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THE TRIASSIC REPTILES FROM DEVON

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Fossil reptiles have been known from the Otter Sandstone Formation in south-east Devon since the 1860s. Early finds were limited, but they indicated relationships with Middle Triassic reptile faunas already known from the Midlands of England. Almost no work was done on the Devon Triassic reptiles until the 1980s, when extensive new collections were made. The fauna of fishes, amphibians, and reptiles includes about ten taxa, and these suggest an Anisian (early Mid Triassic) age for the Otter Sandstone Formation. The fauna fills an important gap between terrestrial tetrapod faunas of the same age in Russia and North America, and shows an unusual mix of Laurasian and Gondwanan elements.

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INTRODUCTION

The Otter Sandstone of Devon, exposed along the coast, and inland, between Sidmouth and Budleigh Salterton, has yielded large collections of fossil fishes, amphibians, and reptiles. Many of the earliest finds, made in the 19th century, were of incomplete specimens. It was assumed that the Otter Sandstone Formation was a source of only sparse vertebrate remains, so no great effort was expended in searching for specimens. This changed in the early 1980s, when Patrick Spencer began amassing a large collection, including taxa that had not been found in Devon before, and indeed some that were hitherto unknown in the British Triassic (Spencer and Isaac, 1983). Spencer and other collectors added to the known fauna in the 1980s and 1990s, and several papers have been published in which the new specimens are described (Benton, 1990; Milner *et al.*, 1990; Benton *et al.*, 1993, 1994; Spencer and Benton, in press).

The limited 19th century discoveries were important at a time when geologists were trying to unravel the true pattern of the evolution of life, and to establish the dating of the rock units of the British Isles. Between 1840 and 1860, palaeontologists established the broad outlines of vertebrate evolution which are still accepted today, and the tetrapods of the British Triassic, which Richard Owen was describing at the time, were an important piece in this jigsaw. Further, the finds of isolated reptile bones in the Otter Sandstone Formation were sufficient to prove its Triassic age.

The purpose of this paper is to review the significance of the reptiles from Devon, firstly in the context of related work in Victorian times, and then in terms of present-day knowledge of Triassic tetrapod evolution.

Repository abbreviations. BGS (GSM), British Geological Survey (Geological Survey Museum), Keyworth, Nottingham; BMNH, British Museum (Natural History), London; BRSUG, Bristol University, Department of Geology Museum; EXEMS, Royal Albert Memorial Museum, Exeter.

SIR RICHARD OWEN AND THE GIANT FROGS AND LIZARDS OF THE TRIASSIC

Richard Owen (1804-1892), Hunterian Professor of Anatomy at the Royal College of Surgeons in London, and later knighted, was the rising star of vertebrate anatomy and palaeontology in Britain in the 1830s. He established an important, and original role for himself, as the acknowledged expert on fossil tetrapods, and naturalists sent him materials from all parts of the British Isles. Skeletal remains and

footprints of fossil tetrapods had been reported from the British Triassic since the 1820s, but only sporadically.

Owen's role, as ringmaster to the scattered provincial collectors, became established rapidly after 1839. He presumably achieved this dramatic takeover of the vertebrate palaeontological world largely because he was stepping into a vacuum, but also because he had an appropriate position (Hunterian Professor; designated rapporteur of the British Association), and he was an indefatigable worker. Not only was he describing all the new Triassic fossils, but he also swept through the, by then, extensive collections of Jurassic marine reptiles, and the sparser fossils of crocodylians and pterosaurs. In addition, he corralled the scattered remains of giant terrestrial Mesozoic reptiles that had been described by Mantell and Buckland, and boldly declared that they represented a major extinct group, which he named the Dinosauria (Owen, 1842b; Torrens, 1992).

In a series of papers in 1841 and 1842, Owen laid the foundations of an understanding of the amphibians and reptiles that lived before the advent of the dinosaurs, in the Middle Triassic. He based his conclusions on two collections, one from quarries in and around Warwick, from Dr Lloyd, and the other from quarries at Grinshill (Figure 1), north of Shrewsbury, from T. Ogier Ward. Owen initially suggested that all the specimens belonged to the temnospondyl amphibian *Mastodonsaurus*, already known from Germany (and usually called *Labyrinthodon* by Owen). He then recognized that the Grinshill animal was distinct from *Labyrinthodon*, and he described it as *Rhynchosaurus articeps*, a new genus and species of reptile (Owen, 1842b, c). Owen regarded *Rhynchosaurus* as a 'lacertian' (i.e., a lizard), but did not connect it with the Warwick material he was studying, which he retained in *Labyrinthodon* (Owen, 1842a).

It has subsequently been realised (e.g. Walker, 1969; Benton, 1990) that all the Grinshill material, and much of that from Warwick, pertains to *Rhynchosaurus*. *Rhynchosaurus* were, for a long time, allied with lizards, as Owen suggested, and with *Sphenodon*, the tuatara, in particular. The link was strengthened by the group name for the sphenodontids, the Rhynchocephalia ('snout heads'), which was often used until 1990. However, rhynchosaurus are almost certainly allied more closely to the archosaurs, the group that includes dinosaurs, birds, crocodiles, pterosaurs, and their Triassic ancestors, than to the lepidosaurs (lizards and sphenodontids) (Carroll, 1977; Benton, 1985, 1990).

A second reptile group is represented at Warwick, and by a

specimen unwittingly described by Owen as an unusual amphibian, *Labyrinthodon scutulatus* (Owen, 1842a, b). Owen (1866) later referred it to the new genus *Rhombopholis*, but its amphibian nature was questioned by Miall (1874). Walker (1969) reinterpreted this specimen, and others from Warwick and Bromsgrove, as a prolacertiform reptile possibly related to *Macrocnemus*, a form well known from the Middle Triassic of northern Italy, Switzerland, Germany, and (?) Spain.

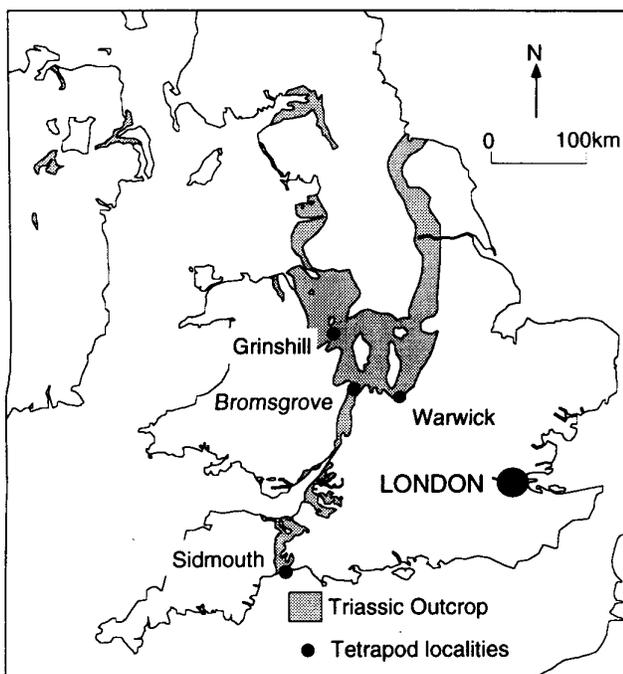


Figure 1. The Triassic outcrop of England, showing the major localities that have yielded Middle Triassic tetrapod remains.

A third English Mid Triassic reptile is represented by teeth called *Cladeiodon* by Owen (1841), together with some other fossils from Warwick. These were regarded as dinosaurian by Huxley (1870) and ascribed by Huene (1908) to *Teratosaurus*, a rauisuchian. However, such generalized archosaur teeth are probably unidentifiable (Benton and Gower, 1997). In addition, Owen figured further archosaur remains in his 1841-2 papers as parts of the amphibian *Labyrinthodon*.

Owen interpreted *Labyrinthodon* as a giant frog-like animal, and this mental image, founded on rather limited material, was later represented in concrete form by Waterhouse Hawkins in one of his famous Crystal Palace models, produced in 1853. The *Labyrinthodon* model shows a strange bug-eyed, wide-mouthed animal, whose jaws are lined with extraordinary large carnivorous teeth. The animal is scaled to a length of about 3 m, with short forelimbs, each equipped with a four-fingered hand, and long large-footed hindlimbs, clearly a frog from hell.

By the end of his frenzy of work on the new bones from Shrewsbury and Warwick, Owen had developed an image of the typical life of the English Triassic, a scene that was dominated by huge frog-like amphibians whose grinning jaws were lined with fearsome teeth. Much smaller herbivorous rhynchosaurs scuttled at their feet, presumably the main food source of the giant *Labyrinthodon*. In the background were the first hints of dinosaurs, known only from their teeth, *Cladeiodon* (sometimes *Cladyodon*).

