
Chapter 6 Mid Devonian fossil fishes sites of Scotland

D.L. Dineley

Introduction: palaeogeography and stratigraphy

Middle Old Red Sandstone sediments accumulated in the tectonically controlled NE–SW-trending Orcadian Basin. This broad structure developed on the margin of Laurussia at about 20° south of the Middle Devonian equator and stretched as far as the Hornelen Basin on the present Norwegian coastline (Figure 6.1). The lower parts of the sequence are lacustrine, but the deposits become more fluvial upwards and laterally towards the margins of the basin, until near the top they are almost entirely fluvial.

Borehole evidence in the North Sea suggests that at times there may have been access from 'Lake Orcadie' to the Devonian sea to the south, in the vicinity of the present mid-North Sea (Marshall, 1992; Marshall *et al.*, 1996).

In total, the basin infill, the 'Caithness Flagstone Series' reached a thickness of over 5000 m. It rests, in part unconformably, upon the Sarclett Group, Lower Old Red Sandstone, and it is in turn, surmounted by the unconformable Dunnet Head (Sandstone) Group (Upper Old Red Sandstone) in Caithness. It was first detailed by Crampton and Carruthers (1914) but more recently has been studied by T.S. Westoll and his group (e.g. Donovan *et al.*, 1974; Westoll, 1977), who were concerned with the biostratigraphy and sedimentology of these strata, the palaeobiology and taphonomy of the vertebrate faunas, and with the sedimentary tectonics (Rogers and Astin, 1991). Westoll's group, and more recently Trewin, have demonstrated that the succession of vertebrate faunas in this series provides a good chronology for this basin, which originated with the work of the Geological Survey (see Dineley and Loeffler, 1993). The complexities of the stratigraphy are shown in (Figure 6.2), where the terminology used is largely that of the Geological Survey. The Palaeontological Association has issued a guide to selected outcrops of the Devonian of Scotland, including several of the Middle Old Red Sandstone localities (Friend and Williams, 1978). Trewin and Hurst (1993) have provided a field guide to the geology of eastern Sutherland and Caithness.

The lake transgression appears to have been a relatively rapid event; for example, in Orkney there is a transition from desiccation-cracked sediments into the lower band of the Sandwick Fish Bed over only 1 m of strata (Trewin, 1976). In marginal situations, such as Gamrie, inundation may have occurred later, and probably as pulses, as indicated by more than one fish-bearing horizon at, for example, Edderton, Tynet Burn and in Orkney. The lake spread out over several differing deposits, such as old lake floors (e.g. Achanarras Quarry), marginal lake deltas, basement bedrock, fluvial deposits (e.g. Black Park, Edderton) and aeolian deposits. At other times there were many smaller localized lakes. Uplands rising with the later Caledonian orogenic movements were high enough to provide a continuous abundant flow of elastic detritus (Parnell, 1985).

During at least one interval, lake waters spread across the whole basin area and on this and many other occasions the organic productivity of the lake was very high. Fish populations rose as the habitat expanded and became more favourable. As a consequence on these occasions the abundance of the vertebrates as fossils also rose and the resulting fish beds are important for correlation. The 'Achanarras horizon', named after the most important quarry exposing beds of this fish stratum, is the foremost such marker horizon. It has a large fauna, species of which are widespread and stratigraphically sensitive.

Fish beds occur at many other horizons within the Middle Devonian sequence, but with more limited lateral extent. The vertebrates (gnathostomes mostly) are used for stratigraphy, and seven zones have been determined in Caithness (Donovan *et al.*, 1974) which span from the mid-Eifelian to the mid- or late Givetian in age. Their characteristic faunas are shown in (Figure 6.3). The gnathostomes are also important in inter-regional correlations, especially with the eastern Baltic and Russian Platform (Blieck *et al.*, 1988).

Environments

The water bodies within the Orcadian Basin were lakes fed by streams from the surrounding highlands under a hot climate, varying between humid and arid. The lakes were never deep, were usually highly productive and are presumed to have had a connection with the sea in the south and east. The Achanarras Fish Bed represents stagnant muds deposited at the bottom of a lake covering some 50 000 km² (Figure 6.1). It contains well-preserved remains of abundant fishes that lived in the upper waters of the Orcadian Lake, and which eventually sank to the deoxygenated lower layers of the lake. There were no predators or scavengers to disturb the carcasses, and little decomposition to destroy the specimens. The essentially laminated nature of the flagstones suggests rhythmic sedimentation under cyclic climatic conditions (Astin, 1985, 1990; Duncan and Hamilton, 1988). It would be seen that at close and regular intervals organic productivity was intense with algal blooms and widespread stromatolitic growth. Vertebrate populations probably fluctuated in consequence (Trewin, 1984). The basin lakes are estimated to have existed for about 10 Ma (rather less than a quarter of the 45 Ma of the Devonian Period) (Duncan and Buxton, 1995).

