



Archosaur remains from the Otter Sandstone Formation (Middle Triassic, late Anisian) of Devon, southern UK

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ABSTRACT

A new jaw from the Middle Triassic (Anisian) Otter Sandstone Formation of Devon confirms the existence of a derived archosaur (avesuchian). Numerous isolated teeth and vertebrae had already suggested the presence of archosaurs in the Otter Sandstone Formation, presumed predators on the fauna of temnospondyls, procolophonids, and rhynchosaurs, but the new fossil is the first to show some diagnostic characters. Other elements in the same block as the jaw, but not necessarily from the same animal, include a possible skull or pelvic bone, a slender long bone, a small tooth (perhaps prolacertiform), and two presumed archosaur dermal scutes. An additional scute is present, as well as the probable distal end of a pubis, perhaps from a large poposauroid archosaur like the Anisian-age *Bromsgroveia* or *Arizonasaurus*. The jaw and pubis represent animals of very different sizes, some 0.8 m and 3 m long in estimated body length respectively.

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1. Introduction

The Middle Triassic Otter Sandstone Formation of the south coast of Devon has been a source of vertebrate fossils since the nineteenth century, with the first published account in 1869 (Whitaker, 1869). Numerous reports have appeared since (summarised by Benton et al., 1994; Benton, 1997; Spencer and Storrs, 2002; Hone and Benton, 2008), and the fauna so far reported consists largely of reptiles. Of these, the rhynchosaur *Fodonyx spenceri* (Hone and Benton, 2008) is by far the commonest fossil taxon, perhaps because this medium-sized herbivore truly was abundant at the time, but also perhaps partly because its tooth-bearing maxilla and mandible are robust, and could survive transport in high-energy streams better than some of the other fossils. Other reptile remains include the small procolophonid *Kapes bentoni* (Spencer and Storrs, 2002), and much rarer fragments of the small diapsid *Coartaredens isaaci* and other unidentified small reptiles (Spencer and Storrs, 2002). Amphibians are represented by rather massive, sculptured dermal bones of the jaws, skull, and shoulder girdle, assigned to *Eocyclotosaurus* sp., 'Mastodonsaurus', and unnamed taxa (Milner et al., 1990). The fish *Dipteronotus cyphus* has also been reported, as well as insects, conchostracans, and plants (Milner et al., 1990; Benton et al., 1994).

Archosaur fossils are rare and incomplete in the Otter Sandstone Formation, and hitherto have been largely undiagnostic. Benton and Gower (1997) reported one or more taxa of archosaurs, possibly a poposauroid like *Bromsgroveia*, represented by 15 teeth, a few vertebrae, a midline skull roof element, and a partial right ischium. An elongate element was identified tentatively as the elongate neural spine of a long-spined 'ctenosauriscid' archosaur (Milner et al., 1990; Benton et al., 1994).

In the past 10 years, further archosaur fossils have been found, and I report here one of the best found to date, the anterior portion of an archosaur mandible. Some other, previously undescribed, archosaur elements are also presented. The Otter Sandstone Formation falls in the first 10 Myr of the Triassic, a time of turmoil as ecosystems were rebuilding themselves following the devastating end-Permian mass extinction. Clarity about the composition of currently poorly known early Middle Triassic vertebrate faunas is essential for understanding the nature of that recovery.

Repository abbreviations. BRSUG, University of Bristol, Department of Earth Sciences, Bristol; EXEMS, Royal Albert Memorial Museum, Exeter; SIDMM, Sidmouth Museum, Sidmouth.

2. Geological setting

The new jaw comes from the Otter Sandstone Formation (OSF) at Port Royal, Sidmouth (Fig. 1), one of several sites that have yielded numerous vertebrate fossils (Benton et al., 1994; Benton and Spencer, 1995; Benton, 1997). The OSF comprises about 120 m of medium- to fine-grained red sandstones that

