

Fossil Fishes of Great Britain

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Chapter 9

British Carboniferous fossil fishes

sites

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INTRODUCTION: PALAEOGEO-GRAPHY AND STRATIGRAPHY

The Carboniferous Period lasted some 65 million years, during which time the palaeogeography of the British Isles areas of the Laurussian continent underwent profound changes. World sea level underwent fluctuations, primarily resulting in a major transgression in early Carboniferous (Dinantian) time and a major



Figure 9.1 Maps of Carboniferous palaeogeographies: (A) Late Tournaisian; and (B) Late Viséan; and (C) Namurian.

regression in the (later) Silesian. The British Isles occupied an equatorial position and a hot climate prevailed: this and the influence of the rising continental uplands were dominating factors affecting environments, sedimentation and the progress of life. During the early Carboniferous, there was a number of land masses traversing the British Isles area in an east-west direction (Figure 9.1). The Caledonian uplands became a major source of clastic sediments. St George's Land extended over central England and much of central and North Wales, as well as the south-eastern area of Ireland. Major areas of Dinantian marine limestone and shale deposition occurred to the south of St George's Land, in the Bristol-South Wales area, as well as across most of southern Ireland. A major marine transgression had occurred over these areas, submerging the southern margins of the Old Red Sandstone continent. Dinantian limestones and shales were also deposited in great thicknesses in central England and eastern Ireland. The Craven Basin, in Derbyshire, South Yorkshire, Lancashire and parts of Cheshire, was bounded by St George's Land to the south, and tongues of land over the East Midlands. In the north, the Askrigg and Cumbrian-Alston blocks ran across North Yorkshire, the Lake District and the Isle of Man, separating the Craven Basin from the Northumberland Basin to the north (Figure 9.1). Further substantial NE-SW-trending land masses were the Southern Uplands and Longford Down blocks, and the Highlands Block, which demarcated the Northumberland Trough in the south and the Midland Valley Basin across central Scotland.

The Late Carboniferous (Silesian) palaeogeography of the British Isles was little changing at first. During Namurian times (mid-Carboniferous), the Craven Basin opened out eastwards, and vast thicknesses of sands, the Millstone Grit, were deposited in the Pennine area. In the succeeding Westphalian, the classic Coal Measures, sandstones, mudstones, coals and limestones, were deposited in large floodplains over South Wales, southern Ireland, central and northern England, and southern Scotland. St George's Land had contracted, losing its northern extension up the east coast of England, and is termed the Wales-Brabant Landmass. The only other area of land lay far to the north-west, extending over the Scottish Highlands, and north-western Ireland, while in the far southwest of England Hercynian tectonism was raising new land.

The biostratigraphy of the marine beds of the Dinantian and Namurian is based on goniatites, conodonts and corals, and the continental sediments are zoned on the basis of miospores. The largely non-marine Westphalian is zoned using miospores, plants and non-marine bivalves (George *et al.*, 1976; Leeder, 1975, 1992; Ramsbottom *et al.*, 1978; Kelling and Collinson, 1992). The main units from areas with fish faunas are shown in Figure 9.2.

Fossil fish faunas are rare in the typical Dinantian limestones of southern and central England, and most are found in the shallower marine successions of the Northumberland Trough (particularly its north-eastern part) and the Midland Valley Basin. Fishes occur at many localities in the marine beds of the Namurian, the best sites being in central Scotland. Fishes are rare higher in the Carboniferous where continental facies are dominant.

ENVIRONMENTS

Environments in the Northumberland Trough changed during the course of the Dinantian. The earliest horizons are transitional between the underlying continental alluvial Upper Old Red Sandstone (Chapter 7) and the overlying Cementstones facies. The Kelso-Birrenswark lavas occur at the Devonian-Carboniferous transition. Rivers draining off the Southern Uplands landmass deposited thick sequences of sandstones in coastal area in the north-eastern part of the Northumberland Trough. The Cementstones represent coastal-plain fluvio-lacustrine facies. The succeeding Border Group records successive advances of a delta system flowing south-west into the Northumberland Basin, and the deltaic deposits are interbedded with marine limestones. The marine sediments with evaporites, stromatolites and restricted marine invertebrate faunas indicate hypersaline conditions. The Border Group higher up contains thick braided river sandstones, as well as coals, related to a major fluvio-deltaic regressive episode.

In the Midland Valley of Scotland, sedimentation at first followed a similar pattern, although the two basins seem to have been separated by the Southern Uplands Block. Upper Old Red Sandstone continental facies pass into the Cementstones, which show evidence for period-

Environments

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		Lower Coal Measures	Lower Coal Measures			Westphalian A		Westphalian A
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		Upper Old Red Sandstone	Upper Old Red Sandstone	Upper Old Red Sandstone	Upper Old Red Sandstone		line to and	eared: Place uvived into i

Figure 9.2 Carboniferous stratigraphy and correlation (after MacGregor, 1960).

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Figure 9.3 Carboniferous outcrops in Britain: present GCR sites are limited to the south of Scotland and to the Border country and the south-east Pennines. Horizons previously yielding fossil fish occur at Oreton (Shropshire), in the Bristol Avon gorge and the west coast of Devon. Midland Valley sites: 54, Wardie; 56, Cheese Bay; 57, Inchkeith; 58, Ardross Castle; 59, Abden. Glasgow area site: 61, Bearsden. Berwickshire sites: 53, Foulden; 55, Glencartholm. Derbyshire: 60, Steeplehouse Quarry.

ic emergence and hypersaline lacustrine conditions. Active volcanism on the southern and northern margins of the Midland Valley Trough gave rise to considerable thicknesses of lavas within the Dinantian successions. Thick oil shale accumulated around Edinburgh, while thick fluvio-deltaic sandstones formed in Fife, suggesting a deep basinal area in the former, and shallower marginal marine environments in the latter (Figure 9.3).

FISH FAUNAS

By Carboniferous times the heavily armoured fishes, agnathans and placoderms, had disappeared. Placoderms are sometimes said to have survived into the basal Carboniferous beds, but evidence for this is equivocal (Gardiner, 1993a). Many Devonian acanthodian and sarcopterygian groups also died out during the Late Devonian, and the balance of Carboniferous faunas was very different from that of the Devonian. Dominant forms were actinopterygians (rayfinned bony fishes) and chondrichthyans (sharks, shark-like forms and chimaeras), with rare acanthodians and sarcopterygians (lobefinned bony fishes; Gardiner, 1993b).

The Carboniferous actinopterygians all belong to an early grade of the group, traditionally called 'palaeoniscids' or 'palaeonisciforms'. This probably includes the basal members of the Chondrostei, which is a taxon now defined as monophyletic, including the sturgeons and paddlefishes, and also the neopterygians (Patterson, 1973; Gardiner, 1984). Actinopterygians first appeared in the Devonian (e.g. Cheirolepis), and by Early Carboniferous times were the dominant freshwater fishes and were also found in smaller numbers in the seas. The 'palaeoniscids' were a very long-lived group, surviving till the Cretaceous Period. They were first described by Agassiz (1833-1845); a monographic contribution followed from Traquair (1877-1914). Substantial descriptions in the 20th century have been given by Moy-Thomas (1938a), Parrington (1949, 1967) Westoll (1944, 1949), Gardiner (1963, 1967a, 1984, 1993b), White (1965) and Gardiner and Schaeffer (1989).

Early actinopterygians were carnivorous, with a jaw of wide gape, and lined with sharp conical teeth. The shape of the maxillary bone in the upper jaw area has an expanded portion posteriorly, with a large part covering the cheek area, and a narrow strip of bone extending forwards, beneath the eye. The whole ventral margin of the maxilla typically bears teeth.

Most early actinopterygians had a fusiform body (Figure 9.4), and body size was usually small or moderate, sometimes reaching 1 m in length. The tail was strongly heterocercal, with the body lobe extending into the upper part and a deeply cleft margin between that and the hypochordal lobe. The notochord extended to the very tip of the tail. This would have given the heavy, bony-scaled fish some upward lift during forward movement. The body was covered with overlapping, rhomboidal scales. In most forms, these typically articulated by means of a peg that fitted into a socket on the base of the scale above it. The fins of early actinopterygians consisted mostly of long, jointed dermal fin rays. Body form was highly variable, as shown by British Carboniferous material (Figure 9.4), such as the deep-bodied Platysomus and the elongate Tarassius (see Figure 9.19). So-called palaeonis-



Figure 9.4 Basal actinopterygian fish morphology (after Lauder and Liem, 1983). (A) *Moythomasia nitida*, Late Devonian, with stout body, large eyes and long jaws, dorsal ridge scales behind the dorsal fin; (B) *Cheirolepis canadensis*, Mid-Late Devonian, elongate with tiny scales; (C) *Aduella blainvillei*, Early Permian, stout body, large scales, arrow points to 'chondrostean hinge', large eyes, suborbital and preopercular bones in head, small mouth; (D) *Andriochtbys tuberculatus*, Early Carboniferous, deep body, small tail and paired fins, large scales and prominent dorsal ridge scales; (E) a characteristic early actinopterygian scale bearing a small peg that articulates with the scale immediately above it.

cids retain many ancestral features, e.g. heavy peg and socket ganoid scales, a spiracle and a heterocercal tail, in which the orientation of the scale rows is reversed.

A cladistic analysis of the palaeonisciforms shows that they are a paraphyletic group, with the majority forming successive stem groups of the Neopterygii (Gardiner, 1984). A cladogram by Gardiner and Schaeffer (1989) shows 27 terminal groups between *Cheirolepis* and the extant neopterygians (Figure 9.5).

Sarcopterygians arose in the Devonian, and radiated substantially during the Carboniferous (Schultze, 1993). They have fleshy lobe-fins, the neurocranium divided into two parts, complex infoldings of the teeth (labyrinthodont structure) and an autostylic jaw suspension (the jaw connects directly with the brain-case). The external part of the bony scales is made of shiny cosmine, which could be periodically resorbed



Figure 9.5 Cladogram of the relationships of the different groups of early actinopterygians (from Gardiner and Schaeffer, 1989). It is based on a preliminary cladogram of a visual comparison of the nasal-temporal bones of the head and also upon a computer analysis of a further large data matrix.

to allow growth to take place in the bony layers. The cosmine enamel and dentine layers are pierced by a well-developed pore-canal system (the lateral line system) similar to that of the osteostracans, which gives the outer surface a punctate appearance.