The Achanarras-age sites illustrate varying conditions in different parts of Lake Orcadie during approximately the same period of time (Figure 6.4). Achanarras yields the greatest number of species, and is the only site at which it is possible to collect good material of several of these forms. Other sites may be interesting because of the superb state of preservation of their material. Specimens from the Moray Firth are very beautifully preserved within nodules because they were closer to the lake margins where carbonate cements were sufficient to nucleate around decaying fish remains.

Fish faunas

Fossil fishes in the Middle Old Red Sandstone of northern Scotland had obviously been observed by local people for many years, but they were not described in print until the 1820s, after Murchison (1827) visited Caithness. His visit stimulated interest, and large collections were made from the 1830s onwards (Andrews, 1982). Louis Agassiz produced as his first *magnum opus* (1833–1845), a description of the many beautiful specimens in Scottish collections including several Middle Devonian taxa or examples. Hugh Miller, the stone mason and poet who became a popular writer on the history and natural history of Scotland, brought public attention to these fossils between 1841 and 1857, especially in his famous book *The Old Red Sandstone or New Walks in an Old Field*. It ran to seven editions.

The Middle Devonian strata of north and north-east Scotland contain some of the most diverse and best-preserved Palaeozoic fish faunas in the world. Many of the species are unique to the area and were perhaps prevented from migrating by the enclosed nature of the Orcadian Lake. Osteichthyans predominate, but placoderms, acanthodians and agnathans are all represented.

Agnathan fishes are rare in the Scottish Middle Old Red Sandstone, and do not occur at the Achanarras horizon. Only two specimens of *Cephalaspis magnifica* are known, both from Spittal Quarry, a Zone 4 locality. Cephalaspids are well documented elsewhere from the Late Silurian to the Late Devonian (see Chapter 1). The Caithness specimens are remarkably large (up to 600 mm long), as are those in the upper Devonian of eastern Canada.

Acanthodians are common, as complete specimens throughout most of the 'fish zones' (Figure 6.3). Active, predatory gnathostomes, the acanthodians ranged in age from Silurian to Permian, and were at their acme in the Devonian. Many of the acanthodians from the Middle Devonian of Scotland were small fishes and were among the earliest to be described.

Typical forms include:

Acanthodii: Climaatiiformes: Diplacanthidae:

Diplacanthus crassisimus Duff, 1842 (syn. *Diplacanthus striatus* Agassiz)

D. tenuistriatus Traquair, 1894

Rhadinacanthus longispinus Agassiz, 1844

Acanthodii: Acanthodiformes: Acanthodidae

Mesacanthus peachi Egerton, 1861

Cheiracanthus murchisoni Agassiz, 1835

Cheiracanthus latus Egerton, 1861

The placoderms were a diverse group of Devonian fishes of which most had a heavily armoured head and trunk shield made up of tuberculated bony plates. The posterior part of the body was unarmoured. Placoderms are absent from Zone 2, but *Coccosteus cuspidatus* appears in Zone 2 in the Lower Stromness Beds of Orkney. Achanarras-age (Fish Zone 3) taxa include:

Placodermi: Antiarchi: Asterolepidae:

Pterichthyodes milleri Miller, 1841

Placodermi: Arthrodira: Coccosteidae:

Coccosteus cuspidatus Miller, 1841

Dickosteus threiplandi Miles and Westoll, 1963

Placodermi: Arthrodira: Homosteidae:

Homosteus milleri Traquair, 1888

Placodermi: Arthrodira: Ptyctodontidae:

Rhamphodopsis threiplandi Watson, 1938

The antiarch *Pterichthyodes milleri* is confined to the Achanarras Horizon. It was about 160 mm long and is virtually the only antiarch in the series. Other antiarchs of the Mid- and Late Devonian epochs were abundant elsewhere throughout the Euramerican province, and latterly the world. The trunk armour supported an armoured and jointed pectoral limb, and the posterior trunk was covered with scales. *Coccosteus cuspidatus*, 400 mm long, is mainly restricted to the Achanarras horizon. It lingered on into the 'Spittal Beds' (Saxon, 1975). This arthrodire, with its heavily armoured head and pectoral region, scaled body and elongated heterocercal tail, is one of the best and longest known in Britain. The headshield was movably articulated with the trunk shield. The jaws bore tooth plates and cusps that provided an effective means of seizing and shearing food. Miles (1969) regarded this level of arthrodire development as fairly advanced and the coccosteids as active but relatively unspecialized predators. *Homosteus milleri* was compressed dorso-ventrally and had short trunk armour. The bony plates are very thick (c. 15 mm) and the plates large. The head plus trunk may be over 300 mm long, making it one of the largest of the Achanarras' fishes.

Higher fish zones show the disappearance of *Coccosteus* and *Pterichthyodes*, and the appearance of the placoderms *Dickosteus threiplandi* (Zones 4 and 5), *Millerosteus minor* (Zone 6), and two new forms, *Watsonosteus fletti* (the small antiarch), *Microbrachius dicki* together with *Asterolepis orcadensis* and *A. thule* in Zone 7.

Palaeospondylus gunni Traquair, 1890 from Achanarras Quarry, and from the Sandwich Beds (Trewin, 1976), is an odd tiny fish that was first brought to Traquair's notice by two Caithness collectors, Alexander and Marcus Gunn. Many palaeontologists have given attention to this enigmatic fossil, and it has been referred to one or other of several fossil groups, or even to specially founded classes or subclasses (Bulman, 1931). Its characteristics have been debated as to whether they are mature or larval. A recent resume (Forey and Gardiner, 1981) suggests that it is a larval gnathostome, probably a dipterid. This convincing argument attempts to identify a synapomorphy with a Recent group rather than using other fossil groups as models, but as Trewin (1986) noted, the distribution of *Palaeospondylus* at Achanarras is quite distinct and different from that of other vertebrates. The puzzle remains.

The Osteichthyes (bony fishes), both actinopterygians (ray-finned) and sarcopterygians (lobe-finned), are abundant in the Achanarras horizon. The earliest records of these are from the Late Silurian, but the first complete specimens are found at the Achanarras horizon. Bony fishes from the Scottish Middle Old Red Sandstone include:

Osteichthyes: Actinopterygii: Cheriolepididae

Cheirolepis trailli Agassiz, 1835

Osteichthyes: Sarcopterygii: Holoptychida: Holoptychiidae

Glyptolepis paucidens Agassiz, 1844

G. leptopterus Agassiz, 1844

Osteichthyes: Sarcopterygii: Osteolepidiformes: Osteolepididae

Osteolepis macrolepidotus Agassiz, 1835

Gyroptychius agassizi Traill, 1841

Osteichthyes: Porolepiformes: Holoptychiidae

holoptychiid indet. (P. Ahlberg, pers. comm., 1995)

'*Holoptychius*'sp.

Osteichthyes: Sarcopterygii: Dipnoi: Dipterida

Dipterus valenciennesi Sedgwick and Murchison, 1828

Cheirolepis trailli, perhaps the most primitive known species of actinopterygian, is restricted to the Achanarras horizon. It was long-bodied, with a heterocercal tail and covered with a shagreen of small acanthodian-like scales, rather than the large thick scales common to more advanced forms. The scales were set in rows, each having a peg and socket to articulate with rows above and below. This species also had its scales and dermal bones coated with a thin shiny tissue, ganoine. The jaw mechanism, too, was novel. The cheek bones formed a rigid plate over the jaw muscles, which in later species were free to allow a wide range of feeding actions to evolve (see (Figure 6.18)).

Sarcopterygians include the rhipidistians, such as *Glyptolepis paucidens*, which first appears in the Achanarras horizon, and continues through to the Mey Subgroup (Zone 6). It was a large fish, averaging about 0.6 m in length, covered in large circular scales ornamented by dentine. It was a predator equipped with two rows of teeth on its jaws. An as yet undescribed holoptychid previously included in *G. paucidens* has a skull length of about 1 m, it is the largest fish in the basin and is very rare. *Osteolepis macrolepidotus*, 0.16 m long on average, is restricted to the Achanarras horizon, but is abundant at some localities (e.g. Cruaday), and rare at others (e.g. Achanarras). *Gyroptychius agassizi* is also virtually confined to the Achanarras horizon. It is 0.3–0.4 m long, and has dorsal fins in a posterior position.