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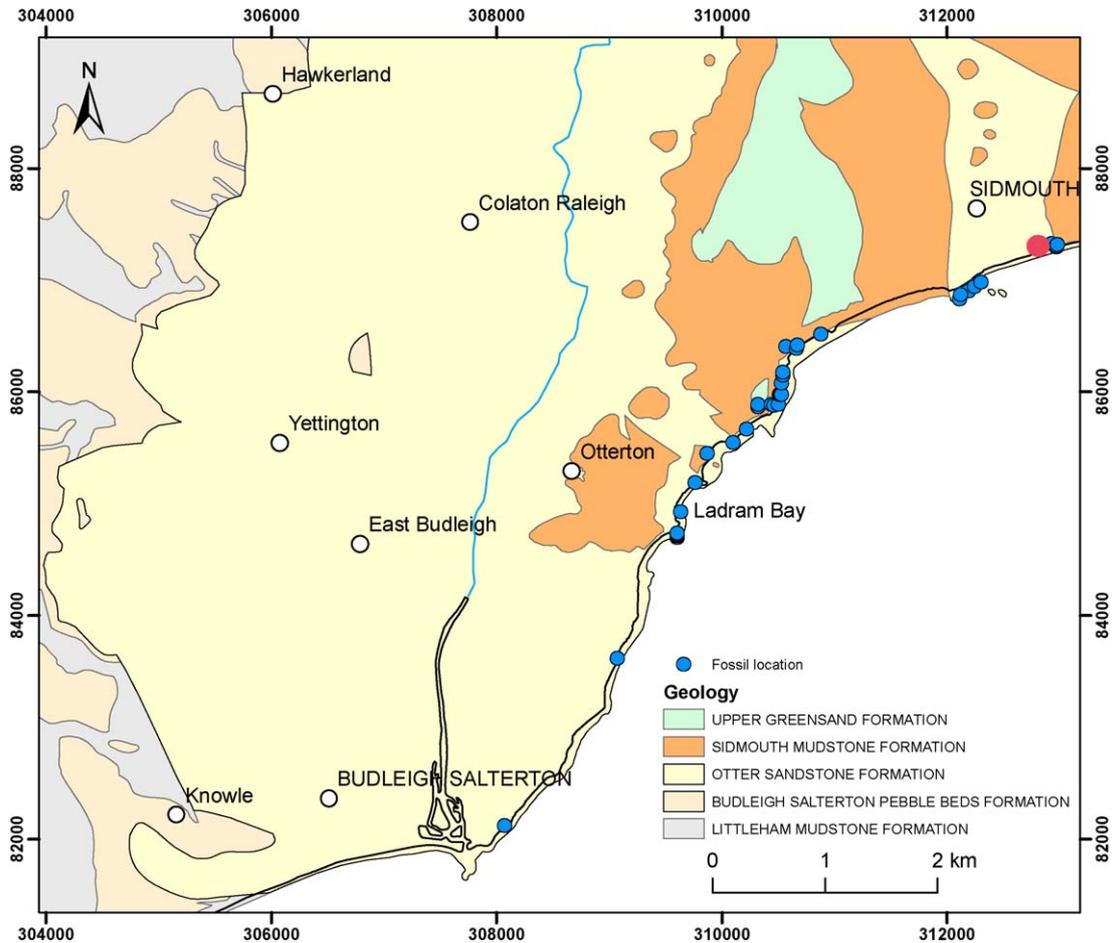


Fig. 1. Map of the coastal outcrop of the Otter Sandstone Formation between Sidmouth and Budleigh Salterton, Devon. The major Triassic formations are indicated, together with principal tetrapod localities (fossil location, blue dots). The Port Royal/Pennington Point locality is marked in red, just east of Sidmouth. Courtesy of Andrew Newell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

rests unconformably on the Budleigh Salterton Pebble Beds Formation (Fig. 2), a 20–30 m thick unit of fluvial conglomerates, and is succeeded by the water-laid siltstones and mudstones of the Sidmouth Mudstone Formation, part of the widespread Mercia Mudstone Group. In its lower part, the OSF contains abundant vertical to subvertical, irregular calcareous structures that have been interpreted as rhizoliths, elements of paleosols or calcretes representing ancient rooting systems. These rhizoliths are not found in situ higher in the OSF, but their broken fragments are common components of reworked intraformational conglomerates, preserved typically as channel lags. The channel sandstones occur in cycles, often with conglomeratic bases, and fine upwards through cross-bedded sandstones to ripple-marked sandstones. The sandstones near the base of the OSF have been interpreted as aeolian, the deposits of transverse barchanoid dune ridges. The middle and upper parts of the OSF are of fluvial origin; the sandstones were deposited by ephemeral braided streams, flowing from the south and southwest (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. The calcrete horizons indicate subaerial soil and subsurface calcrete formation in semi-arid conditions (Purvis and Wright, 1991; Newell, 2006).

The climate was semi-arid, with long dry periods when riverbeds dried out, and seasonal or occasional rains led to violent river action and flash floods. However, there is little evidence for

complete aridity; desiccation cracks and pseudomorphs after halite are uncommon in the OSF. The relative scarcity of plant fossils may reflect oxidising conditions in an arid climate.

The dating of the OSF has long been debated, but it now appears to be well resolved as Anisian. This age had been confirmed by palaeontological comparisons, based on the fishes, amphibians, and reptiles. Several of the OSF fossils were identical with taxa from the continental red bed successions of the English Midlands that had been dated as Anisian by the use of miospores; in particular, the Bromsgrove Sandstone Formation of Bromsgrove and Warwick (Benton et al., 1994). No miospores have been recovered from the OSF.

Identification of the OSF procolophonid as a species of *Kapes* by Spencer and Storrs (2002) confirmed the Anisian age, as *Kapes* is known from the Donguz Svita of Russia, itself dated as middle to late Anisian on the basis of biostratigraphical and magnetostratigraphic evidence. Subsequent detailed magnetostratigraphic work on the OSF by Hounslow and McIntosh (2003) has confirmed the Anisian age: these authors found that the lower parts of the OSF correspond to the early and mid Anisian, and the upper parts, which contain the majority of the macrofossils, correlate with late Anisian and latest Anisian magnetozones (Illyrian Substage; c. 242 Ma) on the marine standard.

The OSF fossils have been found at numerous points along the coastal outcrop, between Budleigh Salterton and Sidmouth (Fig. 1). Particularly rich sites have been Ladram Bay [SY096847–SY104858], High Peak [SY104858], 2 km west of Sidmouth, and Port Royal, just east of Sidmouth [SY12978730]. The tetrapod

