Glencartholm

[NY 376 795]

Highlights

Glencartholm in Dumfries and Galloway is one of the most important Palaeozoic fossil fish sites in the world. It has produced some of the finest specimens of fossil fishes found in the Carboniferous. The fauna is remarkable because of the number of complete fishes discovered, and the variety of forms, over 30 species, which are contained within the assemblage.

Introduction

The fauna from Glencartholm comprises marine brachiopods and bivalves, in addition to the arthropods and fish that have made it famous. So far, about 35 species of fishes have been recorded, many more than most fossil fish sites. Fossils were first discovered at Glencartholm in 1879 by the famous collector A. Macconochie during work for the Geological Survey, as was reported by Geikie (1881). The fishes were first described by Traquair (1881, 1884a, 1884b, 1888a, 1888b, 1890) and the arthropods by Peach (1882a, 1882b). Further collecting took place in 1933–1936 by Moy-Thomas (Schram, 1983), when presumably the use of explosives removed all the accessible fossiliferous strata (Lumsden *et al.,* 1967). The geology of the area has been described by Peach and Horne (1903), who gave a section at the fish site (Nairn, 1954; Lumsden *et al.,* 1967).

It is difficult to identify the precise locality, since some evidence suggests that the Victorian collections may have been made at a slightly different location from the modern ones (Figure 9.16). Several authors referred to a similar faunal assemblage to that from Glencartholm in older Cementstone Group sediments (Westoll, 1948) from a nearby locality at 'Tarras Water Foot' (Geikie, 1881; Traquair, 1881, 1890b, 1903; Moy-Thomas, 1937b; Westoll, 1951). This is probably a confusion with Glencartholm itself; the fossils labelled from Tarras Water Foot are identical to those from Glencartholm, and a separate locality could not be found during resurvey (Lumsden *et al.,* 1967).

Description

The fish bed horizon, low in the Viséan, occurs as a thin unit within the Glencartholm Volcanic Beds at the bottom of the Upper Border Group of the Calciferous Sandstone (Lumsden *et al.,* 1967). In the section for the Langholm area, George *et al.* (1976, p. 42) show these volcanics as largely Holkerian in age. The rocks are poorly exposed, but a complete section was provided by the Archerbeck Borehole (Lumsden and Wilson, 1961). This, however, did not encounter the fossil beds of Glencartholm. Even the local extent of the Glencartholm fish beds is unclear because of faulting at the site, and it has been assumed for many years that the fish bed was worked out (Lumsden *et al.,* 1967). Recently, however, similar fossiliferous shales have been discovered nearby and await detailed excavation (Schram, 1981).

Peach and Horne's (1903) section at the collecting site showed two fossiliferous horizons: the Shrimp Bed, containing crustaceans, fishes and molluscs, and the Scorpion Bed, containing an extensive flora, as well as sparse crustaceans and arachnids. Schram (1983) discovered a black argillaceous limestone containing an almost complete actinopterygian fish, *Acrolepis ortholepis,* the matrix and preservation of which were identified with that of the Shrimp Bed. Nearby, black shales were exposed in the east bank to the north on the upthrow side of a fault that separates it from the original collecting site, and a section 4.87 m long was collected. The fossiliferous unit consisted of fine-bedded black shales with two thin limestone bands, and yielded fossils throughout the section in a manner unlike that described for the original section.

Schram (1983) counted specimens in the extensive collection made by Macconochie, an experienced collector who tended not to discard anything he found. Chordates represent 18% of the fauna, molluscs 33% and crustaceans 37%.

Fauna

Glencartholm is the only known locality for 20 species of fishes, and the type locality for a further six species that are found elsewhere. The majority of fishes are palaeoniscids (24 species) with sharks and holocephalians making up a further seven (Figure 9.17).

Acanthodii: Acanthodiformes: Acanthodidae

Acanthodes nitidus Smith-Woodward, 1891 Type locality

Osteichthyes: Sarcopterygii: Osteolepiformes: Osteolepidae

Megalichthys sp.

Osteichthyes: Sarcopterygii: Rhizodontidae

Strepsodus saurroides Binney, 1841

Strepsodus spp.

Osteichthyes: Sarcopterygii: Actinistia: Rhabdodermatidae

Dumfregia huxleyi (Traquair, 1881) Type and only locality

Osteichthyes: Actinopterygii: Rhadinichythidae

Rhadinichthys canobiensis Traquair, 1909 Type locality

R. canobiensis var. *delicatulus* Traquair Type and only locality

R. canobiensis var. *elegantulus* Traquair Type locality

R. canobiensis var. *pulchellus* Moy-Thomas Type locality

R. macconochii Traquair, 1881 Type locality

R. fusiformis Traquair, 1910 Type and only locality

R. formosus Traquair, 1904

R. tuberculatus Traquair, 1881 Type and only locality

Rhadinichthys sp.

Cycloptychius concentricus Traquair, 1881 Type and only locality

Osteichthyes: Actinopterygii: Canobiidae

Mesopoma politum (Traquair, 1881) Type locality

M. pulchellum (Traquair, 1881) Type and only locality

M. ?crassum (Traquair, 1911) Type and only locality

M. macrocephallum (Traquair, 1890)

Canobius ramseyi Traquair, 1881 Type and only locality

C. elegantulus Traquair, 1881 Type and only locality

Canobius sp.

Osteichthyes: Actinopterygii: Elonichthyidae

Elonichthys serratus Traquair, 1881 Type and only locality

E. pulcherrimus Traquair, 1881 Type and only locality

Osteichthyes: Actinopterygii: Acrolepididae

Acrolepis ortholepis (Traquair, 1884) Type and only locality

Osteichthyes: Actinopterygii: Carbovelidae

Phanerosteon mirabile Traquair, 1881 Type locality

Osteichthyes: Actinopterygii: Holuriidae

Holurus parki Traquair, 1881 Type and only locality

Osteichthyes: Actinopterygii: Platysomidae

Protoeurynotus traquairi Moy-Thomas and Dyne, 1938 Type locality

Paramesolepis tuberculata (Traquair, 1890) Type locality

Platysomus superbus Traquair, 1881 Type locality

Osteichthyes: Actinopterygii: Amphicentridae

Cheirodopsis geikiei Traquair, 1881 Type locality

Osteichthyes: Actinopterygii: Styracopteridae

Styracopterus fukratus (Traquair, 1881) 'Tarras Foot', type locality

Osteichthyes: Actinopterygii: Tarrisiformes: Tarrasiidae

Tarrasius problematicus Traquair, 1881 'Tarras Foot', type and only locality

Chondrichthyes: Elasmobranchii: Ctenacanthiformes: Ctenacanthidae

Goodrichthys eskdalensis Moy-Thomas, 1936 Type and only locality

Onychoselache traquairi Dick, 1978 Type locality

Sphenacanthus costellatus Traquair, 1884 Type and only locality

Chondrichthys: Holocephali: Menaspoidei:

Menaspidae

Deltoptychius armigerus (Traquair, 1888)

Antliodus scoticus Moy-Thomas, 1938 Type locality

Chondrenchelys problematica Traquair, 1888 Type and only locality

Acanthodes nitidus Woodward, 1891 is a slender acanthodian, with the dorsal and anal spines opposite one another. The pelvic spine is inserted relatively posteriorly. The body is covered by scales. These features are considered to be primitive (Forey and Young, 1985).