Rhipidistians occur in other Middle Old Red Sandstone fish zones. Species of the osteolepid *Thursius* occur in Zones 1, 2, 5, and 6, *T. macrolepidotus* in the two lower zones, and *T. pholidotus* in the two upper ones. *Osteolepis microlepidotus* is characteristic of Zone 6, and *Tristichopterus alatus* of Zone 7.

The final sarcopterygian group in the Achanarras horizon are the Dipnoi (lungfishes), such as *Dipterus*, which was able to breath air and probably shared this ability with most other sarcopterygians and perhaps basal actinopterygians. They may all have obtained extra oxygen when the water in which it lived became too stagnant. The dipnoans appeared first in the Lower Devonian and still survive. *Dipterus* had a distinctive palatal tooth plate with tubercles. The species *D. valenciennesii* is ubiquitous, being a typical element of the faunas of Zones 1–5. Described as early as 1829 by Sedgwick and Murchison, it was the first fossil lungfish to be recognized. The species *D. platycephalus* (an invalid taxon perhaps)

appears in Zone 6. Work by Trewin and others is beginning to allow some discussion of the palaeoecology of the gnathostome fishes here. The Estonian palaeontologist E. Mark-Kurik has suggested (1978) that a series of arthrodiran 'zones' in the Scottish Old Red Sandstone may correlate closely with a similar series in the eastern Baltic area (Figure 6.3).

