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 silici-clastic 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 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 sub-aerial 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 elastics 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 elastics 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 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 he 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 dis-conformity 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).

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 southwest 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 southwest 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 nerit-ic 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 lep-tolepids. 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 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 basiptery-gium 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 rbaeticus Duffin, 1982

Pseudodalatias barnstonensis Sykes, 1971

Vallisia coppi Duffin, 1982

Chondrichthyes: Holocephali: Chimaeriformes

Myriacanthus paradoxus Agassiz, 1836

Agkistracanthus mitgelensis Duffin and Ferrer, 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 cotbamensis Egerton, 1854

' *Lepidotes*' sp.

Osteichthyes: Actinopterygii: Neopterygii: Teleostei

Pholidophorus bigginsi 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 chon-drostean *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.

'Temnospondylr: 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 290 655]; Leamington Old Quarry, [SP 325 666]) 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 293 667] 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 tetra-pod 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 126 462]; Woodward, 1904a).

The Bromsgrove Sandstones at Bromsgrove are approximately equivalent in age to the fossil-iferous 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, Brornsgroviscorpio* 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.

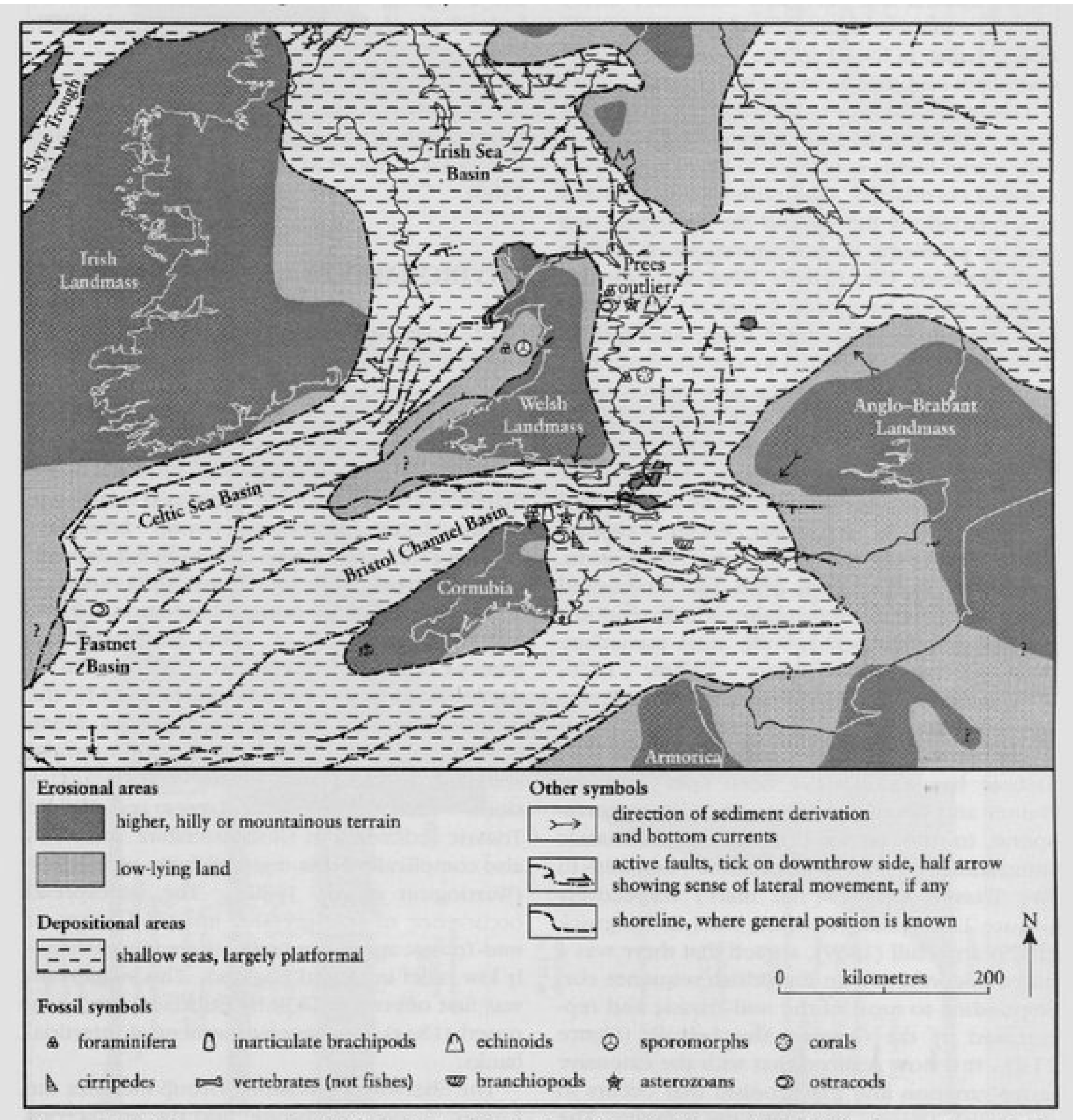
Fish and amphibian sites

Only one GCR site has been selected for inclusion:

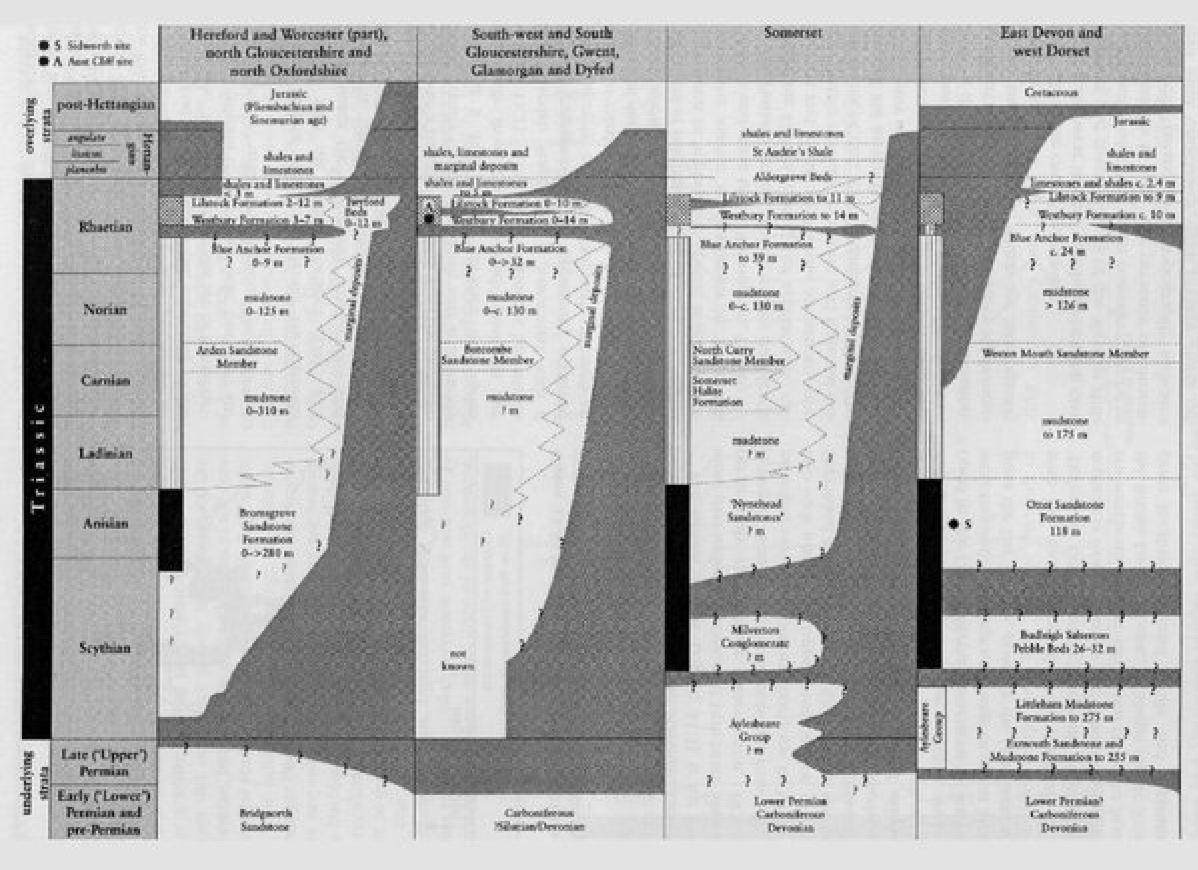
Sidmouth coast section [SY 092 838]–[SY 131 873]. Middle Triassic (Anisian), Otter Sandstone Formation.