The osteolepiform *Megalichthys* is known from the Carboniferous of Great Britain, northern USA and the Lower Carboniferous of Morocco (janvier *et al.,* 1979). Isolated scales have also been recorded from the Namurian of Belgium, and possibly also the Upper Devonian of the Minaussinsk Basin of Russia.

The coelacanth *Dumfregia huxleyi* (Traquair, 1881) has been redescribed by Lund and Lund (1985), who examined nine specimens.

This is an important site for early actinopterygians (palaeoniscids): 25 species have been recorded from Glencartholm and Tarras Waterfoot. The Glencartholm actinopterygians were described by Moy-Thomas and Bradley Dyne (1938), and many of these were further figured by Gardiner and Schaeffer (1989). Several species of *Rhadinichthys* and *Elonichthys* have been noted from Glencartholm, but the taxonomy is confused (see Wardie report).

Rhadinichthys was a fusiform fish, often elongate-fusiform, with an oblique suspensorium and large gape (Figure 9.17). The body scales are rhomboid, and usually denticulated posteriorly. There are two rows of teeth, an inner set of incurved conical teeth and an outer set of small teeth. The most common *Rhadinichthys* at Glencartholm is *R. canobiensis* Traquair (1909), but is listed as *R. fusiformis* by Schram (1983). *R. canobiensis* and *R. macconochii* are long and thin with small paired fins, while *R. tuberculatus* and *R. fusiformis* are more deep-bodied with large paired fins (Moy-Thomas and Bradley Dyne, 1938).

The body of *Cycloptychius* is elongate, with the dorsal fin far back (Figure 9.18). There is a prominent rostrum, and the suspensorium is oblique. There are large conical teeth plus numerous small ones. Three ridge scales lie in front of the dorsal fin. *Cycloptychius* is easily distinguished from *Rhadinichthys* by its scale ornament, shape of the body, and jaw suspension (Moy-Thomas and Bradley Dyne, 1938). It is known also from the Coal Measures of Staffordshire and Northumberland (Lehman, 1966).

Phanerosteon is an unusual early actinopterygian, having lost most of its body scales. It possesses an oblique suspensorium. The genus was described from Glencartholm by Traquair (1881), White (1927) and Moy-Thomas and Bradley Dyne (1938), and their diagnosis has been emended by Gardiner (1985). Moy-Thomas and Bradley Dyne (1938) thought the skull and teeth similar to those of *Elonichthys,* and suggested that the development of scales was arrested in *Phanerosteon,* an example of paedomorphosis.

The genus *Elonichthys* is described in the Wardie site report. *E. serratus* did not exceed 0.12 m in length, and *E. pulcherrimus* did not exceed 0.15 m (Figure 9.14). *Elonichthys serratus* is distinguished by its small delicate fins and small scales with coarsely denticulate posterior margins, *E. pulcherrimus* by its deep-bodied form, and scales with finely denticulate posterior margins (Traquair, 1877; Moy-Thomas and Bradley-Dyne, 1938).

Mesopoma has a short head, and large orbit, and 'not very oblique' suspensorium ((Figure 9.18); Coates, 1993). The teeth are small and conical, extending along the whole length of the maxillary. The genus resembles *Rhadinichthys,*

Aetheretmon, and *Rhadinoniscus* (Moy-Thomas, 1938a; Moy-Thomas and Bradley Dyne, 1938). The *Mesopoma* terminal group (Gardiner and Schaeffer, 1989) is characterized by a small number of branchiostegals, a nearly vertical suspen-sorium, sickle shaped preoperculum, and a more or less triangular maxilla. This group also includes *Styracopterus* and *Canobius.* Until recently, *Mesopoma* was known only from Glencartholm, but it has now been discovered at Bearsden (q.v.) and Bear Gulch, Montana, USA, (Lund, 1982).

Four species of *Mesopoma* are recorded from Glencartholm. *Mesopoma pulchellum* and *M. politum* (Figure 9.18) are easily distinguished, but *M. crassus* is harder to assign generically and is only tentatively placed in the genus *Mesopoma* (Moy-Thomas and Bradley Dyne, 1938). *Mesopoma pulchellum* and *M. politum* are about 0.08 m in length, *M. ?crassus*

is about 0.11 m long. *M. pulchellum* has a row of ridge scales running from the occiput to the dorsal fin, while *M. politum* has only three ridge scales anterior to the dorsal fin.

Canobius was early amongst the 'palaeoniscids' to evolve an almost vertical jaw suspension in place of the primitive oblique jaw suspension. It has a short head with no rostrum and big orbits. *Canobius* is restricted to Glencartholm (Lehman, 1966) where it is represented by three species (Figure 9.17). *Canobius elegantulus* has only three bones in the snout, while *C. ramseyi* possesses also a large central element which bears teeth (Gardiner, 1963; Moy-Thomas and Bradley Dyne, 1938).

Styracopterus has been placed in the *Mesopoma* terminal group (Gardiner and Schaeffer, 1989). It has an almost upright sus-pensorium, very large fulcral scales, and an inequilobate, but not deeply cleft, caudal fin. White (1927) noted the peculiar shape of the maxillary and preopercular bones. Moy-Thomas (1937b) thought that *Benedenius* from the Lower Carboniferous of Belgium was closely related, but Gardiner (1985) disagreed. The genus consists of a single species, *S. fulcratus,* which occurs at 'Tarras Water Foot' (type material), Foulden (q.v.), Coldstream Bridge in Berwickshire and Coomsden Burn in Northumberland. *Styracopterus fulcratus* was described as *Holurus fulcratus* from 'Tarras Water Foot' by Traquair (1881, 1890b) on the basis of five specimens. It represents the same species as that originally described as *Fouldenia ottadinica* from Foulden by White (1927), and has been revised by Gardiner (1985) specimens from Foulden (q.v.).

Platysomids were deep-bodied palaeoniscids with an elongate dorsal fin (Lehman, 1966; Moy-Thomas and Miles, 1971). There are perhaps two families, the Platysomidae (with conical, pointed teeth) and the Amphicentridae (with crushing dentition). Both occur in the Carboniferous and the Permian. Moy-Thomas and Miles (1971) have argued that temporal series in both families illustrate evolution from fusiform to deep-bodied forms:

1. Platysomidae: *Mesolepis* (body deeply fusiform, elongated dorsal fin); *Wardichthys* (deep, rounded body, short dorsal fin well behind the dorsal hump of the body); *Platysomus* (very deep body, unpaired fins elongated).
2. Amphicentridae: *Protoeurynotus* (deeply fusiform); *Eurynotus* (more elongated dorsal fin); *Adroichthys* (short dorsal fin with enlarged dorsal ridge-scales); *Cheirodopsis* (deep, rounded body with elongated dorsal and anal fins); *Cheirodus* (= *Amphicentrum;* very deep rhombic-shaped body, laterally flattened, no pelvic fins).

Platysomus is known from the Carboniferous of England, Scotland, the Netherlands, USA (Mazon Creek), and the Permian of Germany, England, Texas, Canada and Russia, and the Middle Triassic of Australia. Glencartholm is the type locality for *P. superbus* Traquair, 1881 (Figure 9.19).

