Fossil Fishes of Great Britain

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Chapter 10

British Permian fossil fishes sites

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INTRODUCTION: PALAEOGEOGRAPHY AND STRATIGRAPHY

Late Carboniferous earth movements and the closure of the Hercynian (mid-European) ocean greatly enlarged the northern continent of Laurussia and brought it into contact with the southern supercontinent, Gondwanaland. The British Isles area was affected by folding in the south-west of England and block-faulting elsewhere. During the early Permian, much of Britain was upland, with molasse troughs and desert basins extending from the southern North Sea–North German Basin across the eastern side of England, and passing across the Solway Firth area into the Irish Sea Basin (Harwood and Smith, 1986). The depositional areas touched onshore in Northern Ireland, the Hebrides, Morayshire, and in a thin strip from Bristol to east Devon. Early Permian sediments in Britain are red water-laid breccias and conglomerates, derived from neighbouring uplands. They pass up into typical thick dune sandstones, with desert lake and sabkha evaporites that can be correlated to the thick Rotliegendes deposits of mainland Europe. By the end of the Early Permian time most of the area of Britain had been reduced to a low rolling peneplain, generally an arid desert (Smith, 1992). At Kenilworth in the English Midlands the Lower Permian provides a single site for an amphibian–reptile association, which is discussed below. The Permian outcrops in Britain are shown in Figure 10.1.

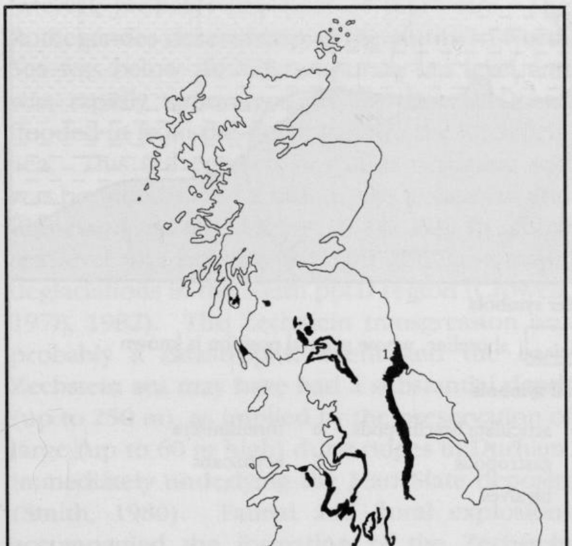

Figure 10.1 Map showing the outcrop of Permian rocks in Great Britain, with the Middridge GCR site indicated (1).

The Late Permian began with a major marine transgression of the Zechstein epicontinental sea over central Europe, the North Sea and the Irish Sea, and extending to the eastern margin of England (Figure 10.2). In north-east England the Zechstein deposits consist of five major sedimentary cycles, each commencing with shelf carbonates, and grading up into evaporites. The base of the first Zechstein cycle (Figure 10.3) in England is represented by the Marl Slate, the only unit to contain significant fish faunas.

While the sedimentary cycles provide a broad framework for lithostratigraphy, correlation elsewhere is difficult on account of the diversity and rapid variation of facies and the absence of fossils. Plants and palynomorphs provide some biostratigraphical control (Pattison *et al.*, 1973). Vertebrates occur in red beds around Elgin in Scotland (Benton and Spencer, 1995) where two GCR Permian reptile sites are designated; Middridge, Co. Durham, is the single proposed GCR Permian fish site. It is a singularly small record, though of great importance in offering a view of vertebrate communities existing during a time of stress in the history of both terrestrial and marine forms of life.

The Marl Slate is a thin, but laterally continuous, bed of bituminous silty shale in north-east England, traceable south from Durham as far as the equivalent Lower Permian Marl near Nottingham. It is correlated with the Kupferscheifer of Germany that contains a similar fauna, and is renowned for its rich fossil assemblage, including algae, ferns and actinopterygian fishes.

The Marl Slate lies immediately below the feature-forming Lower Magnesian Limestone. It rests unconformably upon the Early Permian Yellow Sands, which were dunes filling hollows in the sub-Permian surface, and it passes gradationally up into the Raisby Formation. Over much of the Zechstein Basin, the Marl Slate is less than 0.8 m thick, but in the north-east of England it commonly reaches 1–2 m. The formation is a silty sapropelic dolomite-shale containing sulphide minerals and showing consid-

