,* and assigned to it specimens from Brechin, but White (1958) showed that these two faunas were unrelated, and only the NHM lectotype can now be properly referred to the species. More recent studies by Janvier (1981, 1985a, 1985b), mainly on the osteostracans of Spitsbergen, indicate that '*Cephalaspis*'properly includes only the species *C. lyelli (Figure 5.3)*.

Within the (monophyletic) cornuate osteostracans, Janvier (1985a, 1985b) identified five (monophyletic) groups, two of which are represented by species from the Lower Devonian of Scotland, the cephalaspidians and the scolenaspidians. Both are widely distributed groups, the scolenaspidians being abundant in the Lochkovian of Britain, Spitsbergen, North America and Podolia, and the cephalaspidians being known from Britain, Podolia, Spitsbergen, and possibly also from France and West Germany. However, the distinctions between these groups are based on well-preserved fossils mainly from Spitsbergen, and new work is needed on the osteostracans from the Lower Devonian of Scotland. The species *'Cephalaspis*' *pagei,*'*C. powriei,* and '*C.*' *spinifer* are, however, either primitive scolenaspidians or the oldest relatives to that group because they show incipient scolenaspidian characters (shape of nasohypophysial opening, ornamentation and lateral fields), and may be regarded as sister-species to the scolenaspidians, because they also have cephalaspidian characteristics (Janvier 1985a, 1985b, 1985c) (Figure 5.4).

The occurrence and preservation of osteostracans in Scotland is very different from that of those from the Welsh Borders (see Chapter 4). Articulated and nearly complete specimens of ccphalaspids are relatively well known in Scotland, whereas almost all the Welsh Borders specimens always consist of disarticulated head-shields, scales and fragments. Furthermore, no species in common have been recorded from the two areas, pointing to the lack of a connecting environment between these basins.

The Scottish Lower Devonian thelodonts are also particularly important. The thelodonts were agnathans with a dorso-ventrally flattened head widening into triangular lateral fins, a fusiform trunk with dorsal, anal and caudal fins, and a flexible armour of discrete dermal scales. They are known mainly from isolated scales and are increasingly recognized as good stratigraphical index fossils (Turner and Van der Brugghen, 1993; Turner, 1995). They were highly mobile and are geographically widespread.

The first complete thelodont specimen discovered was described as *Turinia pagei* from Turin Hill (Powrie, 1870), and originally named *Cephalopterus pagei.* Only one entire specimen was then known, obtained by Powrie from a quarry on the north side of Turin Hill. The other material consisted merely of detached scales from the same quarry and from 'Canterland Den'. Henrichsen (1971) suggested that the specimen from Canterland was actually from Turin Hill. Henrichsen (1971) and Gross (1967) referred more particularly to material from Aberlemno Quarry, the only specified site within the wide and vague term Turin Hill. Complete thelodonts have also been found in the Early and Late Silurian of Scotland (see Chapter 2), as well as the Late Silurian of Norway and Oesel (Bougaart and Hout, 1990). Parts of other specimens have been found in Canada (Turner, 1986; Dineley and Loeffler, 1976) and the Welsh Borders (Turner, 1982a). The complete specimens are strikingly uniform in morphology, and vary in size from a few centimetres to over 1 m (Turner, 1986). In 1993 Wilson and Caldwell announced the discovery of new (marine) Silurian and Devonian fork-tailed 'thelodonts' with a body plan very different from that of previously known thelodonts. These fossils suggest a

bilaterally compressed body, large tails and an active predatory mode of life.

The complete thelodont animal from Turin Hill was mentioned by Lankester (1870), who stated that he was unable to assign it to the cephalaspids. *Cephalopterus pagei* remained a problematical 'fish', and was renamed *Turinia pagei,* after its locality, by Traquair (1894a) because the name *Cephalopterus* was preoccupied. When complete thelodonts were discovered in the Silurian rocks in Lanarkshire, Traquair (1899b) realized the true affinities of *Turinia pagei,* and renamed it *Thelodus pagei,* which showed that the previously described coelolepids were not acanthodians or selachians. The genus *Thelodus* had been named by Agassiz (*in* Murchison, 1839) from scales found in the Ludlow Bone Bed at Bringewood. Similar isolated scales were subsequently found at many European Silurian and Early Devonian sites, but their affinities were conjectural until the complete thelodont animals were found. Even so, debate about the affinities of thelodonts, and indeed about whether they constituted a natural group, has continued to the present day (Figure 5.5).

Westoll (1945) compared the Scottish Silurian thelodonts to heterostracans, *Phlebolepis* to anaspids, and he interpreted *Turinia pagei* as a larval unossified cephalaspid. Stensiö (1958, 1964) described possible gill arches and openings in *T. pagei.* Thelodonts are now tentatively regarded as (1) a sister-group of Anaspida and of the lampreys, Petromyzontiformes (Janvier, 1986) or (2) a sister-group of the chondrichthyans or (3) of the heterostracans (Turner, 1991).

