Wardie

[NT 245 771]

Highlights

The Wardie shore section in Lothian has been the source of 18 species of fossil fishes, of which eight were first described from this site, and one of which has never been found elsewhere. Fish specimens have been collected at Wardie for over 150 years, and they provide detailed evidence that the environment around Edinburgh during Early Carboniferous times was a deep lagoon, where thick black sediments accumulated to form the oil shales (Greensmith, 1963). A single specimen of tetrapod material has also been collected from Wardie.

Introduction

Fishes were first discovered at Wardie in the 1830s, and several species were described by Agassiz (1835) from the collections of Lord Greenock. Later collections were reviewed by Traquair (1903), and substantial discoveries in the 1970s (Wood, 1975) led to renewed interest, especially in the remarkable and rare fauna of fossil sharks. The geology of the site (Figure 9.13) has been described by Peach *et al.* (1910), Tait (1925), Waterston (1962b), Mitchell and Mykura (1962), Wood (1975) and Clarkson (1986).

Description

The Wardie Shales are stratigraphically near the middle of the Lower Lothian Group (Wilson, 1974), but their full sequence is nowhere exposed. This site is the type location for the Wardie Shales, and the basal 46 m occur on both sides of Granton Harbour where the rocks occur within the Wardie Syncline. They conformably overlie the Granton Sandstones at the west end of Granton Harbour. Much of the succession is of shale with ironstone nodules. Some of these nodules yield fishes, although the majority contain only spiral coprolites (presumed to be chondrichthyan), and some are barren (Wood, 1975; Clarkson, 1986). Seven horizons yield these nodules; all are distinctive in terms of the relative abundances of different fish species in each (Figure 9.14) and (Figure 9.15).

The first (lower) assemblage is typical of some of the limestone horizons of the Midland Valley, particularly the Lower Limestone Group. It is composed entirely of chondrichthyans, represented by teeth and fin spines. Almost all are bradyodont or anacanthous sharks, which are also common in the Carboniferous Limestone of England and Ireland. The second assemblage, the *Diplodoselache* fauna, is typical of the fish-bearing nodules of the Oil Shale Group, the Burdiehouse Limestone, and the roof shales of the coal seams of the Lower Limestone, Limestone Coal and Upper Limestone groups. Fossils include shark species unique to the Viséan and Namurian of Scotland, *Diplodoselache woodi, Tristychius arcuatus, Onychoselache traquairi* and *Sphenacanthus serrulatus,* osteolepiformes, coelacanths, dipnoans, acanthodians and actinopterygians, as well as one tetrapod specimen.

The siderite nodules ensure the fine preservation of most of the fishes from this site. Elasmobranchs are rare in older collections from the site, possibly because of the difficulty in recognizing shark sections seen in broken concretions (Wood, 1975). Sharks are, however, abundant in the new collections from Wardie, and several species are represented well preserved and almost uncrushed. Acanthodians from Wardie are disarticulated, with scattered scales and spines.

Complete rhizodonts are extremely rare. A gigantic (2.6 m long) specimen of *Rhizodus hibberti* from Wardie, described by Stock (1881, 1883), was preserved in a large flattened nodule and found *in situ,* with only the head damaged by erosion by the sea. The majority of actinopterygians are also well preserved, although crushed flat.

Eighteen species of fishes have so far been recorded from Wardie, which is the type locality for eight of them. Traquair (1903) published a faunal list, based on the collecting from the site of the 19th century, but fishes have continued to be collected from the site in the 20th century, albeit slowly. Renewed interest was stimulated by Stan Wood, who collected

several hundred new specimens in the 1970s (Wood, 1975), some of which were the basis of new descriptions (Dick, 1978, 1981; Dick and Maisey, 1980).

Fauna

Acanthodii: Acanthodiformes: Acanthodidae

Acanthodes sulcatus Agassiz, 1835

Osteichthyes: Sarcopterygii: Osteolepidae

Rhizodus hibberti (Agassiz and Hibbert, 1836)

Megalichthys sp.