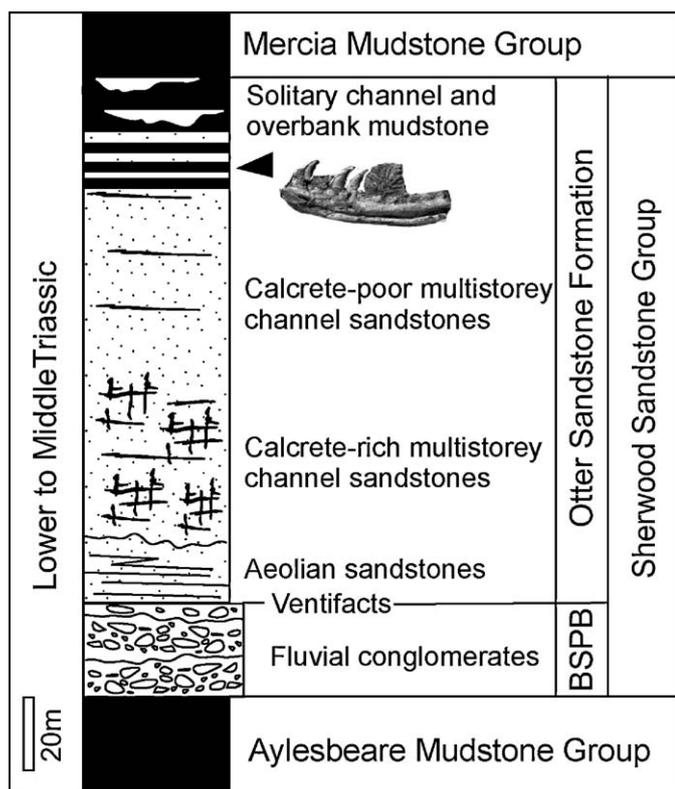


Fig. 2. Stratigraphy of the Otter Sandstone Formation in East Devon coastal exposures. BSPB, Budleigh Salterton Pebble Beds. Approximate level of archosaur jaw find is indicated. *Abbreviation:* BSPB, Budleigh Salterton Pebble Beds Formation. Based on Newell (2006).

fossils are generally isolated elements – jaws, teeth, partial skulls, or single postcranial bones – from channel lag conglomerates. Exceptions are the partial articulated skull and lower jaws of *Fodonyx spenceri*, and the scattered, partial skeleton of that species,

both found separately, and both in overbank coarse sandstones (Hone and Benton, 2008).

3. Description

3.1. Introduction

The new materials include seven individual remains in a beach-worn, rounded block of hard sandstone, collected by Chris Moore about 2000, at Pennington Point, Port Royal, just over the bridge that crosses the River Sid at the east end of the town (OS NGR SY130873). At first, only part of the jaw showed on the surface of the cobble, as well as some enigmatic bone sections on the side. Chris Moore did some preliminary preparation work to expose the whole jaw. Remmert Schouten then completed the preparation work in the Palaeontology Laboratory at the University of Bristol, in 2010, removing the jaw completely from the rock and thereby exposing its medial side, as well as the remaining smaller bones.

The most notable fossil in the block is the anterior portion of an archosaur mandible, but further preparation revealed additional remains deeper in the block: two presumed scutes, a possible cranial or pelvic element, a tiny curved tooth, a slender limb bone, a hollow tooth without serrations, and an unidentified fragment of bone, all contained within the single block. The specimen has been registered under four numbers, the jaw now removed from the block (SIDDM G 1 2010), the scute removed from the block (SIDDM G 2 2010), a plaster cast of the unprepared block (SIDDM G 3 2010), and the remainder of the block (SIDDM G 4 2010). A similar dermal scute to that preserved in the block was found earlier at Sidmouth (exact locality unspecified; BRSUG 27203). A further previously undescribed archosaur specimen is a massive limb element, collected by Mark Hounslow, also at Pennington Point (BRSUG 29009).

3.2. Mandible

The mandible portion, as preserved, is 62 mm long and 12 mm deep (Fig. 3). It consists solely of the dentary from the right side,