THOMAS HENRY HURLEY, OWEN'S NEMESIS

Owen's firmly promoted image of Triassic life was not to last long.

Despite his influential position in society, and in the hierarchy of science, a younger rival soon began to chip away at the evidence he had presented. Thomas Henry Huxley (1825-1895), like Owen, was ambitious and hard-working, and he immediately began to clash with Owen. Huxley (1859, p. 57) gleefully denied the existence of the giant Triassic frog: "I would caution geologists... against supposing that there is any evidence whatever to show that the *Labyrinthodonts* were frog-like animals". In a series of papers, Huxley (1859, 1869, 1870, 1887) described new specimens of *Labyrinthodon*, *Rhynchosaurus*, and '*Cladeiodon*'

In his second paper on the Triassic vertebrates from England, Huxley (1869) announced the first find from the Devon coast sections, a rhynchosaur jaw bone found at the Budleigh Salterton end of the section by William Whitaker, an employee of the Geological Survey of England. In an associated paper, Whitaker (1869) described the location and the succession of rocks between Budleigh Salterton and Sidmouth. These two papers confirmed the Triassic age of the Otter Sandstone Formation.

Further remains from the Sidmouth-Budleigh Salterton section were described by Seeley (1876), Metcalfe (1884), and Carter (1888). Seeley (1876) described some skull remains of a new species, *Labyrinthodon lavis*, further confirming the correspondence of the Devon sections with those already known around Warwick, but the fossils described by Metcalfe and Carter were fragmentary and unpromising.

Nothing more was heard of the Otter Sandstone Formation for some time, although Paton (1974) redescribed the English temnospondyls, including *Labyrinthodon lavis*. The breakthrough came in the 1980s, with the collecting efforts of Patrick Spencer, who showed that fossils could be found all along the coastal exposure of the Otter Sandstone Formation. His new finds were announced in a preliminary note (Spencer and Isaac, 1983), and then described in more detail, the rhynchosaur remains by Benton (1990), the fishes, temnospondyls, and smaller reptiles by Milner *et al.* (1990), the archosaurs by Benton and Gower (1997), and the procolophonids by Spencer and Benton (in press). Benton *et al.* (1994) gave an overview of the whole fauna, and compared it with the other known from the English Middle Triassic.

THE ENGLISH MIDDLE TRIASSIC

The dating of the red sandstones between Sidmouth and Budleigh Salterton was unclear for many years. Sedgwick (1829) recognized that the British New Red Sandstone was equivalent in part to the German Triassic and he considered some units equivalent to the German Buntsandstein and Keuper. Alberti (1834) formalized the three-part division of the Germanic Triassic ('tri' = three) as nonmarine Bunter, marine Muschelkalk, and nonmarine Keuper. Hull (1869) equated the English Bunter Sandstone with the German Buntsandstein (broadly Early Triassic in age) and the Lower Keuper Sandstone with the German Lettenkohle (latest Mid Triassic to early Late Triassic in age). He argued that a major unconformity in the British sequence corresponded to most of the Mid Triassic and represented the Muschelkalk.

The unconformity suspected by Hull (1869) does not exist. Palynological work (summarized by Warrington *et al.*, 1980) has shown that deposits of Mid Triassic age are present in Britain, where correlatives of the Muschelkalk, including brackish-water to littoral marine facies, occur in the upper part of the Sherwood Sandstone Group and lower parts of the overlying Mercia Mudstone Group.

Triassic deposits have a broad U-shaped outcrop in the English Midlands, with a continuation south-westwards to South Wales and Devon (Figure 1). Sediments were deposited in fault-bounded basins in southern and western Britain and on a more regionally subsiding shelf in eastern England. The general sedimentary pattern was complicated locally by the introduction of coarse-grained deposits along basin margins and the deposition of marine-intertidal sediments during Mid Triassic marine incursions. The widespread occurrence of transgressive intertidal facies of Mid Triassic age indicates extremely

low relief in central and southern England and suggests that the contemporary vertebrates were dispersing themselves in lowland areas close to sea level, a suggestion first offered in 1839 by Buckland, who proposed (1844) a palaeoenvironment of intertidal sandbanks.

THE OTTER SANDSTONE FORMATION

The geology and palaeontology of the Otter Sandstone Formation have been studied in some detail by a variety of investigators. Whitaker (1869) gave the first substantial account of the 'New Red' of east Devon and the discovery of a rhynchosaur jaw bone, while Lavis (1876), Metcalfe (1884) and Carter (1888) reported further on the sediments and the occurrence of vertebrate fossils between Sidmouth and Budleigh Salterton. Hutchinson (1879) reported a fossil plant from the sandstones near Sidmouth. Whitaker (1869), Ussher (1876), Irving (1888), Hutchinson (1906), and Woodward and Ussher (1911) presented geological sections of the coastal exposure of the sediments between Sidmouth and Budleigh Salterton, mostly composed from observations made on journeys along the coast in small boats; they termed the Otter Sandstone Formation the 'Upper Sandstone'.

More recent accounts of the sedimentology of the Otter Sandstone Formation, and associated horizons, have been presented by Henson (1970), Laming (1982), Leonard *et al.* (1982), Selwood *et al.* (1984), Mader and Laming (1985), Lorsong *et al.* (1990), Purvis *et al.* (1990), Purvis and Wright (1991), and Newell in Benton *et al.* (1994). The following summary is based on the overview by Benton *et al.* (1994), where further details may be found.

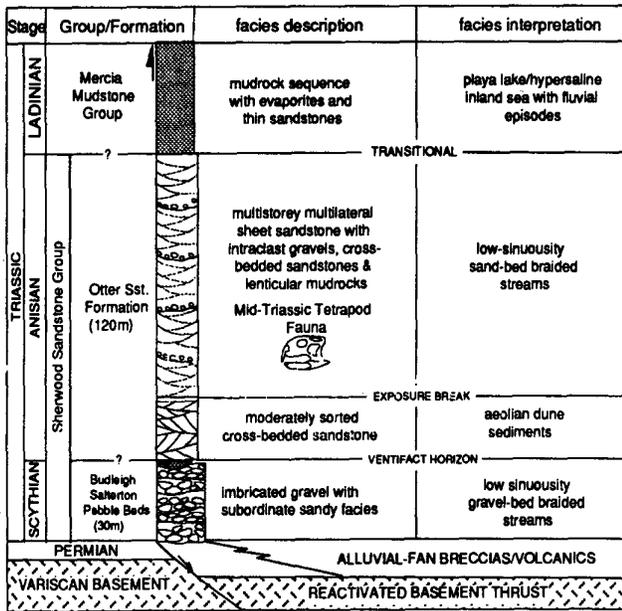


Figure 2. Sedimentology and interpreted depositional environments of the Otter Sandstone Formation and adjacent units, based on fieldwork by A. J. Newell in Benton *et al.* (1994).

The Otter Sandstone Formation comprises about 120 m of medium- to fine-grained red sandstones (Figure 2). These dip gently eastwards in the coast section, and the formation continues northwards to Somerset and eastwards as far as Hampshire and the Isle of Wight beneath younger Triassic sediments, reducing in thickness to 15 m in the east, and 30-60 m beneath Somerset (Holloway *et al.*, 1989). It rests unconformably on the Budleigh Salterton Pebble Beds (Figure 2), a 20-30 m thick unit of fluvial conglomerates derived from the south and west (Henson, 1970; Smith, 1990; Smith and Edwards, 1991). The contact, visible just west of Budleigh Salterton (Figure 3A) [SY 057 815], 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. This contact, and the layer containing ventifacts, has also been noted at inland exposures (Smith and Edwards, 1991, p. 74).

The lowest beds of the Otter Sandstone Formation, exposed west of Budleigh Salterton and in the middle of the foreshore there [SY 064 817], are red, rather structureless, well-sorted sandstones (Henson, 1970; Selwood *et al.*, 1984) (Figure 2).

At Otterton Point [SY 078 819] hard, calcite-cemented, cross-bedded sandstone units (less than 0.5 m thick) contain calcite-cemented rhizoliths up to 1 m deep and other calcrete formations (Figure 3D) (Purvis and Wright, 1991). Purvis and Wright (1991) attributed the large vertical rhizoliths to deep-rooted phreatophytic plants which colonized bars and abandoned channels on a large braidplain. Ussher (1876, p. 380) observed that the sandstones here "contain two or three conglomerate beds, and a few pebbles in false-bedded lines". Irving (1888, p. 153) described "an irregular band of breccia... intercalated with the sandstones, just above high-water mark", and containing fragments of slate, granite, sandstone, and quartzite. Woodward and Ussher (1911, pp. 10-11) traced this 'brecciated horizon' as far as Ladram Bay, 3.5 km to the north-east of Otterton Point.

