J.N.C.C.

Fossil Fishes of Great Britain

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Chapter 11

British Triassic fossil fishes sites

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INTRODUCTION: PALAEOGEOGRAPHY AND STRATIGRAPHY

The continental geography of the British part of northern Pangaea established by the Permo-Carboniferous earth movements was broadly continued into the ensuing Triassic Period. Britain lay beyond the direct influence of the new Tethyan Ocean and only after mid-Triassic times were there occasional brief marine incursions (Figure 11.1). Continental red-bed siliciclastic sedimentation prevailed everywhere under a hot and generally arid climate. The topography was broadly divided between eroding uplands, the massifs of Palaeozoic rocks, and the fault-bounded basins that received sediment from the adjacent horsts (Audley-Charles, 1970, 1992). As Triassic time progressed, the areas of sedimentation enlarged by transgression and the proportion of sand grade and coarser material declined in favour of silt and clay grade fractions. Thus the British Triassic is lithologically roughly divisible into a lower sandstone facies and an upper mudstone facies. Certain basinal areas such as the Worcester Graben and the

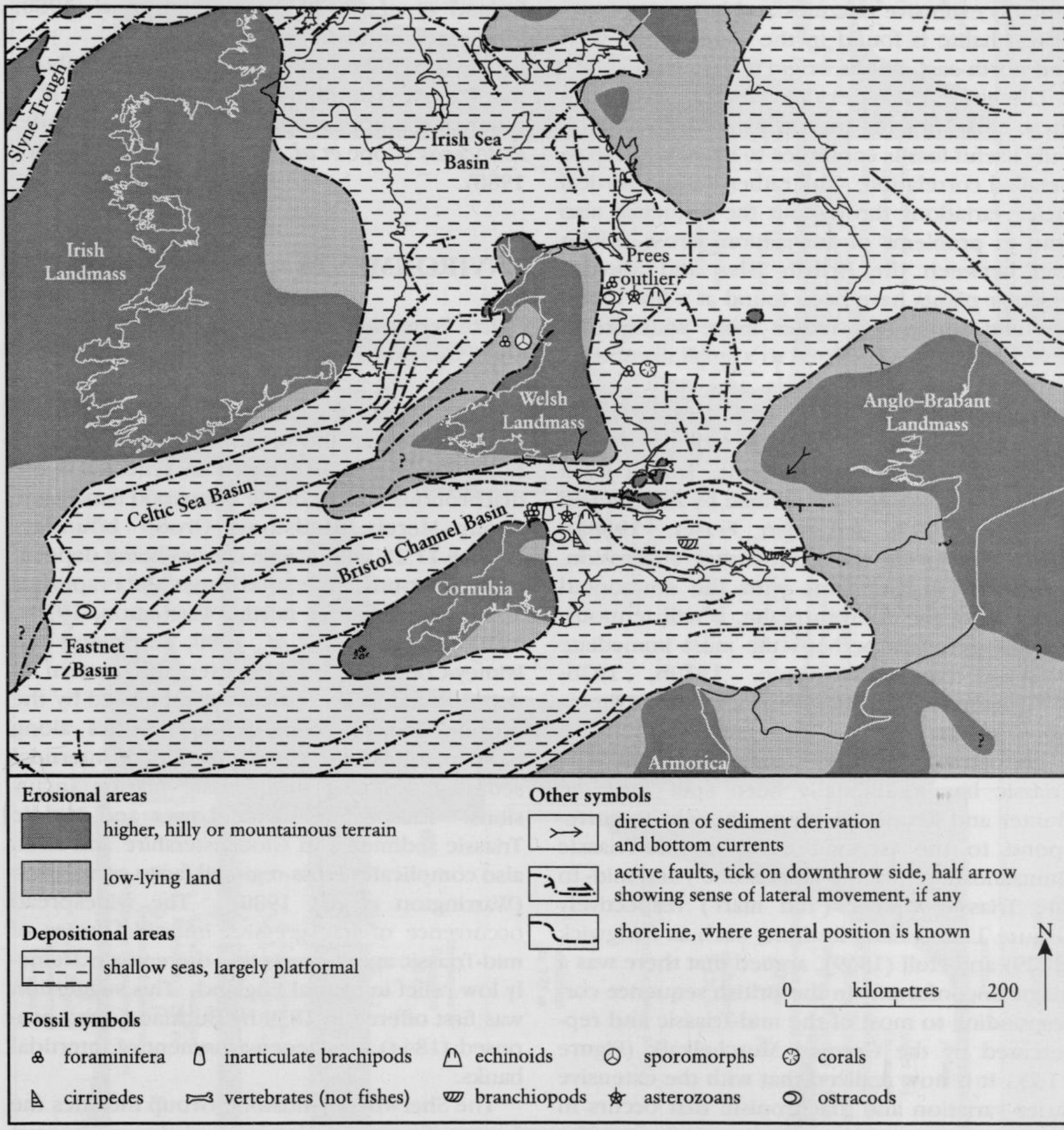

Figure 11.1 Palaeogeography of Britain in late Triassic time (after Bradshaw *et al.*, 1992). Connection with the Tethyan ocean lies via the east and south, with the Boreal ocean via the north.

Bristol and Cheshire Basins subsided at a more rapid pace than others, resulting in the establishment of an axial drainage system that flowed northwards from the Variscan Highlands. The region was part of a very broad dome undergoing fault collapse.

The bulk of Triassic sediment was transported by water, despite the evidence of protracted subaerial conditions. The rocks are the products of vigorous physical weathering, deposited as alluvial fans, braided streams and alluvial plains. Aeolian transport of the finer grades was probably a powerful and persistent influence. There are also extensive calcretes and lacustrine evaporites; halite is found in the south, north-west and north-east, but its origin is uncertain.

Life has left scant evidence of its presence in these environments and the lack of stratigraphically useful fossils continues to be a handicap to detailed correlation. The rather limited vertical facies variations throughout the sequence also lead to problems of correlation across Britain and between the British Isles and abroad. Vascular plants have been found at a few localities and spores are rather more widespread. Invertebrates are confined to a small number of arthropods at lower levels and only in the Rhaetian are marine molluscs, echinoids and other forms known. Triassic vertebrates are limited to a few fishes and tetrapods. Triassic fossil reptile sites have been described by Benton and Spencer (1995; see also Fraser, 1988a). Correlation with the continental succession, principally in Germany, with the ammonoid zonation of the Tethyan realm, is still tenuous. Palynology offers perhaps the most immediate promise (see Warrington, 1970b, 1976; Warrington *et al.*, 1980; Warrington and Ivimey-Cook, 1992).

Lithostratigraphical classification of the Triassic has traditionally been split into the Bunter and Keuper divisions, thought to correspond to the German early to mid-Triassic Buntsandstein ('mottled sandstone') and mid- to late Triassic Keuper ('red marl') respectively (Figure 11.2). Early authors, such as Sedgwick (1829) and Hull (1869), argued that there was a major unconformity in the British sequence corresponding to most of the mid-Triassic and represented by the German Muschelkalk (Figure 11.2). It is now realized that with the extensive facies variation and diachronism that occurs in the British Triassic, this matching is faulty. The Middle Triassic Muschelkalk facies of Germany is not present and modern usage avoids the terms Bunter and Keuper in favour of local formational names (Figure 11.2; Warrington *et al.*, 1980).

Palynological work by Warrington (1970a, 1970b) and Geiger and Hopping (1968) has shown that deposits of mid-Triassic age are present in the British sequence. The correlatives of the German Muschelkalk include brackish water to littoral marine facies and occur in the upper part of the Sherwood Sandstone Group and the lower parts of the Mercia Mudstone Group in central and northern parts of England (Geiger and Hopping, 1968; Warrington, 1974a, 1974b; Ireland *et al.*, 1978; Warrington *et al*, 1980; Warrington and Ivimey-Cook, 1992).

The top of the British Triassic is placed above the Penarth Group within the Blue Lias, at a point of the appearance of the first ammonite, *Psiloceras* (Cope *et al.*, 1980a; Warrington *et al.*, 1980).

ENVIRONMENTS

In late Permian and early Triassic times, renewed and extensional subsidence occurred within the fault-bounded graben and basins of central and southern England. The south-to-north regional palaeoslope and the proximal to distal depositional pattern that developed are reflected in the diachronous nature of the Sherwood Sandstone Group–Mercia Mudstone Group boundary (Figure 11.2), with coarse clastics being deposited in the south, while mudstones and evaporites accumulated farther north (Warrington, 1970a, 1970b; Warrington *et al.*, 1980; Warrington and Ivimey-Cook, 1992). However, this pattern of depositional facies is locally complicated by the introduction of coarse-grained clastics along basin margins and the deposition of intertidal sediments during mid-Triassic marine incursions. Lack of well-dated Lower and Middle Triassic sediments in Gloucestershire and Avon also complicates cross-regional facies correlation (Warrington *et al.*, 1980). The widespread occurrence of transgressive intertidal facies of mid-Triassic age suggests that there was extremely low relief in central England. This suggestion was first offered in 1839 by Buckland, who proposed (1844) a palaeoenvironment of intertidal banks.

The Sherwood Sandstone Group includes the former 'Bunter Sandstone' and the arenaceous (lower) parts of the former British 'Keuper'. Its

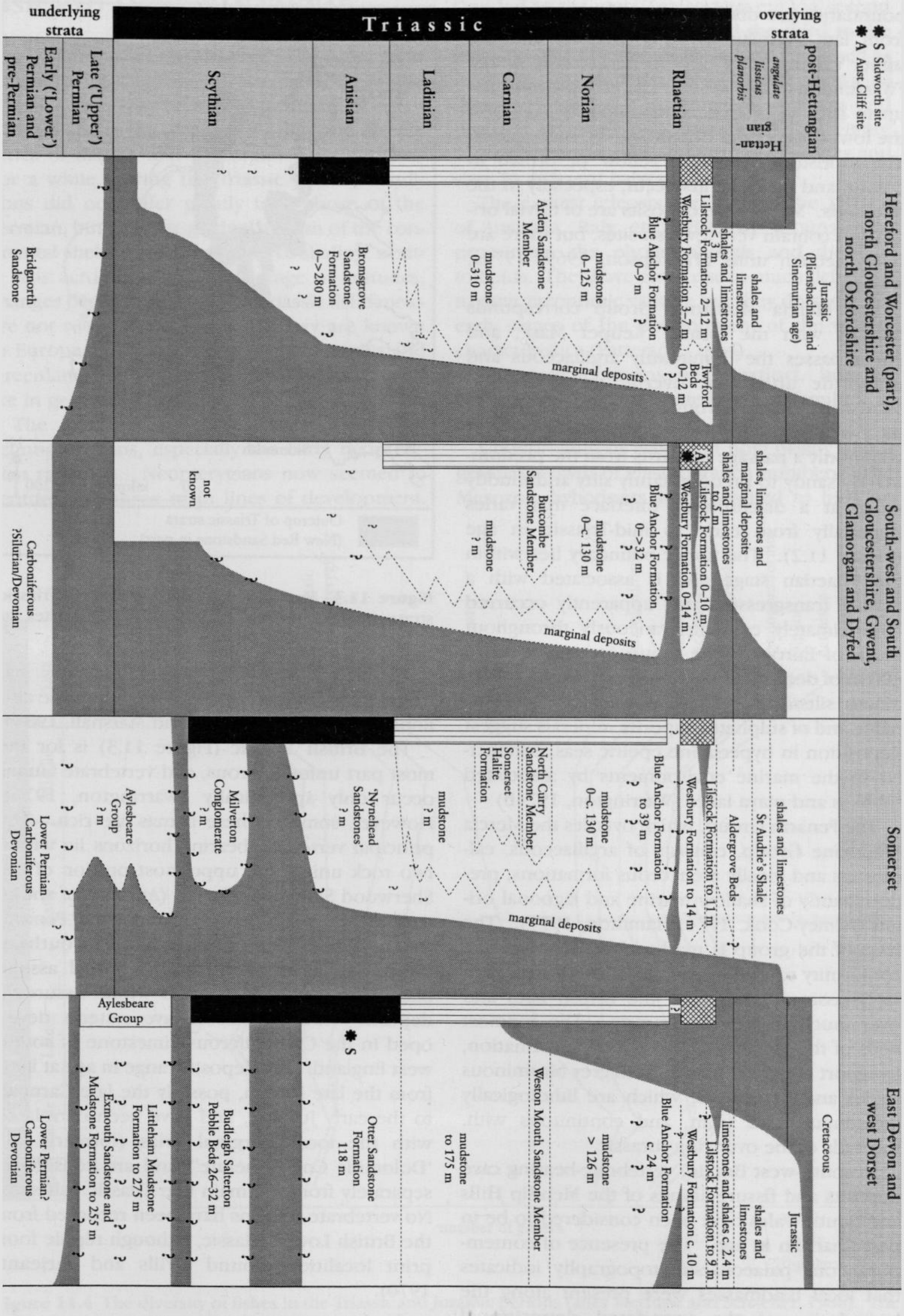

Figure 11.2 British Triassic stratigraphy (after Warrington *et al.*, 1980).

boundaries are diachronous, the lower varying from late Permian to early Triassic, and the upper varying from early to mid-Triassic in age (Warrington *et al.*, 1980). The group comprises up to 1500 m of arenaceous deposits that form the lower part of the British Triassic successions. The sandstones are red, yellow or brown in colour, and pebbly units occur, especially in the Midlands. Most of the deposits are of fluvial origin and contain very few fish sites, but there are many aeolian units (Thompson, 1969, 1970a, 1970b).

