Chapter 8 Late Devonian fossil fishes sites of Scotland

D.L. Dineley

Introduction: palaeogeography and stratigraphy

The Upper Devonian is not so widely represented in Scotland as is the Middle Devonian. Poorly dated successions are known in parts of southeastern Scotland and Northumberland, in the Midland Valley and on Arran (Figure 8.1), resting everywhere unconformably on Lower Old Red Sandstone. In the area of the great Middle Devonian Orcadian Lake (Lake Orcadie) (Chapter 6), which extended from Banffshire and Morayshire to Orkney and Shetland, Upper Devonian strata are recorded only in the Elgin–Forres area, around Nairn, in Sutherland, (Highland) north-east Caithness, and Orkney (Weston, *in* House *et al.,* 1977). Fossil fishes have been recorded from a few locations, but only as isolated scales from the thick Dunnet Sandstone Group of Caithness. No fossils are known from the Hoy Sandstone Group of Orkney.

Upper Old Red Sandstone successions in the Scottish Borders and Midland Valley regions are mostly thinner and finer-grained than the underlying Lower Old Red Sandstone. In some places the Upper Old Red Sandstone facies passes into the Lower Carboniferous. During Late Devonian times, southern Scotland and adjoining areas were mainly land, extending beyond the uplifted Southern Uplands and the Highlands (Figure 8.2). The Midland Valley continued as an alluvial basin, and a further low-lying basin extended from the North Sea area into the eastern Scottish Borders region. Sediment was supplied to these basins from the Northwestern Highlands, the Southern Uplands, and the Cheviot area in northern England. The Midland Valley Upper Old Red Sandstone successions include alluvial fans, braided stream deposits and those of alluvial plains, meandering streams and pedocals (cornstones). In the Scottish Borders (or Cheviot) basin, all the sediments are fluvial in origin, and they are capped in places by a pedocal, followed by the Birrenswark–Kelso lavas, which are dated as earliest Carboniferous.

Correlation on the basis of lithology has been difficult as there is so much lateral variation in these elastic arenaceous deposits. The sparse occurrence of vertebrates has proved to be of considerable stratigraphical use, especially in conjunction with the records from more fossiliferous successions as is the Baltic area and Greenland (see Jarvik, 1961; Blieck *et al.,* 1988; Dineley and Loeffler, 1993). Macroplants and spores have also aided correlation in recent years (see MacGregor, 1979; Richardson, 1974).

In the Orcadian Basin, Upper Old Red Sandstone beds rest unconformably on those of the Middle Old Red Sandstone. The basin still existed in the area (Figure 8.2), but was more widely emergent than during the Middle Devonian time. Many areas experienced no deposition, although considerable thicknesses of sandstones and siltstones accumulated around Elgin and Nairn in the south of the basin, and in north-east Caithness and Orkney in the north. Calcrete soils are present through the Elgin–Nairn sequence and in Ayrshire (Burgess, 1961), indicating more extensive terrestrial conditions in the area than existed during the Middle Devonian. Alternatively, the necessary climatic episodes were more frequent. Wright *et al.* (1993) investigating calcretes in the Upper Old Red Sandstone of the Midland Valley, postulated that these soils represent an interval of non-deposition of several hundreds of thousands of years or longer.

The Upper Old Red Sandstone formations are generally more difficult to assess in chronostratigraphical terms, being largely barren of fossils except for the few vertebrates and some paly-nomorphs. The section on the Berwickshire coast passes conformably upwards from Devonian into Carboniferous, and between Devil's Hole on Rease Sands and Eastern Hole about 170 m of strata are commonly referred to as Devono-Carboniferous, the level of the Devonian-Carboniferous boundary being uncertain (Figure 8.3).