Farther east, calcretes occur more sporadically, and the formation is dominated by sandstones in large and small channels (Figure 3C), with occasional siltstone lenses. The sandstones occur in cycles, often 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 (Figures 2, 3B).

Henson (1970), Laming (1982), and Mader and Laming (1985) interpreted the Otter Sandstone Formation as comprising fluvial and aeolian deposits. Sandstones near the base of the formation are aeolian (Figure 2), and accumulated in dunes produced by easterly winds (Henson, 1970), these being transverse barchanoid dune ridges in modern terminology. The middle and upper parts of the formation are of fluvial origin (Figure 2); sandstones 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, with impersistent rivers fed from reservoirs in breccia outwash fans elsewhere, in turn recharged by flash floods and episodic rainfall. Numerous calcrete horizons occur and indicate subaerial soil and subsurface calcrete formation in semiarid conditions (Mader and Laming, 1985; Lorsong *et al.*, 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. However, there is little evidence of complete aridity; desiccation cracks and pseudomorphs after halite are uncommon in the Otter Sandstone Formation (Lavis, 1876; Woodward and Ussher, 1911; Henson, 1970). The relative scarcity of plant fossils may reflect oxidizing conditions in an arid climate (Laming, 1982, p. 170).

Efforts to date the Otter Sandstone Formation have had to rely on comparisons of the vertebrates with those from other regions. A serious problem in this exercise is the marine Muschelkalk of central Europe which separates comparable nonmarine sediments of the Bunter and Keuper. Walker (1969), Paton (1974), Benton (1990), and others made comparisons with amphibians and reptiles from the Ladinian of Germany, while Milner *et al.* (1990) found more evidence for an Anisian age, based on the fishes, amphibians, and reptiles.

The Middle Triassic tetrapod-bearing sediments of the English Midlands have been dated by the use of miospores; in particular, the Bromsgrove Sandstone Formation of Bromsgrove and Warwick has been assigned an Anisian age (Warrington in Benton *et al.*, 1994). No miospores have been recovered from the Otter Sandstone Formation in Devon, and its age is poorly constrained palynologically by occurrences of Late Permian miospores in the lower part of the New Red Sandstone succession near Exeter (Warrington and Scrivener,

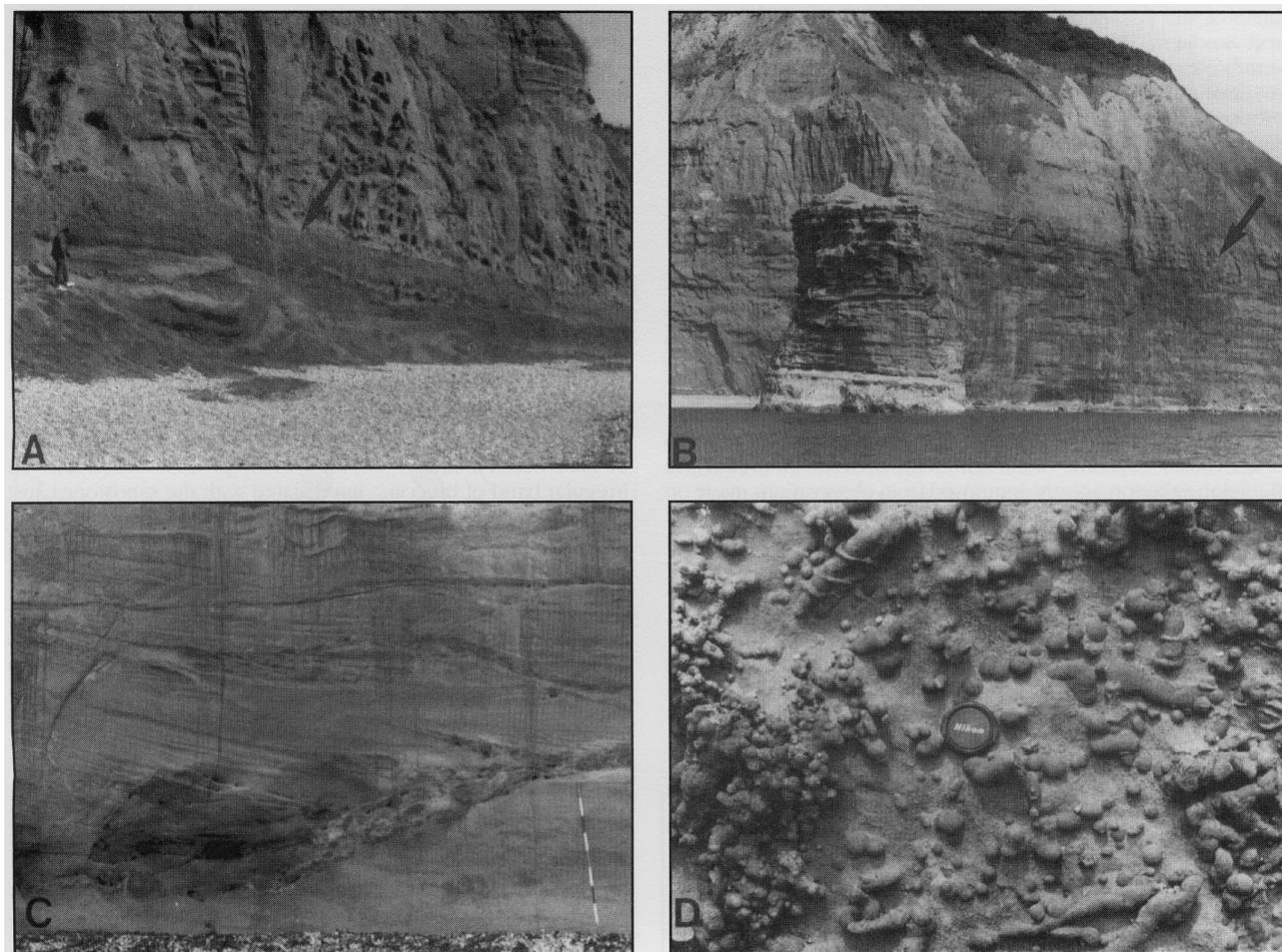


Figure 3. The sedimentology and stratigraphy of the Otter Sandstone Formation. A. The lower contact of the Otter Sandstone Formation with the Budleigh Salterton Pebble Beds (contact marked with an arrow), seen on the coast just west of Budleigh Salterton; note the person for scale. B. The upper contact of the Otter Sandstone Formation with the Mercia Mudstone Group (contact marked with an arrow), seen below Peak Hill, just west of Sidmouth. C. Mudclast-lined erosion surface and cross-bedded sandstones in the Otter Sandstone Formation in Chiselbury Bay; note the metre-pole for scale. D. Calcrete nodules exposed in a vertical cliff section in the Otter Sandstone Formation; the camera lens cap is 50mm in diameter. Photographs by A. J. Newell.

1988, 1990) and Carnian (early Late Triassic) miospores, 135 m above the Otter Sandstone Formation in the Mercia Mudstone Group (Warrington, 1971; Holloway *et al.*, 1989). Though palynological evidence is lacking in Devon, comparisons with the vertebrate faunas of the English Midlands support an Anisian age.

OCCURENCE AND TAPHONOMY OF THE OTTER SANDSTONE VERTEBRATES

Middle Triassic vertebrates have been found at numerous localities along the coast between Budleigh Salterton and Sidmouth (Figure 4). Several specimens collected in the 19th century came from below High Peak [SY 104 858], 2 km west of Sidmouth, and from the mouth of the River Otter, on its east bank [SY 077 820], just east of Budleigh Salterton. Since 1982, extensive collections have been made from at least 15 localities between Budleigh Salterton and Sidmouth [SY 0807 8212 to SY 1066 8639] and just east of Sidmouth [SY 1297 8730], with specimens being collected from fallen blocks of red sandstone and *in situ*, from horizons at the base of the cliff and on the foreshore (Spencer and Isaac, 1983; Benton, 1990; Milner *et al.*, 1990; Benton *et al.*, 1994). Some of the best recent finds of tetrapods have come from Ladram Bay and Chiselbury Bay, parts of the coast not noted as fossiliferous by the Victorian authors.

Recent collections of amphibian and reptile 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 south and west of Chiselbury Bay (Figure 4), tetrapods are less common. The bones are generally in a fine- to medium-grained reddish sandstone that often contains clasts of pinkish, greenish, or ochreous calcrete and mudflakes up to 20 mm in diameter. Fish specimens are more complete, and they are preserved in dark red siltstone, sometimes in association with plant remains and branchiopod crustaceans. Plant remains are preserved in iron oxide in all the lower-energy deposits.

