J.N.C.C.

# *Fossil Fishes of Great Britain*

**D.L. Dineley**

Department of Geology
University of Bristol
Bristol, UK

and

**S.J. Metcalf**

Humber Estuary Discovery Centre,
North East Lincolnshire Council
Cleethorpes, UK

GCR Editor: **D. Palmer**

JOINT NATURE CONSERVATION COMMITTEE

# 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 south-eastern 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 (Westoll, *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.

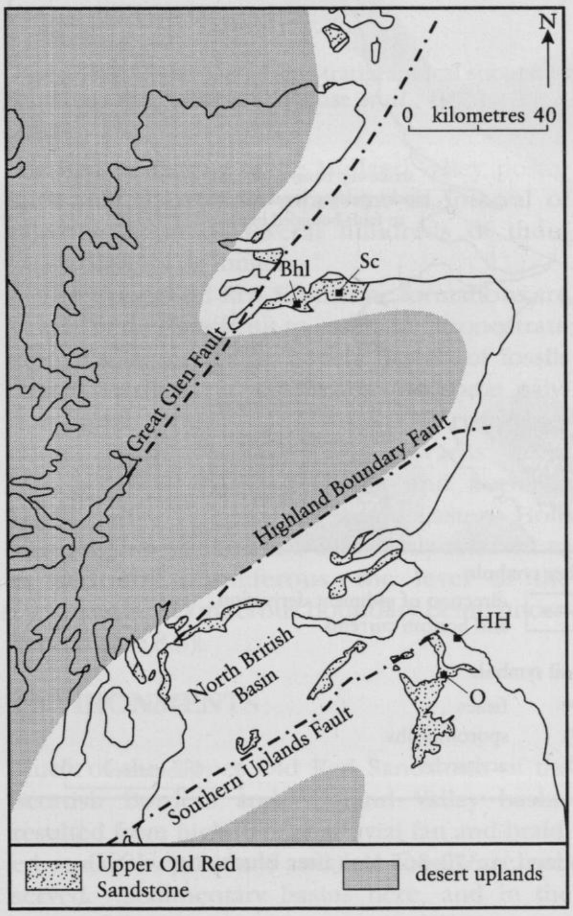



**Figure 8.1** Upper Old Red Sandstone outcrops and locations of GCR sites; O, Oxendean; HH, Hawk's Heugh; Bhl, Boghole; Sc, Scaat (Scat) Craig.

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 clastic 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

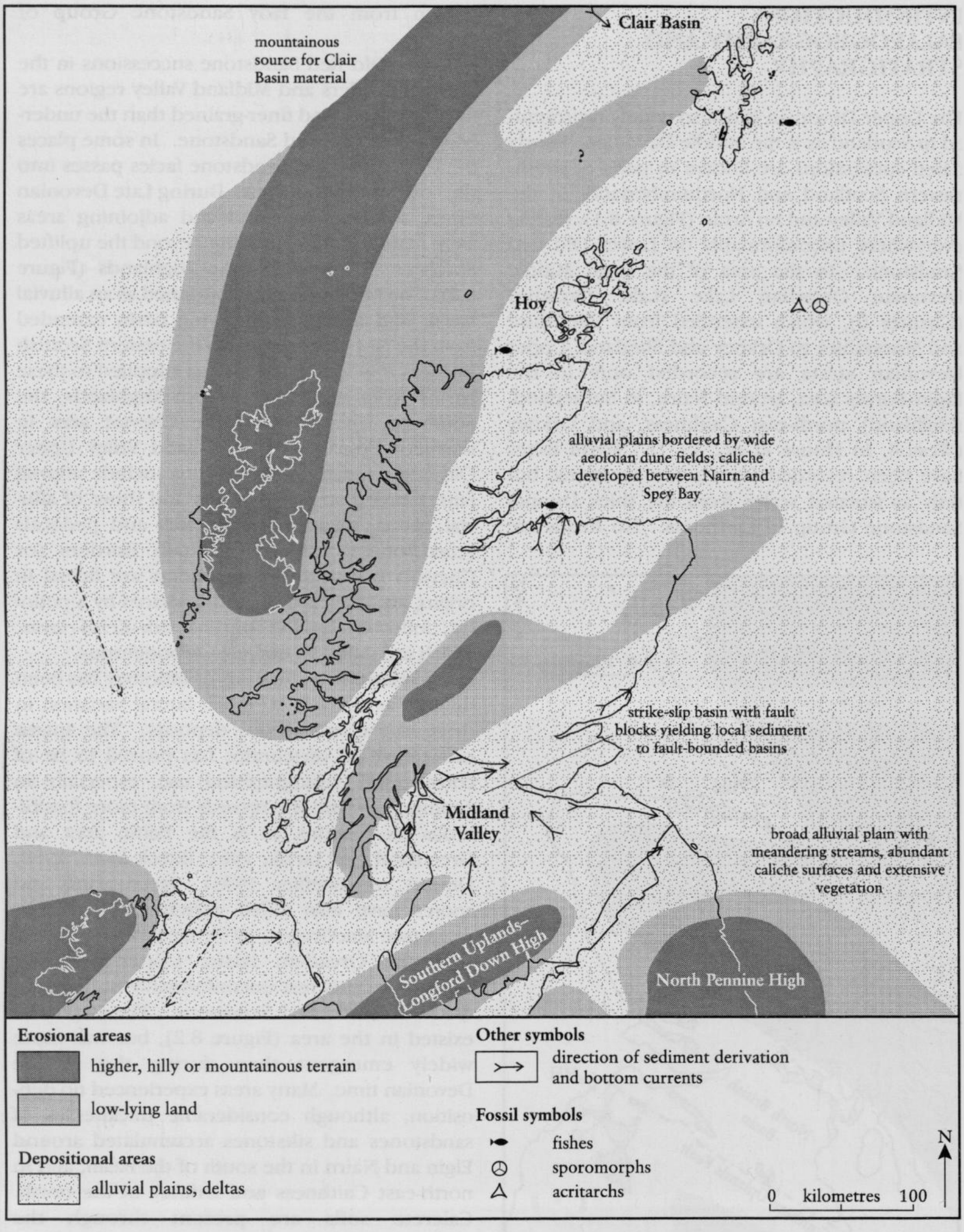



**Figure 8.2** Late Devonian palaeogeography of Scotland, *c.* 370–365 Ma (after Bluck *et al.*, 1992).

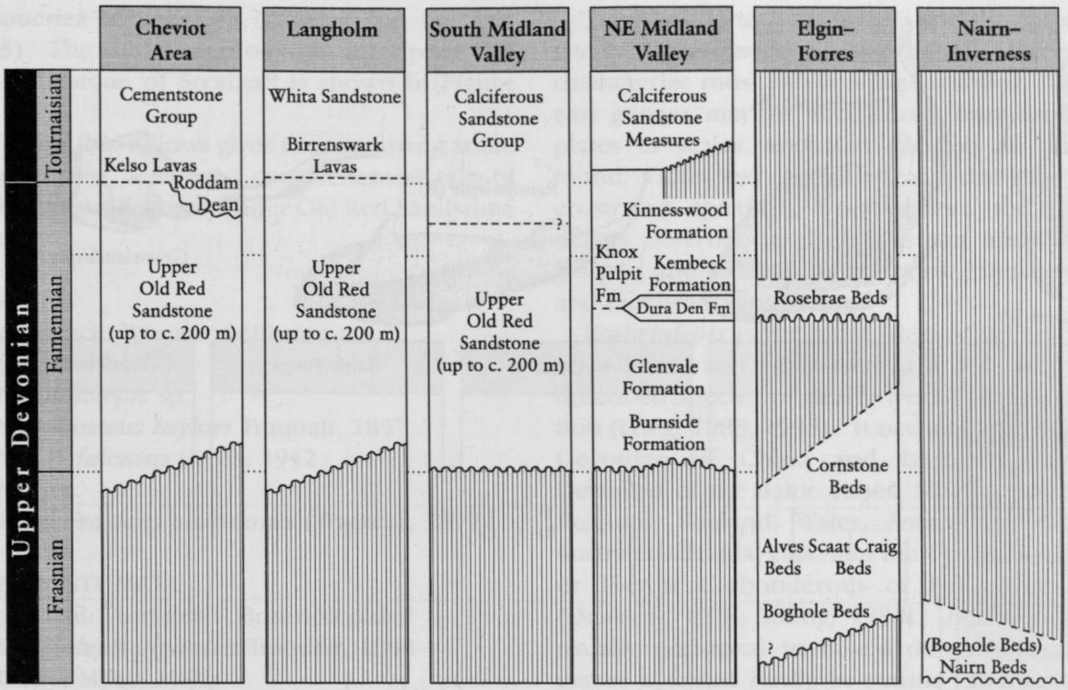



**Figure 8.3** Upper Devonian stratigraphical successions in the Cheviot, Midland Valley and Moray Firth areas of Scotland (after Westoll, in House *et al.*, 1977).