Osteichthyes: Sarcopterygii: Dipnoi

lungfish (T Smithson, pers. comm., 1992)

Osteichthyes: Actinopterygii: Cosmoptychiidae

Cosmoptychius striatus (Agassiz, 1835) Type locality

Osteichthyes: Actinopterygii: Acrolepididae

Nematoptychius greenocki (Traquair, 1867) Type locality.

Osteichthyes: Actinopterygii: Elonichthyidae

Elonichthys robisoni (Hibbert, 1835)

E. striatulus Traquair, 1907

Osteichthyes: Actinopterygii: Gonatichthyidae

Gonatodus punctatus (Agassiz, 1835) Type locality.

Osteichthyes: Actinopterygii: Amphicentridae

Eurynotus crenatus Agassiz, 1835

Wardichthys cyclosoma Traquair, 1875 Type locality.

Osteichthyes: Actinopterygii: Rhadinichthyidae

Rhadinichthys brevis Traquair, 1881 Type locality

R. carinatus (Agassiz, 1835) Type locality.

R. ferox Traquair, 1877 >Type locality.

R. ornatissimus (Agassiz, 1835)

Osteichthyes: Actinopterygii: Platysomidae

a platysomid close to the Amphicentridae

Chondrichthyes: Elasmobranchii: Xenacanthiformes

Diplodoselache woodi Dick, 1981 Type locality.

Chondrichthyes: Elasmobranchii: Ctenacanthiformes

Onychoselache traquairi Dick, 1978

Sphenacanthus serrulatus Agassiz, 1837

Ctenacanthus indet.

TETRAPODA

Aistopoda: Lethiscidae

Lethiscus stocki Wellstead, 1982

Acanthodes sulcatus Agassiz, 1835 was one of the first fishes to be discovered at Wardie, but the type specimen, a patch of scales, is now lost and the characters used to define the species are of little value (Traquair, 1890c; White, 1937; Miles, 1970). White (1937) described new specimens and designated a neotype from Ardross (q.v.), on the possession of 'spines with single longitudinal groove close to and parallel with the anterior border'. Wood (1975) showed that *A. sulcatus* was most common in Beds 4, 5 and 6, and rare in Beds 1, 2 and 3. Miles (1970) described a vertebral column, presumably of *A. sulcatus,* from Wardie (Figure 9.15), which has subsequently been used to illustrate the typical acanthodian condition (Denison, 1979). This specimen is important as 'the most completely preserved acanthodian vertebral column so far available'. It shows 35 perichondrally ossified vertebrae, plus incomplete pectoral, dorsal and anal fin spines, parts of the endoskeletal shoulder girdle and gut contents (probably ostracods). In acanthodians the notochord is persistent, and the vertebral column is represented only by separate neural and haemal arches, which in this specimen are ossified. Each neural arch may be paired and bear a dorsal spine. Only the post-abdominal haemal arches bear spines. There are no ossified ribs.

Several of the species of actinopterygians (Figure 9.14), including *Cosmoptychius striatus* and *Nematoptychius greenocki,* from Wardie have been frequently figured. Species of *Elonichthys* and *Rhadinichthys* have been described from Wardie, but most require redescription.

The genus *Cosmoptychius* was erected by Traquair (1877–1914) for *Amblypterus striatus* of Agassiz, although he later (Traquair, 1890) placed it in *Elonichthys.* Other authors, however (Aldinger, 1937; Gardiner, 1963), found reason to retain the genus *Cosmoptychius. Cosmoptychius striatus* was described and figured by Traquair (1877–1914, 1890b), Watson (1928) and Gardiner (1963). It is the most common fish in the ironstone nodules at Wardie, but most specimens are fragmentary and badly preserved (Traquair, 1877–1914). The species occurs in the Lower Oil Shales of various sites in the Forth region, and at Foulden (q.v.).

Cosmoptychius striatus (Figure 9.14) was no longer than 0.28 m. The ornamentation on the scales and skull roofing bones consists of sharply defined parallel ridges of enamel that occasionally branch and join, and which pass diagonally across the scales, whose posterior margins are therefore delicately denticulated. The species has been mentioned by Watson (1928), Schaeffer (1971), Poplin (1974) and Patterson (1975) since it shows a rare example of an early actinopterygian neurocranium.