The only specimens found *in situ* by Spencer and Isaac (1983), indeterminate bone fragments, came from 'the lowest of three intraformational conglomerates'. Since 1983, four rhynchosaur specimens (EXEMS 60/1985.284, 285, 292, and 7/1986.3) were collected *in situ* from a single horizon at beach level, and a partial rhynchosaur skeleton was found at the top of the foreshore exposures in Ladram Bay in 1990 (EXEMS 79/1992). Fossils probably occur at numerous levels in the Otter Sandstone Formation, but most have been found in fallen blocks on the shore, and the original horizons in the cliffs cannot be identified.

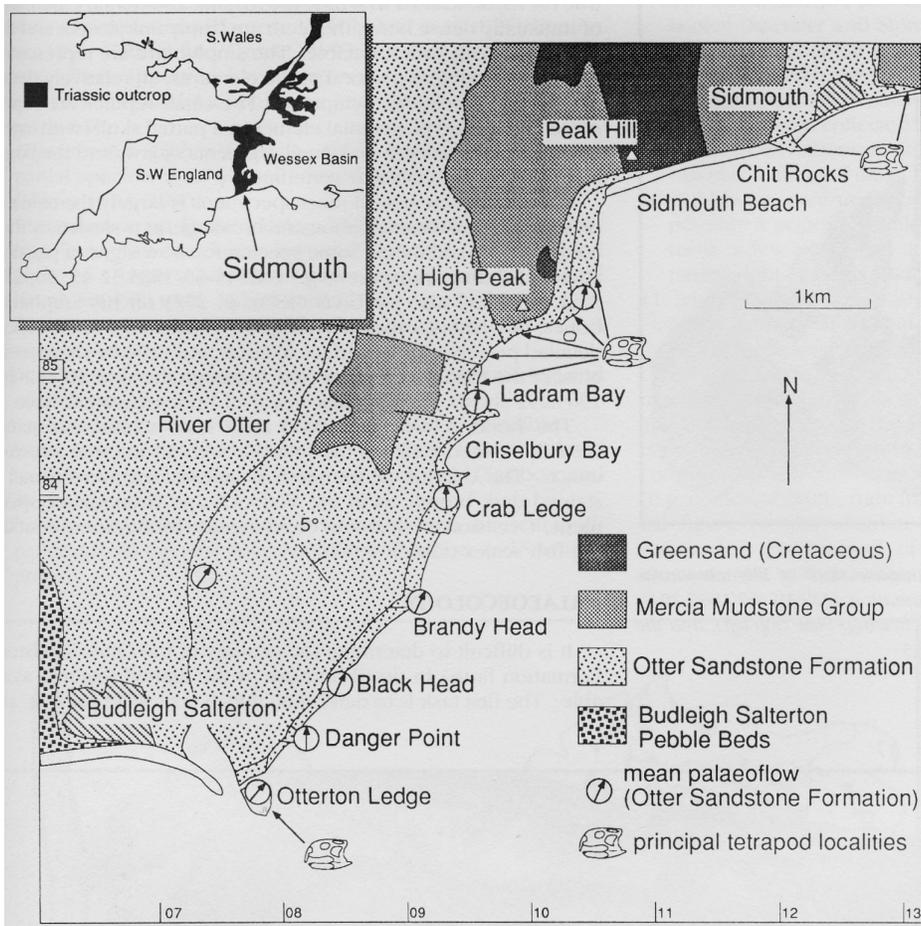


Figure 4. Map of the coastal outcrop of the Otter Sandstone Formation between Sidmouth and Budleigh Salterton, Devon. The major Triassic formations are indicated, together with mean fluvial palaeoflow directions, and principal tetrapod localities. Based on Benton et al. (1994).

The most clearly localized of the older finds is a *Rhynchosaurus* jaw (BGS(GSM) 90494) recovered from a large displaced block on the east bank of the River Otter [SY 0775 8196] "where the sandstone is somewhat brecciform" (Whitaker, 1869, p. 156). Metcalfe (1884) reported white fragments, which he identified as bone, in the "harder parts of the sandstones, at numerous points near Budleigh Salterton and Otterton Point".

The Victorian authors believed that one or more discrete bone beds occurred at the eastern end of the outcrop. Lavis (1876) and Metcalfe (1884) placed it "about 10 feet from the top of the sandstone"; Hutchinson (1906) and Woodward and Ussher (1911) placed it "about 50 feet below the base of the Keuper Marls", some 40 feet (13 m) lower in the section.

Lavis (1876) made his finds in fallen blocks from an "ossiferous zone" consisting of up to four beds, and "characterized by lithological differences, inasmuch as the matrix is composed of much coarser sandstone, containing here and there masses of marl varying in size from that of a pea to that of a hen's egg... In these beds ripple-marks are very plentiful. The fragments of bone which are found in this zone seem to be very slightly waterworn". 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' which 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 a bone-bed can be seen today, and there is no evidence that one ever 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 isolated elements - jaws, teeth, partial skulls, or single postcranial bones. Exceptions are the partial articulated skull and lower jaws of *Rhynchosaurus spenceri* (EXEMS 60/1985.292; Figure 5), the associated humerus, radius, and ulna of that species (EXEMS 60/1985.282), two sets of vertebrae (EXEMS 60/1985.15, 57), and the recently-collected partial rhynchosaur skeleton (EXEMS 79/1992), which comprises much of the trunk, the pelvis, and the hindlimbs, with the bones in close association, but mostly slightly disarticulated.

About half the identifiable tetrapod bones are rhynchosaur remains, and most are parts of the skull, especially the jaw elements (Figure 6). This is a phenomenon of preservation, rather than selective collecting, and probably reflects the high preservation potential of teeth and jaw bones. This is especially true for rhynchosaur in which

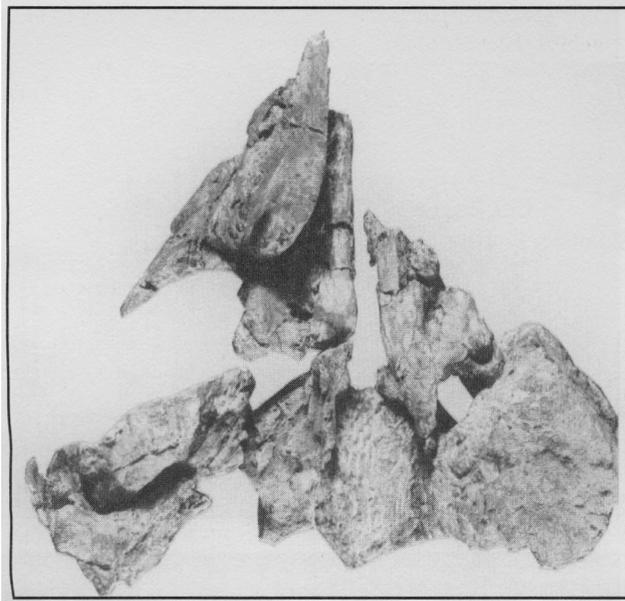


Figure 5. Ventral view of the most complete skull of *Rhynchosaurus spenceri* from the Otter Sandstone Formation (EXEMS 60/1985.292), showing the right maxilla in occlusal (chewing) view (top left), and the posterior angles of the skull. Scale x 0.55

the maxilla and dentary are made of unusually dense bone, the teeth are firmly ankylosed, and the bone is virtually indestructible. The amphibians are represented mainly by skull and pectoral girdle elements, all relatively dense and with characteristic sculpture. The small reptiles are represented by limited postcranial elements, a partial skull (with lower jaws articulated), teeth and small segments of jaw, and the larger archosaur(s) by teeth and vertebrae.

The incompleteness of most specimens is largely the result of predepositional disarticulation and breakage, as is shown by their context in the sediment. Some specimens show signs of possible abrasion during transport (e.g., EXEMS 60/1985.37-45, 56, 284, 312), as noted also by Lavis (1876, p. 277) on his amphibian bones, but others, especially the jaws of procolophonids, show detailed preservation of surface features and delicate sharp teeth. Most of the fossils are undistorted, although the skull EXEMS 60/1985.292 shows slight displacement of bones at suture lines.

The bone is well preserved as a hard whitish substance (usually stained pink by the matrix), with all internal structure intact. The dentine of the teeth is yellow, and the enamel is stained dark brown, as in the Warwick and Bromsgrove specimens. Occasional calcareous coprolites are found, some containing fish scales (Carter, 1888).

