Chapter 9 British Carboniferous fossil fishes sites

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Introduction: palaeogeography 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 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 elastic 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) palaeogeog-raphy 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 Cement-stones 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 evapor-ites, 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 periodic 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 (ray-finned bony fishes) and chondrichthyans (sharks, shark-like forms and chimaeras), with rare acanthodians and sarcopterygians (lobe-finned 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 palaeoniscids 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 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 osteolepi-forms 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 species. Coelacanths were mainly slender 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 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 layer, 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 bradyo-dont 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).

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 elastic sequences of the Scottish Borders and from the mixed-facies Dinantian and Namurian of the Midland Valley of Scotland.

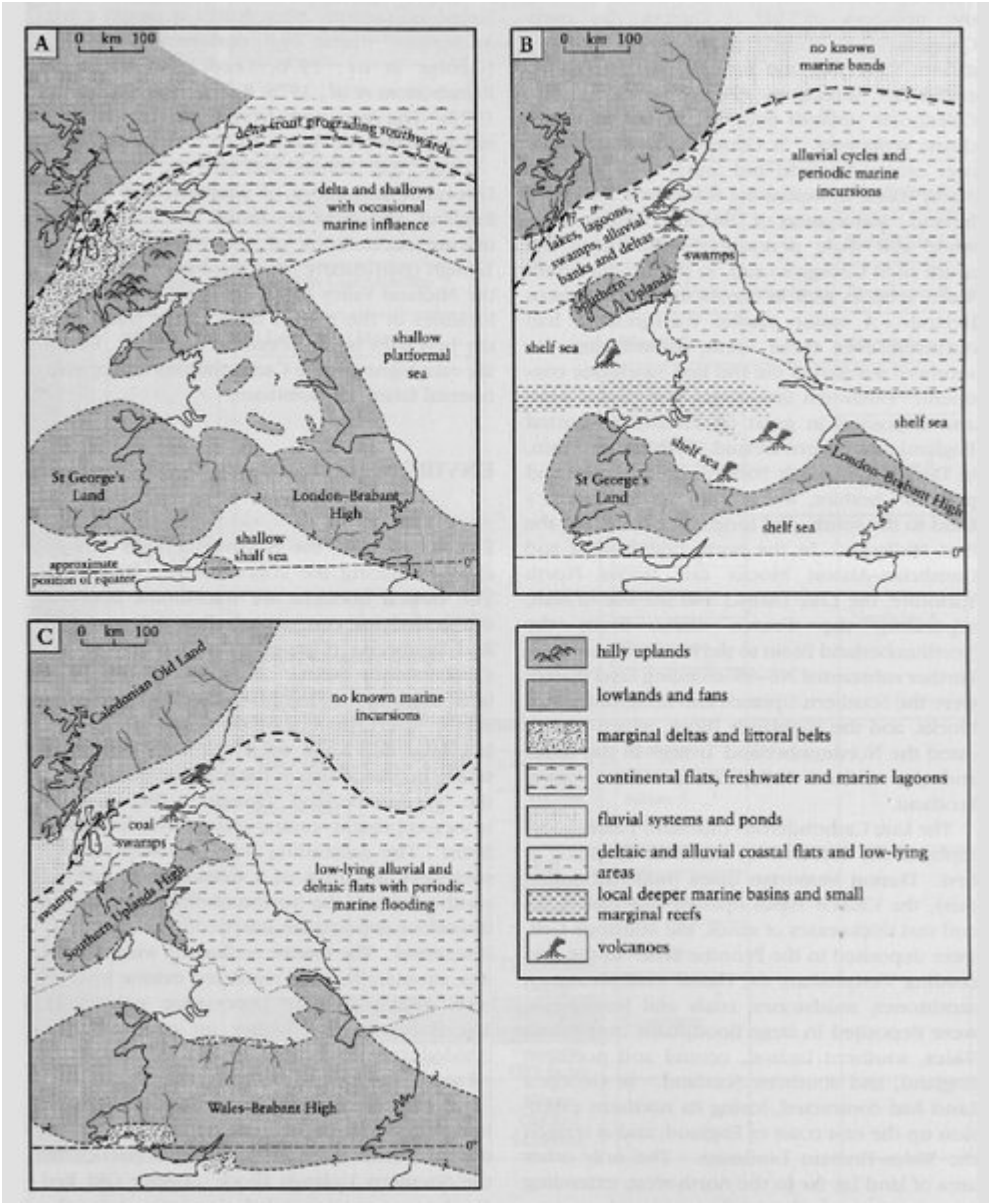
Nine examples are selected for the GCR coverage of British fossil fish sites:

1. Foulden, Borders [NS 921 552]. Courceyan.
2. Wardie, Mid Lothian [NT 245 771]. Courceyan-Holkerian.
3. Glencartholm, Borders [NY 376 795]. Asbian.
4. Cheese Bay, East Lothian [NT 492 856]. Asbian.
5. Inchkeith, Fife [NT 294 830] and [NT 294 822]. Asbian.
6. Ardross Castle, Fife [NO 511 006]. Brigantian.
7. Abden, Fife [NT 276 874]. Brigantian.
8. Steeplehouse Quarry, Derbyshire [SU 288 554]. Brigantian
9. Bearsden, Glasgow, Strathclyde [NS 5305 7325]. Pendleian, basal Namurian.

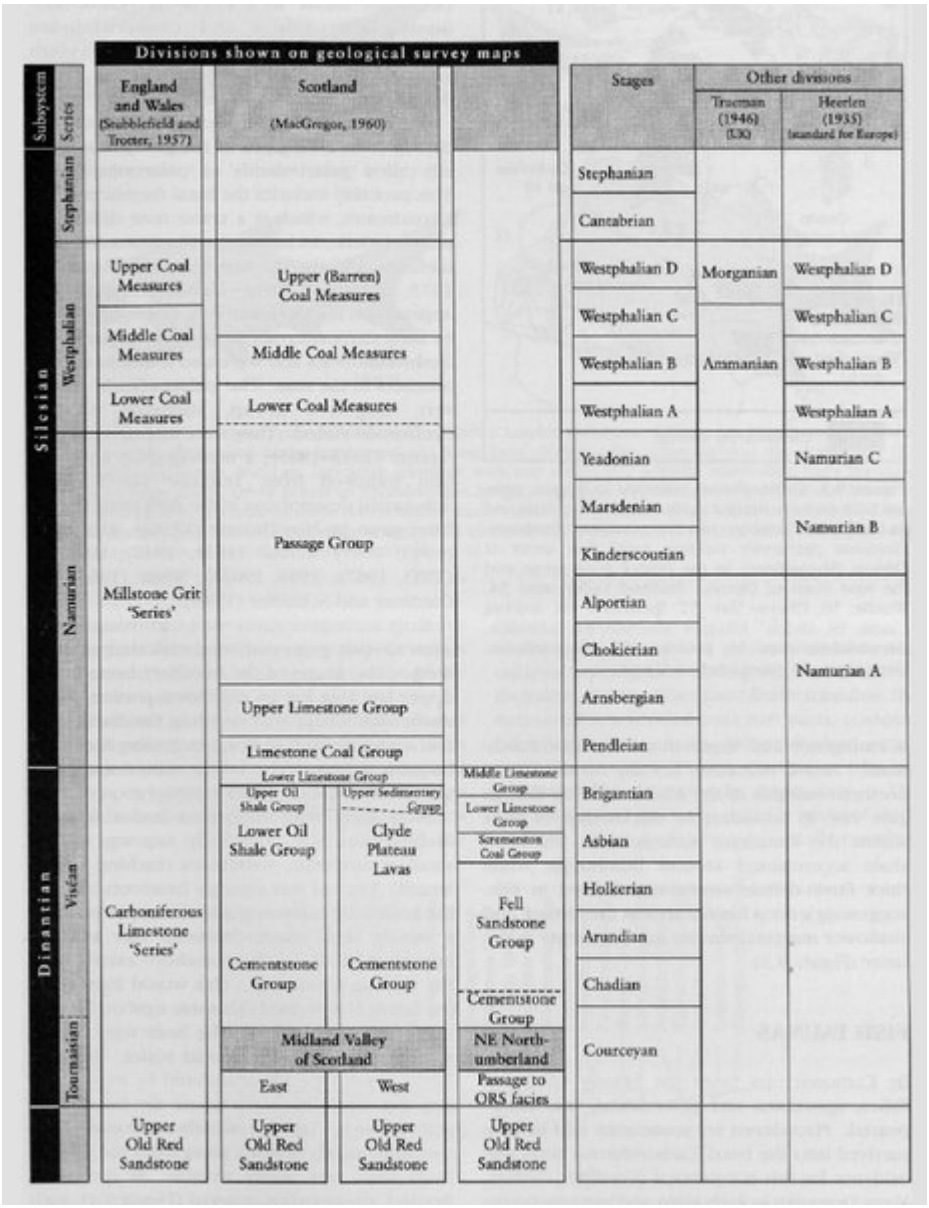
Each presents a fauna that is distinctive for its age, well preserved and perhaps offering further good collecting.