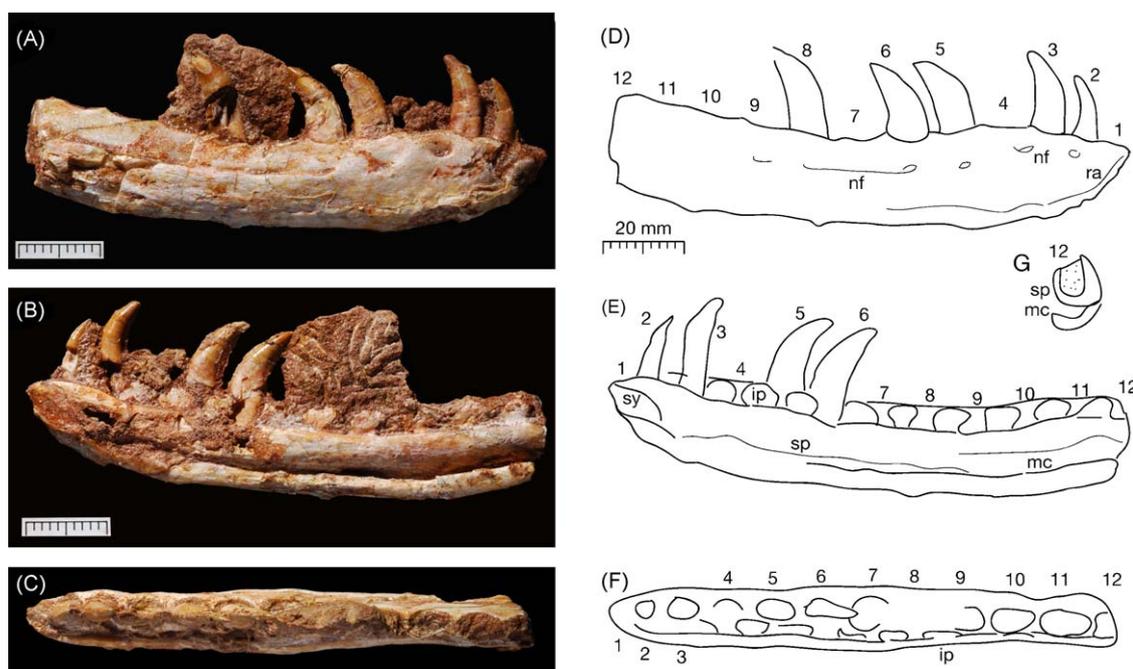


Fig. 3. The lower jaw of a possible poposauroid from the Otter Sandstone Formation (SIDMM G 1 2010), in lateral (A and D), medial (B and E), dorsal (occlusal) (C and F), and posterior (G) views. *Abbreviations:* 1–12, dentary teeth, numbered from the most anterior; ip, interdentary plate; mc, Meckelian canal; nf, nutrient foramen; ra, roughened area; sp, elongate face to which splenial attached; sy, symphysis.

and shows the anterior portion with 12 preserved alveoli and 5 complete teeth. In lateral view (Fig. 3A and D), the mandible shows roughly parallel dorsal and ventral margins, with a slight upturn towards the front of the element. This upturn gives a gentle upwards curve to the tooth row, and so gives the anteriormost three teeth (or the sockets) a slightly anterior tilt. A straight line drawn through the lowest points of the sockets in lateral view shows a 5° tilt between the line through sockets 1–3 and the line through sockets 4–12. There is a long vessel canal beneath sockets 8–6, terminating in a perforation of the bone below socket 6. There are three further nutrient foramina, below teeth 5, 4–3, and 2, and a generally roughened bone surface around the anteriormost part of the dentary.

In medial view (Fig. 3B and E), the most striking features of the dentary margin are the interdental plates. These form substantial subrectangular thin lappets of bone that are centred between the teeth, and wrap around the bases of two teeth. The division between lappets is placed approximately centrally over the lower portion of each tooth. The full extent of the interdental plates is hard to determine because they are so thin, and their edges crumbled under preparation, but they appear to have slightly upwards-curved dorsal margins, 4–5 mm long, that lie almost exactly at the level of the lateral dorsal margin of the dentary. The interdental plates do not appear to meet, but leave a gap at the medial margin of the socket. In medial view, the interdental plates descend, sloping inwards, to a 2.5-mm-wide base that is attached to the more substantial portion of the dentary below. The bone surface of each interdental plate appears to be very porous.

The ventral portion of the dentary in medial view, below the interdental plates, consists of two portions, an upper, rather massive part that encloses the roots of the teeth and forms the dorsal margin of the Meckelian canal (mc, Fig. 3F), and a lower portion that forms a substantial antero-posteriorly running element forming the ventral margin of the Meckelian canal and a longitudinal contact for the unpreserved splenial. At the front of the jaw, the short symphyseal area (sy, Fig. 3E), about 10 mm from front to back, shows where the other dentary attached in life.

The anterior portion of the Meckelian canal would normally be covered in medial view by the splenial, but this element is entirely missing, and had been lost before burial (no trace was found during preparation). The jaw is slightly compressed, but the broken posterior face of the specimen (Fig. 3G) shows that the tooth socket 12 extends 7 mm below the dorsal surface of the mandible, terminating in a narrowing, and slightly curved ventral portion. Beneath the socket is a thin lamina of bone, dividing it from the Meckelian canal (mc, Fig. 3G). The lateral surface of the dentary continues ventrally, forming a thin lateral wall to the Meckelian canal, and then curves round as a thicker ventral wall, curving upwards on the medial surface and terminating in a rounded face that extends forwards as a ridge that would have supported the splenial element for much of its ventral margin (sp, Fig. 3E and G).

The tooth sockets (Fig. 3C and F) measure 4.0 mm × 2.5 mm in antero-posterior width and labio-lingual depth towards the front of the dentary, and 5.5 mm × 3.0 mm further back. The exposed crowns of complete teeth measure as follows: tooth 2 (16 mm ventro-dorsally long, 6 mm antero-posteriorly wide at base), tooth 3 (22 mm long, 8 mm wide), tooth 5 (20 mm long, 9 mm wide), tooth 6 (21 mm long, 10 mm wide), and tooth 8 (24 mm long, 10 mm wide). The lateral margins of the teeth are gently curved, and the anterior and posterior margins broadly curved distally from their bases. The roots of the teeth are oval and do not show the anterior or posterior carinae: the carinae begin in the crown, a few millimetres above the jaw margin at about the same level on anterior and posterior tooth margins, and continue to the distal tooth tip. The carinae are centred on the anterior and posterior tooth surfaces, and they are not offset. The tooth shape, in cross section, changes from oval with broad anterior and posterior margins, to an 'eye' shape with anterior and

posterior points corresponding to the carinae above the jaw line, and the lingual face slightly more convex than the labial. The teeth are recurved, with a smoothly curved posterior margin, and a slight shoulder on the anterior margin. Serrations are seen on both mesial and distal carinae, and there are typically 6 gently pointed serrations per mm, with no variation between carinae nor along the length of the carinae. The tooth enamel surface is smooth, without striations or wrinkles.

3.3. Affinities of the mandible

The Sidmouth mandible (SIDDM G 1 2010) does not show sufficient characters to be identified closely, although it is almost certainly an archosaur and an avesuchian. In the discussion below, following Benton (1999), the terms 'archosaur' and 'Archosauria' refer to the traditional clade that encompasses the latest Permian and Early Triassic *Archosaurus* and *Proterosuchus* and everything above these in the cladogram (often called Archosauriformes), whereas the crown-group, consisting of the crocodile and bird lines, is termed Avesuchia (often called Archosauria).