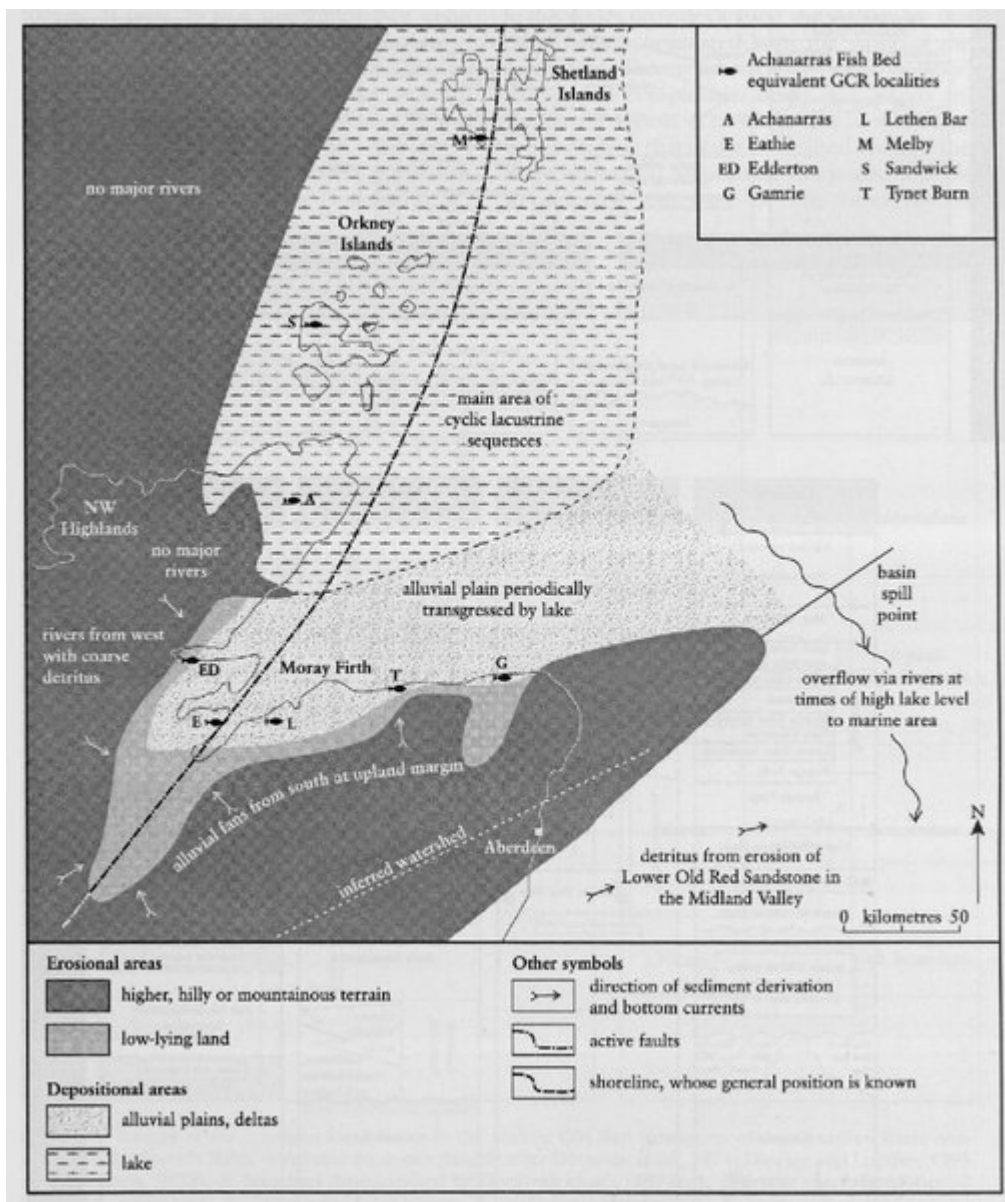
Fish sites

The selected network of GCR sites for the Middle Devonian of Scotland represent a sequence of fish-bearing units of different ages. The oldest (Westerdale Quarry in Highland) may represent an early Eifelian fauna. Several sites containing the important late Eifelian Achanarras horizon have been selected as GCR sites, namely Achanarras Quarry in Highland, Cruaday Quarry in Orkney, Black Park, Edderton in Highland, Den of Findon and Tynet Burn in Grampian, and Melby and Papa Stour in Shetland, a wide geographical range of sites of presumably identical age.

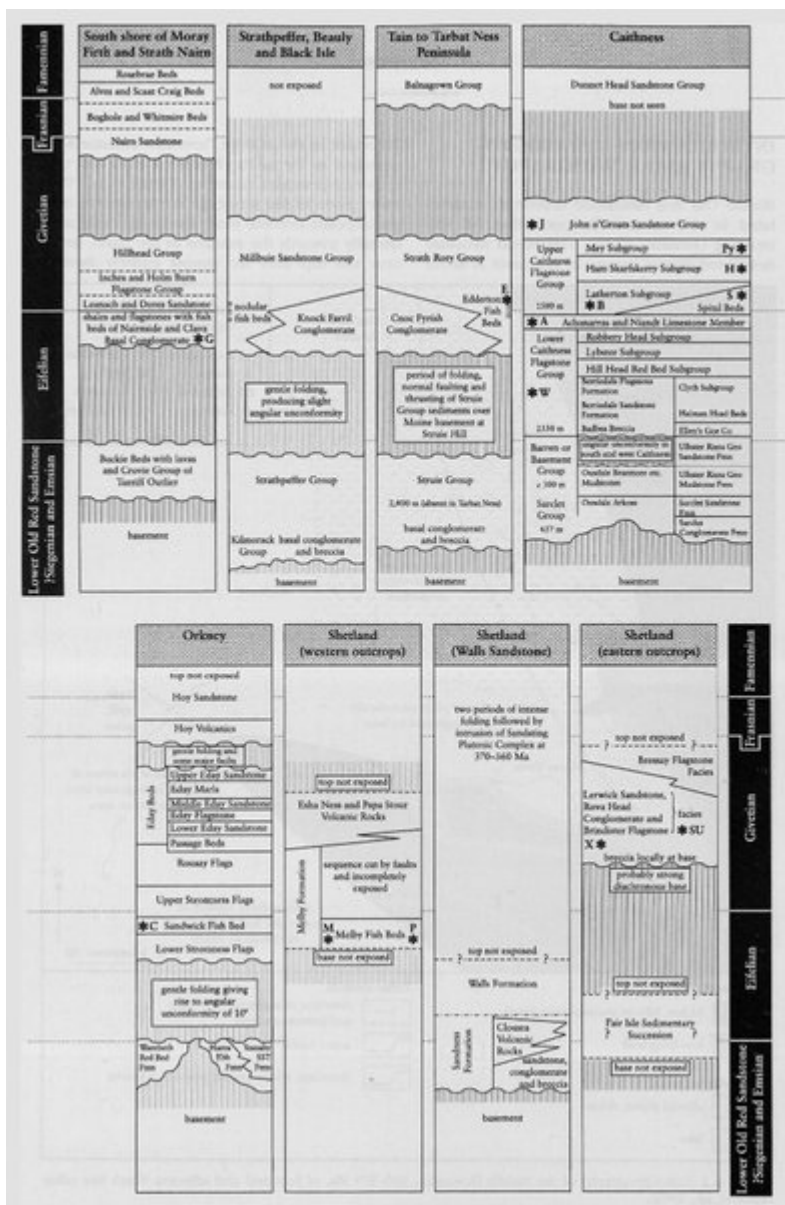
The remaining Scottish Middle Devonian fish sites are all probably Givetian in age, and they document sequences of faunal change in some detail. Dipple Brae in Highland is marginally younger than the Achanarras horizon, as are Spittal Quarry and Banniskirk Quarry in Highland. The Caithness Flagstone sequence is continued with progressively younger fish-bearing horizons represented at Holburn Head Quarry, Weydale Quarry, Pennyland and John o'Groats, all in Highland. In Orkney the Sandwich Fish Beds correlate with the Achanarras horizon at Cruaday Quarry. The Cletts, Exnaboe and Sumburgh Head in Shetland both contain fish beds of latest Givetian age.

