Birk Knowes

[SO 737 346]; [SO 738 348]

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).

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 specimens 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 2.9)A). 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 2.9)B).

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 (Wangsjö, 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 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 Brugghen *et al.* (1997). The new work (Brugghen *et al.,* 1997) shows that *Ainiktozoon* is clearly an arthropod with affinities to the extinct thylacocephalan crustaceans.

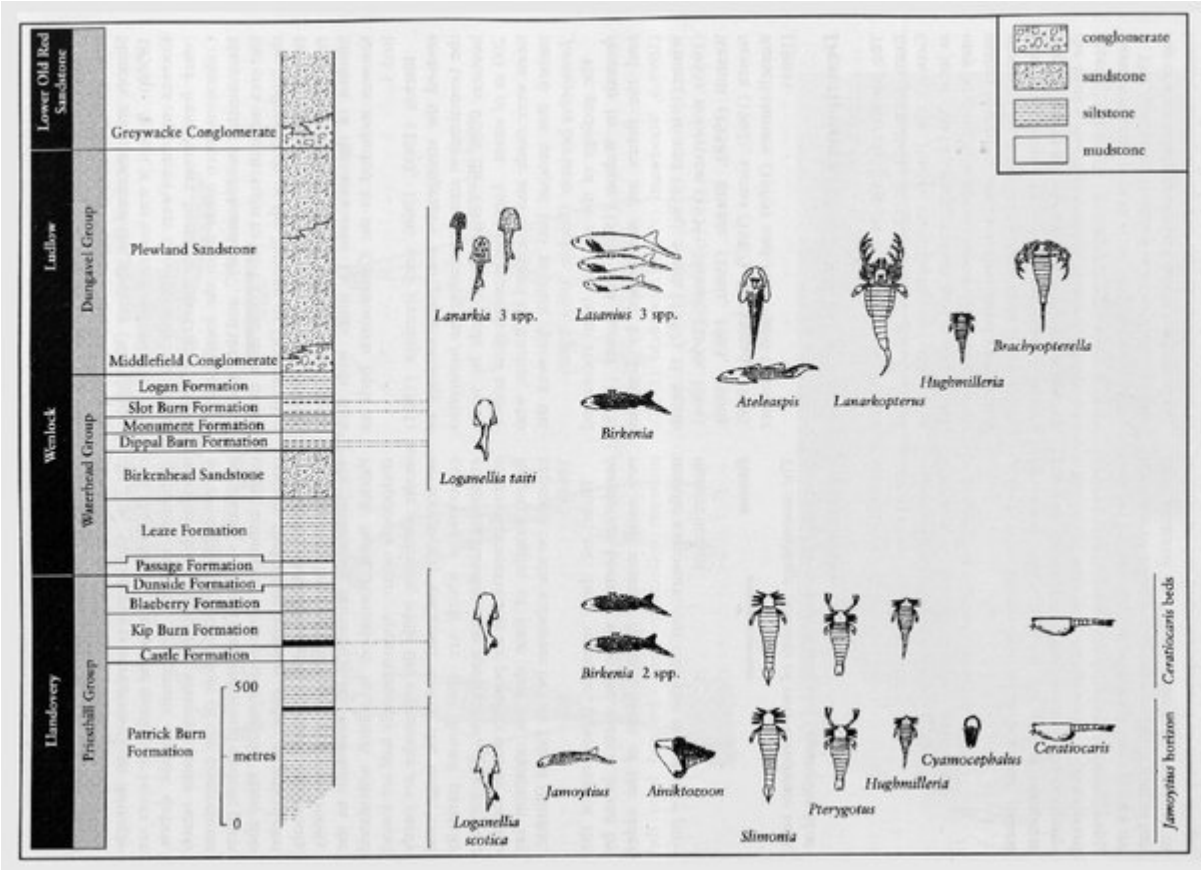
Interpretation

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 benthon-ic 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).