Environments

Much of the Upper Old Red Sandstone of the Scottish Borders and Midland Valley basins resulted from high-energy alluvial fan and braided stream deposition, and few fossils are preserved. Sedimentary basins here, and in the south of the Orcadian Basin, were filling up and becoming emergent (Mykura, 1991; Cope *et al.,* 1992; (Figure 8.2)). Renewed

uplift of the surrounding uplands was accompanied by vigorous erosion. Cornstones formed, indicating pedocal development in tropical, perhaps monsoonal, climates. Terrestrial vegetation was probably restricted to water margins and was never extensive. The fish-bearing units generally represent temporary lakes, where reasonably good-quality specimens are preserved, or river channels, containing transported plates and scales in basal lag conglomerates. Local desiccation events were probably common agents of mortality.

Fish faunas

While a few agnatha remained after the end of Mid-Devonian times, the vertebrate assemblages of the Late Devonian are preponderantly of gnathostomes. A widespread radiation had occurred at the beginning of the Eifelian and widespread changes took place at the start of the Frasnian. Placoderms, excepting the antiarchs, generally declined while the 'bony' fishes became dominant (Ørvig, 1957). Elasmobranchs were widespread in the marine realm. At the end of Famennian time a mass extinction event removed several groups of vertebrates from the scene (Figure 8.4), but the tetrapods were then poised to make an impressive showing in the Carboniferous. Tetrapod origins are now sought amongst the sarcopterygian fishes (Ahlberg and Milner, 1994; Chapter 15), but perhaps a pre-Frasnian fauna contains the most probable candidates. From Scaat Craig, in addition to fishes, tetrapod-like remains have recently been obtained (Ahlberg, 1991). As Young has shown (1981, 1990), the early Devonian provincialism gave way to cosmopolitan faunas in the later part of the period.

Devonian Euramerica has left an abundant record of vertebrate progress with much diversification in response to changing geography and the advances made by the vascular plants. Vertebrate biostratigraphy has made significant strides during the last two decades in North America and much of Europe, Asia and adjacent areas. Australia and Antarctica too have revealed a wealth of late Devonian fossil fishes (Long, 1993). In all of these regions a vertebrate biostratigraphy not greatly different from that of Euramerica is emerging (Dineley and Loeffler, 1993). The faunal succession in the Upper Old Red Sandstone of Scotland is shown in (Figure 8.4).

The list that follows gives taxa occurring at the selected sites. It is not a comprehensive tally of all the known Scottish Upper Old Red Sandstone fishes.

AGNATHA

Heterostraci: Psammosteiformes: Psammosteidae

?Psammolepis sp.

Psammosteus taylori Traquair, 1897

P. cf. *P. falcatus* Gross, 1942

P. indet.

Traquairosteus pustulatus (Traquair, 1897)

GNATHOSTOMATA

Placodermi: Antiarchi: Bothriolepidae

Bothriolepis gigantea Traquair, 1888

B. hayi Miles, 1968

B. major (Agassiz, 1844)

B. paradoxa Agassiz, 1845

B. stevensoni Miles, 1968

B. taylori Miles, 1968

Placodermi: Antiarchi: Remigolepidae

Remigolepis sp.

Placodermi: Antiarchi: Asterolepidae:

'*Asterolepis maxima*' Agassiz, 1844

'*A. alta*' Traquair MS

A. sp.

Placodermi: Arthrodira: Plourdosteidae

Plourdosteus magnus (Traquair, 1895)

P. cf. *magnus*

Placodermi: Arthrodira: Phyllolepida:

Phyllolepidae

Phyllolepis concentrica Agassiz, 1844

Arthrodira *incertae sedis*

Cosmacanthus sp.

Osteichthyes: Sarcopterygii: Osteolepiformes: Eusthenopteridae

Eusthenopteron dalgleisiensis (Anderson, 1859)

E. traquairi Westoll, 1937

?Polyplocodus leptognathus Traquair, 1923

Osteichthyes: Sarcopterygii: Porolepiformes: Holoptychidae

Holoptychius decoratus Eichwald, 1846

H. giganteus Agassiz, 1839

H. nobilissimus Agassiz, 1839

Glyptolepis micra Agassiz, 1841

Osteichthyes: Sarcopterygii: Dipnoi: Dipteridae

(*Conchodus ostreiformis* M'Coy, 1848)