Protoeurynotus is a deeply fusiform amphi-centrid with a nearly vertical suspensorium and triangular maxillary. It is distinguished from *Eurynotus* by the small dorsal fin with anterior ridge scales. *Protoeurynotus traquairi* Moy-Thomas and Dyne, 1938 did not exceed 150 mm in length. It was described by Moy-Thomas and Bradley Dyne from two imperfect specimens. Only the large pectoral tins are preserved in these specimens, and these badly.

The genus *Paramesolepis* was erected by Moy-Thomas and Bradley Dyne (1938) for *Mesolepis tuberculatus* Traquair, 1890, for which Glencartholm is the type locality. It is deeply fusiform with a nearly vertical suspensorium. The head bones are similar to *Mesolepis,* but the teeth are small and the head is larger.

Cheirodopsis has a deep and rounded body, with both the dorsal and anal fins elongated.

The pectoral and pelvic fins are small. There are no teeth on the maxillary and dentary; instead there is a crushing dentition consisting of large coronoid and pterygoid tooth plates (Moy-Thomas and Bradley Dyne, 1938). *Cheirodopsis geikiei* Traquair, 1881 is the commonest fish at Glencartholm, representing 22% of fishes collected at the site by Macconochie and 4% of the total fauna (Schram, 1983). It has been described by Traquair (1881, 1890b) and Moy-Thomas and Bradley Dyne (1938).

Holurus has a fusiform body (not exceeding 130 mm in length), with elongated and rounded dorsal and anal fins. The caudal fin is hetero-cercal but not cleft posteriorly. It possesses small paired fins. The lepidotrichia do not bifurcate and there are no fringing fulcra. There is a row of median ridge scales. The head has no rostrum and the teeth are conical

and medium-sized (Moy-Thomas and Bradley Dyne, 1938). The genus is restricted to the Lower Carboniferous of Scotland (Lehman, 1966) and is represented by a single species from Glencartholm, *H. parki* Traquair, 1881 (Figure 9.19). This has been described by Traquair (1881, 1911), Woodward (1891a) and Moy-Thomas and Bradley Dyne (1938), and is similar to *Tarrasius,* with its elongate median fins, undichotomized lepidotrichia and absence of fulchral scales.

Tarrasius problematicus was named by Traquair (1881) and redescribed after new collections were made by Moy-Thomas (1934) and Moy-Thomas and Dyne (1938). The head resembles that in other early actinopterygians (Jessen, 1973; Lund and Melton, 1982), and the long body has a continuous dorsal, diphycercal caudal fin; anal fin and pelvic fins are absent (Figure 9.19). The pectoral fins have actinopterygian internal structure, but also have rounded fleshy lobes like *Polypterus.* There are no scales on most of the body, with the caudal region only bearing numerous small square scales, like those on *Cheirolepis.* The axial skeleton is like other actinopterygians with two rows of radials below the dorsal and one row above the anal fin, which are more numerous than the neural and haemal spines.

Three species of elasmobranch are known from Glencartholm (Figure 9.20): *Ctenacanthus* and *Goodrichthys* are both genera of Family Ctenacanthidae, and *Sphenacanthus* is *incertae sedis* (Zangerl, 1981). These are some of the most primitive euselachians, and include forms akin to those from Mazon Creek. The genus *Ctenacanthus* was based on isolated spines with longitudinal ornament by Agassiz (1833–45), and there are many species. The type species, *Ctenacanthus major,* from Avon Gorge, Bristol, has never been found in association with other remains. *Goodrichthys,* considered to be a 'ctenacanth' by Moy-Thomas (1936) and Moy-Thomas and Miles (1971), has smooth unornamented teeth and pectinated ribbing on its fin spines, but the ornamentation is greatly reduced in comparison with *C. major.* Apart from this difference, *Goodrichthys* fin spines resemble those of *C. major,* and these fishes may be closely related (Maisey, 1981).

Sphenacanthus is a ctenacanth genus, the type species of which is *S. serrulatus* from Burdiehouse near Edinburgh. It is defined as having spines similar to *Ctenacanthus* and teeth like *Tristychius arcuatus.* The braincase has an elongated otico-occipital region, as in *Tristychius. Sphenacanthus* has fin spines with irregular widely spaced ribs, some with scattered tubercles (Maisey, 1981). *Ctenacanthus costellatus* is unlike other *Ctenacanthus* species, and may belong to *Sphenacanthus* (Maisey, 1981). Traquair (1888c) assigned a shark pectoral fin from Glencartholm to *Tristychius arcuatus* Agassiz, the holotype being spines from Greenside, Glasgow, and noted that the fin was very like that of modern sharks. He later (1903) referred the fin to *T. minor* Portlock. Woodward (1924) noted that the spine of the pectoral fin in this specimen bore *Lophodus*-like teeth on the anterior margin, and related it to the Mesozoic hybodonts. Moy-Thomas (1936) re-examined the Glencartholm specimen, and found that the pectoral and caudal fins were rather more specialized than the hybodontids, so he erected a separate suborder, Tristychii, of the Order Protoselachii. Later still, material collected by S.P. Wood from Wardie showed that the Glencartholm specimen was the same species as the Wardie species, and that they could not be identified with *T. arcuatus* because the fin spines were fundamentally different. They were assigned to the new species *Onychoselache traquairi* Dick, 1978, with the Glencartholm specimen as the holotype ((Figure 9.15)D). In particular, the pectoral spines were shown to be tribasal, hence similar to most hybodontiforms and neoselachians, and not dibasal as was previously supposed.

Zangerl (1981) includes the genus *Onychoselache* in the new Superfamily Hybodontoidea, containing several Palaeozoic shark species that are too poorly known to group into families. The genus is represented by this single species, which is described by Dick and Maisey (1980) based on two specimens only, the holotype from Glencartholm, which is an almost complete fish, probably about 165 mm long, and a second specimen from Wardie of the anterior part of a larger individual, probably 250 mm long, which has a well-preserved head (unlike the holotype). The pectoral fin is distinctive, having a series of 12 or 14 large toothlike denticles along the anterior margin. Similar denticles are present on the head. The caudal fin is supported by elongated and thicker haemal arches, several of which may be jointed, and is slightly heterocercal, probably similar in shape to that of *Tristychius* and *Hybodus.*

Glencartholm Holocephalians (Figure 9.21) include *Deltoptychius armigerus* (Traquair, 1888), the only species of the Family Deltoptychiidae which is known from associated teeth and skeletal remains (Zangerl, 1981). Other species occur in the Lower Carboniferous of Britain, but are known only from teeth, spines and disseminated fragments. The only specimen to show parts of the skull and postcranial skeleton came from Glencartholm (Moy-Thomas, 1936; Patterson,

1965). Scales are known from a second Glencartholm specimen that shows their articulation. A complete specimen of *Deltoptychius* has recently been found at Bearsden (q.v.).

Deltoptychius probably reached about 0.3 m in length, with the headshield about 70 mm of this, and longer than broad. The headshield is fused into a single unit bearing the supraorbital sensory canals. There are no frontal spines as in other chimaeroids. The notochord was uncalcified and there appears to have been no dorsal fin spine (Patterson, 1965). Small scales cover the head and trunk and there are two rows of *Listracanthus*-like spines down the back of the fish. These are longer posteriorly, reaching up to 14 mm in length. The longest ones have the anterior edges of the vertical ridges of the spines bearing elongate tubercles (Patterson, 1965).

