Read at the Annual Conference of the Ussher Society, January 1993

A NEW RHYNCHOSAUR FROM THE MIDDLE TRIASSIC OF DEVON

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Benton, M. J., Hart, M. B. and Clarey, T. 1993. A new Rhynchosaur from the Middle Triassic of Devon. *Proceedings of the Ussher Society,* **8**, 167-171.

A new specimen of *Rhynchosaurus spenceri* Benton, 1990 is described. Rhynchosaurs were medium sized, bulky, herbivores common world-wide in the mid-Triassic. This new specimen adds to evidence of the mid-Triassic age of the Otter Sandstone Formation of Ladram Bay, south-eastern Devon. It has been deposited in the Royal Albert Museum, Exeter, where it is registered as EXEMS 79/1992. The new specimen is the most complete yet found in Devon.

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INTRODUCTION

The Otter Sandstone Formation of Devon has yielded important collections of fossil fishes, amphibians and reptiles (Benton, 1990; Milner *et al.*, 1990; Benton *et al.*, 1993), but few of these finds include articulated parts of skeletons. We report here the most significant, articulated specimen yet found; a partial skeleton of a rhynchosaur.

The specimen was discovered in April 1990 in Ladram Bay [SY 098 852; Figure 1] in red sandstones of the Otter Sandstone Formation (Middle Triassic) by a student field party from the Department of Geological Sciences of the University of Plymouth. It was located *in situ* on a sandstone ledge surrounded by shingle.

Following excavation size, the specimen was passed to M.J.B and Mr Patrick Spencer of Bristol University for further investigation, and was identified as the rhynchosaur *Rhynchosaurus spenceri* Benton, 1990. At this time, the bones were enclosed in six main blocks of sandstone, three of which clearly fitted together, and a number of other smaller pieces. Subsequently it was prepared and conserved by Mr David B. Hill, then Conservator in Bristol City Museum. Cleaning of the sandstone exposed a great number of bones that had previously been concealed. The specimen went on display in the 'Dawn of the Dinosaurs' exhibition in the City of Plymouth Museum from April 1991 to January 1992, and in the Leicestershire Museum in March and April, 1992. It was donated by M.B.H to the Royal Albert Museum, Exeter, where it is registered as EXEMS 79/1992.

THE SHERWOOD SANDSTONE GROUP AND ITS FOSSILS

Mid-Triassic tetrapods were first detected in central Germany and in the Cheshire-Liverpool area in the 1830s in the form of footprints. The first bony remains were found in about 1840 in two locations; Grinshill, just north of Shrewsbury, and from various quarries around Warwick and Leamington Spa. These included remains of a small reptile named *Rhynchosaurus articeps* and a more diverse assemblage of amphibian and reptile bones (Owen, 1842). These included rhynchosaur bones, but they were only recognised as such by Huxley (1869), and the Warwick species named as *Rhynchosaurus brodiei* by Benton (1990).

The first indication of a reptile fauna in the Devon Triassic came in a paper by Huxley (1869), in which he described rhynchosaur jaw bones that were clearly very similar to the Warwick ones, and by Whitaker (1869), who described the geology of the red sandstones between Sidmouth and Budleigh Salterton (Figure 1). Several authors in late Victorian times reported further finds of amphibian and reptile bones (e.g. Seeley 1876; Metcalfe 1884; Carter 1888), but the whole stretch of coastline seems to have been practically ignored until the 1980s. Then, Spencer and Isaac (1983) reported a substantial number of finds of deep-bodied bony fishes, large fish-eating temnospondyl amphibians, tiny procolophonids, meat-eating archosaurs, and others, most of them now in Exeter Museum. The fishes, amphibians, and most of the reptiles were described by Milner *et al.* (1990), and the rhynchosaur by Benton (1990).

