# *Fossil Fishes of Great Britain*

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Chapter 5

# Early Devonian fossil fishes sites of Scotland

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## INTRODUCTION: PALAEOGEOGRAPHY AND STRATIGRAPHY

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

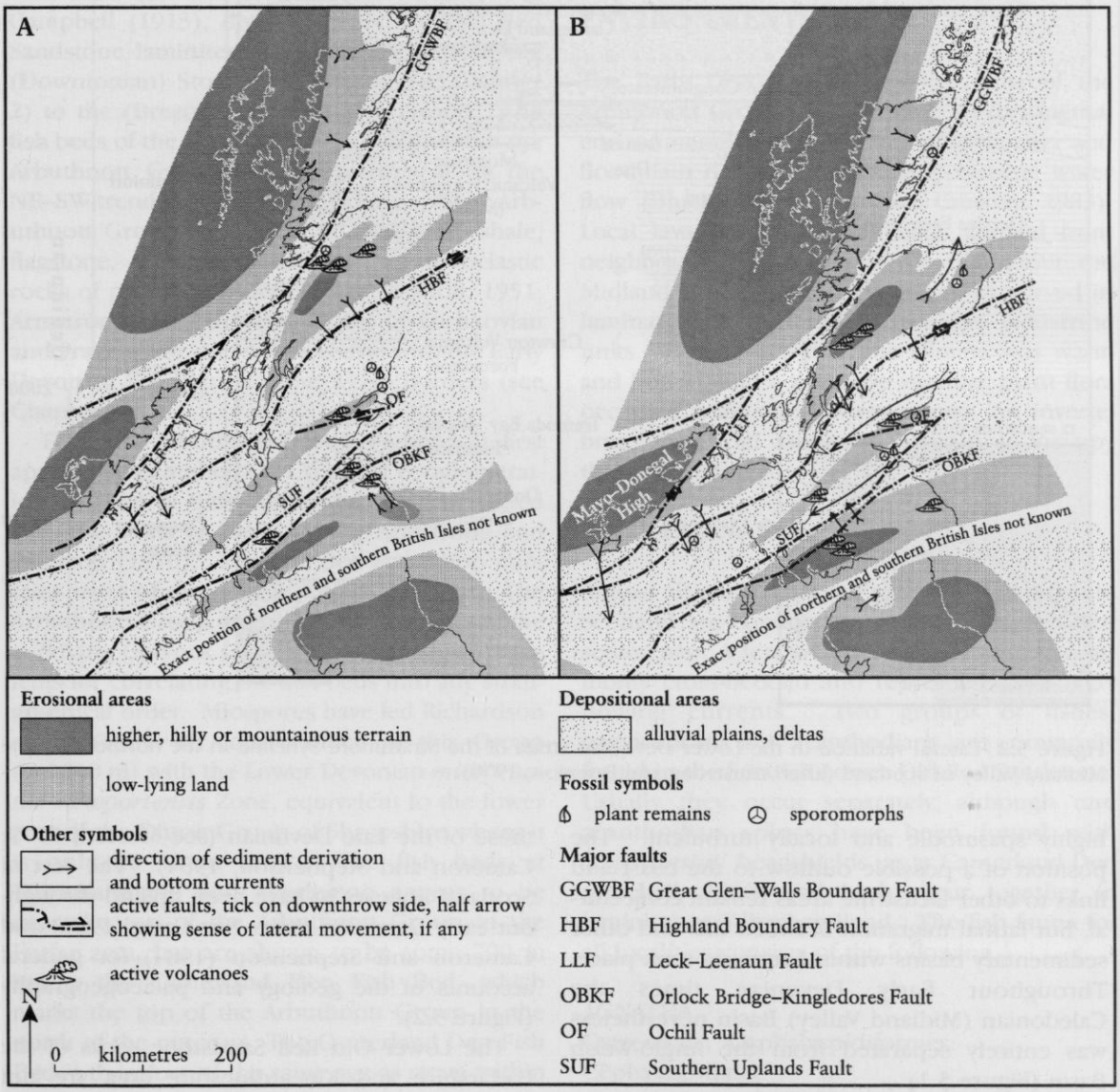


**Figure 5.1** Palaeogeography of the Early Devonian in northern Britain (after Bluck *et al.*, 1992). (A) palaeogeography of Lochkovian time, *c.* 408 Ma; (B) palaeogeography of Late Pragian–Emsian time, *c.* 400 Ma. Continuing movement of the fault-bounded blocks dominated the area of Scotland throughout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

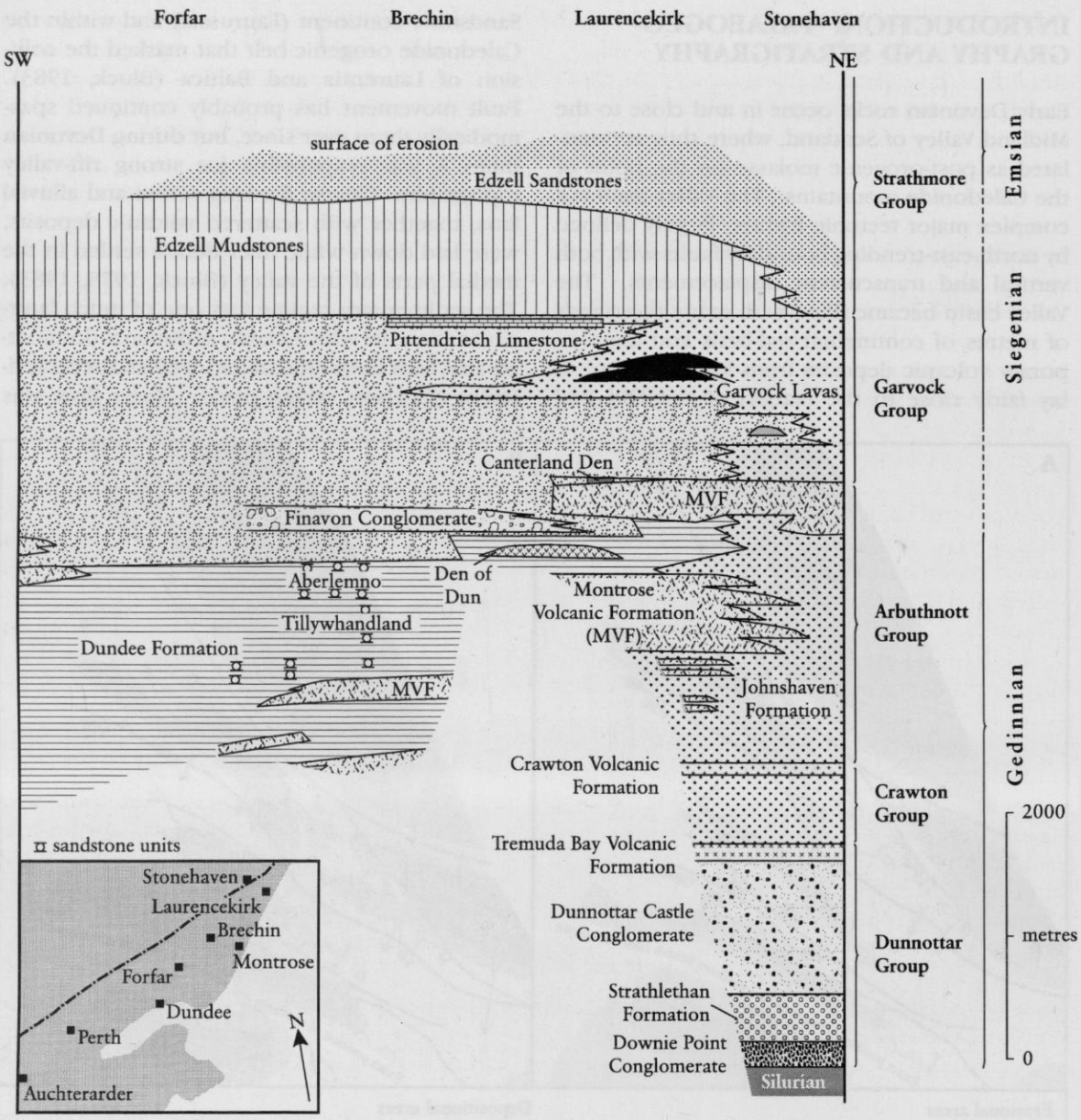


**Figure 5.2** Lateral variation in the Lower Devonian strata of the Strathmore Syncline in the northeast of the Midland Valley of Scotland (after Armstrong and Paterson, 1970).

highly spasmodic and locally turbulent. The position of a possible outflow to the coast and links to other lacustrine areas remain conjectural, but faunal migration between this and other sedimentary basins within Laurussia took place. Throughout Early Devonian times the Caledonian (Midland Valley) Basin nevertheless was entirely separated from the Anglo-Welsh Basin (Figure 5.1).