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 palynomorphs. 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

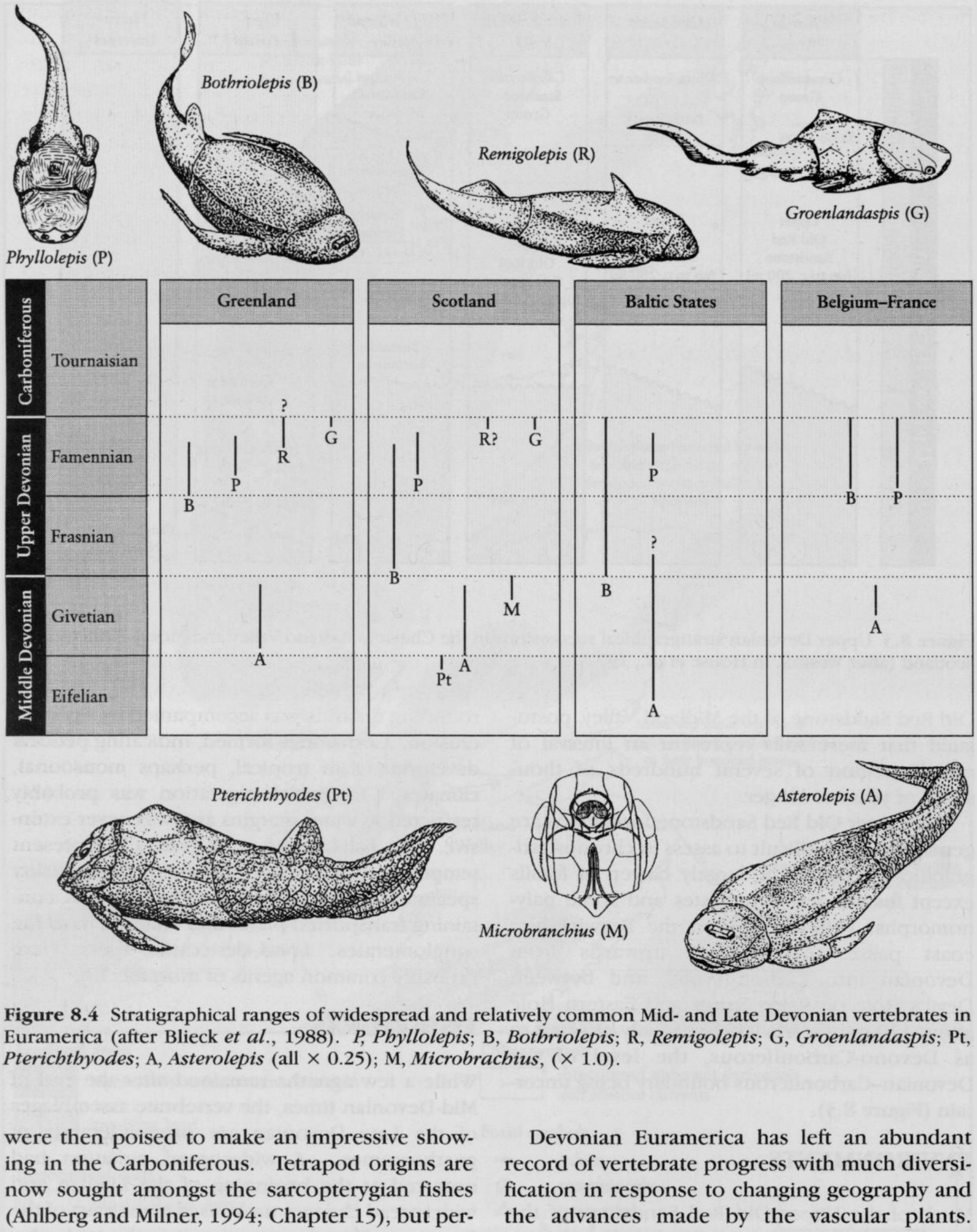



**Figure 8.4** Stratigraphical ranges of widespread and relatively common Mid- and Late Devonian vertebrates in Euramerica (after Blieck *et al.*, 1988). *P, Phyllolepis*; B, *Bothriolepis*; R, *Remigolepis*; G, *Groenlandaspis*; Pt, *Pterichthyodes*; A, *Asterolepis* (all × 0.25); M, *Microbrachius*,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

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 heterostracan 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 Zhang, 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 (Jarvik 1950a).

## OXENDEAN BURN (NT 771561)

### Highlights

Oxendean Burn in Border has produced many plates and carapaces of the placoderm *Bothriolepis*, and it is the only site for the species *Bothriolepis hayi*. Fossil fishes have been found at three levels in the Oxendean Burn, and one of these may represent a catastrophic fish mortality in a drying pool.

### Introduction

The Oxendean Burn drains into the Whiteadder Water on the northern side of the Lammermuir Hills (Figure 8.5). It exposes Upper Old Red Sandstone along its length. The Late Devonian Oxendean Beds there dip east-south-east and yield fishes from three horizons. The fish-bearing beds were discovered in 1961 and they were described by Waterston (1962a) and Miles (1968), who named the site 'Wellrig Burn'.

### Description

The outcrop in the stream is much obscured, and it is difficult to see how all the previously noted fish-bearing exposures fit in to the meas-

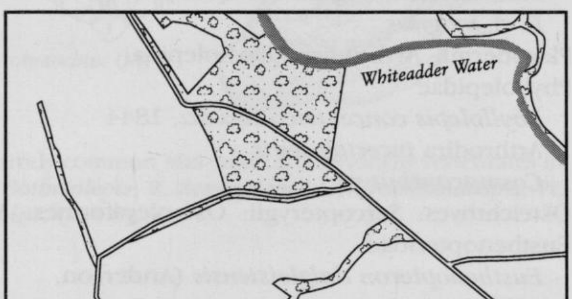



**Figure 8.5** Sketch map of Oxendean Burn area.

ured section, which is as follows (recorded by M.A. Rowlands in 1979):

| | Thickness (m) |
|---|---|
| Red mudstones | 0.4 |
| Massive sandstone, cross-bedded, pink mud clasts and plates of *Bothriolepis hayi* in the base. Locality A of Miles (1968) | 1 |
| Red mottled mudstones with sandstone lenses. ?Locality B of Miles (1968) | 1 |
| Lens of sandstone with thin green mudstones, irregular base with mudclasts (section obscured); red mudstones | 0.4 |
| Sandstone | 0.01 |
| Green mudstones with clay clasts in base; becoming mottled red–green upwards | 1.4 |
| Green mudstone with clay clasts; uneven base | 0.05–0.1 |
| Pale pink micaceous sandstone, cross-bedded | 1 |
| Red mottled mudstones | 1 |
| Red mudstones, mottled micaceous, contains ribs of hard, calcareous siltstone and fine-grained sandstone *c.* 0.2 m thick | 4 |
| – gap (? Waterston's lower fish bed): 0.8 m – | |
| Red siltstone and flaggy purple siltstone | 0.4 |
| – – – – – – – – gap: 0.4 m – – – – – – – – | |
| Bright red siltstones, with micaceous bedding planes and green reduction spots | 1 |
| – – – – – – – – gap: 0.3 m – – – – – – – – | |
| Green and yellow sandstones | 0.2 |
| Yellow sandstone | 0.3 + |

Waterston (1962) noted two fish beds: the lower is 'three inches thick, at the top of a red marl' and packed with *Bothriolepis* plates and areas of *Holoptychius* ornamentation; the upper '20 ft above the lower, is a sandstone rib' and contains disarticulated and disorientated plates of *Bothriolepis*, as well as *Holoptychius* plates and scales, and clay intraclasts. Miles (1968) identified three fish-bearing horizons. Waterston's upper fish bed is Miles' Locality A, described by the latter as a red mudstone and in the base of the overlying lens of fine-grained pink sandstone, and about 4 m wide. Localities B and C of Miles (1968) both yield fossils from

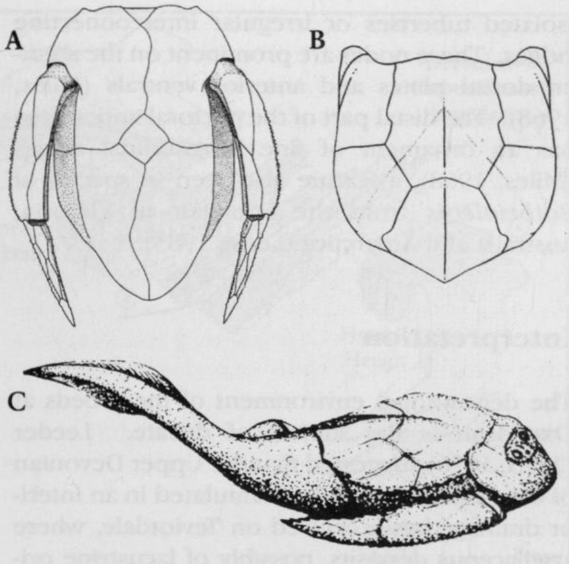



**Figure 8.6** The antiarch *Bothriolepis hayi* Miles (1968) from the Oxendean Beds of Oxendean Burn. (A) restoration of the trunk-armour in ventral aspect based on RSM 11967.34.43 and FR 1867, × 0.2; (B) restoration of the dorsal trunk armour, somewhat flattened, based on RSM 1967.34.16, × 0.2 (after Miles, 1968); (C) reconstruction of *Bothriolepis* (after Long, 1995), × 0.42.

gritty bands within pale pink and buff fine-grained sandstones. Waterston's (1962) lower fish bed was not observed in 1979, and may lie in a gap, as noted above.

### *Fauna*

Placodermi: Antiarchi: Bothriolepidae
*Bothriolepis hayi* Miles, 1968
Osteichthyes: Sarcopterygii: Porolepiformes: Holoptychiida
*Holoptychius* sp.