THE NEW SPECIMEN

The new rhynchosaur specimen adds a great deal to our knowledge of *Rhynchosaurus spenceri*. Before its discovery, 24 other specimens had been found, mainly isolated jaw bones, a few odd vertebrae, a good

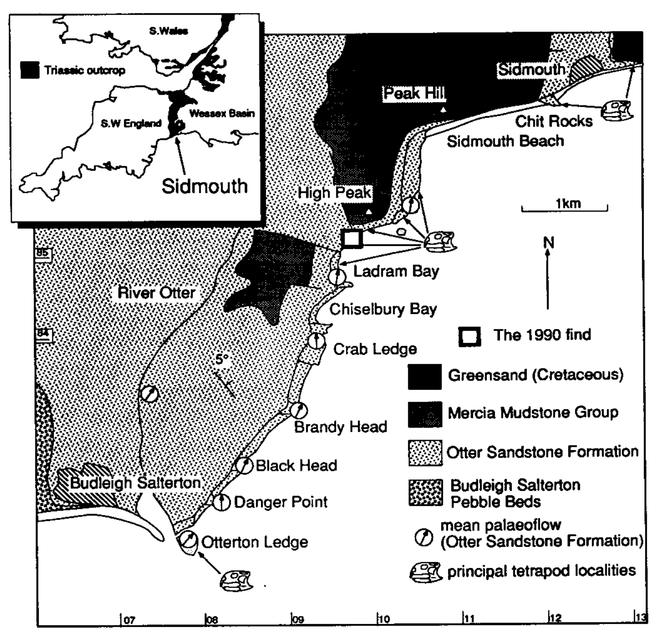

Figure 1: Map of the coastal outcrop of the Otter Sandstone Formation between Sidmouth and Budleigh Salterton, Devon. The major Triassic formations are indicated, together with mean fluvial palaeoflow directions, and principal localities. The site of the new rhynchosaur skeleton is highlighted. (After Benton et al., 1993).

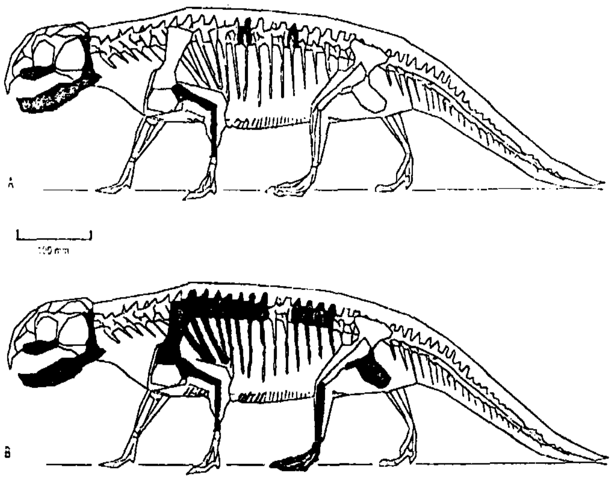

Figure 2: Restoration of the skeleton of Rhynchosaurus spenceri Benton, 1990, in side view. The outline of the skeleton is based on the more complete R. articeps Owen, 1842 from Grinshill, and the bones known up to 1990 are shown in black (a), and those now known as a result of the discovery of the new skeleton (b). (After Benton 1990).

partial skull (EXEMS 60/1985.292), and a partial forelimb (EXEMS 60/1985.282). These are represented on a restored diagram of the skeleton in side view (Figure 2a). The new specimen has much improved our knowledge (Figure 2b).

The specimen (Figure 3) shows a number of red sandstone blocks. The large block at the top of the picture is covered with vertebrae from the back region. These are all slightly disarticulated, but still in close association. The pair of broad ribs at the right hand end of the block are the first two of the trunk region, a feature seen in other rhynchosaurs. The group of the thin rib-like structures at the top right are gastralia, a part of the basket of dermal bone strips covering the underside of the belly region. The broad plates of bone at the other end of the large composite slab are probably hip bones.