PALAEOECOLOGY

It is difficult to determine the ecology of the Otter Sandstone Formation fauna in detail because of the limited material available. The first task is to determine which taxa were present, and this can

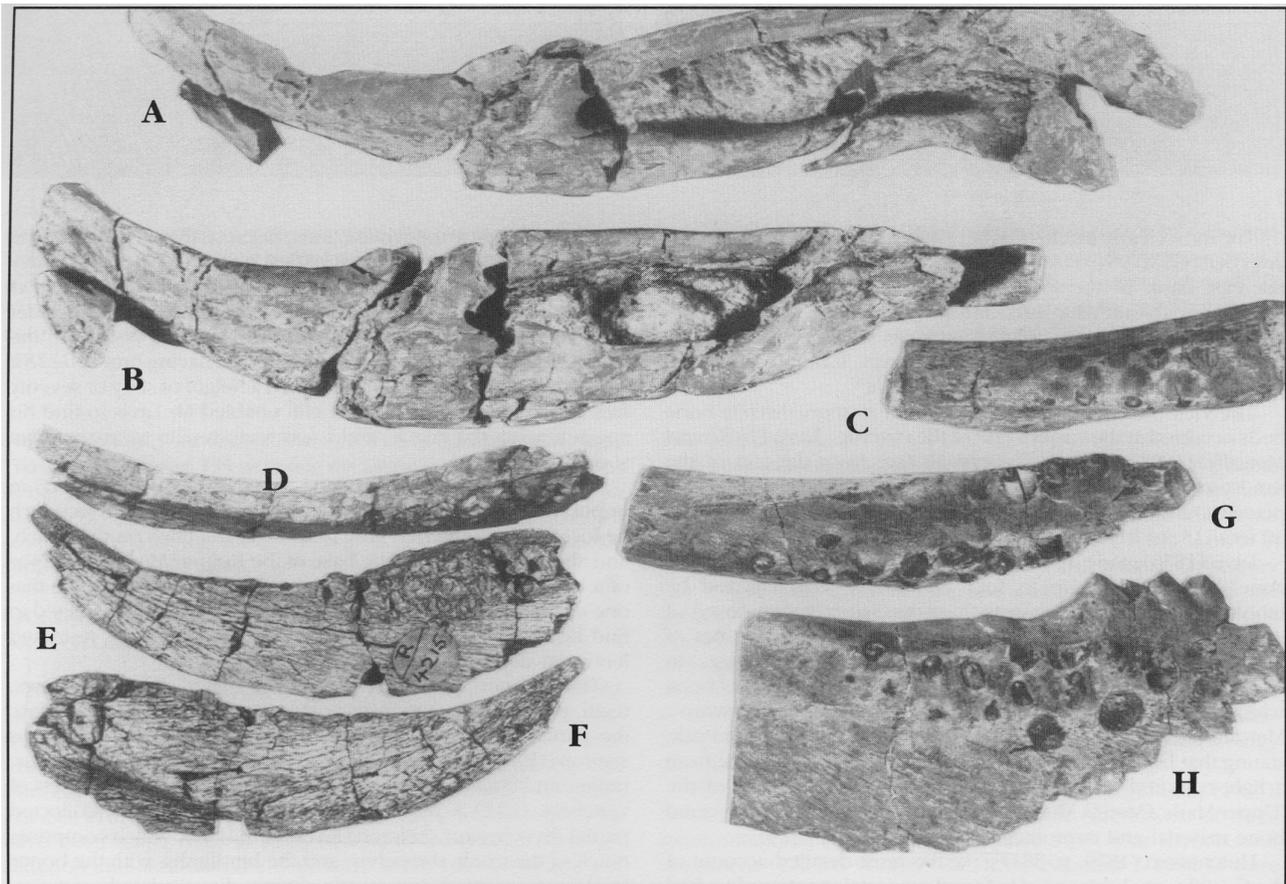


Figure 6. Remains of the lower jaw of *Rhynchosaurus spenceri*. (A, B) Right dentaries (EXEMS 60/1985.292) in occlusal (A) and medial (B) views. (C- E) Anterior part of the right dentary (BMNH R9190 [formerly R4215]) in occlusal (C), medial (D), and lateral (E) views. (F) Fragment of the tooth-bearing portion of a right dentary (EXEMS 60/1985.56) in occlusal view. (G, H) Partial right dentary, showing several tooth rows (EXEMS 60/1985.313), in occlusal (G) and medial (H) views. Scales: A,B x 0.8; C,G,H, x 1.6; D,E,F x 1.3.

now be done fairly completely as a result of current work on the new collections (Benton, 1990; Milner *et al.*, 1990; Benton *et al.*, 1994; Benton and Gower, 1997; Spencer and Benton, in press). There appear to have been one species of fish, two or three of temnospondyl amphibians, and eight or nine of reptiles (Figures 5-9).

1. *Dipteronotus cyphus* Egerton, 1854, several complete and partial specimens of a small, deep-bodied neopterygian fish (Milner *et al.*, 1990).
2. '*Mastodonsaurus lavisi*' (Seeley, 1876) *nomen dubium*, skull fragments, part of a lower jaw, and elements of the pectoral girdle of a large capitosaurid temnospondyl; estimated skull length 500-600 mm. Milner *et al.* (1990) argued that the type specimen of *M. lavisi* was indeterminate, and the taxon is a *nomen dubium*.
3. *Eocyclotosaurus* sp., remains of a skull, about 150 mm long, and other fragments.
4. Capitosaurid *incertae sedis*, posterior part of a mandible.
5. *Kapes* new species, partial remains of a skull, several isolated tooth-bearing elements, and (?) an interclavicle (Spencer and Storrs, in press).
6. Procolophonid *incertae sedis*, jaw remains with different tooth patterns from the new species of *Kapes* (Spencer and Storrs, in prep.).

7. Lepidosauromorph, new taxon, two right dentaries from a tiny animal (Spencer and Storrs, in prep.).

8. *Tanystropheus* sp., a small tooth (Milner *et al.*, 1990).

9. *Rhynchosaurus spenceri* Benton, 1990, skull and mandible remains, isolated maxillae, and postcranial elements, and a partial skeleton collected in 1990 (EXEMS 79/1992); a moderate-sized rhynchosaur with a skull length of 40-175 mm (mean, 116 mm; estimated mean body length 0.8 m; range 0.4-1.3 m).

10. Archosaur *incertae sedis*, one or more taxa of archosaurs, possibly a poposaurid like *Bromsgroveia*, represented by 15 teeth, a few vertebrae, a midline skull roof element, and a partial right ischium (Benton and Gower, 1997).

11. ?ctenosauriscid archosaur, a long neural spine, possibly part of the dorsal 'sail'; this identification is provisional (Milner *et al.*, 1990; Benton *et al.*, 1994).

It is possible to estimate the relative importance of each of the major groups of tetrapods as represented in existing collections, and this may be approached in two ways. The normal approach is to assess the minimum number of individuals (MNI) by counting up the most-represented elements in the collections (e.g. complete skulls, right maxillae, left femora) as an unequivocal figure for the absolute minimum number of individuals required to produce all of the known fossils. The second measure, the non-redundant maximum number of individuals (NRMAX), is based on the initial