The Mercia Mudstone Group corresponds broadly with the former 'Keuper Marl', and encompasses the dominantly argillaceous and evaporitic units that overlie the Sherwood Sandstone Group throughout much of Britain. Its lower boundary may be sharp, but there is commonly a passage upwards from the predominantly sandy to predominantly silty and muddy facies at a diachronous interface that varies regionally from early to mid-Triassic in age (Figure 11.2). The upper boundary lies within the Rhaetian stage and is associated with a marine transgression that apparently occurred approximately contemporaneously throughout much of Europe. The group comprises up to 400 m of dominantly red mudstones with subordinate siltstones. Extensive developments of halite and of sulphate evaporite minerals suggest deposition in hypersaline epeiric seas, connected to the marine environments by associated sabhkas and playa lakes (Warrington, 1974b).

The Penarth Group, which overlies the Mercia Mudstone Group, consists of argillaceous, calcareous and locally arenaceous formations, predominantly of shallow marine and lagoonal origin (Ivimey-Cook, 1974; Hamilton, 1977). The base of the group is marked by a regional disconformity caused by the cessation of continental Triassic deposition in the British Isles and over much of western Europe. The topmost beds of the Penarth Group (Lilstock Formation, Langport Member) pass up into grey bituminous shales and limestones, which are lithologically indistinguishable from, and continuous with, the beds of the overlying Jurassic.

In south-west Britain, vertebrate-bearing cave deposits and fissure-fillings of the Mendip Hills and South Wales have been considered to be in part Rhaetian in age. The presence of contemporaneous palaeokarstic topography indicates that local landmasses were present along the boundaries of the inundated depositional troughs (Warrington *et al.*, 1980; Whiteside and Robinson, 1983; Whiteside and Marshall, 1985).

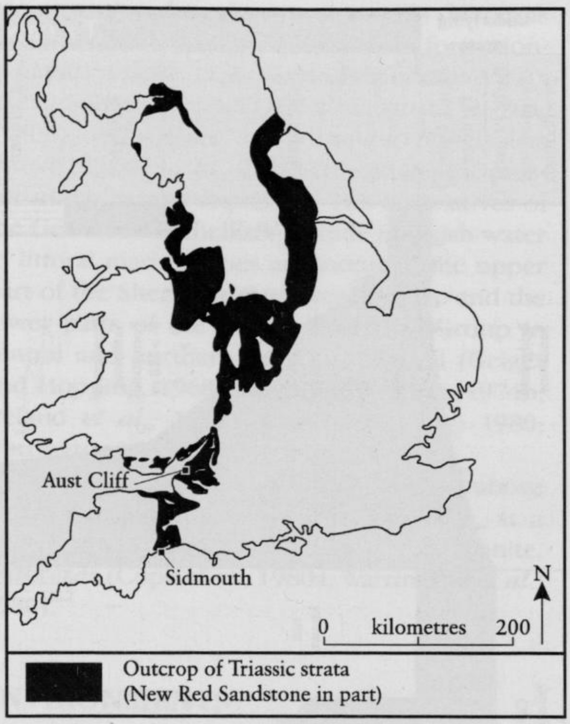

Figure 11.3 Map showing main outcrop of Triassic strata in England and Wales, with GCR sites at Sidmouth and Aust Cliff indicated.

The British Triassic (Figure 11.3) is for the most part unfossiliferous, and vertebrate faunas occur only sporadically (Warrington, 1976). However, some of these faunas are rich. The principal vertebrate-bearing horizons lie within two rock units: the uppermost portion of the Sherwood Sandstone Group (Anisian) of south-west England and the Midlands; the Penarth Group (Rhaetian) of central and southern England. Some of the most unusual assemblages are those which occur within fissure-fill deposits within fossilised cave systems developed in the Carboniferous Limestone of south-west England. The deposits range in age at least from the late Norian, possibly the late Carnian, to the early Jurassic, and have been correlated with the local marginal Trias (formerly the 'Dolomitic Conglomerate') and are considered separately from the main late Triassic fish sites. No vertebrate remains have been recorded from the British Lower Triassic, although reptile footprint localities abound (Wills and Sarjeant, 1970).

FISH AND AMPHIBIAN FAUNAS

The beginnings of the Mesozoic–Cenozoic great expansion of the fishes are to be seen in the Triassic. They may be related to the break-up of Pangaea and to the creation of a new and diverse series of marine and freshwater environments. For a while, during the Triassic period, conditions did not differ greatly from those of the Permian, but with the gradual growth of the continental shelves and the spread of shallow neritic seas across the widening range of latitudes, changes began to take effect. Triassic fish faunas are not relatively widespread. They are known in Europe and Spitsbergen, North America and Greenland, Madagascar, China and Australia and are in general all similar.

The greatest expansion was amongst the actinopterygians, especially the early neopterygian radiation. Neopterygians now seemed to venture into three main lines of development. One led to the gars (*Lepisosteus* etc.), a second to the bowfins (*Amia* etc.) and the third to the teleosts. The first two of these have remained as minor groups, but the teleosts have grown to dominate over all the others in numbers and diversity (McCune and Schaeffer, 1986; Figure 11.4) They acquired a wide range of shapes and sizes in different habitats.

The earliest teleosts appeared in the Triassic of Australia, Italy, etc., with two groups most prominent, the pholidophorids and the leptolepids. They have given rise to much debate as to their taxonomic validity, but they do show the early stages of the development of the teleost characteristics (Patterson, 1964).

The osteolepiforms were extinct, but the coelacanths are represented by two families, as are the lungfishes (Dipnoi).

Chondrichthyan evolution now began with a gradual growth of elasmobranch numbers. The Mesozoic hybodonts were adapted to feed on

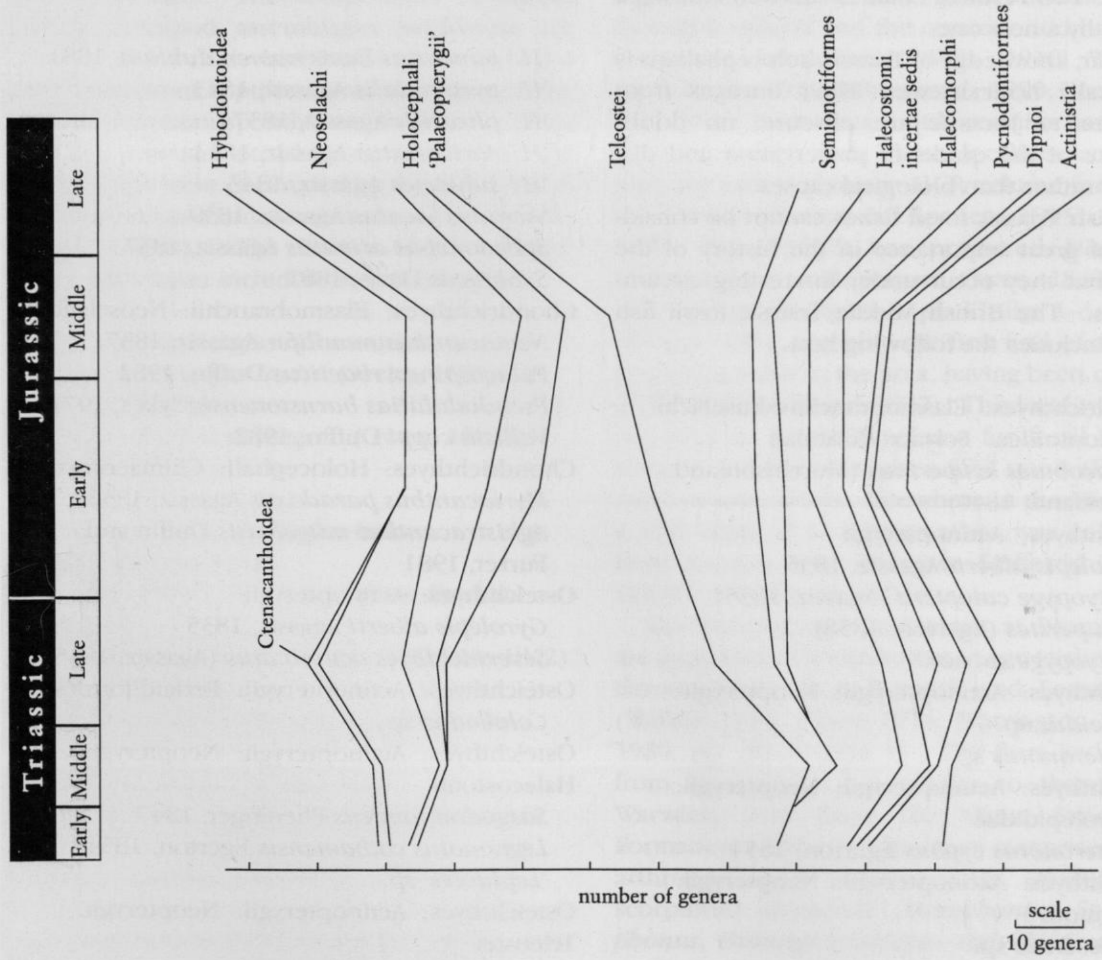

Figure 11.4 The diversity of fishes in the Triassic and Jurassic periods (after McCune and Schaeffer, 1986). The width of each band at the middle of a division reflects the number of genera known from that division.

large, active invertebrates, since they had sharp teeth for biting at the front of their jaws, and blunt crushing teeth at the rear. During the Jurassic, the hybodonts gave rise to modern sharks, with biting teeth, and the skates and rays, which are mainly adapted to feed on benthic invertebrates. During the Mesozoic Era, some hybodonts developed a durophagous dentition (flat teeth for coping with shelled invertebrates etc.), and some elasmobranchs in the Palaeozoic had an early form of this type of dentition with the development of broad-crowned teeth.

The modern sharks and rays are grouped within the neoselachians, which also includes the extinct palaeospinacids, orthacodontids and anacoracids. They are defined by the possession of calcified vertebrae, subterminal hyostylic jaws, U-shaped scapulocoracoid, and only one or two basal segments between the pelvic basipterygium and the clasper shaft cartilage in males (Duffin and Ward, 1983b; Reif, 1977; Maisey, 1975). Two Permian families survived and were joined by a new one.

So far, knowledge of Triassic holocephalians is practically nonexistent. Their lineages from Permian to Jurassic are obscure, no doubt because of the quirks of preservation and discovery rather than biological causes.

British Triassic fossil fishes cannot be considered of great importance in the history of the class, but they occur under interesting circumstances. The British Middle Triassic fossil fish fauna includes the following taxa.

Chondrichthyes: Elasmobranchii: Euselachi: Hybodontoidea: Polyacrodontidae
- *Palaeobates keuperinus* (Murchison and Strickland, 1840)

Osteichthyes: Actinopterygii
- *Gyrolepis alberti* Agassiz, 1835
- *Dictyopyge catoptera* (Agassiz, 1835)
- *D. superstes* (Egerton, 1858)
- *Dictyopyge sp.* nov.

Osteichthyes: Actinopterygii: Neopterygii
- *Perleidus* sp.
- *Dipteronotus* sp.

Osteichthyes: Actinopterygii: Neopterygii: Cleithrolepididae
- *Dipteronotus cyphus* Egerton, 1854

Osteichthyes: Actinopterygii: Neopterygii: Ginglymodi
- *Lepisosteus* sp.

Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
- *'Semionotus' brodiei* Newton, 1887
- *Semionotus metcalfei* Swinnerton, 1928
- *Woodthorpea wilsoni* Swinnerton, 1925

Osteichthyes: Sarcopterygii: Dipnoi
- *Ceratodus laevissimus* Miall, 1878

The Late Triassic fish fauna includes the following taxa:

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea
- *Polyacrodus cloacinus* (Quenstedt, 1858)
- *Lissodus minimus* (Agassiz, 1839)
- *'Hybodus' minor* Agassiz, 1837
- *'H.' austiensis* Davis *nomen dubium*, 1881
- *'H.' cuspidatus* Agassiz, 1843
- *'H.' laeviusculus* Agassiz *nomen dubium*, 1837

The following are hybodonts reported as misidentifications (C. Duffin, pers. comm., 1996):

- *'H.' punctatus* Davis *nomen dubium*, 1881
- *'H.' pyramidalis* Agassiz, 1843
- *'H.' plicatilis* Agassiz, 1837
- *'H.' raricostatus* Agassiz, 1843
- *'H.' sublaevis* Agassiz, 1843
- *'Acrodus' acutus* Agassiz, 1839
- *Sphenonchus armatus* Agassiz, 1837
- *S. obtusus* Davis, 1881

Chondrichthyes: Elasmobranchii: Neoselachii
- *Nemacanthus monilifer* Agassiz, 1837
- *Palaeospinax rhaeticus* Duffin, 1982
- *Pseudodalatias barnstonensis* Sykes, 1971
- *Vallisia coppi* Duffin, 1982

Chondrichthyes: Holocephali: Chimaeriformes
- *Myriacanthus paradoxus* Agassiz, 1836
- *Agkistracanthus mitgelensis* Duffin and Furrer, 1981

Osteichthyes: Actinopterygii
- *Gyrolepis alberti* Agassiz, 1835
- *Severnichthyes acuminatus* (Agassiz, 1835)

Osteichthyes: Actinopterygii: Perleidiformes
- *Colobodus* sp.

