

J.N.C.C.

Fossil Fishes of Great Britain

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Chapter 2

Silurian fossil fishes sites of Scotland

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INTRODUCTION: SILURIAN PALAEOGEOGRAPHY AND STRATIGRAPHY

For much of the early part of the Palaeozoic Era the continents and oceans were very differently disposed from their present arrangement. What has become the north-western part of the European continent was at that time distributed between several continental fragments, or 'terranes'. The seas between them received sediment that was to become strata comprising the Lower Palaeozoic systems of the stratigraphical column. There was continuous movement of the continental masses relative to one another as the processes of oceanic crustal growth and subduction took place. These movements gathered the continents largely into the southern hemisphere and there was also a marked succession of changes in global sea level. Figure 2.1. shows the outcrop of Silurian rocks in the British Isles.

British Lower Palaeozoic stratigraphy shows the influence of each of these dynamic processes and its (Lower Palaeozoic) palaeontology

shows evidence of palaeobiogeographical provincialism. All of this was terminated by the closure of the Iapetus Ocean and the suturing of terranes together to give the Laurussian continent. Thus late Silurian stratigraphy in southern Scotland originated under different conditions and was relatively farther removed from those of England and Wales. The continental collision(s) which produced the northern landmass of Siluro-Devonian times, the Caledonian earth movements, began in the mid- to late Silurian and continued with strong lateral fault activity late into the Devonian period.

During the early part of the Silurian period, Scotland lay in two separate terranes, the northern area forming part of the North American province (Laurentia), and the southern part being attached to Avalonia (i.e. southern Britain and part of western continental Europe; Figure 2.2) (Bassett, 1992). The Iapetus Ocean, which had existed through the earlier part of the Palaeozoic, was narrowing, and final closure was to occur at the end of the Silurian. Thus the once ocean-separated landmasses collided along a suture line that runs across northern England, under the Solway Firth, and across Ireland in a south-westerly direction from near Dublin to just south of the Dingle Peninsula (Figure 2.2).

Throughout Llandovery and Wenlock times (early and mid Silurian), the Southern Uplands area was a diminishing oceanic basin. At its northern margin lay shallower water, from which we have marine strata that occur now within inliers in the Midland Valley, and fossil fishes are found in some of these. Farther north in Argyll, local Old Red Sandstone facies accumulated. In the late Silurian (Ludlow and Přídolí epochs) uplift occurred in the Southern Uplands area, and consequently there is no evidence of deposition for that time in this region. However, the Midland Valley inliers may include sediments that extend into the Ludlow (Cocks *et al.*, 1992). In the the Stonehaven area of the northern part of the Midland Valley (Figure 2.3), some of the continental sediments have yielded fishes, arthropods and land plant debris.

In the typical Southern Uplands Llandovery–Wenlock successions fossil fishes are unknown, but they do occur high in the sequences in the Lesmahagow and Hagshaw Hills inliers in the Midland Valley (Figures 2.3 and 2.4). The stratigraphy of these inliers has been described by Rolfe (1961), Walton (1965), and Robertson (1989). However clear biostratigraphical indices

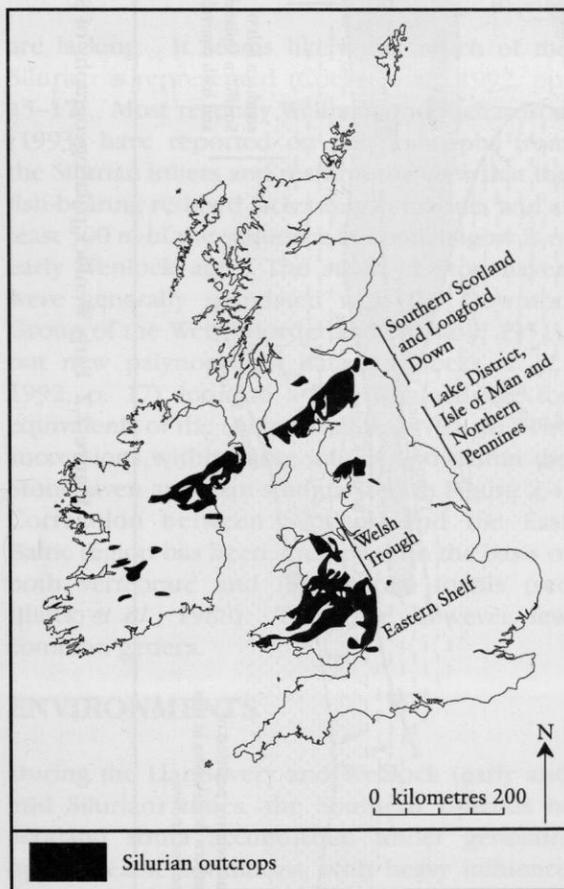


Figure 2.1 Silurian outcrops in Britain.

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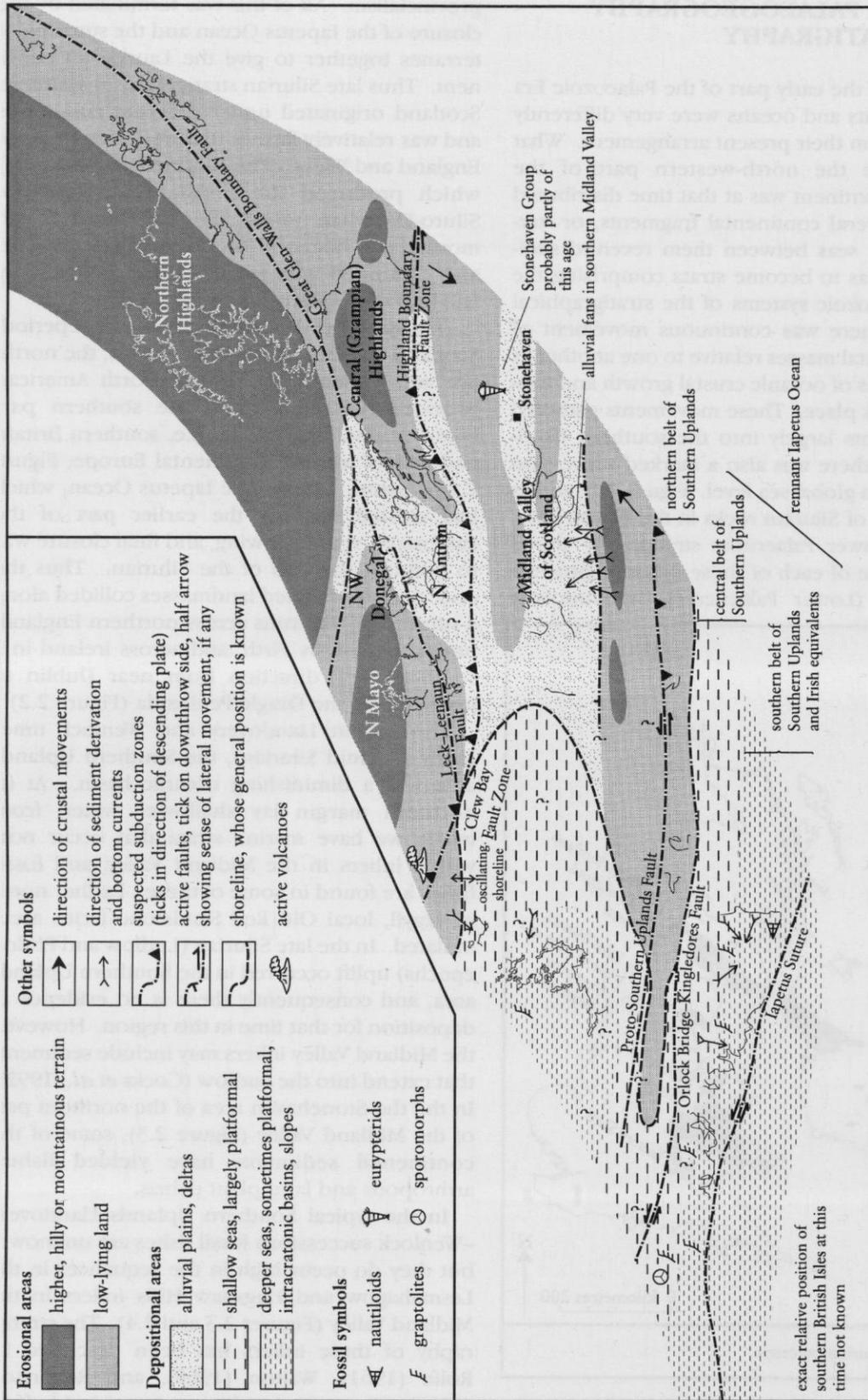


Figure 2.2 Early Wenlock palaeogeography of Scotland (after Bassett, 1992).

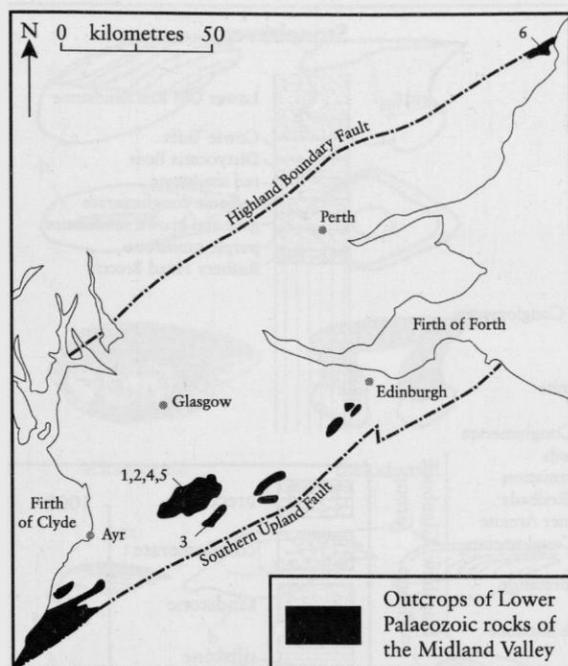


Figure 2.3 Location map of the Lower Palaeozoic inliers of the Midland Valley, showing GCR sites 1-6.

are lacking. It seems likely that much of the Silurian is represented (Cocks *et al.*, 1992, pp. 15-17). Most recently Wellman and Richardson (1993) have reported on palynomorphs from the Silurian inliers and reaffirm the view that the fish-bearing red-bed facies is non-marine, and at least 500 m of the sequence at Lesmahagow is of early Wenlock age. The strata at Stonehaven were generally correlated with the Downton Group of the Welsh Borderland (Westoll, 1951), but new palynomorph data (in Cocks *et al.*, 1992, p. 17) indicate a late Wenlock age for equivalents of the *Dictyocaris* Beds (Band). The successions within these inliers, and within the Stonehaven area, are summarized in Figure 2.4. Correlation between Scotland and the East Baltic region has been attempted on the basis of both vertebrate and invertebrate fossils (see Blicek *et al.*, 1988). There are, however, few common genera.

ENVIRONMENTS

During the Llandovery and Wenlock (early and mid Silurian) times, the Southern Uplands of Scotland strata accumulated under generally open oceanic conditions, with heavy influence from turbidites which fed in from the opposing (northern and southern) margins of the con-

verging continental plates. The Midland Valley inliers south of Glasgow, close to the northern margin of the seaway, show evidence of a mix of shallow marine and (increasing) continental conditions of deposition, while at Stonehouse to the north-east the sediments are non-marine (Figure 2.4).

FISH FAUNAS

By Silurian times the major groups of agnathans and the gnathostomes had become distinct. They were essentially marine organisms throughout most of that period, but freshwater vertebrate faunas were beginning to evolve by Přídolí times or somewhat earlier. This is clear from the record in the undisturbed Silurian of the eastern Baltic and is supported in Scotland, which is clearly part of the same palaeobiogeographical province of that time (Blicek and Janvier, 1991).

The fishes from the Scottish Silurian sites include primitive agnathan forms, and some obscure animals whose affinities are uncertain. At certain levels in some sites these fossils are relatively common. The commonest elements of the fauna are thelodont agnathans, such as *Loganellia scotica* and other species, as well as species of *Lanarkia*. Other fishes include the anaspids *Birkenia* and *Lasanius*, and cephalaspids such as *Ateleaspis*. Rarer specimens include the enigmatic *Jamoytius*, a naked agnathan, and *Aniktozoon*, a problematic fossil, which was thought to have chordate affinities but has recently been diagnosed as belonging to a group of extinct crustaceans (see Birk Knowes report).

AGNATHA

Thelodonti: Thelodonta: Coelolepididae

Thelodus planus Traquair, 1899

Thelodus sp.

Thelodonti: Thelodonta: Turinididae

Turinia pagei (Powrie, 1870)

Thelodonti: Thelodonta: Phlebolepididae

Thelodonti: Thelodonta: Loganellidae

Loganellia scotica (Traquair, 1899)

Sbielia taiti (Stetson, 1931)

Lanarkia horrida Traquair, 1898

L. spinosa Traquair, 1898

L. spinulosa Traquair, 1898

Anaspida: Jamoytiiformes: Jamoytiidae

Jamoytius kerwoodi White, 1946

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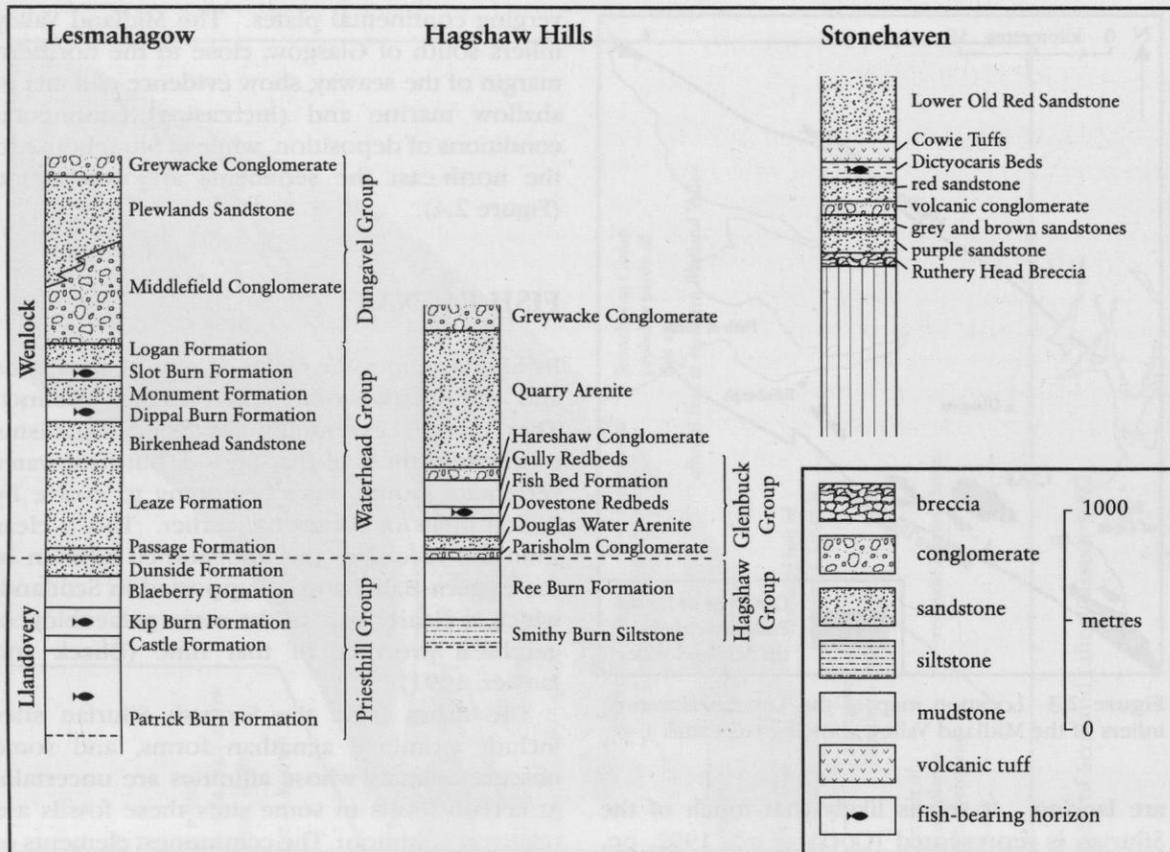


Figure 2.4 Silurian successions in the inliers of the Midland Valley (after Cameron and Stephenson, 1984).