The placoderm *Bothriolepis* and the rhipidistian *Holoptychius,* typical of the late Devonian, characterize most fish-bearing localities. These two genera may be recognized from isolated plates or scales, and that is often all that is found. Other less common taxa include the het-erostracan agnathan *Psammosteus,* the placoderms *Asterolepis, Plourdosteus* and

Remigolepis, and the osteolepiformes *Polyplocodus* and *Eusthenopteron.*

Bothriolepis is the most widespread antiarch placoderm, and it is known from over 100 described species of nearly worldwide distribution (Long, 1983, 1995). It occurs in the Middle Devonian of China and Iran, the Upper Devonian of the Baltic States, Siberia, Scotland, Belgium, England, Wales, Antarctica, Western Australia, Canada, USA, and the Upper Devonian or ?Lower Carboniferous of East Greenland (Denison, 1978; Young, 1981). *Bothriolepis* is usually preserved in fluvial deposits, but the genus is found rarely in marine environments (e.g. Gogo, Australia). Scottish specimens of *Bothriolepis* were recognized very early on and were first described by Agassiz (1833–1845). Because of their box-like dermal armour and arthropod appendage-like pectoral fins they were originally described as turtles or beetles (e.g. Anderson, 1840). Antiarchs were poorly understood for many years, and frequently classified as a group with the ostracoderms (e.g. Woodward, 1891a) rather than with the arthrodires (e.g. Traquair, 1888a, 1888b). It was prolific later material from Canada and Greenland that prompted modern studies of the group, since when attention has returned to the Scottish species (Miles, 1968; (Figure 8.4)).

Unlike most other placoderms, antiarchs such as *Bothriolepis* were freshwater forms, bottom dwellers and 'mudgrubbers' (shown by the presence of mud content in preserved spiral valves; Denison, 1978). *Bothriolepis* also had paired sacs that may have functioned as 'lungs'

(Denison, 1941), which suggests that they inhabited streams and pools that occasionally dried up or became stagnant and deoxygenated (Denison, 1978). The pectoral appendages of *Bothriolepis* may have helped propel the fish along the bottom, or have served as props or braces (Denison, 1978; Young and "Chang, 1992).

The Psammosteiformes, an order of large heterostracan agnathans, existed from early to late Devonian times (Halstead Tarlo, 1965). *Psammosteus* is found in the Middle and Upper Devonian. The Scottish psammosteids have been reviewed by Tarlo (1961a) who found parallels between Scottish and Baltic forms, which is evidence of communication between the two areas. Very distinctive vertebrate faunas distinguishing the Late Devonian and Old Red Sandstone were recognized early in Scotland. Subsequently, the globally cosmopolitan nature of these faunas has become recognized. Recently the study of the vertebrate palaeoecology of the Devonian in the East Baltic area has been given much attention (Mark-Kurik, 1995). Some of the schemes of fish interrelationships may be close to, if not identical to that which prevailed locally in Scotland. For example, Luksevics (1992) postulates one for the Amula (Beds) fauna. Acanthodians are present in the Late Devonian of Scotland but seem to be less abundant than they were earlier. The species *Cosmacanthus malcolmsoni* Agassiz, 1845 was, according to Denison (1979), based on a spinal plate of an arthrodire indet. A single acanthodian zone of *Devononchus concinnus* (Gross, 1930) is proposed for the latest Givetian and Frasnian of Belarussia by Valinkevicius *et al.* (1995), and the genus is widespread in the Late Devonian of northern Europe. As yet, however, it has not been identified in Scotland.