The rhizodontids were a group of osteolepiforms that are known from the Upper Devonian and Carboniferous. They are rather poorly known, mainly because specimens are mostly fragmentary, possibly because of the large size of the animals and the effects of scavenging, transport and burial (Moy-Thomas and Miles, 1971; S.M. Andrews, 1985). Rhizodonts were large, some reaching 6-7 m in length. They were first described from the Lower Carboniferous of Scotland. With widely gaping mouths armed with sharp teeth, they were formidable predators, feeding mainly on fishes. Probably sharklike shaking, tearing and rotating movements were used to rip their prey apart (S.M. Andrews, 1985).

The oldest coelacanths are Mid-Devonian in age (Schultze, 1993), and they have existed to the present day as a low-diversity group, showing little apparent morphological change. The modern coelacanth, Latimeria, is a famous 'living fossil', in a deep oceanic habitat. Carboniferous coelacanths were first described by Agassiz (1833-1845) from the British Carboniferous. During the 19th century many were found in the Coal Measures, and many species were named, but these were extensively synonymized in revisions by Moy-Thomas (1937b) and Forey (1981), leaving a list of eight Coelacanths were mainly slender species. fusiform fishes with two dorsal fins, the posterior being lobed. The tail is diphycercal and three-lobed, a characteristic of the group. The body scales are cycloid, thin and overlapping, and they have a surface ornament of fine ridges or tubercles made of dentine. There are two external nostrils and there is a calcified air-bladder, which is one of the distinctive features of the fossils. Two genera of coelacanths, Rhabdoderma and Diplocercides, are present in the Carboniferous of Britain.

Carboniferous dipnoans belong to five families, the Conchopomatidae, Uronemidae, Ctenodontidae, Sagenodontidae and Gnathorhizidae, the first and last of which arose in the Late Carboniferous (Schultze, 1993). As mentioned previously, lungfishes arose in the Early Devonian, and radiated from the Mid-Devonian to the Early Permian, surviving after that as a low-diversity group, and represented today by three species, each of them a 'living fossil', like the living coelacanth. Many of the Carboniferous lungfishes had evolved considerably in body form since the well-known Mid-Devonian *Dipterus*. The Carboniferous ctenodontids and uronemids showed a symmetrical narrow pointed tail, and the dorsal and anal fins are continuous with it. The bones of the head region are reduced in number and in thickness, and the main teeth are broad cutting tooth plates in the palate.

Acanthodians continued in abundance from



Figure 9.6 Carboniferous chondrichthyans: (A) a cladoselachid persisting from the Late Devonian, $\times 0.16$; (B) a symmoriid, *Denea*, $\times 0.16$; (C) the Late Carboniferous eugenodont *Fadenia*, $\times 0.16$; (D) the Early Carboniferous xenacanthid *Diplodoselache*, \times 0.08; (E) the xenacanthid *Xenacanthus*, $\times 0.08$. Note the differences in cranial and vertebral ossification and fin structure (after Carroll, 1988).

their key role during the Devonian, and the group lived on to the Mid-Permian (Zidek, 1993). Only three of the nine families that arose during Devonian times survived into the Carboniferous, the Ischnacanthidae, Gyracanthidae and Acanthodidae. Most were small fishes, with fusiform bodies, and with spines in front of the fins and along the ventral surface. The head was large, as were the eyes.

The chondrichthyans, or cartilaginous fishes, are represented today by about 700 species of sharks, rays and chimaeras. The Chondrichthyes arose during the Mid- or Late Devonian, and 19 families lived during at least parts of the Carboniferous (Cappetta et al., 1993; Figure 9.6). Most chondrichthyans are marine, but recent work on the deposits and faunal assemblages from the Carboniferous of Scotland suggest that then they were also well represented within fresh or brackish waters. Living chondrichthyans have the following distinguishing features: the cartilaginous skeleton has a prismatic, calcified outer laver, there is no swim bladder, the intestine has spiral valves, they employ internal fertilization and males have claspers, and they have whorl-like arrangements of tooth replacement families. The Devonian shark Cladoselache lacks claspers, but such structures have been demonstrated in many Carboniferous chondrichthyans.

There are two subclasses of chondrichthyans, the Elasmobranchii (sharks, skates and rays) and the Holocephali (chimaeras). The Devonian chondrichthyans were shark-like in appearance, and the typical shark-like form has been maintained ever since, suggesting that these have been the most successful predators in the sea. Most early forms were streamlined and had sharp multicusped (cladodont) teeth, but by the Carboniferous, sharks with pavements of flat crushing teeth had also evolved. Because of their cartilaginous skeleton, fossil sharks are rare, and the discovery of several new groups of sharks in the Carboniferous of Scotland over the last 15-20 years has been highly significant since it adds materially to knowledge of the diversity of the group (Figure 9.6)

Palaeozoic holocephalians included chimaeroids, as well as several other specialized orders (Moy-Thomas and Miles, 1971). There were also several doubtful orders known only from teeth. Many holocephalians had bradyodont teeth, which are distinctive because they have vertical parallel tubes of dentine separated by harder dentine, and they are long-wearing so that a worn tooth has a distinctive pitted appearance. Palaeozoic holocephalians are often loosely called bradyodonts. The head armour of chimaeroids becomes reduced through time, from the large head shield of the Early Carboniferous Deltoptychius, which has a pair of ventral plates on the skull and a pair of mandibular spines, to the Late Permian Menaspis, with its headshield reduced in area and fragmented into a number of plates. The Myriacanthoidea went further. with the reduction and loss of the mandibular plates. Finally, modern chimaeroids have lost all armour. The armour of Deltoptychius suggests that this was the primitive state (Patterson, 1965, 1992).



Figure 9.7 Geological sketch map of southern Scotland and northern England with the positions of the Carboniferous GCR fish sites. Key to localities: A, Abden; B, Bearsden; CB, Cheese Bay; EK, East Kirkton; F, Foulden; G, Glencartholm; I, Inchkeith; R, Ardross Castle; W, Wardie.

FISH SITES

Carboniferous fishes have been reported from many sites and from all Carboniferous series in the British Isles, not least because of the large areas covered by rocks of this age (Figure 9.7). Discoveries of fish faunas are now relatively rare in the Dinantian limestones and in the Westphalian Coal Measures. However, there are to be found, in many museums, extensive collections of Westphalian fishes from collieries and tip heaps of northern England and the Midlands, but their documentation is commonly inadequate. Despite this, much of the material is very good and there is an important literature (see Watson, 1925, 1928). An early classic is Traquair's monograph on British 'ganoid' fishes (1877-1914). The largest and best-preserved faunas come from the Lower Carboniferous marginal clastic sequences of the Scottish Borders and from the mixed-facies Dinantian and Namurian of the Midland Valley of Scotland.

Nine examples are selected for the GCR coverage of British fossil fish sites:

- 1. Foulden, Borders (NS 921552). Courceyan.
- 2. Wardie, Mid Lothian (NT 245771).
- Courceyan-Holkerian.
- 3. Glencartholm, Borders (NY 376795). Asbian.
- 4. Cheese Bay, East Lothian (NT 492856). Asbian.
- 5. Inchkeith, Fife (NT 29390 and NT 294822). Asbian.
- 6. Ardross Castle, Fife (NO 511006). Brigantian.
- 7. Abden, Fife (NT 276874). Brigantian.
- 8. Steeplehouse Quarry, Derbyshire
- (SU 288554). Brigantian 9. Bearsden, Glasgow, Strathclyde
- (NS 53057325). Pendleian, basal Namurian.

Each presents a fauna that is distinctive for its age, well preserved and perhaps offering further good collecting.

Many localities yielding elasmobranch teeth have been exploited in the Dinantian limestones of England and Wales: few of these are now productive. Even the more famous, such as the Bristol Avon Gorge and Oreton, Shropshire, for various reasons no longer qualify for inclusion here. They are invariably no longer accessible and/or have been worked out.

FOULDEN (NS 921552)

Highlights

Foulden in Borders is one of the few sites in the Dinantian of Scotland to yield a significant fish fauna of 12 or more species, six of them being actinopterygians. The fish bed represents a semi-permanent lake within an alluvial coastal plain.

Introduction

The fossil fishes from Foulden have been recognized as internationally important since their discovery in 1910–1912 by T.M. Ovens, who died in 1912 at the age of only 19. His collection of fishes was described by White (1927), who named five new species. Excavations in 1980 and 1981, funded jointly by S.P. Wood, the Nature Conservancy Council, the Hunterian Museum and the Royal Scottish Museum, yielded many new specimens, as well as contextual information determined from careful bed-by-bed collecting. The fishes from Foulden, their taphonomy and palaeoecology were described



Figure 9.8 Sketch map of the GCR site at Foulden.

Foulden





in a thematic series of papers published in 1985 in the *Transactions of the Royal Society of Edinburgh: Earth Sciences* (Anderton, 1985; S.M. Andrews, 1985; Clarkson, 1985; Forey and Young, 1985; Gardiner, 1985; Wood and Rolfe, 1985).

Description

The Fish Bed at Foulden consists of 3.9 m in the base of Bed 16 (Wood and Rolfe, 1985), which is set in a unit of 1.1 m of finely laminated siltstone, becoming more shaly upwards (Figure 9.9). The Fish Bed is further divided into an upper 3.1 m portion, separated from a basal bioturbated part where fossil fishes are less well preserved. It lies within the lower part of the Lower Carboniferous Cementstone Group of Berwickshire and is probably of Tournaisian (Courceyan) age. The fish bed is *c*. 100 m above the base of the Cementstones, which are sparsely fossiliferous, with the exception of Foulden, and its fauna is mainly of ostracods, bivalves and fish fragments, plus some plant material.