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

The Lower Old Red Sandstone rocks of the Forfarshire and Kincardineshire area are not only important stratigraphically, but also contain some key early fossil fish beds. The sequence is composed principally of sandstones, but coarse

conglomerates are prominent in Kincardineshire and along the Highland Border. Thick volcanic units are also present, particularly in the Ochil and Sidlaw Hills, and there are also important shale and mudstone formations (Armstrong and Paterson, 1970). Thin laminites containing fishes and other fossils occur at intervals throughout the sequence. Two other lithologies contain osteostracans, grey flagstones (fine-grained grey sandstone) and also red micaceous sandstones overlying these flagstones, the Garvock Group sediments. Field guides to the geology of the Midland Valley have been provided by Mitchell and Mykura (1960) and Bluck (1973).

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

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

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

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

## ENVIRONMENTS

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

## FISH FAUNAS

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

AGNATHA

Osteostraci: Cephalaspidiformes: Cephalaspididae

*Cephalaspis lyelli* Agassiz, 1835

Type, and only, locality Glamis; doubtful record from Brechin

'*C.*' *pagei* (Lankester, 1870)
Type locality Turin Hill; other sources Aberlemno, Kelly Den, Tealing, Reswallie, Carmylie, Pitairlie, Leysmill
'*C.*' cf. *pagei*
Recorded from Aberlemno, Turin Hill
'*C.*' *powriei* (Lankester, 1870).
Type locality Reisk Quarry, Brechin; other sources Craig nr Montrose, Crombie Burn, Brechin, ?Middleton, Leysmill, Turin Hill
'*Cephalaspis*' *powriei* var. *asper* (Lankester, 1870)
Type locality Turin Hill; other source Reswallie
'*C.*' *powriei* var. *brevicornis* Stensiö, 1932
Type locality Turin Hill; other sources Rossie Priory, Kinblythmont
'*C.*' cf. *powriei* (Lankester, 1870)
Recorded from Turin Hill
'*C.*' *spinifer* Stensiö, 1932
Type locality Turin Hill
'*C.*' *traquairi* Stensiö, 1932
Type and only locality Tulloch Quarry, Galston Moor
'*C.*' *websteri* Stensiö, 1932
Type locality ?Brechin
'*C.*' *watsoni* Stensiö, 1932
Type (?only) locality Rossie Priory
'*C.*' *scotica* White, 1963
Type and only locality Wolf's Hole
'*C.*' sp.
Recorded from Wolf's Hole (White, 1963)
'*Cephalaspis*' sp.
Recorded by Stensiö (1932) from Glamis, Turin Hill, Aberlemno, Leysmill
*Securiaspis caledonica* White, 1963
Type and only locality Wolf's Hole
*Securiaspis waterstoni* White, 1963
Type and only locality Wolf's Hole

Heterostraci: Pteraspidiformes: Pteraspididae
*Pteraspis mitchelli* White, 1963
Type and only locality Wolfe's Hole

Thelodonti: Thelodonta: Turinididae
*Turinia pagei* (Powrie, 1870)
Type locality Turin Hill

GNATHOSTOMATA

Acanthodii: Climatiiformes: Climatiidae
*Brachyacanthus scutiger* Egerton, 1860
*Climatius reticulatus* Agassiz, 1845
*Euthacanthus macnicoli* Powrie, 1870
*E. grandis* Powrie, 1870
*E. curtus* Powrie, 1870
*Parexus recurvus* Agassiz, 1845
*P. falcatus* Powrie, 1870
*Vernicomacanthus uncinatus* Powrie, 1864

Acanthodii: Ischnacanthiformes: Ischnacanthidae
*Ischnacanthus gracilis* Egerton, 1861

Acanthodii: Acanthiformes: Acanthodidae
*Mesacanthus mitchelli* Egerton, 1860
*?Uraniacanthus* sp.

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

Assiduous collecting by early Victorian enthusiasts led to rare osteostracans being found in the 'Arbroath pavement' associated with *Pterygotus* and in the Garvock Group sediments, where they occurred as isolated shields not associated with any other fauna. Only very occasionally have complete cephalaspids been found (Powrie, 1861). Nearly all the osteostracans were found in the 19th century by quarrymen working the sandstones and flagstones. Even 100 years after their first discovery, Stensiö (1932) could only find 141 good specimens, 77 from Scotland and 64 from England (White and Toombs, 1983), on which he based 20 species.

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

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

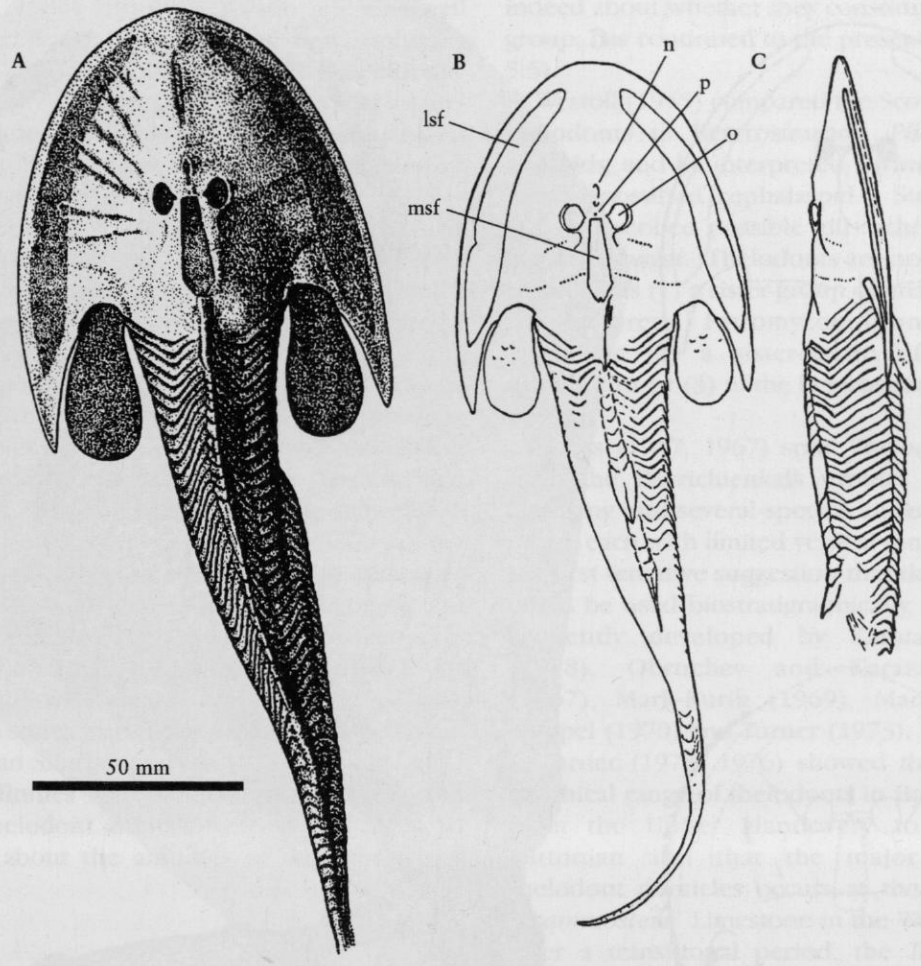


**Figure 5.3** *Cephalaspis lyelli* Agassiz. (A), (B) Dorsal and (C) lateral views of the headshield and trunk region of the lectotype (NHM P 20087) from Glamis, Angus (after White, 1958b): lsf, lateral sensory field; msf, median sensory field; n, nasal hypophysis; o, orbit; p, pineal; pa, pectoral appendage.

includes only the species *C. lyelli* (Figure 5.3).