- Anaspida: Birkeniiformes: Birkeniidae
Birkenia elegans Traquair, 1899
- Anaspida: Birkeniiformes: Lasaniidae
Lasanius problematicus Traquair, 1898
L. altus Smith, 1958
L. ornatus Traquair, 1899
- Osteostraci: Ateleaspidiformes: Ateleaspididae
Ateleaspis tessellata Traquair, 1899
Hemiteleaspis heintzi Westoll, 1945
'Cephalaspis' lornensis Traquair 1898
'Cephalaspis' sp.
- Incertae sedis*
 Petromyzontid?
Monkolepis maculatus Ritchie MS
- Heterostraci: Phialaspidiformes:
 Traquairaspididae
Traquairaspis campbelli (Traquair, 1912)
- GNATHOSTOMATA
- Acanthodii: Acanthodiformes: Acanthodidae
Mesacanthus cf. mitchelli (Egerton, 1861)
- Gnathostomata: Placodermi: Arthrodira
 Arthrodira indet.

Thelodonts were a group of small enigmatic fishes recently discovered to be more diverse than previously thought, and whose entire body was covered with denticles (Turner and van der Bruggen, 1993; Wilson and Caldwell, 1993; Vergoossen, 1992). Their remains are commonly isolated denticles, articulated specimens are rare. In the Scottish Silurian localities, however, articulated thelodont specimens have been found in marine sediments, and these show evidence of true branchial respiratory structures. Discovered in the late 19th century, they have been most important in the interpretation of thelodont anatomy. Our understanding of thelodont anatomy has also been extended by the discovery of groups of internal denticles or denticle-bearing plates inside the snout, within the centre of the headshield and near the branchial openings. Van der Bruggen and Janvier (1993) wondered if some of these denticles were to divert part of the water flow towards the nasal cavities. This may mean that thelodonts had a large median inhalent duct leading to the nasal sacs, and pharyngeal denti-

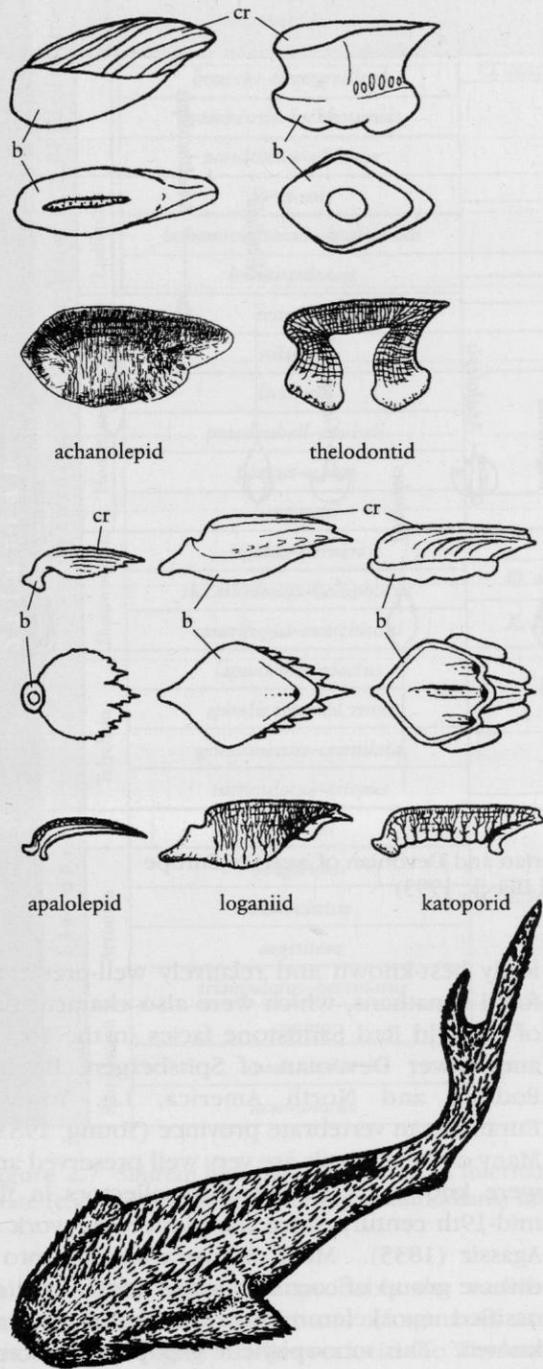


Figure 2.5 The five basic types of thelodont scales, lateral and basal views and sagittal section to show the typical structure: b, base; cr, non-growing crown. The thelodont *Lanarkia* bears large spine-like scales as well as small rotund denticles in regular rows (after Turner, 1973).

cles or tooth-whorls, as would be expected in a theoretical pre-gnathostome. Canadian thelodonts also now suggest a more advanced anatomy than previously thought, with well-formed stomachs and scale structures like those of sharks (Wilson and Caldwell, 1993). Even isolated denticles may be characteristic enough to indicate the species represented, and then to be used in biostratigraphical correlation. Thelodont denticles are important for correlation of both marine Silurian and 'Old Red Sandstone' facies rocks of Silurian and Devonian age which lack other diagnostic fossils, particularly in the East Baltic region (Märss, 1986; Märss *et al.*, 1995; Figures 2.5 and 2.6). Turner (1973) recognized three Silurian thelodont provinces in the northern hemisphere, two of which are found in Britain: the first is present in the Welsh Borders; and the second in the Lesmahagow and Hagshaw Hills inliers, at Ringerike, southern Norway, and in Siberia. This provides evidence regarding the pairing of the Scottish and Baltic fish faunas as a faunal province separate from that of the Anglo-Welsh Borders, and this distributional dichotomy is maintained through the Silurian and early Devonian. It may reflect the separation of the northern and southern basins by an upland extending from North Wales to the southern Baltic.

A recently proposed global microvertebrate zonation of the Silurian system is based largely on thelodonts, with a few acanthodians (Märss *et al.*, 1995). The index species *Loganellia avonia* comes from the Brinkmarsh Beds of the Tortworth inlier, Gloucestershire, while the *Nostolepis gracilis* and *Poracanthoides punctatus* biozones have acanthodian index species. The Devonian follows with the thelodont biozone of *Turinia pagei* (Karatajute-Talimaa, 1978).

The anaspids were a small group of agnathan fishes, including the four orders to which belong respectively *Birkenia*, *Endeiolepis*, *Euphanerops* and *Lasanius*, traditionally assumed to be closely related to the Osteostraci and possibly also to the living cyclostomes (Stensiö, 1958, 1964, 1968; Wängsjö, 1952; Ritchie, 1964; Janvier 1996; Janvier and Blicek 1980). This relationship has been disputed by Janvier (1981) who removed *Jamoytius* and *Endeiolepis* from the Anaspida, which then form a monophyletic group, possibly the sister-group of the Petromyzontiformes, the modern lampreys (Janvier, 1981, 1986). The group was estab-

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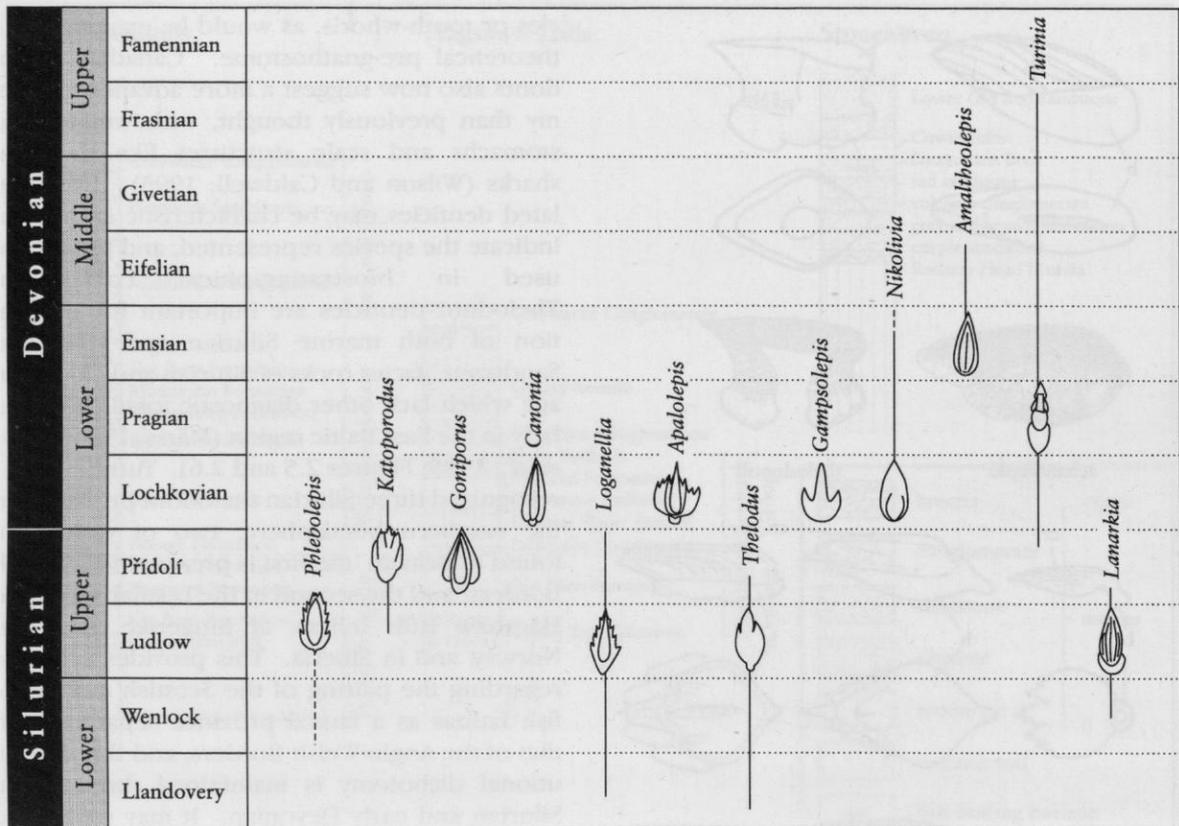


Figure 2.6 Thelodont ranges in the Silurian and Devonian of western Europe (after Janvier and Blicek, 1993).

lished by Traquair (1899a) for two new Scottish genera, *Birkenia* and *Lasanius* from the upper Silurian fish beds of the Lesmahagow and Hagshaw Hills inliers. Since then, specimens have been found elsewhere, in strata dating from the upper Wenlock (Britain, Arctic and western Canada) to the lower Frasnian (Canada). Anaspids are very rare and are mostly known only from fragments or isolated scales. Only in the southern Scottish inliers may British specimens be collected in any numbers. Textbook reconstructions are based mainly upon *Jamoytius*, *Birkenia* and *Lasanius* from the southern Scottish sites. *Birkenia* and *Lasanius* are known only from exoskeletal remains consisting of a large number of narrow, obliquely directed, articulating scales and a row of median dorsal ridge scales. Further material of well-preserved anaspids is now known from Canada, but descriptions have yet to be published. Meanwhile the Scottish sites are important possible sources of further material.

The osteostracans include some of the histor-

ically best-known and relatively well-preserved fossil agnathans, which were also characteristic of the Old Red Sandstone facies in the Přídolí and Lower Devonian of Spitsbergen, Britain, Podolia and North America, i.e. Young's Euramerican vertebrate province (Young, 1981). Many of these fossils are very well preserved and were known to local British collectors in the mid-19th century, since the pioneering work of Agassiz (1835). Most osteostracans fall into a diverse group of cornuate forms which have an ossified exoskeleton and are therefore well known. This monophyletic group is characterized by cornual processes, which are backwards-curving extensions on the head shield, in front of the single pair of fins. These processes have been lost independently by several subgroups, in the derived thyeistids and possibly also in the tremataspids, with their long ossified tadpole-shaped head and body shields (Janvier, 1981). The ancestry of the osteostracans has been traced to *Ateleaspis tessellata* from the upper fish beds of the Lesmahagow and Hagshaw Hills

Fish sites

Silurian	Series		Graptolites	Conodonts	Vertebrates	
	Stages					
	Přídolí		<i>bouceki-transgredlens</i>	<i>O. costeinhomensis</i> – <i>O. e. delorto</i>	<i>K. timanicus</i> – <i>K. lithuanicus</i>	
			<i>branikensis-lochkovensis</i>	<i>O. remscheidensis</i> interval zone	<i>P. punctatus</i> <i>N. gracilis</i>	
			<i>parultimus-ultimus</i>			
	Ludlow	Ludfordian		<i>formosus</i>	<i>O. crista</i>	<i>T. sculptilis</i>
				<i>bohemicus tenuis-kozlowskii</i>	<i>O. snajori</i> interval zone	
		Gorstian		<i>leintwardensis</i>	<i>P. siluricus</i>	<i>A. hedei</i>
				<i>scanicus</i>	<i>A. ploeckensis</i>	<i>P. elegans</i>
				<i>nilssoni</i>	not zoned	<i>P. ornata</i>
	Wenlock	Homerian		<i>ludensis</i>	<i>O. bohémica</i>	<i>P. martinssoni</i>
				<i>praedeubell-deubell</i>		
				<i>parvus-nassa</i>		
		Sheinwoodian		<i>lundgreni</i>	<i>O. sagitta sagitta</i>	<i>L. grossi</i>
				<i>rigidus-perneri</i>	not zoned	
				<i>riccariensis-belophorus</i>	<i>O. sagitta rhenana</i> – <i>K. patula</i>	<i>L. avonia</i>
				<i>centrifugus-murchisoni</i>	<i>K. ranuliformis</i> interval zone	
	Llandovery	Telychian		<i>lapworthi-insectus</i>	<i>P. amorphognathoides</i>	<i>L. scotica</i> – <i>L. sibirica</i>
				<i>spiralis</i> interval zone		
				<i>griestonensis-crenulata</i>	<i>P. celloni</i>	
				<i>turriculatus-crispus</i>		
		Aeronian		<i>guerichi</i>	<i>P. tenuis</i> – <i>D. staurogathoides</i>	
				<i>sedgwickii</i>		
				<i>convolutus</i>		
				<i>argenteus</i>		
				<i>triangulatus-pectinatus</i>		
			<i>cyphus</i>			
Rhuddanian		<i>vesiculosus</i>	<i>D. kentuckyensis</i>	<i>V. crista</i>		
		<i>acuminatus</i>				
					<i>O. ? nathani</i>	

Figure 2.7 Silurian biozones now of use in international correlation. The vertebrates are largely microvertebrate (e.g. scales of thelodonts and acanthodians) taxa (from Märss, 1986).

inliers. This material is probably the earliest known complete osteostracan (fragments are known from slightly earlier rocks in the Wenlock of Gotland; Gross, 1968a, 1968b) and hence is important in agnathan phylogeny. A second school of thought was that the non-cornuate tremataspids were the ancestral osteostracans (Westoll, 1945, 1979; Denison, 1951a, 1951b; Collins, 1981; Halstead, 1982), and then cornua and paired fins, together with reduced body armour and increasing flexibility, evolved secondarily.