The field and laboratory methodology used at Foulden was based on that used in Illinois by Zangerl and Richardson (1963). A large slab was lifted and removed to the laboratory, having been marked up with a grid and north arrows. The Fish Bed is rubbly, which made reassembly difficult. A polished vertical section was cut as a basis for the detailed log, and the beds were stripped off, one by one, their contents being plotted with reference to two marker horizons. The fossils could then be coded for three-dimensional burial position and orientation.

The careful plotting of the fossil content lamina by lamina showed that actinopterygian fishes and malacostracan crustaceans always occur at separate horizons. One level was crowded with small acanthodian fishes, showing a preferred orientation, and plant fragments. Other remarkable horizons were a rhipidistian-rich layer, a coprolite horizon and a bivalve–malacostracan horizon (Figure 9.9).

Fauna

Acanthodii: Acanthodiformes: Acanthodidae Acanthodes ovensi White, 1927 Type and only locality Gyracanthus sp. Osteichthyes: Sarcopterygii: (Actinistia) Coelacanthiformes

cf. Rhabdoderma sp.

Osteichthyes: Sarcopterygii: Osteolepiformes: Rhizodonta

?Strepsodus aulaconamensis Andrews, 1985 Type and only locality

?Strepsodus n. sp.

- Osteichthyes: Sarcopterygii: Dipnoi ?lungfish scale
- Osteichthyes: Actinopterygii: Carbovelidae *Phanerosteon ovensi* (White, 1927) Type and only locality

Osteichthyes: Actinopterygii: Styracopteridae Styracopterus fulcratus (Traquair, 1881)

Osteichthyes: Actinopterygii:

Strepheoschemidae

- Strepheoschema fouldenensis White, 1927 Type locality
- Aetheretmon valentiacum White, 1927 Type locality
- Osteichthyes: Actinopterygii: Cosmoptychidae Cosmoptychius striatus (Agassiz, 1835) cf. Rhadinichthys sp.
- Chondrichthyes: Elasmobranchi: Bradyodonta cf. *Lophodus* sp.

TETRAPODA: ?acanthrosaur incertae sedis

Foulden is the type locality for seven species of fishes, and unique locality for three of these (Figure 9.10). White (1927) noted that the fish assemblage consists of small forms of new actinopterygian (palaeoniscid) genera that are complete, plus larger forms of fishes which are represented by teeth, scales and other isolated fragments which belong to predatory fishes. These latter forms are well known in the Carboniferous, and widely distributed, whereas the small complete forms are rarer, or restricted to Foulden.

All the acanthodians are imperfectly preserved. The swarm of small acanthodians on Bed A had poorly ossified cranial structures, and they were compressed, so that accurate measurements could not be made. The specimens collected by earlier workers, mainly Ovens, are larger, but are also poorly preserved (Forey and Young, 1985). The larger individuals which occur outside this layer are more ossified anteriorly (Wood and Rolfe, 1985). Also, the small specimens only had scale cover on the posterior half of the body. Gyracanthus sp. is based on poorly preserved fragments of spines which were found at several horizons in Bed 16, and from Beds 13 and 14 (Forey and Young, 1985).



Figure 9.10 Foulden acanthodians: (A) *Acanthodes ovensi* White, with a series of immature forms showing the progressive spread of squamation forward during growth (from Forey and Young, 1985): (B) White's (1927) figure of the holotype (NHM P 13137) of *A. ovensi*.

The coelacanth cf. *Rhabdoderma* sp. has been described by Forey and Young (1985) from an almost complete fish discovered in Bed 16 (no accurate horizon given), but preservation is poor.

Rhizodonts were large, and they are normally preserved only as scattered remains. The head of the complete (holotype) specimen of *?Strepsodus aulaconamensis* in the Foulden assemblage has been crushed dorsoventrally and does not allow a detailed study.

Acanthodes ovensi White, 1927 is one of the earliest acanthodid acanthodians. White (1927) described it from seven specimens, of which only the holotype was a full-grown individual, 90–100 mm long. The other specimens were very small, being c. 30–50 mm long. Acantho-

dian material collected from the 1980–1981 dig consists mainly of a crowd of 173 specimens in Bed A. Forey and Young (1985) re-evaluated the species from the type specimens and the new material. *Acanthodes ovensi* is distinguished from Upper Carboniferous and Permian *Acanthodes* by the shape of the tail, the shorter gill chamber, the continuation of the scale cover over the head, and the posterior position of the pelvic fin spine (Figure 9.10).

Gyracanthus sp. is based on fragments of spines found at several horizons in Bed 16 and from Beds 13 and 14 (Forey and Young, 1985). White (1927) also reported *Gyracanthus* sp. indet. from two fragments collected by Ovens.

The coelacanth fishes are a small element in the Foulden fauna. The ornament of the



Figure 9.11 Foulden sarcopterygians: (A) preliminary reconstruction of *?Strepsodus aulaconamensis* sp. with scale cover; (B) *?Strepsodus aulaconamensis* Andrews, with scales omitted to show lepidotrichia and axial skeleton (after S.M. Andrews, 1985) Many of the head and axial skeleton bones are largely conjectural. (C) Coelacanth flank scales (from Forey and Young, 1985).

Foulden coelacanth, cf. Rhabdoderma, is distinctive (Figure 9.11C). Rhabdoderma sp. has been described by Forey and Young from an almost complete fish found in Bed 16, but the preservation is poor. Head bones are ornamented with long ridges parallel to the long axes of the bones or with slightly elongate tubercles, which radiate out from the centre of ossification, or with small rounded tubercles. Forey and Young (1985) described this as an intermediate pattern compared with other Carboniferous and Devonian coelacanths. The Foulden coelacanth is similar to R. ardrossense (see below) in the ornament of the skull roof, but is unique in the fine tubercular ornament on the angular and gular.

Archibald Geikie (1864) reported rhizodont

scales from Foulden, and White (1927) described the material collected by Ovens as scales of *Rbizodus bibberti* and *Strepsodus* sp., plus teeth of *S. sulcidens* and *S. striatulus*. These are form species for different shapes of scale and tooth. The first complete rhizodont discovered at Foulden during the 1980 excavations offered the opportunity to understand rhizodonts as a whole; elements that had previously only been found in isolation could now be linked to their associated parts (S.M. Andrews, 1985).

The rhizodont material from Foulden falls into two size ranges with no intermediates. The small specimens include the first complete rhizodont, and they are by far the smallest rhizodonts so far known (S.M. Andrews, 1985), being from 0.13 to 0.5 m long. The large ones



Figure 9.12 Foulden actinopterygians (after White, 1927). (A) Aetheretmon valentiacum White; (B) Phanerosteon mirabile White; (C) Strepheoschema fouldenensis White.

are 1.3-3.5 m in total length.

S.M. Andrews (1985) gave the name ?Strepsodus anculonamensis to the small fossils and this species is known only from Foulden (Figure 9.11A,B). The larger specimens may belong to the same species, which would imply that the small fishes are juveniles. This idea is supported by the small number of growth lines on the scales of the small specimens, and the large size of the orbit. There are four associated individuals, and several isolated elements of the small specimens, including the complete specimen, which is 345 mm long. A striking feature is a large sclerotic ring formed of numerous plates around the large orbit. The teeth are slender; sigmoidal and conical types occur. The mandibular ramus bears a large symphysial sigmoid tusk, followed by a row of smaller recurved conical marginal teeth (Figure 9.11B). The maxilla has marginal teeth like those of the mandibular. The dermal bones are smooth and ornamented by pits which may be rounded, irregular, or elongated into wavy ridges.

There are ossified fin spines present in the tail, and median fin supports also are present. The notochord is unrestricted by ossified centra. The fins differ from other sarcopterygians in that the scale-covered lobe makes up the bulk of the fin, with the fin-webs merely narrow marginal fringes. The pectoral fins are enlarged into stiff paddles, and the other fins are very small. The pelvic girdle and fin supports are not ossified, which may well be a juvenile feature. The bones of the shoulder girdle, in as far as can be seen, extend ventrally to form a broad and long shield of thick bone (Andrews and Westoll, 1970b).

The scales are cycloid and thin and apparently lack cosmine. They are ornamented by fairly straight fine sub-parallel ridges. Up to two growth lines are seen, but on the internal surface of the scale there is another series of up to ten lines. The internal side of the scale is also ornamented, unlike any other rhizodont, including the scales of the large specimen from Foulden. The overlapping area of the scale is covered by granular denticles arranged in concentric and radiating lines. The main lateral line canal shows as a well-marked groove or fold in the scales. There are at least six subsidiary canals along the flanks.

?Strepsodus sp. is the large form from Foulden, based on two associated specimens and numerous isolated bones and teeth. It is probably the same species as the small form, *?S. anculonamensis* Andrews, 1985, but has some significant differences (S.M. Andrews, 1985). The teeth of the large form are all proportionally stouter than those of the small form.

Actinopterygian fishes are the commonest vertebrate fossils at Foulden and include four rare palaeoniscid species. Foulden is the type and only locality for Phanerosteon ovensi. White's original material consisted of eight specimens, and ten new specimens were collected in 1980-1981. White (1927) claimed that the only differences between P. mirabile (from Glencartholm, q.v.) and Carboveles ovensi were the degree of squamation and the shape of the tail. Gardiner (1985) showed that the tail was the same in the two species, and also that White (1927) had been in error to describe the trunk of C. ovensi as being covered by small round scales; in fact the scales only occurred ventrally behind the pectoral girdle. Phanerosteon ovensi is also distinguished from P. mirabile (Figure 9.12) by the ornamentation on the skull roof and by the extent of scaling on the tail.

The type locality for *Styracopterus fulcratus* is Tarras Waterfoot. Gardiner (1985) included the species *Fouldenia ottadinica* as a synonym of this species. *Fouldenia ottadinica* was originally described by White (1927) from nine specimens from Foulden collected by Ovens. A further 15 specimens were discovered during the 1980–1981 excavations. *Fouldenia ottadinica* had been said (Moy-Thomas, 1937b) to differ from *S. fulcratus* by different-sized opercular and scales with bilobed posterior margins, but Gardiner (1985) showed that bilobed scales only occur on restricted areas of *F. ottadinica*.