The horizons yield numerous plates of *Bothriolepis hayi*. The specimens are mainly detached plates, plus a few articulated individuals, these latter being slightly crushed and distorted. *Bothriolepis hayi* is one of several species recorded from the Berwickshire area by Miles (1968). It was a moderate-sized *Bothriolepis* with trunk armour 150 mm long and a broad, moderately high shield (Figure 8.6). All the material described by Miles (1968) was from individuals of a similar size, interpreted as full-grown adults. *Bothriolepis hayi* is distinguished from other species of *Bothriolepis* by its ornament; the reticular network is broken up by prominent round-topped nodes that may be isolated tubercles or irregular interconnecting ridges. These nodes are prominent on the median dorsal plates and anterior ventrals (Miles, 1968). The distal part of the pectoral appendage has an ornament of fine longitudinal ridges (Miles, 1968), a feature also seen in species of *Bothriolepis* from the Frasnian of Victoria, Australia and Antarctica (Long, 1983).

## Interpretation

The depositional environment of these beds at Oxendean is the subject of debate. Leeder (1973, 1976) suggested that the Upper Devonian of the Scottish Borders accumulated in an interior drainage basin centred on Teviotdale, where argillaceous deposits, possibly of lacustrine origin, occur in the sequence. On the other hand, Paterson *et al.* (1976) considered that the deposits were those of a wide alluvial plain of an easterly flowing river system.

Waterston (1962) interpreted the 'lower fish bed' as having been deposited *in situ* by the killing of fish in a drying pool whereas the contents of the 'upper fish bed' are thanatocoenose (derived) material that has been sorted and stream transported some distance.

*Bothriolepis* has a broad stratigraphical value. In northern Europe, the Middle Devonian *Asterolepis* is replaced by the Late Devonian *Bothriolepis*. However, in the Baltic area, they occur together in an overlapping zone, and in south China *Bothriolepis* is found in much earlier sediments, whereas *Asterolepis* persists well into the Late Devonian (Dineley and Loeffler, 1993, fig. 6.10).

It is difficult to determine the relative stratigraphical relationships of the Berwickshire Upper Old Red Sandstone faunas. Oxendean appears to lie at the same level as the Prestonhaugh Beds on the Whiteadder that yield *Bothriolepis stevensoni* (Miles, 1968). These units have been dated as Famennian, but the evidence is limited (Westoll, *in* House *et al.*, 1977).

## Conclusion

The conservation value of Oxendean Burn results from its production of abundant fossil fish specimens from two or three horizons. The sedimentary environments of these are debated, but they were clearly shallow water and probably lacustrine or associated with fluvial backwaters. Specimens of *Bothriolepis* and *Holoptychius* are fairly common, and fresh excavations may yield much new material.

# HAWK'S HEUGH (NT 790714)

## Highlights

Hawk's Heugh in Border is the only place where British examples of the antiarch *Remigolepis* have been found, and it is therefore important for comparison with sites in East Greenland and Australia that have also yielded this genus. It is also intriguing as a pointer to the possibility of finds of early tetrapods, because elsewhere *Remigolepis* is associated with tetrapod remains.

## Introduction

Hawk's Heugh, on the coastline some 10 km south-east of Dunbar, falls within an extensive, continuous sequence from Upper Devonian to Lower Carboniferous. The geology of the vicinity has been described by George *et al.* (1976). Prof. Sir Frederick Stewart discovered there in 1957 a large bone of *Remigolepis*, an antiarch described originally from Greenland by Stensiö (1931), and this was taken as a hint that tetrapod remains also might occur there, since *Remigolepis* is associated with similar tetrapod remains in Greenland (Andrews, 1978). However, the chances of finding tetrapods in the Pease Bay Beds are small because the fish-bearing bed itself is thin and poorly exposed. There is some doubt locally as to the position of the base of the Carboniferous System and also as to whether the *Remigolepis* horizon might be younger than Devonian. A field guide to the vicinity was provided by Grieg and Davies (*in* Allen and Williams, 1978; Figure 8.7).

## Description

Reddened sandstones and pedocals of Old Red Sandstone facies alternate with sandstones, shales and limestones of the Cementstones (George *et al.*, 1976). The Upper Old Red Sandstone in Pease Bay is cross-bedded, and the grains are well rounded. There are some 350 m of red clastics in this group, the middle part of

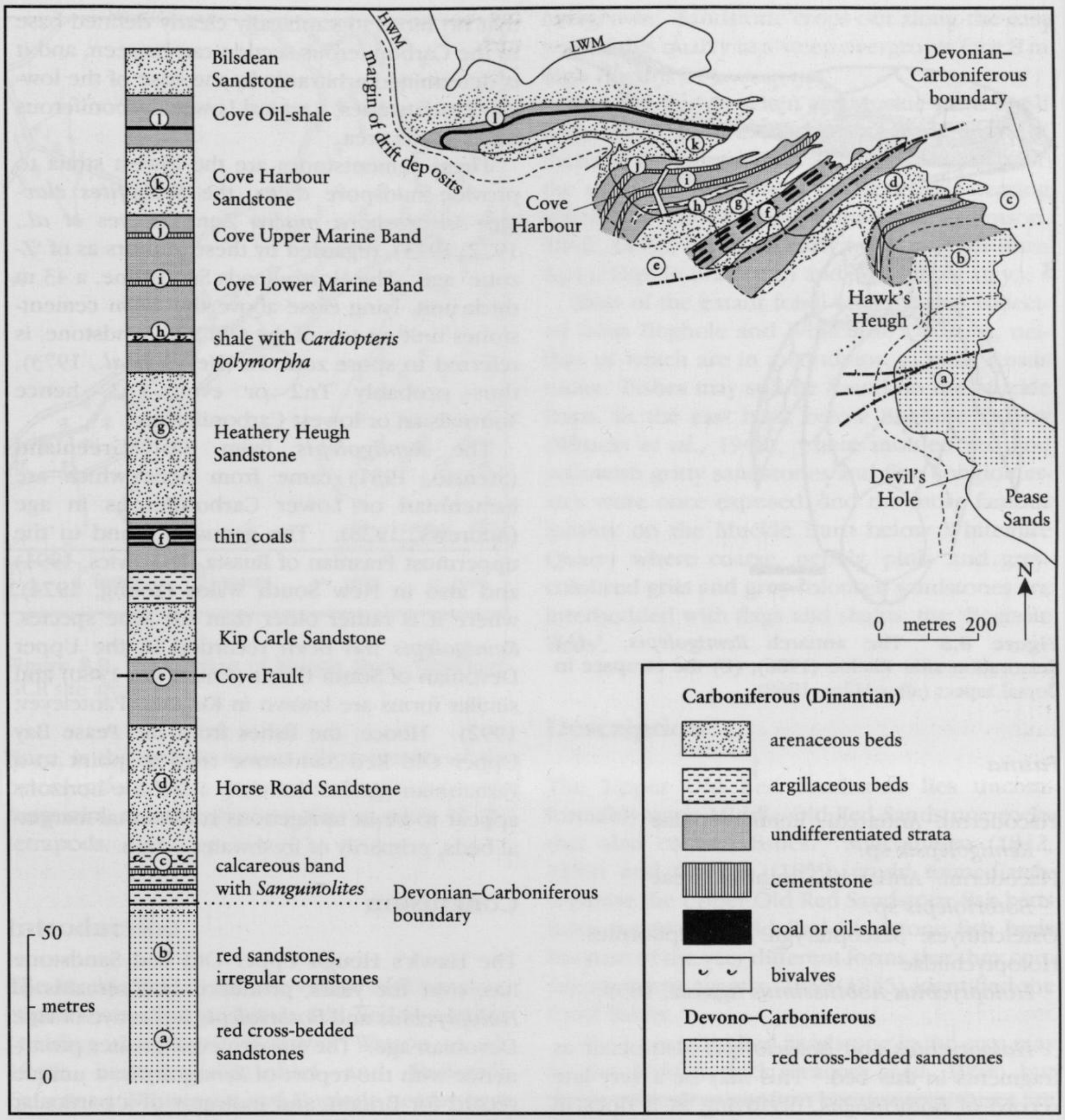



**Figure 8.7** Geological sketch map and section of the Hawk's Heugh (GCR site) coastline (after Greig and Davies, 1978).

which has previously yielded scales of *Holoptychius nobilissimus* in abundance. The Old Red Sandstone passes up into the Cornstone Group, which in turn passes up into Lower Carboniferous cementstones that are rich in plant fragments.

The *Remigolepis* plate was found in a loose block of intraclast conglomerate lithologically comparable to a bed in the cliff above about 6 m below the top of the Cornstone Group at the top of the 'Old Red Sandstone'. The lithology is described as sandstone containing clay galls and lumps of dark calcareous material (Andrews, 1978). The specimen is the anterior median dorsal plate of a large individual. It is 190 mm long, compared to 140 mm in its closest relative, R. *acuta*, from Greenland (Stensiö, 1931). The animal was probably some 330 mm in overall length. *Remigolepis*, assigned to the Family Asterolepidae (Gross, 1965; Denison, 1978), is characterized by the lack of a joint in the pectoral appendage, because of which it was often assigned to its own family or even order, but this is not commonly done now (Figure 8.8).

