
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 'ter-canes'. 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 sub-duction 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 Pridoli 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 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 (Figure 2.3) and (Figure 2.4). The stratigraphy of these inliers has been described by Rolfe (1961), Walton (1965), and Robertson (1989). However clear biostratigraphical indices 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 (West^o11, 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 converging 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 Pridoli 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 *Ainiktozoon*, 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)

Shielia taiti (Stetson, 1931)

Lanarkia horrida Traquair, 1898

L. spinosa Traquair, 1898

L. spinulosa Traquair, 1898

Anaspida: Jamoytiiformes: Jamoytiidae

Jamoytius kerwoodi White, 1946

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. *mittelli* (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 denticles 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 (Marss, 1986; Marss *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 (Marss *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 established 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 *amoytius*, *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 historically best-known and relatively well-preserved fossil agnathans, which were also characteristic of the Old Red Sandstone facies in the Plidoli 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 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 (Weston, 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 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 cyathaspids 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 Marss (1989), and the IGCP Project 328 (Palaeozoic microvertebrates) has encouraged further vertebrate biostratigraphical work on the Silurian (see LeLievre *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. Marss provided the summary figure of distribution and biozones shown in (Figure 2.7); Spitsbergen should now be included.

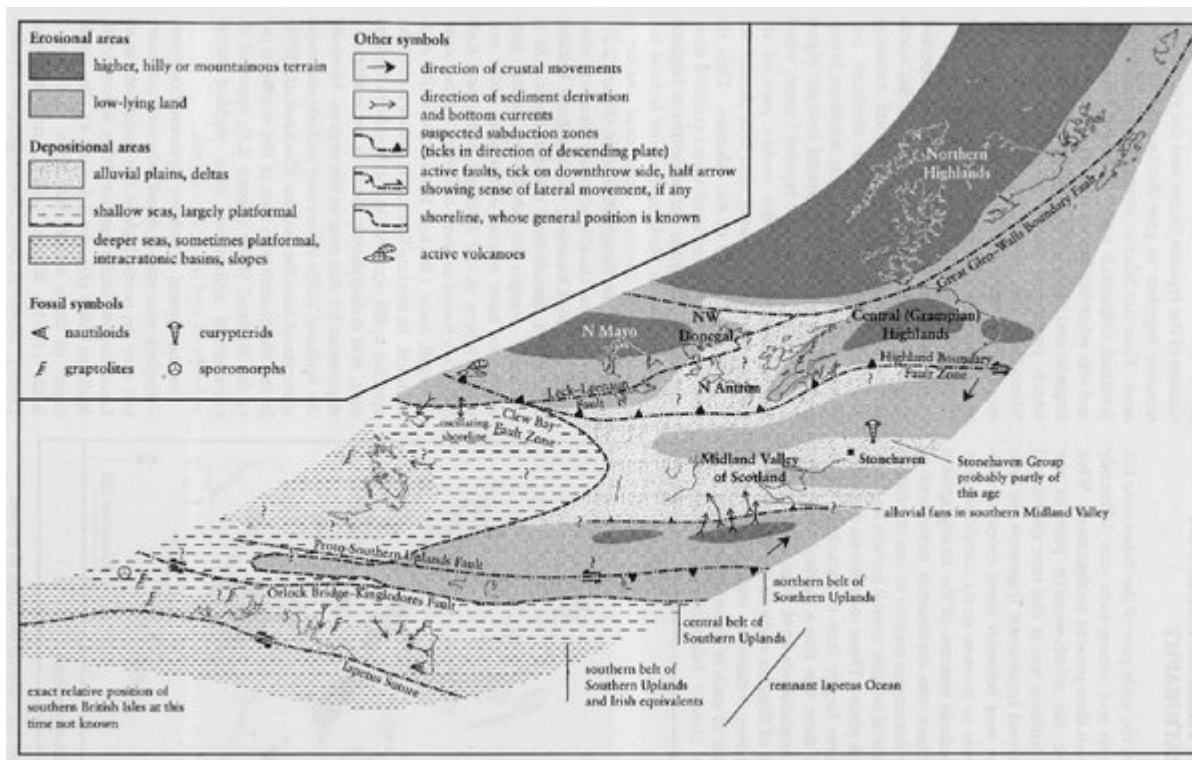
The Scottish Silurian vertebrate sites are distinct from those of the Anglo-Welsh area in respect of both faunas and facies, which reflects the palaeogeographical separation of the two regions during that period. There is, as described above, however, some similarity between the sites in Scotland. Comparison 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.