Gardiner (1984, 1985) regarded *Cosmoptychius striatus* as a stem-group neopterygian, put between the Chondrostei and the Neopterygii, since it possesses several advanced features, including a median posterior myodome, long ascending processes on the parasphenoid, and a dermopterotic. Gardiner and Schaeffer (1989) placed the genus in their *Watsonichthys* terminal group, which also includes *Strepheoschema.* The Family Cosmoptychiidae was erected by Gardiner (1963) for the Lower Carboniferous *Watsonichthys* and *Cosmoptychius.*

The actinopterygian genus *Nematoptychius* is restricted to the Lower Carboniferous of eastern Scotland (Lehman, 1966). It has an inclined suspensorium, both big and small teeth on the maxillary and mandible, a rostrum and a small eye (Gardiner, 1963). *Nematoptychius greenocki* was originally named *Pygopterus greenocki* by Agassiz, without description or figure (Traquair, 1877–1914), and was described first by Traquair (1867) from specimens from Wardie. Traquair (1875) erected the genus *Nematoptychius* for this species. *Nematoptychius greenocki* is up to 480 mm long (Figure 9.14) and has a wide gape, with sharply conical teeth in two rows: an outer row of small, numerous, closely packed teeth and an inner row of large teeth. On the flank the scales are higher than broad. The predatory nature of this fish is proved by a specimen from the Borough Lee Ironstone with an *Acanthodes* in its abdominal cavity, swallowed whole head first (Traquair, 1909, p. 92). Traquair (1877 1914) used an uncrushed and well-preserved specimen of *N. greenocki* from Wardie to illustrate the pattern of cranial bones because it was the finest preserved UK specimen then available and still is in terms of morphology

The name *Elonichthys* was proposed by Giebel (1848) for fishes from the Coal Measures of Halle, Germany, and Traquair (1877–1914) described several species from the Carboniferous of Britain. Characteristics of the genus include two sorts of teeth (tiny and large), the absence of a sub-opercular plate, and large fins. It is a classic 'dustbin' taxon with a history of poor diagnoses preceding the recognition that a new taxon can be properly erected from the material here and elsewhere. *Elonichthys robisoni is* the most abundant palaeoniscid in the Lower Carboniferous of the Forth Basin of Scotland, and occurs in most of the 'estuarine' fish beds from Wardie to the top of the Carboniferous Limestone Series, but never occurring above the lower boundary of the Millstone Grit (Traquair, 1877–1914). The Wardie species was named *E. intermedius* by Traquair (1871) from two specimens that had been described by Agassiz (1835) as *Amblypterus punctatus.* Material of A. *punctatus,* described by Agassiz from Wardie, was shown to be of two genera, one of which was included under *E. robisoni,* and the other became a new genus *Gonatodus* (Traquair, 1877–1914). Traquair (1901) included many synonyms of fishes from the Carboniferous of the Forth area under this species, including *E. intermedius* and *E. pectinatus,* both from Wardie. *Elonichthys striatulus* was first reported from Wardie by Wood (1975), occurring rarely in Beds 6 and 7. Heyler and Poplin (1983) described *E. robisoni* from France and discussed the integrity of *Elonichthys* as a genus.

Gonatodus punctatus was described by Traquair (1877–1914) as a deep-bodied fusiform fish resembling *Elonichthys.* It is 0.14–0.2 m long, with a short head and bluntly rounded snout. The teeth are moderate-sized, slender and cylindrical, with a distinctive bent shape and an in-turning sharply conical apex. They are closely set, unlike those in *Elonichthys.* The pectoral fins are long and pointed, with the dorsal fin posterior to the middle of the back. Gardiner and Schaeffer (1989) recently placed *Gonatodus* in the *Belichthys* terminal group, along with *Aetheretmon,* '*Rhadinichthys*' *carinatus,* and *Phanerosteon.*

Eurynotus occurs in the Lower Carboniferous of Scotland, and the Carboniferous of Ireland, Belgium and Siberia (see Lehman, 1966; Coates, 1994). The trunk is fusiform, and the jaws possess conical teeth or short spheroidals in irregular series on the mandibles, maxillaries and the bones of the buccal platform. The tins have all their fulcrals. A specimen of *E. crenatus* from Wardie was used by Watson (1928) to define the structure of the palate, which had hitherto only been known in *Cheirodus.*