At The Toutties locality has been found the

only undoubted Scottish Silurian heterostracan, *Traquairaspis campbelli* (Traquair). While this family Traquairaspididae is not known elsewhere in the Scottish-east Baltic region, it is found in Canada and in the Anglo-Welsh Basin.

FISH SITES

The policy in selecting Scottish Silurian fish sites has been simple. There are only five or six localities to consider, and each has produced such exceptionally important faunas; because of their age, early in the evolution of fishes, the quality

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of preservation and their role in the taxonomic history of Agnatha, all are designated as GCR sites. Two, Birk Knowes and Dunside, both in the Lesmahagow inlier, are dealt with first, since their fishes are the oldest, probably late Llandovery in age. Then the early Wenlock sites of the Hagshaw Hills (Shiel Burn) and Lesmahagow (Dippal Burn, Slot Burn, Birkenhead Burn) inliers are considered. Finally, two isolated and poorly dated, possibly mid or late Silurian sites are described, Ardmore–Gallanach in the Lorne lavas, and The Toutties, near Stonehaven. Excursion guides to the Hagshaw Hills and Lesmahagow Silurian inliers (Bluck, 1973; Lawson and Weedon, 1992) provide local details of the geology; a similar guide exists for the exposures at The Toutties and Lower Devonian sites in the Midland Valley (Friend and Williams, 1978).

COMPARISON WITH THE FAUNAS OF OTHER REGIONS

Agnathan faunas are now recognized as having an appreciable biostratigraphical value. From the pioneer work of White and Toombs (1948; White, 1950) in the middle part of the 20th century the recognition of distinct Silurian–Devonian vertebrate zones in the Old Red Sandstone facies of England and Wales has been extended to mainland Europe (Blieck, 1984; Janvier and Blieck, 1993), Spitsbergen (Blieck *et al.*, 1987), and Canada (Elliot, 1984; Dineley, 1990). This has largely been on the basis of the ranges of cyathaspidids and pteraspids, but Gross (1967), Turner (1973) and Karatajute-Talimaa (1978) have revealed the value of thelodonts in this field in Britain and the eastern Baltic–Russian outcrops. A recent review of the situation was given by Märss (1989), and the IGCP Project 328 (Palaeozoic microvertebrates) has encouraged further vertebrate biostratigraphical work on the Silurian (see LeLièvre *et al.*, 1995).

In Britain, Turner's (1973) work on the distribution of the thelodonts has remained the prime guide; it has been extended by Karatajute-Talimaa's survey (1978) of the Silurian thelodonts in what was USSR territory. The presence of Silurian vertebrate faunas is now confirmed on all continents except Antarctica; each has its own identity, although there are similarities between them. Märss provided the summary figure of distribution and biozones shown

in Figure 2.7; Spitsbergen should now be included.

The Scottish Silurian vertebrate sites are distinct from those of the Anglo-Welsh area in respect of both faunas and facies, which reflects the palaeogeographical separation of the two regions during that period. There is, as described above, however, some similarity between the sites in Scotland. Comparison with other regions may be made most closely in the case of the eastern Baltic succession. The Baltic–East European platform was a stable unit during Silurian–Devonian times, unlike Scotland, and a lateral passage of facies from offshore marine to freshwater-lagoonal exists at most levels. The vertebrates there are locally numerous and the faunas are more diverse than in Scotland.

There is no doubt that thelodont faunas from Canada and the USA (Turner, 1986), will be reported from many more localities in the future as palaeontological work there expands. Prospects in the Canadian Arctic are so far the most promising (Turner and Dixon, 1971; Dineley, 1992; Wilson and Caldwell, 1993). The Russian Arctic is also yielding abundant material.

BIRK KNOWES (SO 737346; SO 738348)

Highlights

The early Silurian fishes and fish-like organisms from Birk Knowes, near Lesmahagow in Strathclyde, are world-renowned. The strange naked fish *Jamoytius* is among the oldest-known complete jawless fishes, and it may lie close to the origin of the modern lampreys.

Introduction

The 'Jamoytius horizon' (Figure 2.8) outcrops at Birk Knowes, at three small exposures on Logan Water, in the Lesmahagow inlier. The present exposures are indifferent, but could be developed well with care. The fauna is restricted to two species, *Loganellia scotica* and *Jamoytius kerwoodi*, with a possible third, *Thelodus planus*, recorded by Traquair (1898a, 1898b), but regarded by Ritchie (1968) as dubious. The problematic arthropod *Ainiktozoon loganense* Scourfield also occurs. These are associated with a fauna dominated by arthropods (Ritchie, 1968, pp. 24–5).

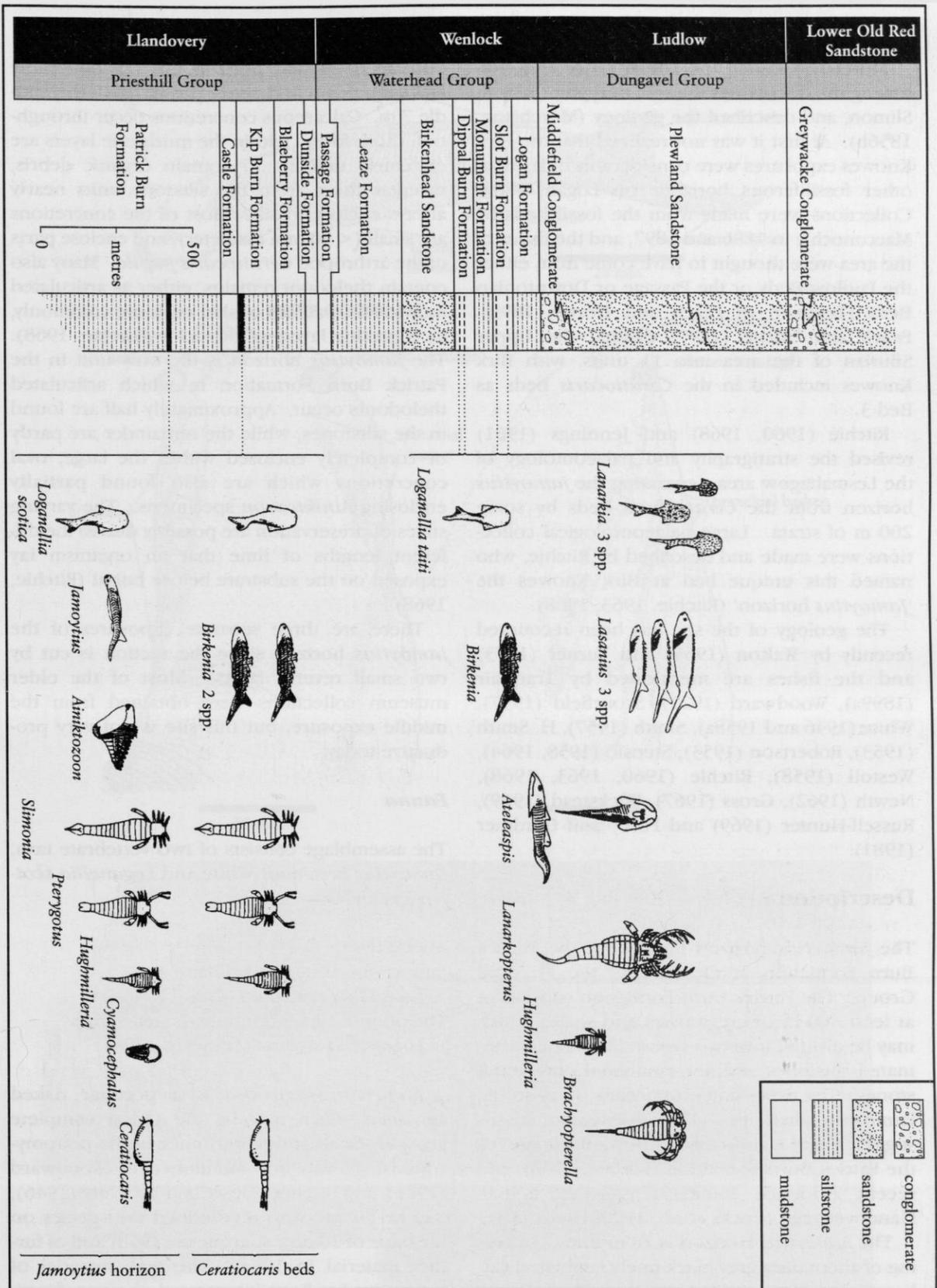


Figure 2.8 The Silurian succession in the Lesmahagow inlier (from Ritchie, 1985). Three vertebrate–arthropod faunal assemblages are distinguished: the *Jamoytius* horizon (lowest), the *Ceratiocaris* Beds in the Kip Burn Formation, and the (latest) fish beds in the Dippal Burn and Slot Burn Formations. *Ainiktozoon* is known only from the *Jamoytius* horizon.

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Murchison visited the Logan Water area, following the discoveries there of eurypterids by R. Slimon, and described the geology (Murchison, 1856b). At first it was not realized that the Birk Knowes exposures were considerably older than other fossiliferous horizons on Logan Water. Collections were made from the fossil beds by Macconochie in 1896 and 1897, and the fishes of the area were thought to have come from either the Ludlow Beds or the Passage or Downtonian Beds (Traquair, *in* Peach and Horne, 1899). Peach and Horne (1899) divided the Upper Silurian of the area into 11 units, with Birk Knowes included in the *Ceratiocaris* beds as Bed 3.

Ritchie (1960, 1968) and Jennings (1961) revised the stratigraphy and palaeontology of the Lesmahagow area, separating the *Jamoytius* horizon from the *Ceratiocaris* Beds by some 200 m of strata. Large palaeontological collections were made and described by Ritchie, who named this unique bed at Birk Knowes the 'Jamoytius horizon' (Ritchie, 1963, 1968).

The geology of the site has been recounted recently by Walton (1965) and Turner (1973) and the fishes are mentioned by Traquair (1899a), Woodward (1921), Scourfield (1937), White (1946 and 1958a), Smith (1957), H. Smith (1953), Robertson (1953), Stensiö (1958, 1964), Westoll (1958), Ritchie (1960, 1963, 1968), Newth (1962), Gross (1967), Wickstead (1969), Russell-Hunter (1969) and Forey and Gardiner (1981).

Description

The *Jamoytius* horizon lies within the Patrick Burn Formation at the base of the Priesthill Group. The Patrick Burn Formation consists of at least 400 m of greywackes and shales which may be divided into two types: dark, finely laminated siltstones and non-laminated olive mudstones. The fishes and crustaceans occur in the laminated siltstones. The invertebrate fossils suggest a late Llandovery-early Wenlock age for the Patrick Burn Formation (Ritchie, 1968), and recent evidence indicates possibly a late Llandovery age (Cocks *et al.*, 1992; Figure 2.8).

The *Jamoytius* Horizon is 10 m thick, consisting of alternating grey-black finely laminated carbonaceous siltstones and non-laminated olive to greyish green mudstones. Macroscopic remains are almost entirely confined to the organic-rich laminated siltstones. The fossils occur through-

out the *Jamoytius* horizon but are noticeably more abundant and better preserved in the middle 7 m. Calcareous concretions occur throughout; those found within the mudstone layers are extremely unlikely to contain organic debris, whereas those from the siltstone units nearly always enclose fossils. Most of the concretions are small (< 50 mm diameter), and enclose parts of the arthropod *Ceratiocaris papilo*. Many also contain thelodont remains, either as articulated individuals, patches of skin or, more commonly, as coprolitic layers of denticles (Ritchie, 1968). The *Jamoytius* horizon is the only unit in the Patrick Burn Formation in which articulated thelodonts occur. Approximately half are found in the siltstones, while the remainder are partly or completely enclosed within the large, oval concretions which are also found partially enclosing *Ainiktozoon* specimens. The varying states of preservation are possibly due to the different lengths of time that an organism lay exposed on the substrate before burial (Ritchie, 1968).

There are three separate exposures of the *Jamoytius* horizon since the section is cut by two small reverse faults. Most of the older museum collections were obtained from the middle exposure, but this site is not very productive today.

Fauna

The assemblage consists of two vertebrate taxa, *Jamoytius kerwoodi* White and *Loganellia scotica* Traquair.

AGNATHA

Jamoytiiformes: Jamoytiidae

Jamoytius kerwoodi White, 1946

Thelodonti: Thelodontida: Loganellidae

Loganellia scotica (Traquair, 1899)

Jamoytius kerwoodi is a peculiar naked agnathan which may be the oldest complete anaspid, or an early forerunner of the petromyzontids. It was first mentioned by Woodward (1921), and has been described by White (1946), and by Ritchie who redescribed the species on the basis of 20 new specimens (1968) and of further material in 1984. The type material of *Jamoytius* has been interpreted as many things, and until recently was usually classified with the anaspids (Robertson, 1953; Stensiö, 1958; Ritchie, 1960, 1968). Re-examination of speci-

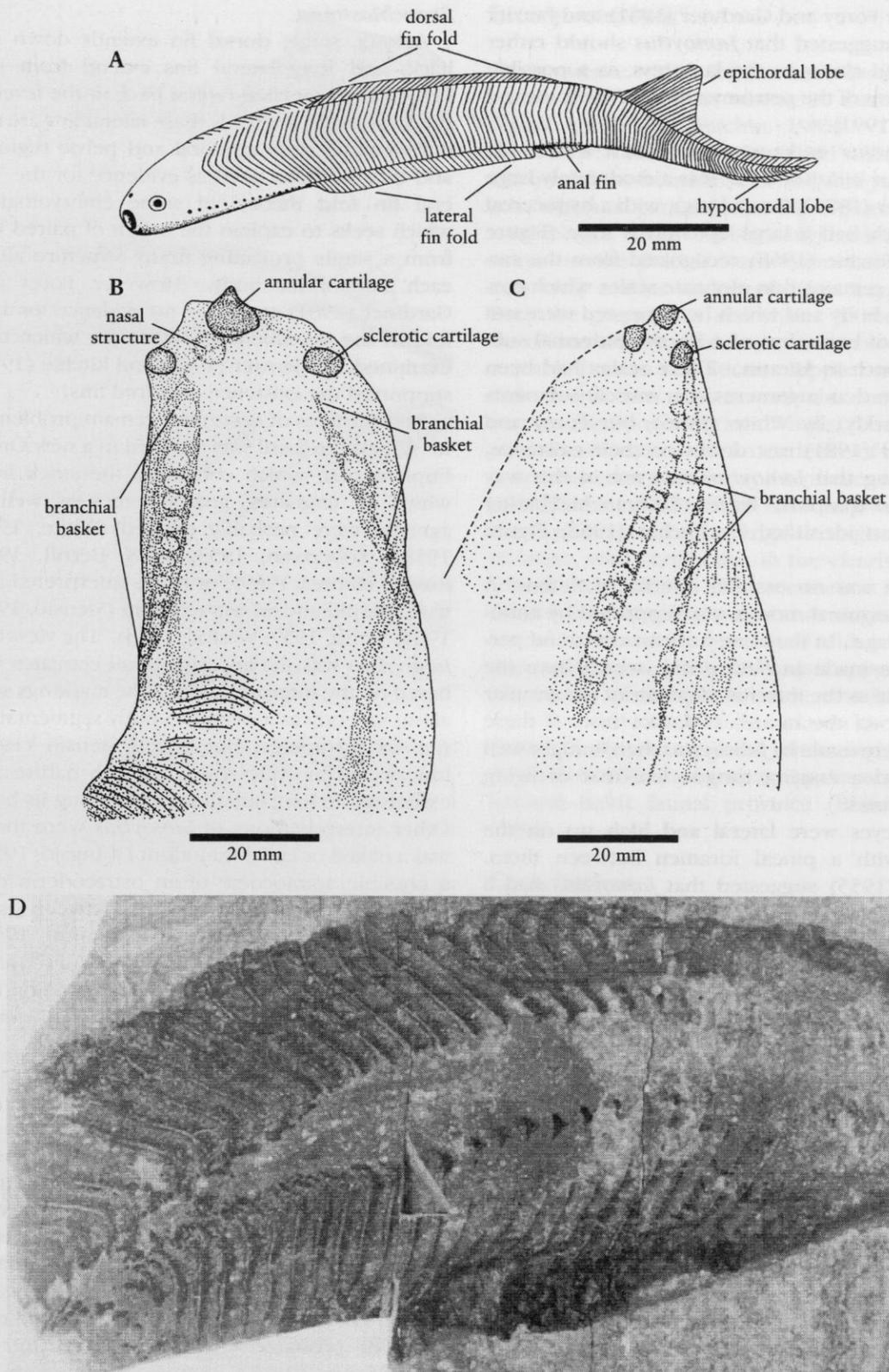


Figure 2.9 (A) a reconstruction of *Jamoytius kerwoodi* White by Ritchie (1968); (B) anterior end of a specimen from Logan Water with poorly preserved trunk scales; (C) anterior end of specimen with no trunk scales visible; (D) part of trunk of *J. kerwoodi* showing somites $\times 1.5$ (GLAHM 101382), Birk Knowes, Upper Llandovery, photographed under water (Photo: courtesy of the Hunterian Museum, Glasgow).