A new excursion guide to the geology of eastern Sutherland and Caithness covers the outcrops on which many of the following sites are located (Trewin and Hurst, 1993).

[References](#)



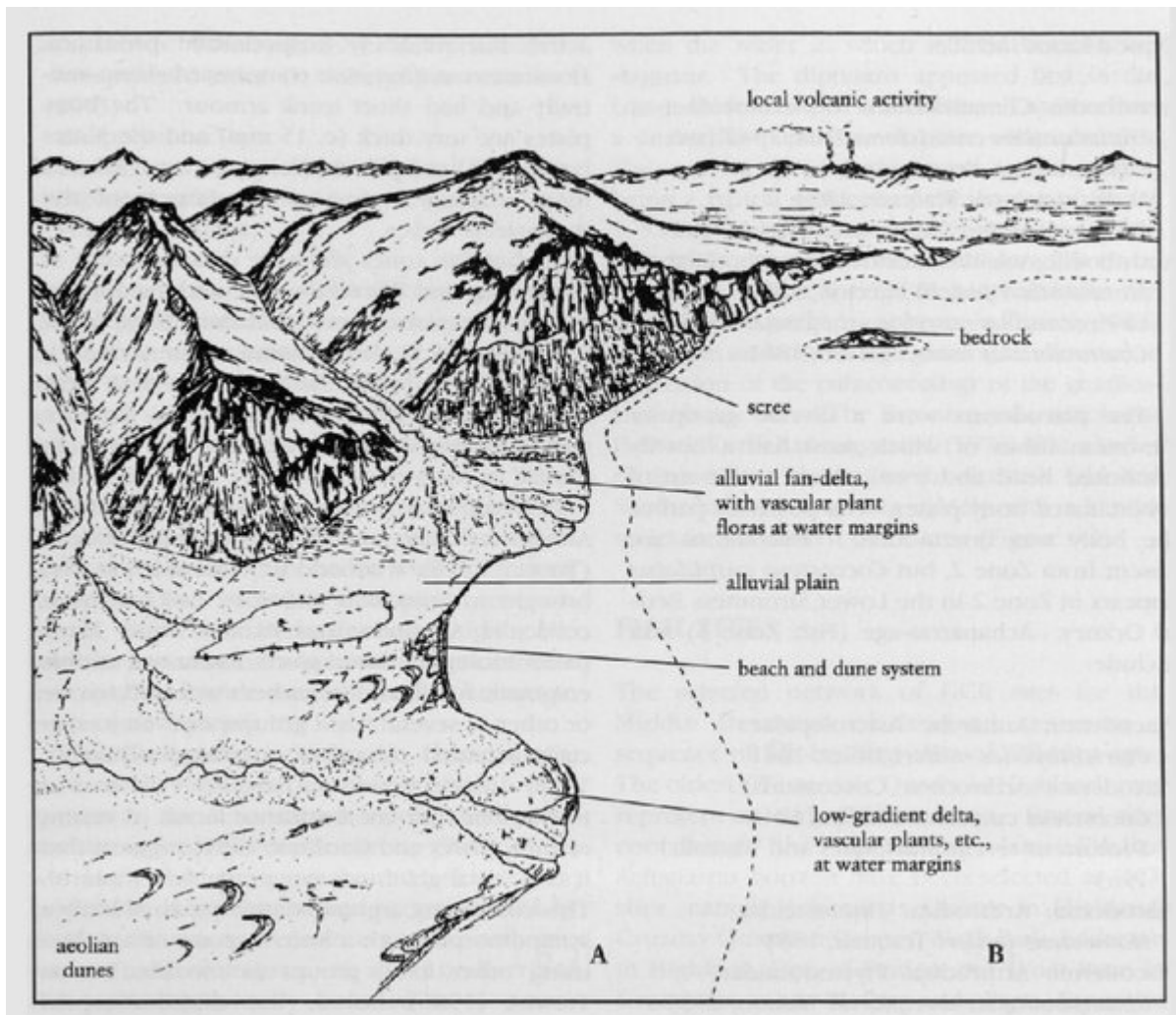
(Figure 6.1) Palaeogeography of the Middle Devonian, 380–375 Ma, of Scotland and adjacent North Sea (after Bluck et al., 1992).