Rhadinichthys carinatus was described by Agassiz (1835) as *Palaeoniscus carinatus,* based on an imperfect specimen from Wardie, and it was later redescribed by Traquair (1877–1914). *Rhadinichthys carinatus* is a slender fish ornamented on the head bones by delicate wavy ridges. The scales are relatively large, quadrate on the flanks, but narrowing towards the ventral line. The posterior margin of the scale has 7–11 sharp denticulations. *Rhadinichthys carinatus* is widespread in the Lower Carboniferous of the Central Valley of Scotland.

Rhadinichthys brevis was a stout and short fish, about 0.1 m long. The cranial roof bones are ornamented with contorted and flattened rugae and the flank scales by a few weak, oblique ridges with five or six denticulations on their posterior border.

Rhadinichthys ferox is known only from Wardie and is rare. No specimens were discovered during collections made by Wood (1975). This species was 0.3 m or more long (cf. (Figure 9.17)A and (Figure 9.17)B), and was ornamented with a distinctive pattern of prominent ridges. The cranial plates are striated and the scales have sharply defined ridges divided

by a diagonal across the scale (Traquair, 1877–1914).

Wardichthys is a platysomid, recognized by its deep but rounded body shape, and short dorsal and anal fins (Lehman, 1966). The genus was erected by Traquair (1875) for a unique specimen, clearly a platysomid, but Traquair separated it because of the head-bones and the scale ornament, which consists of fine tubercles that locally coalesce into short ridges. *Wardichthys cyclosoma* is rare at Wardie, but it is not confined to one bed (S.P. Wood, pers. comm., 1980). Stock (1881) described it as a small fish, 80 mm long, with pectoral or ventral fins and a small dorsal fin.

Wardie is one of only two Carboniferous sites in Britain that commonly yield complete elas-mobranchs (Figure 9.15). Recent discoveries of articulated elasmobranchs in the Lower and Upper Oil Shale groups in the eastern Midland Valley of Scotland have yielded four species from various sites (Dick, 1981); the commonest is *Tristychius arcuatus* (100 specimens), the rarest *Onychoselache traquairi* (one); and there also are *Diplodoselache woodi* (four) and *Sphenacanthus serrulatus* (very rare).

Agassiz (1833–45) noted some poorly preserved teeth from the Burdiehouse Limestone, near Edinburgh, as *Diplodus minitus.* Sixty years later, they could not be traced by Traquair (1903), who suggested that the name should be dropped. In Traquair's (1903) faunal list for Wardie, he recorded *Pleuracanthus* sp., but both this name and *Diplodus* are preoccupied (Dick, 1981). These fragmentary remains probably belong to the xenacanth *Diplodoselache woodi,* the holotype of which is from Locality B of Wood (1975), on the foreshore at Wardie. The locality has yielded three other specimens of *Diplodoselache woodi,* which is characterized by small bicuspid teeth, a single elongate dorsal fin, and a single shallowly inserted dorsal spine (Figure 9.15). Dick (1981) erected the Family Diplodoselachidae, in the Order Xenacanth-iformes (Xenacanthida of Zangerl, 1981), to contain only this genus and species. The xenacanths were freshwater sharks with fusiform body shape and one spine, primitively associated with one expanded dorsal fin. The teeth are of modified cladodont type. Their range is from Upper Devonian to Middle Permian (Zangerl, 1981).

Diplodoselache woodi has a heterocercal tail with a relatively large ventral lobe (Zangerl, 1981). Ribs are absent or, perhaps, uncalcified. The body is covered by denticles. The typical xenacanth elongate dorsal fin is first seen in *Diplodoselache.* The caudal fin lobes are long and the anal fin lies well back, which again could be a precursor of the state in later xenacanths, where there is a 'double' anal fin.

New material of *Onychoselache traquairi* Dick, 1978 collected by Wood from Wardie allowed the reidentification of this shark from Glencartholm (q.v.), which had previously been described as *Tristychius arcuatus.* The Wardie specimen showed that the structure of the spines was fundamentally different.