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

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

The Scottish Lower Devonian thelodonts are also particularly important. The thelodonts

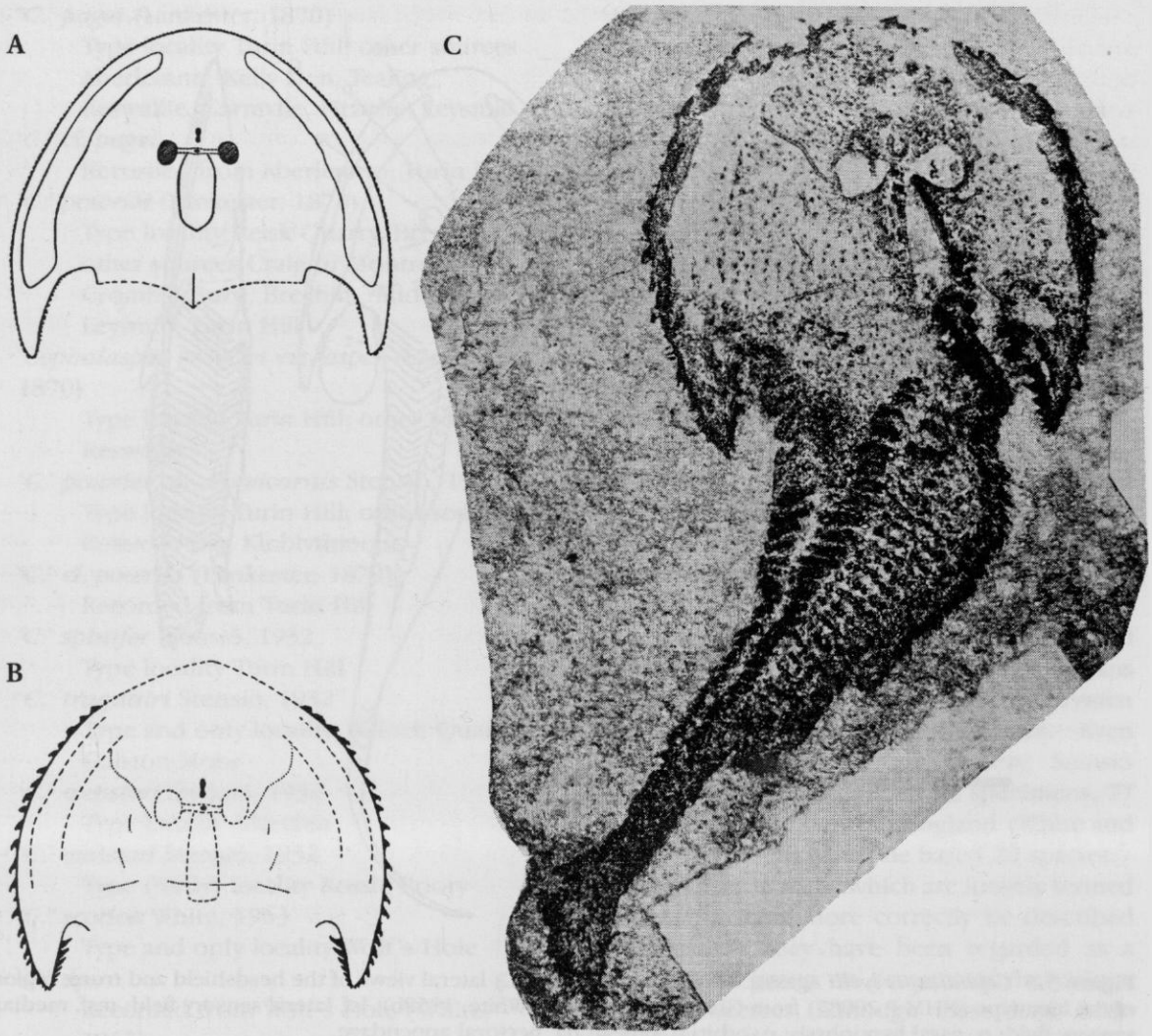


**Figure 5.4** Cephalaspids from the Early Devonian of Scotland (from Stensiö, 1932, © The Natural History Museum, London). (A) *Cephalaspis powriei* Lankester headshield in dorsal view after specimen RSM 138, × 0.8; (B) *C. spinifer* headshield after the holotype RSM 1891.92.149, × 0.8; (C) *C. spinifer*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

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

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

(Turner, 1986). In 1993 Wilson and Caldwell announced the discovery of new (marine) Silurian and Devonian fork-tailed 'thelodonts' with a body plan very different from that of previously known thelodonts. These fossils suggest a bilaterally compressed body, large tails and an active predatory mode of life.

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

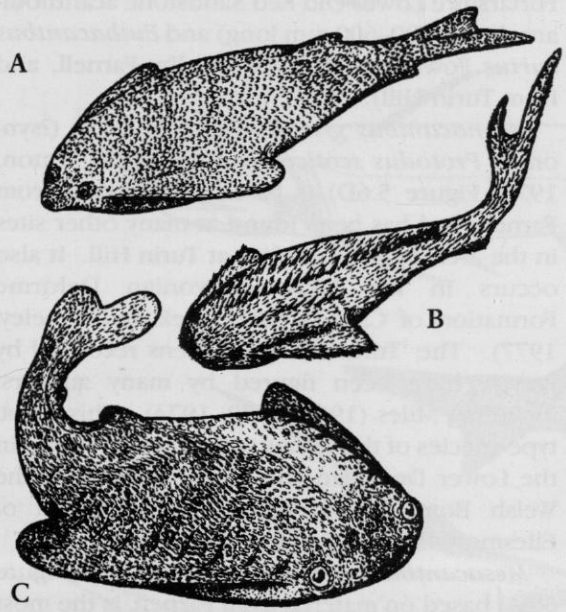


**Figure 5.5** New restorations of Scottish Early Devonian thelodonts by Turner (1992): (A) *Turinia pagei* (Powrie); (B) *Lanarkia spinosa* Traquair; (C) *Loganellia scotica* (Traquair), in which post-pectoral fin and tail are hypothetical. All are *c.* × 0.75.

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

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

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

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

Wilderness Quarry, Gloucestershire (Turner, *in* Allen *et al.*, 1968).

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

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

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

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

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

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

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

*Mesacanthus mitchelli* Egerton, 1860 (Figure 5.6A) based on material from Farnell, is the most abundant of all fishes in Forfarshire and is found in swarms (Powrie, 1870). It is very common at Turin Hill, from whence material was figured by Watson (1937). It is the type species of the genus, which includes species from the Middle Devonian of Caithness, and the Lower or Middle

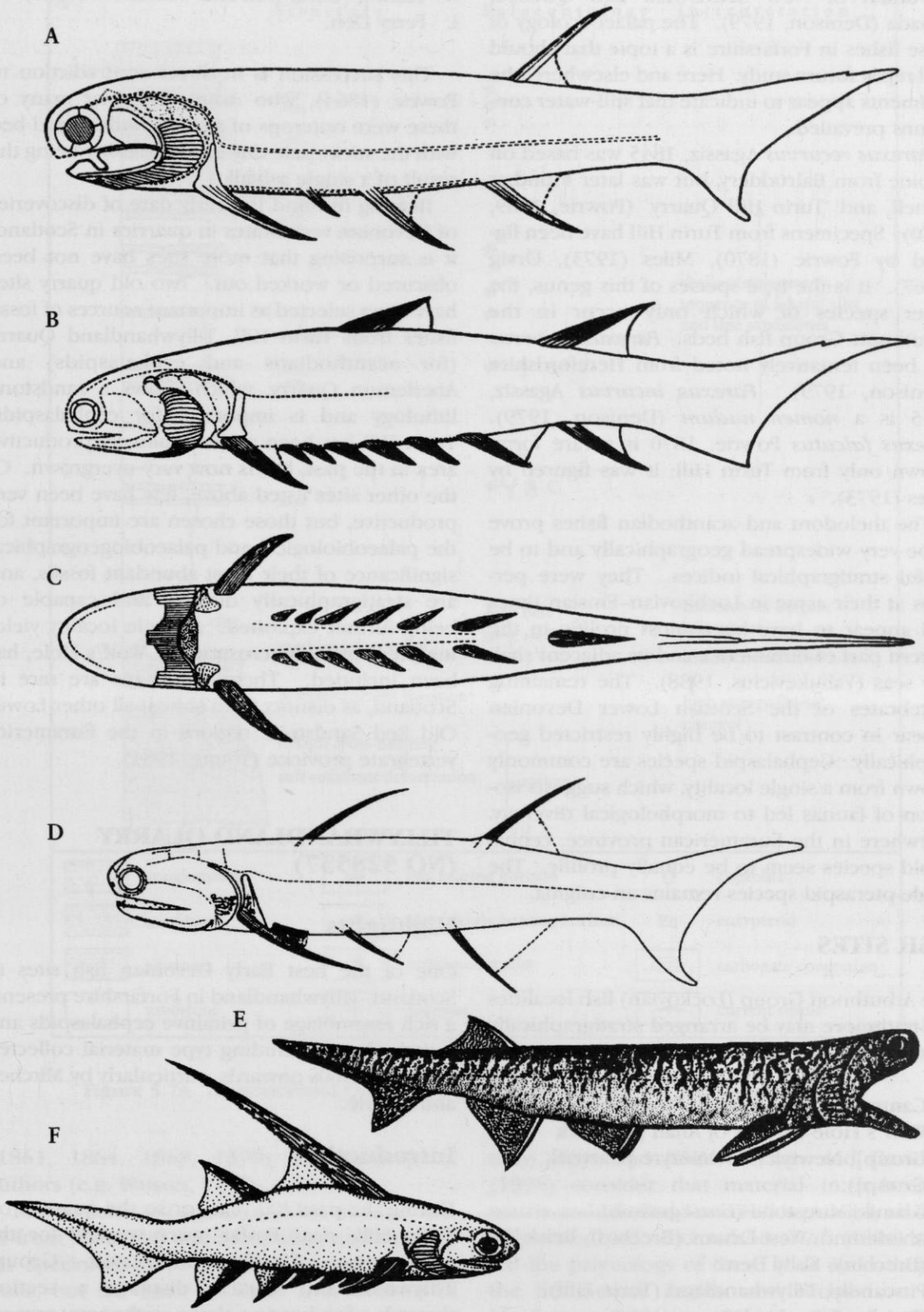


**Figure 5.6** Restorations of acanthodians from the Early Devonian of Scotland. (A) *Mesacanthus mitchelli* (Egerton), × 2.0; (B), (C) *Euthacanthus macnicoli* Powrie × 0.8 in lateral and ventral views; (D) *Ischnacanthus gracilis* (Egerton), × 1.25 approx.; (E) *Mesacanthus* sp. approximately natural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