Gross (1947, 1967) split '*Thelodus scoticus*'from the Beyrichienkalk erratics of northern Germany into several species, including *Turinia pagei,* each with limited vertical range. This was the first tentative suggestion that the thelodonts could be used biostratigraphically, an idea subsequently developed by Karatajute-Talimaa (1978), Obruchev and ICaratajute-Talimaa (1967), Mark-Kurik (1969), Mark-Kurik and Noppel (1970) and Turner (1973).

Turner (1973, 1976) showed that the stratigraphical range of thelodonts in Britain extends from the Upper Llandovery to the Upper Dittonian and that the major change in thelodont denticles occurs at the base of the '*Psammosteus*'Limestone in the Welsh Borders. After a transitional period, the *Turinia pagei* assemblage became established throughout the Dittonian, and possibly also into the Breconian. *Turinia pagei* denticles are abundant in Welsh Border samples, and become established throughout Europe at the same horizon. As mentioned above, Richardson *et al.* (1984) place the occurrence of this species in the middle part of the *micrornatus–newportensis* Palynozone. The changeover at the base of the *Turinia pagei* assemblage zone may match the base of the *Monograptus uniformis* graptolite zone, and should mark the Silurian–Devonian boundary, because such an event occurs in Britain, Europe, Russia, Canada and Australia.

This biostratigraphical use of thelodont scales adds to the importance of the complete specimen of *Turinia pagei* from Turin Hill. These scales show wide individual morphological variations, and complete specimens are essential to prove which scale-form taxa belong together. Besides the complete type specimen, there is now a second articulated piece of *Turinia pagei,* based on a fragment from the Brownstones of Wilderness Quarry, Gloucestershire (Turner, *in* Allen *et al.,* 1968).

Turinia pagei occurs in the Dittonian and possibly also in the Breconian at many localities (Turner, 1973): scales are abundant in the Welsh Borders, the higher red Beyrichienkalk erratics, the Til'ze suite of Lithuania, and the Czortkow horizon of Podolia, and higher in these same successions. In Spitsbergen this species is found in the Vestspitsbergen red-beds (Ørvig, 1969), the *polaris* and *primaeva* beds of the Fraenkelryggen Formation, and possibly also the Kapp Kjeldsen division (Friend, 1961), the Lower Craven Peak Beds of the Toko syncline in Central Australia, and Prince of Wales Island, Arctic Canada. Other species of Turinia are *T.* (*?*) *oervigi* (Karatajute-Talimaa, 1978) from the lower Dittonian of the East Baltic and the Dittonian of England, and *T. australiensis* (Gross, 1971) from the Dittonian?, Lower Devonian of Western Australia, England, the Baltic, Beyrichienkalk, Podolia and Spitsbergen (Turner, 1973). To Turner (in press) it appeared from this that thelodonts adapted to freshwater environments and had become widespread by Dittonian (Lochkovian) time.

Acanthodians occur in the Arbuthnott Group in fine-grained dark-grey laminites which commonly appear varved (?lacustrine) and which occur as thin beds within sequences of green, plant-rich shales and mudstones. Here the acan-thodians are very fragile, and their completeness suggests that they must have died close to their final burial place. They are regarded as active predators, swimming in waters with relatively high organic productivity.

Most Scottish acanthodians were slender, 300 mm long or less, and had large eyes and small nasal capsules, indicating a reliance on sight. The large-toothed Ischnacanthidae were presumably the most predaceous; others with few or no teeth (such as *Euthacanthus*)may have been microphagous.

Acanthodians are known from the Early Silurian to the Early Permian, a span of 150 Ma, but they show low diversity throughout that time. The Silurian forms were marine but non-marine forms appear thereafter. In the first half of the Devonian period the acanthodians had few predators, but with the rise of the earliest ray-finned fishes (actinopterygians) and sharks, they had to compete for food and habitats, and this may have been a factor in their decline to extinction in the Permian (Figure 5.6).

Climatius reticulatus Agassiz, 1845, the first known acanthodian, was named for a spine from Balruddery Den. Later, complete specimens were discovered at Farnell in 1856 (Mitchell, 1859, 1860), and specimens collected by Powrie on Turin Hill are frequently figured (e.g. Watson, 1937; Miles, 1973; Ørvig, 1973). Of these localities, Balruddery yields only spines and poorly preserved material; at Farnell there is no longer any exposure. Nevertheless, the importance of the Scottish sites remains in a historical sense.

Vernicomacanthus uncinatus (Powrie, 1864), with the type and only locality Turin Hill (Powrie, 1870), was originally named as *Climatius uncinatus,* and later made the genotype of *Vernicomacanthus* Miles, 1973. This genus includes one other species, from the Upper Lochkovian (Dittonian) of Herefordshire. *Euthacanthus macnicoli* Powrie, 1870 is the type species of this genus of very primitive toothless climatiids ((Figure 5.6)B, C). The type locality is Turin Hill and the species is common at other sites. Other species of this genus from the Dundee Formation are not recognized by Denison (1979) because they were not adequately characterized. These include *Euthacanthus grandis* Powrie, 1870 (type and only material from Turin Hill; the largest of all the Forfarshire Lower Old Red Sandstone acanthodians, being 300–600 mm long) and *Euthacanthus curtus* Powrie, 1870 (type locality Farrell, and from Turin Hill).