However, both Coton End Quarry, Warwickshire [SP 290 655] and Guy's Cliffe, Warwickshire [SP 293 667] 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).

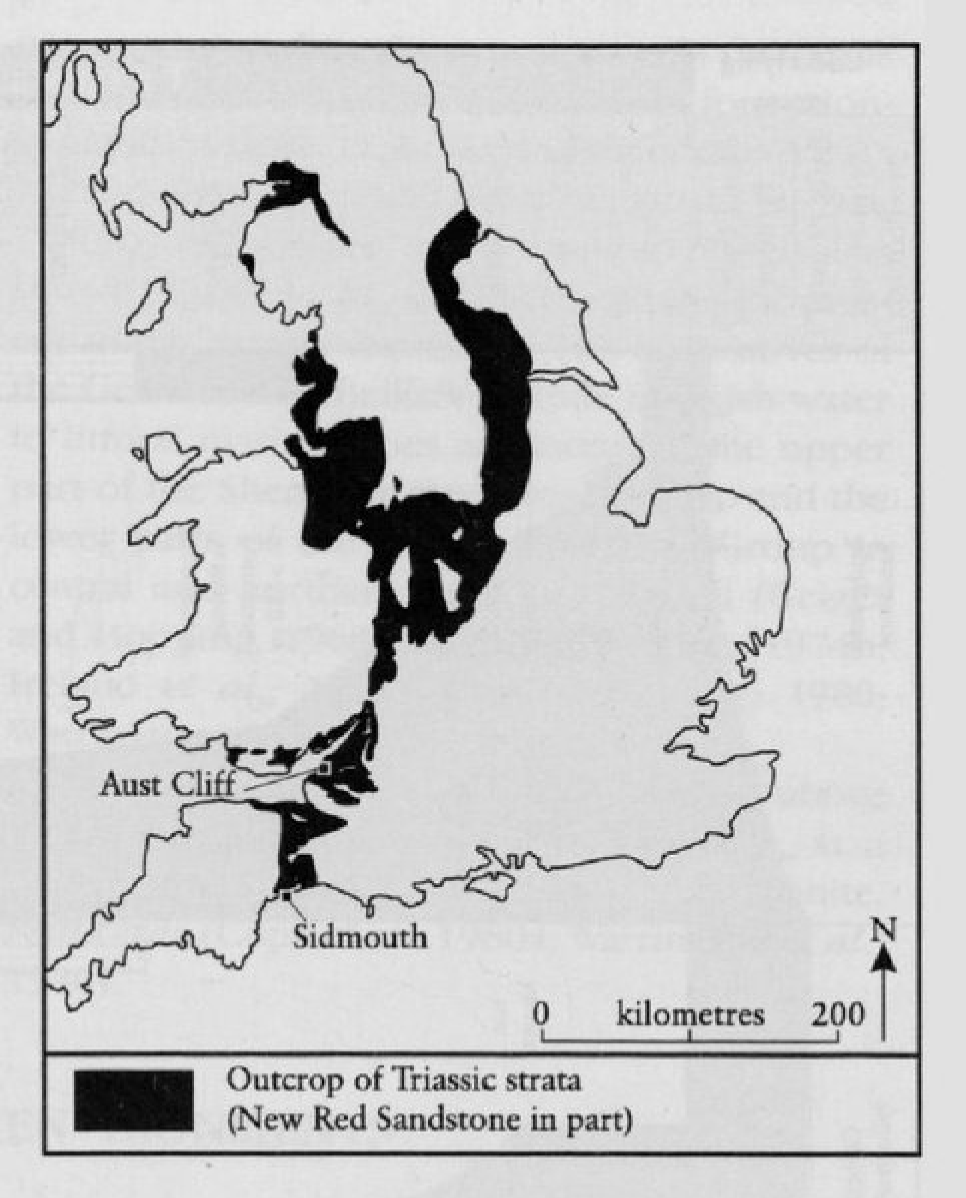
References



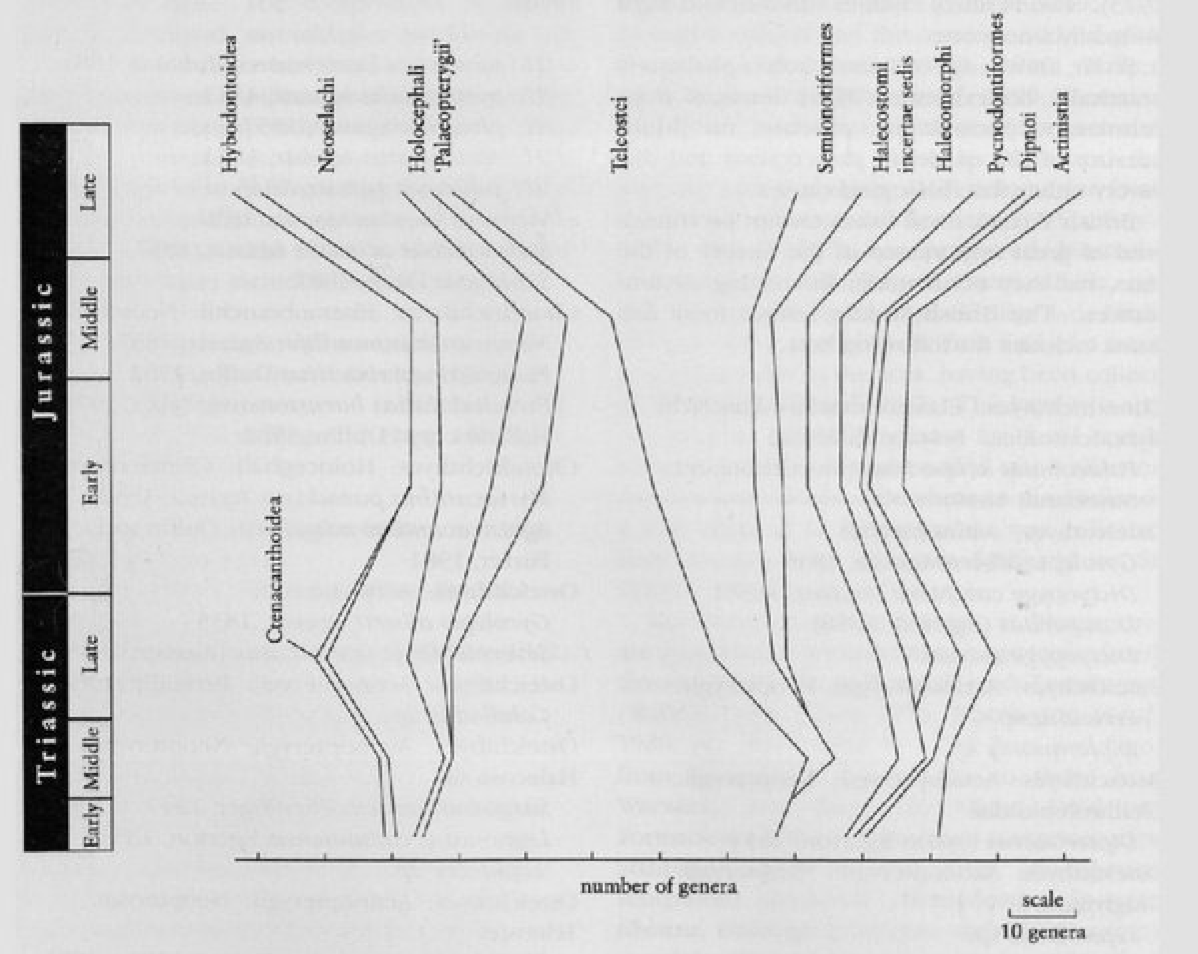
(Figure 11.1) Palaeogeography of Britain in late Triassic time (after Bradshaw et al., 1992). Connection with the Tethyan ocean lies via the east and south, with the Boreal ocean via the north.



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



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



(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.