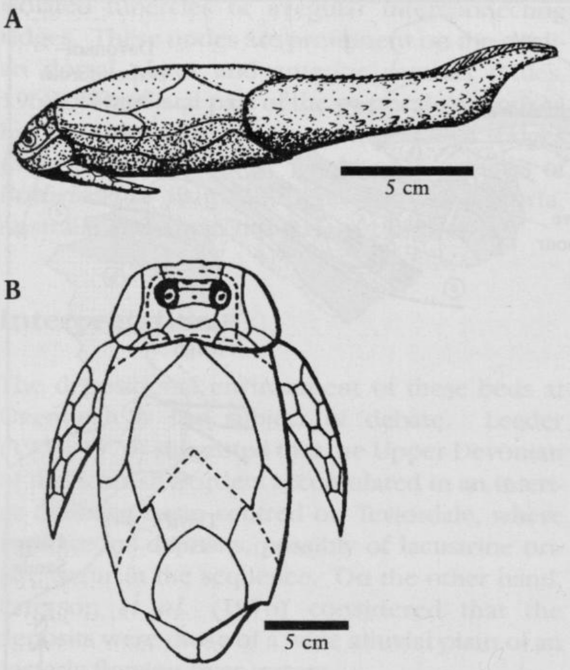



**Figure 8.8** The antiarch *Remigolepis.* (A) Restoration after Ritchie (1986); (B) the carapace in dorsal aspect (after Miles, 1968).

### *Fauna*

Placodermi: Antiarchi: Remigolepidae
*Remigolepsis* sp.
Placodermi: Antiarchi: Bothriolepidae
*Bothriolepis* sp.
Osteichthyes: Sarcopterygii: Porolepiformes: Holoptychiidae
*Holoptychius nobilissimus* Agassiz, 1839

*Holoptychius* and *Bothriolepis* also occur as fragments in this bed. This may be a very late record of *Bothriolepis*, occurring as it does in terminal Devonian beds. *Bothriolepis nielseni* from the East Greenland *Remigolepis* Series is the stratigraphically highest *Bothriolepis* known (Denison, 1978).

## Interpretation

The age of the fish-bearing beds is not clear. The Upper Old Red Sandstone in Pease Bay, source of rare *Holoptychius* scales and of *Remigolepis*, is overlain by 17 m of cementstone and shale with cementstone conglomerate, the Eastern Hole Conglomerate, which is arbitrarily taken to be the basal unit of the Carboniferous (Craig, *in* Craig and Duff, 1975, p. 113). The problem is that no biostratigraphically clearly defined base to the Carboniferous section can be seen, and it is determined arbitrarily by the base of the lowest cementstones, a typical Lower Carboniferous facies in the area.

These cementstones are the lowest strata to provide miospore dates, the *Schopfites claviger–Aurorospora macra* Zone (Neves *et al.*, 1972, 1973), regarded by these authors as of 'Z-zone' age. The Horse Roads Sandstone, a 43 m thick unit, lying close above the 17 m cementstones unit on top of the Old Red Sandstone, is referred to spore zone Pa (Neves *et al.*, 1973), thus probably Tn2 or even Tn3, hence Tournaisian or lowest Carboniferous.

The *Remigolepis* from East Greenland (Stensiö, 1931) came from beds which are Famennian or Lower Carboniferous in age (Andrews, 1978). The genus is found in the uppermost Frasnian of Russia (Luksevics, 1991) and also in New South Wales (Young, 1974), where it is rather older than the type species. *Remigolepis* has been recorded in the Upper Devonian of South China (Pan *et al.*, 1980) and similar forms are known in Kirgizia (Panteleyev, 1992). Hence, the fishes from the Pease Bay Upper Old Red Sandstone tend to point to a Famennian age for the unit. All these horizons appear to be in terrigenous continental-marginal beds, primarily of freshwater origin.

## Conclusion

The Hawk's Heugh Upper Old Red Sandstone has, over the years, produced rare remains of *Holoptychius* and *Bothriolepis* indicative of Late Devonian age. The site achieved greater prominence with the report of *Remigolepis*, a unique record for Britain, and indicator of a particular facies, already noted in Greenland and Australia as bearing some of the most ancient tetrapods. The importance of the site rests in the potential for future discoveries at this coastal site, including more *Remigolepis* material.

# BOGHOLE, MUCKLE BURN (NH 972549)

## Highlights

Several sites along Muckle Burn in Highland have been the source of a rich fauna of up to 17 species of fossil fishes. Boghole, on the Muckle

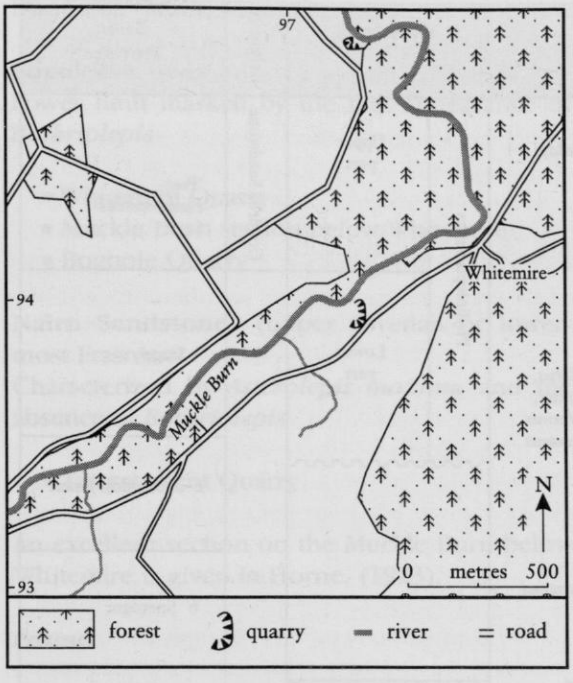



**Figure 8.9** Sketch map of Muckle Burn–Whitemire GCR site area.

Burn, is the unique source of specimens of the osteolepiform sarcopterygian *Eusthenopteron traquairi*, a form close to the ancestry of the tetrapods.

## Introduction

The Muckle Burn, near the village of Whitemire, exposes a section of Upper Old Red Sandstone (yielding *Asterolepis maxima*; Watson *et al.*, 1948) between Glenshiel and Earlsmill. Quarries at Whitemire and Boghole nearby have in the past supplied famous collections of fossil fishes. A stream section near Whitemire has also yielded fossils. Altogether, these localities present a good series of exposures yielding different faunas that illustrate a change from uppermost Middle Devonian at Boghole and Tarrywarrant, to lowermost Upper Devonian at Whitemire and above (House *et al.*, 1977, pp. 80–2).

Tarrywarrant Quarry (NH 970536) is almost completely filled in, with no exposure today. Boghole (NH 972549) is now an overgrown indentation in the steep bank of Muckle Burn with no exposure, although rock cannot be far below the soil cover. Whitemire (NH 972540) is a large quarry which is partially filled and very overgrown. Sandstone crops out along the east wall of this quarry in a steep overgrown face 8 m high (Figure 8.9).

It is not known when the Muckle Burn fossil beds were discovered. Malcolmson knew of them in 1839, and he was the first to describe the threefold division of the vertebrate-bearing strata in the Moray and Nairn area (Malcolmson, 1842, 1859), based on early work at Tynet Burn (q.v.), Dipple Brae (q.v.) and Scaat Craig (q.v.).

Most of the extant fossil material was collected from Boghole and Whitemire Quarries, neither of which are in a condition to yield fossils today. Fishes may still be found on the Muckle Burn, in the east bank below Boghole Quarry (Watson *et al.*, 1948), where mottled red and yellowish gritty sandstones and fine conglomerates were once exposed, and the more famous locality on the Muckle Burn below Whitemire Quarry where coarse, pebbly, pink- and grey-coloured grits and grey-coloured sandstones are interbedded with flags and shales, the 'Boghole Beds'.

## Description

The Upper Old Red Sandstone lies uncomformably upon Middle Old Red Sandstone rocks that also contain fishes. Malcolmson (1842, 1859) and Gordon (1859) could immediately separate the Upper Old Red Sandstone fish beds from the Middle Old Red Sandstone fish beds because of the very different forms that they contained; Louis Agassiz (1833–1845) identified the fossil fishes.

The Upper Old Red Sandstone in the area may be about 450 m thick (Peacock *et al.*, 1968), but this is difficult to confirm because exposures are limited. Most of the rocks are sandstones, rarely red, and more commonly grey, pink, yellow, buff or reddish brown, and sometimes with green reduction mottling. Some beds are pebbly, and conglomerate occurs locally in lenses. Here and there are thin greenish mudstones, and red, brown and green mudstone intraclasts are common. Cross-bedding indicates transport generally south-east and south-west from the Highlands. Pedocals ('cornstones') commonly occur, these being ancient calcrete soil horizons indicating emergent conditions in a tropical climate.