The teeth show a number of diagnostic characters that allow the jaw to be assigned to sequential nested clades. First, the teeth are laterally compressed, and not oval, showing a sharp anterior and posterior margin, a feature shared by archosaurs and *Prolacerta* (Juil, 1994; Dilkes, 1998). Further, the teeth are recurved, meaning they curve from the base of the crown to the tip, and the curve makes the tips point backwards, also a feature of archosaurs and *Prolacerta* (Dilkes, 1998). Further, as in most Archosauria, the teeth are implanted in sockets (theodont), and they bear serrations on the anterior and posterior carinae (Benton and Clark, 1988; Juil, 1994). The teeth allow no closer identification of the affinities of this jaw because they are of the generalised archosaurian type seen from the Triassic to the Cretaceous in most carnivorous clades.

A closer identification of the Sidmouth animal may come from the interdental plates. Interdental plates are not seen in *Prolacerta* or other archosauromorphs outside Avesuchia (Juil, 1994), and yet these structures are seen in 'rauisuchians' and dinosaurs, and so presumably in all Avesuchia. The uncertainty about the occurrence of interdental plates is because these are relatively delicate structures, being thin sheets of bone over the labial sides of the teeth, and they might be lost during preservation or preparation. Perhaps the most basal archosaur to exhibit such interdental plates is *Euparkeria* (Senter, 2003), in which case these structures place the Sidmouth jaw in the clade consisting of *Euparkeria* + Avesuchia. The interdental plates of the Sidmouth jaw are unlike those seen in the Late Triassic 'rauisuchians' *Teratosaurus*, *Postosuchus*, and *Fasolasuchus* (Benton, 1986; Brusatte et al., 2009), where the interdental plates form a continuous thin bone sheet over the medial sides of the teeth, separated from the remainder of the medial surface of the dentary by a definite dental groove that shows openings between the teeth. Saurischian dinosaurs, on the other hand, generally show separate interdental plates (Rauhut and Hungerbühler, 1998), which may be the primitive condition, as seen in *Euparkeria* (Senter, 2003) and in the Sidmouth jaw.

In attempting to identify the jaw to a clade within Avesuchia, there are several candidate taxa that have been found already in the Anisian (Poposauroidea, Rauisuchioidea, Dinosauromorpha), as well as the basal archosaurian clades Proterochampsidae, Euparkeriidae, Erythrosuchidae, or that had ghost ranges extending back into the Anisian (Ornithosuchidae, Aetosauria, Pterosauria) (Brusatte et al., 2010; Nesbitt et al., 2010). However, there are relatively few apomorphic characters in the mandible and teeth that assist identification to these clades, and in any case, the Sidmouth jaw shows the less derived ('primitive') condition of

these. For example, Brusatte et al. (2010) note three dentary characters that may be phylogenetically informative in Avesuchia:

- (71) dentary, teeth: present up to anterior tip (0); absent at anterior tip but present posteriorly (1); completely absent (2);
- (72) dentary, expansion of anterior region relative to main body: absent (0); present (1);
- (73) dentary, length of symphysis: antero-posteriorly short (0); antero-posteriorly expanded and deep (1).

The Sidmouth jaw shows the primitive condition for character 71, dentary teeth present to the anterior tip, which means it is not an aetosaur or an ornithischian dinosaur, as is evident in any case, and it is excluded from some other clades of crurotarsans, pterosaurs, and dinosaurs that entirely lose their teeth. The Sidmouth jaw also shows the primitive condition for character 72, an unexpanded anterior dentary tip, and this means it is not a phytosaur and it is excluded from some 'rauisuchian' clades. Finally, the Sidmouth jaw shows a short symphysis, also a primitive character. Taking account of the exclusions, the Sidmouth jaw could belong to Poposauroidae, Rauisuchoidea, Ornithosuchidae, or basal Dinosauromorpha, among the candidate avesuchian clades.

Among basal Dinosauromorpha the only Anisian taxon so far, *Asilisaurus* (Nesbitt et al., 2010), has a pointed dentary with short, peg-like teeth ankylosed to the bone, so very different from the Sidmouth jaw. This does not exclude, however, that the Sidmouth jaw might have come from another kind of basal dinosauromorph or basal avemetatarsalian. The Ornithosuchidae are possible candidates for comparison – the dentary of *Ornithosuchus* from the Lossiemouth Sandstone Formation of Elgin, NE Scotland, is very similar in shape (Walker, 1964), showing the parallel dorsal and ventral margins, and the elevation of the jaw line and change of angle between dentary teeth 1–3 and the seven posterior teeth. *Ornithosuchus*, and other ornithosuchids are known so far only from the Late Triassic, some 10–15 Myr after the OSF, and they were generally twice or three times the size of the Sidmouth animal, having skulls 30–50 cm long. Further, they have fewer dentary teeth – 10 in *Ornithosuchus* and *Riojasuchus*. Nonetheless, a small Anisian ornithosuchid would be an exciting find, extending the range of the clade much deeper in the Triassic than currently known, but in line with the ghost ranges (Brusatte et al., 2010).