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mens by Forey and Gardiner (1981) and Janvier (1981) suggested that *Jamoytius* should rather be placed closer to the lampreys, as a possible sister-form of the petromyzontids (Arsenault and Janvier, 1991).

Jamoytius is known only from the single species at Birk Knowes. It is a moderately large agnathan (180–200 mm long), with a hypocercal tail which had a large epichordal lobe (Figure 2.9A). Ritchie (1968) recognized from the carbonized remains thin elongate scales which covered the body and which he suggested were not formed of bone, but of a horny epidermal substance such as keratin. These scales had been interpreted as myomeres (i.e. muscle segments of the body) by White (1946), but Forey and Gardiner (1981) cast doubt on their existence, suggesting that *Jamoytius* was not in this way similar to anaspids. Traces of a branchial basket were also identified by Ritchie (1968; Figure 2.9B).

There was no ossified internal skeleton. A simple terminal mouth was supported by annular cartilage. In the same horizon are round perforations made in *Dictyocaris* which have the same size as the internal diameter of the annular cartilage of the mouth of *Jamoytius*. If these holes were made by *Jamoytius* then it might well have had a rasping tongue like that of living cyclostomes.

The eyes were lateral and high up on the head, with a pineal foramen between them. Berrill (1955) suggested that *Jamoytius* had a pair of widely separated eyes with relatively large eye-cups which were primitive and similar to those of a developing lamprey larva. Ritchie (1968) found specimens that showed the branchial apparatus, which indicated that *Jamoytius* could not have been an ancestor of the modern Acraniata, but this was in turn dismissed by Wickstead (1969) who stated that there were in fact close similarities between the branchial structure of *Jamoytius* and that of the lancelet (*Branchiostoma*) during metamorphosis. Wickstead's (1969) interpretation of *Jamoytius* as a possible immature acraniate that showed both adult and larval characters, i.e. with gills, in the form of pouches surrounded by a branchial basket, as in larval *Branchiostoma*, was not accepted by later investigation. Forey and Gardiner (1981) and Janvier (1981) argued that *Jamoytius* is closer to present-day lampreys, and that the branchial basket, paired eyes and annular cartilage are not features of larval

Branchiostoma.

A long, single dorsal fin extends down the back, and long lateral fins extend from just behind the branchial region back to the level of the anal fin. In anaspids these lateral fins are not differentiated into pectoral and pelvic regions, and this has been used as evidence for the 'lateral fin fold theory' of some embryologists, which seeks to explain the origin of paired fins from a single projecting fleshy structure along each side of the body. However, Forey and Gardiner (1981) could see no evidence for a fin fold in the specimens of *Jamoytius* which they examined, but Janvier (1981) and Ritchie (1984) supported the existence of paired fins.

The affinities of *Jamoytius* remain problematic. At first the fossil was ascribed to a new Order Euphanerida, which contained the stock from which all craniates, gnathostomes as well as agnatha were probably derived (White, 1946, 1958a; Robertson, 1953, 1958; Berrill, 1955; Russell-Hunter, 1969), or it was interpreted as a true anaspid and an ostracoderm (Stensiö, 1958, 1964; Smith, 1957; Westoll, 1958). The view that *Jamoytius* was the ancestor of all craniates was based on the interpretation of the markings seen along its body as a primitive body segmentation (i.e. as myomeres; but which Stensiö (1958) interpreted as scale rows) and the nature and extent of the long lateral fin folds along its body. Other interpretations of *Jamoytius* were that it was a naked or larval thelodont (Wängsjö, 1952), a possible ammocoete of an ostracoderm or a secondarily naked intermediary between ostracoderms and *Branchiostoma* (Smith, 1953). Ritchie recently (1984) added a new description of *Jamoytius* and has reiterated his opinion that the genus is probably a close relative, if not an ancestor, of the petromyzontids.

Loganellia scotica (Traquair, 1898a) occurs both in the *Jamoytius* horizon and in the younger fish beds of the Lesmahagow and Hagshaw Hills inliers at Shanks Castle, Seggholm, Birkenhead Burn and Shiel Burn. The type locality is Dunside, but Birk Knowes is the earliest Scottish occurrence and the site of the first report of complete articulated thelodonts. Other thelodont remains in the formation consist of pockets of disarticulated denticles of probable coprolitic origin (Ritchie, 1968; Figure 2.10).

Loganellia scotica was originally named *Thelodus scoticus* by Traquair and described by him in 1898. Gross (1967) split the previously

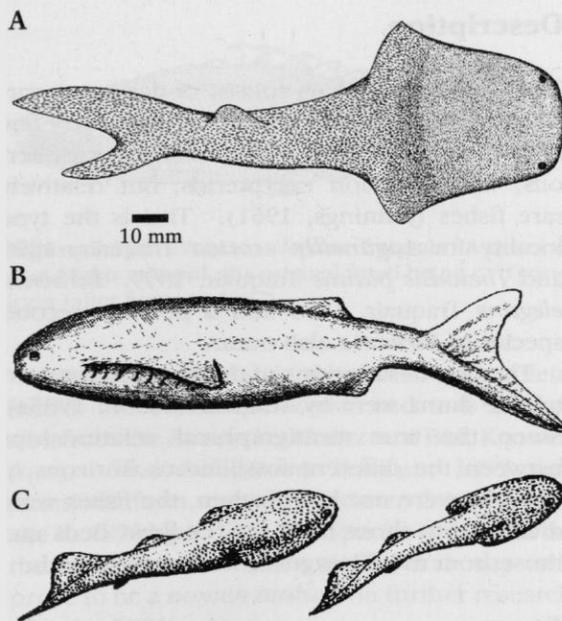


Figure 2.10 The thelodont *Loganellia scotica* (Traquair); (A) Traquair's original reconstruction in dorsal view (from Miles, 1971); (B) Turner's (1970) reconstruction in lateral view; (C) Janvier's (1996) representations of *Turinia*.

described '*Thelodus scoticus*' into five species of which *Loganellia scotica* was one. J.M. Vergoossen (1992) has described 'scale sets', several scales fused together, from the branchial areas of the *L. scotica* from the '*Jamoytius*' horizon, and it is apparent that there are remaining problems in the interpretation of thelodont scale variations and patterns. *L. scotica* also occurs in Oesel (Estonia), Germany, Siberia and Timan and is used for correlation between these areas and Britain. The species ranges in age from late Llandovery to Wenlock, and has been regarded as a marine form with a wide geographical range within the Euramerica province. *Ainiktozoon loganense* Scourfield was described from a collection of 29 specimens in the Hunterian Museum, Glasgow, and Ritchie (1968, p. 24) found several more specimens, describing its occurrence as 'moderately common'. The material has also been described by Russell-Hunter (1969), Ritchie (1985) and most recently Bruggen *et al.* (1997). The new work (Bruggen *et al.*, 1997) shows that *Ainiktozoon* is clearly an arthropod with affinities to the extinct thylacocephalan crustaceans.

Interpretation

The sequence within the Priesthill Group represents a transition from marine to fluviatile and deltaic conditions (Ritchie, 1985). Thus the *Ceratiocaris* Beds were deposited under different conditions from those of the *Jamoytius* horizon, which in part explains the different faunal assemblages. The fossil-bearing laminated siltstones in the Patrick Burn Formation are the only truly marine sediments (Jennings, 1961). Both the greywackes and shales of the Patrick Burn Formation have slump structures reflecting unstable bottom conditions. Ripple marks indicate current directions towards the north-northeast for the Formation as a whole. The bottom muds were anoxic with no evidence of benthonic or infaunal organisms, and molluscs were very rare (Ritchie, 1968). The Baltic equivalents of the Lesmahagow rocks range through a variety of facies, with vertebrates in the clearly marine (Blieck *et al.*, 1988). The vertebrates from the three fish-bearing horizons are amongst the oldest in Britain and are typically of mid- or surface-water swimmers. Only *Ateleaspis* appears to be adapted to a benthonic lifestyle. Similar faunas are found in Mid-Silurian rocks in the eastern Baltic. These taxa are so far not known from the Anglo-Welsh Silurian and are perhaps part of a Scottish-Baltic faunal province (Blieck *et al.*, 1988).

Conclusion

Birk Knowes is one of the key Silurian vertebrate localities in the British Isles. It is the source of the extraordinary fossil fish *Jamoytius* which is so important to the understanding of relationships between fossil and living agnathans. The locality has the advantage of being datable by the presence of good specimens of the thelodont *Loganellia scotica* and can be correlated to the Wenlockian of the East Baltic (Märss, 1986). Its early date and the nature and number of the fossil vertebrates make it of high conservation value.

DUNSIDE (SO 746362, SO 751371) (POTENTIAL GCR SITE)

Highlights

This site, near Lesmahagow in Strathclyde, is the original type locality of the rare primitive

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thelodont *Loganellia scotica*. Other early fishes have been found here, and the site is internationally important because of the rarity of such ancient fish assemblages.

Introduction

A stream section on Logan Water in the Lesmahagow inlier exposes the only known outcrop of the fish-bearing *Ceratiocaris* Beds. These are the lowest beds of the Kip Burn Formation of the Priesthill Group, of latest Llandovery or earliest Wenlock age (Figure 2.8). Murchison visited the area following the discovery of eurypterids by Robert Slimon, and subsequently published a description of the geology (Murchison, 1856b). Hunter (1885) gave the first written record of fishes collected from a nodule horizon at this site. Slimon had collected specimens of *Thelodus* and *Birkenia* during his original survey, but these remained unrecognized until his collection was re-examined following the description of fishes from other collections (MacNair, 1905). At this stage it was not realized that the Birk Knowes exposures were older than those on Logan Water and the fish species were all grouped together.

The geology of the site has been described by Murchison (1856b) and more recently by Jennings (1961), and the fish fauna by Hunter (1885), Traquair (1899b, 1905a) and MacNair (1905; see Figures 2.4 and 2.8).

Description

The *Ceratiocaris* Beds consist of dark grey, carbonaceous, laminated siltstones with a very few olive mudstone bands. They are very fossiliferous, with common eurypterids, but relatively rare fishes (Jennings, 1961). This is the type locality for *Loganellia scotica* Traquair, 1899 and *Thelodus planus* Traquair, 1899. *Birkenia elegans* Traquair, 1899 and a possible second species of *Birkenia* also occur.

The first descriptions of the Lesmahagow vertebrate fauna were by Traquair (1899b, 1905a). Since the true stratigraphical relationships between the different fossiliferous horizons in the area were not known then, the fishes were divided into those from the 'Ludlow' Beds and those from the 'Passage' or Downtonian beds.

Fauna

AGNATHA

Thelodonti: Thelodontida: Loganellidae

Loganellia scotica Traquair, 1898

Anaspida: Birkeniiformes: Birkeniidae

Birkenia elegans Traquair, 1898

Traquair described *Thelodus scoticus* and *T. planus*, both of which must have come from this site, and an indeterminate form from the 'Ludlow' Beds, and he listed *Birkenia elegans* as coming from the 'Passage' Beds.

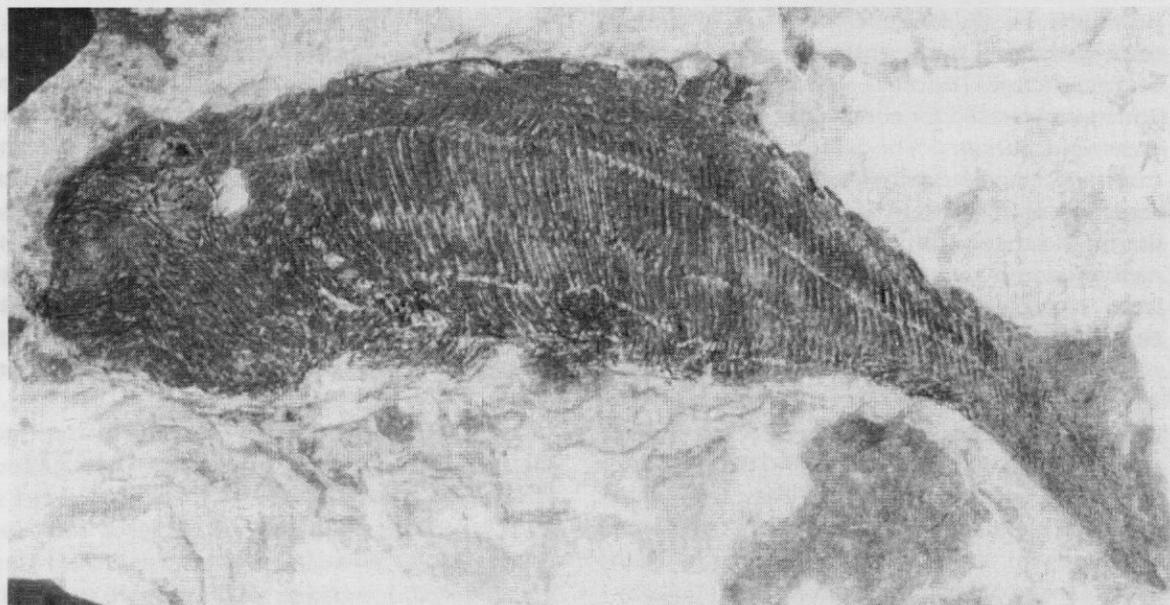


Figure 2.11A *Birkenia elegans* Traquair. Well-preserved specimen from the ?Wenlockian of Birkenhead Burn, Shanks Castle, photographed under water, $\times 2$, GLAHM V 8384 (Photo: courtesy of the Hunterian Museum, Glasgow).

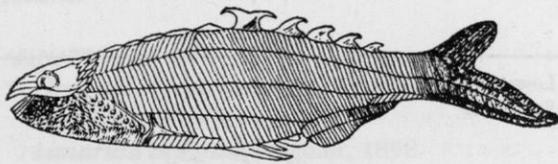


Figure 2.11B *Birkenia elegans* Traquair. A restoration of this anaspid, the original fossil being c. 10 cms long (after Stetson, 1927).