Interpretation

The Oil Shales of the Midland Valley of Scotland were deposited on the floor of a large lagoon which, at its greatest extent, was up to 50 km wide from east to west. It was frequently isolated from the open sea (Greensmith, 1965; Dick, 1981). The deposition of the Oil Shales took place under conditions similar to those found in thermally stratified lakes, whereas the other sediments were deposited under different conditions. Eutrophic periods immediately before and after deposition of oil shales are indicated by the presence of pyrite, plant material and fish-bearing nodules; the preservation of the fine detail of fishes, especially the sharks, needs undisturbed and stagnant conditions (Zangerl and Richardson, 1963; Dick, 1981). Dick (1981) states that the presence of articulated skeletons together with the distribution of fish-bearing nodules through considerable thicknesses of shale, rather than in discrete bone beds, suggests that these fish were the normal inhabitants of the lagoon in which the Oil Shales were deposited, rather than individuals trapped or washed in when the outlet to the sea was cut off. Hesselbo and Trewin (1984) have pointed out that the preservation of elasmobranchs, particularly, requires stagnant-water conditions similar to those in a thermally stratified lake, and that fish faunas should be used with care as environmental indicators because many groups today can tolerate a wide range of salinities.

Sharks were found in all beds except Bed 1. Elasmobranchs are normally said to occupy marine habitats (Zangerl, 1981, p. 36), but the Wardie fauna must be non-marine because of its actinopterygians, flora and the absence of marine invertebrates (Wood, 1975). This is not a new problem; Paterson (1837), remarking on the juxtaposition of marine and

freshwater forms at Wardie, suggested that the sediments could have been laid down in an estuary which received marine incursions. Wood (1975) hypothesized a marginal habitat, such as a lagoon or estuary, and Dick (1981) noted two shark faunas in the Early Carboniferous of Scotland: the *Diplodoselache* fauna, characteristic of the lagoon or lake in which the Oil Shales of the Midland Valley accumulated, and the anacanthous sharks. The presence of the latter represent occasional marine episodes and indicates that there was no permanent barrier between the lagoon and the open sea.

Diplodoselache woodi possesses features of xenacanths, anacanthous and ctenacanth sharks. The relationship between xenacanths and other early elasmobranchs is obscure. Some authors have suggested a dichotomy between the xenacanths and all other elasmobranchs (Moy-Thomas and Miles, 1971; Zangerl, 1973; Schaeffer and Williams, 1977). Dick (1978, 1981) disputed this, arguing that xenacanth origins lay within the (anacanthous) ctenacanth assemblage because *D. woodi* displays several synapomorphies with the xenacanths.