Ischnacanthus gracilis Egerton, 1861 (?synonym *Protodus scoticus* Newton, 1892; Paton, 1976; (Figure 5.6)D) is based on material from Farnell, and has been found at many other sites in the area, being abundant at Turin Hill. It also occurs in the Lower Devonian Delorme Formation of Canada (Bernacsek and Dineley, 1977). The "furin Hill' specimens recorded by Powrie have been figured by many authors, including Miles (1966, 1970, 1973). This is the type species of this genus, which is also found in the Lower Devonian and Upper Silurian of the Welsh Borders, and the Lower Devonian of Ellesmere Island, Canada.

Mesacanthus mitchelli Egerton, 1860 (Figure 5.6)A based on material from Farnell, is the most abundant of all fishes in Forfarshire and is found in swarms (Powrie, 1870). It is very common at Turin Hill, from whence material was figured by Watson (1937). It is the type species of the genus, which includes species from the Middle Devonian of Caithness, and the Lower or Middle Devonian of New Brunswick and Quebec, Canada (Denison, 1979). The palaeoecology of these fishes in Forfarshire is a topic that should well repay future study. Here and elsewhere, the sediments appear to indicate that still-water conditions prevailed.

Parexus recurvus Agassiz, 1845 was based on a spine from Balruddery, but was later found at Farnell, and 'Turin Hill Quarry' (Powrie, 1869, 1870). Specimens from Turin Hill have been figured by Powrie (1870), Miles (1973), Ørvig (1967). It is the type species of this genus, the other species of which only occur in the Arbuthnott Group fish beds. *Parexus recurvus* has been tentatively noted from Herefordshire (Denison, 1979). *Parexus incurvus* Agassiz, 1845 is a *nomen nudum* (Denison, 1979). *Parexus falcatus* Powrie, 1870 is a rare form, known only from Turin Hill; it was figured by Miles (1973).

The thelodont and acanthodian fishes prove to be very widespread geographically and to be useful stratigraphical indices. They were perhaps at their acme in Lochkovian–Emsian times and appear to have been most prolific in the eastern part of Euramerica and its adjacent shallow seas (Valiukevicius, 1988). The remaining vertebrates of the Scottish Lower Devonian appear in contrast to be highly restricted geographically. Cephalaspid species are commonly known from a single locality, which suggests isolation of faunas led to morphological diversity. Elsewhere in the Euramerican province, cephalaspid species seem to be equally prolific. The single pteraspid species remains an enigma.

Fish sites

The Arbuthnott Group (Lockovian) fish localities of Strathmore may be arranged stratigraphically (Armstrong and Paterson, 1970):

vii. Canterland Den (Den of Morphie).

vi. Wolf's Hole (Bridge of Allan [Garvock Group]; Newtyle, Auchentyre [Garvock Group]).

v. Glamis; Mirestone (Carsegownie); Aberlemno; West Drums (Brechin); Reisk (Brechin); Kelly Den.

iv. Pitscandly; Tillywhandland (Turin Hill); Pitairlie; Crombie Den.

iii. Rossie Den; Balruddery Den; Reswallie; Famell; Duntrune; Myreston; Carmylie; Leysmill; Three Wells.