A stratigraphical sequence has been established through the Upper Devonian of Highland

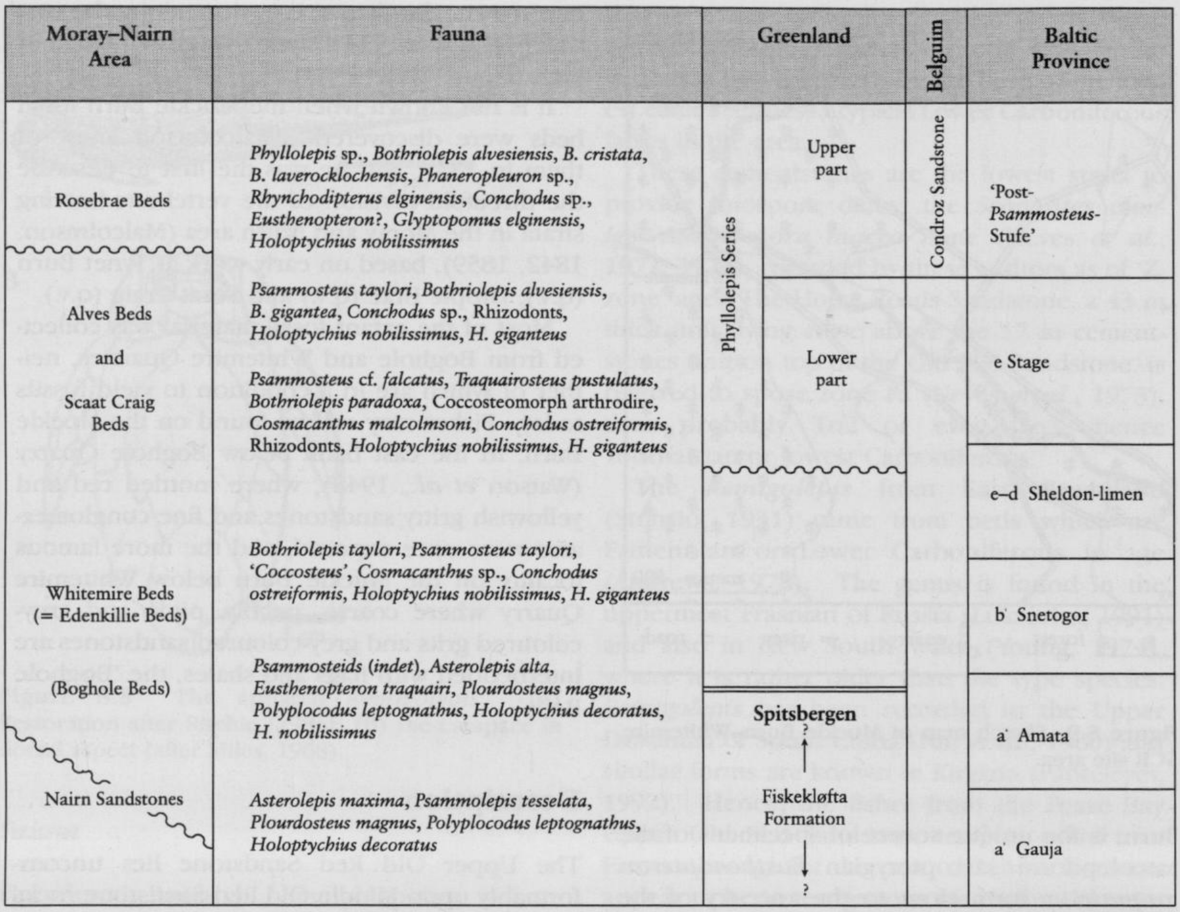



**Figure 8.10** Suggested correlation of the Upper Old Red Sandstone of the Moray–Nairn area with the successions in Greenland, Spitsbergen, Belgium and the Baltic Province (after Miles, 1968; Westoll, 1977).

based on fish faunas (Traquair, 1897a, 1905a, 1905b; Westoll, 1951, *in* House *et al.*, 1977; Figure 8.10). The Nairn Sandstones are characterized by *Asterolepis maxima* and the absence of *Bothriolepis*. The overlying Alves and Scaat Craig Beds include *Bothriolepis major* and other species, and *Holoptychius*. Traquair's highest unit, the Rosebrae Beds, contains *Phyllolepis concentrica* and *Glyptopomus minor*, among others. The two lower units appear to coalesce in the Elgin–Forres area, since *Asterolepis* and *Bothriolepis* are found together at Boghole (Muckle Burn), as well as at Whitemire and on the Findhorn, a unit termed by Westoll (1951) the Boghole Beds.

These divisions were further discussed by Tarlo (1961a), Miles (1968), Peacock *et al.* (1968) and Westoll (*in* House *et al.*, 1977), and the chrononstratigraphical situation appears somewhat complex. The Rothes and Heldon Hill faults separate three outcrops of Upper Old Red Sandstone in the Elgin–Nairn area. The uppermost unit, the Rosebrae Beds, rests with minor unconformity directly on the Alves Beds in the west, and on a new unit, the Cornstone Beds, in the east. The Cornstone Beds overlie, and interdigitate with, the Scaat Craig Beds. Hence the Scaat Craig Beds and the Cornstone Beds together, in the east, are approximate lateral equivalents of the Alves Beds in the west. Below these are the Boghole Beds, and below them, in the farthest west of the area, the Nairn Beds. These two lower units seem to merge in the Elgin–Forres area: Miles restricted the term Boghole Beds to the lower part of Westoll's (1951) usage, the units that lack *Bothriolepis*. He also introduced the term Edenkillie Beds for the upper part, with *B. taylori*, and terminating at the base of the Alves Beds where *B. gigantea* makes its appearance.

Stratigraphical relationships in the Muckle

Burn area (Miles, 1968) are:

**Edenkillie Beds**
Lower limit marked by the first appearance of *Bothriolepis*

- Whitemire Quarry
- Muckle Burn section below Whitemire
- Boghole Quarry

**Nairn Sandstone** (upper Givetian or lowermost Frasnian)
Characterized by *Asterolepis maxima* and the absence of *Bothriolepis*

- Tarrywarrent Quarry

An excellent section on the Muckle Burn below Whitemire is given in Horne, (1923).

***Fauna***

The faunal assemblages from each of the sites, based on Miles (1968), are listed below. Abbreviations are: T, Tarrywarrant; B, Boghole; M, Muckle Burn below Whitemire; W, Whitemire Quarry; N, Nairn Sandstones; E, Edenkillie Beds.

AGNATHA
Heterostraci: Psammosteiformes:
Psammostiidae
*Psammosteus taylori* Traquair, 1897 W, N, E
Psammosteid indet. B, M, N

GNATHOSTOMATA
Placodermi: Antiarcha: Bothriolepidae
*Bothriolepis taylori* Miles, 1968.
Type locality W, E
*'Asterolepis maxima'* Agassiz, 1845 T, N
*'A. alta'* Traquair, MS. ?Only locality B, N
*A.* sp. M, N
Placodermi: Arthrodira: Coupteidae
*Plourdosteus magnus* (Traquair, 1895)
B, M, N
*P.* sp. (cf *magnus*) W, E
Arthrodira indet.
*Cosmacanthus* sp. W, E
Osteichthyes: Sarcopterygii: Dipnoi: Dipterida
*Conchodus* sp.
*Conchodus ostreiformis* M'Coy, 1848 W, E
Osteichthyes: Sarcopterygii: Osteolepiformes
*Psammolepis* ? sp. T, N
*Polyplocodus leptognathus* Traquair,1923
B, N
*Polyplocodus* ? M, N
*Eusthenopteron traquairi* Westoll, 1937
Type and only locality B, N
Osteichthyes: Sarcopterygii: Porolepiformes:
Holoptychidae
*Holoptychius nobilissimus* Agassiz,1839
B, N, E
*H. decoratus* Eichwald, 1846 B, N
*H. giganteus* Agassiz,1845 W, E

The occurrence of the heterostracan *Psammosteus taylori* Traquair was given by Traquair (*in* Horne, 1923), but no material was described and Miles (1968) could trace none.

Stensiö (1948) predicted that the *Bothriolepis* remains from Whitemire, usually referred to *B. major*, would prove to be a new species, and indeed Miles (1968) established the species *B. taylori* for this material. It is the oldest bothriolepid from the Moray Firth area, and probably also from Scotland. It is closely related to *B. gigantea*, which is found at many sites in the overlying Alves Beds.

The holotype of *Asterolepis maxima* Agassiz, 1845 is said to come from Boghole, although all other specimens are from Kingsteps, Nairn. There are no obvious differences between the asterolepids from these two places, although Traquair (MS) erected the new species *A. alta* on the basis of specimens from Boghole. Miles (1968) retained '*A. alta*' to distinguish this species from those more usually called *A. maxima*, and a more formal solution to this problem is still required.

*Plourdosteus magnus* (Traquair, 1895) was named as a species of *Coccosteus*, for material from Kingsteps, Nairn. The genus was founded by Ørvig (1951) on Upper Devonian fossils from Escuminac, Canada, and it also occurs in the Upper Old Red Sandstone of the Baltic region. The arthrodire *Cosmacanthus* sp. was recorded by Traquair (*in* Horne, 1923), but has not been confirmed (Miles, 1968).

The osteolepiform sarcopterygian *Polyplocodus leptognathus* was identified by Traquair (*in* Horne, 1923), but Miles (1968) states that the name *Polyplocodus* should not be applied to this particular form.

*Eusthenopteron* was established by Whiteaves (1881, 1886) for *E. foordi* Whiteaves, 1881 from the Upper Devonian of Escuminac Bay, Canada. *Eusthenopteron traquairi* Westoll, 1937 is a new species based on a single fronto-ethmoid shield and fragments of head bones in the RSM.

Boghole is the type, and possibly only locality. Westoll (1940) described *E.* cf. *traquairi* from the Rosebrae Beds, but Jarvik (1952) suggested that this specimen might be similar to *E. dalgleisiensis* (Anderson) from Dura Den, Fife (Anderson, 1859). The dipnoan *Conchodus ostreiformes* is present amongst specimens in the RSM.

## Interpretation

Westoll (1978) argued that the Nairn and Boghole beds were late Givetian in age, and hence latest Mid-Devonian. However, the Boghole Beds are usually dated as early Frasnian, and hence basal Late Devonian (Westoll, *in* House *et al.*, 1977; Friend and Williams, 1978), close to the Mid–Late Devonian boundary (Marshall and Allen, 1982), and perhaps equivalent in age to the Sumburgh Head (q.v.) and Bressay fish beds in the Shetland Middle Old Red Sandstone Basin.