Strepheoschema fouldenensis is a deep-bodied fish described originally from six specimens (White, 1927) and emended by Gardiner (1985) after the collection of a further 23 specimens from the 1980–1981 excavations. The line of the body (Figure 9.12) is marked by enlarged paired median ridge scales, which is a feature unique to *Strepheoschema* and *Aetheretmon*. Gardiner (1985) designated a new family, the Strepheoschemidae, to include this genus and *Aetheretmon*, which had originally been included in the Rhadinichthidae (Gardiner, 1967a).

Aetheretmon valentiacum is the most common early actinopterygian at Foulden, represented by many juveniles (Figure 9.12A). White (1927) described it from six specimens. Gardiner (1985), using the type material, plus 44 new specimens and material from Crooked Burn, showed that there was a continuous series of skull and scale ornamentation types, and concluded that only one species was represented by the two species originally described from Foulden, plus two from Coomsden Burn (White, 1927; Moy-Thomas, 1938a). Aetheretmon valentiacum was a fusiform fish which had unarticulated pectoral fin rays, a feature of many stemgroup neopterygians (Gardiner, 1985). The fulcral ridge scales above the tail are long and pointed, and there is a pair of large ventral ridge scales in front of the anal fin (presumably around the vent), similar to those of Strepheoschema.

Three fragments of *Cosmoptychius striatus* were recognized by Gardiner (1985) from the distinctive size, shape and ornamentation of a maxilla. This species is characteristic of the Lower Oil Shale Group of the Forth region and 'its occurrence at Foulden is unexpected' (Gardiner, 1985, p. 65). The remainder of the material consists of palaeoniscid scales, cf. *Rhadinichtbys*.

Wood and Rolfe (1985, p. 6) reported a single ?tetrapod scute, possibly an acanthracosaur from Bed 16.

Interpretation

The setting is interpreted as fresh- to brackishwater, with a hint of marine influence. The Cementstones environment was an 'extensive, low relief monotonous, silty to muddy floodplain crossed by occasional small sluggish meandering rivers. The floodplain passed imperceptibly seawards into coastal mudflats. The rivers frequently flooded onto the floodplain depositing silt and mud' (Anderton, 1985, p. 9). The floodplain was the scene of numerous crevasse splays from breached channel banks, and was subject to occasional marine inundations. Shallow, ephemeral and probably brackish lakes

Foulden

could have supported restricted faunas, but they would have low preservation potential on a drying floodplain. The Foulden Fish Bed represents a semi-permanent, relatively deep and relatively freshwater lake (Anderton, 1985). The lake was established where sedimentation did not keep pace with tectonic subsidence, and the area became increasingly submerged, becoming first a swamp, then becoming totally submerged as a shallow lake, some 5 m deep, which gradually silted up. As suggested by S.M. Andrews (1985), if this was a shallow area which could seasonally flood, it would provide a safe environment for small fishes, into which large predators could gain access at times of higher levels of water, in order to breed, or possibly to seek prey.

In discussing the possible causes for the mass mortalities in the fish bed, Anderton (1985) compared the lacustrine environment with that of Achanarras (q.v.). Unlike that Middle Devonian lake, the shallow lake at Foulden shows no evidence of a permanently stratified and eutrophic environment: there is little evidence of varved sediments, and the lake was very shallow. However, temporary stratification could have occurred during hot calm weather and, when followed by storms and deposition of sediment, would have provided a mechanism for the preservation of the fauna (Anderton, 1985). It may be assumed that the many fossils represent a school of young individuals killed off by local environmental changes (Wood and Rolfe, 1985).

Otoliths, possibly of acanthodians, are known from Foulden.

The complete specimens of rhizodonts from Foulden offer new opportunities for functional interpretation. S.M. Andrews (1985) compared the pectoral fin of rhizodonts with the paddles of plesiosaurs and ichthyosaurs. Rhizodont teeth are deeply rooted, superficially similar to crocodiles, to help retain struggling prey.

The ornamentation on the internal side of the scale of the rhizodont *?Strepsodus aulacona-mensis* may be a juvenile feature. The bosses at the centre of each scute were previously thought to be for attachment, or insertion of muscle. The articulating scales of the Foulden material led S.M. Andrews (1985) to suggest that the boss was merely to thicken up this area of body cover. The differences in stoutness of the teeth between the small and large forms of *?Strepsodus* may be the result of growth (and

possible associated change of diet) or may simply represent different regions of the mouth. The small and large forms were found at different horizons, and their distribution may represent a partial separation in the population, perhaps by depth or by seasonal floods. In the latter case, it could mean that the large fishes moved into previously inaccessible areas to breed, so that on return to normal conditions the young fishes could live in safer shallow waters.

Conclusion

Although the fish assemblage (12 spp. or more) from Foulden is relatively small, the fact that several species appear to be unique to the site suggests a somewhat special, perhaps confined lake and gives the site its conservation value. Small complete individuals and small juveniles dominate the assemblage, but sometimes much larger fishes had access to the area. *?Strepsodus aulaconamensis* and *Acanthodes ovensi* are represented by juveniles, and there is evidence of larger members of what are, or are most probably that same species. Excavations in 1980–1981 proved the richness of the site, and its potential for the future.

WARDIE (NT 245771)

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,



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

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 vield these nodules; all are distinctive in terms of the relative abundances of different fish species in each (Figures 9.14 and 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 fishbearing 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



Figure 9.14 Actinopterygians in nodules from the Wardie Shale, Wardie, (A)–(D) are all $c. \times 0.66$. (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), $c. \times 0.5$.

and spines.

Complete rhizodonts are extremely rare. A gigantic (2.6 m long) specimen of *Rbizodus hib-berti* 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.

K. ornatissimus (Agassiz, 1835)
Osteichthyes: Actinopterygii: Platysomidae
a platysomid close to the Amphicentridae
Chondrichthyes: Elasmobranchii:
Kenacanthiformes
Diplodoselache woodi Dick, 1981
Type locality.
Chondrichthyes: Elasmobranchii:
Ctenacanthiformes
Onychoselache traquairi Dick, 1978
Sphenacanthus serrulatus Agassiz, 1837
Ctenacanthus indet.

TETRAPODA

Aïstopoda: 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 *Elonichtbys*. 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 *Elonichtbys*. 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 fins 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 9.17A and 9.17B), 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 elasmobranchs (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 Xenacanthiformes (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.



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).

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 fishbearing 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 airbreathing 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.

GLENCARTHOLM (NY 376795)

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.

Glencartholm



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

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%.

British Carboniferous fossil fishes sites

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 fulcratus (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 cov-



ered by scales. These features are considered to be primitive (Forey and Young, 1985).

The osteolepiform *Megalichtbys* 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 buxleyi* (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

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.

been emended by Gardiner (1985). Moy-Thomas and Bradley Dyne (1938) thought the skull and teeth similar to those of *Elonichtbys*, 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 suspensorium, 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 pulcbellum* 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 pulcbellum* and *M. politum* are about 0.08 m in length, *M. ?crassus* is about 0.11 m long. *M. pulcbellum* 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 suspensorium, 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. Mov-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 Burn Berwickshire and Coomsden 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); *Adroichtbys* (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 amphicentrid 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 fins 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 col-

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. lected 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 heterocercal 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 mediumsized (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 'cte-

Figure 9.20 Glencartholm elasmobranchs. (A) *Sphenacanthus costellatus* Traquair, restoration (after Moy-Thomas, 1936); (B) *Goodrichichthys 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.

nacanth' 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, *Goodrichtbys* 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 *Lopbodus*-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 9.15D). 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

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.

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 *Listracantbus*-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 volsellorbinus*, 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 Lagerstätten 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 guiet 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 were 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.

CHEESE BAY (NT 492856)

Highlights

Cheese Bay, Lothian, is the type locality for *Rhadinichthys formosus* Traquair, 1904, a small actinopterygian. The fish fauna consists of 15 species, some of which lived in highly saline drying pools.

Introduction

The Cheese Bay (or Gullane) section is only occasionally exposed at low tide. The so-called 'Shrimp Bed' and associated black shales have yielded a rich and diverse assemblage of fishes. The beds occur in the Lower Oil Shale Group of the Calciferous Sandstone Series, dated (George *et al.*, 1976, p. 49) as Asbian (late Viséan). The discovery of fish in this section by Macconochie was first reported by Traquair (1904) and described in detail by Traquair (1907), Briggs and Clarkson (1983) and Hesselbo and Trewin (1984).

Description

The section at Cheese Bay consists of 5 m of laminated dolomites and mudstones that are truncated by faulting and lack of exposure (Hesselbo and Trewin, 1984). Fishes occur at three horizons (Traquair, 1907; Figure 9.22). They are

Figure 9.22 Section of the Cheese Bay GCR site.

common in the shales below the 'Shrimp Bed', but rare within it. Large specimens are represented in the assemblage by scales of *Rbizodus* from just below the Shrimp Bed, which must have been from an animal of up to 10 m in length (Andrews, *in* Hesselbo and Trewin, 1984).

Besides the fish fauna, the 'Shrimp' Bed contains numerous specimens of crustaceans, with *Tealliocaris* particularly numerous, and in various stages of growth. Many of these are preserved whole (Traquair, 1907) or only partly disarticulated. Most of the in-situ 'Shrimp Bed' is reported recently to have been removed by person(s) unknown (R.L. Paton, pers. comm., 1995).

Fauna

Acanthodii: Acanthodiformes: Acanthodidae Acanthodes sp.

Osteichthyes: Sarcopterygii: (Actinistia) *Rbabdoderma* sp.

Coelacanthus sp.

- Osteichthyes: Sarcopterygii: Rhizodontida *Rhizodus hibberti* (Agassiz and Hibbert, 1836)
- Osteichthyes: Actinopterygii: Elonichthiidae Gonatodus punctatus (Agassiz, 1835)
 - E. robisoni (Hibbert, 1835)
 - *E. robisoni* sub. var. *intermedius* Traquair, 1907
- E. striatulus Traquair, 1907
- Osteichthyes: Actinopterygii: Cosmoptychiidae Cosmoptychius striatus (Agassiz, 1835)
- Osteichthyes: Actinopterygii: Pygopteridae Nematoptychius greenocki (Traquair, 1867)
- Osteichthyes: Actinopterygii: Rhadinichthyidae Rhadinichthys brevis Traquair, 1881
 - *R. elegantulus* Traquair, 1881
 - R. formosus Traquair, 1904
 - Type locality
 - R. ornatissimus (Agassiz, 1835)
- Osteichthyes: Actinopterygii: Platysomidae Wardichthys cyclosoma Traquair, 1875

TETRAPODA

Tetrapod *incertae sedis*: an unidentified postranial skeleton (RSM; M. Coates, pers. comm.)