Below this slab is another composite piece, containing a very fine hind limb, which lacks the femur. Hence this limb starts at the knee joint, at the top, and the obvious large bone running down is the tibia; a narrower fibula lies behind. Below these are some small ankle bones, and then the long powerful toes extend to the left, most of them complete, fully articulated, and equipped with deep claws. At the right-hand end of this block are some ends of ribs, and a broad plate of bone, probably the scapula (shoulder blade). The smaller slab at the bottom left of the picture contains a few vertebrae, and some bones of the shoulder girdle and forelimb, and there are a number of other vertebrae present.

RHYNCHOSAURS

Rhynchosaurs were common, widespread, herbivores, during the Mid- and early Late Triassic (Benton 1990). At first sight, a rhynchosaur would have looked like a pig with a rather heavy head (Figure 4). The Devon rhynchosaur was nearly 1 m long, based on the currently-known sample of incomplete specimens. The body was thought to be relatively bulky, with a barrel-like rib cage, slender limbs, and a long tail. The fat body was doubtless necessary to accommodate a long gut, a common feature of herbivorous animals.

The unusual curved snout of rhynchosaurs was used by Owen (1842) to name the group ('rhynchosaur' means 'snouted reptile'; Figure 2). The lower jaw is deep, which suggests powerful jaw-closing muscles. The arrangement of teeth is unique among animals; there are two or three rows on both the upper and lower jaws, and these are separated by shallow grooves. The jaws meet in a very precise way, when closed, with no possibility of sideways or back-and-forwards movement. This would have allowed the rhynchosaur to chew tough vegetation.

In the neck region, *Rhynchosaurus* had relatively large ossified hyoid bones, which suggests that it had a large powerful tongue (The hyoid is seen in the Shrewsbury specimens). In addition, there is a curved snout: this is composed entirely of the paired premaxillae, which are rooted deeply within the other bones of the top of the snout. Most of the length of the premaxillae is exposed and was probably covered with a horny sheath in life - there is evidence for this in the parallel striations running the length of the bones. It seems likely that *Rhynchosaurus* used its snout bones for digging and/or gathering up food: the deep rooting of the premaxillae meant that they could withstand large pulling forces as the animal scraped its snout backward through hard soil or tangled undergrowth.

The final clue to feeding is in the feet: the claws on each toe are larger than expected, narrow from side to side, and rather pointed (Figures 2, 3). In all regards, these are the claws of a scratch-digger, an animal that digs by raking its toe claws through hard earth. However, it is likely that the claws in *Rhynchosaurus* were used to dig up roots and tubers. Plant fossils from the Otter Sandstone Formation (Benton et al., 1993) include the horsetail-like *Schizoneura*. *Rhynchosaurus* was probably eating horsetails, and other low-level Triassic plants such as seed ferns and cycads.

THE MIDDLE TRIASSIC IN DEVON

The sedimentology of the Otter Sandstone Formation has been recently studied in some detail (Newell 1992). The formation is about 120 m thick, and the beds dip gently eastwards. It rests conformably on the Budleigh Salterton Pebble Beds, a 20 to 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 [SY 057 815], is marked by an extensive ventifact horizon 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.

At its base the Otter Sandstone Formation is aeolian in origin. Overlying the ventifact horizon are approximately 15 m of sandstones which display truncated cross sets which are thought to reflect the deposits of small barchan dunes. A thin claystone deposit within these sands represents a small interdune lake. Above these deposits, occurring immediately to the east of the mouth of the River Otter, the sandstone units indicate deposition within braided streams. Extraformational clasts are seen within this lower part of the formation. Fossil bone debris has been recorded from this location (Whitaker 1869; Figure 1).

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 horizons. Purvis and Wright (1991) attribute the large vertical rhizoliths to deep-rooted phreatophytic plants which colonised bars and abandoned channels on a large braidplain.