*Eusthenopteron* appears in the succession at the same time as *Bothriolepis*, not only in Scotland, but also in Escuminac Bay, Canada, and the Baltic area. Westoll (1937) suggested that this assemblage might represent a zonal index. *Bothriolepis* is useful biostratigraphically since it occurs in late Devonian continental deposits of ancient Laurasia and all the Gondwana continents (Denison, 1978) and has over 100 species (Dineley and Loeffler, 1993).

Andrews and Westoll (1970a) suggested that *Eusthenopteron traquairi* resembled the pike (*Esox*) in its aquatic mode of life, and that it may also have been capable of short journeys 'walking' overland using the pectoral fins as limbs. They averred that in *Ichthyostega* the paired limbs developed to manoeuvre in confined spaces in water, and also to move about on land for short periods of time, possibly while searching for new waters. Locomotion out of the water was perhaps prompted by reasons such as drying up the pools, anoxia in the waters or predator pressure.

The vertebrate fauna of the Upper Old Red Sandstone is typified in the sites mentioned above and others support a correlation with areas in Greenland, Spitsbergen and mainland Europe (Figure 8.10). The late Devonian vertebrate (fishes) fauna was effectively cosmopolitan throughout the Euramerican Province, and generally similar worldwide.

## Conclusion

The fish-bearing bands exposed in the Boghole Beds at Boghole have yielded an important earliest Late Devonian (Frasnian) fauna. The conservation value lies in the diversity of the fauna with over 15 species of placoderms, acanthodians and sarcopterygians. Specimens have come to light from many quarries and stream sections in the area. Unfortunately, the quarries are no longer extant, but the stream exposures still produce specimens, and could be excavated for more substantial studies.

# SCAAT CRAIG (NJ 237568)

## Highlights

The Scaat Craig site in Highland is an isolated exposure of Upper Old Red Sandstone that has yielded a unique fauna of fish scales and bone fragments, and is the type locality for three species, and a number of tetrapod-like bones have been reported recently (Ahlberg, 1991, 1995), the first material evidence (as distinct from trackways) in Britain of such advanced vertebrates in the Devonian (Chapter 15).

## Introduction

'Scaat Craig' was originally the name of a knoll in the valley of the Longmorn Burn, south-east of Elgin, long since overgrown and indistinguishable. There are two exposures, the first behind the garden of 'Greenbank' house at NJ 237568, the second 300 m away opposite the railway bridge (Figure 8.11).

The discovery of the site, the first source of Old Red Sandstone fishes in the Moray Firth area in 1826, and the early years of collection at Scaat Craig by Mr John Martin, of the Elgin Institution, were eloquently recorded by Patrick Duff (1842, pp. 27–8), a local enthusiast.

Scaat Craig received a famous visit by J. Malcolmson and Patrick Duff, in 1838, but they did not collect anything. Although unsuccessful on his first visit to Scaat Craig, Malcolmson took to London some specimens that had previously been collected, and they caused great excitement when exhibited at the Geological Society. A tooth was immediately figured in Murchison's *Silurian System* (1839). Later in 1838

Malcolmson took specimens from here and from Cromarty to show to scholars on the continent, and a little later he went on to discover the Middle Devonian fish beds at Dipple Burn (q.v.), Tynet Burn (q.v.), Lethen Bar and Clune in 1838 and 1839. J.G. Malcolmson (1842, 1859), Gordon (1859) and A.G. Malcolmson (1921) noted that the Scaat Craig beds could not be traced laterally owing to the thickness of drift cover.

Malcolmson gave Richard Owen in London some Scaat Craig teeth, for which he (Owen, 1840–1845) erected six species of a new genus, *Dendrodus*, (*D. biporcatus*, *D. strigatus*, *D. sigmoideus*, *D. compressus*, *D. latus* and *D. incurvus*) so called because of microscopic plant-like ramifications seen in cross-section. Owen thought them to be fish teeth, and suggested that *Dendrodus* might have linked some extinct group of fishes with the labyrinthodonts. Patrick Duff (1842, p. 30) and Hugh Miller (1858) realized that these tooth taxa probably referred to specimens already named from their scales from Scaat Craig. Duff (1842) was also first to figure fish specimens from Scaat Craig, later described by Agassiz (1844–1845), such as *Cosmacanthus malcolmsoni*.

The date of the discovery of the site is important because it was so early; it predated Hugh Miller's finds on Cromarty (Miller, 1830). Gordon (1859) and Horne (1923) suggested that fossil fishes were first found at Scaat Craig in 1836, but this later date seems unlikely, because by 1838 there was enough material already collected for it to be distributed around Europe by J.G. Malcolmson, and it contradicts Duff's (1842) account. Oddly, however, the same John Martin who first collected at Scaat Craig, later (Martin, 1837) failed to mention any organic remains from these strata.

Agassiz (1835, 1844–1845) figured material from Scaat Craig in the first systematic work on fossil fishes. Other early workers who described or mentioned the site include Duff (1842), Roberts (1863), Traquair (1888a), Taylor (1910) and Mahood and Spriggs (1919). Important early collections were made by Duff, Malcolmson, Brickenden (now in NHM), Grant, Jenkins, Gordon and the Elgin Museum (Malcolmson, 1859; Traquair, 1895). More recently, tetrapod-like bones have been recognized in collections from this site, thus pushing back the earliest record for a stem-tetrapod to the Frasnian (Ahlberg, 1991, 1995).

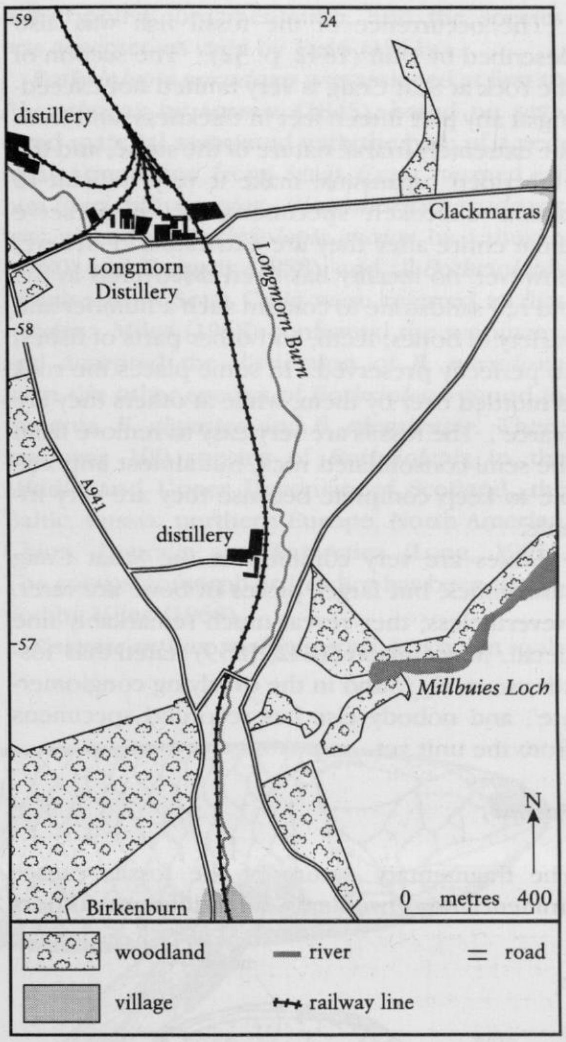



**Figure 8.11** Scaat Craig GCR site sketch map.

## Description

The strata at Scaat Craig are bright red, grey and yellow, coarse, friable, pebbly sandstones, rich in scales and fish fragments, and which overlie conglomeratic sandstones. The site is now rather overgrown, but Duff (1842, p. 28) described it when it was much clearer: 'The deposit at Scat Craig ... (being) composed of soft sandstone and conglomerates, passing from coarse to the fine grained; but even the coarsest conglomerate of Scat Craig, containing rounded masses, larger than a hen's egg, of granite, gneiss, graywacke, mica slate and augite, embedded in a calcareous cement, are not of the oldest conglomerate, as is proved by isolated masses of a still older brecciated conglomerate being found embedded in it.' (Figure 8.11).

The occurrence of the fossil fish was also described by Duff (1842, p. 32): 'The section of the rock at Scat Craig is very limited not exceeding at any part fifteen feet in thickness; and from the extremely friable nature of the stone, and the embedded organisms, make it very difficult to obtain unbroken specimens, or to preserve them entire after they are extricated. I believe, however, no locality has been discovered in the old red sandstone to contain such a number and variety of bones, teeth, and other parts of fishes, so perfectly preserved. In some places the rock is mottled over by them, while at others they are scarce'. The fossils are very easy to remove from the semi-consolidated rock, but almost impossible to keep complete because they are very friable.

Scales are very common in the Scaat Craig sandstones, but larger pieces of bone are rarer. Nevertheless, they reveal much remarkably fine detail. Malcolmson (1842, 1859) stated that 'fossils are rarely found in the overlying conglomerate', and nobody else has recorded specimens from the unit yet.