Devonian of New Brunswick and Quebec, Canada (Denison, 1979). The palaeoecology of these fishes in Forfarshire is a topic that should well repay future study. Here and elsewhere, the sediments appear to indicate that still-water conditions prevailed.

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

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

## FISH SITES

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

vii. Canterland Den (Den of Morphie).
vi. Wolf's Hole (Bridge of Allan [Garvock Group]; Newtyle, Auchentyre [Garvock Group]).
v. Glamis; Mirestone (Carsegownie); Aberlemno; West Drums (Brechin); Reisk (Brechin); Kelly Den.
iv. Pitscandly; Tillywhandland (Turin Hill); Pitairlie; Crombie Den.
iii. Rossie Den; Balruddery Den; Reswallie; Farnell; Duntrune; Myreston; Carmylie; Leysmill; Three Wells.
ii. Tealing (Coral Den and Whitehouse Den).
i. Ferry Den.

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

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

## TILLYWHANDLAND QUARRY (NO 528537)

### Highlights

One of the best Early Devonian fish sites in Scotland, Tillywhandland in Forfarshire presents a rich assemblage of primitive cephalaspids and acanthodians, including type material collected from the 1860s onwards, particularly by Mitchell and Powrie.

### Introduction

During the past 200 years or so the quarries on Turin Hill, near Forfar, were worked for the sandstones of the Arbuthnott Group. Tillywhandland Quarry displays a section through a fish-bearing clastic–carbonate–organic laminite, and it yields a rich fauna of acanthodians and cephalaspids. Fish specimens, probably from this site, have been reported by Powrie

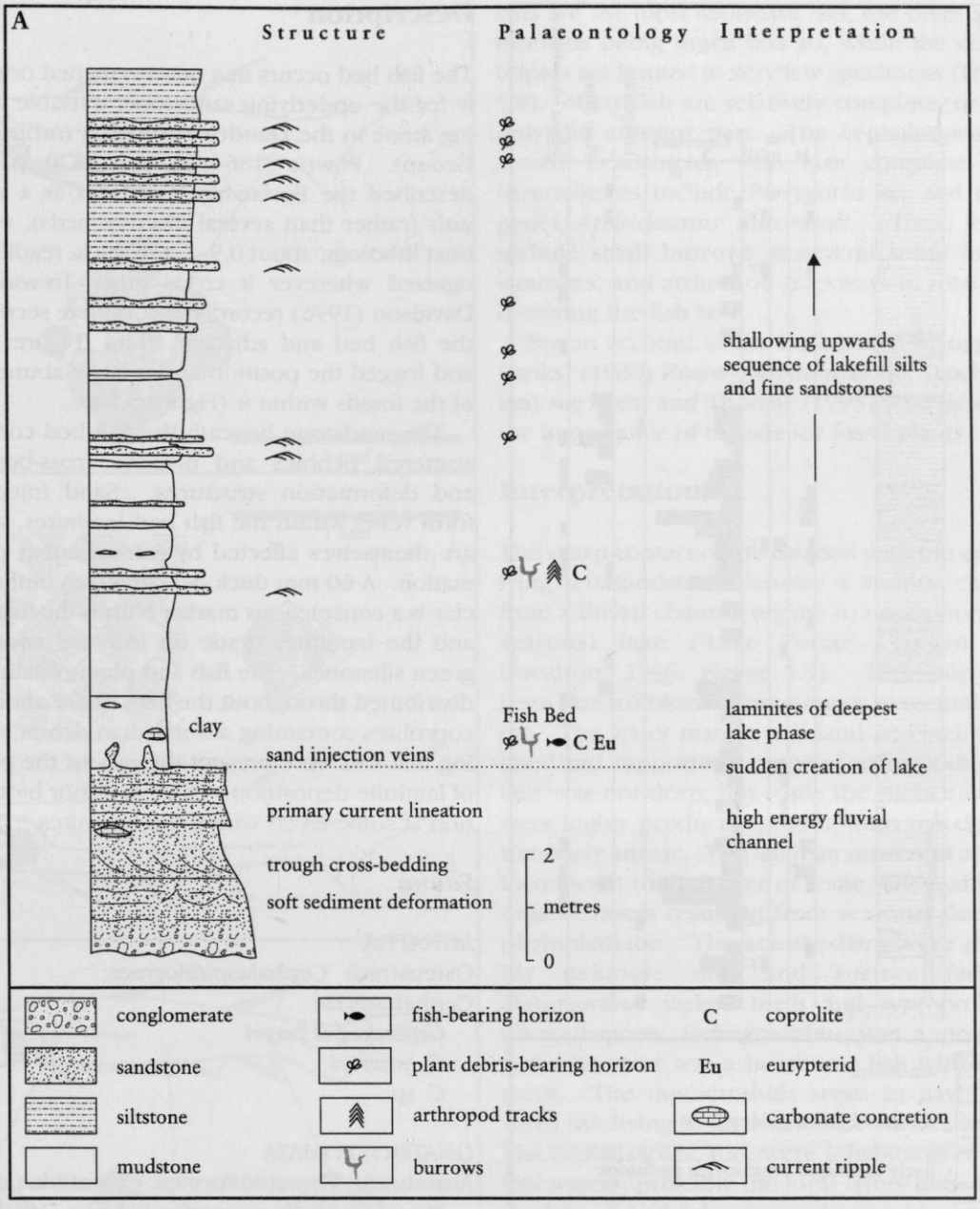


**Figure 5.7A** Tillywhandland Quarry: the succession (after Trewin and Davidson, 1996).

(1861, 1864, 1869, 1870) and subsequent authors (e.g. Watson, 1937).

Powrie collected a great number of fossil fishes from Turin Hill and other sites, and many of his specimens were the basis of type descriptions, but the exact localities and horizons of material from 'Turin Hill' are not known. Nor is it certain if there is one or several fossil fish beds at Turin Hill. From examination of collections in Montrose Museum (Mitchell Collection), RSM and NHM, Trewin and Davidson (1996) consider that material in a laminite matrix and labelled Turin Hill is possibly all from Tillywhandland. Richardson *et al.* (1984) studied the palynology of these beds and others in the Strathmore region and Richardson and MacGregor (1986) ascribed the Tillywhandland fish bed to the basal Lockovian *micronatus–newportensis* Zone.