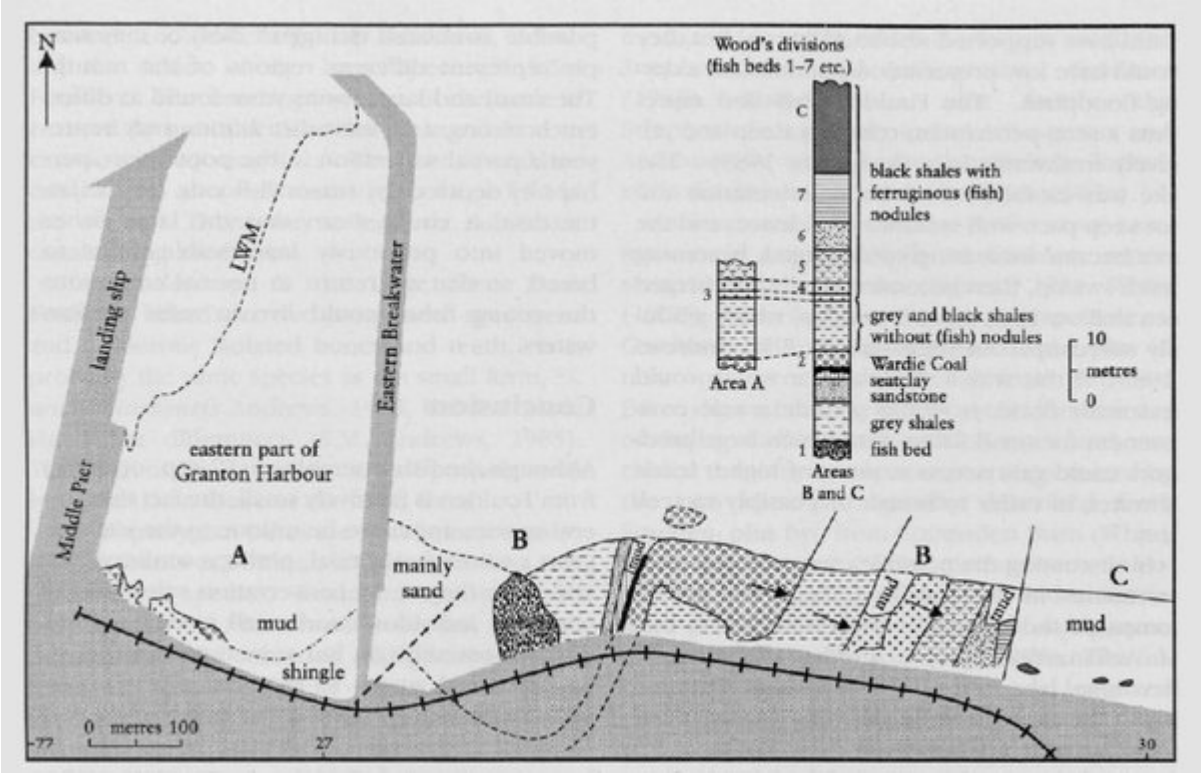
The long caudal fin lobes and the anal fin, lying well back in *Diplodoselache,* could have facilitated an efficient sinusoidal swimming motion. There is no evidence of any form of air-breathing organ to enable xenacanths to survive low oxygen conditions, so they were probably restricted to the surface waters of lakes. *Diplodoselache* probably was a medium-sized predator living in the surface waters of a lagoon (Dick, 1981).

Rhizodonts were voracious predators with sharp teeth, and which often must have reached a large size (over 1 m). They are presumed to have inhabited deeper waters.