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.

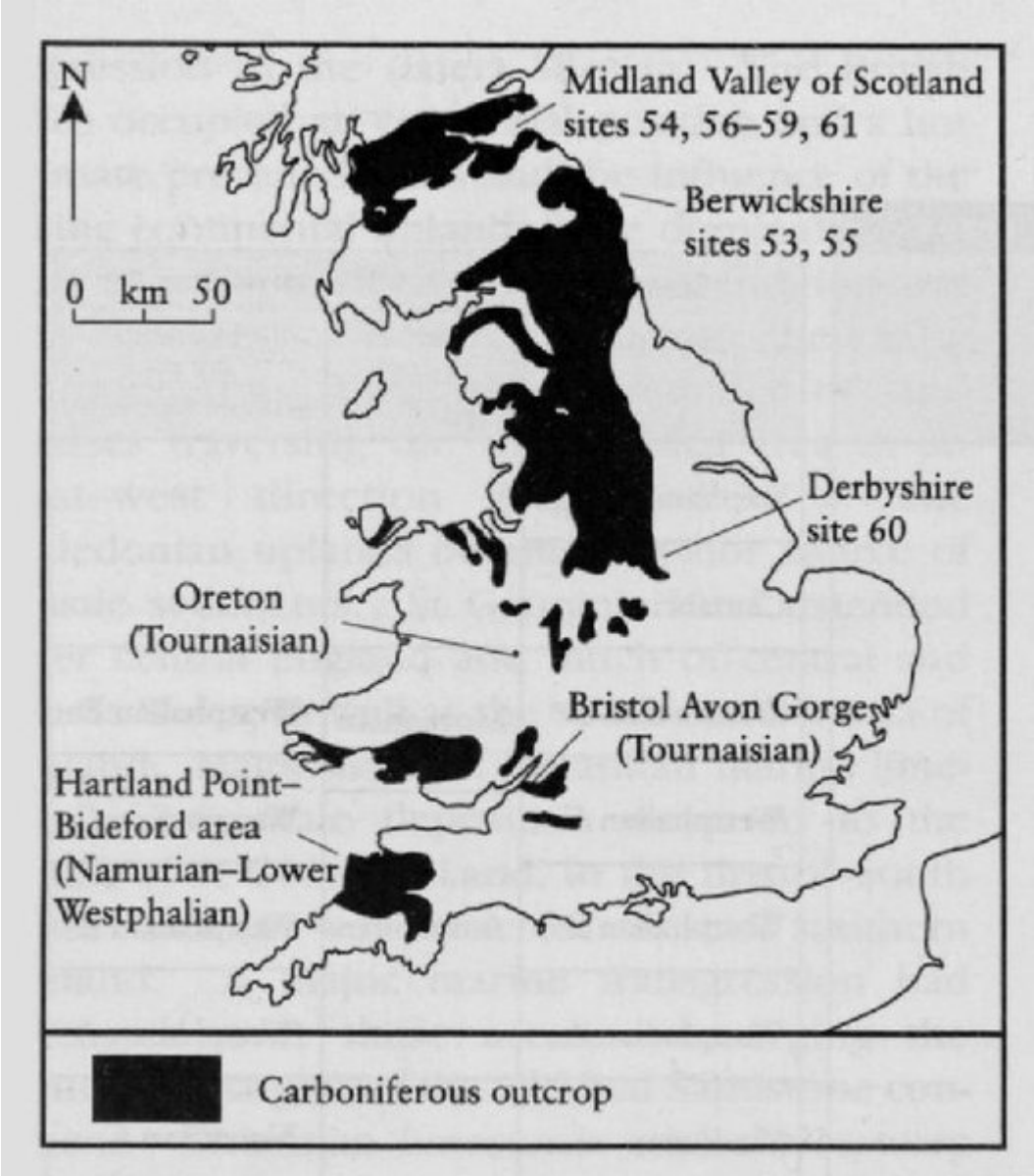
References



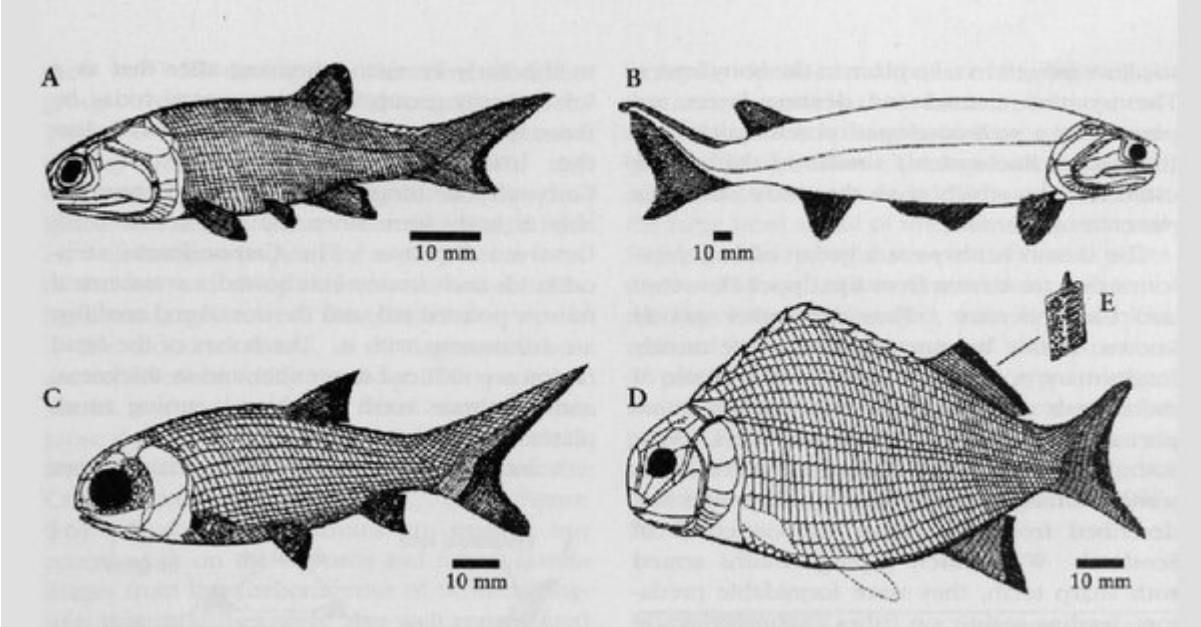
(Figure 9.1) Maps of Carboniferous palaeogeographies: (A) Late Tournaisian; and (B) Late Viséan; and (C) Namurian.