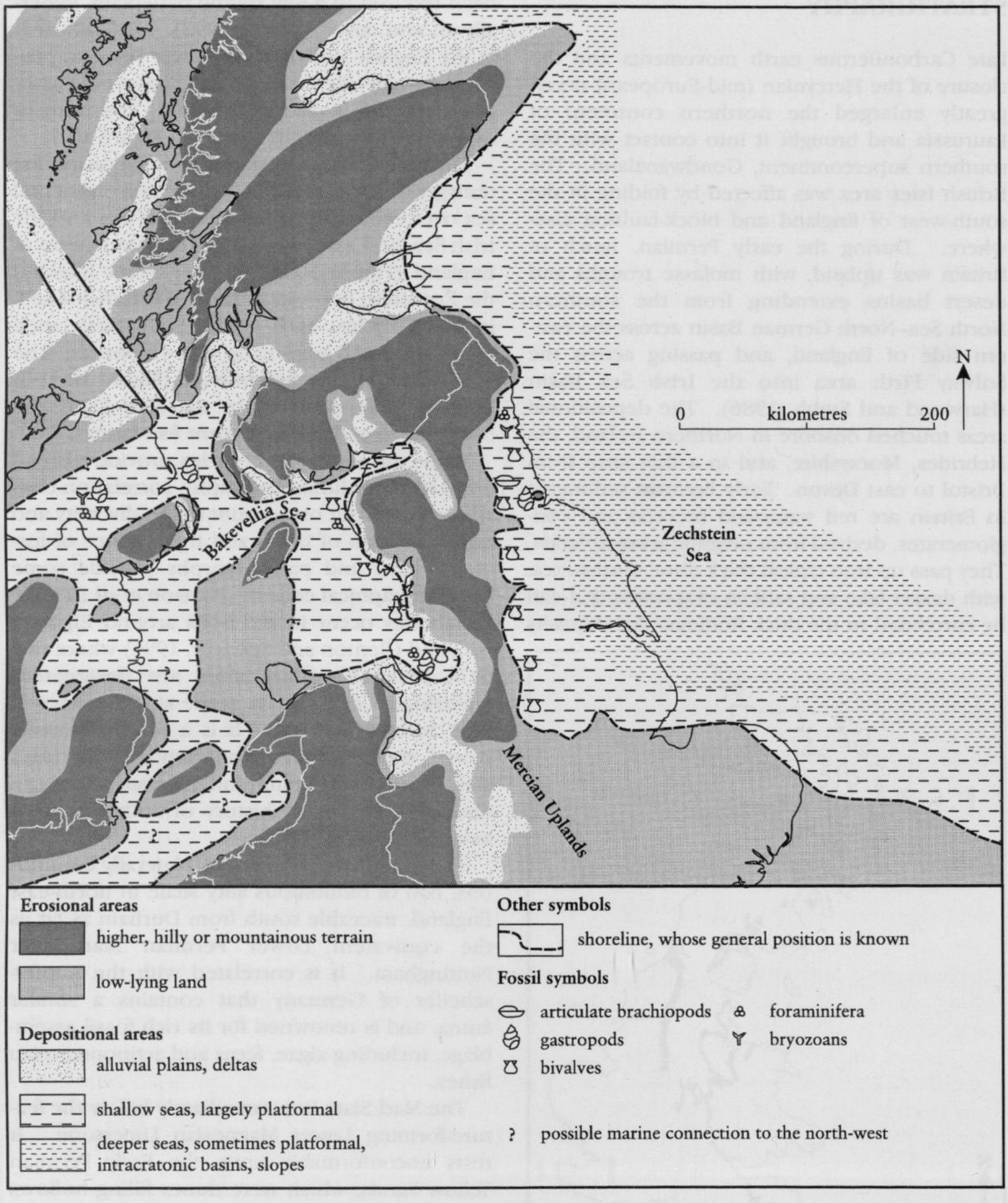

Figure 10.2 Palaeogeographical map showing Britain during the early part of the English Zechstein Cycle 1 and equivalents, *c.* 255 Ma (after D.B. Smith, in Cope *et al.*, 1992). Symbols indicate various invertebrate fossils.

Groups	Cycles	Yorkshire Province (outcrop area)	Durham Province (Co. Durham, east Tyne)	Yorkshire Province (East and North Yorkshire)	North Germany and Holland
Upper Permian Don Group	EZ1 b EZ1 a	Sprotbrough Member (b), Wetherby Member (a): Cadeby Formation Marl Slate	Hartlepool Anhydrite Ford Formation Raisby Formation Marl Slate (*Middridge site*)	Hayton Anhydrite Cadeby Formation Marl Slate	Werraanhydrit Zechsteinkalk Kuperschiefer
Lower Permian		basal Permian (yellow) sands and breccias	Yellow (basal Permian) sands and breccias	basal Permian sands and breccias	Rotliegendes (red beds)

Figure 10.3 Correlation of part of the Permian succession of northern England with that in North Germany and Holland (after Smith, 1989).

erable lithological variation. Generally speaking, quartz silt is abundant towards the base, and there are well-developed carbonate laminites in the upper part. There is no bioturbation, and the biota indicates deposition in an anoxic environment (Turner and Magaritz, 1986).

ENVIRONMENTS

The Marl Slate is the initial deposit of the Zechstein transgression (Smith, 1979, 1980, 1992), and represents a relatively short time interval, probably less than 20 000 years. The Rotliegendes desert basin of the southern North Sea was below the contemporary sea level and was rapidly submerged as the Boreal Ocean flooded in from the north to form the Zechstein Sea. This sea covered northern Germany and was bounded to the south by the Bohemian and Rhineland massifs (Figure 10.4). Rise in global sea level was possibly brought about by major deglaciations in the south polar region (Crowell, 1978, 1982). The Zechstein transgression was probably a catastrophic event and the early Zechstein sea may have had a substantial depth (up to 250 m), as implied by the preservation of large (up to 60 m high) dune ridges in Durham, immediately underlying the Marl Slate deposits (Smith, 1980). Faunal and floral explosions accompanied the formation of the Zechstein Sea, and this was then followed by a progressive impoverishment of the biota as the seas dwindled (Pattison *et al.*, 1973).

Deposition of the Marl Slate was seasonal (Brongersma-Sanders, 1965, 1971), which produced alternating carbonate-rich and organic-rich layers. The organic-rich layers are considered to be the result of seasonal phytoplankton blooms (Brongersma-Sanders, 1971). Removal of organic material depleted the water mass of essential nutrients, which caused a reduction in productivity, leading in turn led to a decrease in numbers of phytoplankton blooms, thus causing the greater separation of organic layers as seen in the laminites. It is likely that in some years no organic layer was formed.