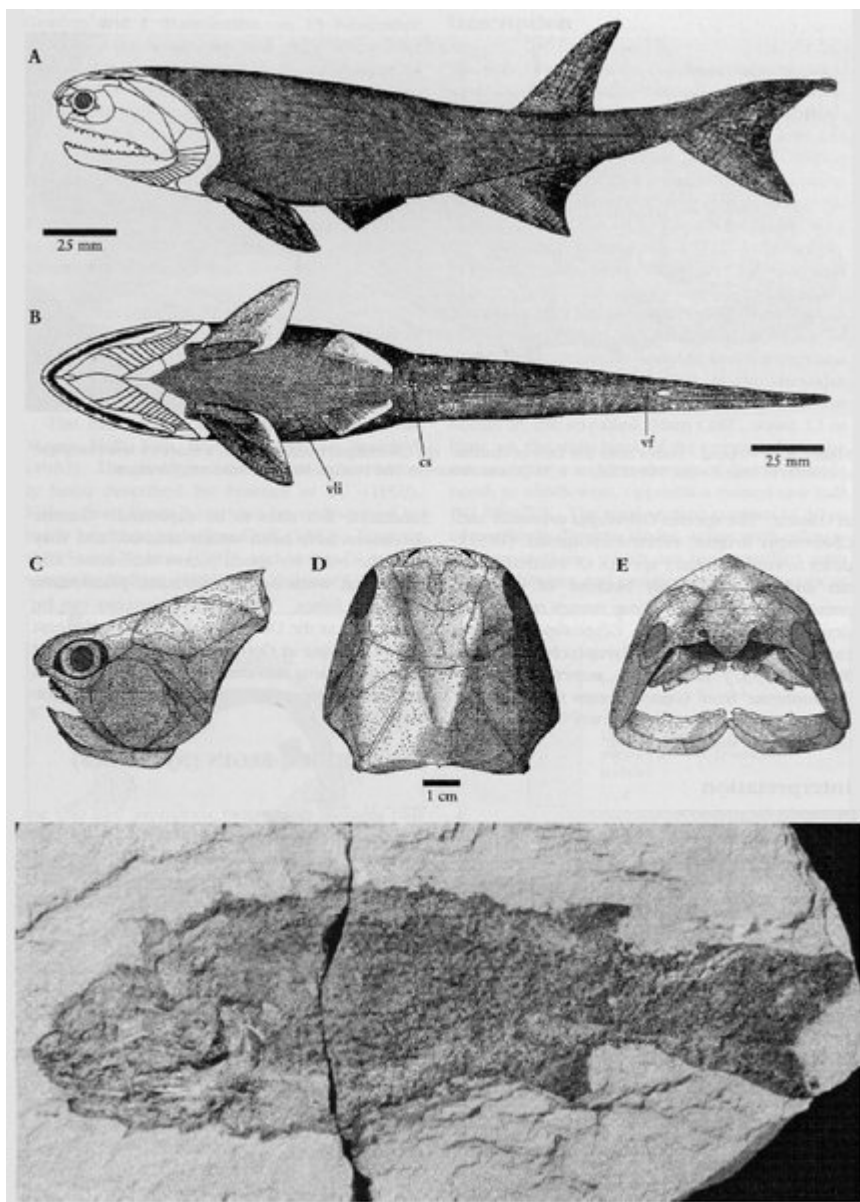
(Figure 6.2) Stratigraphical sections of the Middle Old Red Sandstone of Scotland, Orkney and Shetland, with GCR sites shown. A, Achanarras Quarry; B, Banniskirk Quarry; C, Cruaday Quarry; D, Dipple Brae; E, Blackpark; F, Edderton; G, Gamrie, Den of Findon, Tynet Burn; H, Holburn Head Quarry; J, John o'Groats; M, Melby; P, Papa Stour; Py, Pennylands; S, Spital Quarry, Su, Sumburgh Head; W Weydale Quarry; X, Exnaboe (after Mykura (1991), Donovan et al. (1974) and others).