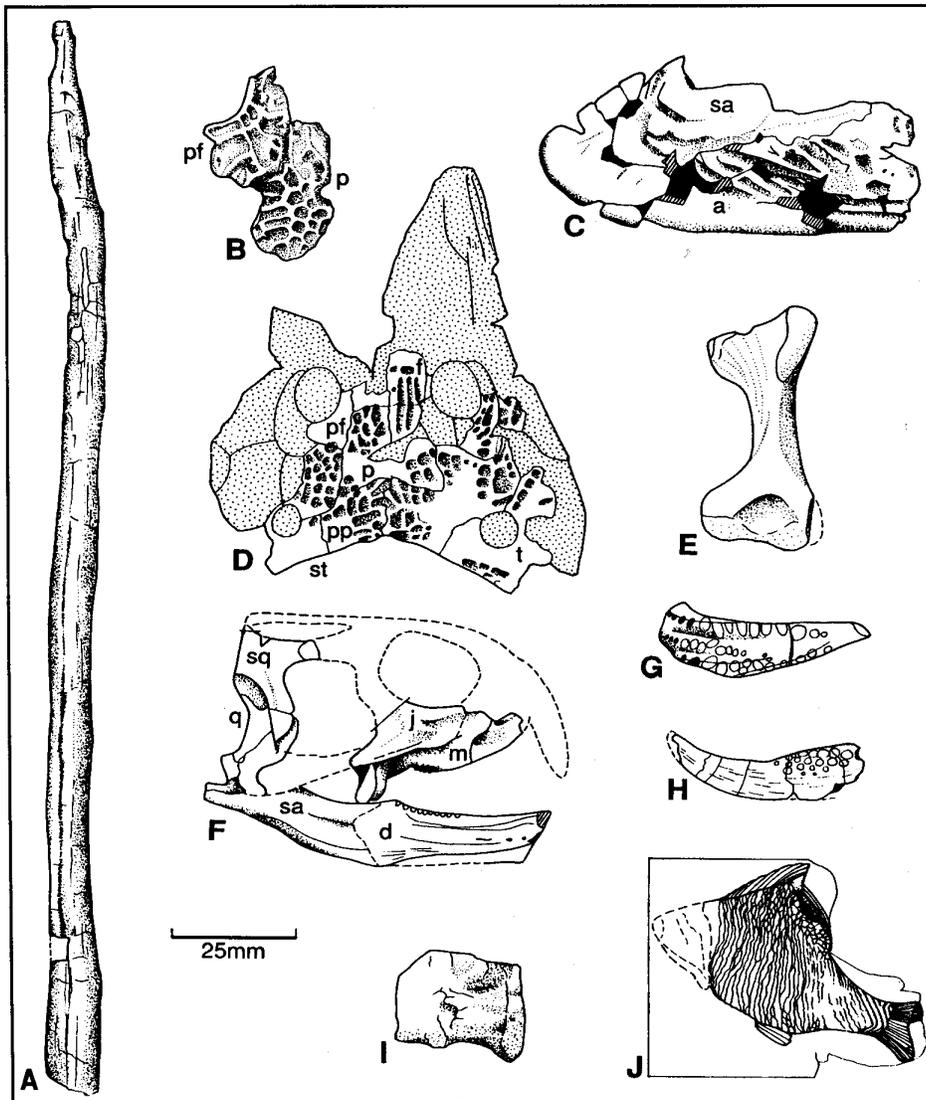


Figure 7. Larger elements of the Otter Sandstone Formation fauna from Devon. A. Spine of an unknown vertebrate, possibly a dorsal neural spine of a ctenosauriscid archosaur (EXEMS 60/1985.88). B. Fragment of the skull roof of *Mastodonsaurus lavisi* in dorsal view (EXEMS 60/1985.287). C. Posterior portion of a right mandible of an unknown capitosaurid, in lateral view (EXEMS 60/1985.78). D. Incomplete skull roof of *Eocyclotosaurus* sp., in dorsal view (EXEMS 60/1985.72). E. Remains of *Rhynchosaurus spenceri*; left humerus in ventral view (EXEMS 60/1985.282) (E), restored skull in right lateral view (EXEMS 60/1985.292) (F), right maxilla in ventral view (EXEMS 60/1985.292) (G), and right dentary in lingual view (BMNHR9190) (H). I. Vertebra of an archosaur (BRSUG 26206). J. The neopterygian ('palaeonisciform') fish *Dipteronotus typhus* (EXEMS 60/1985.293). Abbreviations: a, angular; d, dentary; f, frontal; j, fugal; m, maxilla; p, parietal; pf, postfrontal; pp, postparietal; q, quadrate; sa, surangular; sq, squamosal; st, supratemporal; t, tabular. (A, I, original; B-D, J, after Milner *et al.*, 1990; E-H, after Benton, 1990.)

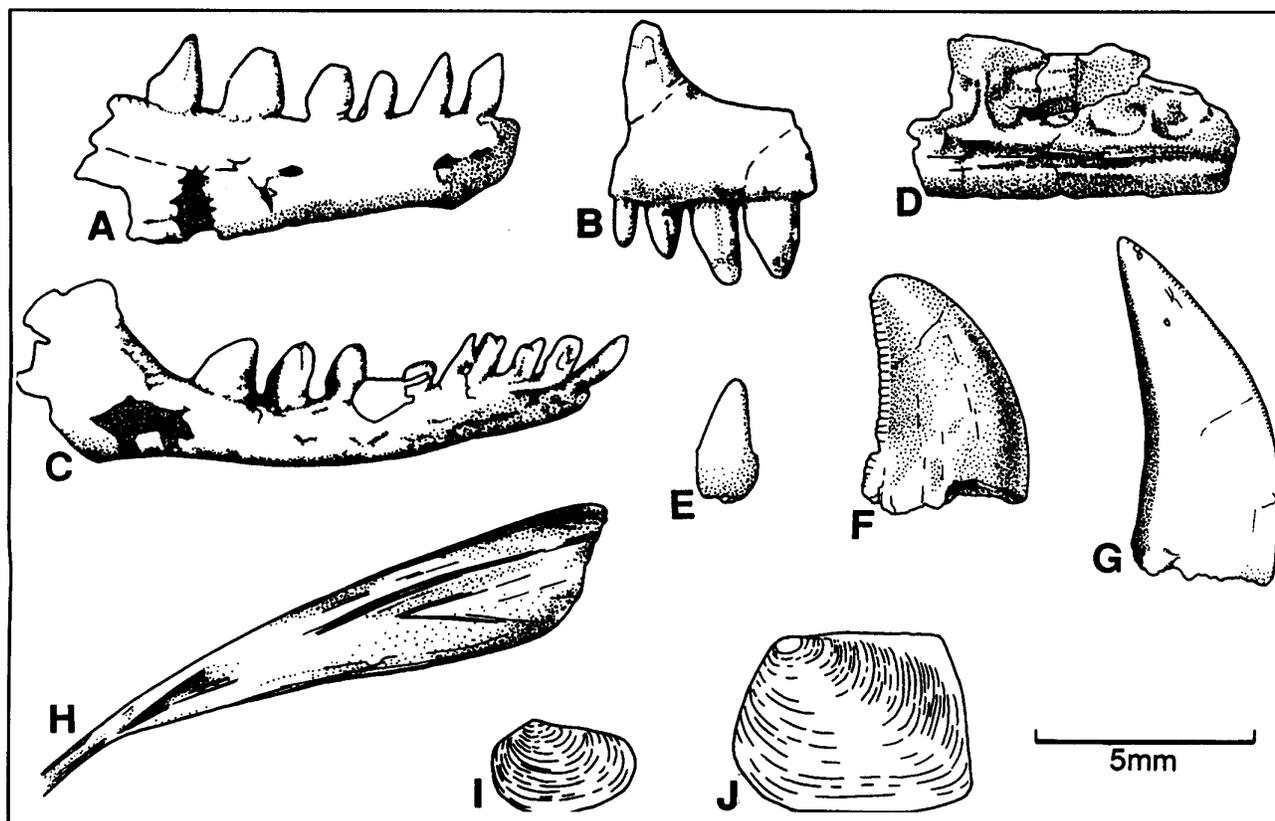


Figure 8. Smaller elements of the Otter Sandstone Formation fauna of Devon. Right dentaries (A, C) and a left maxilla (B) of a procolophonid, all in lateral view (EXEMS 60/1985.311, 3, and 154). D. Dentary fragment of an unknown small pleurodont reptile, showing pits for teeth, in lingual view. E. Tooth of ?*Tanystropheus*, showing small accessory cusps (EXEMS 60/1985.143). F, G. Recurved teeth of two kinds of unknown archosaurs (BRSUG 26206, 26207). H. Unidentified insect wing (BRSUG 26225). I, J. Carapaces of the conchostrac Euestheria (BRSUG 26227). (A-C, E, after Milner et al., 1990; D, F-J, original.)

assumption that every bone found separately represents a different individual (Benton *et al.*, 1994). An attempt is made to discover all isolated bones that can be fitted together, or which can be associated as being probably the remains of a single individual.

It is likely that the MNI underestimates the number of individuals present in an ancient fauna, while the NRMAX overestimates the number. In cases such as the Otter Sandstone fauna, where isolated elements dominate, the NRMAX probably gives a better estimate of true numbers, especially where detailed collecting data are available. For example, the Devon tetrapods have been collected from numerous sites along a 7 km coastal section, and site information is taken into account in associating material: a left and a right maxilla found 4 km apart are unlikely to come from the same individual, although the MNI figure would imply that! The NRMAX figures are used here.

It is not clear, however, which of these measures should give the best *proportional* estimates. There is no reason, for example, why an MNI value based on skulls for one species should be in proportion with that based on right femora for another; indeed, it is more likely that such figures, based of necessity on different skeletal elements, will not be in proportion to true ancient diversities. The NRMAX could be a better proportional estimator for preservation of ancient faunas if all taxa and finds are equally well documented. Of course, both the MNI and NRMAX are influenced by preservation factors, and neither can give a good estimate of the original *living* faunal compositions.

The composition of the Devon fauna (Benton *et al.*, 1994, figure 7.16) is similar to those from Warwick and Bromsgrove, but very different from the Grinshill 'fauna', which consists of one species

only, *Rhynchosaurus articeps*, although footprints indicate a more varied mix. Comparisons with the Bromsgrove fauna are difficult because fossils are so sparse, and so incomplete that many are not clearly identifiable. In both the Devon and the Warwick faunas, the rhynchosaur *Rhynchosaurus* dominates (48% and 31% of all individuals respectively). Amphibians are marginally less abundant in Devon (25%) than in Warwick (29%), and archosaurs likewise (18% in Devon, 31% at Warwick).