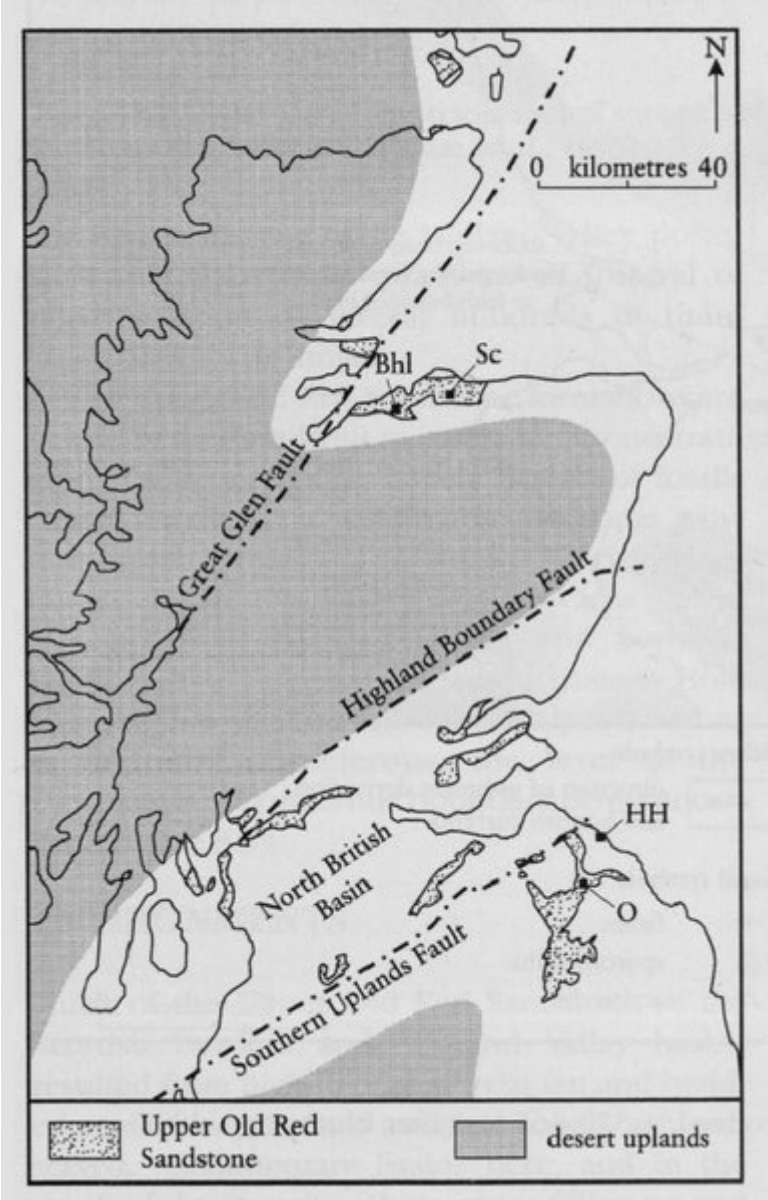
Fish sites

Fragments of *Bothriolepis* and *Holoptychius* bone have been recorded from many Scottish Late Devonian sites, but few localities have produced relatively complete specimens. For example, the Elgin District Geological Survey memoir (Peacock *et al.,* 1968) lists 25 late Devonian localities within the relatively small outcrop area: only two of these have yielded (relatively complete) specimens. Four sites, yielding abundant, well-preserved and/or significant fossils, are selected here for the GCR coverage, to represent the southern and northern occurrences, i.e. the 'Lake Cheviot' basin and the 'Orcadian' basin. Oxendean Burn and Hawk's Heugh in Borders show typical faunas of several taxa from the Scottish Borders Basin. Boghole/Muckle Burn and Scaat Craig in Highland have produced two excellent fossil fish faunas, the first early in the Late Devonian, the second rather later. Each represents an environment, community of vertebrates and stratigraphically important moment in Late Devonian time. The famous Dura Den site (Anderson, 1859; Woodward, 1912; Attridge, 1956) once yielded a wealth of osteichthyans of similar age to the latter oarvik 1950a).