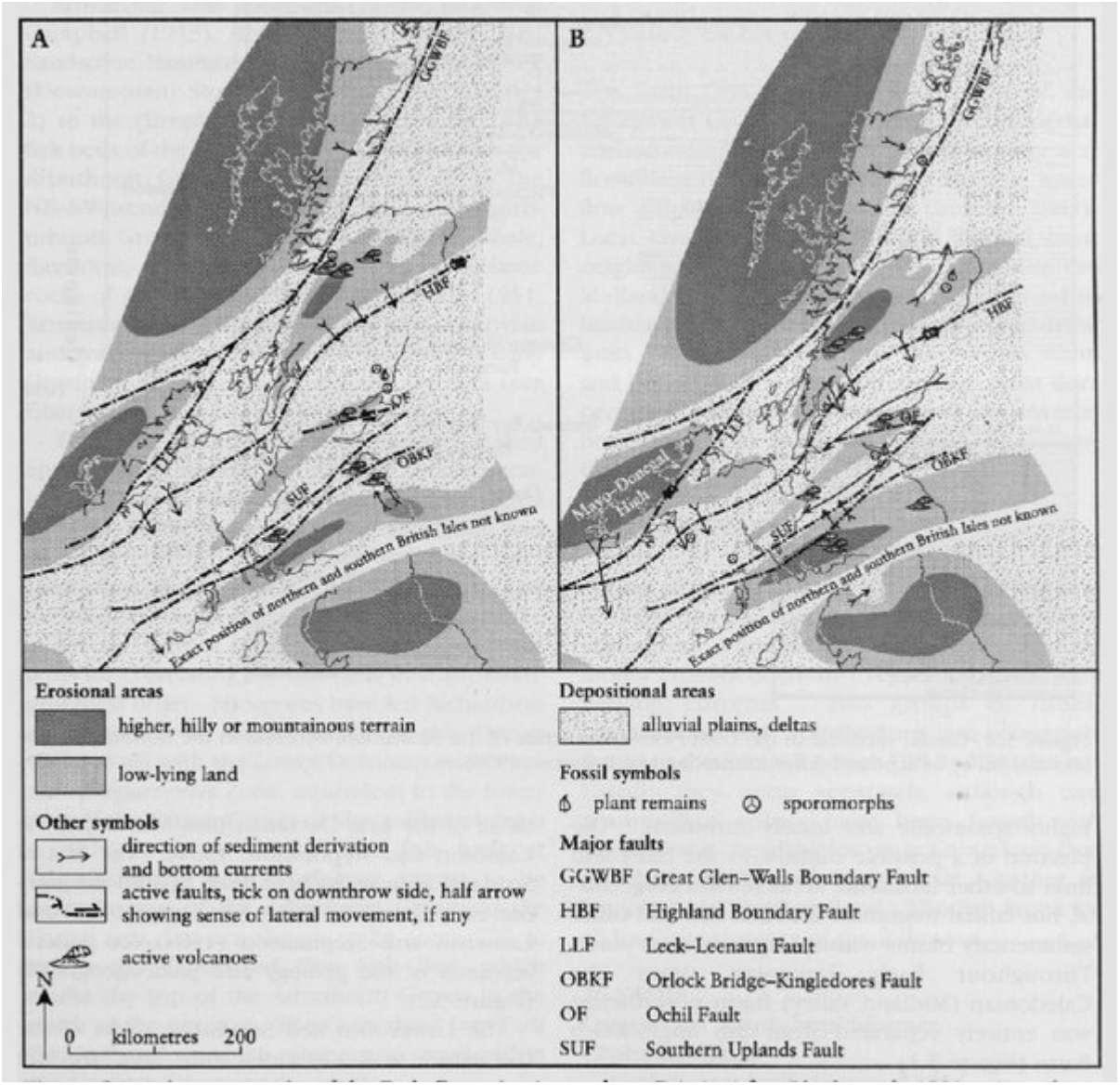
ii. Tealing (Coral Den and Whitehouse Den).

i. Ferry Den.

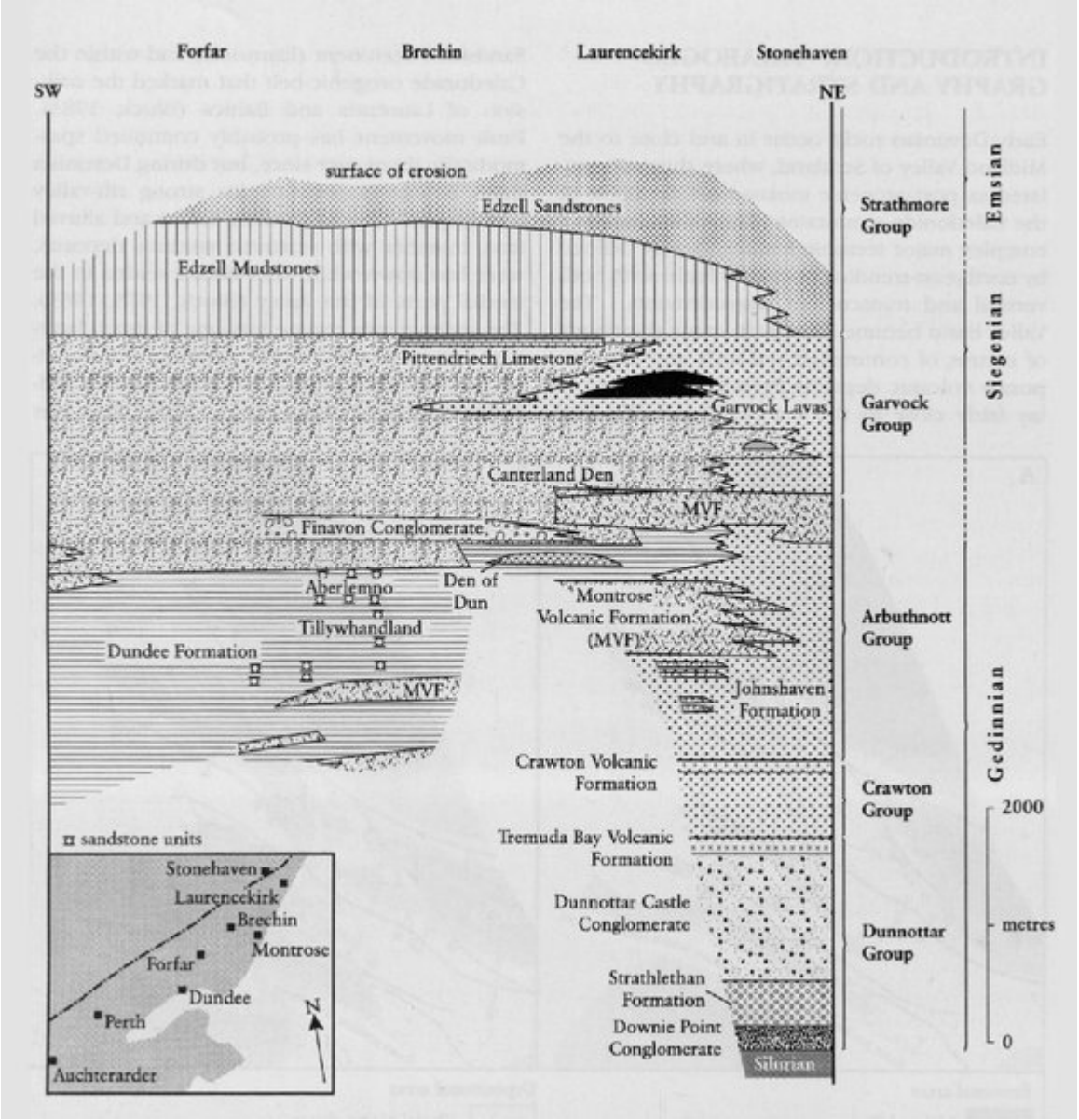
This succession is in direct contradiction to Powrie (1864), who maintained that many of these were outcrops of a single widespread bed with the sticky pale clay at each locality being the result of a single ashfall.