Loganellia scotica is the earliest, complete British articulated thelodont, and it is known also from the *Jamoytius* Horizon at Birk Knowes (q.v.). *Thelodus planus* Traquair, 1899 was described from a single specimen found at the site in 1898 by A. Tait. The species is defined on the ornamentation of the scales, and may well prove to be a *nomen nudum* on further research (Turner, 1991).

Birkenia is rare in the *Ceratiocaris* Beds, but is the most common fish in the overlying fish beds of Lesmahagow and the Hagshaw Hills (see Shiel Burn and Slot Burn reports). The finds here are the stratigraphically lowest record of *Birkenia* in Scotland, and the material may represent a new species, rather than *B. elegans* as recorded (Figure 2.11A, B).

Interpretation

The locality at Dunside has produced a very similar vertebrate and arthropod fauna to that at Birk Knowes, but it dates from a slightly younger formation. The main differences between the two assemblages lie in the absence of *Jamoytius* and *Ainiktozoon* at Dunside, and the presence there of *Birkenia*. *Birkenia* cf. *elegans* was recently reported together with thelodont denticles from County Mayo, north-western Ireland (Palmer *et al.*, 1989), in a postulated extension of the Midland Valley of Scotland. The implication is of an aquatic connection between these two areas, some 500 km or more in length (see Figure 2.2).

Conclusion

The conservation value of this key early Silurian fish site lies in its remarkable fauna of up to four fish species, associated with predatory eurypterid arthropods. It differs from the nearby older site, Birk Knowes, in the presence of the anaspid fish *Birkenia*.

SHIEL BURN (SO 777291)

Highlights

A rich fauna of up to ten species of fishes, including representatives of three major groups, occurs in two horizons. Silurian fishes are very rare globally, and this is the best and richest fish site in the Hagshaw Hills area, Strathclyde.

Introduction

Shiel Burn on Shiel Hill drains into Monks Water in the Hagshaw Hill inlier (Figure 2.12). Several exposures of a fish-bearing bed have been discovered in the Fish Bed Formation (Rolfe, 1960, 1961). One occurs on the bank of Glenbuck Loch, and the other on Shiel Burn. The Fish Bed Formation is part of the Glenbuck Group, dated as perhaps early Wenlock in age (Cocks *et al.*, 1992). Discoveries there date back to the 19th century. In 1896 Macconochie found fragments of fishes in the Lesmahagow and Hagshaw Hills inliers for the Geological Survey, between 1897 and 1899 he and Tait collected much of the material described by Traquair (1898b, 1899b, 1905a). This material included the first known anaspids and the first articulated thelodonts.

Description

On Shiel Burn the two units of the fish bed are 18 m apart (Figure 2.13), exposed at the head of a waterfall above an excavated slot, in the north bank of the burn. The lower, poorly fossiliferous unit is 0.6–0.9 m thick; the upper unit is 1.2–1.5 m thick and is subdivided into an upper laminated part with common anaspids and thelodonts and a lower, poorly laminated part with only a few fish remains which are commonly disarticulated but may otherwise be well preserved (Ritchie, 1963). The fish specimens occur in a dark grey finely laminated siltstone, and they are initially hard to detect since they are preserved flat. After some weathering, however, the fossils appear ochreous, and detail can be highlighted by immersion in water.

The fishes include a number of thelodonts, anaspids and cephalaspids, as described below (Slot Burn), since this site and Slot Burn (q.v.) in many ways are comparable. Märss and Ritchie (1998) recently completed a detailed study of rare articulated Thelodonts from Shiel Burn.

Silurian fossil fishes sites of Scotland

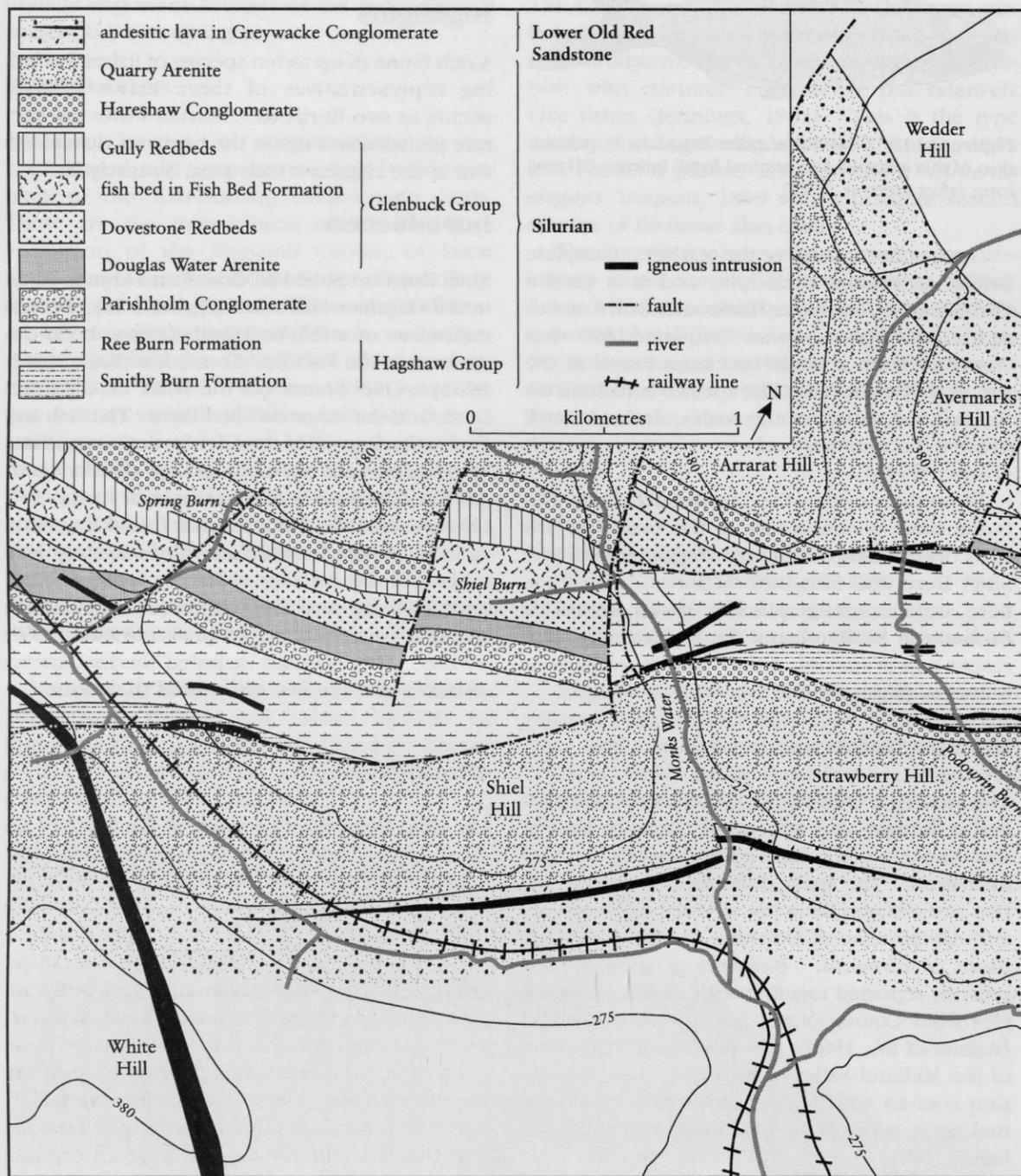


Figure 2.12 Map of the geology in the vicinity of Shiel Burn (after Rolfe, 1961).

Shiel Burn

Fauna

AGNATHA

Thelodonti: Thelodontida: Loganeliidae

Shielia taiti (Stetson, 1931)

Lanarkia horrida Traquair, 1898

L. spinosa Traquair, 1898

L. spinulosa Traquair, 1898

Anaspida: Birkeniiformes: Birkeniidae

Birkenia elegans Traquair, 1898

Anaspida: Birkeniiformes: Lasaniidae

Lasanius problematicus Traquair, 1898

L. alatus Smith, 1958

L. armatus Traquair, 1899

Osteostraci: Ateleaspidiformes: Ateleaspididae

Ateleaspis tessellata Traquair, 1899

Incertae sedis

Monkolepis maculatus Ritchie, 1963

Interpretation

The strata on Shiel Burn are coarsely varved light and dark fine clastics, which may suggest deposition in lake waters, where oxygen levels were low. The fish specimens are preserved in abundance, and in good condition, which suggests mass mortality events, as found in many later Old Red Sandstone localities. The good quality of the preservation suggests that there were no scavenging or burrowing organisms in the anoxic sediments.

The Fish Bed Formation is exposed on the shore of Glenbuck Loch nearby. Its basal unit consists of 6.5 m of light grey sub-greywacke, and continues as cycles of grey-green sandstones, sometimes with breccias at their bases, grading up into siltstone or mudstone. Several fish beds have been found here, one immediately above the basal sub-greywacke and another

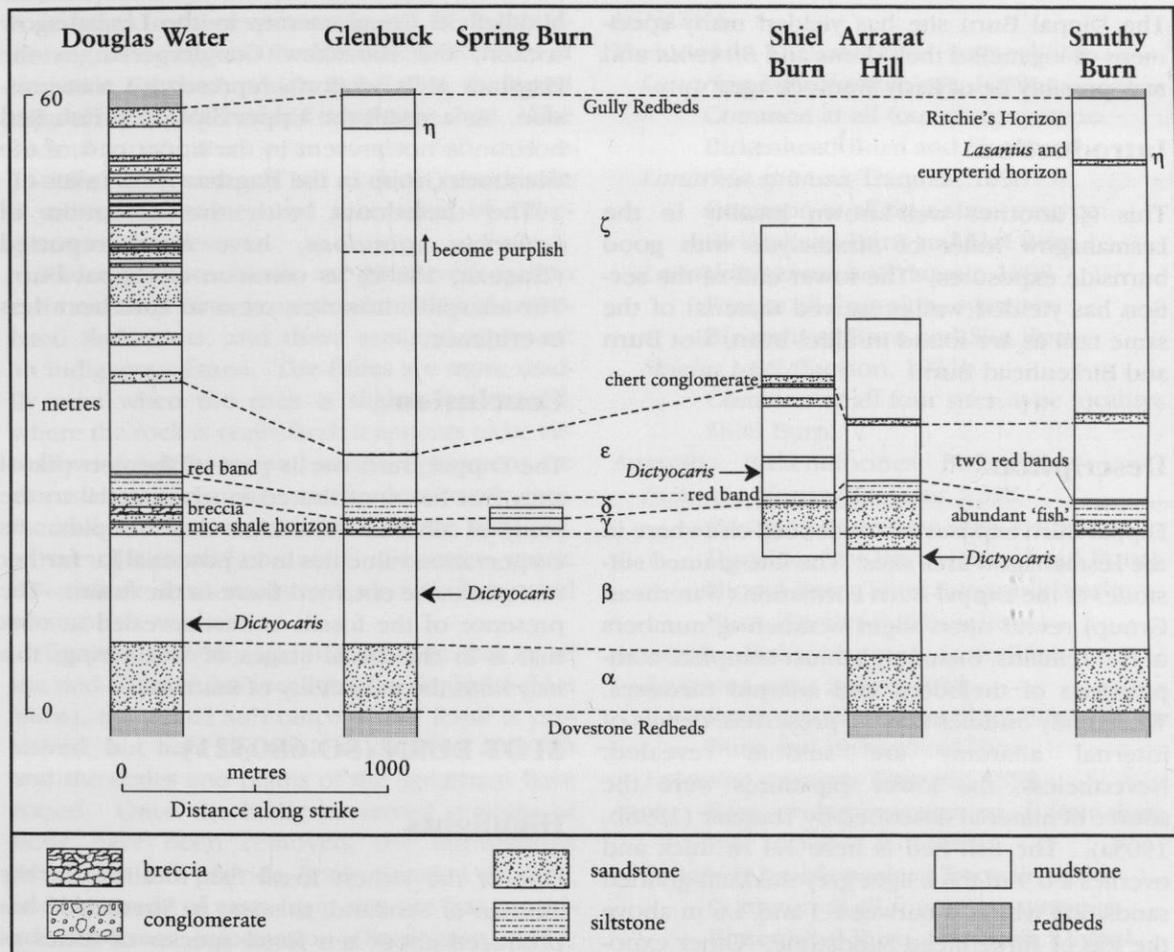


Figure 2.13 Stratigraphical sections in the Hagshaw Hills Silurian inlier to show the Fish Bed Formation (after Rolfe, 1961). The Greek letters refer to six divisions distinguished by Rolfe (1961).

Silurian fossil fishes sites of Scotland

12 m above this. The fossils include fishes, eurypterids, *Spirorbis* and a possible calcareous alga. These are all marine fossils. The environment of deposition is interpreted as a relatively deep body of water, perhaps a lagoon or basin partly separated from open water by a sill.

Conclusion

The conservation value of this site lies in its faunal diversity and relatively fossiliferous strata. This is a rich fish site, which has produced ten species of thelodonts, anaspids and cephalaspids. It has been productive for 100 years, and still yields abundant material.

DIPPAL BURN (NS 693318) (POTENTIAL GCR SITE)

Highlights

The Dippal Burn site has yielded many specimens of loganellid thelodonts and *Birkenia* and may possibly be of Early Wenlock age.

Introduction

This is another well-known locality in the Lesmahagow inlier of Strathclyde with good burnside exposures. The lower end of the section has yielded well-preserved material of the same taxa as are found in Shiel Burn, Slot Burn and Birkenhead Burn.

Description

Dippal Burn exposes fish beds seen elsewhere in the Lesmahagow area sites. The fine-grained siltstones of the Dippal Burn Formation (Waterhead Group) reveal upon slight weathering numbers of fish remains, including almost complete compressions of thelodont and anaspid carcasses. While body outlines may be preserved, details of internal anatomy are seldom revealed. Nevertheless, the lower exposures were the source of material described by Traquair (1898b, 1905a). The fish bed is here 1.4 m thick and overlies a 0.9 m thick light grey medium-grained sandstone which is between 3 and 4.6 m above the top of Birkenhead Sandstone. Other exposures of the fish bed occur at NS 703325, NS 703328, NS 711336 and NS 717340.

Fauna

AGNATHA

Thelodonti: Thelodontida: Loganellidae

Shielia taiti (Stetson, 1931)

Loganellia scotica Traquair, 1898

Lanarkia horrida Traquair, 1898

L. spinosa Traquair, 1898

L. spinulosa Traquair, 1898

Anaspida: Birkeniiformes: Birkenidae

Birkenia elegans Traquair, 1898

Anaspida: Birkeniiformes: Lasaniidae

Lasanius problematicus Traquair, 1898

Interpretation

Ritchie (MS) has correlated the Dippal Burn fish bed with the main fish bed of the Fish Bed Formation of the Hagshaw Hills inlier at Slot Burn (q.v.). Jennings (1961) determined that the conglomerate, which occurs in the section some way above the fish bed in both areas (the Middlefield Conglomerate in the Lesmahagow section, the Hareshaw Conglomerate in the Hagshaw Hills section), represents a transgression. As a result the Upper Slot Burn Fish Bed horizon is not present in the upper part of the Glenbuck Group in the Hagshaw Hills inlier.

The thelodonts, with the exception of *Lanarkia spinulosa*, have been reported (Traquair, 1898b) as common at Dippal Burn. The anaspids, however, seem to have been less in evidence.

Conclusion

The Dippal Burn site is part of the network of sites that has contributed much material to the study of Silurian thelodonts and anaspids. Its conservation value lies in its potential for further material to be obtained there in the future. The presence of the fossils is best revealed in rock that is in the initial stages of weathering; this may limit the availability of material.