Osteichthyes: Actinopterygii: Neopterygii: Halecostomi
- *Sargodon tomicus* Plieninger, 1847
- *Legnonotus cothamensis* Egerton, 1854
- *'Lepidotes' sp.*

Osteichthyes: Actinopterygii: Neopterygii: Teleostei
- *Pholidophorus higginsi* Egerton, 1854–1855

Osteichthyes: Sarcopterygii: Dipnoi:

Ceratodontidae
Ceratodus latissimus Agassiz, 1839

Newton (1887) noted a number of fish specimens from the Upper Keuper (?Norian) in a quarry at Shrewly, Warwickshire, which he called *Semionotus brodiei*. However, in a comprehensive study of the Semionotidae of Europe, McCune (1986) declared '*S.*' *brodiei* Newton 1887 from the Upper Keuper near Shrewsbury to be *nomen dubium* on account of its poor preservation, and similarly that Swinnerton's (1928) single specimen of *S. metcalfei* is a *nomen dubium* though the specimen bears resemblance to *S. kapffi*. From the Bunter Sandstone (Anisian) near Kidderminster, White (1950c) described part of the trunk of a fish seeming to resemble the typical Triassic chondrostean *Perleidus*.

Fossil amphibians occur in the freshwater and terrestrial deposits of the Middle Triassic succession in Britain. The components of Middle Triassic tetrapod assemblages worldwide are similar, and include herbivorous, insectivorous and carnivorous reptiles, in association with the fish-eating temnospondyl amphibians. These faunas continued into the early part of the late Triassic, but were decimated by the late Carnian and late Norian extinction events (Benton, 1991, 1994a, 1994b). The British Middle Triassic amphibian fauna includes the following taxa:

'Temnospondyli': Mastodonsauridae
'*Mastodonsaurus lavisi*' (Seeley, 1876) *nomen dubium*
'*Mastodonsaurus jaegeri*' (Owen, 1842a) *nomen dubium*
Mastodonsaurus sp.
'Temnospondyli': Benthosuchidae
Eocyclotosaurus sp.
'Temnospondyli': Cyclotosaurinae *incertae sedis*
'*Cyclotosaurus pachygnathus*' (Owen, 1842) *nomen dubium*
'Temnospondyli': Capitosauridae *incertae sedis*
Capitosauridae *incertae sedis*
'Temnospondyli': Stenotosaurinae *incertae sedis*
Stenotosaurus stantonensis (Woodward, 1908)
'*Stenotosaurus (Cyclotosaurus) leptognathus*' (Owen, 1842) *nomen dubium*
indeterminate temnospondyl fragments

MID-TRIASSIC OF CENTRAL AND SOUTHERN ENGLAND

Numerous localities in the English Midlands and along the Devon coast have yielded fossil fish and amphibian remains of Mid-Triassic age. They are all derived from the uppermost part of the Sherwood Sandstone Group, which is known as the Bromsgrove Sandstone Formation in the Midlands, and the slightly younger Otter Sandstone Formation of the Devon coast.

There are several old quarries in the Bromsgrove Sandstone Formation (Anisian) of the Warwick area that have yielded fragmentary fish and amphibian remains, but only the Guy's Cliffe and Coton End sections are extant. A number of localities in Leamington and Warwick (e.g. Coton End, SP 290655; Leamington Old Quarry, SP 325666) have produced remains of the temnospondyl amphibians *Mastodonsaurus*, '*Cyclosaurus pachygnathus*' and '*C. leptognathus*' and of the palaeoniscoid fish *Gyrolepis alberti* and the ceratodontid lungfish *Ceratodus laevissimus* (Wills, 1910; Walker, 1969; Paton, 1974; Milner *et al.*, 1990; Benton *et al.*, 1994). Numerous reptile remains have also been recovered from these localities and the sites are included in the GCR volume for fossil reptile sites (Benton and Spencer, 1995). Guy's Cliffe (SP 293667) has produced *Mastodonsaurus* sp. (= M. *jaegeri*; Owen, 1842a, pp. 537–538, pl. 44, figs 4–6, pl. 37, figs 1–3; Miall, 1874, p. 433), probably the first find of a tetrapod to be made in the area, having been collected in 1823 (Buckland, 1837). This locality is also recorded in the GCR volume for fossil reptile remains and has been given SSSI status (Benton and Spencer, 1995). Elsewhere in the Midlands a fine skull of *C. leptognathus* was collected from Stanton, near Uttoxeter, Staffordshire; SK 126462; Woodward, 1904a).

The Bromsgrove Sandstones at Bromsgrove are approximately equivalent in age to the fossiliferous horizons at Warwick and Leamington (Walker 1969; Paton 1974; Warrington *et al.*, 1980, pp. 38–9, table 4). The flora and fauna from Bromsgrove are similar to those from Warwick, and from the Otter Sandstone Formation of Devon. The fauna comprises a few arthropods and conchostracans (*Euestheria*), scorpionid arachnids (*Mesophonus*, *Spongiophonus*, *Bromsgroviscorpio* and *Willsiscorpio*), annelids (*Spirorbis*) and a bivalve (?*Mytilus*). The vertebrates include the shark *Palaeobates*

[Acrodus] keuperinus, the early actinopterygian *Gyrolepis alberti*, the perleidid *Dipteronotus cyphus* and the lungfish *Ceratodus laevissimus* (Old *et al.*, 1987; Milner *et al.*, 1990), as well the capitosaurid amphibians '*Cyclotosaurus pachygnathus*' and *Mastodonsaurus* (Wills, 1916, pp. 2–7, figs 2–4, pl. 2; Paton 1974), and reptiles (Benton *et al.*, 1994; Benton and Spencer, 1995). The Bromsgrove fauna is associated with a rich flora that includes sphenopsids (horsetails and relatives) and gymnosperms (cycads, cycadeoids and conifers).

The Otter Sandstone Formation (Anisian) of Devon is best exposed along a series of fine sea cliffs between Budleigh Salterton and Sidmouth. Inland the formation has a poorly exposed outcrop in east Devon around the districts of Budleigh Salterton and Sidmouth and further inland beyond Honiton. All the fossil vertebrates have been recovered from the cliff exposures. The recent discovery of a rich vertebrate fauna from several localities between Budleigh Salterton and Sidmouth has provoked interest in the Otter Sandstone as a productive source of Middle Triassic vertebrates. The locality was known to the late Victorians, who had collected some of the first known remains of the reptile *Rhynchosaurus* and good material of *Mastodonsaurus* from the same localities, but their finds had been rather sparse.

FISH AND AMPHIBIAN SITES

Only one GCR site has been selected for inclusion:

Sidmouth coast section (SY 092838–SY 131873). Middle Triassic (Anisian), Otter Sandstone Formation.

However, both Coton End Quarry, Warwickshire (SP 290655) and Guy's Cliffe, Warwickshire (SP 293667) have been designated SSSIs for their fossil reptiles and amphibians and are included in the GCR volume for fossil reptile sites (Benton and Spencer, 1995).

SIDMOUTH (SY 092838–131873) (POTENTIAL GCR SITE)

Highlights

The Otter Sandstone Formation at Sidmouth in Devon is the richest active Middle Triassic vertebrate-bearing site in the British Isles. Six or more species of fish and amphibian have been found here, most of them recently, and the site represents one of the most promising localities of its age anywhere in the world.

Introduction

The fossiliferous beds occur in the series of high cliffs to the west of Sidmouth between Chiselbury Bay (SY 092838) and Chit Rocks (SY 121869), and at Port Royal, just east of Sidmouth (SY 12978730). The whole locality (Figure 11.5) is important as one of the most productive sources of vertebrates of mid-Triassic age in Britain, and fresh finds are made every year after cliff falls. However, it is difficult and dangerous to collect from the cliff face and most of the fossils have come from fallen blocks on the foreshore, or *in situ* from ledges at beach level.

Whitaker (1869) distinguished 'red sandstone' overlain by 'red marl' in the New Red Sandstone at High Peak (SY 144858), which is in turn overlain by Cretaceous Upper Greensand, and he reported the first finds of vertebrates from the Otter Sandstone Formation. Lavis (1876) reviewed the Sidmouth coast in more detail, and Seeley (1876) described a fine lower jaw and other bones of the tetrapod *Mastodonsaurus lavisi*. Hutchinson (1879) further reported fossil plant remains that he identified as stems of an equisete or calamite. Ussher (1876), Metcalfe (1884), Carter (1888), Irving (1888, 1892, 1893), Hull (1892) and Woodward and Ussher (1911) discussed the stratigraphy and dating of the coastal section near Sidmouth, with particular attention to occurrences of fossil vertebrate material. Metcalfe (1884) figured remains of the reptile *Rhynchosaurus*, together with *Mastodonsaurus* jaws and other bones collected from fallen blocks near High Peak, while Carter (1888) described further remains, including fish scales and coprolites.

A second phase of work on the Otter Sandstone Formation coast section began in the 1960s. Laming (1966, 1968) and Henson (1970) provided further information on the sedimentology and stratigraphy of the formation. Warrington *et al.* (1980), Laming (1982) and Warrington and Scrivener (1990) discussed the problems of correlating the Otter Sandstone with other Triassic sequences. Leonard *et al.* (1982), Selwood *et al.* (1984), Mader and

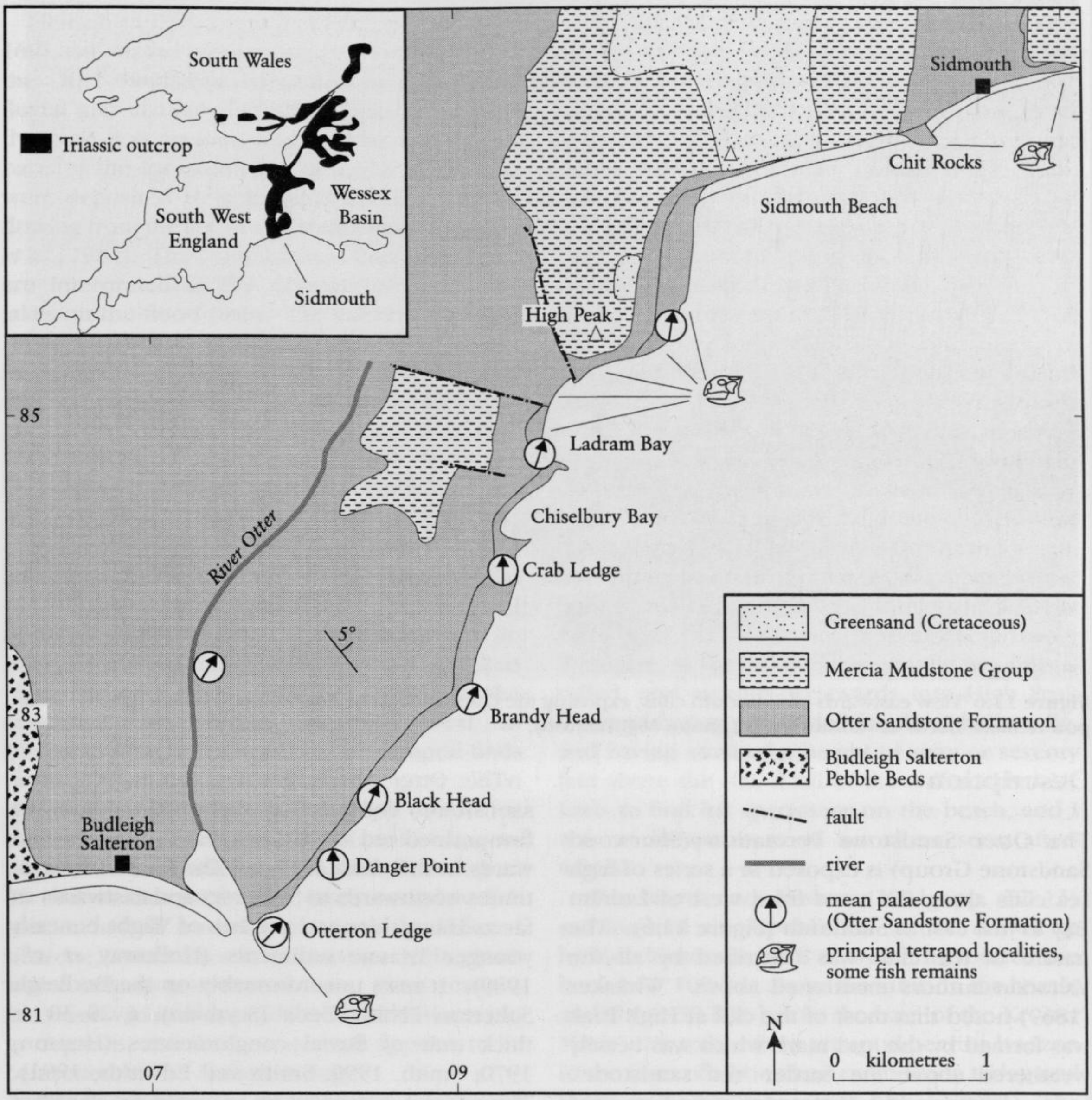

Figure 11.5 Map of coastal outcrop of the Otter Sandstone Formation between Sidmouth and Budleigh Salterton, South Devon (from Benton and Spencer, 1995).

Laming (1985), Lorsong *et al*. (1990), Smith (1990), Purvis and Wright (1991), Smith and Edwards (1991) and Wright *et al*. (1991) carried out studies on the sedimentology of the Otter Sandstone Formation, focusing on the paleosols and other climatic indicators. Spencer and Isaac (1983), Milner *et al*. (1990), Benton (1990) and Benton *et al*. (1994) described collections of fishes and tetrapods made between 1982 and 1994 by P. Spencer that greatly enlarged the faunal list.