It is possible to infer likely food chains for the Otter Sandstone fauna (Figure 10). The top carnivores in Devon were archosaurs, probably a rauisuchian like *Bromsgroveia* from Warwick and Bromsgrove, and some others, which preyed on the temnospondyl amphibians, the rhynchosaurs, and the smaller reptiles. The amphibians presumably fed almost exclusively on fishes. The rhynchosaurs were herbivores, feeding on elements of the equisetalean and coniferalean flora found in association at Bromsgrove. Smaller (100-150 mm) procolophonid reptiles may also have had herbivorous diets, feeding on low herbaceous plants, so far unrepresented in Mid Triassic collections. The lepidosauromorph and the tanystropeid may have fed on arthropods, represented by scorpions from Bromsgrove.

Fishes are known from the Otter Sandstone, specimens of the deep-bodied perleidid 'palaeonisciform' bony fish *Dipteronotus*, about 60-70 mm long, represented by several entire specimens (Milner *et al.*, 1990), and coprolites containing fish scales (Carter, 1888). The fish fauna might have been more extensive, by comparison with those from Warwick and Bromsgrove, which have yielded specimens of the shark *Acrodus*, the lungfish *Ceratodus*, and the perleidid *Dipteronotus typhus*.

Rare plant remains, including rhizomes and stems referable to

Schizoneura, and invertebrate remains, including arthropod cuticle, an insect wing, and branchiopod crustaceans (*Euestheria*, *Lioestheria*), have been found in the Otter Sandstone Formation (Figure 8; Benton *et al.*, 1994). Rhizoliths indicate the existence of a contemporary indigenous vegetation interpreted as comprising conifers and phreatophytic plants (Purvis and Wright, 1991). Plants and invertebrates are better known from Bromsgrove (Old *et al.*, 1991), probably a comparable assemblage. These include giant horsetails such as *Equisetites arenaceus*? and *Schizoneura paradoxa* (roots, pith casts, leaves), and conifers and conifer-like plants such as *Chiropteris digitata*?, *Yuccites vogesiacus* (leaves and stems), *Voltzia*? (pith casts and decorticated stems), *Aethophyllum*, and cones (*Strobilites*, *Willisiostrongobromsgrovensis*, *W willisi*). Invertebrates include the annelid *Spirorbis*, a bivalve, *Mytilus*?, the branchiopod crustacean *Euestheria*, and several species of scorpions.

Psilophyte plants in the associations from Worcestershire and Devon probably populated damp tracts bordering river channels or in floodplain areas; the conifers may reflect drier habitats. Scorpions signify dry terrestrial habitats, but the crustaceans indicate the existence of seasonal pools of fresh to brackish water. Temnospondyl amphibians indicate the existence of at least seasonal bodies of fresh water, necessary for breeding, on a floodplain that was inhabited also by herbivorous rhynchosaurs and procolophonids, and the carnivorous rauisuchians.

SIGNIFICANCE OF THE DEVON TETRAPODS

The tetrapods from Devon now represent a reasonably extensive

fauna, important for two reasons, (1) filling a gap in knowledge, and (2) contributing to our understanding of major faunal change through the Triassic.

Terrestrial tetrapod faunas of Anisian age are rare worldwide, and especially in Europe (Ochev and Shishkin, 1989). The rarity in Europe is explained by a major marine episode represented by the Muschelkalk over Germany, central Europe, and parts of France and the Iberian peninsula. The only other nonmarine tetrapod faunas of Anisian age from Europe are isolated remains in the uppermost Bunstansandstein of Germany and the more extensive faunas from the Donguz Svita of the Urals in Russia. Elsewhere in the northern hemisphere, one tetrapod fauna of probable Anisian age is known from the Holbrook Member of the Moenkopi Formation, North America, but remains are sparse.

Terrestrial tetrapod faunas of Anisian age are commoner in Gondwana. These include the basal member of the Zarzaitine Formation in North Africa, the Ermaying Formation of China, the Yerrapalli Formation of India, possibly the Manta Formation of Tanzania, the Ntawere Formation of Zambia, the Omingonde Formation of Namibia, and possibly the 'Cynognathus Zone' of South Africa and the Puesto Viejo and Rio Mendoza formations of Argentina, the last two traditionally usually dated as Olenekian (= late Scythian), that is, Early Triassic (e.g. Anderson and Cruickshank, 1978; Benton, 1983), but re-dated by comparison with the Russian faunas as Anisian (Ochev and Shishkin, 1989; Shubin and Sues, 1991).

The Otter Sandstone Formation shares some of its components with faunas from other parts of the world. The temnospondyl *Eocyclotossaurus* is known also from the Ober Bunstansandstein of

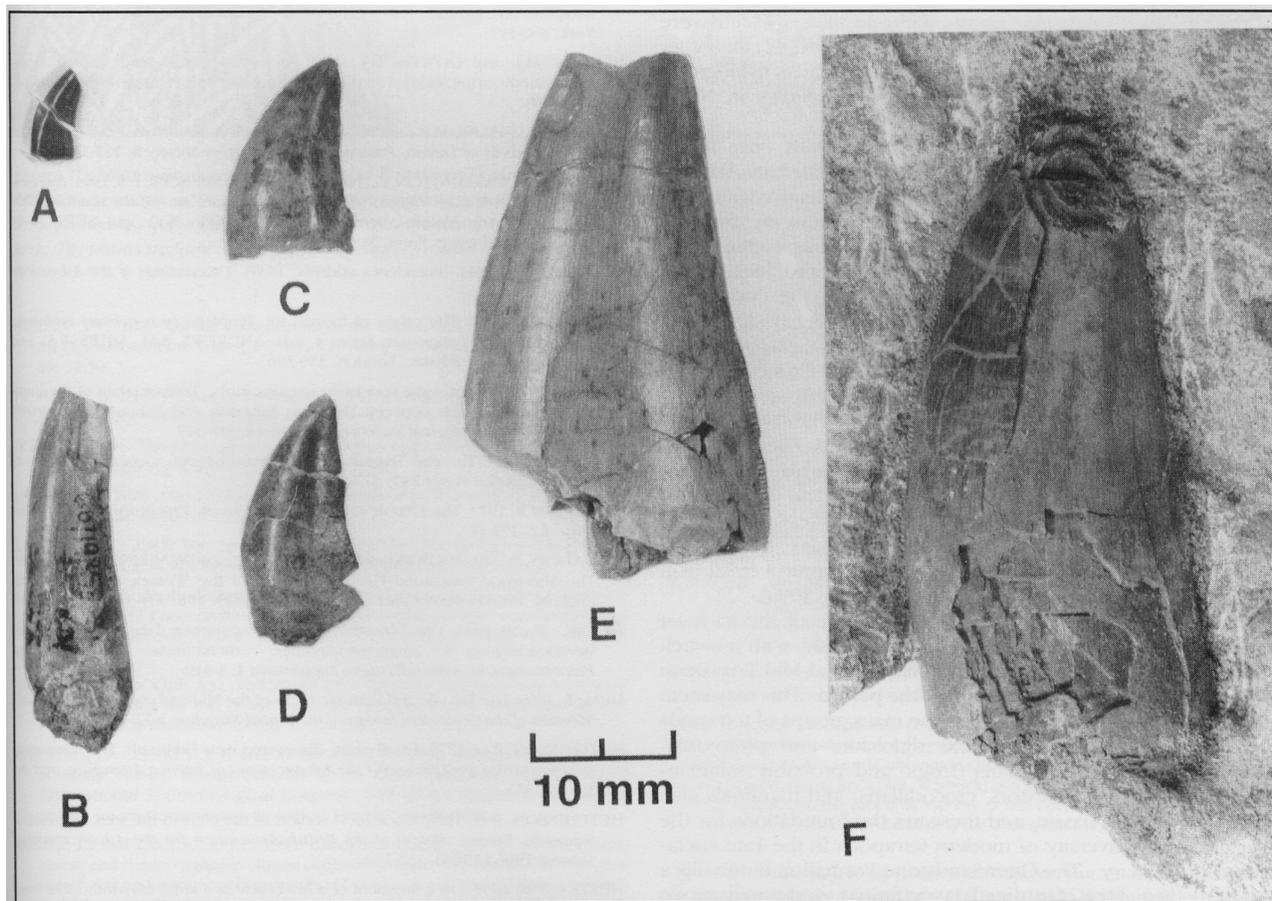


Figure 9. Archosaur teeth from the Mid Triassic of Devon, showing four of the five types. A, Type-1 tooth, tiny and elongate, EXEMS 60/1985.115. B, Type-3 tooth, long and slender, EXEMS 60/1985.28. C, D, Type-4 teeth, short and broad, EXEMS 60/1985 (C) and EXEMS 60/1985.76 (D). E, F, Type-5 teeth, large, EXEMS 60/1985.177 (E) and BRSUG 26212 (F).