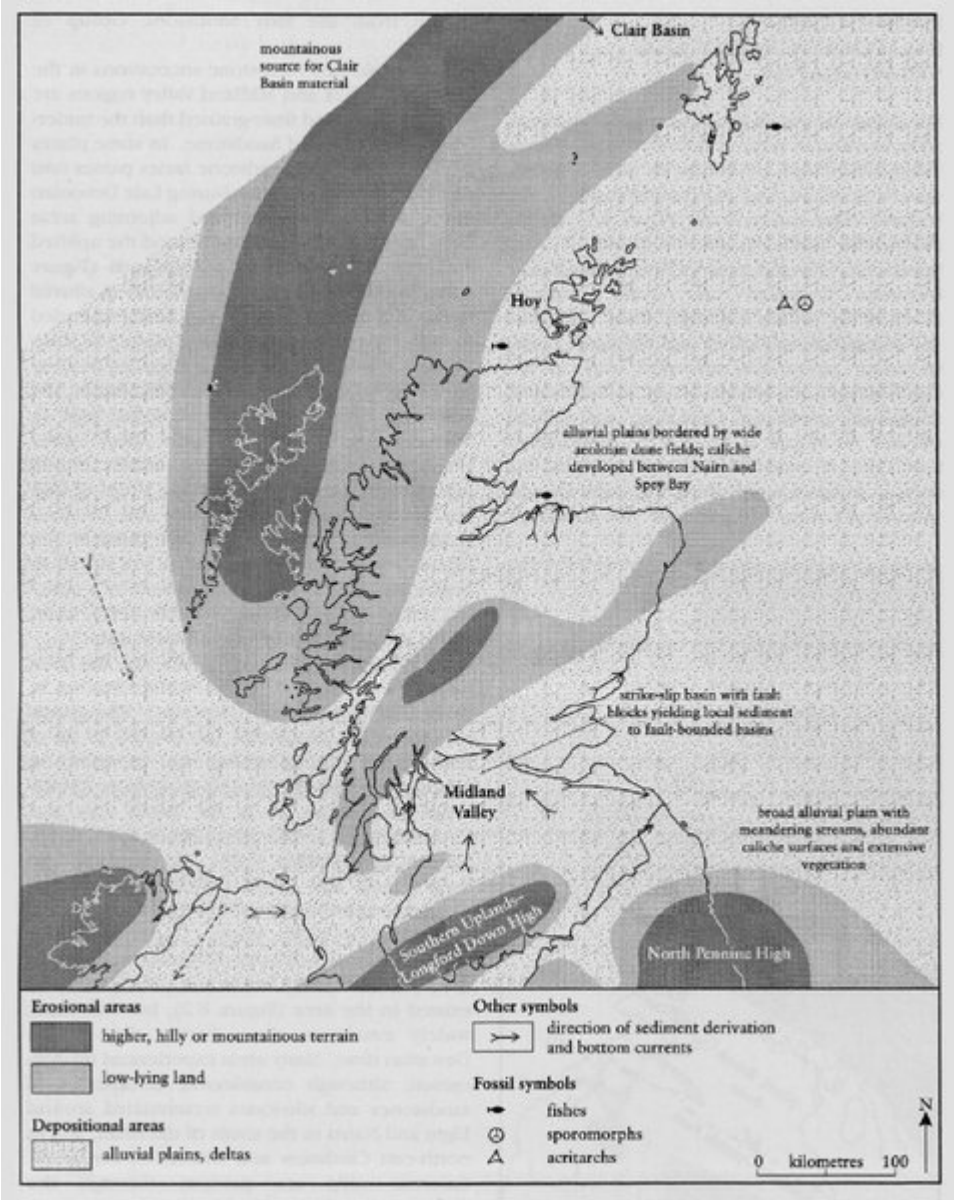
Comparison with other regions

The Late Devonian Epoch was one of widely cosmopolitan fish faunas; placoderms, chondrichthyes and osteichthyes were much in evidence and a few of the agnathans were still extant. The most important new feature amongst the Late Devonian vertebrates was the advent of the tetrapods, examples of which are now known from Euramerica and Gondwana. Thus the British Upper Old Red Sandstone fossil fish sites yield material comparable to that from northern and eastern Canada and the USA, as well as East Greenland and the eastern Baltic. The Main Devonian Field of Russia has also provided similar material. Late Devonian fish assemblages in China and other parts of East Asia, Australia and Antarctica include similar placoderms and osteichthyes. Work on microvertebrate remains from these and intervening areas is increasingly providing a means of stratigraphical correlation and integration of a vertebrate stratigraphy with one based on conodonts. In particular, the Scottish Old Red Sandstone succession of vertebrate faunas may be correlated to those in East Greenland and the eastern Baltic. Migration between these parts of the old Euramerican continent was possible from time to time, if not continually throughout the Devonian.