The Otter Sandstone Formation has been regarded as 'sparsely fossiliferous' (Spencer and Isaac, 1983). This impression may be the result of the steepness and height of the cliffs, and the fact that most fossils so far collected have come from fallen blocks on the shore. The Sidmouth to Budleigh Salterton section has yielded the largest number of remains of fossil vertebrates from the New Red Sandstone of Devon, and one of the widest ranges of fossil tetrapods from the British Middle Triassic, and it has continued to produce new fossils.

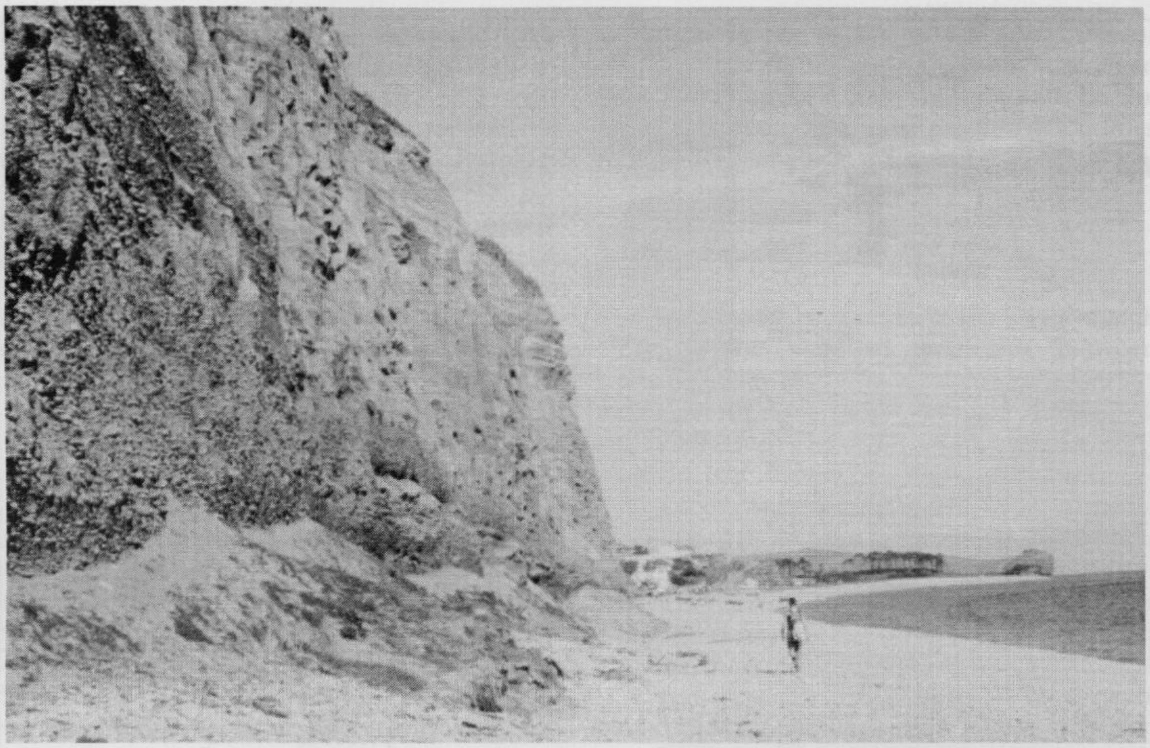

Figure 11.6 View eastwards of Sidmouth cliffs, exposing the Otter Sandstone Formation in which fish and tetrapod remains occur at various levels (photo: M.J. Benton).

Description

The Otter Sandstone Formation (Sherwood Sandstone Group) is exposed in a series of high sea cliffs along the coast from west of Ladram Bay to just east of Sidmouth (Figure 11.6). The nature of the cliffs was described by all the Victorian authors mentioned above. Whitaker (1869) noted that most of the cliff at High Peak was formed by the 'red marl' which was heavily weathered above the harder 'red sandstone'. Irving (1888, pp.152–3) stated that the latter was underlain by 'massive, strongly current-bedded (Bunter) sandstones' which continue to the mouth of the Otter River. The succession is summarized below, with measurements estimated from Lavis (1876, fig. 1), on the assumption that High Peak is 155 m high (contour on 1:50 000 OS topographical map).

	Thickness (m)
CRETACEOUS	
Chalk gravel	5
Greensand	30
– – – – – – – unconformity – – – – – – –	
TRIASSIC	
Upper (Keuper) Marls (unnamed formation of Mercia Mudstone Group)	60
The Otter Sandstone Formation	*c.* 60

The Otter Sandstone Formation (the 'red sandstone') comprises *c.* 118 m of medium- to fine-grained red sandstones that dip gently eastwards in the coast section. The formation continues northwards to Somerset and eastwards as far as Hampshire and the Isle of Wight beneath younger Triassic sediments (Holloway *et al.*, 1989). It rests unconformably on the Budleigh Salterton Pebble Beds (Scythian), a 20–30 m thick unit of fluvial conglomerates (Henson, 1970; Smith, 1990; Smith and Edwards, 1991). The contact is marked by an extensive ventifact horizon (Leonard *et al.*, 1982) that represents a non-sequence of unknown duration, and is interpreted by Wright *et al.* (1991) as a desert pavement associated with a shift from a semi-arid to an arid climate.

Calcretes occur abundantly at Otterton Point, Budleigh Salterton, but farther east they are rarer, and the formation is dominated by sandstones in large and small channels, with occasional siltstone lenses. The sandstones occur in cycles, commonly with conglomeratic bases, and fine upwards through cross-bedded sandstones to ripple-marked sandstones. The Otter Sandstone Formation is capped by water-laid siltstones and mudstones of the Mercia Mudstone Group.

Henson (1970), Laming (1982, pp. 165, 167, 169), and Mader and Laming (1985) interpreted the Otter Sandstone Formation as comprising fluvial and aeolian deposits. Sandstones near the base are aeolian, and middle and upper parts of the formation are of fluvial origin and were deposited by ephemeral braided streams flowing from the south and south-west (Selwood *et al*., 1984). The comparatively thin mudstones are interpreted as the deposits of temporary lakes on the flood plain. The calcretes indicate subaerial soil and subsurface calcrete formation in semi-arid conditions (Mader and Laming, 1985; Lorsong *et al*., 1990; Mader, 1990; Purvis and Wright, 1991). The climate was semi-arid, with long dry periods when river beds dried out, and seasonal or occasional rains leading to violent river action and flash floods.

Recent collections of fish material and amphibian bones have come from the top 40 m or so of the Otter Sandstone Formation and occur in all lithologies, but most commonly in intraformational conglomerates and breccias (Spencer and Isaac, 1983). Lower in the sequence, in breccias exposed west of Chiselbury Bay, the abundance of tetrapod finds declines significantly. The bones are generally in a fine- to medium-grained reddish sandstone that commonly contains clasts of pinkish, greenish or ochreous calcrete and mud flakes up to 20 mm in diameter. The more complete fish specimens are, however, preserved in dark red siltstone, sometimes in association with plants and conchostracan crustaceans. Plant remains are preserved in iron oxide in all the lower-energy deposits, and their occurrence appears to be controlled by the sedimentology.

The only specimens found *in situ* by Spencer and Isaac (1983, p. 268) came from 'the lowest of three intraformational conglomerates', but these were 'indeterminate bone fragments'. It is likely that fossils occur at numerous levels throughout the Otter Sandstone Formation, but most have been found in fallen blocks on the shore, and locating the original horizons in the cliffs is difficult.

The Victorian authors believed that one or more discrete bone beds occurred at the eastern end of the outcrop. Lavis (1876) and Metcalfe (1884) put the bone bed 'about 10 feet from the top of the sandstone'; Woodward and Ussher (1911) placed it 'about 50 feet below the base of the Keuper Marls', some 40 ft (13 m) lower in the section.

Metcalfe (1884) gave further details of this locality at High Peak, stating that bones were found in fallen blocks of sandstone from a light-coloured band in the cliff close below the base of the 'Upper Marls' (Mercia Mudstone Group). Carter (1888) recovered bone material and coprolites from this locality.

Hutchinson (1879, p. 384) gave the most detailed account of the fossiliferous horizons. He found equisetalean stems in a bed at the top of the sandstone and 'about eight or ten feet above' two or three 'White bands' that appear as clear horizons in the cliff face. Then, 'one or two steps below' the White bands 'is what I venture to call the Saurian or Batrachian band, in which Mr Lavis found his Labyrinthodon; but I cannot exactly say how many feet this band is below the white bands, because the fall down of the under cliff has concealed the stratification at this place; but it may be fifty feet below, and amongst the beds of red rock. Be that as it may, the Saurian band rises out of the beach somewhere under Windgate, as the hollow between the two hills is called, and ascends westwards into High Peak Hill, and having proceeded for about half-a-mile, and having attained a height of sixty or seventy feet above the sea, a fall of the cliff enabled Mr Lavis to find his specimens on the beach, and I was so fortunate as to see them soon afterwards.'

Woodward and Ussher (1911, pp. 12–13) summarized an unpublished section drawn up by Hutchinson in 1878 in which he located the bone bed '100 feet above the talus on the beach, and about 50 feet below the base of the Keuper Marls'. No trace of any tetrapod-bearing horizon in the form of a bone bed can be seen today, and there is no evidence that one existed. The Victorian geologists evidently expected to find bones at discrete levels, and had no concept of restricted lenticular deposits, such as channel lags.

The tetrapod fossils are generally preserved in a fine- to medium-grained, orange to reddish sandstone that often contains sedimentary clasts, including reworked rhizolith concretions, up to 20 mm in diameter, and claystone intraclasts that may have a pinkish, greenish or ochreous colour. The bones generally occur as isolated elements: jaws, teeth, partial skulls or single postcranial bones, but some occur in articulation. The bones generally show little obvious sign of abrasion, and some tiny reptile and fish jaws are exquisitely preserved. More details of taphonomy were given by Benton *et al.* (1994) and Benton and Spencer (1995).

About half of the identifiable tetrapod bones are rhynchosaur remains. The amphibians are represented mainly by skull and pectoral girdle elements, all relatively dense and with characteristic sculpture. Specimens of the fish *Dipteronotus cyphus* obtained from a claystone lens east of Windgate are extremely well articulated and occur in association with a 'still-water' fauna of branchiopod crustaceans.

Fauna

The list of fishes and temnospondyl amphibians is compiled from Milner *et al.* (1990) and Benton *et al.* (1994).

Osteichthyes: Actinopterygii: Neopterygii: Cleithrolepididae
Dipteronotus cyphus Egerton, 1854
Complete specimens, pieces of flank, individual scales and spines (EXEMS = The Royal Albert Memorial Museum, Exeter)
Osteichthyes: Actinopterygii
Gyrolepis(?) and others
Scales
Actinopterygii: Neopterygii: Ginglymodi
Lepisosteus sp.
Scales in coprolites
Osteichthyes: Actinopterygii: Semionotidae
Lepidotes

TETRAPODA
'Temnospondyli': Mastodonsauridae
'*Mastodonsaurus lavisi*' (Seeley, 1876) *nomen dubium*
Holotype. The posterior part of right mandible (NHM R.4215). Skull fragments and part of a lower jaw (NHM, EXEMS)
'Temnospondyli': Benthosuchidae
Eocyclotosaurus sp.
Remains of a skull, and other fragments (EXEMS)
'Temnospondyli': Capitosauridae
Capitosauridae *incertae sedis*
Posterior part of mandible (EXEMS)
'Temnospondyli'
indeterminate temnospondyl fragments (EXEMS)

Interpretation

Attempts to recover palynomorphs from the Otter Sandstone Formation have so far not been successful (Warrington, 1971). Its age is poorly constrained by occurrences of Late Permian miospores in the lower part of the Permo-Triassic succession near Exeter (Warrington and Scrivener, 1988, 1990) and Carnian taxa in the Mercia Mudstone Group, 135 m above the Otter Sandstone Formation. The only other biostratigraphical indicator is the vertebrate fauna. Walker (1969, 1970), Paton (1974) and Benton (1990) favoured a Ladinian age for the fauna, but Milner *et al.* (1990) argued that an Anisian age was most likely. The association of the perleidid fish *Dipteronotus cyphus* (Anisian–basal Ladinian) with some of the reptile remains identifies the Anisian as the only shared date.

The remains of three temnospondyl amphibians ('*M. lavisi*', *Eocyclotosaurus* sp., capitosaur *incertae sedis*) are abundant in the Otter Sandstone Formation. These were all aquatic superficially crocodile-like forms, and they were probably carnivores or piscivores which fed at the waterside. The new eocyclotosaur material represents the first find of a benthosuchid from the Middle Triassic in Britain. It is a fairly well-preserved partial skull, but specifically indeterminable and identified only as *Eocyclotosaurus* sp. (Milner *et al.*, 1990). It is similar to *Eocyclotosaurus* species from France and Germany.

The fossils of '*Mastodonsaurus lavisi*' show some resemblance to material from Coton End and Bromsgrove (Paton 1974, pp. 265–82) and these show closest resemblance to *M. cappelensis* from the Upper Buntsandstein (Anisian) of Baden-Württemburg, Germany (Milner *et al.*, 1990). The material consists of jaw and some skull bones that are not specifically diagnostic, as Paton's (1974) description of the species was based upon *Mastodonsaurus* generic characters only. However, Milner *et al.* (1990) suggested that the species should retain its name for practical purposes, but as a *nomen dubium*. *M. lavisi* is the largest temnospondyl in the Otter Sandstone herpetofauna with an estimated skull length of 500–600 mm. It may have grown to at least 2 m.