SLOT BURN (SO 680321)

Highlights

One of the richest fossil fish localities in the Silurian of Scotland, this site in Strathclyde has produced about ten fossil species of fishes of widely varying groups, and much information about their habitats and palaeobiology.

Introduction

This locality, in the Lesmahagow inlier, is the best known of the mid-Silurian Scottish fish beds, and is the locality from which much of the original vertebrate material was collected by the Geological Survey (Traquair, 1899b, 1905a). It is probable, therefore, that Slot Burn was the site from which most of the type material came for Traquair's descriptions, although he gave no type localities. The site is known also as Segholm or Seggieholm. The problem of the locality of the collecting sites of many specimens in old collections recurs frequently.

Description

The fishes come from beds within the Slot Burn Formation of the Waterhead Group. The upper fish bed both here and at Birkenhead Burn (q.v.), is in two discrete units, which were recognized by Peach and Horne (1899, pp. 578–9). It is revealed in this exposure as red shaley mudstone grading up into the laminated siltstones of the main fish bed, which is 1–1.3 m thick and topped by thinly bedded mudstone bed. The second productive layer of the fish bed is 14–18 m upstream and is 1 m thick, lying above a yellow sandstone, and succeeded by olive-green mudstones.

The vertebrate fossils are preserved as thin carbonaceous films or as the denticles of articulated thelodonts, and these remains represent an indigenous fauna. The fishes are more readily seen when the rock is slightly weathered; where the rock is really fresh it appears to be virtually unfossiliferous and smaller specimens are almost invisible. They are predominantly fragmented in the marginal parts of the fish bed, where the well-laminated siltstones grade upwards or downwards into a poorly laminated siltstone or mudstone.

Traquair (1899b) was first to note that in all the mid-Silurian fish localities, bar Segholm (Slot Burn), the actual substance of the fossil is preserved, but here the shale is decayed and soft and the scales and plates of the agnathans have rotted. Once the badly preserved remains of bone have been removed, the impressions which are left provide finely detailed moulds, and the study of casts from this site has provided important information (Parrington, 1958; Ritchie, 1967). The fossils are commonly less than 10 cm long.

Ritchie made a large collection from trenches here in the early 1960s, and he attempted a study of relative abundance through the fish bed (1963, p. 5). Most forms were present throughout the fish bed in approximately similar proportions, with only three exceptions where one or other species dominated a horizon. Particularly important was a pyritiferous siltstone 50 mm thick within the mudstone succession that yielded many well-preserved ostracoderms associated with the articulated arthropod *Lanarkopterus*. It also produced several specimens of the ?petromyzontid *Monkolepis maculatus*.

Fauna

For comparison the fish fauna of Slot Burn (and of the nearby Shiel Burn, Birkenhead Burn, and Dippal Burn) is listed here.

AGNATHA

Thelodonti: Thelodontida: Loganellidae

Lanarkia horrida Traquair, 1898

Common at all four sites; syntype:
Birkenhead Burn and Slot Burn

Lanarkia spinosa Traquair, 1898

Common at all four sites; syntype:
Birkenhead Burn and Slot Burn

Lanarkia spinulosa Traquair, 1898

Rare at all four sites; syntypes:
Birkenhead Burn and Slot Burn

Shielia taiti (Stetson, 1931)

Common at all four sites; type locality:
Shiel Burn

Anaspida: Birkeniiformes: Birkeniidae

Birkenia elegans Traquair, 1898

Common at all four sites; syntypes:
Dunside, Slot Burn, Birkenhead Burn,
Dippal Burn, Shiel Burn and Lynslie
Burn (Pentland Hills inlier)

Anaspida: Birkeniiformes: Lasaniidae

Lasanius altus Smith, 1958

Rare; recorded from Shiel Burn, Slot
Burn and Birkenhead Burn

Lasanius armatus Traquair, 1899

Rare, probably present at all four sites;
type locality: Slot Burn

Lasanius problematicus Traquair, 1898

Common at all four sites; syntypes:
Birkenhead Burn, Slot Burn, Dippal
Burn, Shiel Burn, Smithy Burn
(Hagshaws) and Lynslie Burn

Silurian fossil fishes sites of Scotland

Osteostraci: Ateleaspidiformes: Ateleaspidae

Ateleaspis tessellata Traquair, 1899

Rare; recorded at all four sites.

Lectotype: selected by Heintz (1939)
from Slot Burn

Incertae sedis

Monkolepis maculatus Ritchie, 1963

Rare; recorded only at Shiel Burn and
Slot Burn; ?type locality

The Waterhead Group and the Glenbuck Group fish beds all have a comparable fauna with similar diversity. The first descriptions were usually based upon Geological Survey collections from all the sites on the two horizons, and rarely has a species been given a single type locality in subsequent work.

The upper fish beds of the Lesmahagow and Hagshaw Hills inliers contain two genera of complete thelodont animals. Other known articulated thelodonts are from the Silurian and Devonian of north-west Canada (Wilson and Caldwell, 1993) from the Devonian of New Brunswick, Canada (*Thelodus macintoshi*), from the Upper Silurian of Oesel in the Baltic (the Phlebolepidae), and undescribed forms from Ringerike, Norway (Ritchie, 1967) which are similar to *Sbielia taiti*.

Sbielia taiti (Stetson, 1931) is common in the Dippal Burn and the Fish Bed formations. These were first recognized by Traquair (1899b) as small poor specimens of *Thelodus scoticus* (Figure 2.14A) which might constitute a new species. Stetson (1931) obtained new material

from the collector, Tait, and named the new species after him, choosing a type specimen from Shiel Burn which had been figured by Traquair (1899b, plate 1, fig. 4). This type specimen is particularly important because it shows traces of internal structure. Eight black streaks were interpreted as branchial bars by Stetson (1931), and discussed by Westoll (1945) and Stensiö (1958) who thought that they represent extrabranchial atria. Ritchie (1963) discovered similar structures in *Loganellia scotica*, and decided that they represent branchial pouches, and that the thelodonts were therefore very different from the Heterostraci with which they had previously been linked (Ritchie, 1968). In a specimen of *Sbielia taiti* from Shiel Burn, the orbit is visible as a distinct circular hole. *Sbielia taiti* is usually 70–100 mm long, but sometimes larger specimens, over 150 mm long, have been found. *Sbielia taiti* has also been recorded from the late Silurian of Ringerike (Norway), Siberia and Pennsylvania (Giffin, 1979).

Lanarkia species are distinguished from *Loganellia* by their sharp, hollow, conical spines which lack a basal plate (Traquair, 1899b). *L. borrida* and *L. spinosa* are both fairly common, *L. spinulosa*, the largest form at 200 mm long, being rare. Ritchie (1963) identified possible small (20–30 mm long) young *Lanarkia* sp. in the weathered lithology of Slot Burn. These had large eyes but all the other adult features were present. Turner (1992) suggested that *L. 'borrida'* and *L. spinosa* were different growth stages and that *L. spinulosa* was a possible sexual dimorph of *L. spinosa* (Figure 2.14B).



Figure 2.14A The thelodont *Thelodus scoticus* (GLAHM V8304), ?Upper Llandoverly at Birk Knowes, c. $\times 1$ (Photo: courtesy of the Hunterian Museum, Glasgow).

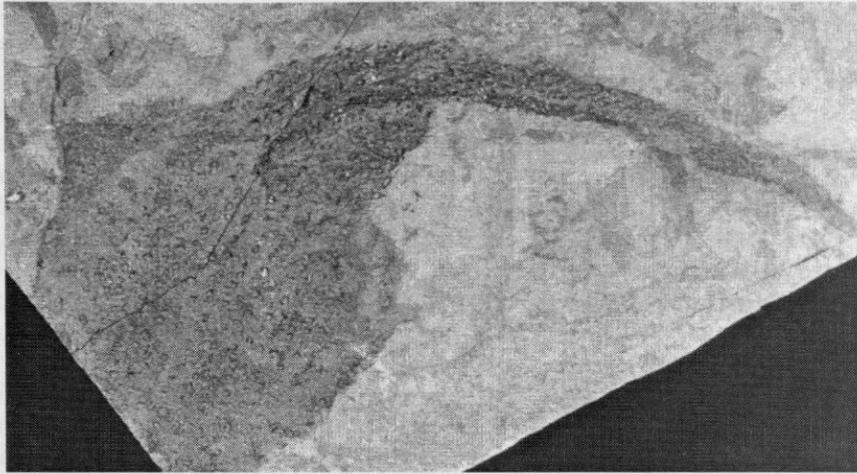


Figure 2.14B The thelodont *Lanarkia borrida* (GLAHM V2302), ?Wenlock at Seggholm, ?Slot Burn; at about natural size (Photo: courtesy of the Hunterian Museum, Glasgow).

The anaspid *Birkenia* is 20–100 mm long, and is typically found laterally compressed (see Figure 2.11A). It is one of the most common and well-preserved forms in the fish beds of Slot Burn, Dippal Burn and Glenbuck. The body is covered with dorso-ventrally elongated scales and the fifth and ?adjacent median dorsal scutes are distinctively double-hooked. The dorsal flank scales of *Birkenia* slope downward and backward in the posterior half of the body, instead of downward and forward as in the other scaled anaspid genera, and clearly do not reflect the form of the myotomes (see Birk Knowes report). There is evidence that in *Birkenia* the size, but not the number, of scales increased with age (Parrington, 1958).

Anaspids have a hypocercal tail, but when Traquair (1899b, 1905a) first reported *Birkenia*, he assumed that the tail was heterocercal, and so he figured *Birkenia*, and the other anaspids from southern Scotland, upside down. He did not identify the orbital openings or discuss the position of the mouth, both of which have a peculiar orientation in his reconstruction. Anaspids were correctly orientated by Kiaer (1924), following research on better-preserved anaspids from Ringerike, Norway, which showed the position of the pineal and nasal openings. Stetson (1928) redescribed *Birkenia elegans* using new material collected by Tait and by Strachan (Museum of Comparative Zoology, Harvard), basing his reconstruction on the

Ringerike anaspids.

Heintz (1958, p. 77) reconstructed the head of *Birkenia*, which is covered with small plates and scales, and which has a distinctive, large Y-shaped pineal plate containing the pineal opening and forming the posterolateral margin of the single nasal opening. The arrangement of plates is similar to that of *Pterygolepis* from Norway, although Smith (1957) compared it with the cephalic shield of cephalaspids. A paired 'round patch' defined by scale pattern and antero-ventral to the orbit is a distinctive feature of *Birkenia*, but its function is unclear.

There has been some debate about the nature of the mouth of anaspids, and this has a bearing on whether recent Cyclostomata (with suctorial mouths) descended from anaspid-like primitive forms (Stensiö 1927, 1939b; Obruchev, 1949; Balabaj, 1956). Heintz (1958) suggested that the mouth of *Birkenia* was a vertical split or ovoid opening at the bluntly rounded front end of the head similar to that of other known Agnatha, as was also independently proposed for anaspids generally by Parrington (1958) and Stensiö (1958). Heintz (1958) concluded that *Birkenia* did not have a suctorial mouth, but rather one like *Branchiostoma* that was adapted to microphagous feeding with cirri, mucous glands, cilia and an endostyle. Denison (1961) thought that this was unlikely, and suggested that some kind of suctorial device was present in anaspids. He also disputed the idea that the

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anaspids sucked up food from the sea floor (Parrington, 1958) because the hypocercal tail would give lift to a fish whose other features suggest an active lifestyle rather than one specialized for bottom-feeding.

Jarvik (1959) described the caudal fin of *Birkenia*, and Ritchie (1964) described a specimen possessing a fin membrane extending beyond the scale-covered portion, and also a possible membranous lateral fin comparable with those of *Rhyncholepis* from Norway. Ritchie (1980) perceived fin-folds preserved in Ringerike anaspids, and produced a model for anaspid stability and lifestyle in which he regarded the anaspid as being active and free-swimming, feeding anywhere between the surface and the bottom.

The other anaspid genus in these fish beds, *Lasanius* (Figure 2.15A, B), lacks a scale covering and its only hard parts are a row of 17–24 spinous dorsal scutes, an oblique row of six ossicles associated with the branchial openings and 5–10 post-cephalic rods immediately behind the branchial ossicles. The remainder of the animal may be preserved as a carbonized stain. Since Traquair's (1899b, 1905a) original account, *Lasanius* has been redescribed by Simpson (1926), Stetson (1927), Bulman (1930), Parrington (1958) and Ritchie (1963) and discussed by many authors. Two species were recognized by Traquair, *L. problematicus* (Figure 2.15A, B), which is common, and the smaller, rarer *L. armatus*.

Lasanius has six branchial ossicles, representing the number of branchial pouches, but the number of dorsal scutes and of post-cephalic rods varies between and within species. The

post-cephalic rods, behind the branchial ossicles, may vary in number even between the two sides of an individual. Stetson (1927) thought that these L-shaped structures supported the gills, but Bulman (1930) suggested that the rods were inserted between myotomes. Parrington (1958) showed that *L. problematicus* had between seven and nine rods, and that this number was not based on size or maturity of an individual. He also showed that each L-shaped structure supported a lateral spine, and supported the suggestion of Bulman (1930) and Stensiö (1939b) that the lateral spine in turn supported a primitive pectoral fin or a fin-fold.

Little is known about the structure of the head of *Lasanius*. None of the anterior parts of the head has ever been found, and reconstructions have been based on other anaspids. Parrington (1958) identified paired lens-shaped structures on the head of *L. problematicus* that he interpreted as the remains of the eyes.

Parrington (1958) regarded *Lasanius* as an active swimmer, which used its hypocercal tail to acquire an inverted vertical position in order to 'hoover' through the bottom mud using its auctorial mouth to feed on minute organisms. Phylogenetic relationships of the Anaspida and Petromyzontida were discussed by Arsenault and Janvier (1991). *Lasanius* and *Birkenia* are very closely related, based on maximum convergence of derived characters.

Ateleaspis tessellata Traquair, 1898 is the earliest relatively complete British cephalaspid known, pre-dating the more typical cornuate forms of the Devonian by many millions of years. *A. tessellata* was discovered in 1897 by Macconochie and Tait (Traquair, 1898a, p. 74).

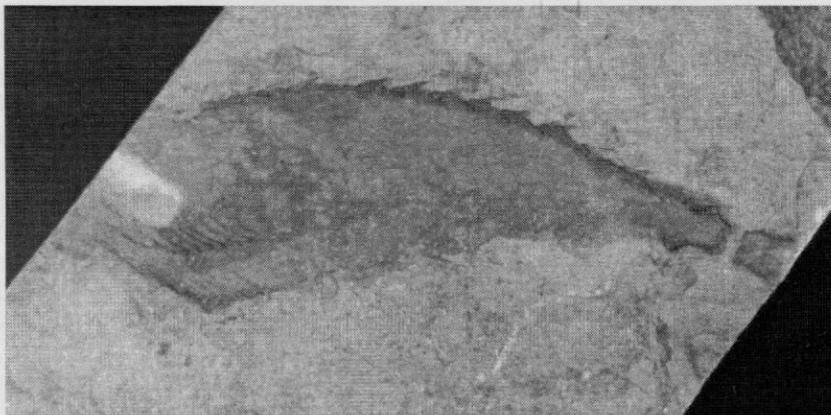


Figure 2.15A The anaspid *Lasanius problematicus* Traquair. Specimen from an unidentified horizon, Segholm (Slot Burn), c. $\times 2$, GLAHM V 2286 (Photo: courtesy of the Hunterian Museum, Glasgow).