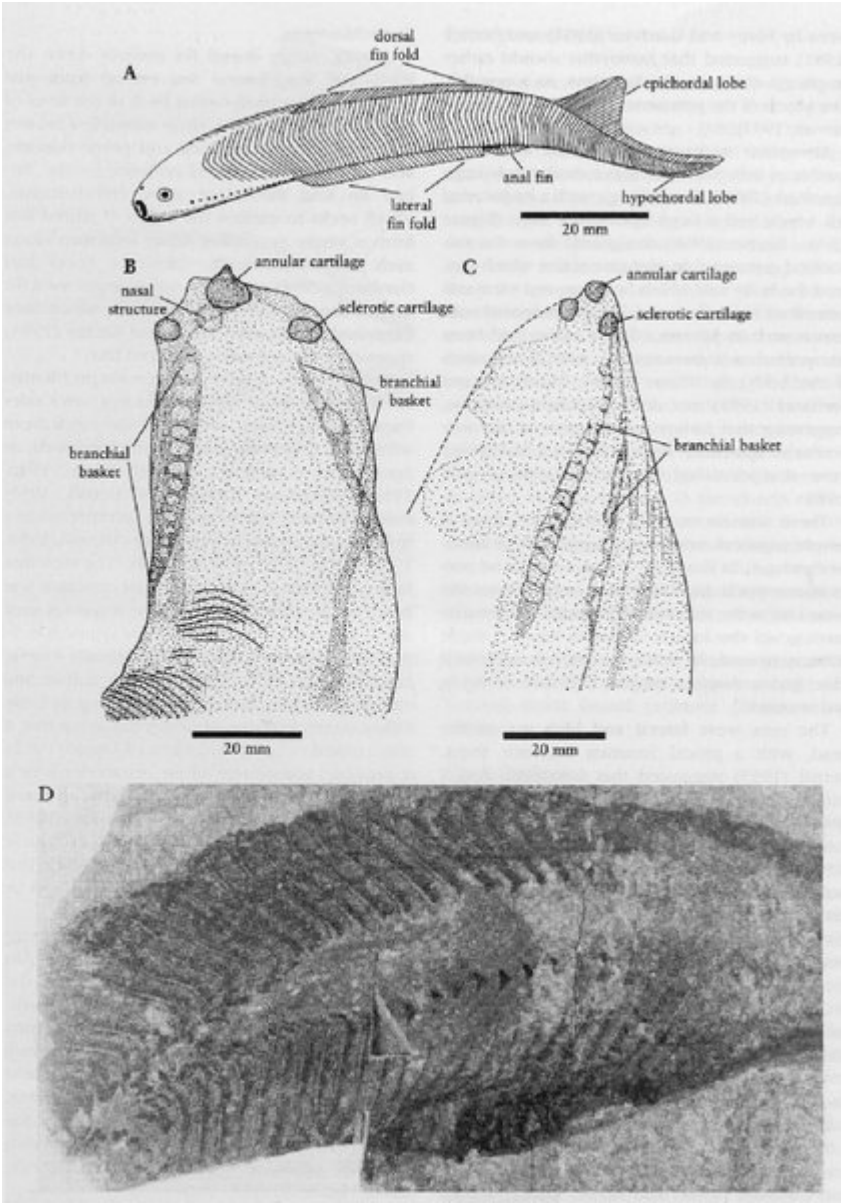
Conclusion

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 (Marss, 1986). Its early date and the nature and number of the fossil vertebrates make it of high conservation value.

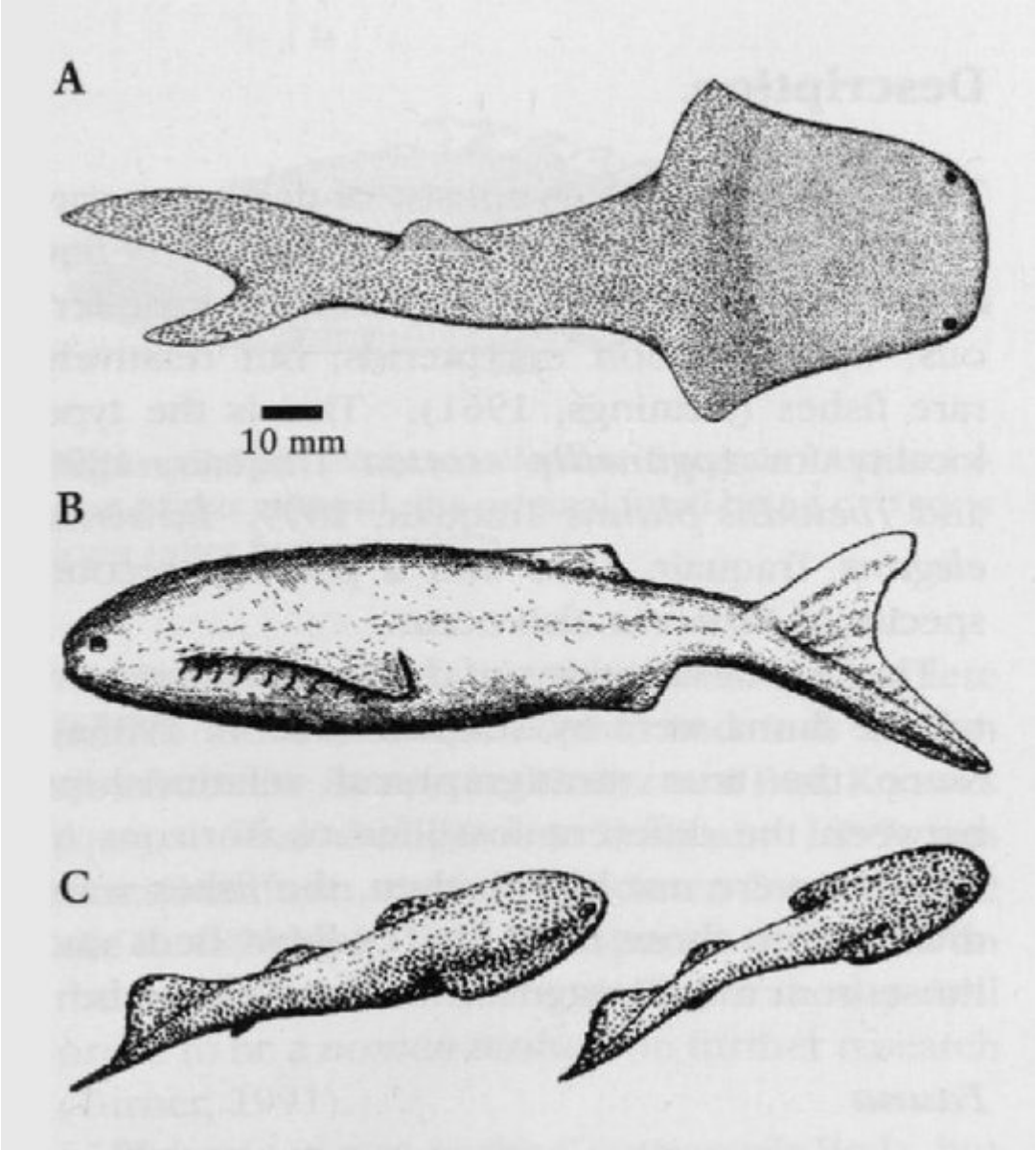
References



(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.



(Figure 2.9) (A) a reconstruction Jamoytius kerwoodi White by Ritchie (1968); (13) 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 x 1.5 (GLAHM 101 382), Birk Knowes, Upper Llandovery, photographed under water (Photo: courtesy of the Hunterian Museum, Glasgow).



(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.