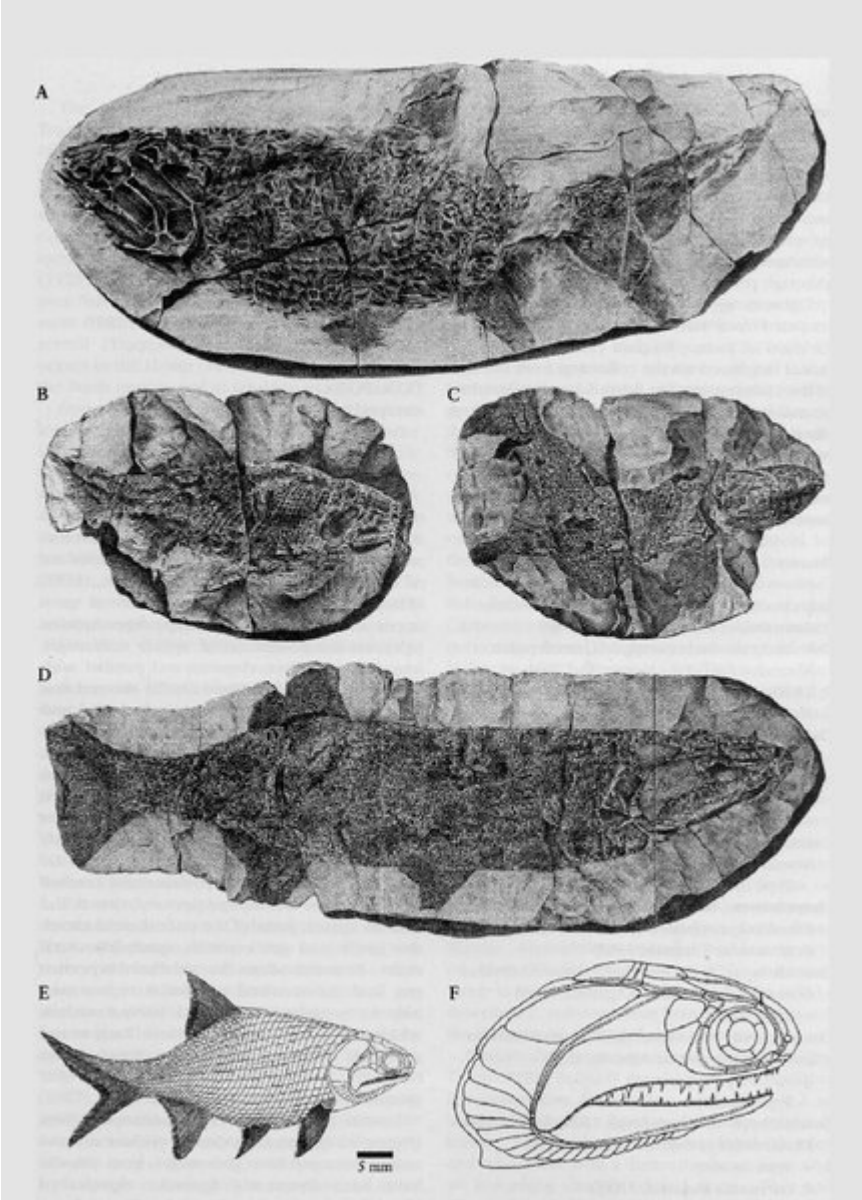
Conclusion

The Wardie locality has a significant conservation value because it has produced very many fossil fish specimens over the past 150 years, including superb examples of early actinopterygians and rare sharks. The 18 species described so far from Wardie include eight type specimens, many collected in the 1970s. The success of recent collecting shows the potential of the site for future finds.