Turner and Magaritz (1986) concluded that the anoxic events were of much shorter duration than 20 000 years, the first sapropelic event lasting 5000 years, the second only a few hundred years. The freshwater flooding peaks represent less than 1000 years, indicating that there were drastic and rapid changes taking place not only in the Zechstein Sea but also involving ocean-wide chemical cycles.

FISH FAUNAS

Permian fossil fish faunas are not well known, being very limited in number and distribution worldwide. No record of Permian agnathans has been discovered and the placoderm fishes had become extinct by Early Carboniferous time. It is not known to what extent this is related to the gathering of the continents to Pangaea, where extremely arid, hot climates prevailed in the north and glaciations covered much of the southern latitudes. Certainly there would have been a reduction in the variety of habitats that had existed in the Carboniferous times. The demise of the acanthodians also may have been similarly related to habitat reduction as well as to the rise of new competitive groups. The osteolepiform lobe-fins, too, died out in Early Permian time. The Chondrostei, however, more than survived, diversifying and giving rise to the holostean stock from which the teleosts later evolved. Coelacanth fishes are known from a few Permian rocks.

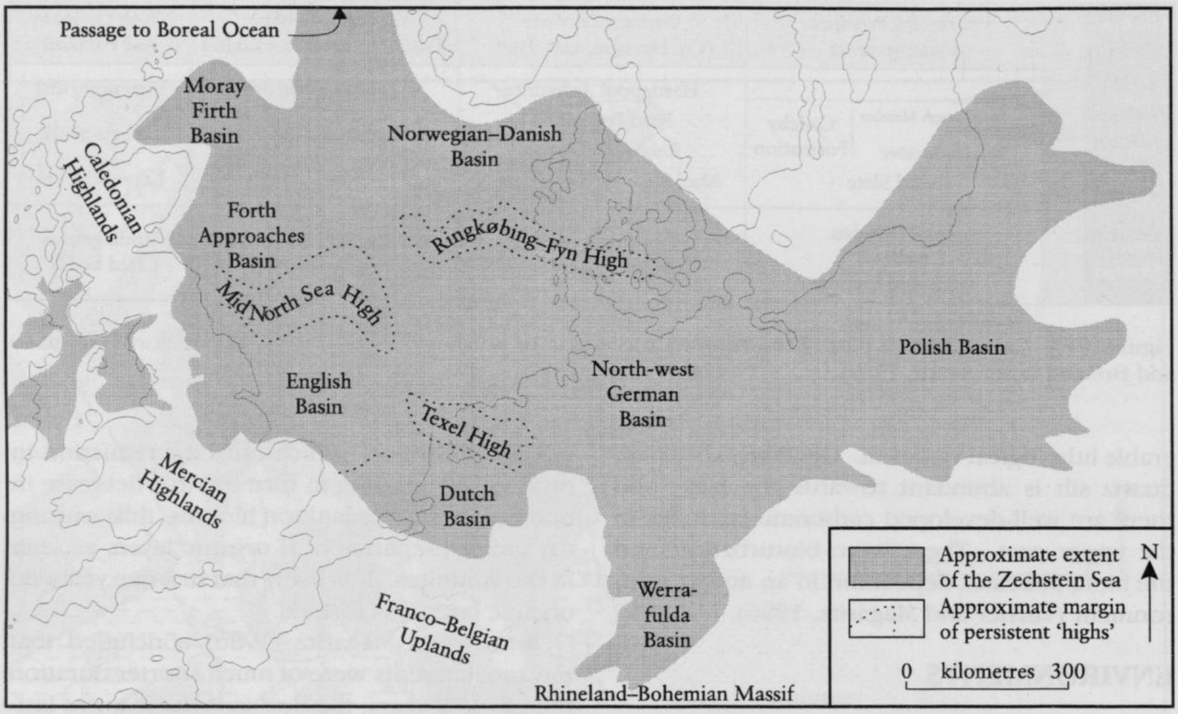

Figure 10.4 The Zechstein Sea, showing the major sub-basins and the land masses (after Smith, 1992). Sea depth was nowhere more than 30 m; the English Basin was less than 250 mm deep.

Diminishing numbers of chondrichthyans survived in both marine and freshwater environments; the elasmobranchs were soon to recover and continue a gradual expanding diversity from then on. During the Permian, cladoselachian sharks were replaced by hybodonts, which are considered to be ancestral to all modern sharks, skates and rays. Hybodontiform sharks are poorly known apart from isolated mineralized skeletal elements, and it is difficult to establish a classification (Maisey, 1982; Duffin, 1985). The pleuracanth sharks entered fresh waters, while the hybodonts continued successfully in the marine realm.

Permian fishes have been described from several parts of the world and from both marine and non-marine deposits. The relatively well-preserved and locally numerous examples from the Kuperschiefer of Germany attracted attention early in the 19th century (Schlotheim, 1820; Germar, 1842). Those in the Marl Slate of Co. Durham were discovered at about the same time and were described a little later (King, 1850). Very little research has been done recently. Permian fish faunas from other parts of the world have been recorded in North America (Hussakof, 1911), Greenland (Aldinger, 1937), Australia, Brazil and East Asia.

FISH SITES

Several fish sites have been reported in the Marl Slate of the Durham area, but the most productive fossil locality is Middridge, and it is selected as a potential GCR fish site.

MIDDRIDGE (NZ 249252) (POTENTIAL GCR SITE)

Highlights

Middridge in Durham is the relatively most productive British Permian fossil fish locality. It is the source of specimens of 13 species of fossil fishes, including 11 bony fishes, a chimaera and a coelacanth.