### *Fauna*

The fragmentary nature of the fossils causes nomenclatural problems, with different authors assigning different names to isolated scales, plates and bone fragments, and faunal lists for Scaat Craig by different authors may differ substantially. The faunal list given here is that of Miles (1968):

AGNATHA
Heterostraci: Psammostiformes:
Psammosteidae
*Psammosteus* cf. *falcatus* Gross, 1942
*Traquairosteus pustulatus* (Traquair, 1897).
Type (and ?only) locality

GNATHOSTOMATA
Placodermi: Antiarchi: Bothriolepidae
*Bothriolepis paradoxa* (Agassiz, 1845)
Type locality
Placodermi: Anthrodira indet.
Coccosteomorph arthodire indet.
*?Cosmacanthus malcolmsoni* Agassiz, 1845
[Not an acanthodian, Denison 1979, p. 58]
Type and only locality
Osteichthyes: Sarcopterygii: Osteolepiformes
Rhizodonts indet.
Osteichthyes: Sarcopterygii: Porolepiformes
*Holoptychius nobilissimus* Agassiz, 1839
*H. giganteus* Agassiz, 1845
*?H. decoratus* Eichwald, 1846

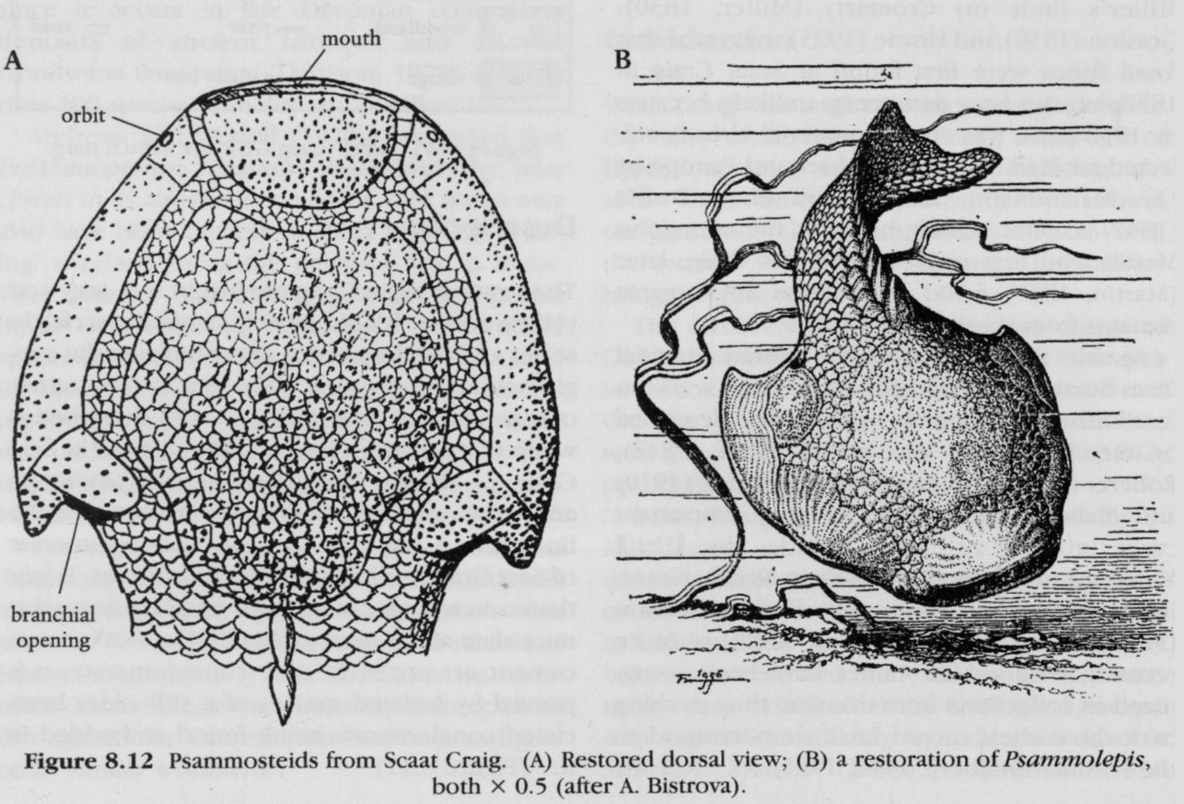



**Figure 8.12** Psammosteids from Scaat Craig. (A) Restored dorsal view; (B) a restoration of *Psammolepis*, both × 0.5 (after A. Bistrova).

Dipnoi: Dipteridae
*Conchodus ostreiformis* M'Coy, 1848
Type locality.

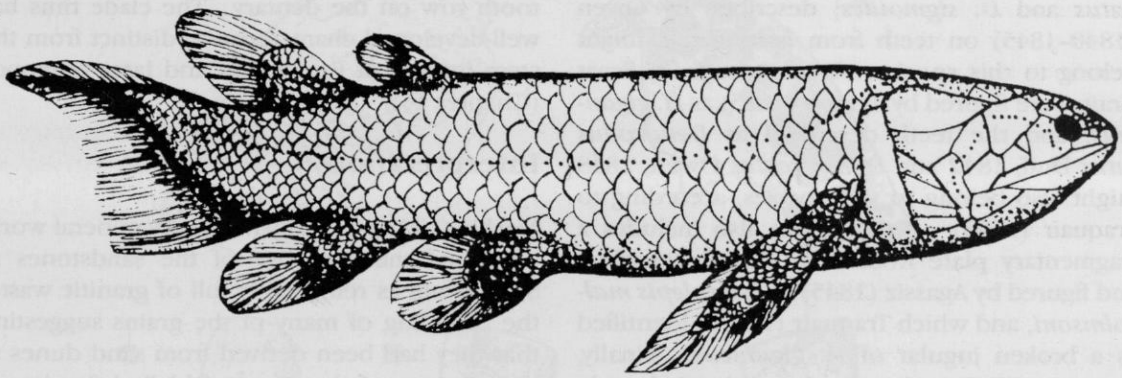
TETRAPODA: Elginerpetontidae
*Elginerpeton pancheni* Ahlberg, 1995
Type and only locality.

Psammosteid heterostracans (Figure 8.12) are represented by several specimens from Scaat Craig. The record of *Psammosteus* cf. *falcatus* is based on the abraded distal tip of a branchial plate, described by Traquair (1895) as *Psammosteus* sp., and redescribed by Tarlo (1961a) and Miles (1968). *Psammosteus falcatus* is known from the Upper Devonian of Ellesmere Island, Central Poland and Timan, where its short time range makes a useful zone fossil. *Traquairosteus pustulatus* was assigned to *Psammosteus* by Traquair (1897a), based on psammosteid plate fragments from Scaat Craig with a distinctive 'rippled' ornamentation, and the species was accepted as valid by Tarlo (1961a).

*Bothriolepis paradoxa* was assigned at first to *Placothorax* by Agassiz (1845), based on scattered material associated with the base of a pectoral appendage from Scaat Craig, termed by him *Pterichthys major*. *Placothorax paradoxus* was placed in *Bothriolepis major* by Lahusen (1880) and Traquair (1888), and all *Bothriolepis* remains from Scaat Craig were referred to that species. Miles (1968) confirmed the synonymy, and accepted the distinction of *B. paradoxa* from the other species of *Bothriolepis* found in the area, *B. gigantea* and *B. alvesiensis*. There are over 100 species of *Bothriolepis* in the Middle and Upper Devonian of Scotland, the Baltic, Russia, northern Europe, North America, China, Australia and Antarctica (Long, 1995). The coccosteomorph arthrodire has been identified by Miles (1968).

*Cosmacanthus malcolmsoni* is known only

A



B

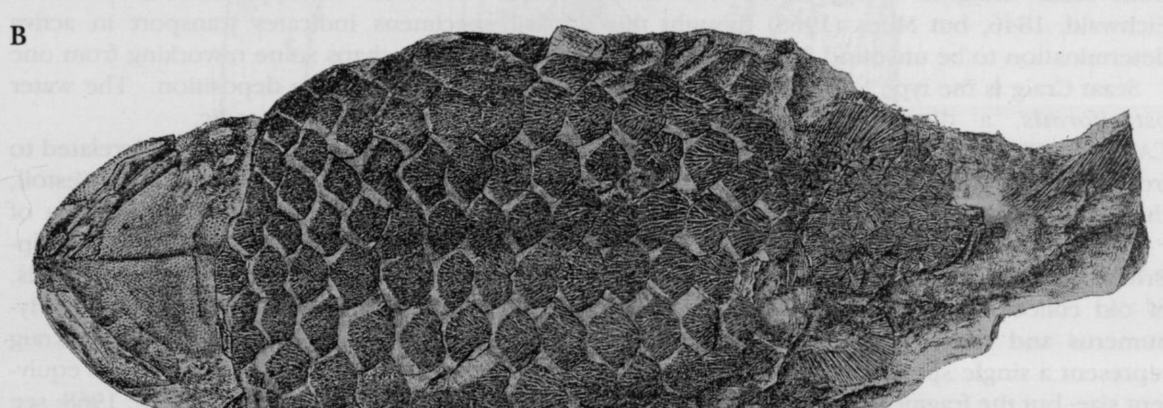


**Figure 8.13** (A) *Holoptychius nobilissimus* Agassiz, a restoration from Scaat Craig, × 0.2; (B) *Holoptychius* specimen from Classbinnie, Perthshire, figure in ventral aspect, × 0.3 (after Murchison, 1872).

from three pieces of spine from Scaat Craig. The holotype was presumably found and figured by Duff (1842, pl. 7, fig. 5), before the formal description of Agassiz (1845, p. 121, pl. 33). A current view is that the specimens may be placoderm spinals resembling Phylctaeniidae, and the taxon is listed under 'Arthrodira *incertae sedis*' by Denison (1978, 1979). This referral is based on a third specimen discovered by Traquair (1897a, pp. 381–2, pl. 10, figs 2, 3) in the Brickenden Collection at the NHM. Only new material of this species can resolve the argument.