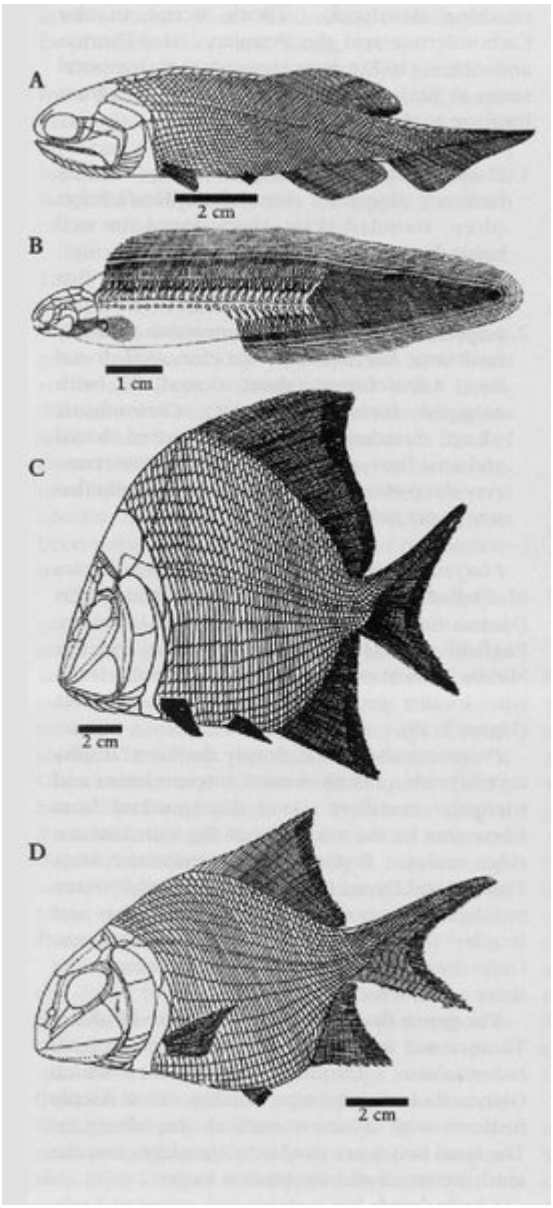
(Figure 9.2) Carboniferous stratigraphy and correlation (after MacGregor, 1960).



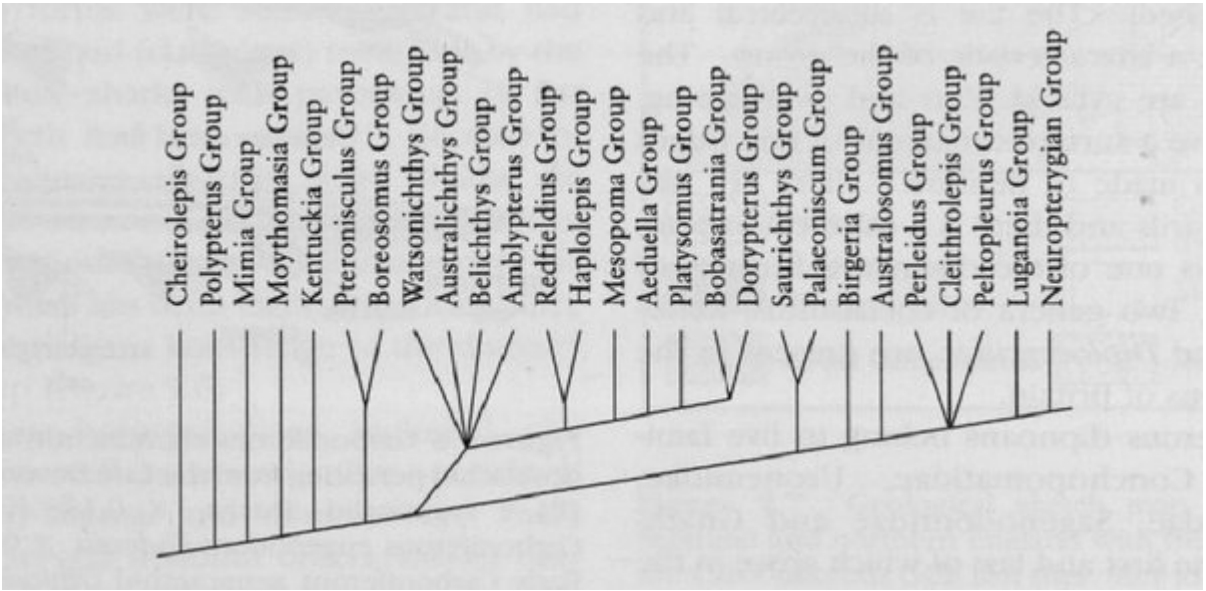
(Figure 9.3) Carboniferous outcrops in Britain: present GCR sites are limited to the south of Scotland and to the Border country and the south-east Pennines. Horizons previously yielding fossil fish occur at Oreton (Shropshire), in the Bristol Avon gorge and the west coast of Devon. Midland Valley sites: 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.