The holotype, and most of the isolated specimens of *Deltoptychius armigerus* (Figure 9.21) are spines, which were shown by Moy-Thomas (1936) to have been borne on the angle of the mandible. There is a much variation in shape and ornamentation. The Glencartholm specimen shows that the anterior border of the spine, when complete, is much longer than it is in any of the isolated examples, and that the two spines almost met in the midline. Patterson (1965) determined that there was a single pair of mandibular teeth-plates like *D. acutus* from the Carboniferous Limestone of Armagh and northern England, and a posterior pair of tooth plates. *Chondrenchelys problematica* (Figure 9.21) was named by Traquair (1888c), and redescribed by Moy-Thomas (1935), Patterson (1965) and Lund (1982). *Chondrenchelys* is a small elongate fish, with a long continuous dorsal fin and a body tapering to a point. It has bradyodont tooth plates, but is different from other chondrichthyans, and has been placed in a separate order, the Chondrencheliformes, by Moy-Thomas (1939) and Lund (1977). Traquair (1888c) said C. *problematica* was 'one of the strangest fishes' of the fauna at Glencartholm. The species is unique to the site, and remained the sole representative of the order, until a second chondrencheliform, *Harpagofututor volsellorhinus,* was discovered in the Bear Gulch Limestone (Lund, 1982). Lund (1982) tentatively included in the order two similar form genera, *Platyxystrodus* and *Solenodus,* based on teeth from North America and Britain.

In *Chondrenchelys problematica* there are about 100 well-developed ring-shaped calcifications in the notochordal sheath, comparable to those of modern chimaeroids; they are not true centra as they might appear (Patterson, 1965; Zangerl, 1981). *Chondrenchelys* has a diphycercal tail, which is not seen as a primitive feature of the group, but as being associated with a specific mode of locomotion. The dentition consists of two large pairs of tooth plates in each jaw.

Chondrenchelys is the oldest holocephalian in which claspers are known, representing the only evidence of typical chondrichthyan sexual dimorphism in early holocephalians. In the Palaeozoic, only a few species show the condition of the pelvic area for both adult males and the females (Zangerl, 1981). Unlike modern chimaeroids, the pectoral and pelvic girdles have left and right halves unfused, very like xenacanthid sharks. However, the vertebral column, skull and dentition of *C. problematica* are typically holocephalian. The similarities to xenacanthids are probably convergent, and based on a similar eel-like swimming mode (Moy-Thomas and Miles, 1971).

Interpretation

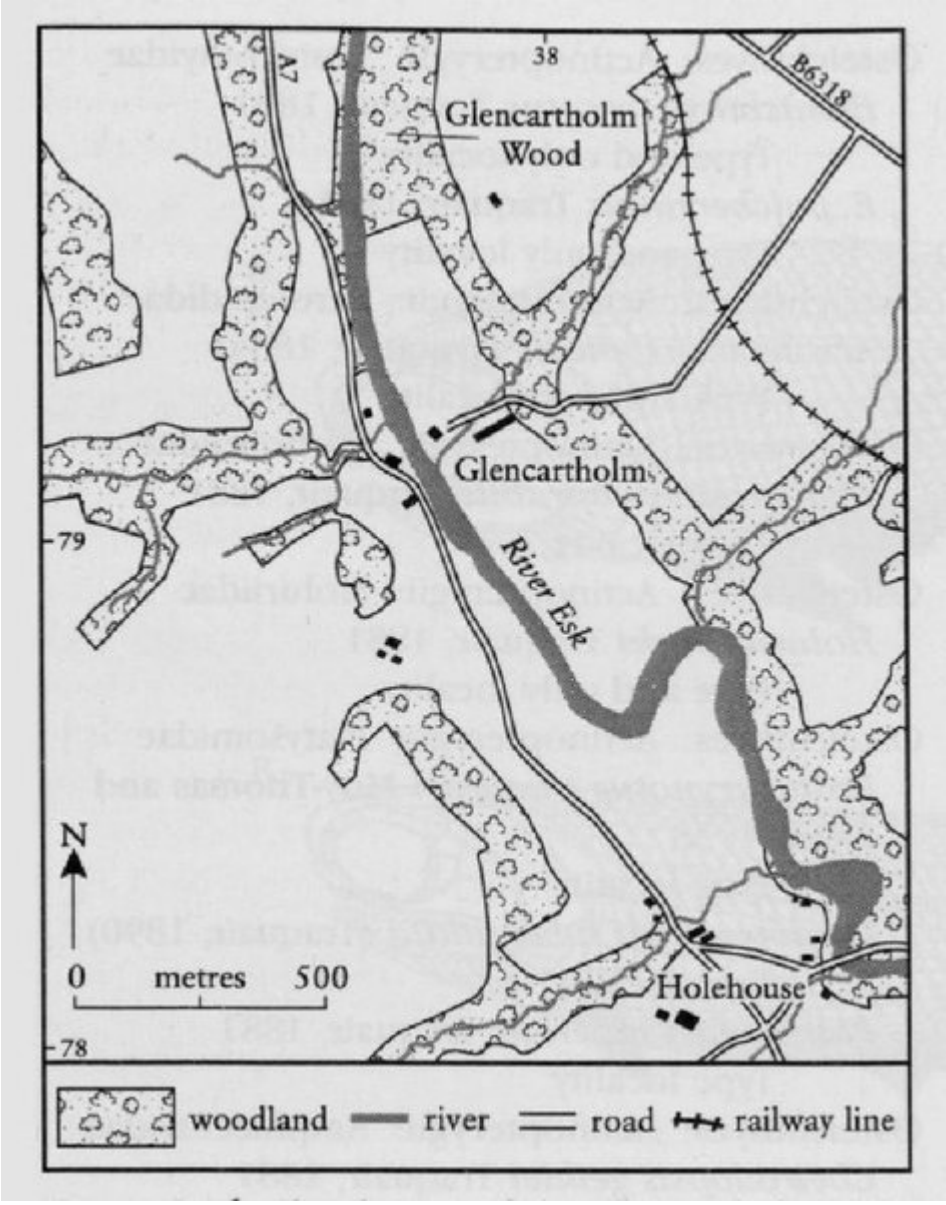
The conditions of preservation of the Glencartholm fauna, where organic body fossils persist while calcareous shells frequently do not, having been demineralized or replaced, indicate conditions of quick burial, low oxygen and low pH, allowing whole bodies to remain intact but mineral content to be attacked by the acid conditions (Schram, 1983). The Glencartholm biota represents a death assemblage, perhaps similar to the younger Carboniferous Lagerstatten of Bear Gulch and Mazon Creek, all three of which represent nearshore marine environments (Schram, 1983). The marine invertebrates do not occur in the same layers as the fishes. Malacostracans (shrimps) at the three sites show assemblages of related species in similar trophic positions and habitats over wide geographical areas over long (70–80 Ma) periods (Schram, 1981, 1983; Factor and Feldman, 1985). The nearshore marine habitat contains nectonic and benthic malacostracans that show that conditions were conducive to animal life within the water column and at the sediment–water interface. The fish species show similar genera and families at Bear Gulch and Glencartholm, even when these represent specialized forms. The sites differ in that there are no coelenterates, annelids or soft-bodied problematica at Glencartholm, although these are common at Bear Gulch and Mazon Creek. Lund and Lund (1985) found it plausible to postulate an estuarine or similar environment (for *Dumfregia*).