Introduction

Many museum specimens of fossil fish have been obtained in the past from Middridge Quarry. The flora and fauna from this quarry is the most prolific for the Marl Slate in Durham (Mills and Hull, 1976). The Late Permian Marl Slate exposed in a quarry and railway cutting 1 km SSW of Middridge, and close to East Thickley and Thickley Wood, has long been known for its rich fossil plant, invertebrate and vertebrate assemblages. There is another quarry, Old Towns Quarry (NZ 257246), about 1 km to the south-east, and closer to Newton Aycliffe than to Middridge. However, the fish site is almost certainly the former, sometimes termed Thickley Quarry. Extensive collections were made in the 19th century, and these include many specimens of fishes, as well as the 'amphibian' *Lepidotosaurus*, and the reptiles *Protorosaurus* and *Adelosaurus* (see Benton and Spencer, 1995, p. 21).

The sections of the quarry that lie near the railway line, and in the side of the railway cutting are now rather overgrown and the Marl Slate is no longer visible. However, a new excavation in the floor of the eastern end of the old quarry exposes a good section right through the Marl Slate and gives clear access to the fossiliferous beds (Mills and Hull, 1976, pp. 137–8; Bell *et al.*, 1979).

Description

As Benton and Spencer report (1995, p. 22): 'Middridge Quarry and railway cutting expose sections in the lower portion of the Upper Permian which rests unconformably on Carboniferous sediments. Typical sections taken in the new pit at Middridge show the following sequence (Bell *et al.* 1979, p. 445):

	Thickness (m)
Lower Magnesian Limestone	4 +
Marl Slate	2.58–2.76
calcareous laminated siltstones and thin silty limestones	(1.47–1.60)
laminated limestone (upper invertebrate bed)	(0.02–0.03)
calcareous laminated siltstones and thin silty limestones	(1.09–1.13)
Basal Permian Breccia	
Calcareous breccia (lower invertebrate bed) with abundant *Lingula* in the top 0.02–0.03 m	0.38–0.42
– – – – – – – unconformity – – – – – –	
Lower Coal Measures	
Thin-bedded micaceous sandstones and shales	1.20

The new pit exposed the Basal Breccias (?Lower Permian) which may be equivalent to the breccias observed elsewhere in Durham, Yorkshire and North Nottinghamshire lying below the Lower Permian Yellow Sands (Smith *et al.* 1974; Smith 1989; Smith and Taylor 1992). The Yellow Sands are not seen at Middridge.

The Marl Slate is well represented, compared with the thicknesses of 0–3 m elsewhere in south Durham. It comprises a succession of rusty brown-weathering, thinly laminated calcareous siltstones and thin silty limestones rich in bituminous and other organic material. There is a thin, highly fossiliferous laminated limestone (upper invertebrate bed) just over 1 m above the base of the Marl Slate. Pyrite, galena and sphalerite occur as spherulitic aggregates, small veins and as a partial replacement of some fossils (Bell *et al.*, 1979).

Numerous fossils have been found in the Marl Slate at Middridge, in addition to the reptiles and amphibians [two reptile species and one amphibian?] (Pattison *et al.*, 1973; Bell *et al.*, 1979). These include 12 genera of plants (Thallophyta, Pteridophyta, Pteridospermae, Coniferales), as well as a wide selection of invertebrates (foraminifers, bryozoans, brachiopods, bivalves, nautiloids and ostracods) and fish. The fishes are represented by isolated scales and fragments, as well as by a few complete flattened specimens ... Some fish remains are found in coprolites deposited by other fishes or by tetrapod predators.'

Fauna

Osteichthyes: Sarcopterygii: Actinistia
Coelacanthus granulatus Agassiz, 1839
Osteichthyes: Actinopterygii: Palaeoniscidae
Acrolepis sedgwicki Agassiz, 1833
Reticulolepis (Acrolepis) exsculpta (Kurtze, 1839) Westoll, 1934
Palaeoniscus freieslebeni Blainville, 1818 (includes *P.comptus* (Agassiz, 1835) and *P. elegans* (Sedgwick, 1850))
P. longissimus Agassiz, 1835
P. macropthalmus Agassiz, 1835
Pygopterus humbolti Agassiz, 1833 (includes *Pygopterus mandibularis* Agassiz, 1844)
Osteichthyes: Actinopterygii: Platysomidae
Globulodus macrurus (Agassiz, 1835)
Platysomus gibbosus (Blainville, 1818) (including *Platysomus striatus* Agassiz, 1833)
Osteichthyes: Actinopterygii: Dorypteridae
Dorypterus hoffmani Germar, 1842
Osteichthyes: Actinopterygii: Semionotidae
Acentrophorus glaphyrus (Agassiz, 1835)

A. altus (Kirkby, 1862)
Chondrichthyes: Holocephali
Janassa bituminosa (Schlotheim, 1820)
Elasmobranchii
Wodnika striatula Münster, 1843

In addition to the fishes, reptiles and amphibians, invertebrates and vascular plants are numerous at Middridge (see Benton and Spencer, 1995, p. 22).

The fossil assemblage from the Marl Slate consists of diapsid reptiles and palaeoniscid fishes; the inarticulate brachiopod *Lingula* also occurs. The fishes are mainly fusiform palaeoniscids, such as *Palaeoniscus* and *Acrolepis*, and some deep-bodied palaeoniscids, such as *Platysomus*. Most palaeoniscids were small, with thick rhomboidal scales, and triangular dorsal and anal fins. The suborder appeared in the Devonian, became more numerous in the Carboniferous and extended into the Mesozoic.