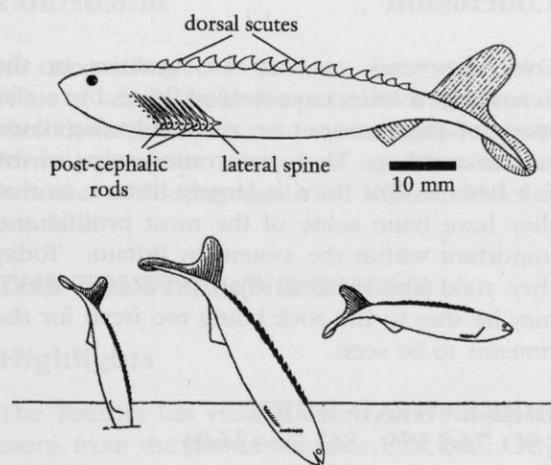


Figure 2.15B The anaspid *Lasanius problematicus* Traquair. Restoration in lateral view and possible feeding and swimming positions as suggested by Parrington (1958).

Using specimens from Slot Burn, Birkenhead Burn and the Pentland Hills, Traquair named and then described and figured it in 1899. Better material was subsequently discovered, allowing further details (Traquair, 1905a) to be added to the original description. Heintz (1939) compared the species to *Aceraspis* and *Hirella* from younger rocks at Rudstangen, Norway. He selected a lectotype from Slot Burn. Unfortunately, after over 40 years of collecting, only 20 specimens of *Ateleaspis* were known, consisting mostly of small fragments. It is one of the rarest elements in the vertebrate fauna from these fish beds (Ritchie, 1967). All the known material of *Ateleaspis* is distorted and flattened, which emphasizes the polygonal pattern of the mucous canal system across the head shield (Figure 2.16). Traquair (1899b) and Parrington (1958) thought that this represented incomplete ossification of the headshield. Parrington (1958) suggested that *Ateleaspis* was therefore an immature cephalaspid. The cephalaspid headshield is described in more detail in Chapter 3.

Ritchie (1967) gave an account of the genus based on new material from Slot Burn, Birkenhead Burn, Shiel Burn and Smithy Burn. His reconstruction is based mainly upon a fairly complete mould from Slot Burn, which allowed latex casts to be produced. The pectoral fins were shown to have a sinus separating them from the trunk, which was similar enough to *Aceraspis* for Ritchie (1967) to decide that they

represented the same genus. Previously, the mistaken belief that *Ateleaspis* lacked such a sinus had led to the idea that it was at a very early stage in the development of fins (Heintz, 1939; Westoll, 1945, 1958). Janvier (1980, 1981), on the other hand, thought that *Aceraspis* showed several characters which were more derived than *Ateleaspis*, and he retained the distinction between the two genera.

Monkolepis maculatus Ritchie MS is a long, narrow segmented organism, possibly over 90 mm in length, with no trace of fins or a branchial apparatus. Three carbonized circular structures towards the end of the fossil are interpreted as the remains of an annular buccal cartilage and sclerotic cartilages, similar to those in *Jamoytius*. The original specimen of this agnathan was first referred to *Jamoytius kerwoodi* (Ritchie, 1960), but new material indicated that it was a different organism. Janvier (1981) removed *Jamoytius* from the anaspids, and made it a possible sister-group of the Petromyzontida, the modern lampreys, and the annular buccal cartilage seen in *Monkolepis* might suggest that this species also was related to the lampreys.

Interpretation

The upper fish beds of the Lesmahagow and Hagshaw Hills inliers are finely laminated pyritiferous siltstones indicating stagnant bottom conditions and deposition within large bodies of quiet water. The entire section at Lesmahagow can be regarded as showing a gradual decrease in salinity upwards from the marine Patrick Burn Formation into fluvial and deltaic conditions by the time of the Waterhead Group. These environmental changes may explain the differences between the faunas of the lower and the upper Lesmahagow fish beds.

The stratigraphical relationships among the mid-Silurian fish sites of the Hagshaw Hills and Lesmahagow inliers (Shiel Burn, Slot Burn, Birkenhead Burn) are complex (see Figure 2.4). They were first identified as exposures of the 'Passage' or Downtonian Fish Bed (Peach and Horne, 1899), hence probably late Ludlow in age, but Jennings (1961) showed that the upper fish beds represented two horizons, not one. Dippal Burn in the Lesmahagow inlier is approximately stratigraphically equivalent to Shiel Burn in the Hagshaw Hills inlier, and these are 100 m or so below the Slot Burn and Birkenhead Burn

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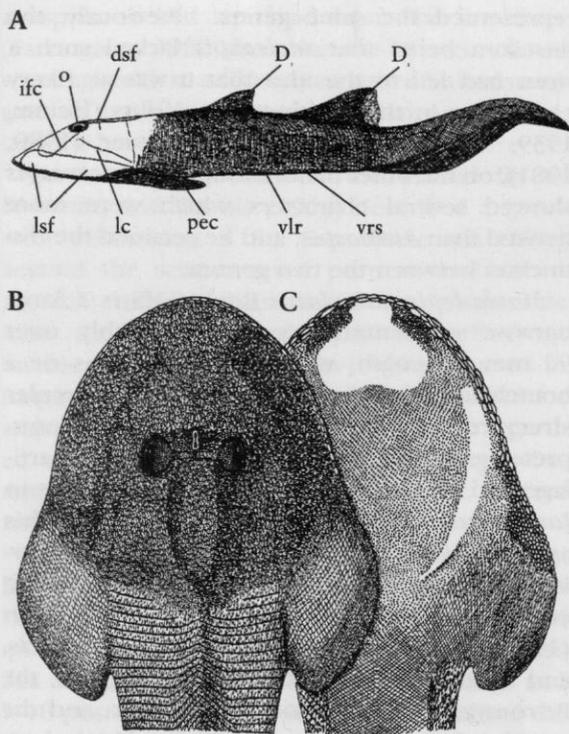


Figure 2.16 *Ateleaspis tessellata* Traquair. (A) Reconstruction in lateral view, *c.* $\times 0.3$; and of the headshield and front part of the trunk; (B) in dorsal and (C) ventral view, *c.* $\times 0.5$, (after Ritchie, 1967): cmm, transverse sensory canals; D1 and D2 anterior and posterior dorsal fins; dsf, dorsal sensory field; ifc, infra-orbital sensory canal; lc, lateral sensory canal; lsf, lateral sensory field; o, orbit; pec, left pectoral fin; vlr, ventro-lateral ridge; vrs, ventro-lateral scales.

fish beds (both in the Lesmahagow inlier).

Debate has persisted about the dating of these Silurian fish beds, there being little upon which to correlate them to the type Silurian sections. The detailed collecting and field research by Rolfe (1960, 1961, 1973a, 1973b) and Ritchie (1960, 1967, 1985) finally distinguished between these discrete horizons and indicated that there were four clearly distinguished fossiliferous horizons in the Lesmahagow inlier: (1) the *Jamoytius* horizon, (2) the *Ceratiocaris* Bed, (3) the Dippal Fish Beds and (4) the Slot Burn Fish Beds. These upper two horizons have a very similar fauna of almost equal diversity, and were referred to the Upper Wenlock or Middle Ludlow (Ritchie, 1967; Janvier, 1985a), but may have an older Wenlock age (Cocks *et al.*, 1992). As stated above, Wellman and Richardson (1993) have found microfloras giving an early Wenlock date.

Conclusion

Over the years, at least 14 localities in the Lesmahagow inlier have yielded fishes, but so far many of these cannot be accurately correlated one to another. The conservation value of the fish beds in Slot Burn is largely historic in that they have been some of the most prolific and important within the system in Britain. Today they yield less material than previously, which may be due to the rock being too fresh for the remains to be seen.

BIRKENHEAD BURN (SO 763359, SO 764360)

Highlights

A rich mid-Silurian fish fauna, consisting of nine species of thelodonts, anaspids and cephalaspids, has been found at this site. It has provided type specimens of three species of thelodonts *Lanarkia horrida*, *L. spinosa* and *L. spinulosa*.

Introduction

Two fish beds are exposed on Birkenhead Burn in the Lesmahagow inlier of Strathclyde, one being 1.0–1.2 m thick, the other 4.6 m. They were considered by Jennings (1961) to be of Slot Burn Formation age. Peach and Horne (1899) first described the site, and remarked on the constant association of the fish fauna with eurypterids in the upper fish bed.

Description

The fish beds are grey laminated mudstones, the fishes and eurypterid remains being preserved as thin grey to black films. The geology, stratigraphical relations and fish fauna of the site are described in the Slot Burn report (q.v.).

Interpretation

The Birkenhead Burn fish beds are comparable to those from Slot Burn (q.v.), and may belong to the Slot Burn Formation, but this correlation is uncertain. Differences in the composition of the fauna and some stratigraphical uncertainties suggest that the fauna may be of slightly different age, i.e. equivalent to the fish beds in the Dippal Burn Formation.

Conclusion

An outstanding fossil fish site, the conservation value of which lies in the richness of its fauna of thelodonts, anaspids, and cephalaspids, the site forms part of the network of agnathan-bearing localities of Silurian age in the Midland Valley of Scotland.

THE TOUTTIES (NO 881866)

Highlights

The Toutties has yielded many good fish specimens from the Cowie Harbour Fish Bed. This Grampian site is important because the age may be latest Silurian (although that is controversial), and this represents one of the few British fish faunas of that age outside the Anglo-Welsh Borderland region.

Introduction

The Cowie Harbour Fish Bed crops out on the foreshore just south of the old harbour jetty to the north of Stonehaven, within rocks called 'The Toutties' (Figure 2.17). The geology of the site has been described by Campbell (1911, 1912b), Denison (1956), Armstrong and Paterson (1970) and Armstrong *et al.* (1978), and the fish fauna by Traquair (1912), Campbell (1913), Westoll (1945), White (1946, 1950a), Ritchie (1960, 1964) and Janvier (1981).

Description

In this vicinity Late Silurian strata rest unconformably on the much older (Cambrian age) Highland Boundary Group, which has been highly folded. The fish bed lies within the vertical Silurian strata and is faulted out at the southern end of the outcrop where the bed disappears under the low-tide mark in Cowie Harbour. Armstrong and Paterson (1970) divided the Upper Silurian 'Downtonian' Stonehaven Group into the lower Cowie Formation (730 m thick) with the fish bed in its upper part, and the overlying Carron Formation (820 m thick). The fish bed occurs in a sequence of alternating grey sandstones and shales, with brown, grey and red cross-bedded fluvial sandstones below and above (Figure 2.18).

The Cowie (Harbour) Fish Bed (also called the *Dictyocaris* Band or Member) was first

described by Campbell (1911). Fossils had been collected for the Geological Survey by Macconochie in 1881, but the first agnathan fossils were not found until 1912, when a fish spine was discovered in a grey mudstone rich in the arthropod *Dictyocaris*. Cephalaspids also were found in a reddish sandy mudstone below this grey bed (Campbell, 1912a, 1912b).

Fauna

The recorded fish fauna from the Cowie Harbour Fish Bed includes an anaspid, a heterostracan and a cephalaspid.

AGNATHA

Anaspida: Birkeniiformes: Birkeniidae
Birkenia sp.

Osteostraci: Ateleaspidiformes: ?Ateleaspididae
Hemiteleaspis heintzi Westoll

Heterostraci: Phialaspidiformes:
Traquairaspididae

Traquairaspis campbelli (Traquair, 1913)

The anaspid is represented by possible scutes of *Birkenia* recorded by Campbell (1913). Ritchie (1960, 1964) also reported the discovery of an anaspid which, with its well-developed lateral fin folds, resembles the Norwegian genera *Pharyngolepis* and *Pterygolepis*.

Some of the remains noted by Campbell (1912) were regarded by Traquair (1912) as cephalaspid scutes and plates. Westoll (1945) described a new genus and species of hemicyclaspid *Hemiteleaspis heintzi*, based on the impression of a single, incomplete head shield plus several separate scales from Cowie Harbour. Scales were also found, in association with *Dictyocaris* at nearby Tewel Burn. Westoll (1945) considered that *Hemiteleaspis* was intermediate in form between the cephalaspids *Aceraspis* (which Westoll considered to be ?latest Ludlow in age) from Rudstangen, Norway, and *Hemicyclaspis* from the Downtonian (Přídolí) of the Welsh Borders and Jeløy, Norway. Janvier (1981, p. 131) regarded the hemicyclaspids as successive outgroups of the derived cornuate Osteostraci, with *Ateleaspis* from Slot Burn (q.v.) as the most primitive, followed by *Aceraspis* and *Hirella*, then *Hemiteleaspis* and finally *Hemicyclaspis* (Figure 3.14).

Traquair (1912) named a new species of heterostracan from the Cowie Harbour Fish Bed as *Cyathaspis campbelli*. When White (1946)

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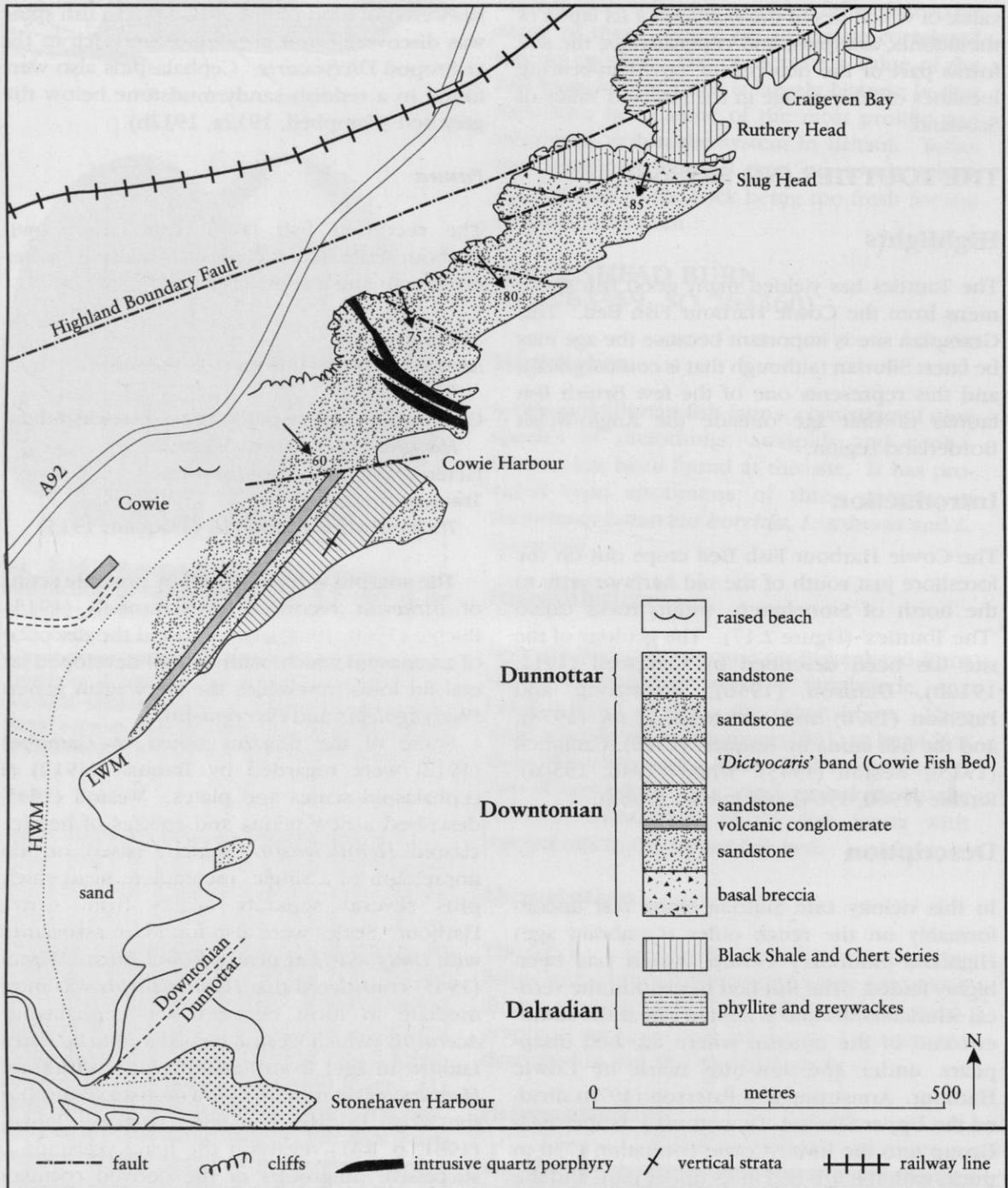


Figure 2.17 Geological sketch-map of the coast to the north of Stonehaven (after McGregor, 1978); The Toutties is the area of foreshore south of Cowie Harbour.