Farther east, calcretes occur more sporadically, and the formation is dominated by sandstones in channels, with occasional siltstone lenses. These represent the deposits of a series of sandy braided rivers. The succession exposed in Ladram Bay consists of multi-storey sandbodies with a sheet-like geometry. The major erosive bounding contacts which define the sandbodies are commonly floored by a lag conglomerate. These contacts can be traced laterally for hundreds of metres across the sections as fairly planar features. Locally, deep scouring is reflected by large scale trough cross sets of conglomeratic sandstone. The lag conglomerates are composed solely of intraformational debris; typically claystone, calcrete palaeosol pebbles, early cemented sandstone and, rarely, bone material. The specimen was recovered from such a sand-body, exposed at a time of low beach level, approximately 150 m to the west of the Ladram Bay slipway. Within these sandbodies which are typically 1 m to 3 m thick - cross-bedded, current rippled, low angle- and parallel-laminated sandstones represent bar forms and bedforms present within the braided river. These stratal packages are related by a complex series of

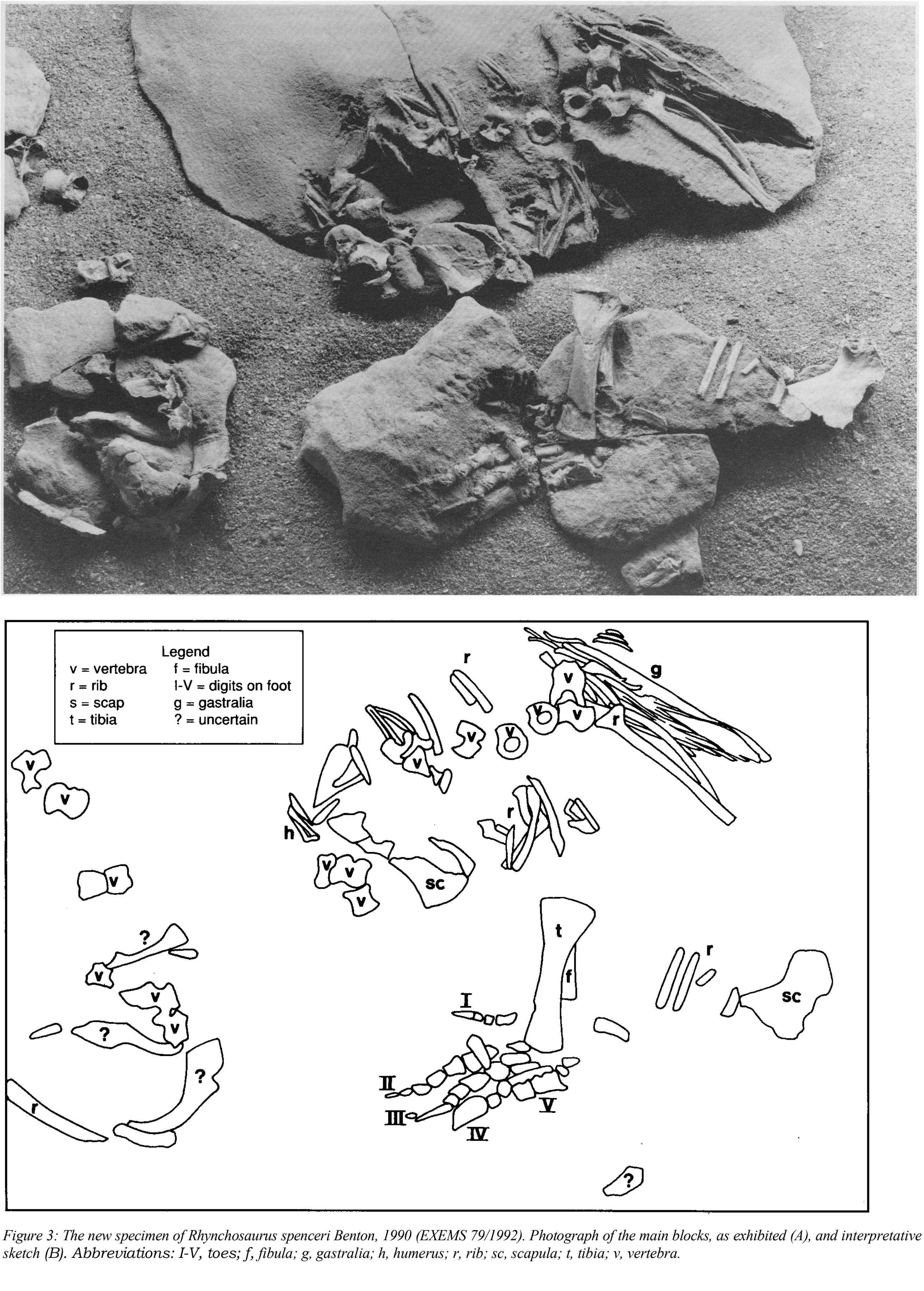

Figure 3: The new specimen of Rhynchosaurus spenceri Benton, 1990 (EXEMS 79/1992). Photograph of the main blocks, as exhibited (A), and interpretative sketch (B). Abbreviations: I-V, toes; f, fibula; g, gastralia; h, humerus; r, rib; sc, scapula; t, tibia; v, vertebra.

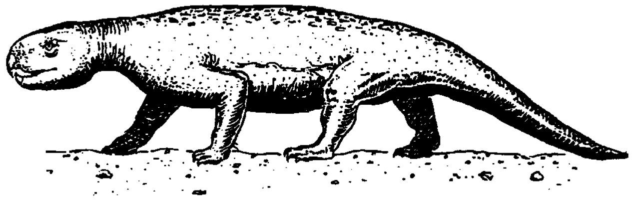

Figure 4: Side view reconstruction of the Devon rhynchosaur Rhynchosaurus spenceri Benton, 1990. (Reproduced by permission of Tristram Besterman, Plymouth City Museum & An Gallery).