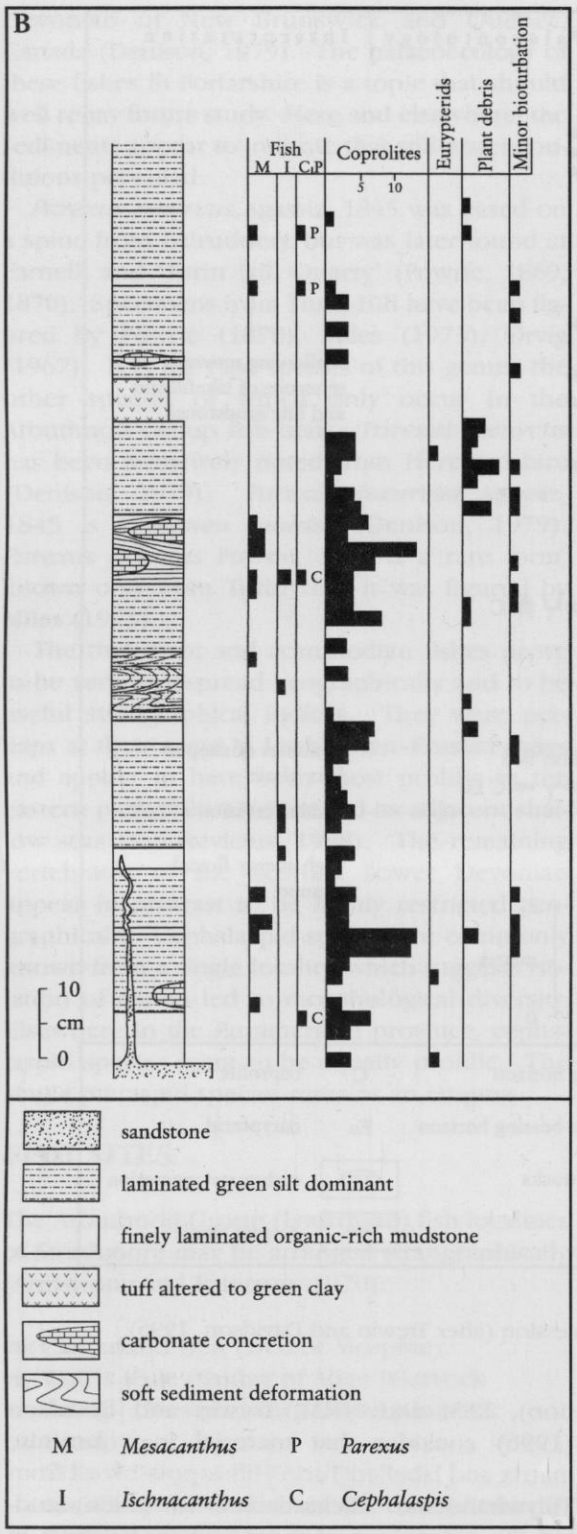


**Figure 5.7B** Tillywhandland Quarry: the recorded positions of the fauna and flora within the fish bed (after Trewin and Davidson, 1996).

## Description

The fish bed occurs in a quarry opened originally for the underlying sandstone, a usable building stone in the Dundee Formation (Arbuthnott Group). Powrie (1864, p. 414; 1870, p. 285) described the Forfarshire Fish Bed as a single unit (rather than several discrete beds), of distinct lithology, about 0.9–2.4 m thick, readily recognized wherever it crops out. Trewin and Davidson (1996) recorded a complete section of the fish bed and adjacent strata (Figure 5.7A) and logged the position and relative abundance of the fossils within it (Figure 5.7B).

The sandstone beneath the fish bed contains scattered pebbles and displays cross-bedding and deformation structures. Sand injections form veins within the fish bed laminites, which are themselves affected by soft-sediment deformation. A 60 mm thick pale green to buff sticky clay is a conspicuous marker within the fish bed, and the laminites grade up into the overlying green siltstones. The fish and plant remains are distributed throughout the bed, as are abundant coprolites containing acanthodian debris, showing that fish were present thoughout the period of laminite deposition. There is minor bioturbation at some levels within the laminites.

### *Fauna*

AGNATHA
Osteostraci: Cephalaspidiformes:
Cephalaspidae
*Cephalaspis pagei*
*C. powriei*
*C.* sp.

GNATHOSTOMATA
Acanthodii: Climatiidiformes: Climatiidae
?*Brachyacanthus scutiger* Egerton, 1860
*Climatius reticulatus* Agassiz, 1845
*Euthacanthus macnicoli* Powrie, 1864
*Euthacanthus* sp.
Acanthodii: Ischnacanthidiformes:
Ischnacanthidae
*Ischnacanthus gracilis* (Egerton, 1861)
?*Uraniacanthus* sp.
Acanthodii: Acanthodiformes: Acanthodidae
*Mesacanthus mitchelli* (Egerton, 1861)
*M.* sp.

Trewin and Davidson (1996) found that *Mesacanthus mitchelli* and *Ischnacanthus gra-*

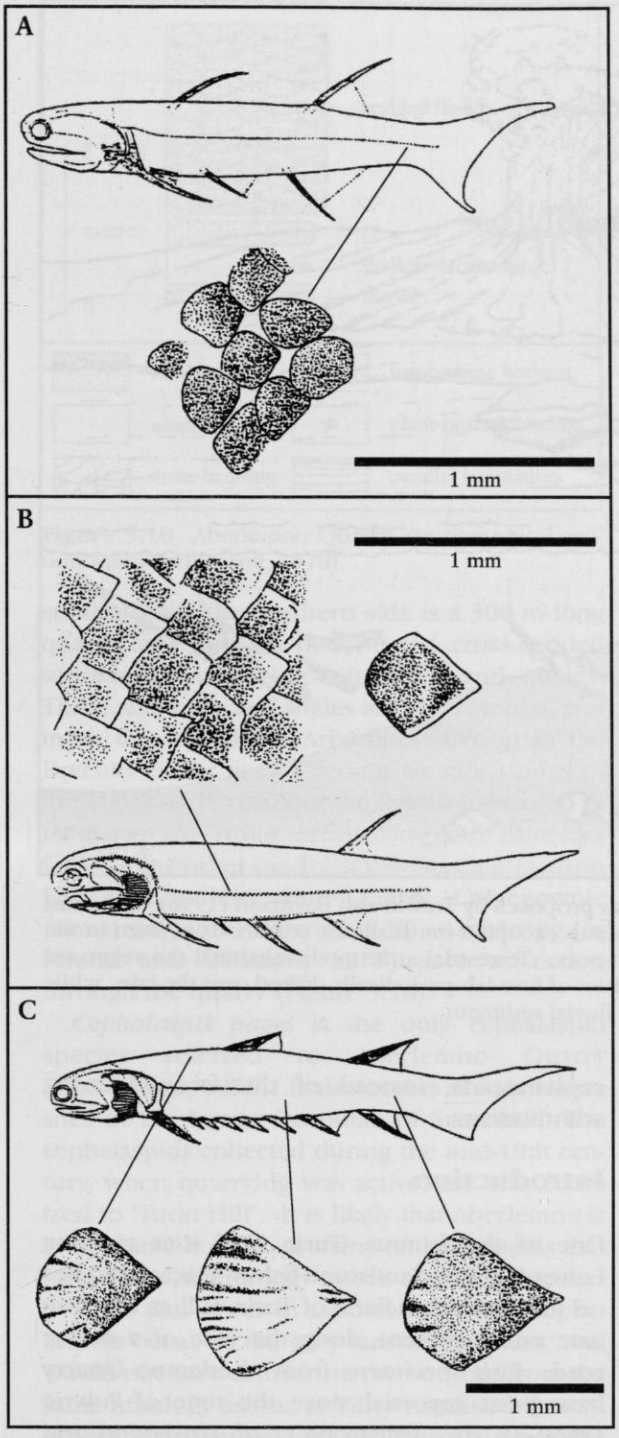


**Figure 5.8** Characteristic acanthodian scales from Tillywhandland Quarry. (A) *Ischnacanthus gracilis* (Egerton), NHM P 62266, scales rhombic, sub-rhombic or polygonal, relatively flat to gently convex and smooth; (B) *Mesacanthus mitchelli* (Egerton), P 140 and 10892, scales smooth with flat crowns, sharp posterior point; (C) *Euthacanthus macnicoli* Powrie, scales with simple ribs, very flat crowns with five to ten well-spaced grooves. (Courtesy V.T. Young.)

*cilis* are the most abundant fish, the other acanthodians being much less so, while the cephalaspids are limited to very few specimens (Figure 5.8). Many fish are relatively complete, or lack only the anterior part. The cephalaspids are mostly headshields with rare complete fish. Invertebrates include *Pterygotus* sp. and millipedes *Archidesmus macnicoli*. Trace fossils include small burrows at several levels in the laminites, and arthropod trackways in siltstones overlying the fish bed.

For an account of the flora which belongs to Banks' (1980) *Zosterophyllum* Zone, (Lochkovian) see Cleal and Thomas (1995) who describe the importance of the site for fossil plants.

## Interpretation

The sharp contact of the fish bed with the underlying red sandstone denotes a sudden change from a fluvial channel regime to deposition in a seasonal lake ('Lake Forfar'; Trewin and Davidson, 1996; Figure 5.9). This may have been due to volcanic damming or to tectonic tilting. The water margin and land was well vegetated and supported a range of arthropods. The lake was not deep, but while the surface waters were highly productive, the bottom was discontinuously anoxic. The laminae represent annual increments to the order of some 2000, with the organic layers resulting from seasonal decay of phytoplankton. The acanthodians were probably nektonic mid and surface feeders. *Mesacanthus* lacked teeth and was probably microphagous; *Ischnacanthus* was a predator and *Climatius* was a benthonic fish with sharp teeth. The mesacanthids seem to have been shoal fish living in the shallow or surface waters. The cephalaspids, too, were inhabitants of shallow waters, probably the local rivers rather than the lake. Small fish were perhaps subject to predation from the large pterygotid eurypterids.