Some aspects of the fish fauna also give indications of the environment. In North America and northern Europe, the sarcopterygian *Megalichthys* occurs in coal measures, and therefore was probably a freshwater fish, whereas the specimen from Morocco indicates that it may also have inhabited deltaic and brackish water and possibly also used aestivation burrows (Janvier *et al.,* 1979). In modern fishes, a deep body such as in the platysomid *Platysomus superbus,* is associated with life in quiet waters. The diets of the fishes can also be reconstructed. Some of the fishes ate malacostracans, as indicated by specimens from Bear Gulch, where shrimp remains have been found within shark and coelacanth skeletons, and in many coprolites (Schram, 1983). Food preferences of the sharks are inferred from the style of the dentition, as well as rare preserved gastro-intestinal contents and coprolites. Analogies may be sought in the Late Carboniferous Mecca fauna of North America, where preserved food residues vary palaeogeographically. In the marginal areas of these basins, where body fossils are common, food residue masses of sharks contain almost exclusively fish remains, but in the more central areas of the basins where preserved fish skeletons are extremely rare in black shales, the abundant gastric residue masses and shark coprolites contain only remains of arthropods (Zangerl and Richardson 1963; Zangerl, 1981). This may be the result of periodic natural fish traps along the fringes of the basin leading to abnormal trophic relationships, whereas in deeper central waters sharks fed primarily on arthropods (Zangerl, 1981).

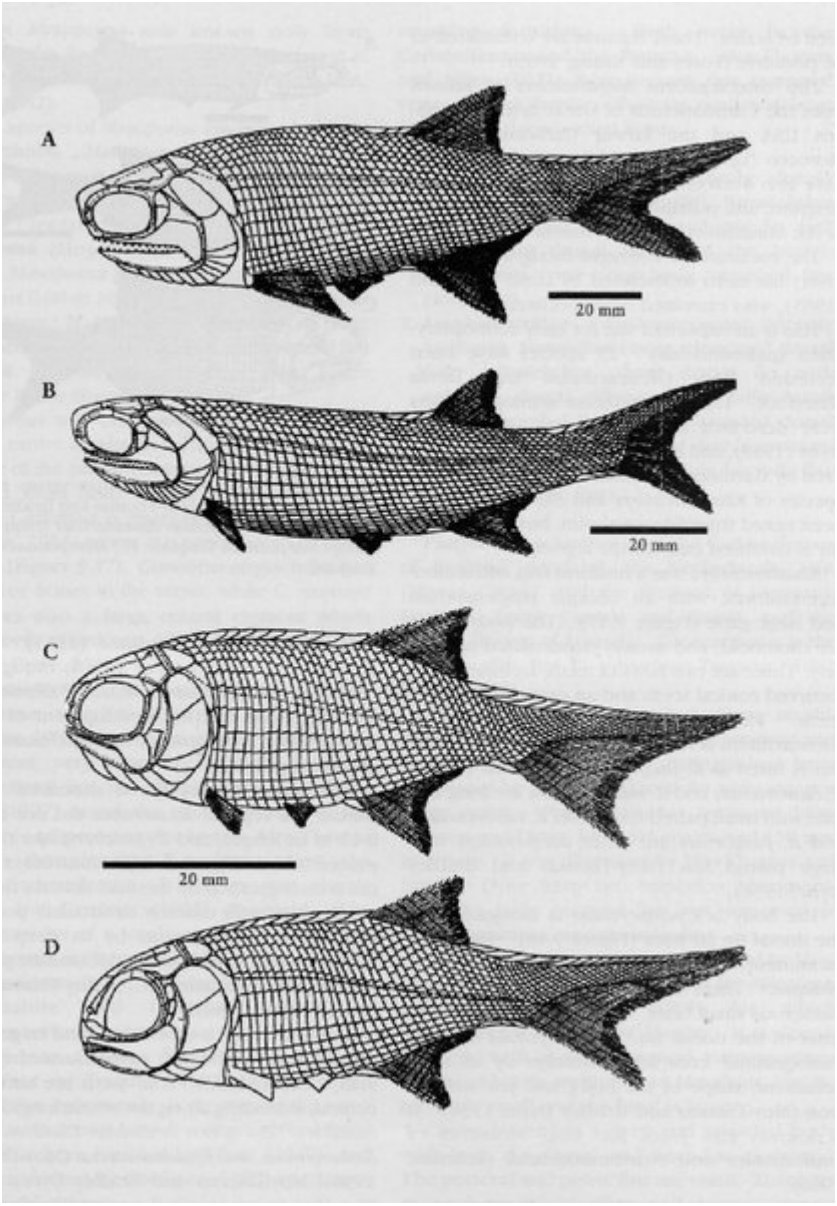
Conclusion

Glencartholm has been the source of the richest Carboniferous fish fauna in the British Isles, and one of the richest in the world, hence its conservation value. Over 35 species have been recorded, for many of which this site is the source of the type specimens. Several species are known only from Glencartholm. Many of the collections are Victorian in age, but substantial excavations wcrc carried out in the 1930s and in the 1960s (B.G. Gardiner, pers. comm., 1996). Exploratory trenching in the 1980s showed the further potential of the site for more finds of fossil fishes.