hierarchical bounding contacts which define the style of the bar forms, the channels and the entire fluvial system. Interpretation of these has shown that the river was subjected to rapidly fluctuating discharge - possibly seasonal fluctuations - which was perennial. These rivers may have been ephemeral. Lenticular channel-fill deposits, consisting of sandstone and claystone, are recognised and suggest palaeochannel depths in the order of 1 m to 2.5 m. Although claystone is inferred to have existed formerly in greater quantities (being seen as rip-up mud flakes in intraformational conglomerates) it is rare *in situ*. Thin beds (2 cm to 10 cm) are noted draping bar-form deposits, while thicker (a few tens of cms) beds are seen as erosional remnants of abandonment/floodplain deposits. The climate was semi-arid, and the limited evidence of desiccation cracks and pseudomorphs after halite (see Henson 1970) may be the result of the erosive nature of the fluvial system. The relative scarcity of plant fossils may reflect oxidising conditions in a relatively arid climate (Laming 1982, p. 170).

The specimen described herein was probably unfortunate enough to fall into the river or 'become incorporated' during a period of fairly rapid deposition enabling it to be buried fairly quickly and not subjected to excessive transportation.

TAPHONOMY OF THE TETRAPOD REMAINS

Tetrapod fossils in the Otter Sandstone Formation are generally isolated elements - jaws, teeth, partial skulls, or single postcranial bones, apart from the new skeleton, and two specimens noted earlier. About half of the identifiable tetrapod bones found are rhynchosaur remains, and most of these are parts of the skull, especially the jaw elements. 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 rhynchosaurs in which 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 related to fluvial transportation. Some specimens show signs of possible abrasion during transport, but others, especially the jaws of