The Toutties

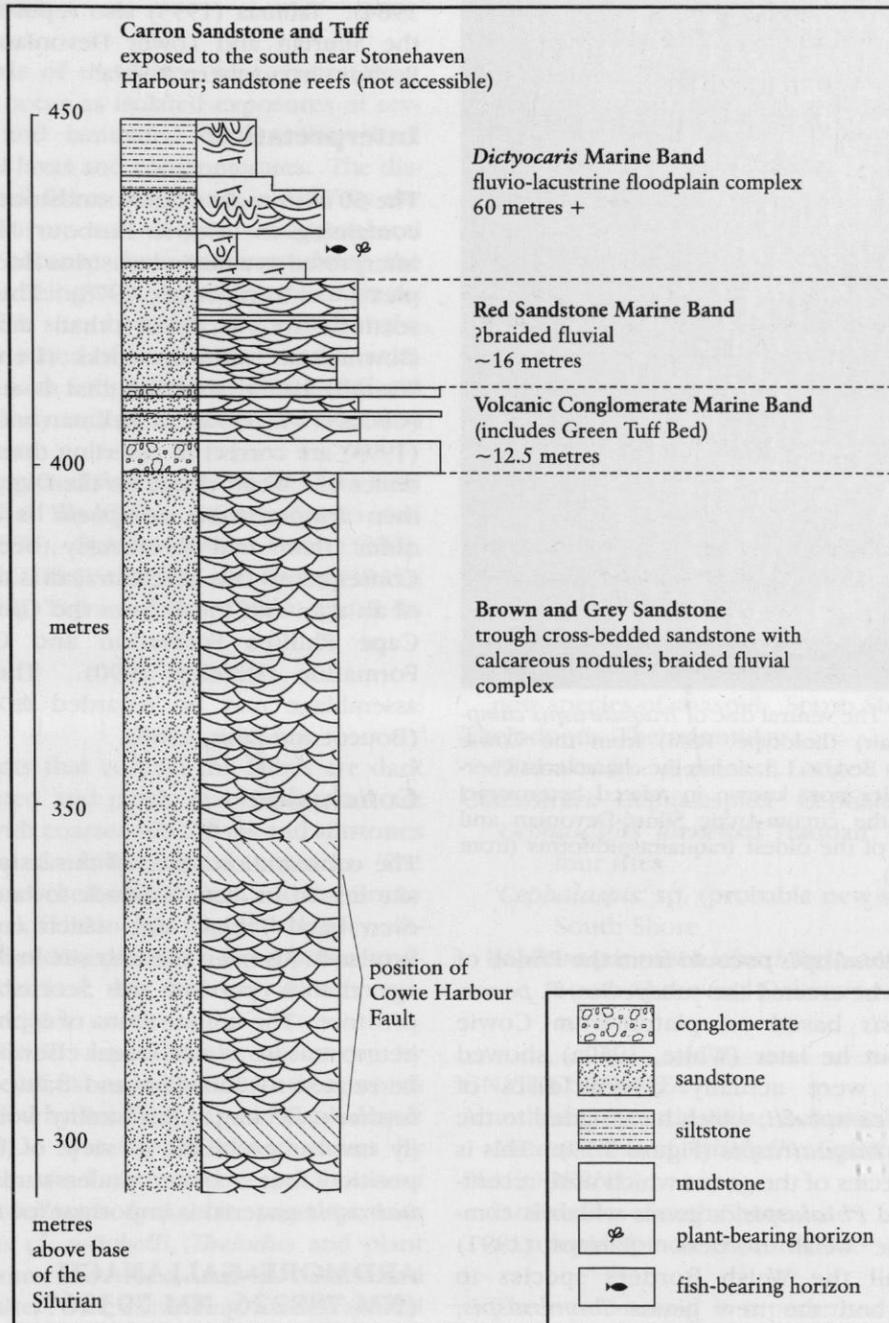


Figure 2.18 Stratigraphical log of the uppermost part of the Downtonian at The Toutties (after MacGregor, 1968).

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Figure 2.19 The ventral disc of *Traquairaspis campbelli* (Traquair) (holotype, RSM) from the Cowie Harbour Fish Bed, $\times 1.3$. It has the characteristic serrated tubercles now known in related heterostraci throughout the circum-Arctic Siluro-Devonian and may be one of the oldest traquairaspidiforms (from Kiaer, 1932b).

described *Phialaspis pococki* from the Přídolí of Shropshire, he erected the subspecies, *P. pococki cowiensis* based on plates from Cowie Harbour, but he later (White, 1950a) showed that these were actually ventral discs of *Cyathaspis campbelli*, which he assigned to the new genus *Traquairaspis* (Figure 2.19). This is the type species of the genus which until recently contained *Phialaspis*, a genus which is common in the Welsh Borders. Tarrant (1991) removed all the Welsh Borders species to *Phialaspis* and the new genus *Toombsaspis*, leaving *T. campbelli* as the sole species of *Traquairaspis*. It may be related to *Rimasventeraspis angusta* (Denison, 1963) from the Přídolí of Yukon, Canada, these two species forming the Family Traquairaspididae, according to Tarrant (1991).

In recent years traquairaspidids have been recorded from the Downtonian (Přídolí) of the

Mackenzie Mountains, Northwest Territories, Canada (Dineley and Loeffler, 1976) and the Peel Sound Formation and other units in the Central Arctic Islands (Dineley, 1990; Elliot, 1984). Talimaa (1995) also reports them from the Silurian and Lower Devonian of Timan-Pechova in northern Russia.

Interpretation

The 60 m or more of grey sandstones and shales containing the Cowie Harbour Fish Bed are interpreted as a fluvio-lacustrine floodplain complex (Armstrong *et al.*, 1978). This is the only section in Scotland that may contain Downtonian (Přídolí) rocks (Denison, 1956; Westoll, 1977), although that is still uncertain (Cocks *et al.*, 1992). If Wellman and Richardson (1993) are correct in asserting that there is evidence of a Wenlock age for the Dictyocaris Beds, then *Traquairaspis campbelli* is substantially older than had previously been thought. Consequently this heterostracan is thereby more of an age with those from the Canadian Arctic Cape Phillips Formation and Cape Storm Formation (Dineley, 1990). The vertebrate assemblage may be regarded as non-marine (Boucot and Janis, 1983).

Conclusion

The conservation value of this as an important site lies in its ?late Wenlock to late Ludlow or even basal Přídolí age, which is unique for Scotland. Also, it is the only site in Britain of that age that is part of the Scottish-Baltic fish province. The unique fauna of cephalaspids and heterostracans is not found elsewhere but may be related to Canadian and Baltic forms. Any further collecting at this locality would necessarily involve problems in view of its foreshore position, but a better understanding of *Traquairaspis* material is important for taxonomy.

ARDMORE-GALLANACH
(NM 788226, NM 793267,
NM 798267, NM 826271)

Highlights

The important fish beds in this outcrop occur in association with the Lorne lavas, and the fishes and associated plants give this volcanic sequence a biostratigraphical age. Up to eight species of

fishes have been reported, providing a remarkable insight into a fish assemblage at the Silurian–Devonian boundary.

Introduction

The fish beds of the Lorne area, near Oban, Strathclyde, occur as isolated exposures of several flaggy and laminated beds within thick sequences of lavas and conglomerates. The discovery of fossil fishes and plants in 1897 by the Geological Survey was of great stratigraphical importance because their presence dated the Oban lavas as being of Lower Old Red Sandstone age. Four fish sites have been reported in the area: on the island of Kerrera and on the mainland at Gallanach Lodge, Selma Cottage Cliff and Dalintart railway cutting, of which only the first two are extant.

The geology and fish faunas of the area have been described by Geikie (1897), Symes and Traquair (1898), Symes (1898), Pratt (1900), Kynaston and Hill (1908), Lee and Bailey (1925), Stensiö (1932), Tarlo and Gurr (1964) and Tarlo (1967).

Description

The sediments that contain the fishes are dark grey, laminated and partly pyroclastic, and are associated with coarser siltier flags and siltstones with ripple marks and scattered sun cracks. The fish beds are marked at Gallanach and Kerrera by the presence of distinctive flaggy dark grey siltstones with bedding planes covered with rounded, usually cracked, thin dark grey films, possibly of algal origin.

Geikie (1897) reported the discovery by Macconochie of fishes in the Oban area, which were identified by Peach as parts of *Cephalaspis* (Pratt, 1900). Symes (1898), with notes by Traquair, reported the discovery of a new species, *Cephalaspis lornensis*, together with *Mesacanthus* cf. *mittelli*, *Thelodus* and plant remains from the then newly discovered Gallanach site. In ascending stratigraphical order the four sites are as follows.

1. South shore of the island of Kerrera, south-west of Ardmore: grey flaggy shales, containing two fish beds, one exposed to the south-west of Ardmore, which has produced the majority of specimens, and a second to the east that has also yielded fish remains. The Kerrera site has proved to be important, having yielded a large collection of almost-complete fossils to L.B.H. Tarlo and P. Gurr in the 1960s. Unfortunately, the whereabouts of these specimens is unknown now (1996).
2. Gallanach Lodge: grey fine-grained flags intercalated within conglomerate.
3. Selma Cottage Cliff, near Selma Cottage, Oban: a greenish grey calcareous shale. This site was the original source of cephalaspids to the first collectors, but no longer exists. It is probably the site referred to as Carrick Villa by Traquair (1898b).
4. Dalintart railway cutting: a grey bituminous shale. There are two exposures 250 m apart, north-east of Dalintart Farm, Glen Crutten, 1 mile (1.6 m) E of Oban. A section is given by Kynaston and Hill (1908, p. 71).

Fauna

The fish fauna consists of about eight species of agnathan, acanthodian and placoderms:

AGNATHA

Heterostraci: Anaspida

new species of anaspid: South Shore

Thelodonti: Thelodontidae

Thelodus sp.: Gallanach Lodge

Osteostraci: Cephalaspida: Cephalaspidae

'*Cephalaspis*' *lornensis* Traquair, 1898: all four sites

'*Cephalaspis*' sp. (probable new species): South Shore

(*Gylenaspis maceacheni* Tarlo and Gurr, MS: South Shore and Dalintart railway cutting)

GNATHOSTOMATA

Acanthodii: Acanthodida: Acanthodidae

Mesacanthus cf. *mittelli*: Gallanach Lodge

PLACODERMI

?arthrodire: South Shore

arctolepid spines: South Shore

The new anaspid is represented by a single unlocated specimen, which Gurr suggests came from the second, eastern fish bed at Ardmore. *Thelodus* was reported by Symes and Traquair (1898), but the original material has been lost (S. Turner, pers. comm., 1982) and no new material has been collected. '*Cephalaspis*' *lornensis* Traquair, 1898 was described fully by Stensiö (1932). The lectotype is from 'Carrick

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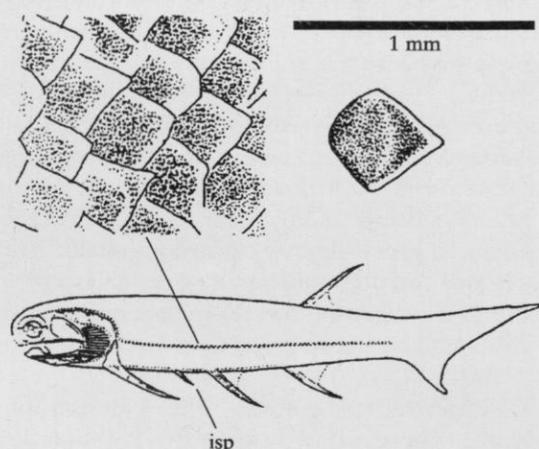


Figure 2.20 *Mesacanthus mitchelli* (Egerton) restoration in lateral view, approximately natural size (after Watson, 1937): isp, intermediate spine; with details of squamation of specimen from Tillywhandland (from Young, 1995).

Villa'. It is a cephalaspid with short cornua, narrow pectoral sinuses and broad interzonal part. *Gylenaspis* is a new species of ateleaspid which awaits description.

The jawed vertebrates from Kerrera are represented by fragmentary remains of an acanthodian compared with *Mesacanthus mitchelli* (Egerton, 1861; Figure 2.20) from the Dundee Formation of Forfarshire (Pragian, early Devonian), and two placoderms, a possible arthrodire and an arctolepid have been reported but not figured.

Interpretation

No age has been defined for the Kerrera beds beyond 'Lower Old Red Sandstone', but this represents a facies that includes beds dated elsewhere as late Silurian and early Devonian. Gurr and Tarlo (1967) and Halstead (1993) gave a Gedinnian (= Lochkovian, earliest Devonian) age for the Kerrera site, based on the *Gylenaspis* that Tarlo listed as the last ateleaspid. However, Halstead (1993, p. 578) did not mention this record later, noting the last ateleaspids as

Hemicyclaspis murchisoni and *Ateleaspis robustus* from the Přídolí of the Welsh Borders and Norway. Spores from a temporary excavation at the camp site north of Gallanach are of Lower Old Red Sandstone affinity (J.E.A. Marshall, pers. comm., 1982). Plants from the Gallanach fish bed have a Downtonian (Přídolí) appearance (C.J. Cleal, pers. comm.)

Unpublished studies by the late L.B.H. Tarlo and P. Gurr suggested that the beds within which the fossiliferous layers occur show repeated cyclothems, representing subtidal and intertidal sediments, and that the Kerrera deposits were probably laid down in a tidal basin, a regime intimately associated with cycles of volcanic activity from more than one centre and supporting a brackish-water vertebrate fauna.

The age of the Kerrera cephalaspids is critical to understanding the evolution of the group in Europe, since Kerrera and Oban were geographically midway between the Welsh Borders and Spitsbergen, two identified areas of cephalaspid evolution in the Late Silurian–Early Devonian (Dineley, 1973; Janvier, 1985a). Further studies may give some indication of the migration routes for genera between the two areas. The gnathostome remains (if such they are) may also be important, representing some of the oldest recorded placoderms in Britain. Arthrodires occur in the Lower Devonian of the Anglo-Welsh Basin (White, 1961), and are widespread throughout all the Lower Devonian vertebrate provinces of the world (Young, 1981).

Conclusion

The age of the Lorne fish sites is of considerable interest since it coincides with the transition from marginal Ludlow-age sediments to the continental Old Red Sandstone facies, and some of the fish specimens may be among the oldest within their groups. The conservation value lies in the uniqueness of the fauna at the species level and the possibility of establishing the age through further study and excavation of the fish-bearing strata.