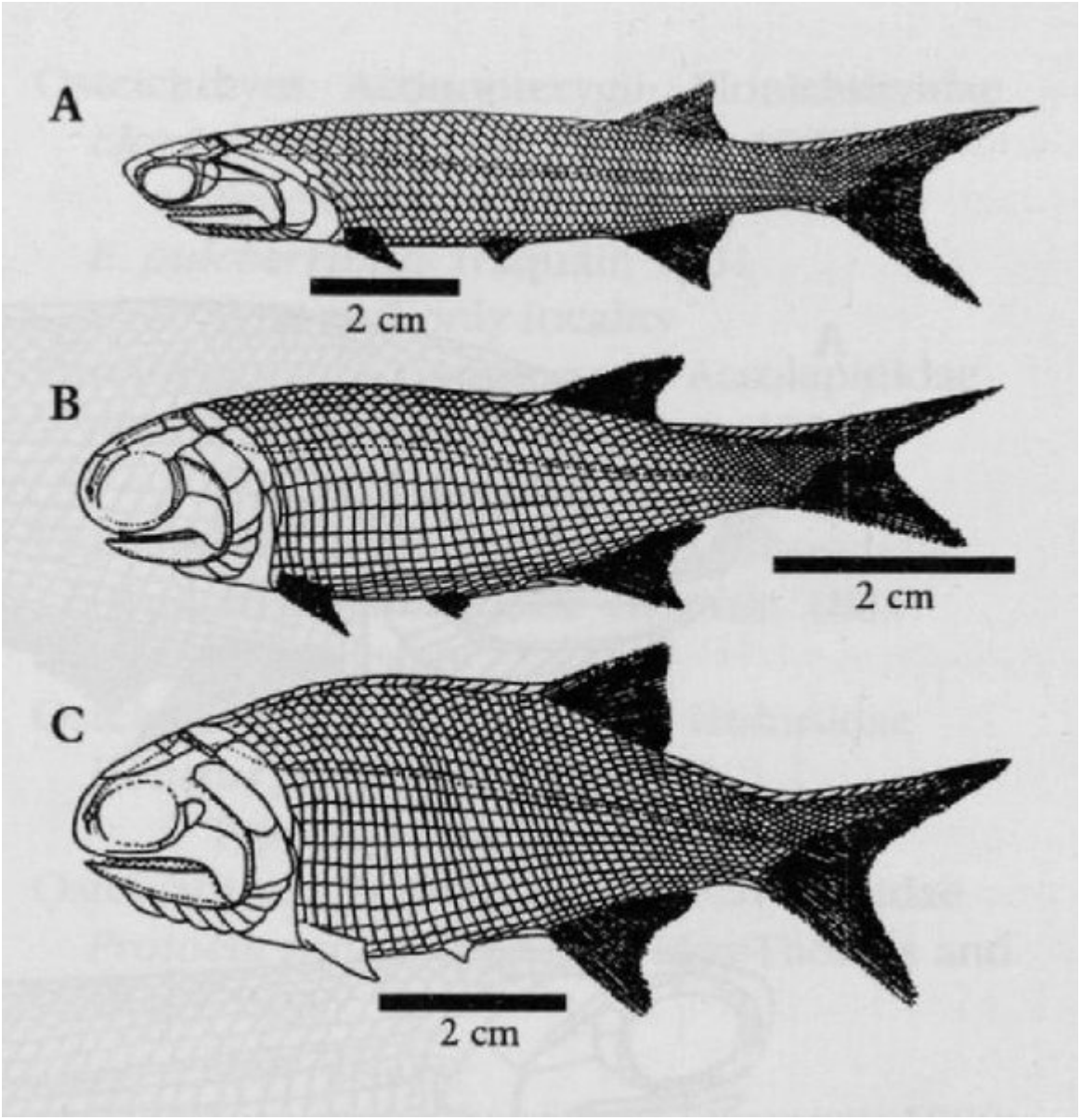
References



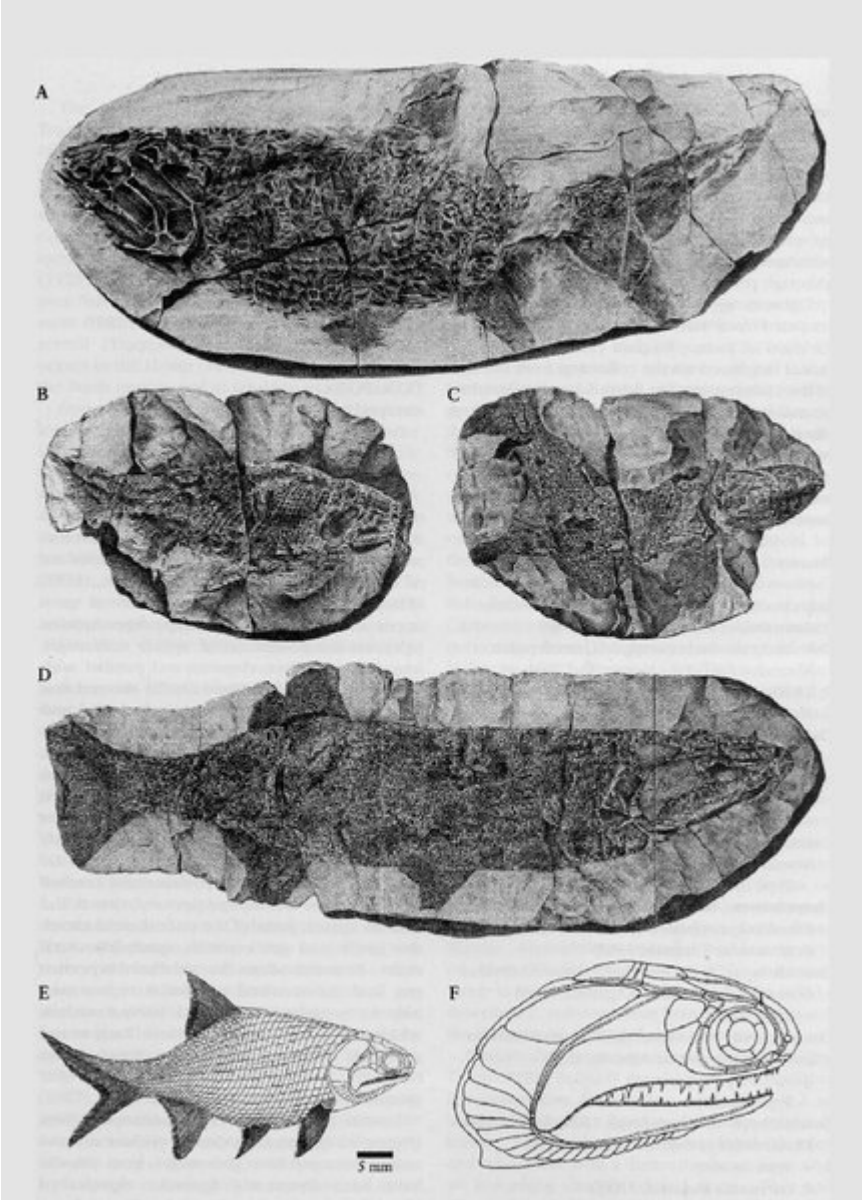
(Figure 9.16) Sketch map of the Glencartholm GCR site, Berwickshire.



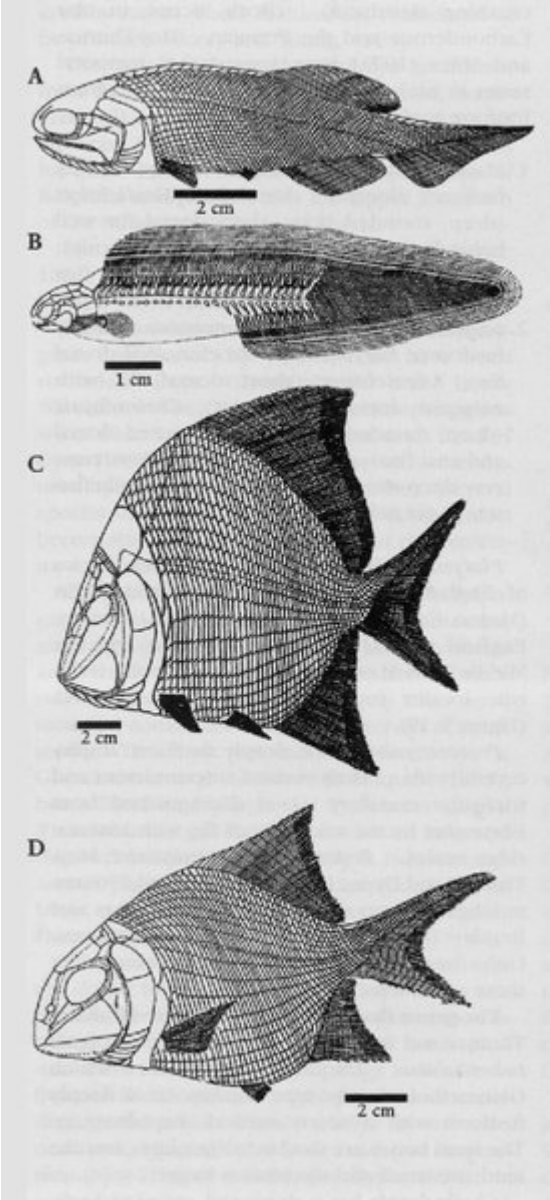
(Figure 9.17) Some of the relatively more common Glencartholm actinopterygians: restorations in lateral view by Moy-Thomas and Bradley Dyne (1938). (A) Rbadiniththys fusiformis Traquair; (B) R. canobensis Tranquair; (C) Canobius ramsayi Traquair; (D) C. elegantulus Traquair.