The other temnospondyl material consists of a partial right mandible, identified by Spencer and Isaac (1983) as that of *Cyclotosaurus* sp., but considered by Milner *et al.* (1990) to be

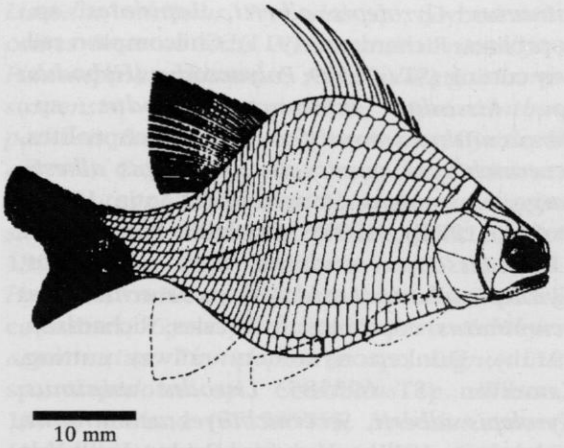

Figure 11.7 Otter Sandstone Formation fish: *Dipteronotus cyphus* Egerton.

undiagnostic capitosaurid and several indeterminate temnospondyl specimens (Milner *et al*., 1990).

Dipteronotus cyphus, a deep-bodied perleidid fish (7–10 cm long) which possesses a dorsal hump, is represented at Sidmouth by many well-preserved partial and complete remains (Figure 11.7). Specimens of *D. cyphus*, including the holotype, have been obtained elsewhere only at Bromsgrove, from the upper member of the Bromsgrove Sandstone Formation. The Otter Sandstone specimens are better preserved than those from Bromsgrove and the species was redescribed from two partial Sidmouth specimens (Gardiner, *in* Milner *et al*. 1990). *Dipteronotus* is known also from the Scythian of Europe and the Carnian–Norian of Morocco.

The only other fishes recovered from the Otter Sandstone are some poorly preserved actinopterygian specimens, probably *Gyrolepis* from the same laminated mudstones as *D. cyphus* and *Lepidotes* (=*Lepidotus*) scales that occur within coprolites, probably attributable to the fish-eating amphibians. *Gyrolepis* is a genus known from several localities in the English Midlands including the Bromsgrove Sandstone Formation of Bromsgrove (Sherwood Sandstone Group) and the Colwick Formation of Colwick Wood, Nottinghamshire, the Arden Sandstone Member of Leamington, Warwickshire, and the Dane Hills Sandstone Member of Aylestone Road in Leicester and Spinney Hills, Leicestershire (all Mercia Mudstone Group; Gardiner, *in* Milner *et al*., 1990). The presence of the three temnospondyl amphibians, which were aquatic carnivores, suggests a rich fish fauna of which only three genera have been recovered. However, much unidentified fish material has been collected in recent years (P. Spencer, pers. comm., 1994) which may prove the existence of a much more diverse assemblage.

The only plants so far found in the Otter Sandstone Formation are stems and leaves of large horsetails (Hutchinson, 1879), and recently found *Schizoneura*, a form also known from the Bromsgrove Sandstone Formation (Benton and Spencer, 1995).

Comparison with other localities

The Otter Sandstone fauna and flora is comparable to that of the Bromsgrove Sandstone Formation at Bromsgrove, Guy's Cliffe and Coton End, Warwickshire. Outside the British Isles, the fauna compares with Early to Mid-Triassic faunas from France (Grès à *Voltzia*) and Germany (Buntsandstein) and Mid- to Late Triassic faunas from Germany (Lettenkeuper; Milner, *et al*., 1990).

Conclusion

The Otter Sandstone Formation exposed along the coast at Sidmouth offers vast potential for study of mid-Triassic amphibian and fish faunas. There are no mainland European freshwater faunas of the same age, since the Muschelkalk marine transgression occupies that interval of time. The assemblage comprises the richest mid-Triassic continental amphibian fauna in Britain and probably in western Europe. New finds, including as yet undescribed fish remains, continue to be made *in situ* and in fallen blocks, with erosion constantly supplying new specimens. This potential and the importance of past finds give the site its conservation value.

LATE TRIASSIC OF CENTRAL AND SOUTH-WEST ENGLAND

Late Triassic fish faunas have been obtained in south-west and central England from two main sources: the 'Rhaetic Bone Bed' in the Penarth Group, and from the cave and fissure fillings in the region of the Severn estuary, which are treated separately towards the end of this chapter. The 'Rhaetic Bone Bed' is actually several ossiferous horizons of varying duration and lateral extent that occur within an unusual sequence at the base of the Westbury Formation, over a wide geographical area (Dawkins, 1864).

The Penarth Group is entirely Rhaetian in age (Warrington *et al.*, 1980). The Westbury Formation is the basal unit of the Penarth Group and is lithologically a thin (1–15 m) band of black, pyritic shales with occasional limestone lenses, shell beds and thin sandstones. The formation is best exposed in south-west Britain, where the base of the unit is characterized in some sections by distinctive bands of a bone and intraclast conglomerate, which are approximately 0.1–0.3 m thick. It is these bone beds that form a basis for much of the present knowledge of Rhaetian vertebrate palaeontology. The Westbury Formation lithologies show cyclical sedimentation, suggesting fluctuating but generally shallow water depths during deposition (Hamilton, 1977; Ivimey-Cook, 1974). Localized channels, bioturbation, fragmented shell horizons and the concentrated bone beds all confirm the shallow-water nature of the Westbury sea (Ivimey-Cook, 1974).

FISH SITES

Typical Rhaetian localities that yield fish material include the following.

DEVON: Culverhole Point (SY 275893; *Hybodus minor*, *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, *Sargodon tomicus*, fish scales, teeth and coprolites; Richardson, 1906); Axminster (SY 3098; *Pseudodalatias barnstonensis*; Sykes, 1974); Axmouth (SY 2691; *Hybodus minor*, *Gyrolepis alberti*; *Severnichthyes acuminatus*; Agassiz, 1833–1845, 1839; Dames, 1888).

SOMERSET: Bagley, near Wedmore (ST 457462; *Lissodus minimus*, *Sargodon tomicus*, *Severnichthyes acuminatus*; Boyd-Dawkins, 1864); Ben Knowle, Wookey (ST 515449; *Lissodus minimus*, *Gyrolepis alberti*; Boyd-Dawkins, 1864); Blue Anchor Bay–Watchet coastline (ST 042432–167456; *Lissodus minimus*, *Hybodus* sp., *Nemacanthus monilifer*, *Palaeospinax rhaeticus*, *Pseudodalatias barnstonensis*, shark coprolites, *Agkistracanthus mitgelensis*, *Gyrolepis alberti* , *Severnichthys acuminatus*, *Sargodon tomicus*, *Legnonotus cothamensis*; Richardson, 1911b; Hamilton and Whittaker, 1977; Sykes, 1977; Storrs and Gower, 1993; Storrs, 1994; Duffin, 1994); Charlton Mackrell railway cutting (ST 417212; *Lissodus minimus*, *Gyrolepis alberti*, *'Lepidotes'* sp., coprolites; Richardson, 1911); Chilcompton railway cutting (ST 626509; *Polyacrodus* (*Hybodus*) sp., *Lissodus minimus*, *Hybodus* sp., *Nemacanthus monilifer* , shark coprolites, *Severnichthyes acuminatus*, *Gyrolepis alberti*, *Sargodon tomicus*; Savage, 1977; Antia, 1979b; Duffin, 1980b, 1994); Dunball, Puriton (ST 3141; *Lissodus minimus*, *Hybodus minor*, *Gyrolepis alberti*, *'Lepidotes'* sp., *Severnichthyes acuminatus*, coprolites, fish scales; Richardson, 1911b); Dunkerton colliery railway cutting, Camerton (ST 695585; *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; Richardson, 1911b); Hapsford Bridge, Vallis Vale (ST 755490–756489; *Lissodus minimus*, *Hybodus* sp., holotype specimen of *Vallisia coppi* , ?neoselachian calcified vertebrae, shark coprolites, *Severnichthyes acuminatus*, *Gyrolepis alberti*, *Sargodon tomicus*; Duffin, 1982); Langport railway cutting (*Gyrolepis alberti*, coprolites, other fish remains; Richardson, 1911b); Milton Lane, Wells (ST 545455; *Lissodus minimus*, *Gyrolepis alberti*, fish scales; Richardson, 1911b); Sparkford Hill railway cutting (ST 604254; *Lissodus minimus*, *Gyrolepis alberti*, fish scales; Richardson, 1911b); Three-Arch Bridge railway cutting, Shepton Mallet (ST 594433; *Gyrolepis alberti*, coprolites, other fish remains; Richardson, 1911b); Uphill railway cutting (ST 317589; *Lissodus minimus*, *Hybodus minor*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; Richardson, 1911b).

SOUTH GLOUCESTERSHIRE (AVON): Aust Cliff, Severn estuary (ST 566898; 16 species, including one type specimen; see site report; Sykes, 1974; Storrs, 1994); Barnhill Quarry, Chipping Sodbury (ST 725830; *Hybodus minor*, *Lissodus minimus*, *Gyrolepis alberti*, *Sargodon tomicus*, *Severnichthyes acuminatus*; Reynolds, 1938; Macfadyen, 1970); Brislington (ST 635704; *Hybodus minor*, *Gyrolepis alberti*, *Severnichthys acuminatus*; Kellaway, 1933); Cotham Road, Bristol (ST 586739; *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, fish coprolites; Rendle-Short, 1904); Horton (ST 7684; *Gyrolepis alberti*; *Severnichthyes acuminatus*; Richardson, 1902); Lilliput, Chipping Sodbury (ST 7381, *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes* sp.; Richardson, 1904); Manor Farm Quarry (ST 575895; *Polyacrodus* (*Hybodus*) *cloacinus*, *Lissodus minimus*, *Hybodus* sp., Hybodontiformes *incertae sedis*, *Nemacanthus monilifer*, *Palaeospinax rhaeticus*, *Pseudodalatias barnstonensis*, shark coprolites, *Myriacanthus padoxus*, *Severnichthyes acuminatus*, *Gyrolepis alberti*, *Colobodus* sp., *Sargodon tomicus*, *Legnonotus cothamensis*, *Pholidophorus higginsi*, *Ceratodus latissimus*; P. Davis, pers. comm., 1995); Pylle Hill, Totterdown (ST 598718; *Hybodus minor*, *Lissodus minimus*, shark coprolites, *Gyrolepis alberti*, *Severnichthyes acuminatus*, *Pholidophorus* sp., *Legnonotus* sp., '*Lepidotes*' sp., *Ceratodus* sp.; Wilson, 1891); Redland (ST 585753; *Hybodus minor*, *Lissodus minimus*, shark coprolites, *Gyrolepis alberti*, *Severnichthyes acuminatus*, *Pholidophorus* sp., *Legnonotus* sp., '*Lepidotes*' sp., *Ceratodus* sp.; Rendle-Short, 1904); Stoke-Gifford (ST 6280; *Hybodus minor*, hybodont spines, *Gyrolepis alberti*, *Severnichthyes acuminatus*, fish scales; Rendle-Short, 1904).

GLOUCESTERSHIRE: Coomb Hill (ST 764940; *Hybodus minor*, *Lissodus minimus*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; Richardson, 1902); Charfield (ST 723924; *Lissodus minimus*, *Hybodus minor*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, coprolites; Richardson, 1904); Chaxhill (ST 737887; *Gyrolepis* sp.; Richardson, 1902); Garden Cliff, Westbury-on-Severn (SO 718128; *Polyacrodus (Hybodus) cloacinus*, *Lissodus minimus*, *Hybodus* sp., *Nemacanthus monilifer*, *Pseudodalatias barnstonensis*, shark coprolites, *Severnichthyes acuminatus*, *Gyrolepis alberti*, *Sargodon tomicus*, *Ceratodus latissimus*; Etheridge, 1872; Savage and Large, 1966; Macfadyen, 1970; Sykes, 1977; Storrs, 1994); Tites Point, Purton Passage, Severn estuary (SO 692047; holotype of *Hybodus minor*; Storrs, 1994); Wainlode Cliff, Severn estuary (SO 845257; *Lissodus minimus*, *Hybodus minor*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, fish debris; Etheridge, 1872; Storrs, 1994).

GLAMORGAN: Coity (SS 925814; hybodont spines, *Sargodon tomicus*, other fish teeth; Francis, 1959); Cowbridge (SS 999745; *Hybodus minor*, *Lissodus minimus*, *Gyrolepis alberti*, *Sargodon tomicus*, '*Lepidotes*' sp., *Severnichthyes acuminatus*, fish scales, teeth and coprolites; Richardson, 1905); Dinas-Powys (ST 155712; *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; fish scales and teeth; Richardson, 1905); Penarth Head-Lavernock Point coastline (ST 186697–188682; *Lissodus minimus*, *Hybodus minor*, *Nemacanthus monilifer*, *Pseudodalatias barnstonensis*, *Sargodon tomicus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; '*Lepidotes*' sp., fish scales; Etheridge, 1872; Storrs, 1994); St. Mary's Well Bay, Sully (ST 175676; *Gyrolepis alberti*, '*Lepidotes*' sp., *Sargodon tomicus*; Richardson, 1905); Stormy Down (SS 846806; *Hybodus minor*, *Severnichthyes acuminatus*; Newton, 1899; Francis, 1959).