New material of small coelacanths have been found here by S.P. Wood, either *Coelacanthus* or *Rhabdoderma* (T.R. Smithson, pers. comm., 1992).

Rhadinichthys formosus is described by Traquair (1904) as being similar to *R. ferox* (from Wardie, q.v.) in scale ornamentation, but resembling *R. brevis* (also from Wardie) in its general shape. It is 140 mm long and deeply fusiform, with a large dorsal and anal fins. The moderate-sized scales are ornamented with sharp ridges separated by a diagonal across the scale. The posterior border of the scale is delicately denticulated. The cranial roof bones are marked with fine contorted and interrupted striae.

Interpretation

Briggs and Clarkson (1983) compared the Cheese Bay Shrimp Bed with the Granton Shrimp Bed, and suggested that conditions were similar between the two sites, which they described as 'stromatolite communities', having been preserved on tidal flats in nearshore intertidal or subtidal conditions where the fossil concentrations may represent dried-out pools. The fishes would have been periodic introductions. Study of the whole Granton sequence showed fluctuating salinity conditions within a stagnant pool caused by marine incursions that also caused mass mortalities of the indigenous fauna (Cater, 1987). Thus the faunal assemblage at Granton, and by implication in the Shrimp Bed, is envisaged as having consisted of marine forms, which were brought in by incursions of the sea, plus a specialized indigenous fauna that lived in brackish waters with possibly fluctuating salinities. Cater (1987) interpreted the Granton Shrimp Bed as representing periodically exposed mud flats with pools, and the shales above and below as low-energy stagnant lagoons. By implication, the faunal assemblages from Cheese Bay can be separated into coelacanths, the actinopterygian Wardichthys, and the acanthodian Acanthodes occurring in the fluctuating salinity plus marine incursion beds, and the other actinopterygians occurring within the lagoons. The fish fauna is similar to that from the Wardie Shales which is of slightly younger age (Cater, 1987).

Conclusion

The conservation value of the Cheese Bay site results from the production of a good fauna of fossil fishes of mid-Dinantian age, associated with crustaceans and other fossils including the important discovery of tetrapod remains. Recent sedimentological study has enhanced understanding of the unusual periodically evaporitic conditions. Detailed logging and collecting could provide information about the environments in which the fishes lived, because the assemblage is probably at least two communities mixed together *post mortem*, and further confused by indiscriminate collecting. The discovery of tetrapod remains demonstrates the continuing potential of the site.

INCHKEITH (NT 294830 AND NT 294822)

Highlights

A good fauna of 13 fossil fish species has been reported from the island of Inchkeith in the Firth of Forth, Fife. The site is especially important since it has also yielded tetrapod bones.

Introduction

Fishes were first reported from Inchkeith by Davies (1936) from more than one locality. In 1979 one of these localities was excavated using explosives to remove the overlying lavas. The results of this were the retrieval of several 'amphibian bones' (S. Turner, internal NCC report), as well as associated fish remains.

Description

Steeply dipping shales, mudstones, limestones and sandstones, about 120 m thick, interbedded with lavas, making up a total of about 290 m, are exposed on the Island of Inchkeith (Davies, 1936). The middle of the sequence is thought to lie near the horizon of the Burdiehouse Limestone (Davies, 1936, p. 777; Mitchell and Mykura, 1962), a unit exposed near Edinburgh that lies at the junction of the Lower and Upper Oil Shale groups. The age is Viséan, and proba-

Figure 9.23 Sketch map of Inchkieth.

bly Brigantian (George et al., 1976, p. 49).

The tetrapod bones found in 1979 came from a welded ash band between two thin ostracodbearing horizons that were full of fish scales, lying between two lava flows. The tetrapod remains were found together with rhipidistian and lungfish bones (S. Turner, pers. comm., 1982).

Fauna

- Acanthodii: Climatiiformes: Gyracanthidae *Gyracanthus* sp.
- Osteichthyes: Sarcopterygii: (Dipnoiformes) Sagenodus sp.

Uronemus sp.

- Osteichthyes: Sarcopterygii: Rhizodontidae Strepsodus?
 - *Rhizodus* cf. *hibberti* (Agassiz and Hibbert, 1836)
- Osteichthyes: Actinopterygii: Gonatodidae *Pseudogonatodus* sp.
- Osteichthyes: Actinopterygii: Elonichthyidae Elonichthys robisoni (Hibbert, 1835)
- Osteichthyes: Actinopterygii: Acrolepidae *Nematoptychius* sp.
- Osteichthyes: Actinopterygii: Platysomidae *Eurynotus* sp.
- Chondrichthyes: Elasmobranchii Ageleodus sp. (= synonym of Callopristodus) Callopristodus sp. Cynopodius crenulatus Traquair, 1881 Pleuracanthus sp. (= Xenacanthus)

TETRAPODA: ?Adelogyrinidae cf. *Palaeomolgophis*

Interpretation

The vertebrate assemblage does not support the opinion of the Geological Survey that the Inchkeith sediments are in the Lower Oil Shale Group, but suggests that they lie in the Viséan Middle Oil Shales Group (Smithson, 1985, p. 127). It is a freshwater facies with predatory species of osteichthyan predominant in the fauna. The elasmobranchians also include large predatory forms. Tetrapod bones include a rib (Andrews and Carroll, 1991; Smithson, 1985) and jaw fragments. The association of beach shales, ostracod and plant-rich beds with the vertebrates (fishes and tetrapods) in a volcanic set-

ting is comparable to the situation at East Kirkton (q.v.).

Conclusion

The Inchkeith site has a conservation value based on its varied fauna of mid-Dinantian fishes and rare tetrapod remains. Recent excavations have shown that the potential of the site is good, given the means of effecting the removal of hard volcanic units adjacent to the fossil layer.

ARDROSS CASTLE (NO 511006)

Highlights

Twelve species of fossil fishes have been found at Ardross Castle in Fife, and these include the original specimens of four species, and two species not found elsewhere. Some of the specimens are well enough preserved to show details of how they decomposed before being buried.

Introduction

The fossil-bearing strata crop out on the foreshore below the ruins of Ardross Castle. Although invertebrates have been found in fair numbers, fishes are rather rare at Ardross, and only now and again are a few specimens found (White, 1937). One of the first people to note the occurrence of fossils at Ardross was Thomas Brown (1861), who described actinopterygian scales, teeth and scales of *Holoptychius*, and a specimen of *Amblypterus ?striatus*. Peach (1902) summarized the fauna, which was described by Traquair (1905c). White (1937) described the fishes from the site, including new specimens and two new species.

Description

The fishes from Ardross occur in the *Crangopsis* Bed in the Calciferous Sandstone Series, a unit dated as Brigantian (late Viséan) in age by George *et al.* (1976, p. 53). The specimens are preserved in a fine-grained mudstone with a low lime content.

One of the most interesting features of the fossils from this site is the fact that several of them show obvious signs of in-situ disruption and decomposition prior to burial. The scattering of bones shows this: for example, one specimen had lost a large piece from its back, the preorbital region had been scattered, the caudal region telescoped and all the fins disturbed.

Fauna

The fish assemblage from Ardross Castle is large in numbers of species, but these are represented by very few specimens. Twelve species of fishes have been recorded from Ardross, and in addition 16 species of invertebrates and two plants (White, 1937) occur.

Acanthodii: Acanthodiformes: Acanthodidae Acanthodes sulcatus Agassiz, 1835 Neotype locality Osteichthyes: Sarcopterygii: Actinistia: Rhabdodermatidae Rhabdoderma ardrossense Moy-Thomas, 1937 Type and only locality Coelacanth indet. (= Coelacanthopsis curta Traquair, 1905) Osteichthyes: Actinopterygii: Rhadinichthyidae Rhadinichthys carinatus (Agassiz, 1835) Rhadinoniscus wrighti White, 1937 **Type** locality Osteichthyes: Actinopterygii: Elonichthyidae Elonichthys robisoni (Hibbert, 1835) Osteichthyes: Actinopterygii: Cosmoptychiidae Watsonichthys pectinatus (Traquair, 1877) Osteichthyes: Actinopterygii: Amphicentridae Cheirodus crassus Traquair, 1890 Chondrichthyes: Holocephali Deltoptychius armigerus (Traquair, 1888) Eucentrurus paradoxus Traquair, 1905 Type locality for unique specimen helodont teeth Chondrichthyes: Elasmobranchii Euphyacanthus semistriatus (Traquair, 1894)

The Order Acanthodiformes is distinguished from all other acanthodians by having only a single dorsal fin and spine, in a posterior position. *Acanthodes*, the type genus, is known from the Lower Carboniferous to Lower Permian, virtually worldwide. The type locality for *A. sulcatus* is Wardie (q.v.), but the original material is lost. This was a large acanthodian (about 20 cm long), similar to *A. wardi* Egerton. White (1937) redescribed *A. sulcatus* based on an Ardross complete specimen and separated this species from *A. wardi* and *A. nitidus* on its straight styliform bone and the nature of the scales.

The coelacanth Rhabdoderma ardrossense is

one of the five species recorded from the Carboniferous of Britain that is still recognized as distinct (Forey, 1981): the 15 invalid species that had been erected on the basis of scale ornament are better interpreted as variants of R. elegans or R. tinglevense. Rhabdoderma ardrossense is known from only two specimens, which were described by Moy-Thomas (1937c) and Forey (1981). In Britain, Rhabdoderma is restricted to the Carboniferous, and mainly to the Late Carboniferous. The type species, R. elegans from Linton, Ohio, shows the braincase completely ossified in the adult. Rhabdoderma is classified as the primitive sister-group to the Suborder Coelacanthoidei (Forey, 1981; Figure 9.24).