The pale green to buff clay appears to be the weathering product of a volcanic ash-fall and the termination of the lake's existence was the result of increased sediment input. The origin of the fish fauna and possible connections with other water bodies remain obscure. Recent studies, as yet unpublished have not been able to confirm that the Tillywhandland fish bed is the same stratum as is exposed elsewhere (R. Davidson, pers. comm.).

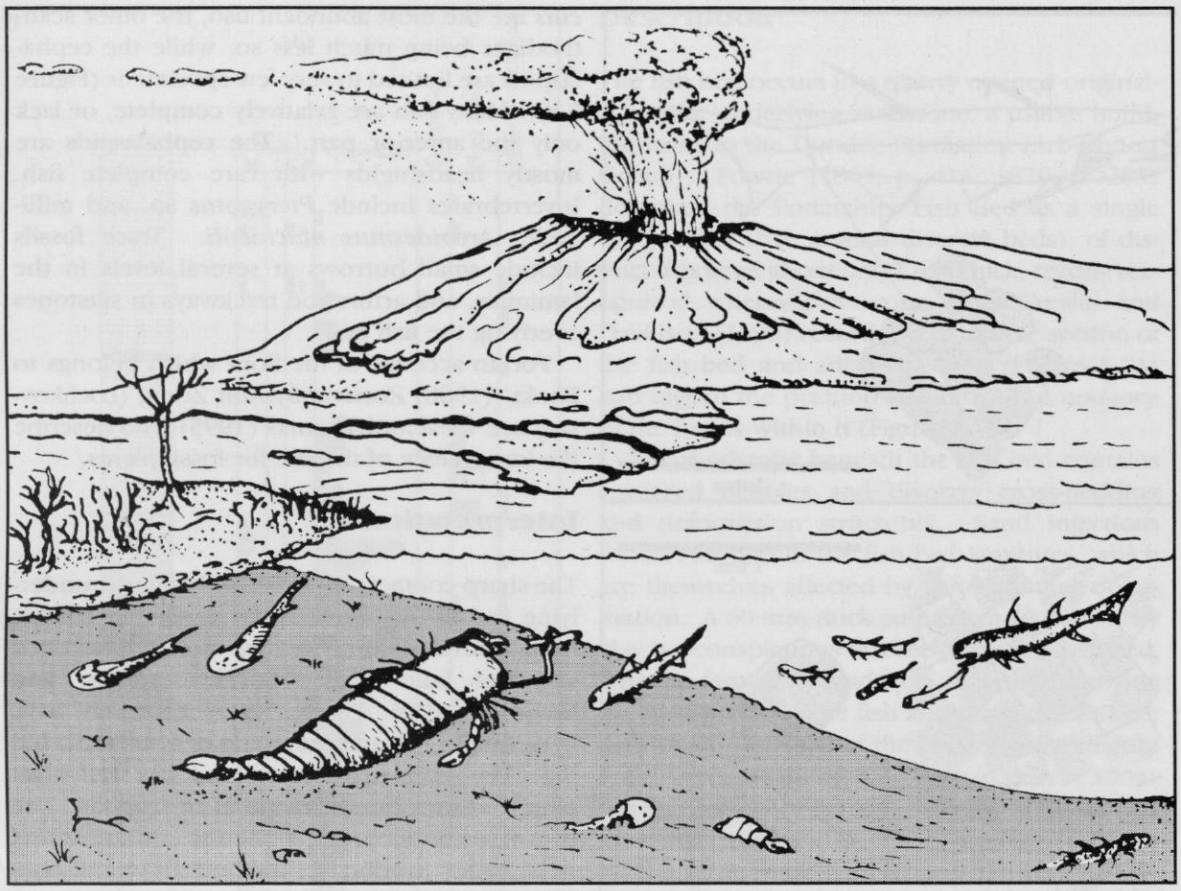

**Figure 5.9** A restoration of the margins of 'Lake Forfar' as proposed by Trewin and Davidson (1996). A vagrant benthos of cephalaspids, eurypterids and other invertebrates occupied the shallows; acanthodians lived in the open waters. Bottom conditions were probably oxygen-poor. Terrestrial arthropods inhabited the vegetated land adjacent to the lake. From nearby volcanoes quantities of fine ash periodically drifted over the lake, while there was throughout a seasonally variable input of fine fluvial sediment.

## Conclusion

As one of the best Lower Devonian fish localities in Scotland, its conservation value is enhanced by it being the site richest in acanthodian fishes. It is one of the numerous quarries that formerly existed in the Turin Hill area, and it is one of the few that shows good sections, and in which fossil fish have been found recently. There is a continuing potential for investigation here.

# ABERLEMNO QUARRY (NO 526551)

## Highlights

Aberlemno Quarry in Forfarshire is a famous site that has been yielding excellent specimens of osteostracan fishes since the 1860s. It is distinct from Tillywhandland Quarry nearby since the faunas are dominated by the heavily armoured cephalaspids, instead of the free-swimming acanthodians.

## Introduction

One of the famous 'Turin Hill' sites yielding Lower Old Red Sandstone fishes, this section lies on the north-east flank of Turin Hill as an elongate entrenchment along the side of a minor road. Fish specimens from Aberlemno Quarry have been reported since the time of Powrie (1869–1870). Armstrong *et al.* (*in* Friend and Williams, 1978) described the succession in the local exposures of the Dundee Formation, Arbuthnott Group.

## Description

The southern side of the quarry is marked by extensive spoil heaps of shale and green mud-

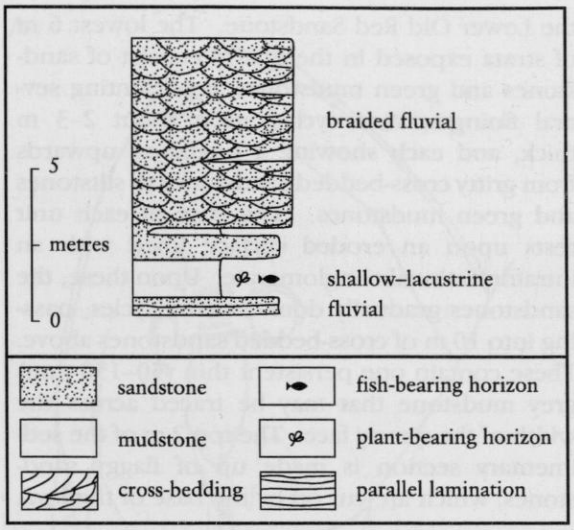


**Figure 5.10** Aberlemno Quarry, stratigraphical section (after Armstrong, 1978).

stones, while the northern side is a 300 m long quarry face through massive red cross-bedded sandstones overlying siltstones and shales. These siltstones and shales are the 'fish bed' and mark the top of the Arbuthnott Group in the Brechin–Forfar area, overlain by sandstones of the Melgund Formation, the lowest formation of the Garvock Group (Armstrong and Paterson, 1970). The other quarry at this horizon in Turin Hill area is Mirestone Quarry, Carsegownie (Armstrong and Paterson, 1970). Armstrong (*in* Friend and Williams, 1978) gave a section through the quarry (Figure 5.10).

*Cephalaspis pagei* is the only cephalaspid species referred to Aberlemno Quarry (Henrichsen, 1971). It also occurs at many other sites in the Lower Devonian of Scotland. The cephalaspids collected during the mid-19th century, when quarrying was active, are only localized to 'Turin Hill'. It is likely that Aberlemno is at the same horizon as many of these fossils that have a similar lithology to this quarry, particularly those that occur in sandstone. Other cephalaspids occur in the grey laminated shales, and would not have come from this site, but from the same lithology as that at Tillywhandland Quarry. Acanthodian spines are also known, as is the arthropod *Dictyocaris*.

The plant fossils are well known and the palaeobotany of this site is described by Cleal and Thomas (1995). The *Zosterophyllum* Zone flora here is regarded as the best example anywhere, though other instances occur in South Wales and the Welsh Borders, Spitsbergen, the Czech Republic and Siberia.

***Fauna***

The exact provenance of many osteostracans present in the collections is not certain, but it is most likely that the following were derived from Aberlemno.