GWENT: Bishton (ST 390873; *Gyrolepis alberti*, fish scales, teeth and coprolites; Richardson, 1905); Cadoxton (ST 124696; *Lissodus minimus*, *Gyrolepis alberti*, '*Lepidotes*' sp.; Richardson, 1905); Goldcliff (ST 366831; *Hybodus minor*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; Strahan, 1899; Richardson, 1905); Llanwern (ST 353878; *Lissodus minimus*, *Gyrolepis alberti*; Richardson, 1903); Milton (ST 367884; *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; Richardson, 1903); Lis-Werny (ST 339880; *Gyrolepis alberti*; Richardson, 1905); Sedbury (ST 555930; *Lissodus minimus*, *Hybodus minor*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, *Sargodon tomicus*, fish teeth, scales and coprolites; Richardson, 1903).

LEICESTERSHIRE: Barrow-on-Soar (SK 573173; *Hybodus minor*, *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*; *Pseudodalatias barnstonensis;* Woodward, 1889b; Sykes, 1974); Wigston (SK 603991; fish remains including *Pholidophorus higginsi*; Quilter, 1889; Woodward, 1889c; Richardson, 1909); Spinney Hills brickpits (SP 604045; *Lissodus minimus*, *Hybodus minor*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Sargodon tomicus*, *Severnichthyes acuminatus*, *Pholidophorus higginsi*, *Ceratodus latissimus*; fish coprolites; Woodward, 1889c; Kent, 1968); Glen Parva brickworks (SP 5689; *Hybodus minor*, *Lissodus minimus*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Sargodon tomicus*, *Severnichthyes acuminatus*, *Pholidophorus higginsi*, *Ceratodus latissimus*, fish coprolites; M. Browne 1889, 1894a,1894b; Fox-Strangways, 1903; Horwood, 1916).

NOTTINGHAMSHIRE: Bantycock Pit (SK 811502) and Staple Pit (SK 805499; *Lissodus minimus*, *Hybodus minor*, *Nemacanthus monilifer*, *Pseudodalatias barnstonensis*, *Severnichthyes acuminatus*, *Gyrolepis alberti*, *Sargodon tomicus*, '*Lepidotes*' *barnstonensis*, '*Lepidotes*' sp.; Martill and Dawn, 1986); Barnstone cutting (SK 739358; type specimen of *Pseudodalatias barnstonensis*, '*Lepidotes*' *barnstonensis*, '*Lepidotes*' sp.; Sykes 1971, 1974, 1979; Sykes *et al.*, 1970); Beacon Hill (SK 810530; *Lissodus minimus*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, shark fin rays, fish scales and teeth; Johnson, 1950); Bunny cutting (SK 578211; *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, fish scales and teeth; Kent, 1953); Owlthorpe (SK 666336; *Hybodus* sp., *Lissodus minimus*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, other fish remains; Ivimey-Cook and Elliot, 1969); Stanton-on-the-Wolds (SK 637312; *Hybodus minor*, *Lissodus minimus*, *Nemacanthus monilifer*, *Gyrolepis alberti*, *Severnichthyes acuminatus*, *Sargodon tomicus*, *Ceratodus* sp.; Lamplugh *et al.*, 1909).

LINCOLNSHIRE: Lea railway cutting, Gainsborough (SK 8189; *Hybodus minor*, *Lissodus minimus*, *Nemacanthus monilifer*, *Pseudodalatias barnstonensis*, *Gyrolepis alberti*, *Sargodon tomicus*, *Severnichthyes acuminatus;* Burton, 1867; Sykes, 1974).

YORKSHIRE: Thornton-le-Beans (SE 397902; fish remains; Sykes, 1977).

Rhaetian sediments in a large glacial erratic at Linksfield, near Elgin, Morayshire (NJ 223641), have produced remains of fishes including *Lissodus minimus*, '*Hybodus*', '*Sphenonchus*', and '*Lepidotes*', and reptiles (Woodward and Sherborn, 1890; Storrs, 1994).

Of these numerous localities, one stands out clearly from the rest in the abundance of its fauna, its accessibility and potential for future research and is therefore selected as a potential GCR site:

Aust Cliff, (ST 565895–572901). Upper Triassic ('Rhaetian'), 'Rhaetic Bone Bed', Westbury Formation.

AUST CLIFF (ST 565895–ST 572901) (POTENTIAL GCR SITE)

Highlights

Aust Cliff exposes the best section of the 'Rhaetic Bone Bed' in Britain, and is the type locality for the large palaeonisciform chondrostean *Severnichthyes acuminatus* (Agassiz), the hybodont shark *Lissodus minimus* (Agassiz) and the dipnoan lungfish *Ceratodus latissimus* Agassiz.

Figure 11.8 Aust Cliff, north of the Aust Service Area: the pale band of the Penarth Group high in the cliff face contains lenses of Rhaetic Bone Bed (photo: G. W. Storrs).

Table 11.1 Aust Cliff section (based on Reynolds, 1946; Hamilton, 1977; Warrington *et al.*, 1980).

			Thickness (m)
		Blue Lias (Hettangian)	(variable)
JURASSIC	Lower Lias	*planorbis* Beds	
TRIASSIC		Pre-*planorbis* Beds	(variable)
Penarth Group		Lilstock Formation	*c.* 3.40
		Westbury Formation	*c.* 4.30
Mercia Mudstone Group		Blue Anchor Formation	*c.* 7.0
		Red mudstones	*c.* 30.0
CARBONIFEROUS		Carboniferous Limestone	(variable)

Introduction

Aust Cliff, at the eastern end of the Severn (Road) Bridge (Figure 11.8), is Britain's most prolific site for Rhaetian fossil fish. The cliff exposure was first described by Buckland and Conybeare (1824), and subsequent accounts have been given by many authors, including Strickland (1841), Etheridge (1868), Short (1904), Reynolds (1946), Hamilton (1977) and Storrs (1993, 1994). The Aust section has yielded important collections of marine and terrestrial reptiles, as well as abundant fish remains. Aust Cliff is the type locality for the large primitive actinopterygian *Severnichthys acuminatus* (Agassiz), the hybodont shark *Lissodus minimus* (Agassiz) the lungfish *Ceratodus latissimus* Agassiz and *Synectodus rhaeticus* (Duffin).

The bone beds of the Westbury Formation at this locality have been important in Triassic vertebrate palaeontology and have played an important role in the discussion of bone-bed formation and diagenesis. The site is fairly accessible, subject to erosion and occasionally produces good specimens.

Description

Aust Cliff exposes a section through the Upper Triassic and the lower part of the Lower Jurassic (Figure 11.9). It represents the truncated face of a ridge of Triassic and Lower Jurassic rocks surrounded by alluvium. A very gentle anticlinal structure is shown, cut by five small faults with throws to the south ranging from *c.* 1 m to 4.5 m (Figure 11.9). Both flexing and faulting have been explained by compaction of the Mercia Mudstone Group sediments. The Mesozoic succession exposed in the cliff is readily subdivided lithologically and biostratigraphically. The lower part of the cliff consists of the Mercia Mudstone Group, including the Blue Anchor Formation (formerly the 'Tea Green Marls'). Macrofossils are generally absent from these beds, but occur abundantly in the overlying dark and lighter grey sediments of the Penarth Group (including the 'Rhaetic' of earlier authors). Limestones and shales at the top of the cliff are the lowest part of the Lias. This Mesozoic succession rests unconformably on the upturned edges of a Carboniferous Limestone ridge exposing the Lower Dolomites that dip about 15° SW. The section (based on Reynolds, 1946; Hamilton 1977; Warrington *et al.*, 1980) is given in Table 11.1.

The vertebrate remains are found predominantly in the 'Rhaetic Bone Bed' that occurs in places at the base of the Westbury Formation, the subdivisions of which are (Reynolds 1946):

	Thickness (m)
8. Greenish-black shales	0.3
7. Hard grey limestone ('upper *Pecten* Bed')	0.13
6. Black Shales	2.4
5. Hard pyritous limestone ('lower *Pecten* Bed')	0.18
4. Black shales, hard fissile paper-shale above	1.2
3. Bone Bed	0.02–0.15
'Tea Green Marls' [= Blue Anchor Formation]	

The 'Bone Bed' occurs as lenses of grit or intraformational conglomerate (or breccia) with a calcite-cemented sandy matrix on top of the

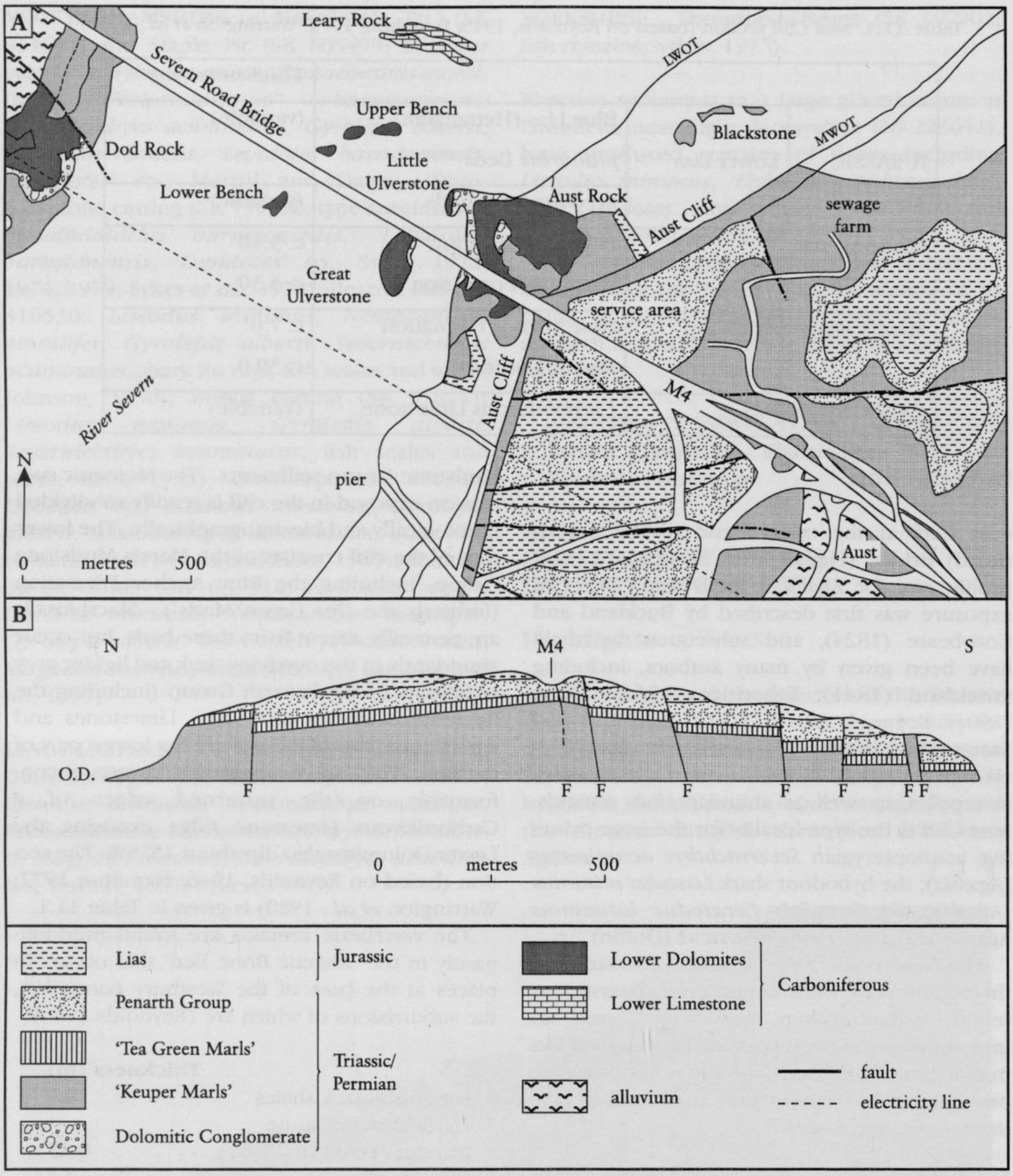

Figure 11.9 The Rhaetian at Aust Cliff: (A) geological map; (B) stratigraphical section (both from Benton and Spencer, 1995, after Hamilton, 1977).

Blue Anchor Formation, the surface of which may be ripple-marked. The conglomeratic component is made up mainly from clasts of the Blue Anchor Formation sediments, together with quartz pebbles and bone fragments. Many of the fragments of Blue Anchor Formation sediment are plastically deformed, which suggests that they were still soft when incorporated into the bone bed. The quartz pebbles are mainly of vein quartz, are mostly well rounded, and are probably derived from older beds (although Wickes, 1904, suggested that they might represent stomach stones, or gastroliths, swallowed by plesiosaurs to aid in the digestion of food).

The vertebrate remains are mainly phosphatized bones, teeth and scales. They are disarticulated and commonly rounded and worn, indicating some *post-mortem* transport. Coprolites (faecal droppings), some possibly of sharks, are also abundant: these contain crustacean fragments and abundant fish scales, and they are heavily phosphatized, containing from 25–50% calcium phosphate (Duffin, 1979c).