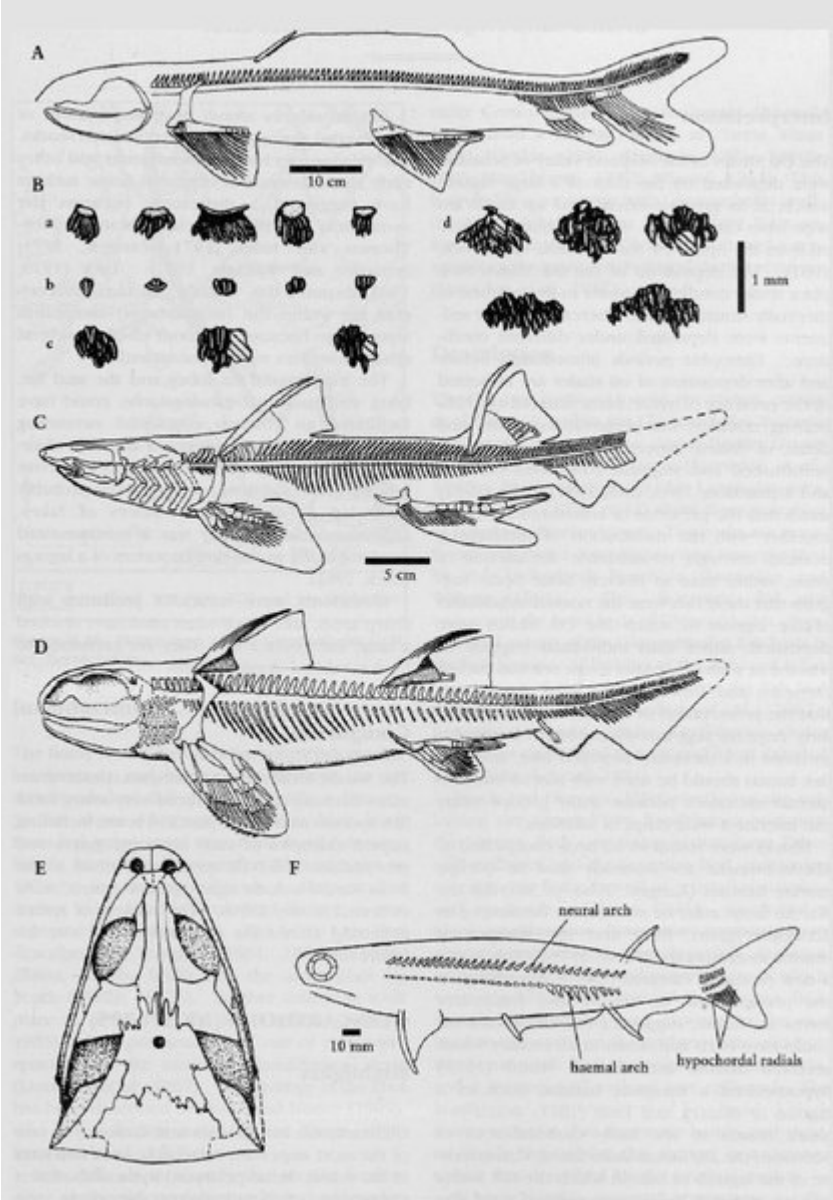
References



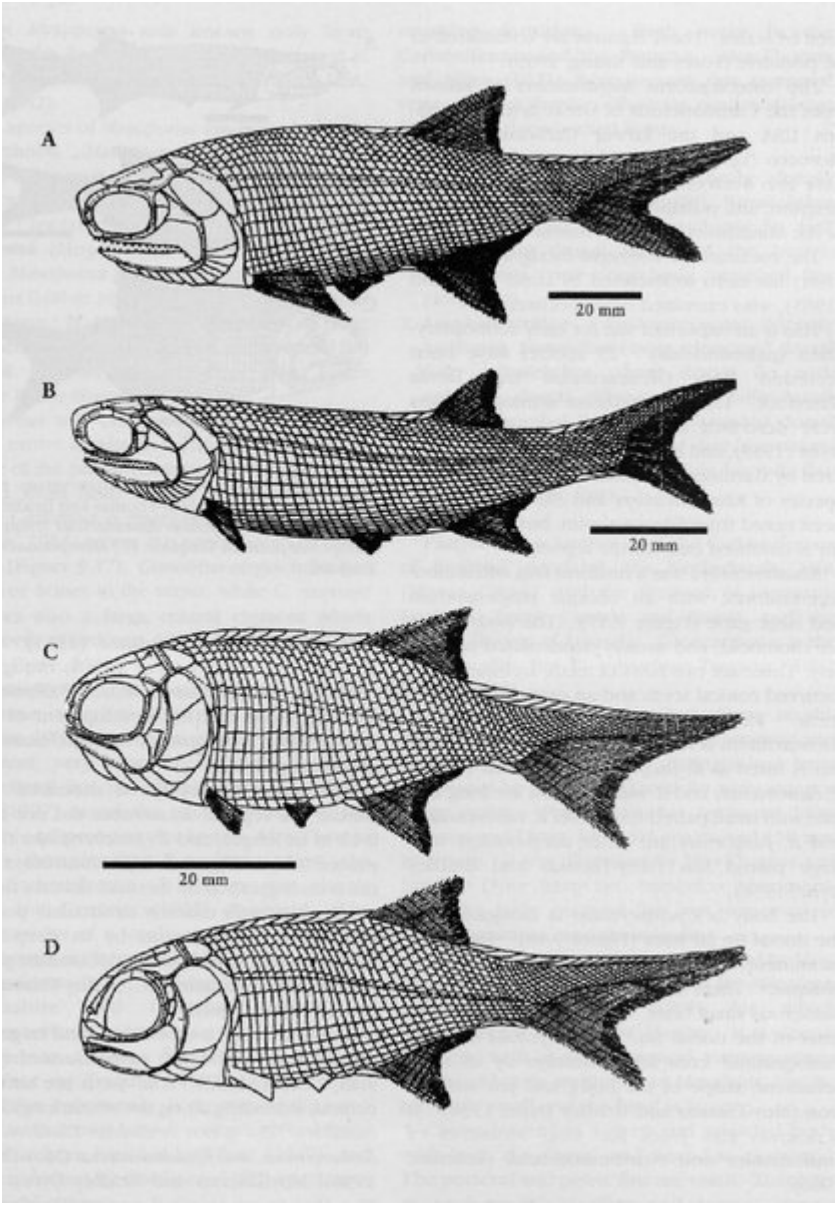
(Figure 9.13) Sketch map and geological section at the Wardie GCR site, East Lothian (after Wood, 1975).



(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 9.15) 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 9.17) 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.