Bearing in mind the early date of discoveries of Devonian vertebrates in quarries in Scotland, it is surprising that more sites have not been obscured or worked out. Two old quarry sites have been selected as important sources of fossil fishes from Turin Hill, Tillywhandland Quarry (for acanthodians and cephalaspids) and Aberlemno Quarry, which shows a sandstone lithology and is important for cephalaspids. Turin Hill has been a phenomenally productive area in the past, but is now very overgrown. Of the other sites listed above, few have been very productive, but those chosen are important for the palaeobiological and palaeobiogeographical significance of their most abundant fossils, and are stratigraphically distinct and capable of being further exploited. A single locality yielding pteraspidid heterostracans, Wolf's Hole, has been included. These agnathans are rare in Scotland, as distinct from almost all other Lower Old Red Sandstone regions in the Euramerica vertebrate province (Young, 1981).

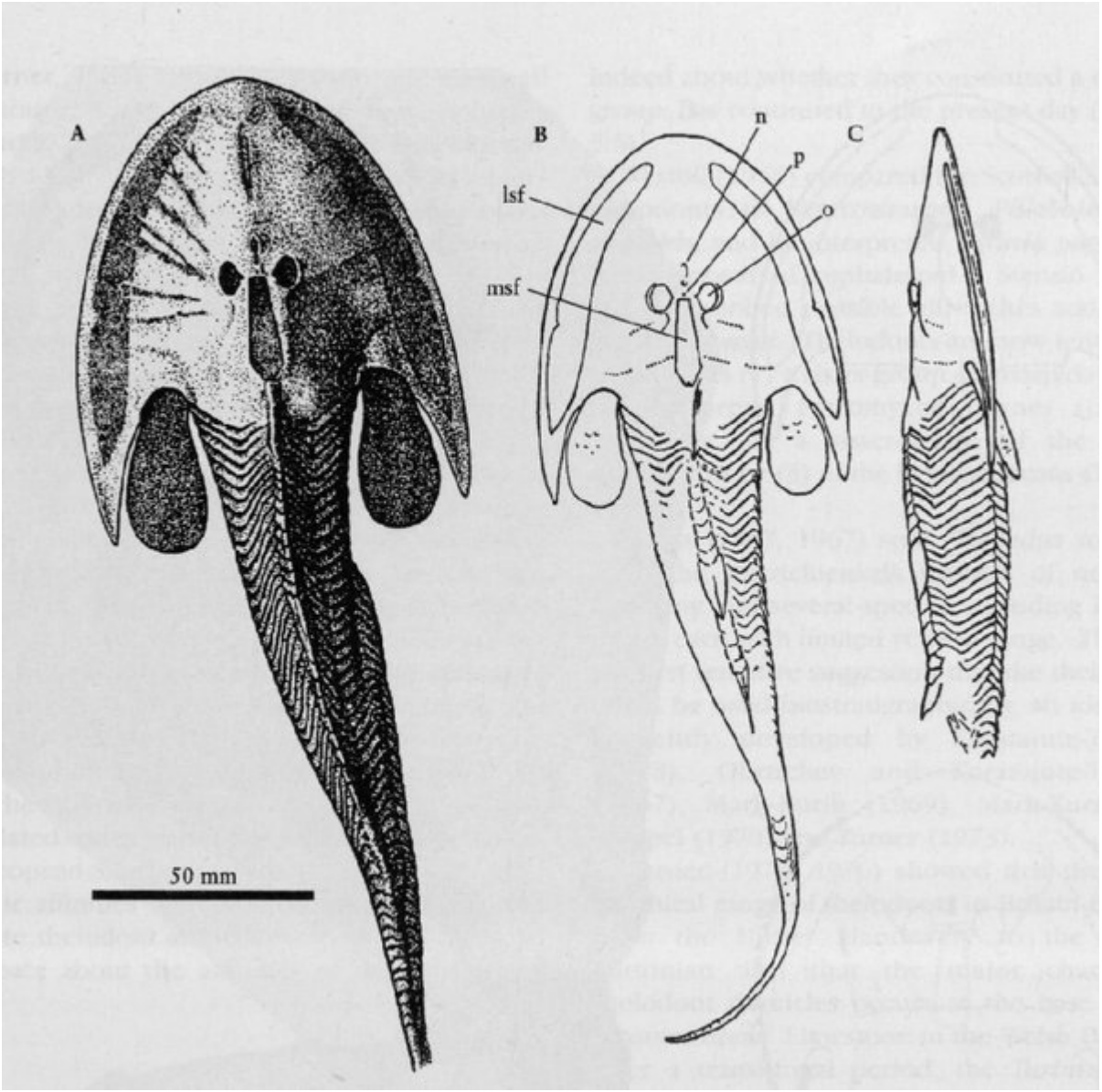
References



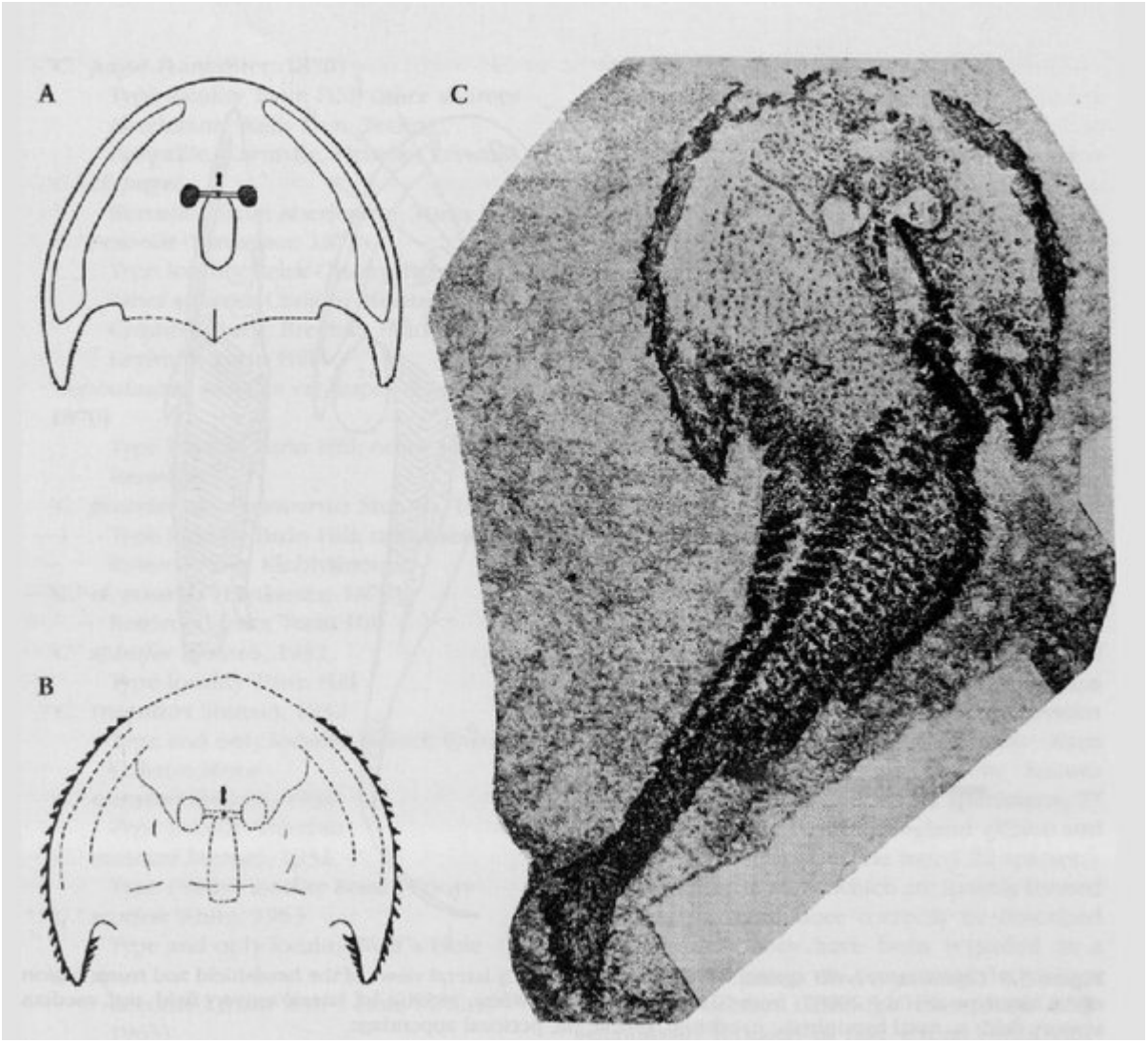
(Figure 5.1) Palaeogeography of the Early Devonian in northern Britain (after Bluck et al., 1992). (A) palaeogeography of Lochkovian time, c. 408 Ma; (B) palaeogeography of Late Pragian–Emsian time, c. 400 Ma. Continuing movement of the fault-bounded blocks dominated the area of Scotland throughout this interval, with uplift continuing to the north and south of the Midland Valley.