According to the classification of Sykes (1977), the Bone Bed had a part-primary and part-secondary origin. The indications of primary deposition include the condition and orientation of the fossils, and the poorly sorted nature of the deposit. However, most of the fossils, and other clasts, show signs of abrasion, which indicates that the deposit is largely reworked. This is borne out by finds of teeth of the Carboniferous fishes *Psephodus magnus*, *Psammodus porosus* and *Helodus* in the bone bed, presumably reworked from the local Carboniferous Limestone or the Coal Measures. Macquaker (1994) and Storrs (1993, 1994) concluded that the bed represents a tempestite.

Vertebrate remains are most abundant in the impersistent Bone Bed. A similar fish fauna, though less abundant than in the Bone Bed, occurs in the succeeding basal sands of the Westbury Formation and also at the base of the limestone bands, and in the shales. Reynolds (1946, p. 32) described further vertebrate accumulations that occur within arenaceous limestone units (known as the '*Pullastra*' beds, after the predominant bivalve component *Pleurophorus [Pullastra] elongatus*) which occur at the base and directly above the lower *Pecten* bed (Bed 5 in above log) within the black shale units. The limestone bands frequently contain selenite and quartz pebbles, up to 12 mm across (Sykes, 1977). They have yielded specimens of *Severnichthyes* and other fish remains, as well as terrestrial tetrapod material (Reynolds, 1946). Scattered vertebrate remains have also been recovered from within the lower black shale unit (Bed 4 of Reynolds, 1945; Sykes, 1977). Bone-rich debris is also locally present in the topmost layers of the green marls at the base of the Rhaetian sequence where the marl is intensely bioturbated. These occurrences of reptile and fish bones in Rhaetian horizons at Aust, other than in the basal bone bed itself, are classified as trace bone beds (Sykes, 1977, p. 220).

Fauna

Dozens of slabs with fish bones and teeth are preserved in BRSMG, BRSUG, NHM, BGS(GSM), CAMSM and in most other British collections. Many tooth and fin spine specimens collected during the 19th century were identified to species, and made the types of new species and new genera, but there is no point in listing all of these since there is rarely enough evidence for such precise determination (see Storrs, 1994, for discussion).

Chondrichthyes: Elasmobranchii: Euselachii: Hybodontoidea
- *Polyacrodus (Hybodus) cloacinus* (Quenstedt, 1858)
- *Lissodus (Acrodus) minimus* (Agassiz, 1839)
- *Hybodus* sp.
- Hybodontiformes *incertae sedis*

Chondrichthyes: Elasmobranchii: Neoselachii
- *Nemacanthus monilifer* (Agassiz, 1837)
- *Palaeospinax rhaeticus* Duffin, 1982
- *Pseudodalatias barnstonensis* Sykes, 1971

Chondrichthyes: Elasmobranchii
- shark coprolites

Chondrichthyes: Holocephali: Chimaeriformes
- *Myriacanthus paradoxus* Agassiz, 1836

Osteichthyes: Actinopterygii:
- *Severnichthyes acuminatus* (Agassiz, 1835)
- *Gyrolepis alberti* Agassiz, 1835

Osteichthyes: Actinopterygii: Neopterygii: Perleidiformes
- *Colobodus* sp.

Osteichthyes: Actinopterygii: Neopterygii: Holostei: Halecostomi
- *Sargodon tomicus* Plieninger, 1847
- *Legnonotus cothamensis* Egerton, 1854

Osteichthyes: Actinopterygii: Neopterygii: Teleostei
- *Pholidophorus higginsi* Egerton, 1854–1855

Osteichthyes: Sarcopterygii: Dipnoi: Ceradontidae

Ceratodus latissimus Agassiz, 1839

A fauna of psammodont and cochliodont shark tooth plates (e.g. *Cochliodus*, *Psammodus*, *Psephodus*, *Helodus* and *Ctenoptychius*) has been recovered from the basal bone beds in the Westbury Formation, and especially from those at Aust. However, these have been secondarily reworked from Carboniferous limestones, and are not considered further here.

Interpretation

The Bone Bed is assumed to have been deposited under marine coastal conditions. The conglomerate shows signs of rapid deposition and winnowing by wave action and shoreline currents. It has been suggested (Macquaker, 1994; Storrs, 1993, 1994) that the Aust bone bed represents a storm deposit: a mass of rocks and fossils picked off the shoreline, and carried back down into deeper water by a storm surge ebb current, or exhumed and redeposited from penecontemporaneous shallow-water sediments. Other authors suggest that reworking of strand-line deposits produced by the Rhaetian transgression might equally have produced the bone bed. This occurred with overstep across the former playa-type sediments of the Mercia Mudstone Group, a palaeoenvironment of intrinsically low relief. Although the palaeontological evidence does not give precise dating, it is probable that the marine flooding phase occurred very rapidly and would have had a strong erosive force. Kent (1970), for example, suggested that the whole of the Midlands was submerged by the transgression almost simultaneously.

Fish remains are extremely common in the Bone Bed at Aust (Figure 11.10). These include the teeth and fin spines of sharks, and teeth and scales of primitive, heavily scaled bony fish. The most common reptile remains are ichthyosaurs and plesiosaurs, with a few possible dinosaurs. In the past the most characteristic remains of the Aust Bone Bed were tooth plates of the lungfish *Ceratodus latissimus* Agassiz 1839, so much so that these rocks were once referred to as the '*Ceratodus* Beds' (Storrs, 1994). Aust Cliff is the type locality for this species, a form similar to the extant *Neoceratodus* from Australia. The teeth are extremely variable in size and shape, hence Agassiz (1839) named ten other species of the genus based upon Aust specimens. These were recognized as junior synonyms of *C. latissimus* by most later authors (e.g. Woodward, 1889a; Sykes *et al*., 1970). *Ceratodus parvus* Agassiz is considered by some (e.g. Sykes *et al*., 1970) to represent a smaller species of dipnoan in the Westbury Formation, although the most recent review of the Aust specimens suggests that it is a junior synonym of *C. latissimus* (Storrs, 1994, p. 237). Today this species is much less common in the fallen blocks of the Bone Bed and the '*Ceratodus* Beds' may have represented an impersistent lens of concentrated, reworked material (C. Trueman, pers. comm., 1994).

Rhaetian shark material is common throughout the Westbury Formation at Aust Cliff and consists of isolated teeth, dermal denticles and fin spines. At least two genera of hybodont shark are known, along with three possible neoselachians and a shark of unknown but possibly neoselachian affinity (Figure 11.10). The hybodont sharks are represented by *Polyacrodus cloacinus* (Quenstedt) and *Lissodus minimus* (Agassiz). The latter species is based upon small, low-crowned, multicuspid teeth recovered from Aust Cliff in the 19th century and described by Agassiz (1839) as *Acrodus minimus*. The Westbury Formation specimens were more recently assigned to *Lissodus* Brough, a genus described from articulated material from the late Triassic of Africa by Duffin (1985, p. 123). Hybodont fin spines are also common in the Westbury Formation at Aust and many were traditionally assigned to the Jurassic genus *Hybodus*. However, most of these spines are undiagnostic and their names are considered *nomines dubia* by most modern authors (for review see Storrs, 1994). The cuspidate teeth described as '*Hybodus*' *minor* Agassiz may, in fact, be from the anterior dentition of a problematic neoselachian taxon rather than a hybodont shark, possibly a palaeospinacid (Maisey, 1977a), and the fin spines assigned to this particular genus are not distinguishable from those of *Polyacrodus* or *Lissodus* (Storrs, 1994).

Nemacanthus monilifer Agassiz is another shark described from fin spines and the type locality is Aust Cliff. This fin spine is, however, readily distinguished from '*Hybodus*' as it possesses two rows of sharp tubercles on the poste-

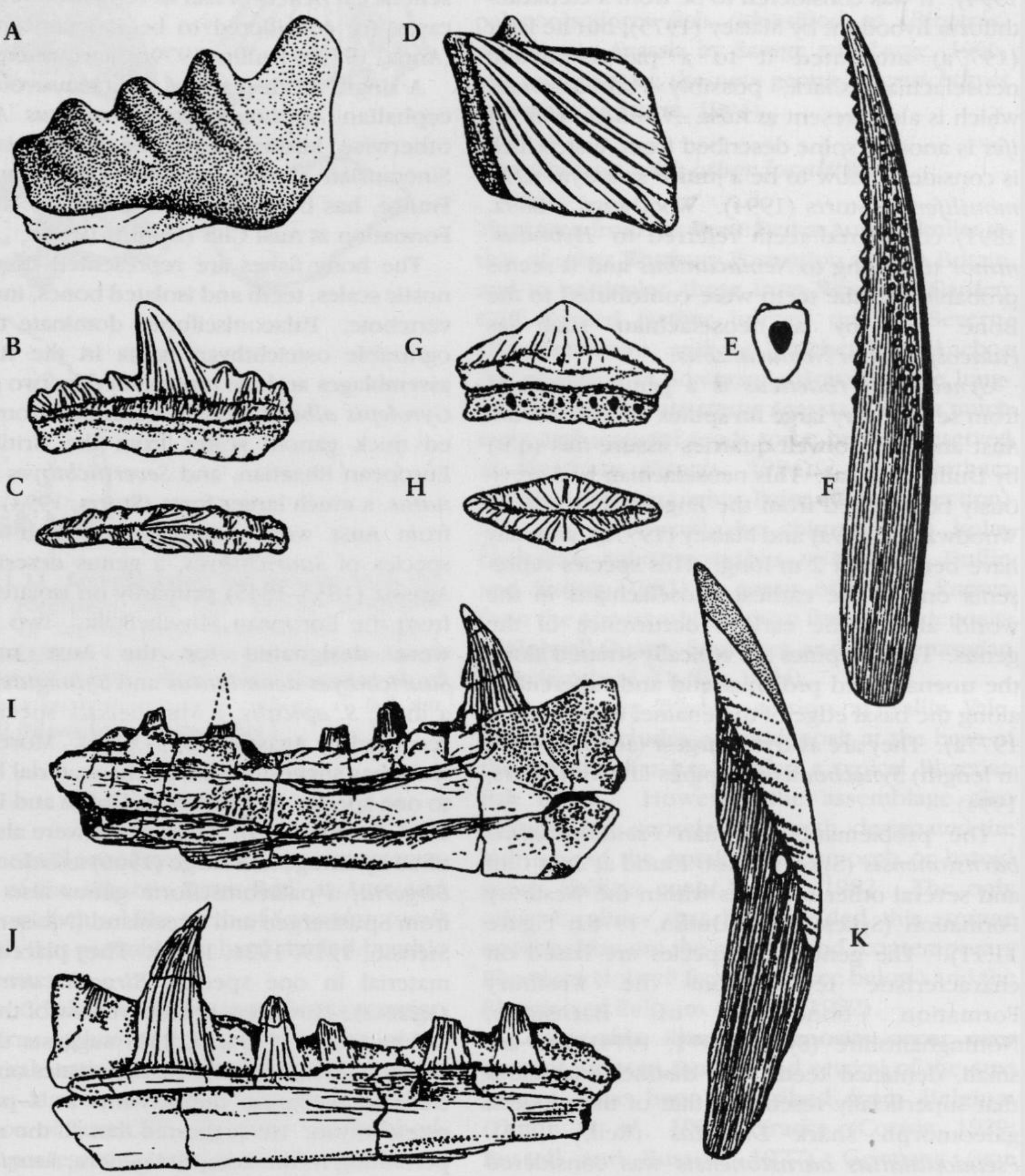

Figure 11.10 Fossils from the Rhaetic Bone Bed, Aust Cliff: (A) idealized characteristic tooth plate of *Ceratodus latissimus* Agassiz (*c.* 6 cm long) in occlusal aspect; (B), (C) *Polyacrodus cloadcinus* (Quenstedt), idealized tooth (*c.* 2.5 cm in antero-posterior length) in lingual and apical aspects; (D) *Gyrolepis alberi* Agassiz, idealized scale (*c.* 0.5 cm long; (E), (F) *Nemacanthus monilifer* Agassiz, reconstructed fin spine (*c.* 12 cm long) in transverse section and right lateral aspects; (G), (H) typical *Lissodus minimus* (Agassiz) tooth (*c.* 0.3 cm in antero-posterior length, in lingual and apical aspects; (I), (J) *Severnichthys acuminatus* (Agassiz) neotype, dentary, BRSMG 7976 (*c.* 10.5 cm long) in left lateral aspect and medial aspect; (K) fin spine of the rare *Palaeospinax rhaeticus* Duffin (*c.* 7 cm long). (All figures from Storrs, 1994.)

rior edge and is finely tuberculated on both sides from the middle to the distal end (Storrs, 1994). It was considered to be from a ctenacanthiform hybodont by Maisey (1975), but he later (1977a) attributed it to a palaeospinacid neoselachian shark, possibly *Palaeospinax*, which is also present at Aust. *Nemacanthus filifer* is another spine described from Aust, which is considered now to be a junior synonym to *N. monilifer* by Storrs (1994). Woodward (1889a, 1891) considered teeth referred to '*Hybodus*' *minor* to belong to *Nemacanthus* and it seems probable that the teeth were contributed to the Bone Bed by a neoselachian such as *Palaeospinax* or *Nemacanthus*.