The majority of Marl Slate 'palaeoniscid' early actinopterygians belong to the family Palaeoniscidae, which is known from the Devonian to the Permian. *Acrolepis* occurs in the Carboniferous of Scotland and the Permian of Durham, the Kupferschiefer of Germany and the Permian of Russia (Aldinger, 1937). *Acrolepis* is included in the '*Pteronisculus*' group of stem-group actinopterygians by Gardiner and Schaeffer (1989). *Acrolepis sedgwickii* is a well-preserved example of the genus (Gardiner and Schaeffer, 1989, fig. 3B) and *A. exsculpta* is distinguished by ornamented lepidotrichia, and was made a separate genus, *Reticulolepis*, by Westoll (1934).

Palaeoniscus is widespread in the Permian. It occurs in the Marl Slate, the Kupferschiefer, and the Permian of Russia and Greenland (Aldinger, 1937). The '*Palaeoniscum*' group of Gardiner and Schaeffer (1989) includes *Palaeoniscum* (sic) and some species of *Elonichthys* and *Cosmolepis* from the Carboniferous, and is probably paraphyletic. *Palaeoniscus freieslebeni* (Figure 10.5) is known from the Marl Slate and Kupferschiefer, plus the Permian of Russia and Greenland, and the Eotrias of Spitsbergen and Karroo of South Africa (Piveteau, 1966). In Germany it comprises about 90% of all fish finds in the Kupferschiefer (Schaumberg, 1978)

Platysomids include deep-bodied and laterally compressed forms. In modern fishes this shape is associated with life in quiet waters. The genus *Globulodus* is restricted to the Marl Slate and the Kupferschiefer. The proportions of its body are similar to *Mesolepis* from the Carboniferous. Its dentition indicates a diet mainly of shellfish. *Platysomus* is also known from the Carboniferous. The *Platysomus* group of Gardiner and Schaeffer (1989) includes several genera besides *Platysomus*, e.g. *Cheirodopsis* and *Amphicentrum*.

Dorypterus was a deep-bodied, laterally compressed fish and is known from the Upper Permian of Germany and Durham. The body is naked with a very long dorsal fin behind the head. The fins are similar to platysomids, but the skull is reduced and most of the scales and teeth are lost. It is the only known representative of the Order Dorypterida, whose affinities have not been determined (Schaeffer, 1973) and is known from a single species *D. hoffmani* that occurs in the Kupferschiefer and the Marl Slate. *Dorypterus hoffmani* was first described and named by Germar (1842) from a specimen from the Kupferschiefer of the Eisleben district, Germany. The first English examples were described by Hancock and Howse (1870a) from four specimens collected by J. Duff from the Marl Slate of Middridge in the 1860s and 1870s (Figure 10.6). These were redescribed by Gill (1925) and Westoll (1941).

Many families of Mesozoic fishes have neopterygian features, including the ancestral features of the teleosts. The earliest known neopterygian is *Acentrophorus*, which is distin-

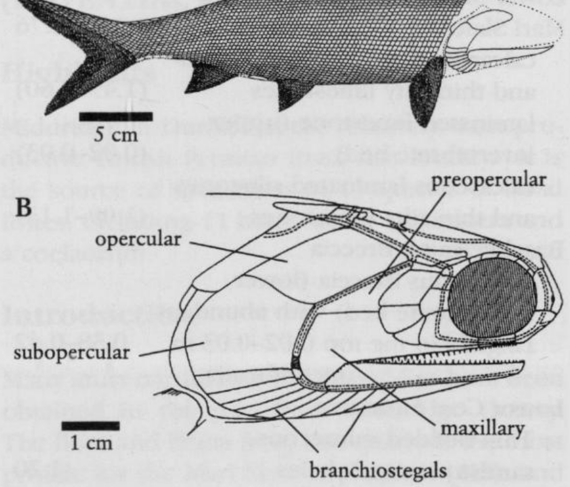

Figure 10.5 The palaeoniscid *Palaeoniscus freieslebeni* Blainville: (A) restored lateral view (after Aldinger, 1937); (B) reconstruction of the head (after Westoll, 1941).

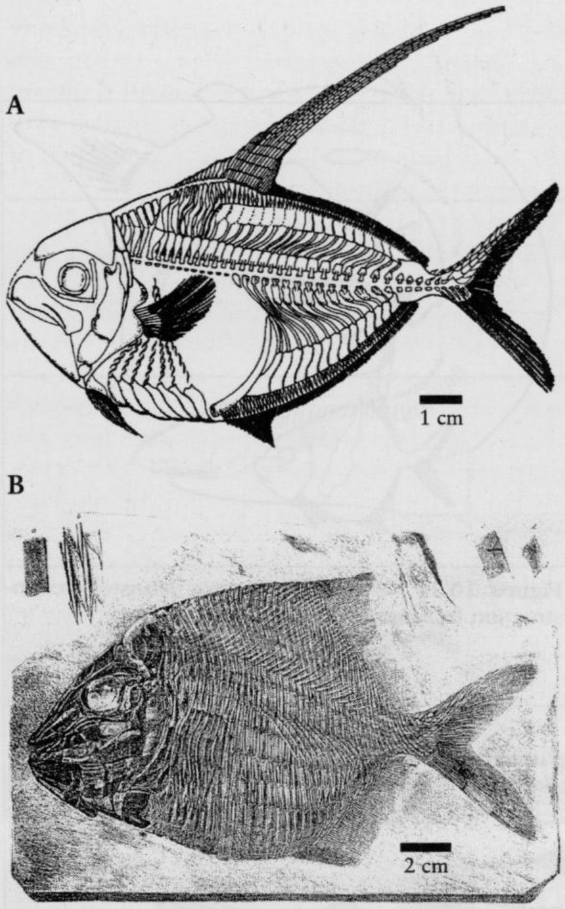

Figure 10.6 (A) *Dorypterus hoffmanni* Germar, restoration in lateral view (after Westoll, 1941); (B) *Platysomus striatus* Agassiz (from King, 1850).