| | | Scotland | | | | Baltic | | | | | |
|----------|----------------------------------|------------------------------------|---|-------------------------|----------------------------|-----------------------|-----------------------------------|---------------------|---|--|--|
| | | Caithness stratigraphical units | Z | Vertebrates | | Stratigraphical units | Vertebrates | | | | |
| Givetian | Upper Caithness Flagstones Group | John o'Groats Group | 7 | Watsonosteus | Trilobosteus | Renslandia | Microbrachius | Gauja | <i>A. ornata</i> | | |
| | | Mey Beds Subgroup | 6 | Millerosteus | Thursius pholidotus | | | Burtnicki | <i>A. dellei</i> <i>P. tuberculatus</i> | | |
| | | Ham-Skarfskerry Subgroup | 5 | Dickosteus | Gyroptychius milleri | Osireolepis | Asterolepis (Bonaay, Orkney only) | | | | |
| | | Latheron Subgroup | 4 | Dickosteus | Gyroptychius milleri | Osireolepis panderi | Glyptocephalus paucidentis | Homocentrus milleri | Diplerus sulfureus | Arküla | <i>A. estonica</i> <i>P. pauli</i> <i>P. palaeformis</i> |
| Eifelian | Lower Caithness Flagstones Group | Achanarras horizon | 3 | Cocosteus | Osireolepis macrolepidotus | Gyroptychius agassizi | Pterichthyodes | Chirolophis | Narva | <i>Asterolepis estonica</i> <i>Sch. striatus</i> | |
| | | Wick Flagstone Fm | 2 | Thursius macrolepidotus | Gyroptychius agassizi | | | Rhamphodopsis | | | |
| | | Ellens Goe Conglomerate (Red Beds) | 1 | Thursius macrolepidotus | | | | Palaeospondylus | | Pärnu | <i>Sch. heterolepis</i> |
| Emsian | | Sarcelt Group | | | | | | | | | |

(Figure 6.3) Ranges of the common fossil fishes in the Middle Old Red Sandstone of the Orcadian Basin compared with the Eastern Baltic vertebrate biozones (largely after Donovan et al., 1974; Dineley and Loeffler, 1993; and Mark-Kurik, 1978). Z, Biozones distinguished by Donovan et al., (1974): 1, *Thursius macrolepidotus*; 2, *Cocosteus cuspidatus*; 3, *Palaeospondylus gunni*; 4, *Dickosteus threiplandi*; 5, *Asmussia murchisoniana*; 6, *Millerosteus minor*; 7, *Watsonosteus fletti*. A, *Asterolepis*; P, *Psammosteus*; Sch, *Schizosteus*.



(Figure 6.4) Diagrammatic reconstruction of the marginal environments around the Middle Devonian Orcadian Basin of Scotland and the North Sea at a time of high stable water level (after Trewin, 1986). The shallow-water well-oxygenated zone (A) provided a variety of habitats for the fish, which were ultimately preserved in the deeper deoxygenated zone (B).



(Figure 6.18) Fishes from the Den of Findon. (A), (B) *Cheirolepis trailli* Agassiz, restorations of lateral and ventral views respectively (from Pearson and Westoll, 1979). (C)–(E), *Coccosteus cuspidatus* Agassiz: (C) restoration of the fish head in lateral view; (D) restoration of the head and trunk shields in dorsal view; (E) restoration of the skull in anterior view (after Miles and Westoll, 1968). Fishes from the Den of Findon. (F) *Cheirolepis trailli* Agassiz, a more or less complete specimen in lateral view, T00382/A, x 0.75 (Photo: courtesy The Natural History Museum, London).