Synechodus rhaeticus is a genus described from several very large fin spines identified from Aust and the Holwell quarries fissure fills (q.v.) by Duffin (1982a). This neoselachian had previously been noted from the English Rhaetian by Woodward (1889a) and Maisey (1977a), and may have been about 2 m long. This species represents one of the earliest neoselachians in the world and is the earliest occurrence of the genus. The fin spines are typically striated along the unenamelled proximal end and tuberculate along the basal edge of the enamel coat (Maisey, 1977a). They are also the largest (at above 7 cm in length) *Synechodus* fin spines known (Storrs, 1994).

The problematic selachian *Pseudodalatias barnstonensis* (Sykes) is also found at Aust Cliff and several other localities within the Westbury Formation (Sykes, 1974; Duffin, 1978a; Figure 11.11). The genus and species are based on characteristic teeth from the Westbury Formation bone-beds of Barnstone, Nottinghamshire (Sykes, 1971, 1974) and are small, denticled teeth with distinct enameloid that superficially resembles that of the modern galeomorph shark *Dalatias* (Reif, 1978). *Pseudodalatias barnstonensis* was considered to be related to the hybodont sharks by Reif (1978), whilst Duffin (1982b) suggested that it was closer to the neoselachian grade.

Shark coprolites and fossilized spiral intestinal tract contents have been extensively described from the Rhaetic Bone Bed at Aust and other localities (Duffin, 1979c). Some of these contain the remains of ingested prey, such as fish scales, crustaceans (Hamilton, 1977) and even a reptile (Storrs, 1994). However, they remain problematic as many of the other Rhaetian fishes, such as the palaeoniscoids and the lungfishes may have possessed a spiral intestinal tract (Storrs, 1994). Less structured phosphatic masses may represent faecal pellets of fish or reptiles, but in some cases are considered to be inorganic nodules (Antia, 1979b; Duffin, 1979c; Macquaker, 1994).

A single tooth plate of the chimaeroid holocephalian *Myriacanthus paradoxus* Agassiz, otherwise known from the Hettangian and Sinemurian (Lower Jurassic) of England and France, has been recovered from the Westbury Formation at Aust Cliff (Duffin, 1994).

The bony fishes are represented by undiagnostic scales, teeth and isolated bones, including vertebrae. Palaeonisciforms dominate the recognizable osteichthyan fauna in the Rhaetian assemblages and are represented by two genera, *Gyrolepis alberti* Agassiz, described from isolated thick ganoid scales from the British and European Rhaetian, and *Severnichthyes acuminatus*, a much larger form (Storrs, 1994). Teeth from Aust were originally assigned to two species of *Saurichthyes*, a genus described by Agassiz (1833–1845) primarily on isolated teeth from the European Muschelkalk. Two species were designated for the Aust material, *Saurichthyes acuminatus* and *S. longidens*, and a third, *S. apicalis*, a Muschelkalk species, was recorded by Agassiz (1833–1845). More recent work has suggested that all the material belongs to one species (see review in Duffin and Delsate, 1993; Storrs, 1994). These teeth were also identified by Savage and Large (1966) as belonging to *Birgeria*, a palaeonisciform genus also known from Spitsbergen and Greenland (Nielsen, 1949; Stensiö, 1919, 1921, 1932). They placed all the material in one species, *Birgeria acuminata* (Agassiz). However, a recent review of the material by Storrs (1994, p. 231) suggests that this diagnosis was based on characteristics only sufficient to recognize the remains as a primitive osteichthyan. He suggested that all the material pertaining to the accepted genera, *Saurichthyes* and *Birgeria*, represents a new genus of palaeoniscoid fish. This is because the pseudolabyrinthodont dentition differs from *Saurichthys*, and the possession of a large, probably overhanging or recurved rostrum, distinctive bone sculpture and large teeth differs from *Birgeria*. The new species, *Severnichthyes acuminatus* (Agassiz), represents a large (up to 60 cm long), carnivorous primitive actinopterygian, probably similar in form to the pike-like *Birgeria* (Storrs, 1994, p. 234). Aust is the type locality for *Severnichthyes acuminatus* (Figure

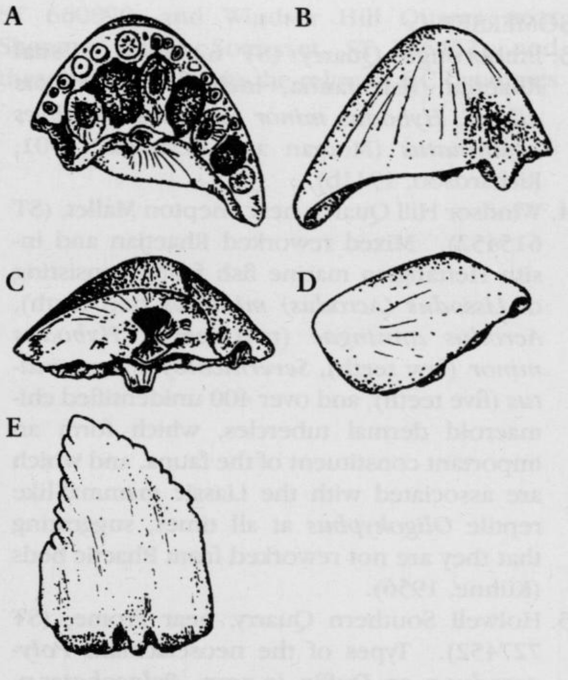

Figure 11.11 Representative fish remains from the Westbury Formation, Aust Cliff. (A)–(D) rostropremaxillary of *Severnichthys acuminatus* (Agassiz) BRSMG Cd222, *c.* 3 cm long, in platal, anterodorsal and left lateral aspects. (E) idealized ?lower tooth of *Pseudodalatius barnstonensis* (Sykes), *c.* 0.3 cm long. (All figures from Storrs, 1994.)

11.11).

Semionotid osteichthyans are a common component of the 'Rhaetic Bone Bed' at Aust and include small chisel-like teeth of *Sargodon tomicus*, a fish that probably ate hard-shelled benthic invertebrates.

The poorly known macrosemiid neopterygian *Legnonotus cothamensis* Egerton is represented by several articulated specimens from the Cotham Marble Member of the Lilstock Formation of Aust Cliff. This tiny, shallow-bodied fish possessed a large dorsal fin which was joined to its body for approximately half its length (Storrs, 1994).

The Liassic poorly defined teleost genus *Pholidophorus*, known from the Cotham Marble Member at Aust Cliff, is represented by *P. higginsi* Egerton and *P. nitidus* Egerton. However, the second species appears to be a junior synonym of *P. higginsi* (Storrs, 1994). This genus has also been reported from other Rhaetian deposits, including the fissure-fill sediments of the Bristol region (Whiteside, 1986).

Temnospondyl amphibians have been reported from Aust, based on mandibles named *Metopias diagnosticus* (e.g. Reynolds, 1946), but these turn out to be the teeth and jaws of the palaeonisciform fish (identified as '*Birgeria*' *acuminata* Agassiz by Savage and Large, 1966, but representing the new genus *Severnichthyes acuminatus* Storrs, 1994).

Comparison with other localities

The fauna from the Bone Bed at Aust is similar to that of other Westbury Formation sites in Britain and in particular, those from Westbury Garden Cliff located farther upriver on the Severn, Gloucestershire, and the Watchet–Blue Anchor Bay coastline in Somerset. However, the lungfish *Ceratodus latissimus* Agassiz, 1839 is much rarer and material tends to be better preserved at Westbury (Storrs, 1994). The Cotham Member at Blue Anchor Point (Watchet section) has also produced the chimaeriform holocephalian *Agkistracanthus mitgelensis* Duffin and Furrer (1981), a genus otherwise known from the apparently Rhaetian fissure-fill deposits of Holwell Quarry, Somerset, and the Hettangian of Switzerland (Duffin, 1994).

The Upper Triassic section at Vallis Vale, Somerset, includes a clay deposit at the base of the section that has yielded a typical Rhaetian fish fauna. However, the assemblage also includes rare neoselachian teeth, designated the holotype of the possible galeomorph or batoid genus *Vallisia coppi* Duffin, 1982. The only other localities that have yielded this strange neoselachian are the nearby (and ?contemporary Rhaetian) Holwell fissure fill (see below) and the Rhaetian of Belgium (Duffin, 1982).

Comparable Rhaetian deposits occur over most of western Europe and several of the Aust genera have been described from Belgium (Duffin *et al.*, 1983), France (Corroy, 1929; Russell and Russell, 1977), Germany (von Huene, 1933, 1935; Dreyer, 1962), Poland (Duffin and Gazdzicki, 1977) and Switzerland (Peyer, 1944). The sediments are similar to those of the Penarth Group in southern Britain, and are likely to have been deposited in adjacent or contiguous structural basins (Storrs, 1994).

Conclusion

Aust Cliff exposes the best section of the Rhaetian beds with the 'Rhaetic Bone Bed' in Britain. Aust is the type locality for three species of fish and is one of the best late Triassic sites for lungfish remains. The bone beds of the Westbury Formation at this locality have a considerable conservation value for Triassic vertebrate palaeontology (Storrs, 1994), and have played an important role in the discussion of bone-bed formation and diagenesis (e.g. Antia, 1979).

VERTEBRATE-BEARING FISSURE DEPOSITS OF SOUTH-WEST ENGLAND

Cave and fissure systems developed in the Carboniferous Limestones of the Mendips and Glamorgan during the Late Triassic and earliest Jurassic contain abundant vertebrate remains. The Mendips and parts of South Wales appear to have comprised an archipelago of low islands, and the fissures preserve a record of the diverse and often insular faunas of the time (Robinson, 1957; Tarlo, 1962; Halstead and Nicoll, 1971; Kermack *et al.*, 1973; Fraser, 1985, 1986, 1988b). The nature of the palaeokarst and the geology of the caves was reviewed by Simms (1990); Savage (1993) reviewed the potential of the palaeokarst for further vertebrate finds.

FISH SITES

The numerous vertebrate-bearing fissure and cave fill deposits of southern England and South Wales that have yielded fish remains, as well as reptilian and mammalian material (Benton and Spencer, 1995) are listed below.

GLOUCESTERSHIRE

1. Slickstones (Cromhall) Quarry (ST 704916). Typical Rhaetian fishes including *Gyrolepis*, *Hybodus minor* and *Severnichthyes acuminatus* occur in the covering sediments at Cromhall (Walkden and Fraser, 1993). These are important as they indicate a Rhaetian and possibly Westbury Formation age for the fissure, and confirm that the infilling is of a saline intrusion (i.e. neptunian dyke) type.
2. Tytherington Quarry (ST 660890). Typical reworked Rhaetian fish fauna including *Pholidophorus*, *Gyrolepis*, *Hybodus minor* and *Severnichthyes acuminatus* (Marshall and Whiteside, 1980; Whiteside and Marshall, 1985).

SOMERSET

3. Emborough Quarry (ST 623505). Usual Rhaetian fish fauna, including *Gyrolepis alberti*, *Hybodus minor* and *Severnichthyes acuminatus* (Morgan and Reynolds, 1901; Richardson, 1911b).
4. Windsor Hill Quarry, near Shepton Mallet, (ST 615452). Mixed reworked Rhaetian and in-situ Hettangian marine fish fauna consisting of *Lissodus (Acrodus) minimus* (ten teeth), *Acrodus anningae* (two teeth), *Hybodus minor* (few teeth), *Severnichthyes acuminatus* (five teeth), and over 400 unidentified chimaeroid dermal tubercles, which form an important constituent of the fauna, and which are associated with the Liassic mammal-like reptile *Oligokyphus* at all times, suggesting that they are not reworked from Rhaetic beds (Kühne, 1956).
5. Holwell Southern Quarry, near Frome, (ST 727452). Types of the neoselachians *Polyacrodus* n. sp. Duffin, in prep., *Palaeobates* n. sp. Duffin, in prep., and the hybodont sharks 'Hybodont' n. gen. n. sp. Duffin and Herman, in prep., and *Palaeospinax rhaeticus* Duffin, 1982. Other remains include *Polyacrodus (Hybodus) cloacinus*, *Lissodus (Acrodus) minimus*, *Hybodus* sp., *Nemacanthus monilifer*, *Pseudodalatias barnstonensis*, *Vallisia coppi*, shark coprolites, placoid, hybondontoid and ctenacanthid scales, *Agkistracanthus mitgelensis*, *Severnichthyes acuminatus*, *Gyrolepis alberti*, *Colobodus* sp., *Sargodon tomicus*, *Lepidotes* sp., *Ceratodus latissimus*. Full lists are given in Kühne (1956) and Duffin (1978, 1982, 1994). The material sorted by Charles Moore in the late 19th century (Moore, 1867, 1881) included over 70 000 undiagnosed fish remains (including 45 000 '*Acrodus*' teeth) and 29 mammal teeth (Robinson, 1957; Savage, 1993).

None of these sites could be selected as having a greater or lesser claim as a candidate GCR site to represent British Triassic fissure-fill fish faunas. The fish faunas are similar to those of bedded Rhaetic deposits, and in some cases have been reworked from substantially earlier sediments. The contemporary fossil reptile and/or mammal faunas of several fissure sites are unique (Slickstones (Cromhall Quarry), Gloucestershire, ST 704916; Durdham Down, Avon, ST 572747; Emborough Quarry, Somerset, ST 623505; Tytherington Quarry, Gloucester, ST 660890; and Windsor Hill Quarry, near Shepton Mallet, Somerset, ST 615452), and these are included in the relevant GCR volumes (Benton and Spencer, 1995). Several localities have been entirely worked out, and new ones are found when suitable sites are excavated.