guished from 'chondrosteans' by the presence of an interopercular and the separation of the maxilla from the opercular series (Schaeffer, 1973; Figure 10.7). *Acentrophorus* is classified among the Semionotidae, which includes many other genera from the Mesozoic, *Semionotus* from the Triassic and *Lepidotes* from the Upper Triassic and Lower Cretaceous. *Acentrophorus* (Figure 10.7) is small (about 7 cm long), and covered with overlapping cycloid ganoid scales. The tail is heterocercal, but the axial lobe is reduced to a single row of scales. (In later neopterygians it became reduced to a homocercal tail.) The jaw suspension is upright and teeth are present only at the front.

Chondrichthyans from the Marl Slate include holocephalians. The petalodontids are an extensive group of chondrichthyans that appear in the Lower Carboniferous and continue into the Permian. Very little is known of the body form of

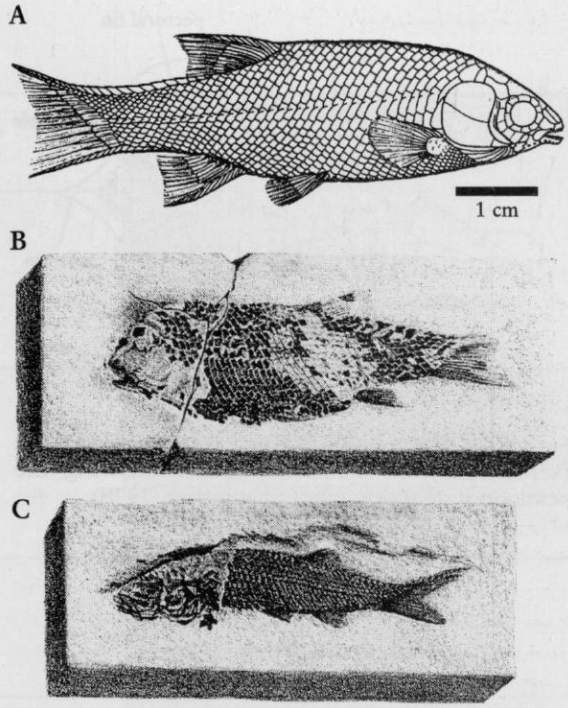

Figure 10.7 (A) the semionotid *Acentrophorus* restored in lateral view (after Gill, 1925), with specimens, (B), (C) from the Marl Slate, Middridge (natural size) (figured by King, 1850).

these soft-bodied fishes, but rare specimens of *Janassa* show that this petalodont had a dorsoventrally compressed body and large pectoral fins like a small modern-day ray (Hancock and Howse, 1870b). *Janassa bituminosa* (Figure 10.8) has a large rostral cartilage in the head, and some cartilages in the pectoral and pelvic fins are preserved. It has no fin spines. The tail tapers to a point, with a large epichordal lobe. This fish was stenophagous (i.e. feeding upon a limited or single type of food) and its stomach contents include broken brachiopod shells, crinoids, foraminifera and fragments of large crabs.

The coelacanth *Coelacanthus granulatus* (Figure 10.9) is the type species of this genus, and described by Schaumberg (1978) based only on German specimens. It was a small- to medium-sized fish, slender and with a narrow head, big eyes and deeply opening lower jaw. There were two dorsal fins, only the posterior of which was lobed, and the lepidotrichia of the anterior dorsal fin articulates directly with the internal element. The tail was typical for coelacanths and was three-lobed. The swim bladder was calcified.

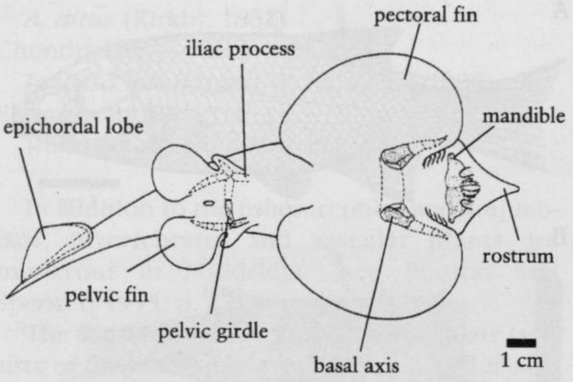

Figure 10.8 The holocephalian *Janassa bituminosa* (Schlotheim) in ventral view, and showing the petalodont dentition (after Shaumberg, 1978).

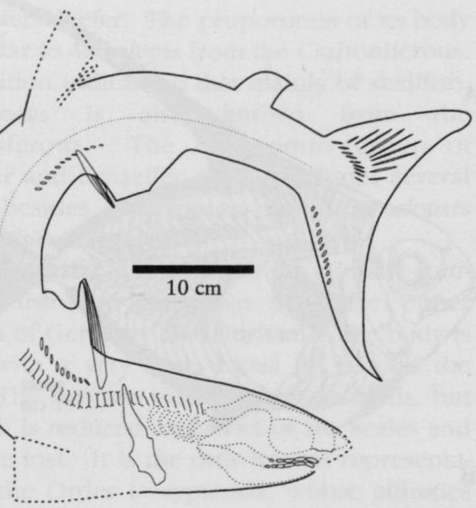

Figure 10.10 *Wodnika striatula* Munster, reconstruction by Schaumberg (1978).