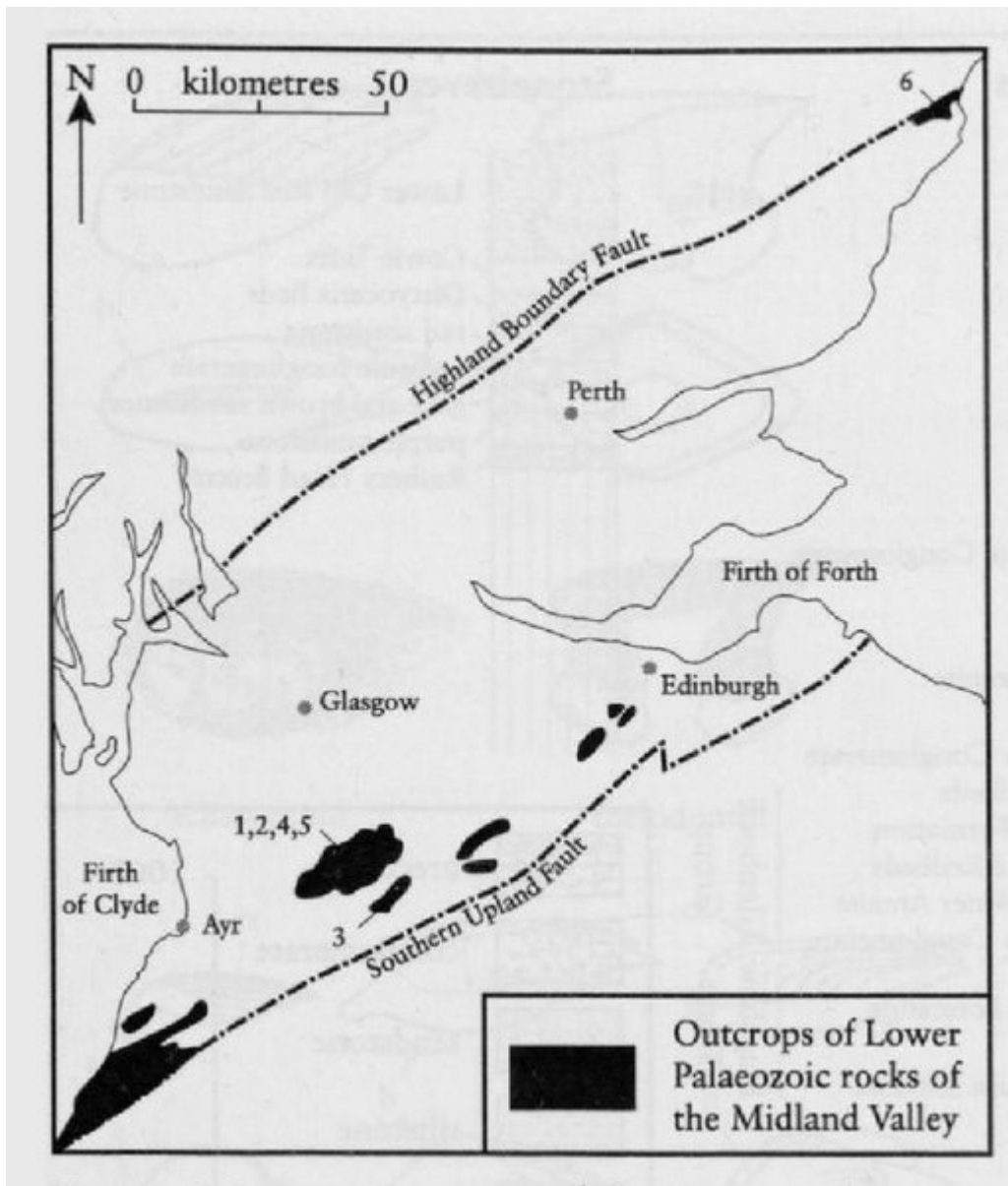
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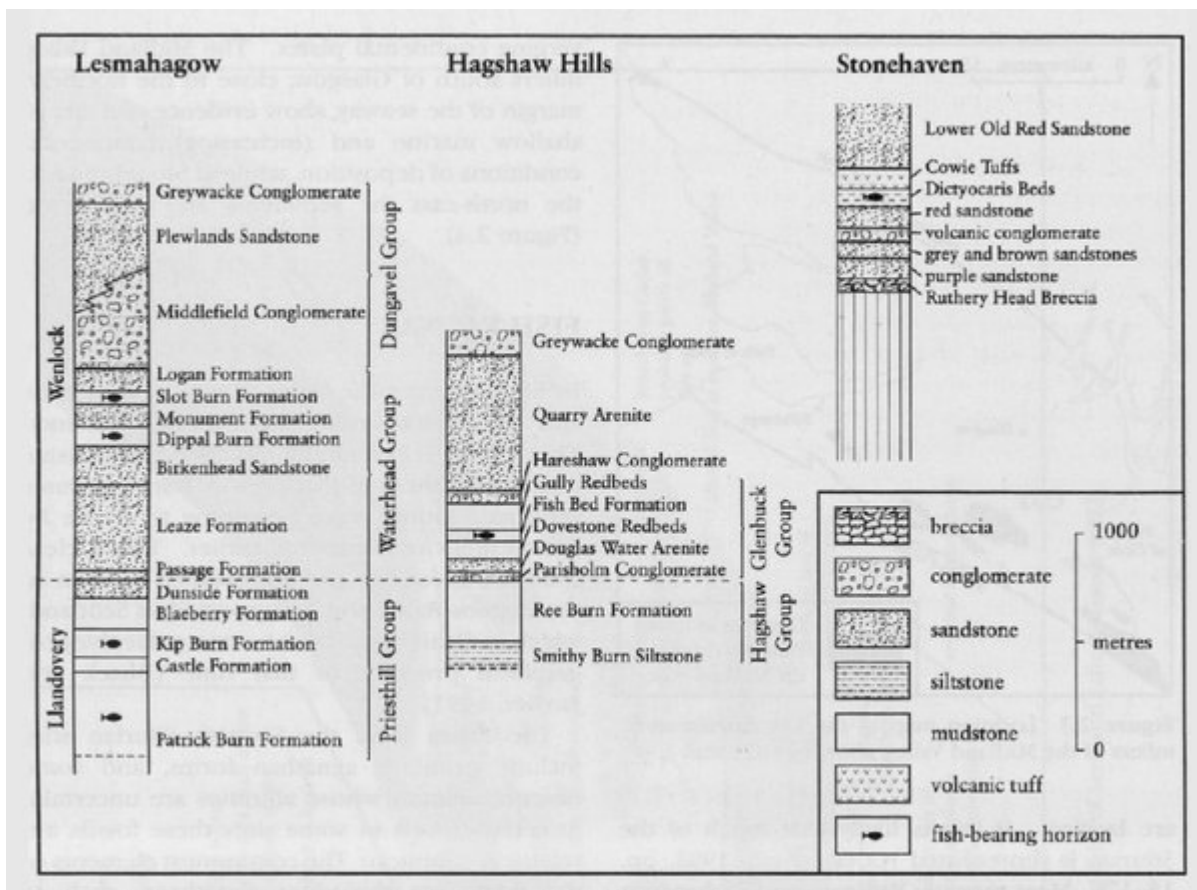
(Figure 2.1) Silurian outcrops in Britain.