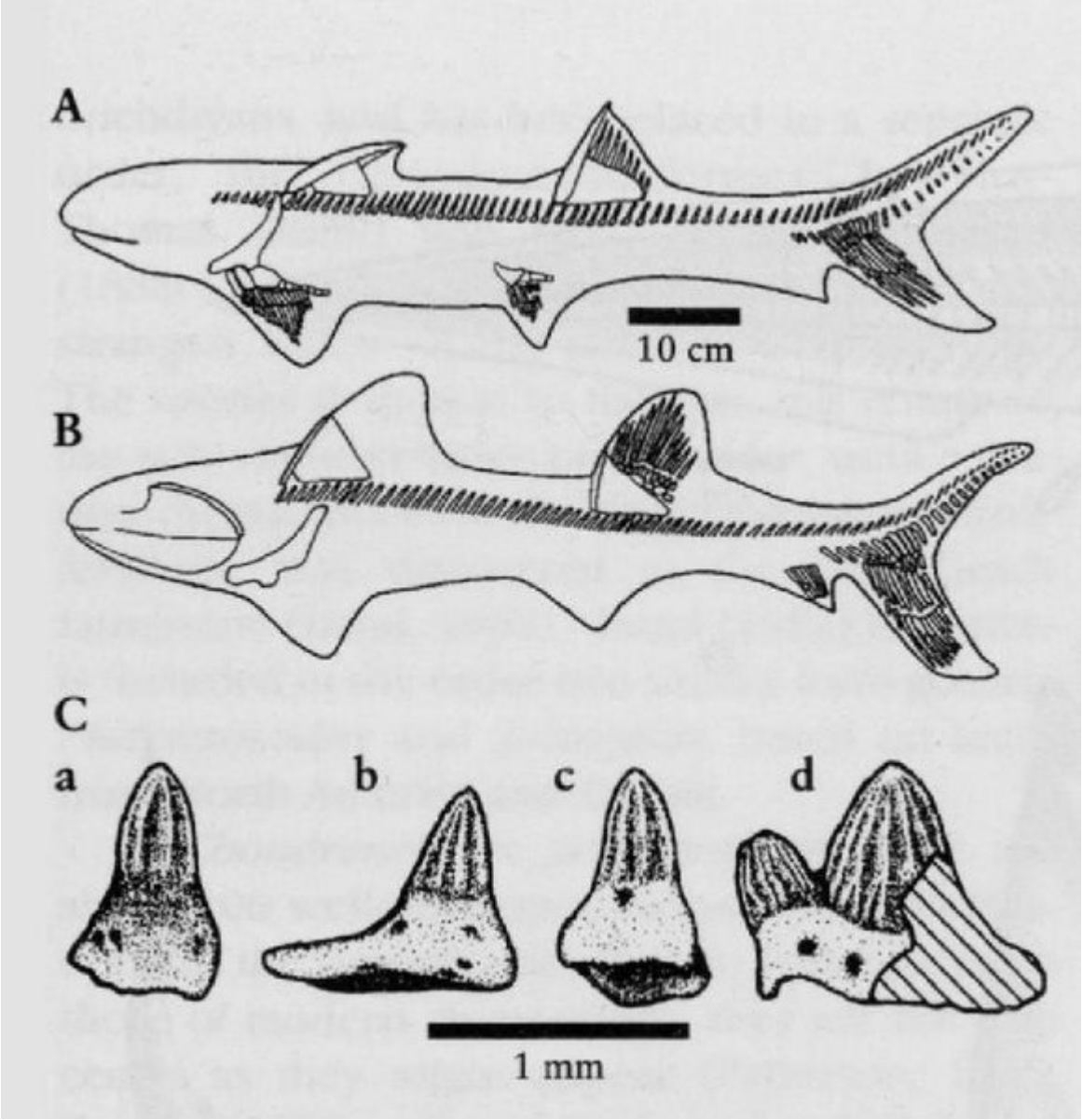
(Figure 9.18) Glencartholm actinopterygians: restorations in lateral view by Moy-Thomas and Bradley Dyne (1938). (A) Cycloptychius concentricus Traquair; (B) Mesopoma politum Traquair; (C) Mesopoma crassum Traquair.



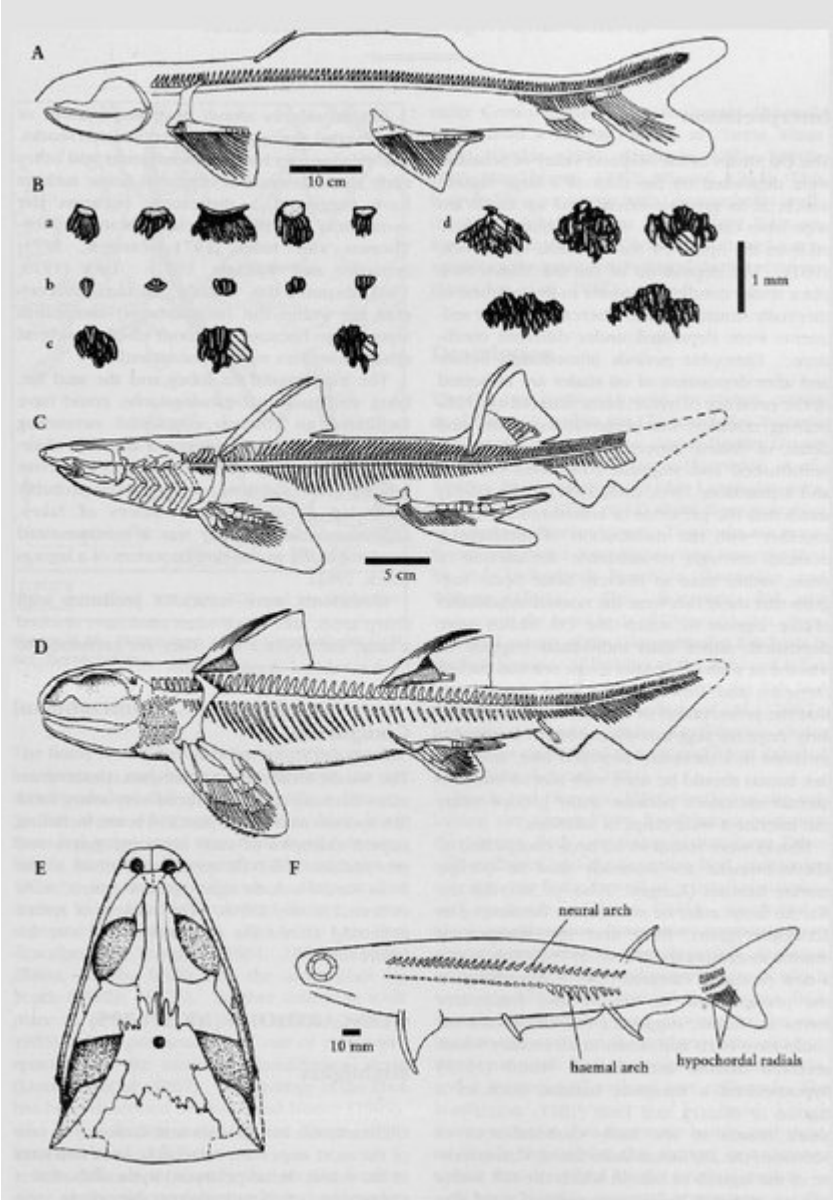
(Figure 9.14) Actinopterygians in nodules from the Wardie Shale, Wardie, (A)–(D) are all c. X 0.66. (A) Cosmoptychius striatus Agassiz, specimen in nodule; (B) Elonichthys robisoni Hibbert; (C) Rhadinichthys ferrox Traquair; (D) Nematoptychius greenocki Traquair; (E) Gonatodus punctatus Agassiz, restoration from Gardiner (1967a); (F) Nematoptychius greenocki Traquair, restoration of the head by Gardiner (1963), c. x 0.5.