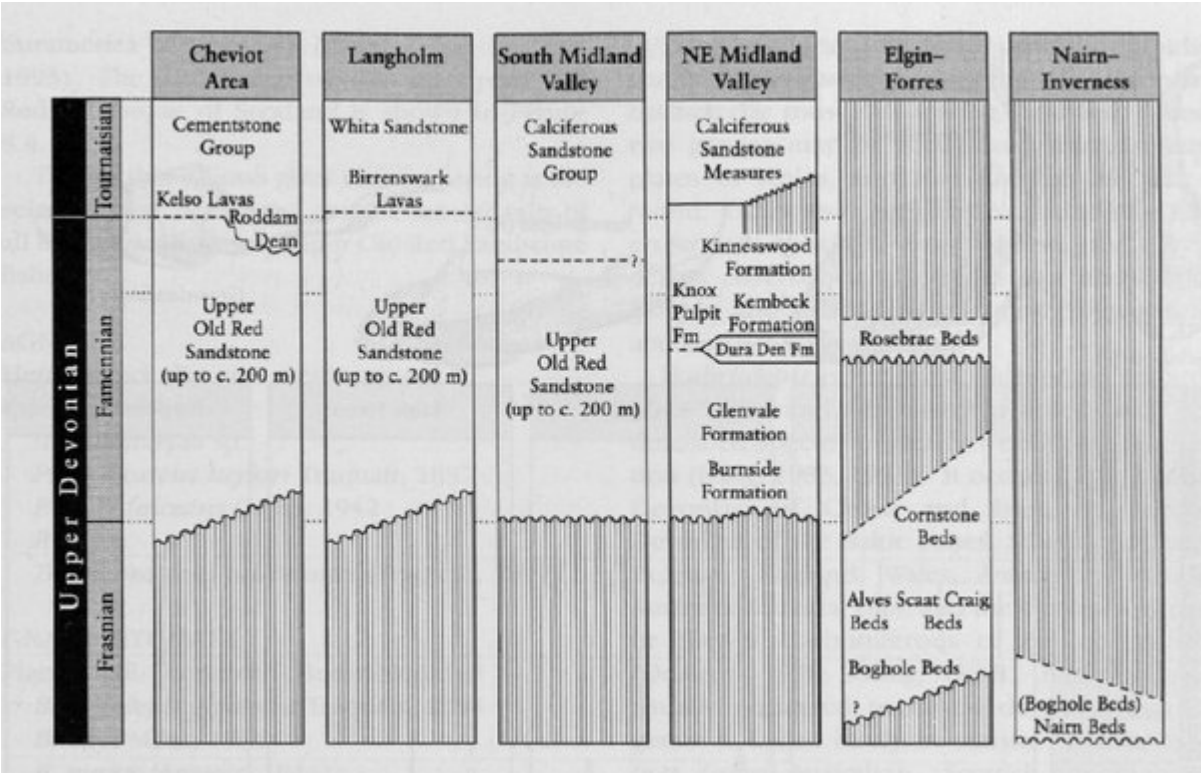
References



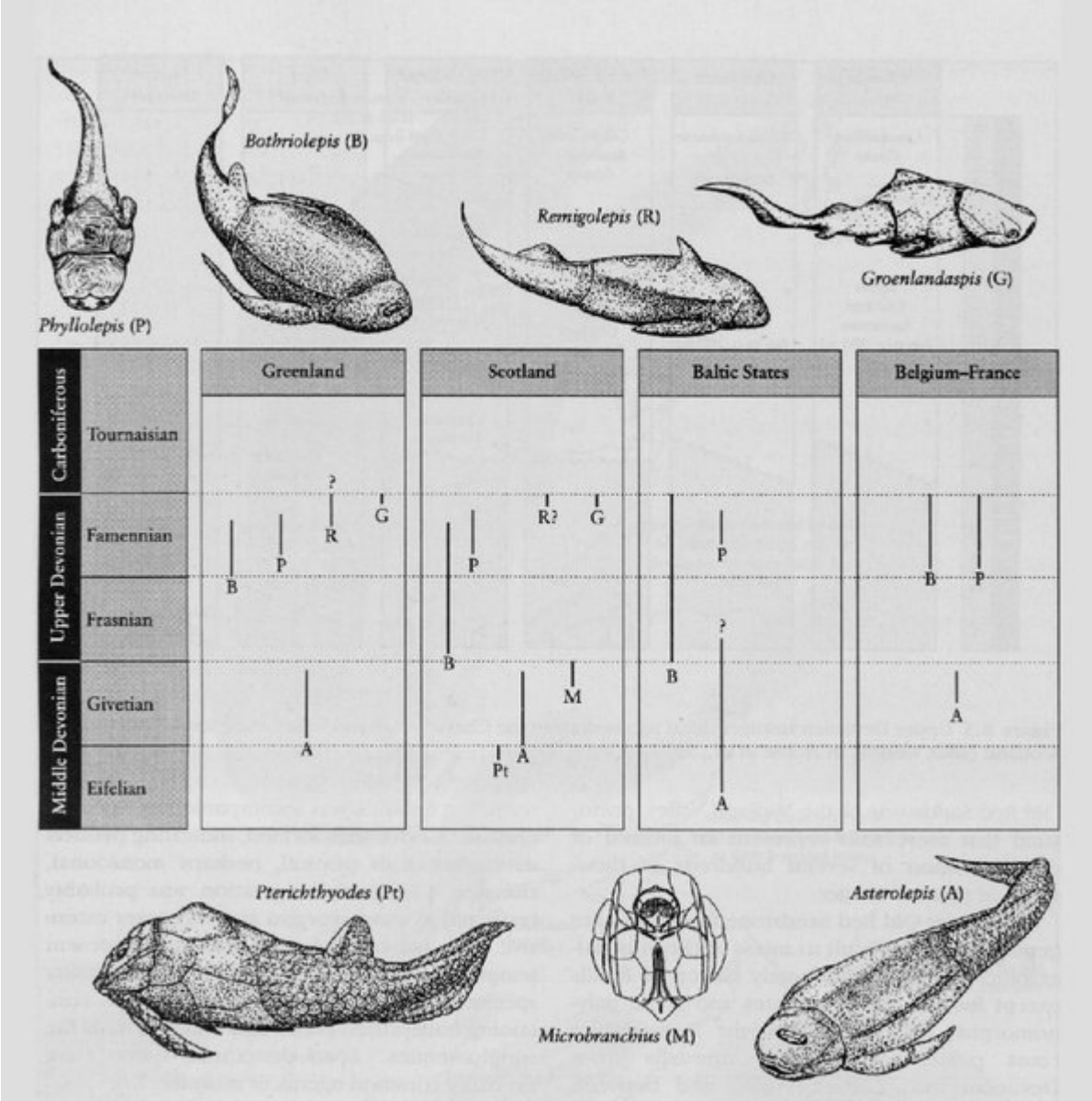
(Figure 8.1) Upper Old Red Sandstone outcrops and locations of GCR sites; 0, Oxendean; HH, Hawk's Heugh; Bhl, Boghole; Sc, Scaat (Scat) Craig.



(Figure 8.2) Late Devonian palaeogeography of Scotland, c. 370–365 Ma (after Bluck et al., 1992).



(Figure 8.3) Upper Devonian stratigraphical successions in the Cheviot, Midland Valley and Moray Firth areas of Scotland (after Westoll, in House et al., 1977).



(Figure 8.4) Stratigraphical ranges of widespread and relatively common Mid- and Late Devonian vertebrates in Euramerica (after Blieck et al., 1988). P, Phyllolepis; B, Bothriolepis; R, Remigolepis; G, Groenlandaspis; Pt, Pterichthyodes; A, Asterolepis (all x 0.25); M, Microbrachius, (x 1.0).