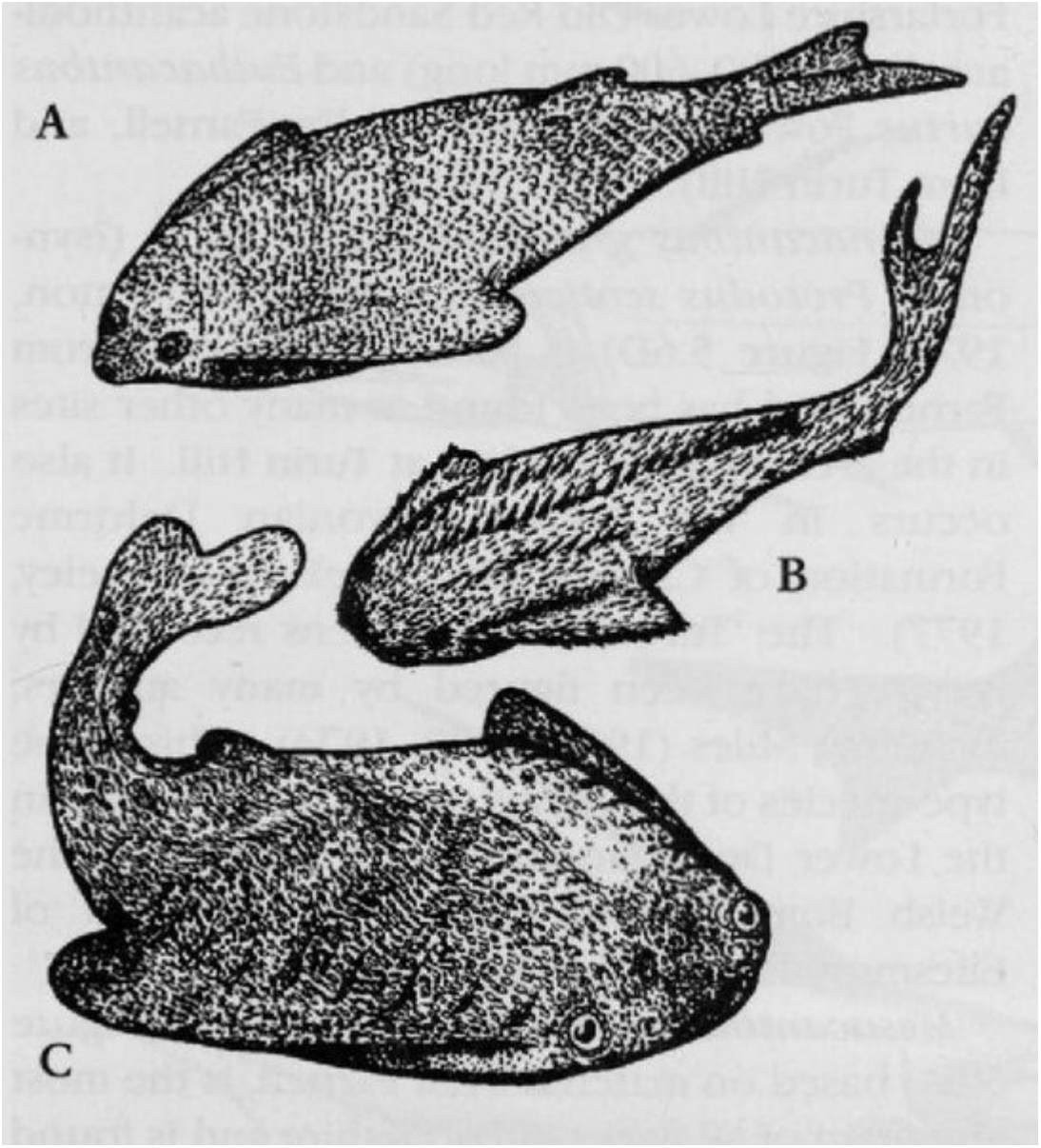
(Figure 5.2) Lateral variation in the Lower Devonian strata of the Strathmore Syncline in the northeast of the Midland Valley of Scotland (after Armstrong and Paterson, 1970).