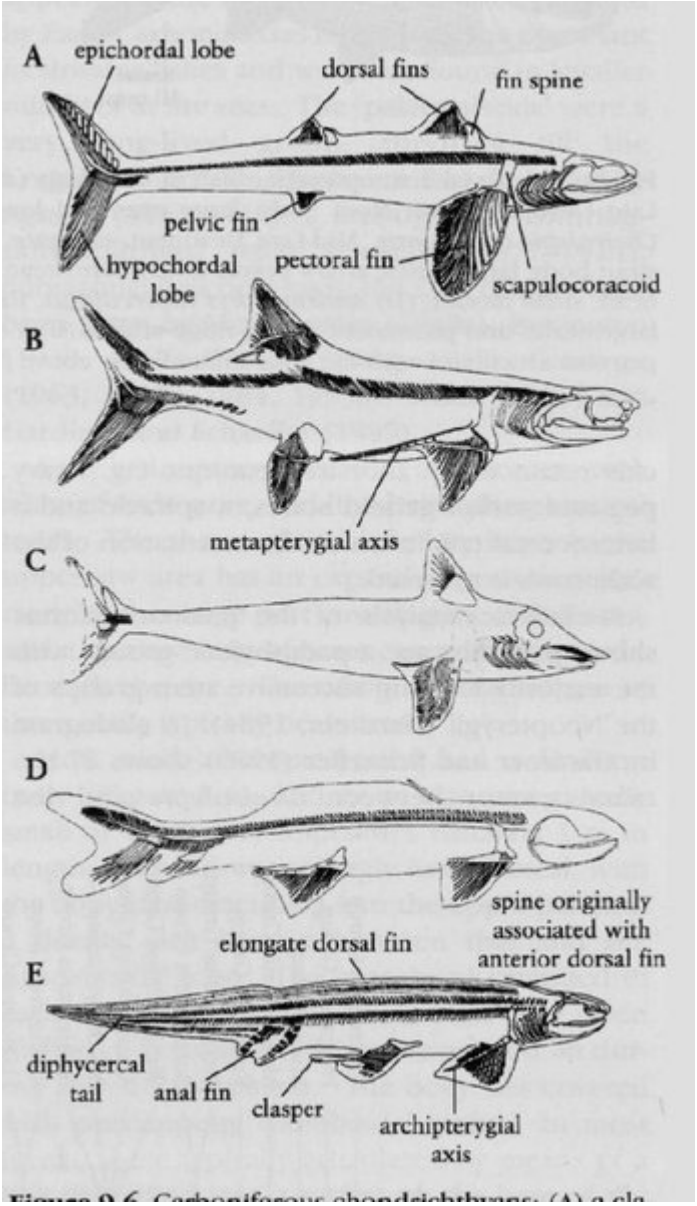
(Figure 9.4) Basal actinopterygian fish morphology (after Lauder and Liem, 1983). (A) Moythomasia nitida, Late Devonian, with stout body, large eyes and long jaws, dorsal ridge scales behind the dorsal fin; (B) Cheirolepis canadensis, Mid-Late Devonian, elongate with tiny scales; (C) Aduella blainvillei, Early Permian, stout body, large scales, arrow points to 'chondrostean hinge', large eyes, suborbital and preopercular bones in head, small mouth; (D) Andriochthys 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.