A specimen of *Rhadinichthys carinatus*, originally said to be from Wardie (q.v.), was described by White (1937) from Ardross. The specimen shows signs of having decomposed fairly extensively prior to burial; the head bones have all but gone, the scales are scattered and some of the fins are missing.

Rhadiniscus is distinguished from *Rhadinichthys* by fewer branchiostegal rays and the more divided lepidotrichia. It is confined to

the Lower Carboniferous of Scotland (Lehman, 1966), and is an elongated early actinopterygian with a stout caudal peduncle, rhombic body scales which are strongly serrated behind, and with a very oblique suspensorium. Only small marginal teeth are known and the branchiostegal rays never exceed four pairs (White, 1937). *Rhadinichthys wrighti* was described by White (1937) from a single specimen which lacks skull and ventral fins (Figure 9.24B).

A nearly complete specimen of *Elonichthys robisoni* from Ardross Castle was described by White (1937) and had originally been referred to a new species by Traquair, but White (1937) synonymized it with the species from Burdiehouse (Traquair, 1877–1914). This species is the commonest fish in the Lower Carboniferous of the Forth Basin.

Watsonichtbys (Figure 9.24) is distinguished from *Elonichthys* by the presence of an epipreopercular, by a rounded snout, by the very long, fringed anal fin and by the lepidotrichia of the pectoral fins being separated at the base (Lehman, 1966). It is known from the Lower Carboniferous of Scotland and the Upper Dwyka (Karroo System) of South Africa

Figure 9.24 Ardross Castle site fossil actinopterygians: (A) *Watsonichtbys pectinatus* Traquair, skull in lateral view (after Gardiner, 1963); (B) *Rhadiniscus wrighti* White, skull in lateral view; (C) the coelacanth *Rhabdoderma*, restoration in lateral view (after Forey, 1981).

(Gardiner, 1963; Lehman, 1966). Only one species occurs in Scotland, W. pectinatus from Gilmerton. The Watsonichthys terminal group (Gardiner and Schaeffer, 1989) includes Rhabdolepis, Cosmoptychius, and Strephamongst eoschema others, besides Watsonichthys. Watsonichthys lacks a postileithrum, a feature that is common in lower actinopterygians such as Cheirolepis and Stegotrachelus (Gardiner and Schaeffer, 1989). Watsonichthys pectinatus, a large fusiform species reaching almost 1 m in length, was described by Gardiner (1963).

Cheirodus crassus was 0.14–0.15 m long and the same height. A nearly complete specimen was described by White (1937), which showed for the first time the shape and other features of this species, which had previously only been known from the type suite of seven scales from Abden (q.v.; Traquair, 1890c).

The holocephalan Eucentrurus paradoxus Traquair, 1905 is based on a distorted unique specimen, and is the sole representative of the Eucentruridae bradvodonts (Mov-Thomas 1937d) of the Order Chondrenchelyiformes. This order contains three species, Chondrenchelys problematica, Harpagofututor volsellorbinus and E. paradoxus. The head of E. paradoxus is an undescribable mass that contains a bradyodont-type tooth plate, and the body made up of minute 'spinelets' (Traquair, 1905c; Moy-Thomas, 1937d). The remains of pectoral and pelvic girdles and of calcified centra in the tail can be seen. Zangerl (1981) stated that Euphyacanthus semistriatus was described from spines and cannot be assigned with certainty to any group of elasmobranchs because the remains are too fragmentary.

Other fish species from Ardross Castle are more fully described in the Foulden, Glencartholm and Abden reports (q.v.).

Interpretation

In the absence of detailed sedimentological information to the contrary, this environment could be compared to that at Granton (Briggs and Clarkson, 1983; Cater, 1987), where shrimps mostly represent an indigenous fauna inhabiting a stagnant lagoon with fluctuating salinities into which marine incursions brought marine forms and caused mass mortalities of the existing species. This might explain the rarity of fish specimens at Ardross Castle, and decomposition shown by some specimens.

The coelacanth *Rhabdoderma* is a common species in the Late Carboniferous of Europe and North America, where its distinctive scales occur commonly in freshwater deposits. There are also some occurrences in marine beds, which suggests a euryhaline habit.

Conclusion

The conservation value of the Ardross Castle site lies in the diversity of its fish fauna, which may include 12 species of acanthodians, coelacanths, actinopterygians, sharks and holocephalians. Specimens are rare, perhaps because of inimical environmental conditions. The assemblage of fishes is different from that at other sites of equivalent age in the Forth area, notably in the low percentage of small actinopterygians. Elsewhere, these dominate the faunal assemblage, and those present at Ardross are common forms, such as *Elonichthys robisoni* and *Rhadinichthys carinatus*, both of which may have been able to tolerate a wide range of habitat.

ABDEN (NT 276874)

Highlights

The fish fauna from Abden near Kirkcaldy in Fife is one of the youngest from the Scottish Early Carboniferous, and it is the source of about nine species, including the original material of one species. Sharks are rare, which may indicate a somewhat unusual marine environment.

Introduction

Fossil fishes were originally found at Abden in Victorian times, and they were described first by Traquair (1890c). More recent work on Carboniferous fishes, such as papers by Moy-Thomas (1937c), Patterson (1965) and Forey (1981), has redescribed material from Abden.

Description

The Abden Bone Bed occurs in the Uppermost Calciferous Sandstone Series of the Brigantian (late Viséan) of Fife. Westoll (1951) also includ-

Figure 9.25 Sketch map of the GCR site at Abden.

ed the Blackband Ironstone fauna from Niddrie and the Ardross Shrimp Bed as the 'Abden Fauna'. These rocks crop out on the foreshore north of Abden Rocks, Kinghorn Burgh (Figure 9.25).

Fauna

- Acanthodii: Acanthodiiformes: Acanthodidae *Acanthodes* sp.
- Osteichthyes: Sarcopterygii: (Actinistia) Diplocercides davisi (Moy-Thomas, 1937) (= Rhabdoderma(?) abdenense Moy-
 - Thomas, 1937)
- Osteichthyes: Actinopterygii: Amphicentridae Cheirodus crassus Traquair, 1890 Type locality

Eurynotus crenatus Agassiz, 1835

- Osteichthyes: Actinopterygii: Acrolepidae
- Nematoptychius greenocki (Traquair, 1867) Chondrichthyes: Holocephali: Menaspidae

Deltoptychius armigerus (Traquair, 1888) Chondrichthyes: Elasmobranchii:

Ctenacanthiformes

Tristichius arcuatus Agassiz, 1837

Interpretation

Traquair (1890c) noted the presence of a coelacanth at Abden, but did not describe it. Moy-Thomas (1937c) named several forms, Rhabdoderma ? davisi from the Carboniferous Limestone of Armagh and R. ? abdenense for Traquair's coelacanth from Abden. These were both based on isolated head bones, and Mov-Thomas (1937c) recognized the similarity between these two species, and with Diplocercides. Forey (1981) also noted the similarity in the ornamentation on the gulars, operculum and cleithrum between these two species and D. kayseri and D. beiligenstockiensis from the Devonian of Germany, and he synonymized the two British species as Diplocerides davisi (Mov-Thomas, 1937c).

A specimen termed cf. *Rhabdoderma* sp. from Foulden was described by Forey (1981) as having the same style of ridged ornament on the cleithrum as *Rhabdoderma ?abdenense* and *Diplocercides*, but it otherwise showed ornament and shape of head bones which relate it to *Rhabdoderma*. Thus Forey (1981) showed that the ornament pattern must be more general than previously supposed, but he did not, in that paper, remove *davisi* from the genus *Diplocercides*.

The actinopterygian Cheirodus has a lozengeshaped deep body with two marked angles, one on the dorsal side and one in front of the anal fin. The anal and dorsal fins are long-based; there are small pectorals, and although it has been thought that it had no pelvic fins (e.g. Lehman, 1966), material from Bearsden (q.v.) shows their presence. Cheirodus is known from the Carboniferous of England, Scotland and the USA (Lehman, 1966). Gardiner and Schaeffer (1989) place the genus in their Platysomus terminal group. The original description of Cheirodus crassus Traquair, 1890 was based on seven isolated scales from Abden (Traquair, 1890c), which have coarse ornament. Some scales also occur at Beith, associated with dentary plates (Traquair, 1890c). White (1937) redescribed the species on the basis of an almost complete specimen from Ardross Castle (q.v.).

Patterson (1965) figured two examples of holocephalan mandibular spines from Abden, as part of a series to illustrate the variation in their style of shape and ornamentation. These may be termed *Deltoptychius armigerus*.

The particular faunal assemblage from Abden

was referred to as the 'Abden Fauna' by Westoll (1951). He regarded it as different from the more typical 'Marine Fauna' of, for example the Hurlet Limestone (containing elasmobranchs), although both are considered to be marine.

Conclusion

Abden produced some good fish specimens in the late 19th and early 20th centuries, hence its conservation value. The fauna differs from that of other localities of similar age in the rarity of sharks. Further collecting of fish specimens, and study of the sedimentology, may demonstrate whether these faunal differences truly reflect an unusual environment of marine deposition.

STEEPLEHOUSE QUARRY (SU 288554)

Highlights

Fossil fishes are very poorly known from Dinantian limestone sequences, and Steeplehouse Quarry in Derbyshire has produced the best fauna from this kind of offshoremarine facies. This site is the oldest UK stratigraphical occurrence of a neoselachian (modern-type) shark, and of the shark *Lissodus*, and the fish assemblage is dominated by sharks that lived in and around an ancient coral reef.

Introduction

A new fish bed was discovered in the early 1960s at Steeplehouse Quarry, Derbyshire, in a 1.5 m unit of crinoidal limestones with shale partings (Ford, 1964). A unit of these limestones, 1 m thick, contains large numbers of dermal denticles of *Petrodus patelliformis* plus other rarer fish teeth and fragments. Fish remains were first noted in this quarry by Shirley (1958), and the rich deposits were discovered soon after by Ford.