The remaining groups for comparison are the rauisuchian clades Rauisuchoidea and Poposauroidae. Galton and Walker (1996) and Benton and Gower (1997) independently identified a 'poposaurid rauisuchian' *Bromsgroveia* from the Bromsgrove Sandstone Formation of Warwick and Bromsgrove, in the English West Midlands. Subsequent study has shown that *Bromsgroveia* is a close relative of *Arizonasaurus* from the Anisian Moenkopi Formation of Arizona, USA (Nesbitt, 2003, 2005; Butler et al., 2009; Brusatte et al., 2010), as well as a number of other basal archosaurs from the Middle and Late Triassic such as *Lotosaurus*, *Poposaurus*, *Sillosuchus*, *Hypselorhachis*, *Effigia*, and *Shuvosaurus*, the clade Poposauroidae. Within Poposauroidae, *Shuvosaurus* and *Effigia* comprise the Shuvosauridae, but the other taxa form an unresolved multitomy. Earlier studies had identified a smaller poposaurid clade, the Poposauridae (*Poposaurus*, *Postosuchus*, *Bromsgroveia*), and a further poposaurid clade of long-spined forms, the Ctenosauriscidae (*Ctenosauriscus*, *Bromsgroveia*, *Hypselorhachis*, *Lotosaurus*). However, recent cladistic studies (e.g. Brusatte et al., 2010) have failed to identify either family, and the 'ctenosauriscids', with elongate neural spines forming a dorsal 'sail', are not confirmed as a clade.

Poposauroidae is sister clade of Rauisuchoidea in the cladistic analysis of Brusatte et al. (2010), which together form the clade Rauisuchia, but earlier cladistic analyses, and others in progress, do

not find a monophyletic Rauisuchia, some of them placing certain 'rauisuchians' on the stem to Crocodylomorpha. Poposaurid synapomorphies include (Weinbaum and Hungerbühler, 2007; Brusatte et al., 2010) lack of osteoderms, incipient perforated acetabulum (paralleled in derived crocodylomorphs), three or more sacral vertebrae (paralleled in some rauisuchoids, e.g. *Batrachotomus*, *Saurosuchus*), gracile sacral ribs, laterally facing sacral rib articulations, anterior cervical neural spines longer antero-posteriorly than high, anterior cervical centra longer than high, a crest above the acetabulum that trends anterodorsally, a deep fossa anterior to the crest, and an articulation for the first sacral rib reaching the anterior margin of the preacetabular process medially. *Bromsgroveia* from the English Midlands shows the iliac/sacral characters, and so is a poposaurid, and the archosaur remains previously reported by Benton and Gower (1997) from the OSF were compared with those of *Bromsgroveia*, although they lacked diagnostic features.

The Sidmouth jaw is nearly identical in shape to that of the poposaurid *Arizonasaurus* (Nesbitt, 2005, Fig. 13), but only about a quarter of the size. The two resemble each other in general, non-apomorphic characters such as the roughly parallel jaw margins, the slight elevation and change of angle between teeth 4–12 and 1–3, where the first three point slightly backwards, the marked nutrient foramina below the tooth row, the separate, somewhat oval-shaped interdental plates, the long narrow anterior extension of the Meckelian canal, and the short symphysis and pointed anterior jaw tip. Note, however, that the interdental plates of the new OSF jaw are larger and deeper than those in *Arizonasaurus*, so the two cannot be the same taxon.

In summary, the Sidmouth jaw could represent a basal dinosauromorph or avemetatarsalian, a basal ornithosuchid, a rauisuchoid, or a poposaurid. Circumstantial evidence hints at the last as most likely because poposaurids are definitively identified already from the Anisian worldwide, and from the English Anisian in particular.

Poposaurids such as *Ctenosauriscus*, *Arizonasaurus*, and *Lotosaurus* had a 'sail' composed of elongate neural spines on the dorsal vertebrae. Milner et al. (1990), Benton et al. (1994), and Benton and Gower (1997) tentatively identified an elongate neural spine among the OSF fossils (EXEMS 60/1985.88) as a possible elongate neural spine, although noting that it was narrower than such spines in poposaurids. Butler et al. (2009) rightly stressed this point, and the elongate OSF bone may be one of the unusual, straight ribs from the anterior two or three dorsal vertebrae of the rhynchosaur *Fodonyx* (cf. Hone and Benton, 2008, Fig. 4E), as identified in other rhynchosaurs by Benton (1983, 1990).

The dentary fragment, at 62 mm long, scales to a lower jaw some 120–125 mm long, and so a total body length of 750–800 mm, based on the proportions of *Arizonasaurus*, which ranged from 2 to 4 m long, and whose dentary is about four times the size of the Sidmouth dentary.

3.4. The other isolated elements

The block SIDMM G 4 2010 contains five other elements, four still in situ, and one removed from the block (Fig. 4), a possible skull or pelvic bone (bone 1, Fig. 4A and B), a slender long bone (bone 2, Fig. 4A and B), a small tooth (t, Fig. 4B), and two possible dermal scutes (sc, Fig. 4A–D).