(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.



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

Series	Stages	Silurian		Graptolites	Conodonts	Vertebrates
Pridoli				<i>bouceki-transgredlens</i>	<i>O. costeinbomensis</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>parultimus-ultimus</i>		<i>N. gracilis</i>
Ludlow	Ludfordian			<i>formosus</i>	<i>O. crista</i>	<i>T. sculptilis</i>
				<i>bohemicus tenuis-kozlowski</i>	<i>O. snajori</i> interval zone	
				<i>leintwardensis</i>	<i>P. siluricus</i>	
	Gorstian			<i>scanicus</i>	<i>A. ploeckensis</i>	<i>A. bedei</i>
				<i>nilssoni</i>	not zoned	<i>P. elegans</i>
Wenlock	Homerian			<i>ludensis</i>	<i>O. bohemia</i>	<i>P. martinssoni</i>
				<i>praedeubell-deubell</i>		
				<i>parvus-nassa</i>		
				<i>lundgreni</i>		
	Sleinwoodian			<i>rigidus-perneri</i>	not zoned	<i>L. grossi</i>
				<i>riccarionensis-belophorus</i>	<i>O. sagitta rhenana</i> – <i>K. patula</i>	<i>L. avonia</i>
				<i>centrifugus-murchisoni</i>	<i>K. ramuliformis</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>		
	Rhuddanian			<i>cyphus</i>	<i>D. kentuckyensis</i>	
		<i>vesiculosus</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 Marss, 1986).