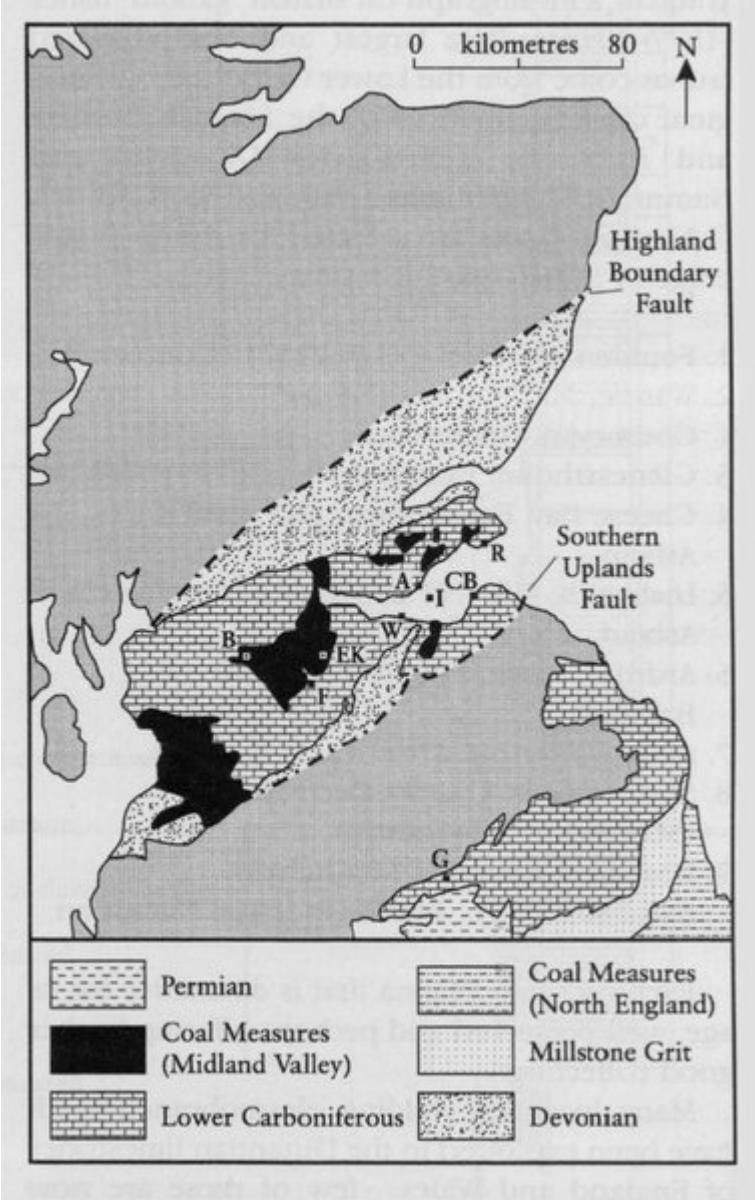
(Figure 9.19) Glencartholm actinopterygians: restorations in lateral view by Moy-Thomas and Bradley Dyne (1938). (A) Holurus parki Traquair; (B) the elongated Tarrasius problematicus Traquair, once thought to be a crossopterygian (after Moy-Thomas, 1937b); (C) Platysomus superbus Traquair; (D) Cheirodopsis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



(Figure 9.5) 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.



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



(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.