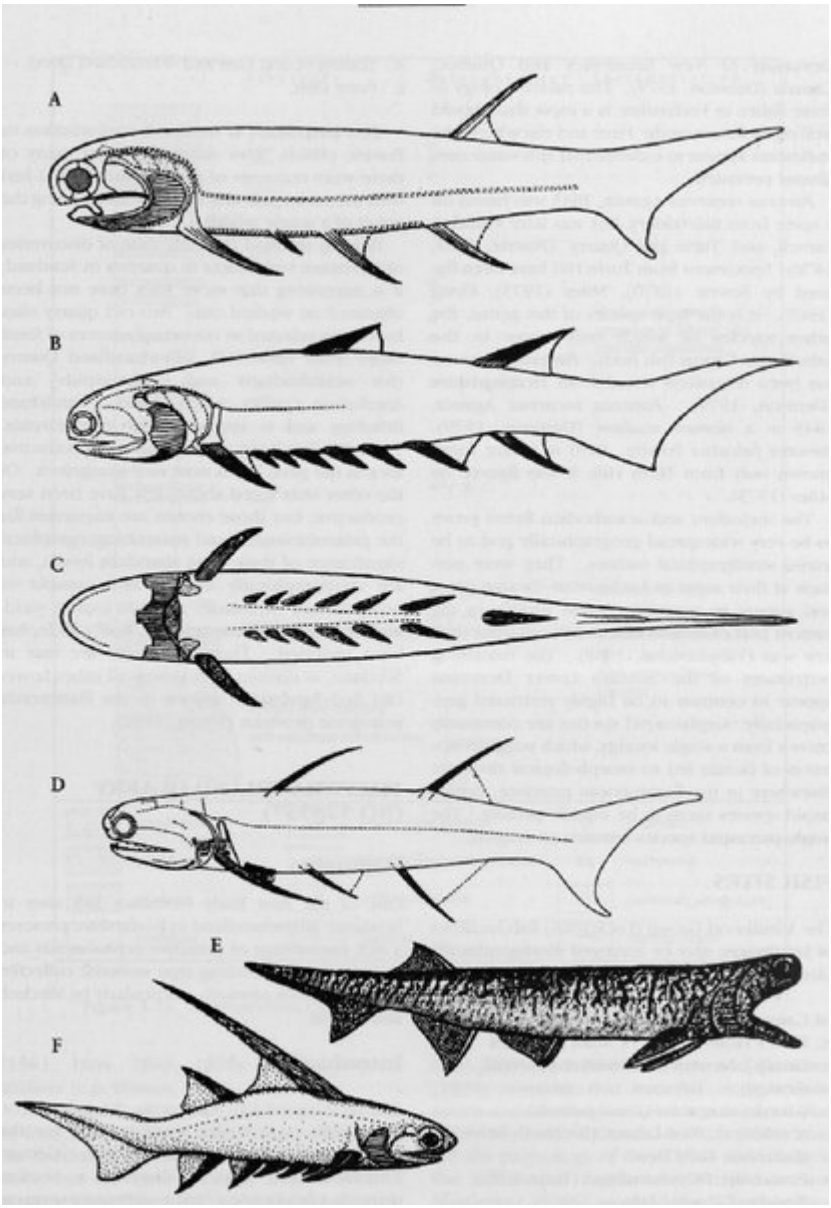
(Figure 5.3) Cephalaspis lyelli Agassiz. (A), (B) Dorsal and (C) lateral views of the headshield and trunk region of the lectotype (NHM P 20087) from Glamis, Angus (after White, 1958b): lsf, lateral sensory field; msf, median sensory field; n, nasal hypophysis; o, orbit; p, pineal; pa, pectoral appendage.



(Figure 5.4) Cephalaspids from the Early Devonian of Scotland (from Stensiö, 1932, © The Natural History Museum, London). (A) Cephalaspis powriei Lankester headshield in dorsal view after specimen RSM 138, x 0.8; (B) C. spinifer headshield after the holotype RSM 1891.92.149, x 0.8; (C) C. spinifer complete animal in dorsal view, x 0.7.



(Figure 5.5) New restorations of Scottish Early Devonian thelodonts by Turner (1992): (A) Turinia pagei (Powrie); (B) Lanarkia spinosa Traquair; (C) Loganellia scotica (Traquair), in which post-pectoral fin and tail are hypothetical. All are c. x 0.75.



(Figure 5.6) Restorations of acanthodians from the Early Devonian of Scotland. (A) Mesacanthus mitchelli (Egerton), x 2.0; (B), (C) Euthacanthus macnicoli Powrie x 0.8 in lateral and ventral views; (D) Ischnacanthus gracilis (Egerton), x 1.25 approx.; (E) Mesacanthus sp. approximately natural size (taken with permission from J. Long, 1995); (F) Parexus sp., approximately natural size. From various sources.