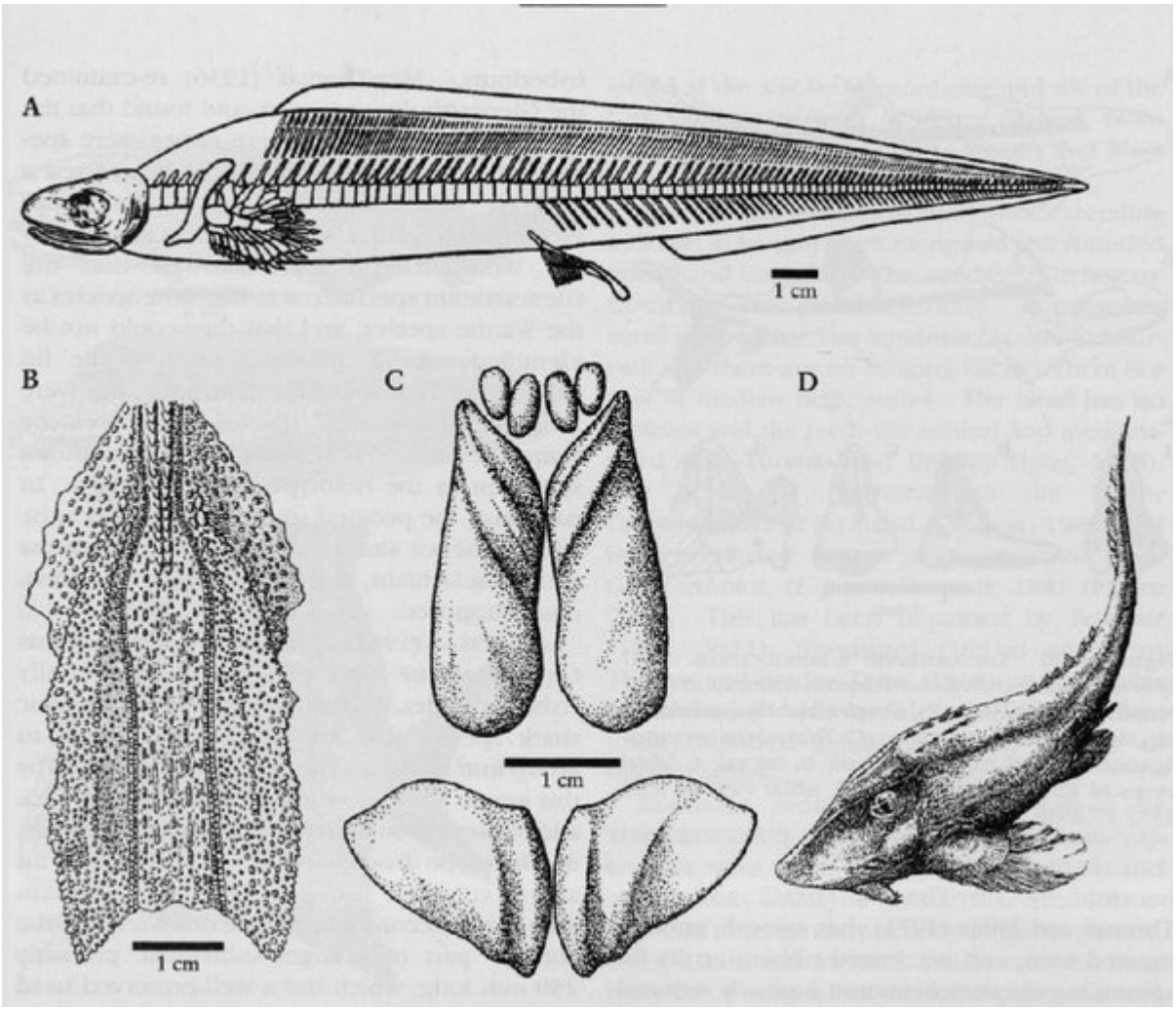
(Figure 9.19) Glencartholm actinopterygians: restorations in lateral view by Moy-Thomas and Bradley Dyne (1938). (A) Holurus parki Traquair; (B) the elongated Tarrasius problematicus Traquair, once thought to be a crossopterygian (after Moy-Thomas, 1937b); (C) Platysomus superbus Traquair; (D) Cheirodopsis geikiei Traquair. (C) and (D) are typical deep-bodied actinopterygians.



(Figure 9.20) Glencartholm elasmobranchs. (A) Sphenacanthus costellatus Traquair, restoration (after Moy-Thomas, 1936); (B) Goodrichichthvs eskdalensis, Moy-Thomas restoration; (C) Tristychius arcuatus Agassiz, isolated teeth; a, lingual; b, lateral; c, labial views of RSM 1972.276.461A; d, labial view of RSM 1972.27.460B.



(Figure 9.15) Wardie elasmobranchs; (A) Diplodoselache woodi Dick, restoration of the skeleton, after Dick (1981); (B,a) scales from the anterior part of the trunk; (B,b) scales from the anal fin; (B,c) flank scales; (B,d) scales from head, body and tail; (C) Tristychius arcuatus Agassiz restoration of the skeleton (after Dick, 1978); (D) Onychoselache traquairi Dick, restoration (after Dick, 1978); (E) The Wardie tetrapod Lethiscus stocki Wellstead, a restoration of the dorsal surface of the skull (after Wellstead, 1982); (F) the Acanthodes sulcatus Agassiz restoration after Moy-Thomas and Miles (1971).



(Figure 9.21) Glencartholm holocephalians. (A) Chondrenchelys problematica Traquair in lateral restoration after Patterson (1965). (B) Deltoptychius armigerus Traquair, restoration of the headshield in dorsal view based on NHM P 11372 (after Patterson, 1966); anterior at top, incompletely fused tesserae make up the central part of the shield. (C) Dentition restored as if seen in front of wide-open mouth. (D) Deltoptychius, restoration of the fish courtesy of the Hunterian Museum, Glasgow; overall length of the specimen from Bearsden (q.v.) c. 60 cm.