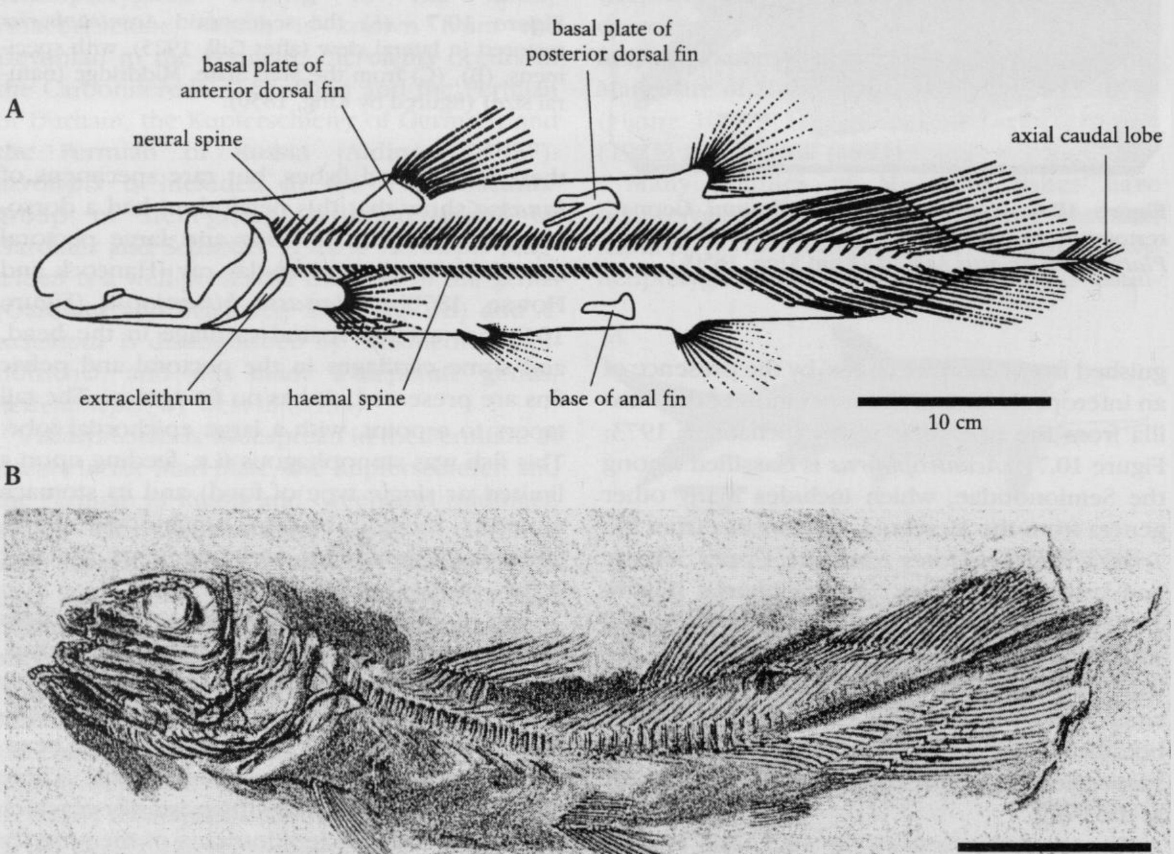

Figure 10.9 (A) *Coelacanthus granulatus* Agassiz, a restoration in lateral view (after Moy-Thomas and Westoll, 1935); (B) specimen from the Marl Slate, Middridge, figured by King (1850).