AGNATHA
Osteostraci: Cephalaspidiformes:
Cephalaspididae
*Cephalaspis pagei* (Lankester, 1870)
*C.* cf. *C. pagei*
'*C.*' *powrei* (Lankester, 1870)
'*C.*' *powrei* var. *asper* (Lankester, 1870)
'*C.*' *powrei* var. *brevicornis* Stensiö, 1932
'*C.*' cf. *powrei*
'*C.*' *spinifer* Stensiö, 1932

## Interpretation

The Aberlemno section may be interpreted as largely a braided fluvial sequence with a thin intercalation of a shallow lacustrine fish-bearing layer. The upper part of the Arbuthnott Group is diachronous and interdigitates with the lower part of the Garvock Group. This means that the Aberlemno fish bed is not the youngest fish bed of the Arbuthnott Group as a whole, since Canterland Den (Den of Morphie) lies above it (Armstrong and Paterson, 1970, p. 23). Much of this may have been due to the spread of shallow bodies of lake water. The fauna and flora recorded from the Arbuthnott Group (Edwards, 1980; Edwards and Fanning, 1985) suggest a Lochkovian age, and the fishes and eurypterids indicate an age not older than the base of the Dittonian (Westoll, *in* House *et al.*, 1977). Richardson *et al.* (1984) regarded the 'Aberlemno horizon' as falling in the middle subzone of *micromatus–newportensis* Zone of the Lochkov Stage, basal Dittonian of the Welsh Borderland. A radiometric age of 407 ± 6 Ma was determined by Thirlwall (1983) for the lower part of the Arbuthnott Group and Richardson *et al.* (1984) calculated from this an age of 410 ± 6 Ma for the base of the Devonian. The age of the Aberlemno fish bed cannot therefore be much less.

## Conclusion

The conservation value of Aberlemno Quarry results from it being the best surviving site on Turin Hill where fossil fishes occur in fine sand-

stone or siltstone, and shales. It is likely that many of the excellent specimens of cephalaspids found in the 19th century came from Aberlemno, but there are problems in identifying particular localities from the older literature. The site exposes the fish-bearing sandstones, and upon excavation could yield more specimens.

## WOLF'S HOLE QUARRY (NS 790981)

### Highlights

Wolf's Hole Quarry has been the source of only a small number of fossil fish specimens, but these present a unique faunal assemblage. This includes the original material of four agnathan fish species, *Pteraspis mitchelli*, *Cephalaspis scotica*, *Securiaspis waterstoni* and *Securiaspis caledonica* (Figure 5.11).

### Introduction

Wolf's Hole Quarry, near Bridge of Allen in Forfarshire, has yielded fossil fish specimens from a coarse, pinkish brown quartz- and feldspar-rich sandstone. This lithology, as determined from museum specimens, matches the sandstones seen in the basal and middle parts of the section exposed today. All the specimens were found in the 1860s and 1870s when the sandstones were worked for building stone. Nothing has been found since, so the fishes were probably entombed in one, or several, lens-like accumulations, in a similar fashion to the preservation of cephalaspids and pteraspids in the Welsh Borders.

The first record of fossil fishes from Wolf's Hole Quarry was given by H. Mitchell (1862), who noted *Pteraspis*. A little later, 'unaware of Mitchell's discoveries', Powrie (1870, p. 285) also collected some specimens of *Cephalaspis* and *Pteraspis* from the site. The rather small total collection from the quarry is housed in Montrose Museum (Mitchell Collection) and the National Museum of Scotland (Powrie Collection).

### Description

Wolf's Hole Quarry exposes 25 m of massive cross-bedded sandstones with some siltstones, overlain by a basic amygdaloidal lava at the base of the Sheriffmuir Formation in the upper part of the Lower Old Red Sandstone. The lowest 6 m of strata exposed in the quarry consist of sandstones and green mudstones, representing several fining-upward cycles, each about 2–3 m thick, and each showing a gradation upwards from gritty cross-bedded sandstones to siltstones and green mudstones. The base of each unit rests upon an eroded surface lined with an intraformational conglomerate. Upon these, the sandstones gradually dominate the cycles, passing into 10 m of cross-bedded sandstones above. These contain one persistent thin (50–150 mm) grey mudstone that may be traced across the width of the quarry face. The top 2 m of the sedimentary section is made up of flaggy sandstones, which are cut off by the base of the lava.

#### *Fauna*

AGNATHA
Osteostraci: Cephalaspidiformes:
Cephalaspididae
*'Cephalaspis' scotica* White, 1963
*Securiaspis waterstoni* White, 1963
*S. caledonica* White, 1963
Heterostraci: Pteraspidiformes: Pteraspididae
*Pteraspis mitchelli* (Lankester, 1868)

Five recognizable fragments of cephalaspid headshields are known from Wolf's Hole Quarry (Figure 5.11). Powrie (1863) was the first to mention their occurrence, recording them as *Cephalaspis lyelli*, which at that time was the name applied to all cephalaspids discovered in Scotland. When White (1963) re-examined these specimens, he concluded that they represented three new species, one cephalaspid and two securiaspids. *Cephalaspis scotica* is based on a unique imperfect cephalic shield, which Stensiö (1932) had noted was similar to *C. websteri* Stensiö, although it probably could not itself be attributed to the latter species. *Securiaspis caledonica* and *S. waterstoni* are also each represented by single cephalic shields in the original descriptions (White, 1963). *Securiaspis* is confined elsewhere to the Lower Devonian in the Welsh Borders and Spitsbergen (Janvier, 1985), and this is the only occurrence in Scotland.

*Pteraspis mitchelli* was first discovered at Wolf's Hole Quarry by H. Mitchell (1862), and it was named after him by Powrie (1864), but without designation of a holotype. Three specimens were figured by Lankester (1868), but the first

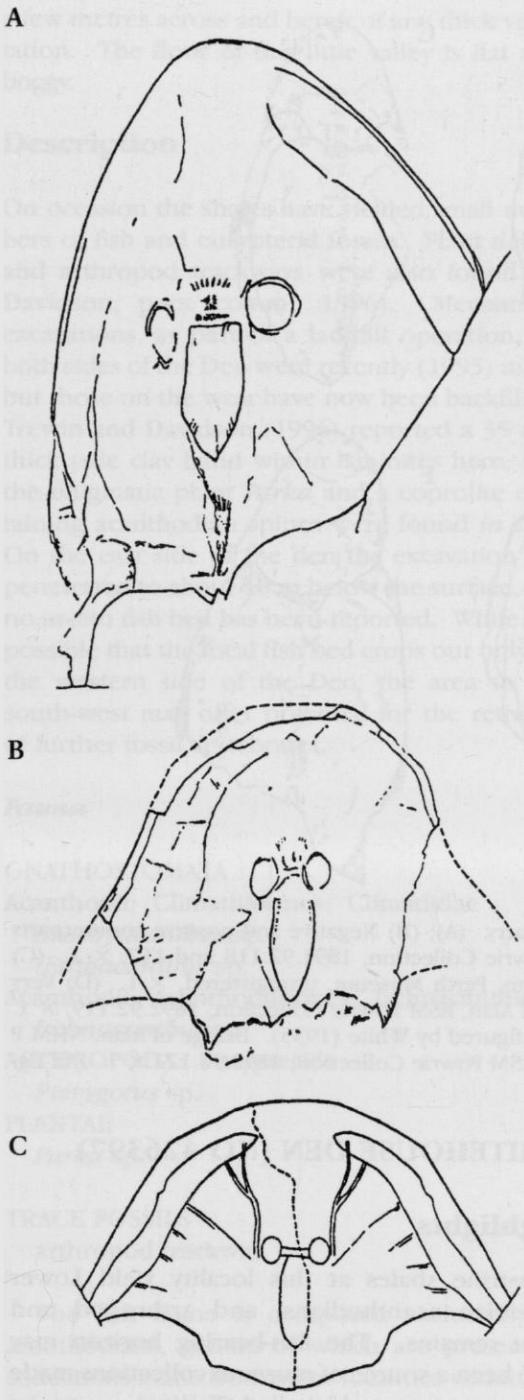


**Figure 5.11** Cephalaspids from Wolf's Hole Quarry. (A) *Cephalaspis scotica* White, imperfect headshield is dorsal aspect, holotype RSM Powrie collection 1981.92.135, × 2. (B) *Securiaspis waterstoni* White, imperfect headshield in dorsal aspect, holotype, Perth Museum, unregistered, × 1. (C) *Securiaspis caledonica* White, external impression of headshield. Area to left of dotted line is restored. Perth Museum, unregistered, slightly less than natural size. (From White, 1963)

adequate description of *P. mitchelli* was given by White (1963), who designated one of Lankester's (1868) figured specimens as the lectotype (Figure 5.12). *Pteraspis mitchelli* is very rare, being known from only a few large pieces of dorsal shield, and some fragments that include scraps of ventral shield. It is readily distinguished by its large rostrum and small cornua. Blieck (1981, 1985) noted the similarities of this species to both *P. rostata* and to *Protopteraspis*, but resisted (1985) moving it to *Protopteraspis*.