The enigmatic 'bone 1' (Fig. 4A and B) has a blade-like portion 28 mm across in both directions, and the whole piece is 57 mm long, the 'shaft' being 30 mm long and 7 mm wide at the narrowest, broadening to a spoon-shaped 13 mm-broad distal end. This distal end, to the right in the figure, is a definite termination, so the first possible identification, as an archosaur pubis seems unlikely: poposaurids such as *Arizonasaurus* (Nesbitt, 2005, Fig. 24) and

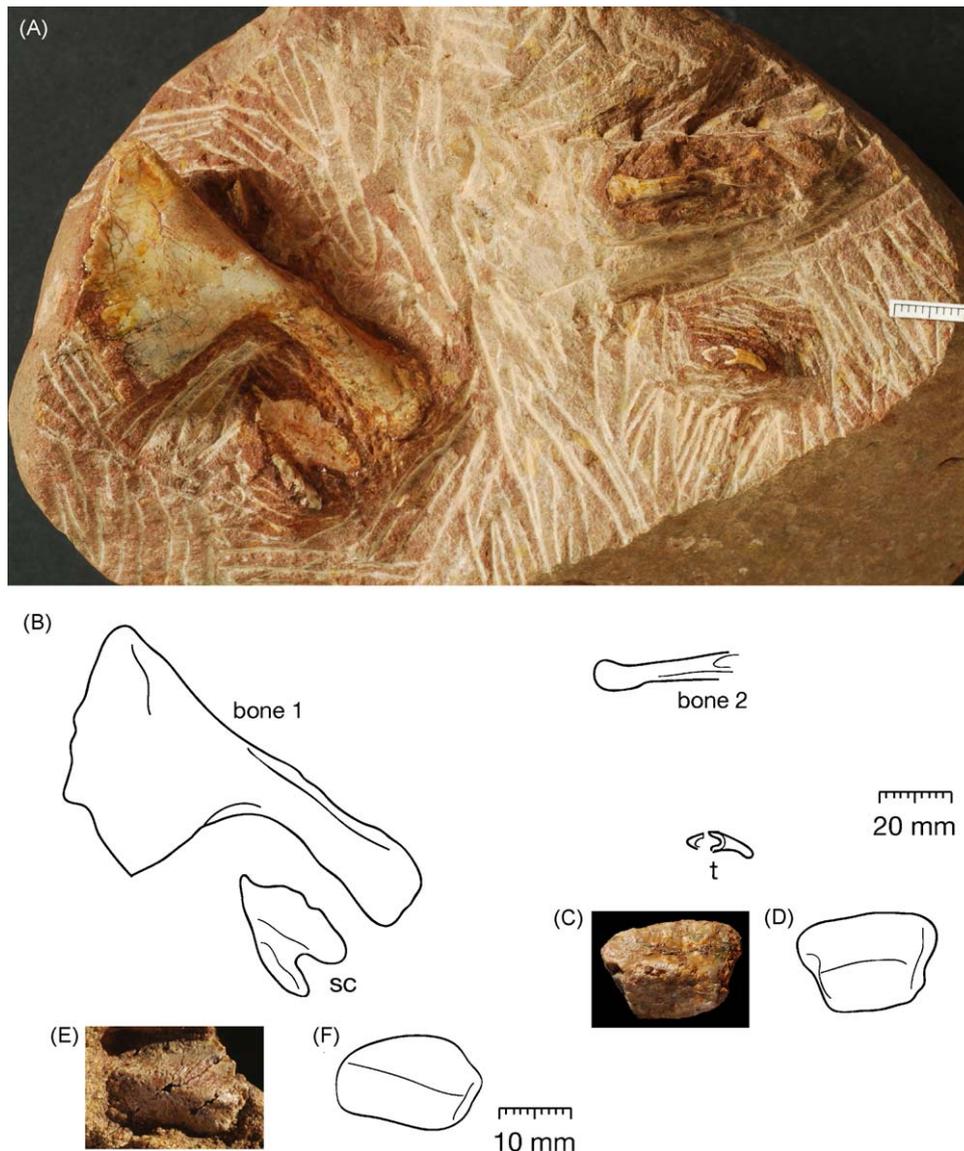


Fig. 4. Isolated bones in the same block as the archosaur jaw from the Otter Sandstone Formation (SIDMM G 4 2010), as a photograph (A), and interpretive drawing (B) of what lies below where the jaw was removed, and an isolated scute (SIDMM G 2 2010) (C and D). (E and F) an additional scute (BRSUG 27203), found separately, and about half the size of the others. Note the differing scale bars for A–D and E–F. Abbreviations: sc, scute; t, tooth.

Effigia (Nesbitt, 2007, Fig. 42) have a long, slender ventral pubic process, three or four times as long as the narrow process in 'bone 1'. The ischia of these taxa are also long and slender, and typically fused. It also cannot be matched with any skull bones (? possible quadrate or pterygoid) of such archosaurs, nor does it correspond to any typical rhynchosaurian elements seen in *Fodonyx* (Hone and Benton, 2008).

The slender limb bone (bone 2, Fig. 4A and B) is 20 mm long as preserved, with slightly expanded ends, one of which is rather damaged. The preserved end is 4.5 mm across, and the shaft narrows to 2.5 mm. This might be a metatarsal of an archosaur – the poposaurid *Effigia* has such long slender metatarsals, whereas the metacarpals, and the hand as a whole, are considerably shorter and relatively broader (Nesbitt, 2007, Fig. 47). These elements are not known in *Arizonasaurus* (Nesbitt, 2005).

The small isolated tooth (t, Fig. 4A and B) is not evidently archosaurian, being apparently somewhat circular in the cross section of the root, and with a crown that is slightly recurved, but only slightly compressed and with sharp anterior and posterior edges that lack serrations. The tooth is damaged across the root,

revealing a substantial hollow interior portion, suggesting the tooth is not mature. The top of the crown bears an oblique flattened facet, presumably a wear facet. This tooth is presumably from a diapsid, perhaps an archosauromorph, but probably not an archosaur. In the oblique wear facet and general shape, it matches the anterior incisiform teeth of the enigmatic OSF diapsid *Coartaredens* (cf. Milner et al., 1990, Fig. 6B; Spencer and Storrs, 2002, Fig. 8), but it is about ten times the size (15 mm vs. 1–2 mm). It is safest probably to assign the tooth to an unknown archosauromorph diapsid, perhaps a prolacertiform.