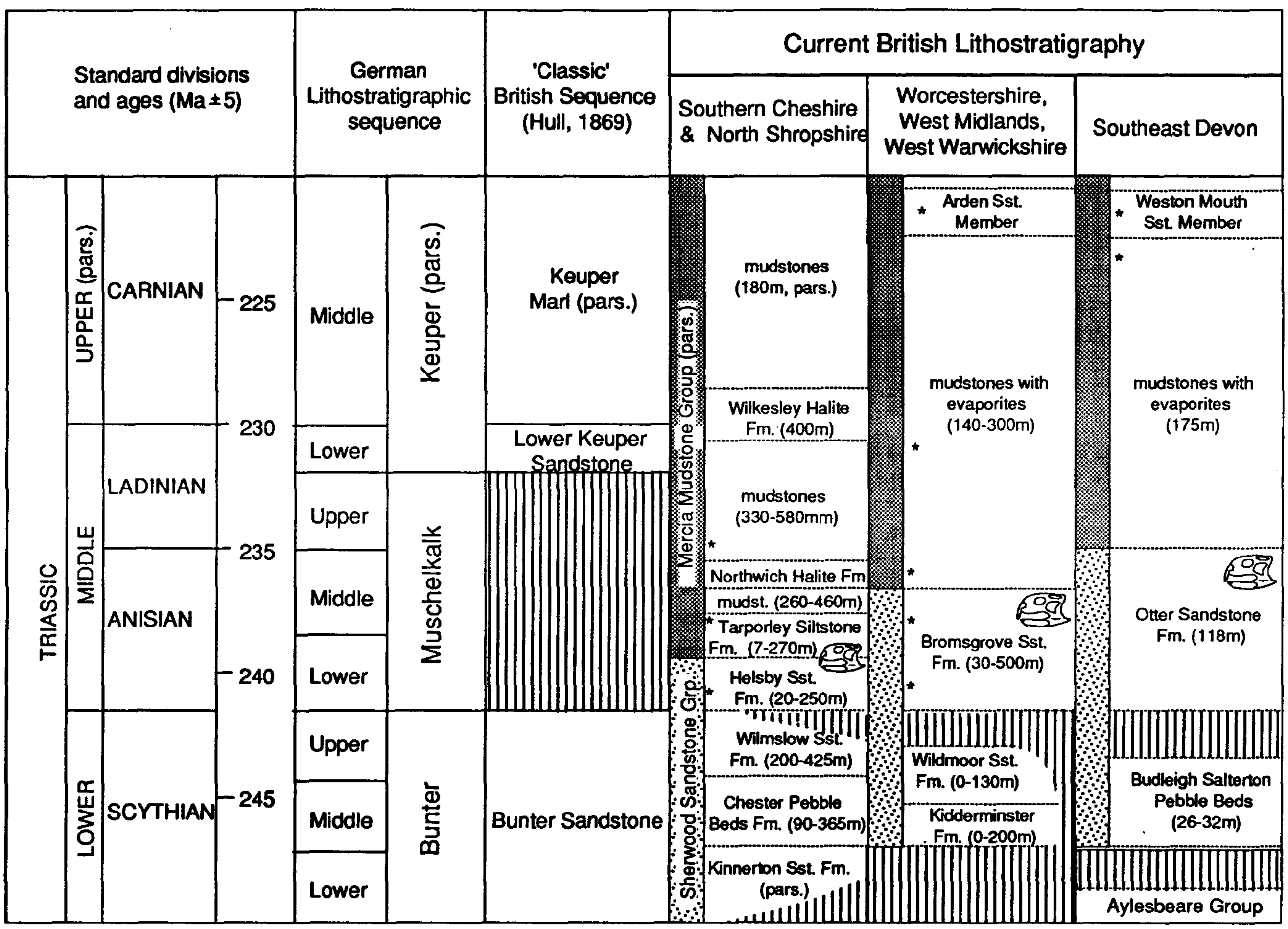

*Figure 5: Stratigraphic setting of the British Mid-Triassic tetrapod faunas. Correlations of the standard Triassic divisions and the German Triassic sequence with the British Triassic for currently recognised lithostratigraphic units, are illustrated. Skulls - - levels of main tetrapod faunas; * - - palynological evidence of age; ages (Ma ± 5) after Forster and Warrington (1985). (After Benton et al., 1993.)*