Ford (1964) suggested that Steeplehouse Quarry might be the type locality of M'Coy's (1848a) original description of *Petrodus patelliformis* for several reasons (see below). Bulk sampling by Ward and Duffin between 1972 and 1979 provided several rare teeth including two new species of shark (Duffin and Ward, 1983a; Duffin, 1985).

Description

The beds in the quarry are part of the Cawdor Limestones at the top of the Lower Carboniferous (Dinantian) succession in Derbyshire, and referred to the P¹ goniatite Subzone of the Upper Viséan (Shirley, 1958; Ford, 1964; Duffin and Ward, 1983a). This unit is dated as latest Viséan (late Brigantian), and probably P² Subzone, by George *et al.* (1976, p. 30).

A varied fauna of invertebrates found in both the limestones and the shale partings includes corals, brachiopods, bryozoans and crinoids (Ford, 1964). The fish remains are present as scattered pieces throughout the 1 m of limestones, but are concentrated at the top of each limestone bed and within the shale parting itself. Samples of the shale partings reached 20% by weight of dermal denticles. The shale partings die out laterally southwards; and the presence of denticles within the limestone also thins rapidly westwards. Their occurrence was shown to be concentrated within a small thickness of beds over an area not more than 50 m across from north to south (Ford, 1964). Duffin and Aldridge have continued to study microvertebrate material from Steeplehouse Quarry and have kindly provided additions to the formal list.

Fauna

Chondrichthyes: Elasmobranchii incertae sedis Cooleyella fordi (Duffin and Ward, 1983) Lissodus wirkworthensis Duffin, 1985 Thrinacodus ferox (Turner, 1982) Pristodus cf. falcatus Davis, 1884 Protocrodus sp. Symmorium cf. reniforme Cope, 1893 ?Triodus sp. 'Harpagodens' (= Thrinacodus) Petrodus patelliformis M'Coy, 1848 Cladodus sp. Indeterminate xenacanth, petalodont, and hybodont teeth, dermal denticles and plcoid scales Osteichthyes: Actinopterygii Indeterminate actinopterygian teeth, scales, and vertebrae

Denticles described as *Petrodus* or *P. patelliformis* are known worldwide in the Carboniferous (Zangerl and Richardson, 1963; Chorn and Reavis, 1978). Denticles of this type occur on many different kinds of chondrichthyans, in the same way as those called Listracanthus (Zangerl, 1981). A specimen, from the Upper Carboniferous of Arkansas, USA, is described with Petrodus denticles in association with teeth which can be identified as Carcharopsis (Zangerl, 1981). Listracanthus denticles consist of dense dentine and have been thought to be spines in the past because they may be 0.05 m long, or more. Petrodus denticles consist of trabecular dentine beneath a thin layer of orthodentine (Zangerl, 1981). Zangerl (1981) believed that Listracanthus has a dermal skeleton of listracanthi and petrodi, whereas Petrodus was a very large animal (about 1 m long) armoured exclusively with petrodi, and with a dentition of Carcharopsis teeth. Neither Listracanthus nor Carcharopsis have been recorded from Steeplehouse Quarry.

M'Coy (1848a) regarded *Petrodus patelliformis* as 'abundant in some parts of the Derbyshire limestone' but gave no locality. The type material was collected by Hopkins, who discussed the Derbyshire limestones (Hopkins, 1834) without referring to any fish localities. Green and Strahan (1887) did not list Steeplehouse as a fish locality, and did not list *Petrodus patelliformis* as occurring at the other Derbyshire fish sites, so Ford (1964) suggested that it is possible that this is the type locality for the species.

Only dermal denticles have been found at Steeplehouse, and they have been assumed to represent a hybodont (Ford, 1964), identical denticles being found on a specimen from Pendlesides in association with a pectoral girdle and skull, and used to describe the species as a hybodont (Moy-Thomas, 1935). This has since been referred to a new genus and species, *Moyacanthus thomasi* Zangerl, 1981, but the denticles are removed from the species description because they are ubiquitous in the Carboniferous and do not appear to have any specific relationship to the bones in the specimen, being described as 'strewn amongst the cartilages' (Zangerl, 1981).

The teeth of *Lissodus* are distinct from other hybodont teeth (Figure 9.26). They are small to moderately large, with deep crowns. A small labial peg is present and supported by a labial root buttress in some species (Duffin, 1985). *Lissodus* is widespread, known from freshwater and marine deposits from the Lower Carboniferous (Viséan) to Upper Cretaceous (Maastrichtian) of Britain, north-west Europe, Russia, USA and South Africa (Duffin, 1985, 1989). This is its oldest site. It is normally thought of as a Mesozoic genus, many species occurring in the Jurassic and Cretaceous.

Lissodus wirkworthensis is represented by 29 teeth, 1–2 mm long obtained by bulk sampling from Steeplehouse Quarry (Duffin, 1985).

Duffin and Ward (1983a) erected a new family, the Anachronistidae, for teeth found in the Lower Carboniferous of England and Wales, and the Early Permian of Nevada, USA. *Anachronistes fordi* from Steeplehouse is the type species. Recently, however, Duffin, Richter and Neis (in prep.) have amended the diagnosis while reporting *Anachronistes* to be a junior synonym of *Cooleyella* Gunnell (1933). Duffin (1980a) and Duffin and Ward (1983a) suggest that the arcuate or V-shaped basal root face is typical of neoselachians of superorders Squalomorphii, Squatinomorphii or Galeomorphii, and this is probably a synapomorphic character.

The neoselachian *Cooleyella* shares several characters such as the labial buttress and the central vascular root pit with the teeth of the Early Jurassic *Squatina* and *Orectolobus*. The teeth of *Cooleyella* are envisaged as being arranged in distinct tooth rows, either as in *Squatina*, or with an overlap between lateral blades of teeth in successive tooth rows. The tooth shape shows that this shark was adapted to a durophagous and bottom-living habit. Duffin and Ward (1983a) suggested that it might have been dorso-ventrally flattened, with large pectoral fins, like the recent wobbegong (*Orectolobus*) and angel shark (*Squatina*).

Thirty-five teeth of *Cooleyella fordi*, varying from 1–2 mm in length, were obtained from Steeplehouse Quarry by Duffin and Ward (1983a). A single tooth was also found in Clwyd, North Wales. These are typical neoselachian teeth with a conical central cusp, well developed lateral blades and a basal flange, a V-shaped basal face to the root, and root vascularization. These specimens represent the earliest known neoselachian.

The pheobodont shark *Thrinacodus ferox* has now appeared at Steeplehouse Quarry (Duffin, 1993a) and teeth ascribed to this taxon have also been recorded from Late Devonian (Famennian) to Early Viséan rocks in Australia, Thailand, Poland, Morocco, New Mexico and China.

Figure 9.26 Steeplehouse Quarry elasmobranchs. Teeth of the hybodont selachian *Lissodus wirksworthensis* Duffin: (A) NHM P60741 in labial view; (B) P 60739 in occlusal view; (C) holotype P 60740 in occlusal view; (D) in lingual view; (E) labial view; (F) P 60752 in occlusal view; (G) labial view; (H) lingual view; (I) P 60748 in occlusal view; (J) labial view (after Duffin, 1985).

Interpretation

The coarse clastic nature of the denticle-bearing deposit, with the larger fossils being little-worn, indicates rapid deposition of material derived from nearby. Reef limestones are situated within a distance of few hundred metres, so Ford (1964) envisaged a depositional site close to a reef complex, perhaps as a result of inter-reef scour plus subsequent deposition in off-reef waters. It is also possible that a shoal of Petrodus inhabited the reefs, which would explain the presence of their remains through such a thickness of strata (Ford, 1964). Duffin and Ward (1983a) note the presence of xenacanth shark teeth in the assemblage, and suggest that certain faunal elements could not be indigenous to the reef complex, but have been transported in from freshwater areas, possibly from lagoons.

Other instances of shark teeth in off-reef calcarenites and 'Beach Beds' have been reported from Bolt-Edge Quarry (SK 088798; Davis, 1886) and Treak Cliff (SK 139829; Barkes and Holroyde, 1896). They are within strata of much the same age but are equally local, being virtually untransported accumulations of fish debris from large numbers of fishes.

Conclusion

The sharks from Steeplehouse Quarry are an unusual and varied assemblage and provide the site with its conservation value. The habitat and the fauna are very different from the fish assemblages of the same age in Scotland. Further sampling at Steeplehouse Quarry is possible, and bulk processing techniques, as used by Duffin and Ward (1983a), would produce many more specimens.

BEARSDEN (NS 53057325)

Highlights

Bearsden in Glasgow, Strathclyde, is one of the most important fossil shark sites in the world, and many discoveries have been made there in recent years. It is the source of 14 species of fishes, including complete and superb specimens of sharks, and several unique bony fishes.

Introduction

The fish beds in shales in the Manse Burn at Bearsden were discovered in 1981 by S.P. Wood (Wood, 1982). In 1981 the NCC financed an excavation to expose these shales, and a temporary quarry, 5×3 m in area was worked, bed by bed, through the shales exposed there, by a team of workers from the Hunterian Museum led by Wood. Many new species were discovered, including complete fossil sharks, which are usually only known from teeth and spines because it takes unusual preservation environments to preserve the cartilaginous skeletons. The site also yielded the first complete *Deltoptychius*.

Several publications have appeared since Wood's (1982) announcement of the site. Dick *et al.* (1986) referred to the sharks, Clark (1990, 1991) has described some of the crustaceans, and Lowney (1983) and Coates (1993) have described new actinopterygians from the site.

Description

The Bearsden site exposes the Manse Burn Formation, which has been dated as Pendleian (earliest Namurian = earliest Serpukhovian), E¹ Zone, based upon spore, conodont and goniatite analysis. Clark (1989) defined the Formation as including the shales from the Top Hosie Limestone Marine Band to the base of the first thick sandstone. The Manse Burn Formation (Figure 9.27) has been divided into six members on the basis of sedimentology and the Shrimp Member, the fossil content: Posidonia Member, the Nodular Shale Member, the Platey Shale Member, the Betwixt Member and the Lingula Member. These members correspond roughly to the 'beds' A-E described by Wood (1982).