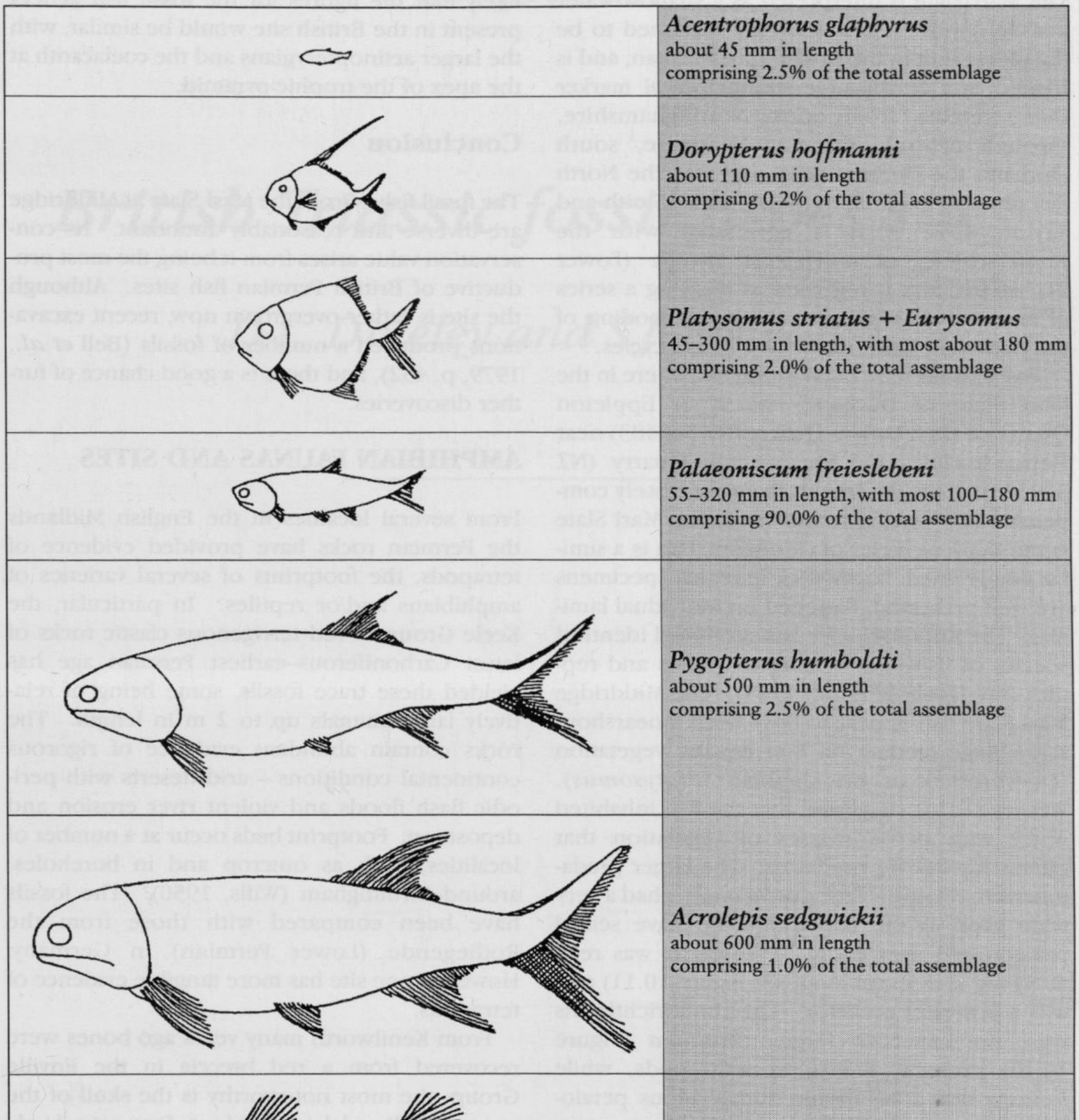

Figure 10.11 Components of the fossil fish fauna from the German Kupferschiefer, probably closely comparable to that at Middridge. Palaeoniscids make up more than 90% of the assemblage, while the larger actinopterygians and the coelacanth constitute less than 5% at the top of the trophic pyramid (after Schaumberg, 1978).

Interpretation

The Marl Slate is interpreted as a shallow-water marine deposit. It is generally reckoned to be the oldest unit in the British Late Permian, and is treated as a correlatable stratigraphical marker that stretches from north Nottinghamshire, through central and east Yorkshire, south Durham, the Durham coast and into the North Sea (Smith *et al.*, 1974; Smith, 1989; Smith and Taylor, 1992). It is correlated with the Kupferschiefer of north-west Europe (Lower Zechstein), and is regarded as marking a series of anoxic events prior to the main flooding of the Zechstein Basin in the first of five cycles.

Fossil fishes have been found elsewhere in the Marl Slate of Durham, namely at Eppleton Quarry or High Downs Quarry (NZ 360483) near Hetton-le-Hole, and Quarrington Quarry (NZ 329378). Outside Britain, the most closely comparable fish-bearing formation to the Marl Slate is the Kupferschiefer of Germany. This is a similar fine-grained, flaggy rock in which specimens are well preserved, flattened on individual laminae. The Kupferschiefer has produced identical species of fishes, invertebrates, plants and reptiles (see Haubold *et al.*, 1985). The Middridge Marl Slate fish appear to have been a nearshore assemblage feeding on soft aquatic vegetation (*Dorypterus*) or on shellfish (*Platysomus*). Westoll (1934) suggested that the fish inhabited water with dense masses of vegetation that offered shelter for predators. The larger predators were relatively few; *Coelacanthus* had a very wide gape to the jaw and could have seized palaeoniscid prey easily. *Pygopterus* was relatively big (i.e. 50 cm long; see Figure 10.11) and was a powerful predator. The chondrichthyans were not especially large. *Wodinka* (Figure 10.10) probably fed upon arthropods, while *Janassa* was a benthonic durophagous petalodont (Malzahn, 1986).

Schaumberg (1978) has made a study of the fossil fish assemblages of the German Kupferschiefer and estimated the percentages of the different genera present (Figure 10.11). It is likely that the figures for the fossil fish genera present in the British site would be similar, with the larger actinopterygians and the coelacanth at the apex of the trophic pyramid.

Conclusion

The fossil fishes from the Marl Slate at Middridge are diverse and reasonably abundant. Its conservation value arises from it being the most productive of British Permian fish sites. Although the site is rather overgrown now, recent excavations produced a number of fossils (Bell *et al.*, 1979, p. 452), and there is a good chance of further discoveries.

AMPHIBIAN FAUNAS AND SITES

From several localties in the English Midlands the Permian rocks have provided evidence of tetrapods, the footprints of several varieties of amphibians and/or reptiles. In particular, the Keele Group of red terrigenous clastic rocks of latest Carboniferous–earliest Permian age has yielded these trace fossils, some being of relatively large animals up to 2 m in length. The rocks contain abundant evidence of rigorous continental conditions – arid deserts with periodic flash floods and violent river erosion and deposition. Footprint beds occur at a number of localities, both as outcrop and in boreholes, around Birmingham (Wills, 1950). The fossils have been compared with those from the Rotliegende (Lower Permian) in Germany. However, one site has more tangible evidence of tetrapods.

From Kenilworth many years ago bones were recovered from a red breccia in the Enville Group; the most noteworthy is the skull of the stegocephalian labyrinthodont *Dasyceps bucklandi* Lloyd (von Huene, 1910) and the maxilla of the theromorph reptile *Oxyodon*.