procolophonids, show detailed preservation of surface features and delicate sharp teeth. The disarticulation of the new skeleton occurred before final burial, and may indicate slight movement of the bones by water currents. The overall incompleteness of the specimen may be the result of rapid collecting. The bone tissue is well preserved as a hard white apatite (stained pink by the matrix), with all internal structure intact. The dentine of the teeth is yellow, and the enamel is stained dark brown.

AGE OF THE OTTER SANDSTONE FORMATION FAUNA

The age evidence for the Otter Sandstone Formation has been reviewed by Benton *et al.* (1993). This formation is poorly constrained palynologically by occurrences of Late Permian miospores in the lower part of the Permo-Triassic succession near Exeter, and Carnian (Late Triassic) taxa in the Mercia Mudstone Group, 135 m above the Otter Sandstone Formation.

Miospores provide an independent means of correlation of British Triassic deposits, with the stages based upon marine faunas in the Tethyan realm. Within the last 30 years, formations in the Sherwood Sandstone and Mercia Mudstone Groups in many parts of Britain have been assigned ages on the basis of comparison of miospore assemblages with those documented from independently dated Triassic sequences elsewhere in Europe (evidence summarised in Figure 5), and these indicate that the vertebrate faunas in the Midlands are pre-Ladinian and not older than Anisian. Though palynological evidence is lacking in Devon, these findings support the interpretation of the comparable Devon tetrapod fauna as Anisian in age (Milner *et al.,* 1990; Benton *et al.,* 1993).

Milner *et al.* (1990) noted that the British *Mastodonsaurus* specimens from Devon, Bromsgrove and Warwick, indicate an Anisian to Carnian age, based on comparisons with German material. The other amphibian genus, *Eocyclotosaurus,* is more useful, being known from the *Voltzia* Sandstone of France and the Lower Röt of Germany, both dated as latest Scythian or early Anisian in age, and from the Holbrook Member of the Moenkopi Formation of Arizona, USA, dated as early Anisian. Hence, the amphibians would appear to indicate an Anisian age for the Devon, Warwick and Bromsgrove faunas.

The reptiles generally point to a Mid-Triassic, possibly Anisian, age for all the formations (Milner *et al.,* 1990). The procolophonids, the tanystropheid, and the rauisuchian archosaurs could all be Anisian or Ladinian in age, although Milner *et al.* (1990) prefer an Anisian age on the basis of the primitive nature of the Devon procolophonid. The three species of *Rhynchosaurus* fall in the phylogeny of rhynchosaurs (Benton 1990) between *Stenaulorhynchus* from the Manda Formation of Tanzania (generally dated as Anisian) and the Hyperodapedontinae *(Hyperodapedon, Scaphonyx),* which are all Carnian in age. Hence, the rhynchosaurs, present in all four regions, might indicate a Ladinian age.

SUMMARY

This new specimen of *Rhynchosaurus spenceri* Benton 1990 is the most complete reptile yet found in the Triassic of Devon. It complements the holotype and the many other fragmentary specimens already known from the area. Detailed palaeontological work on the specimen is yet to be completed.

ACKNOWLEDGMENTS

We are grateful to David Hill, then of Bristol City Museum, for the superb preparation work he has carried out on the new rhynchosaur specimen, to Ailbhe Duane and Meriel FitzPatrick for their initial sighting of the specimen, to Tristram Besterman of the City of Plymouth Museums and Art Gallery for help in arranging the conservation and preparation of the specimen, and to Exeter City Museums Service for their current care of the material. Ms M. Luscott-Evans is thanked for the preparation of the final manuscript.

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