Germany, the Holbrook Member of North America, and the Zarzaitine Formation of North Africa (Ochev and Shishkin, 1989). Rhynchosaurs of possible Anisian age have been reported only from the Manda Formation (*Stenaulorhynchus*) and Yerrapalli Formation (*Mesodapedon*). This is an unusual observation since rhynchosaurs are the commonest element of the Otter Sandstone Formation fauna, but they are absent in the northern hemisphere outside England. The procolophonid *Kapes* is shared between the Otter Sandstone Formation and the Yarenskian Gorizont (upper Olenekian) and the Donguz Svita (Anisian) of Russia (Spencer, in press).

The Otter Sandstone fauna expands current understanding of tetrapod faunal evolution during the Triassic (Benton, 1983; Shubin and Sues, 1991; Benton, 1994a, b). After the massive late Permian extinction event(s), many major groups of tetrapods disappeared, most notably several temnospondyl groups, the pareiasaurs, large herbivores, and most lineages of mammal-like reptiles. Ecosystems were destroyed worldwide, with the loss of most medium and all large herbivores, and all medium and large carnivores. Earliest Triassic faunas worldwide were dominated by the medium-sized herbivorous dicynodont *Lystrosaurus*, but several groups of small synapsids, diapsids, and anapsids that had survived the mass extinction, diversified and slowly added complexity to terrestrial ecosystems. The Otter Sandstone Formation fauna, dated as Anisian, and hence less than 10 Myr after the end of the Permian, shows this diversification, with Palaeozoic survivors like the temnospondyls, procolophonids, and prolacertiforms, but a number of essentially new Triassic groups, especially the rhynchosaurs and archosaurs. The Otter Sandstone Formation fauna is typical of the global picture, since faunas were essentially cosmopolitan (Shubin and Sues, 1991), but it is unusual in two ways: (1) like other European Triassic faunas, it lacks synapsids (mammal-like reptiles), which were abundant in North America and in Gondwana; and, (2) like other British Triassic faunas, it is dominated by rhynchosaurs, a group not known elsewhere in Europe, only sporadically in North America, but abundantly in Gondwana.

These Middle Triassic faunas continued with only minor variations into the Carnian, the earlier part of the Late Triassic. Many Carnian faunas continued to be dominated by rhynchosaurs; temnospondyl amphibians, rauisuchian archosaurs, dicynodonts and other synapsids, procolophonids, and the like continued as key elements (Benton, 1983, 1994a, b; Shubin and Sues, 1991). New forms included very rare dinosaurs. At the end of the Carnian, some 220 Myr ago, the rhynchosaurs, dicynodonts, and chiniquodonts, some families of temnospondyls, and some other reptile families disappeared. This was a sizable extinction event in terms of the loss of diversity, but it was especially serious in the loss worldwide of all medium and large herbivores, the rhynchosaurs, dicynodonts, and chiniquodonts (Benton, 1983, 1986, 1993, 1994a, b). Following the end-Carnian extinction event, new tetrapod groups radiated, the dinosaurs, crocodylomorphs (including, later, the crocodiles), pterosaurs, lepidosaurs (including ancestors of the lizards), turtles, and mammals. This postulated extinction event is controversial (e.g. Olsen and Sues, 1986; Sepkoski, 1989; Hallam, 1990).

Tetrapod evolution on land underwent one of its most traumatic episodes of change during the Triassic, with a switch from essentially Palaeozoic taxa in the Early and Mid Triassic to essentially modern taxa by the end of the period. This may seem an unusual statement, since two of the main groups of tetrapods at the end of the Triassic were dinosaurs and pterosaurs. However, modern amphibians (frogs, and probably salamanders), turtles, lizard ancestors, crocodylians, and mammals also originated in the Triassic, and these set the foundations for the later growth in diversity of modern tetrapods in the Late Cretaceous and Tertiary. The Otter Sandstone Formation fauna fills a gap in the sequence of earlier Triassic faunas, and it may prove critical in making stratigraphic and palaeogeographic links between Russian and North American faunas, and between Laurasia and Gondwana.

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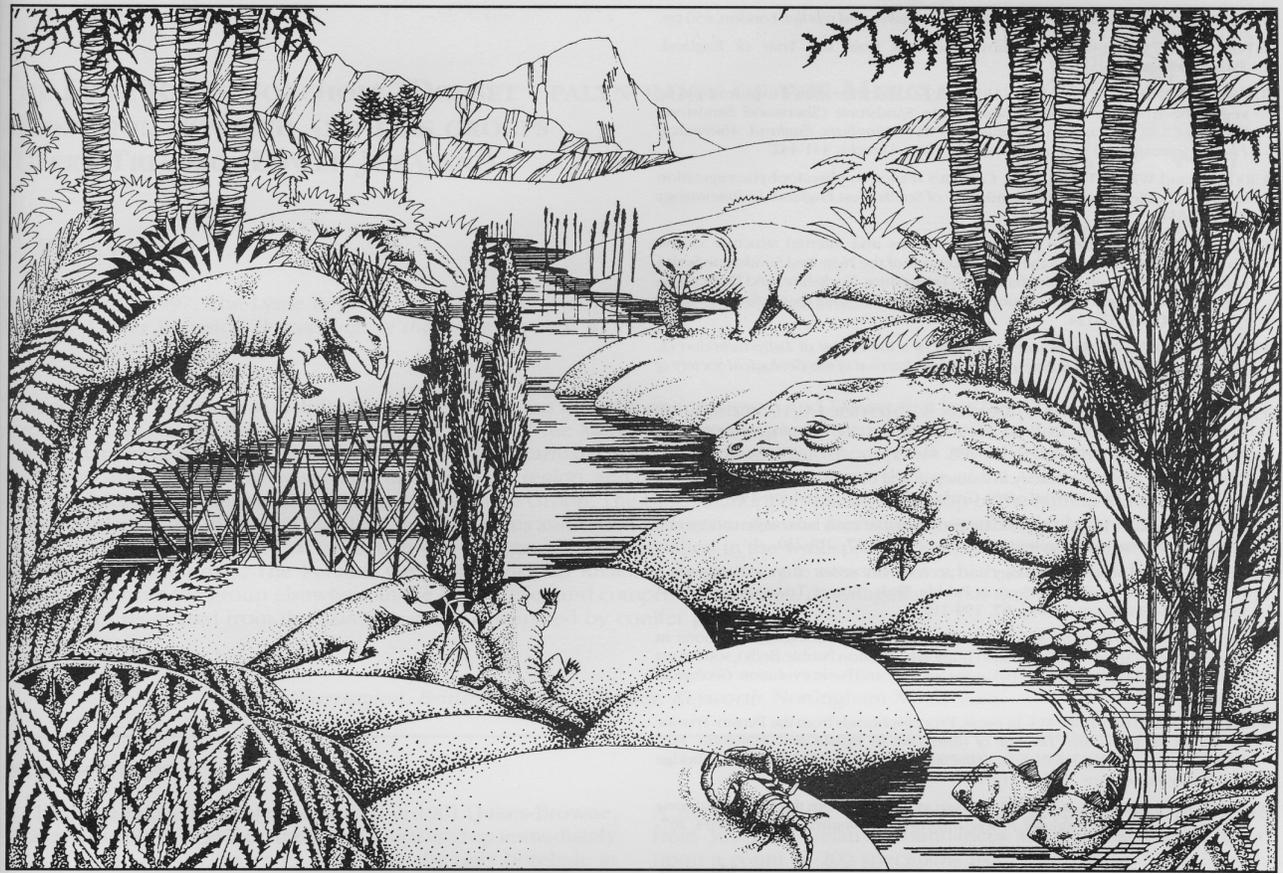


Figure 10. Imaginary scene during the Mid Triassic in Devon, based on specimens from the Otter Sandstone Formation between Sidmouth and Budleigh Salterton. A scorpion (mid-foreground) contemplates a pair of procolophonids on the rocks. Opposite them, a hefty temnospondyl amphibian has spotted some palaeonisciform fishes, *Dipteronotus*, in the water. Two *Rhynchosaurus* stand in the middle distance and, behind them, a pair of *rauisuchians* lurk. The plants include *Equisetites* (horsetails) around the waterside and *Voltzia*, a conifer tree. Drawn by Pam Baldaro, based on her colourpainting.

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