## Interpretation

Pteraspidids are very rare in Scotland, although they are common in the Welsh Borders. The only other place in Scotland where pteraspidids have been discovered is Auchtertyre, near Newtyle, which also yields rare *Pteraspis mitchelli*. White (1963) argued that pteraspids were inhabitants of moving waters, are usually found within current-bedded deposits and are rarely associated with other vertebrates except a few isolated cephalaspid headshields. The cephalaspids may have favoured the Scottish Old Red Sandstone lakes and backwaters, whereas pteraspids ventured more readily into moving waters. Cephalaspids are present, though rare in the Scottish Middle Old Red Sandstone and in the ?lacustrine or lagoonal Escuminac Formation (Upper Devonian) of eastern Canada. White (1963) suggested that *P. mitchelli* might have been a peculiar species in being adapted to conditions that were avoided by the rest of the pteraspids. This argument does not take into account that the fossils from Wolf's Hole are, in fact, found in current-bedded deposits that are unlike the lacustrine silts and fine sandstones of the other Scottish Lower Old Red Sandstone fish sites. The assemblage and sedimentology here are closer to those found in the Dittonian of the Welsh Borders, where they are considered to be fluvial in origin. This pteraspid material was also considered by Blieck (1981, 1984), who was not without some doubt about its taxonomy, noting possible affinities with *Protopteraspis* and similarities to *P. rostrata*. Meanwhile it remains the only pteraspid from Scotland. This possible affinity with *P. rostrata* is of interest since the only pteraspid from Ireland is *P. rostrata* from the Fintona Beds of County Fermanagh (Harper and Hartley, 1938). Perhaps then the

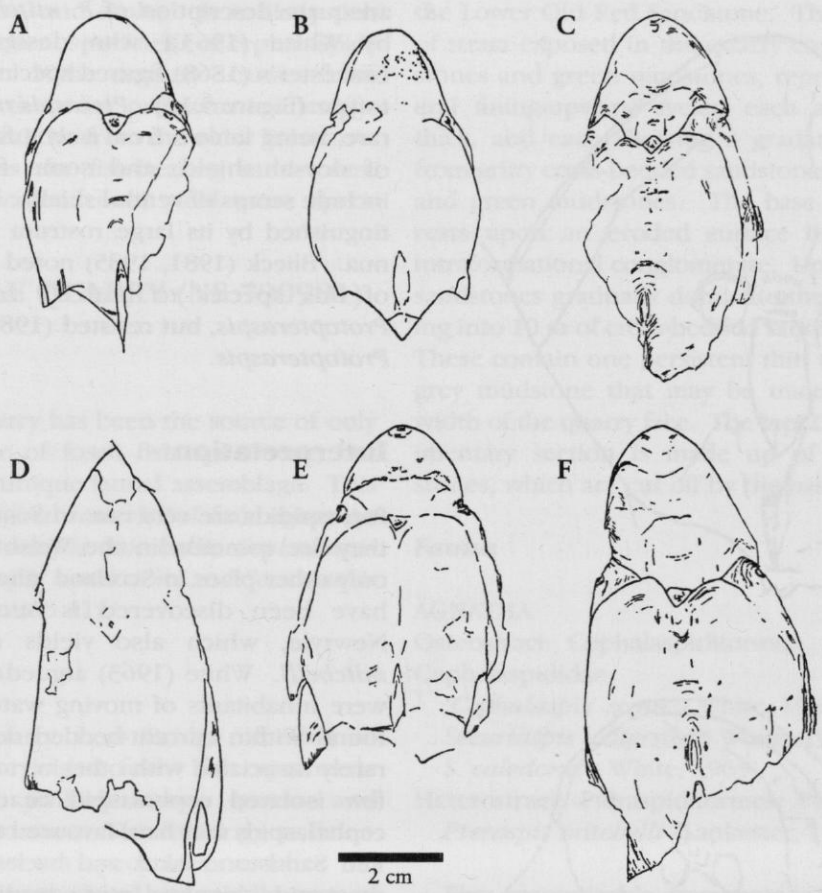


**Figure 5.12** *Pteraspis mitchelli* Powrie from Wolf's Hole Quarry. (A), (B) Negative and positive counterparts of a small dorsal shield. Lectotype, Bridge of Alan, RSM Powrie Collection, 1891.92.118 and 117, × 1. (C) External impression of imperfect dorsal shield, Bridge of Alan, Perth Museum, unregistered, × 1. (D) Very imperfect dorsal shield figured by Lankester (1868), Bridge of Alan, RSM Powrie Collection, 1892.92.119, × 1. (E) External impression if imperfect dorsal shield. Specimen figured by White (1935). Bridge of Alan, NHM P 16808, × 1. (F) external impression of small dorsal shield. RSM Powrie Collection, 1892.92.122 × 1. (All figures from White, 1963.)

Caledonian basin was directly linked to that in the north of Ireland.

## Conclusion

Wolf's Hole Quarry has produced a limited, but important, fish fauna, hence its conservation value. The specimens include type specimens of four species, and in some ways the conditions of deposition may be more comparable with some of the fluvial sandstone deposits of the Early Devonian of the Welsh Borders. The occurrence of *Pteraspis* is unusual for Scotland and may indicate a link with northern Ireland and the Anglo-Welsh Basin. The site has not yielded any specimens recently, but the fish-bearing sandstones are exposed and could be worked again in the future.

# WHITEHOUSE DEN (NO 426397)

## Highlights

Lacustrine shales at this locality yield Lower Devonian acanthodians, and arthropod and plant remains. The fish-bearing horizon may have been a source of museum collections made many years ago and labelled 'Tealing'.

## Introduction

This locality near Tealing in Tayside has, over the past few years, been excavated and has revealed sandstones and shales of the Lower Devonian Arbuthnott Group (Armstrong and Paterson, 1970). Situated some 300 m south-east of Lorance Hill, the Den is in a shallow depression,

a few metres across and bereft of any thick vegetation. The floor of this little valley is flat and boggy.

## Description

On occasion the shales have yielded small numbers of fish and eurypterid fossils. Plant debris and arthropod trackways were also found (R. Davidson, pers. comm., 1996). Mechanical excavations, as part of a landfill operation, on both sides of the Den were recently (1995) made but those on the west have now been backfilled. Trewin and Davidson (1996) reported a 35 mm thick pale clay band within laminites here, and the enigmatic plant *Parka* and a coprolite containing acanthodian spines were found *in situ*. On the east side of the den the excavation has penetrated to about 10 m below the surface, but no in-situ fish bed has been reported. While it is possible that the local fish bed crops out only on the western side of the Den, the area to the south-west may offer potential for the retrieval of further fossil vertebrates.

### *Fauna*

GNATHOSTOMATA
Acanthodii: Climatiiformes: Climatiidae
*Brachyacanthus* sp.
?*Euthacanthus* sp.
Acanthodii: Acanthodiformes: Ischnacanthidae
*Ischnacanthus* sp.
ARTHROPODA: Eurypterida
*Pterygotus* sp.
PLANTAE
*Parka* sp.

TRACE FOSSILS
arthropod trackway

The fish fauna is composed exclusively of acanthodians, genera of which are present in collections made from other localities within the Arbuthnott Group of this region and housed in several museums (Montrose Museum, National Museum of Scotland and the Natural History Museum). *Cephalaspis* has so far not been collected at Whitehouse Den.

## Interpretation

This site is one of three in the vicinity of Tealing village from which fossil fish now in museum collections may have been obtained in considerable number in the past. The laminites at this and other localities nearby have been interpreted by Trewin and Davidson (1996) as lacustrine deposits formed within the hydrologically open Lake Forfar under a seasonal climatic regime. The lake floor may have been poorly oxygenated and laminite deposition was terminated by the influx of silts and current-rippled sands.

The acanthodian fish fauna indicates an active mid- to upper-water population of small predatory species. The food supply was, presumably, invertebrates, living in or near aquatic or water-margin vegetation. The significance of the ash fall for the lake ecology is not clear, but it may have produced a short episode of toxicity and increased fish mortality.

### *Comparison with other sites*

As stated above, two localities in the neighbourhood of Tealing village have yielded acanthodian fishes from a lithology similar to that at Whitehouse Den. It is probable that all are at the same horizon and include the pale clay noted by Powrie (1864) as common to many fish beds locally. The section at Tillywhandland is now the most completely investigated and was the main source of specimens in laminite lithologies, labelled 'Turin Hill' (Trewin and Davidson, 1996). However, it is not considered that Tillywhandland and Whitehouse fish beds are at the same level in the succession (Armstrong and Peterson, 1970).

## Conclusion

Recent investigation of this site has shown that its conservation value lies in its potential as a source of fossil acanthodians, some of which may be well preserved. It may also yield fossil taxa such as cephalaspids found hitherto at Tillywhandland and other sites not far away.