Rhizodonts indet., recorded by Miles (1969), include jawbones described as *Polyplocodus* sp. by Traquair (1895) and loose teeth which he referred to *Sauripteris crassidens*, both identifications considered doubtful by Miles.

Scattered scales of *Holoptychius nobilissimus* Agassiz, 1839 are common at Scaat Craig. Traquair (1895) suggested that *Dendrodus strigatus* and *D. sigmoides*, described by Owen (1840–1845) on teeth from Scaat Craig, might belong to this species. Two scales from Scaat Craig were figured by Agassiz (1845) as *H. giganteus*, and the teeth described as *Dendrodus latus* Duff, 1842 and *D. bifurcatus* Owen, 1848 might also belong to this species, according to Traquair (1895). This species also includes a fragmentary plate from Scaat Craig, described and figured by Agassiz (1845) as *Asterolepis malcolmsoni*, and which Traquair (1897a) identified as a broken jugular of H. *giganteus*. Finally, Traquair (1897a) described an abraded scale from Scaat Craig as *Holoptychius decoratus* Eichwald, 1846, but Miles (1968) thought this determination to be unsound (Figure 8.13).

Scaat Craig is the type locality for *Conchodus ostreiformis*, a dipnoan palatal tooth (in CAMSM). Westoll (1951) recorded this species from the Rosebrae Beds, but Miles (1968) noted that the record is undocumented.

Ahlberg (1991) reported the earliest known British tetrapod, on the basis of re-examination of old collections from Scaat Craig. A tibia, humerus and some incomplete jaws possibly represent a single species, all being of a consistent size; but the fragmentary nature of the specimens makes it impossible to link together these isolated bones, which all show tetrapod, or very tetrapod-like features. The tibia represents the earliest tetrapod-like hind limb, comparable to specimens from the lower Famennian of Greenland.

More recently collecting at Scaat Craig has produced some 13 taxonomically different unique and phylogenetically specimens (lodged in RSM, NHM, BGS(GSM), OUM and LEICSM) studied by Ahlberg (1995). *Elginerpeton pancheni* (Figure 8.14) is represented by jaw fragments and possibly by limb and pelvic remains. Ahlberg accepts them as evidence of a clade (including *Obruchevichthys* from the late Frasnian of Latvia and Russia) that is the sister group of all other tetrapods. This new genus was a large tetrapod with overall jaw length of 400 mm. The coronoid teeth are only slightly larger than the marginal and a premaxilla indicates a narrow triangular skull. Overall the animal may have resembled *Ichthyostega*, but no hand or feet bones are known.

Ahlberg (1995) places *Elginerpeton* in a new stem group of tetrapods, differing from all other known Devonian tetrapods in its rounded infradentary margins and in having an accessory tooth row on the dentary. The clade thus has well-developed characteristics, distinct from the stem lineage of Famennian and later tetrapods (Chapter 15).

## Interpretation

Mackie (1902), a pioneer of heavy mineral work, described the character of the sandstones at Scaat Craig as remarkably full of granitic waste, the rounding of many of the grains suggesting that they had been derived from sand dunes at the margins of the Upper Old Red Sandstone basin. The water-worn appearance of numerous fossil specimens indicates transport in active streams and perhaps some reworking from one site to another prior to deposition. The water flow was powerful and episodic.

The Scaat Craig Beds have been correlated to late Frasnian equivalents in the Baltic (Westoll, *in* House *et al.*, 1977). The determination of *Psammosteus falcatus* led Tarlo (1961a) to separate the Scaat Craig Beds from the Alves Beds, placing them between the Alves and the overlying Rosebrae Beds. However, the Scaat Craig Beds are more usually considered a facies equivalent of the Alves Beds (Peacock *et al.*, 1968; see also Muckle Burn account). *Bothriolepis paradoxa* together with *Holoptychius*, occurs at one other locality, Redhall Quarry, Fochabers, and this is therefore correlated with the Scaat Craig Beds.

The abundance of vertebrate remains collect-

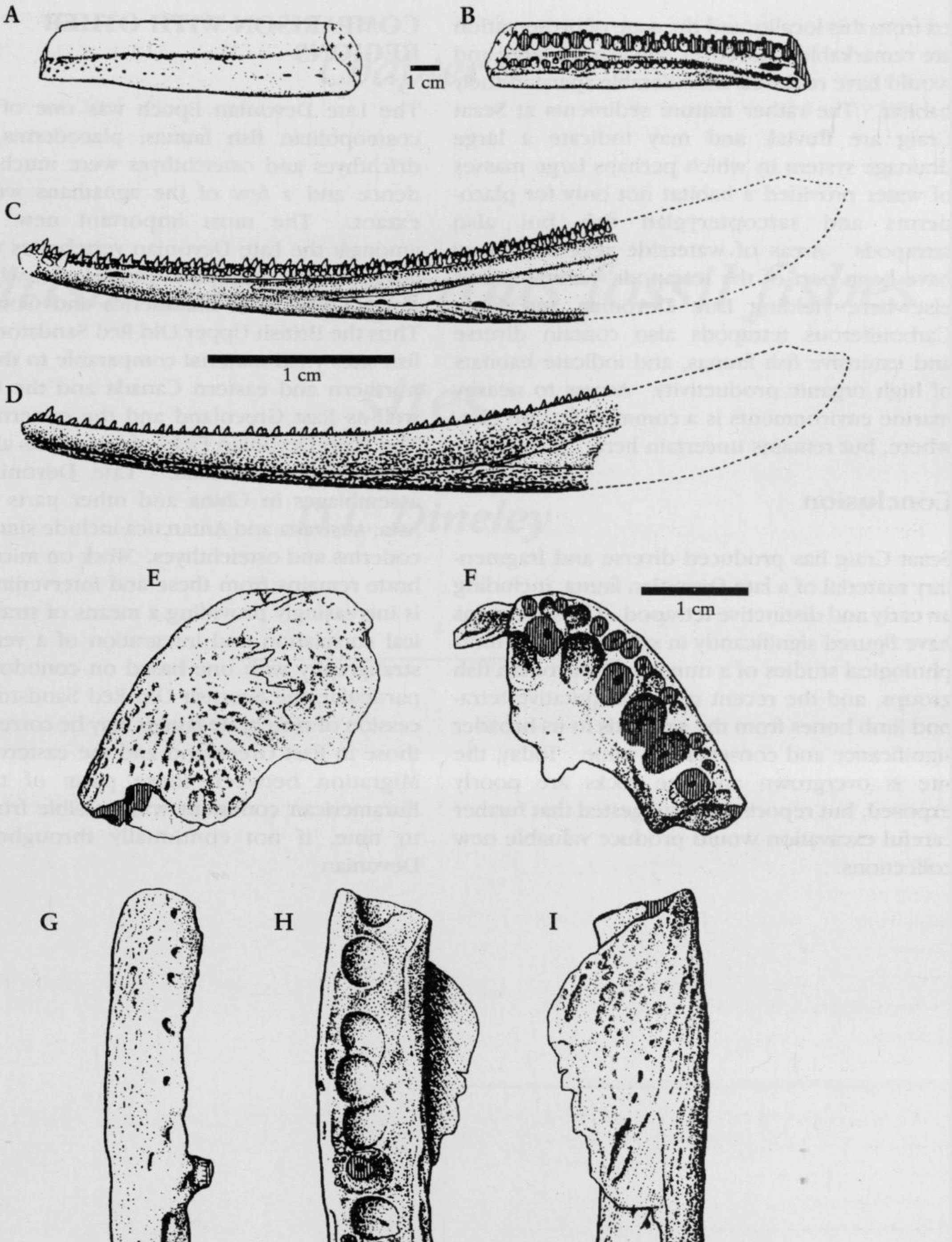



**Figure 8.14** Fossil tetrapod bone fragments from Scaat Craig (from Ahlberg, 1995). (A), (B) *Elginerpeton pancheni* Ahlberg, holotype RSM G 1967.17.1, in ventro-lateral and dorsal views. (C), (D) Reconstruction of the mandible in lateral and mesial views: brackets indicate parts of the jaws preserved in different specimens. (E), (F) the premaxilla, OUM Geol. Col D796, anterior part in dorsal and ventral views. (G)–(I) the posterior part of the premaxilla, NHM P9776, in lateral, ventral and dorsal views (vertical hatching = broken bone).

ed from this locality and the state of preservation are remarkable. Moreover, the fish are large and would have required considerable space in their habitat. The rather mature sediments at Scaat Craig are fluvial, and may indicate a large drainage system in which perhaps large masses of water provided a habitat not only for placoderms and sarcopterygian fish but also tetrapods. Areas of waterside vegetation may have been part of the tetrapods' habitat. Sites elsewhere yielding Late Devonian and Early Carboniferous tetrapods also contain diverse and extensive fish faunas, and indicate habitats of high organic productivity. Access to nearby marine environments is a common feature elsewhere, but remains uncertain here.

## Conclusion

Scaat Craig has produced diverse and fragmentary material of a late Devonian fauna, including an early and distinctive tetrapod. The specimens have figured significantly in systematic and morphological studies of a number of Devonian fish groups, and the recent report of putative tetrapod limb bones from the site adds to its broader significance and conservation value. Today, the site is overgrown and the rocks are poorly exposed, but reports have suggested that further careful excavation would produce valuable new collections.

## 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.