The fossil fishes and abundant crustaceans are in finely laminated shales of the Shrimp Member, which has now been identified at several other localities nearby (Clark, 1989). Some specimens were collected from weathered exposures along Manse Burn, but most came from the temporary quarry. Of the fishes, all but *Acanthodes* are restricted to certain beds. Some actinopterygians occur only in marine phases, others are restricted to transitional beds. The sharks *Stethacanthus* and *Tristychius* are mutually exclusive. *Tristychius* probably represents the non-marine *Diplodoselache* fauna described by

Bearsden

Figure 9.27 (A) Sketch map of the Bearsden area, Glasgow, with the stratigraphical section (B) found in the Manse Burn Formation (after Wood, 1982).

Dick (1981) from the Oil Shales of Edinburgh (Wood, 1982).

Fauna

Acanthodes sulcatus occurs throughout the Bearsden section, and is not restricted to marine or brackish sediments. One specimen collected in 1981 contained the first known specimen of a Carboniferous acanthodian braincase (Wood, 1982). Dipnoans are absent, and there is a single isolated coelacanth head in the collection (Wood, 1982).

The marine actinopterygian fauna from Bearsden is unique (Figure 9.28), and bears no relationship to the marine palaeoniscids from Glencartholm (q.v.) or from South Africa (Wood, 1982). There are as many as eight species (Coates, 1988), of which Coates (1993) described three new species of Mesopoma, a genus already widely known from the Early Carboniferous of Scotland, and a new species of the new genus Frederichthys, a platysomid (Figure 9.28B). Several fine specimens of Cheirodus crassus Traquair, 1890 have also been discovered at Bearsden. They show for the first time that pelvic fins were present in this species. Outside North America, complete Carboniferous marine sharks are known only from Glencartholm (q.v.) and the Edinburgh area, and non-marine sharks are known exclusively from the Edinburgh area (Dick, 1978, 1981; Dick and Maisey, 1980; Wood, 1982). None of the marine sharks discovered at the Edinburgh Bearsden occur at or Glencartholm sites. The non-marine shark Tristychius arcuatus is present at Bearsden and in the Edinburgh area, but is absent at Glencartholm.

Stethacanthus is a shark from Bearsden which has a peculiar large toothed triangular 'brushorgan' attached to the dorsal spine. The Bearsden material is referred to S. altonensis, which was first described from the Mississippian of Ohio, based on a large series of unornamented spines, i.e. spines unaccompanied by the 'brush'. Complete specimens from the Bear Gulch Limestone of Montana allowed a fuller description (Williams, 1979, 1985; Lund, 1984). Wood (1982) suggested that the S. cf. altonensis from Bearsden may be synonymous with imperfect material Cladodus neilsoni from East Kilbride (Traquair, 1897b), but the name Stethacanthus is retained here.

Stethacanthus is sole genus of the Family Stethacanthidae, known from the Late Devonian (Famennian) to Late Carboniferous (Moscovian) mainly of North America (Cappetta *et al.*, 1993). The taxonomy of species of *Stethacanthus* is

Figure 9.28 Bearsden actinopterygians: (A) Mesopoma carricki Coates in lateral restoration (after Coates, 1993); (B) Frederichthys musadentatus Coates, a composite restoration after the holotype GLAHM V 8286 (from Coates, 1993). (Continued on p. 309.)

much disputed (Williams, 1979, 1985; Zangerl, 1981, 1984; Lund, 1984, 1985a, 1985b, 1986).

Several complete specimens of Stethacanthus were found at Bearsden, but the following description is based on the Bear Gulch specimens, which might not be the same species (Figure 9.29C). The Bearsden specimens have been briefly described by Wood (1982), but await detailed examination. They show details of braincase, gill-rakers and gut contents, never before seen in related material, and refute the interpretations of Zangerl (1981; M.Coates, pers. comm., 1992). The brush spine is a broad triangular object whose outer surface is unornamented and which articulates with the mobile 'brush'. It is much larger in the male. This is not a typical shark fin spine as it lacks an outer layer of orthodentine. The outer layer is probably trabecular dentine and it surrounds a conical central (pulp?) cavity (typical shark spines are like enlarged denticles in structure). Since the cavities in the trabecular dentine represent what is left of the pulp cavity, and since these extend to the spine's surface, the spines were probably covered by epidermis (Zangerl, 1981). The 'brush' consists of fine fibres radiating upward and backward from the postero-ventral corner of the spine. The well-preserved Bearsden specimens show that it was calcified, thick, apparent-

Figure 9.28 – *contd.* Bearsden actinopterygians: (C) *Melanecta annaea*, GLAHM V 8255, \times 2, photographed in UV light; (D) *Mesopoma carricki*, GLAHM V 8254, \times 1.5, photographed in toluene; (E) *Cheirodus* sp., GLAHM, \times 1.25 (Photos: courtesy of Hunterian Museum,, Glasgow).

ly inflexible and triangular in shape (Wood, 1982).

There is no trace of shagreen denticles like those that are normally found in the skin of some sharks, except for patches on the 'brushorgan' and head and along part of the lateral line (Zangerl, 1981). Stethacanthus has modified denticles covering the dorsal surface of the head and the upper edge of the 'brush'. These are monocuspid, and those of the dorsal fin have polygonal bases that fit together into a mosaic pattern. The belt of denticles is between seven and nine wide at the front tapering to four or five at the posterior end of the 'brush', and differs between male and female specimens. The male has a median row of denticles which are lengthened and straighter than the other denticles. These reach approximately 20 mm in height (Lund, 1974). The Bearsden specimens are described as increasing in size posteriorly in the male (Wood, 1982).

There is much variety in brush-organ shape, character of denticles and of the joints between the parts (and the brush-organ is often all that is preserved of a specimen). This could possibly be because more than one species is represented in the collections from North America.

The males were larger and had claspers. The pectoral fins were typical of the Symmoriida, and made up of two parts, a triangular 'metaptery-gium' followed by a long, jointed free axial whip (Figure 9.29). This axial whip extends backwards well beyond the pelvic fins in the Bearsden male. Wood (1982) suggested that it could have been used to grip the female during copulation.

Wood (1982) described a Bearsden specimen of a dorsal spine and basal plate in articulation identical with that of the 'primitive' Upper Devonian *Cladoselache*. Maisey (1977a) suggested that the unornamented dorsal spine of *Cladoselache* was deeply inserted, but Wood suggests that it might have been shallowly based like that seen in the life position in the Bearsden shark. Both species differ from most sharks in having the dorsal fin completely covered by epidermis (Zangerl, 1981).

Tristychius is a hybodont with fusiform body and relatively large fins. Not enough is known to group the Palaeozoic hybodonts adequately into families (Dick, 1978; Zangerl, 1981, p. 56). *Onychoselache traquairi* is presumably that described by Wood (1982) as 'a second shark species'; 125 mm long, with small cladodont teeth and a series of radials above the vertebral column.

Two Bearsden specimens of the first complete fossil bradyodont, Deltoptychius sp., to have been found in Britain await description (Figure 9.29B). They show how five separately named fossil fragments fit together to form one animal and that the eyes of Deltoptychius had previously been restored in entirely the wrong part of the head (M. Coates, pers. comm., 1992). Deltoptychius is the only genus of the Family Deltoptychiidae, defined as chimaeroids in which the headshield is fused into a single plate bearing the supraorbital sensory canals. Incomplete material of D. armigerus is known from several Scottish Early Carboniferous localities (Glencartholm, Ardross Castle and Abden; q.v.).

Interpretation

The shales of the Manse Burn Formation may have been deposited in conditions of varying salinity and oxygenation. The Shrimp Member, which contains the fishes and many crustaceans, shows evidence of sequential marine and nonmarine environments, subject to seasonal fluctuations (Coates, 1993). The four marine communities proposed by Schram (1981) at Glencartholm occur together, indicating a broader range of ecological niches at Bearsden (Wood, 1982).

The 'brush-organ' is one of the strangest features of Stethacanthus. Dorsally, the 'brush' forms a platform that bears many dermal denticles (Zangerl, 1981). Lund (1974) misinterpreted this three-dimensional pectoral spine assemblage as a flat first dorsal fin. Williams (1979) reexamined the Bear Gulch specimens and noted the three-dimensional nature of what is now preserved flattened. The 'brush' was vertically hinged upon the spine. Williams (1979) interpreted the function of the brush-organ complex as being for sexual display, rather than locomotion, as Lund (1974) had thought. The male brush and spine are larger than the female and have a bigger platform with larger denticles. The male has a median row of lengthened denticles, the female has its smallest brush denticles along the midline. Zangerl (1981) described how the jointing could be used to change the shape of the organ, perhaps for sexual display, or could possibly be used as a threat, because the top of the head and the denticled brush-organ could

Figure 9.29 Bearsden fishes: (A) the acanthodian *Acanthodes* sp., GLAHM unnumbered photo in toluene and figured as a restoration in lateral view; (B) *Deltoptychius*, GLAHM unnumbered photo in toluene at \times 0.3; (C) *Stetbacanthus* sp. (the 'Bearsden Shark') GLAHM V8246 at \times 0.25 (Photos: courtesy of Hunterian Museum,, Glasgow). (Continued on p. 312.)

Figure 9.29 – *contd.* Bearsden fishes: (D) reconstruction of the *Stethacanthus* skeleton (after Zangerl, 1981); (E) the Bearsden shark *Stethacanthus* sp., $c. \times 0.1$.

take on the appearance of an enormous toothstudded mouth. Wood (1982) suggested that the brush could have had a more violent purpose during foreplay, by comparison with some extant sharks that damage the females during sex.

Conclusion

The conservation value of the Bearsden site arises from its importance as one of the best Carboniferous fish sites in the world, and may be ranked alongside Glencartholm (q.v.) and Bear Gulch, Montana. Well-preserved fossil fishes of this age are universally rare, and the Bearsden sharks are the best-preserved cartilaginous fishes known from the Palaeozoic, matched only by species from the Bear Gulch Limestone in Montana. The collection also includes the first well preserved Carboniferous acanthodian braincase.

The controlled excavation of a small area of the fish-bearing units in the Manse Burn Formation in 1981 showed the wealth of the fauna, not only of fishes, but also of crustaceans, and the potential here for future excavation and