The two putative scutes (sc, Fig. 4A–D) are similar in size, about 38 mm long and 26 mm wide. The first scute (sc, Fig. 4A and B) is seen in ventral or interior view, and this is a concave surface, with both sides sloping in towards a deep midline. The lateral margins (long sides) of the presumed scute are rough and perhaps damaged, while the narrow sides are pointed at one end and deeply scalloped at the opposite end. The pointed and scalloped ends (sc, Fig. 4A and B) could represent the overlapping structures, where the pointed end overlay the scalloped, and so the pointed end would be anterior. The isolated scute (SIDMM G 2 2010; Fig. 4C and D), located originally close to the medial side of the mandible,

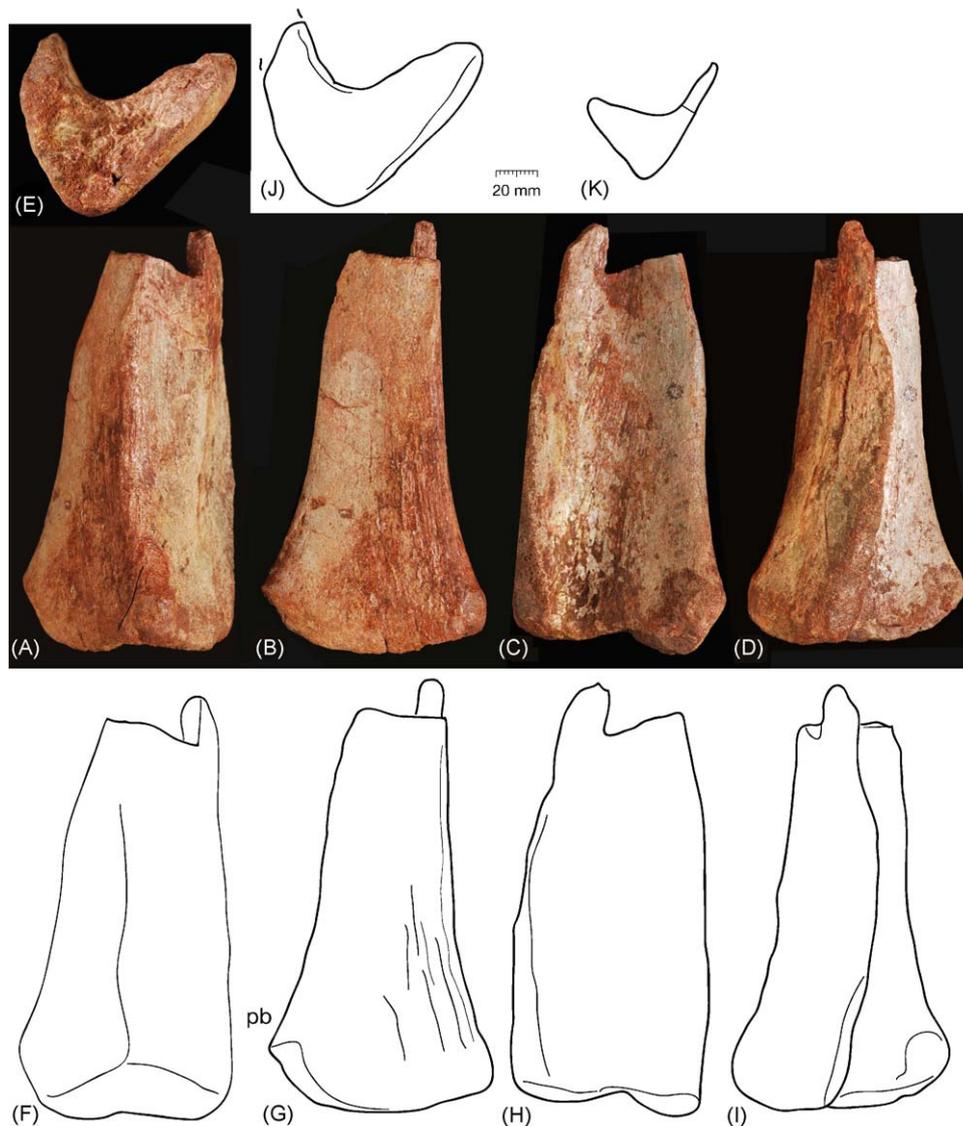


Fig. 5. Possible distal end of a right pubis of an *Arizonasaurus*-like archosaur from the Otter Sandstone Formation, BRSUG 29009, shown in putative anterior (A and F), lateral (B and G), posterior (C and H), lateral (D and I), articular (E and J), and broken-end view (K). Abbreviation: pb, pubic boot.

is pictured in external view, and shows a midline ridge, and slight indentations at either end, perhaps indicating areas of overlap with adjoining scutes. The overall surface appears to be smooth, rather than sculptured, but the specimen might have been eroded. How much of the outline of the two presumed scutes is real, and how much has been lost during predepositional transport, is not clear.

A third scute, found separately (BRSUG 27203; Fig. 4E and F) is smaller, 18 mm long and 12 mm wide, but it shows a similar shape, with a roughly midline ridge on the outer surface, higher at the putative anterior end (Fig. 4E and F, left on the image) and lower at the posterior end, where it was perhaps overlapped by the next osteoderm.

Sculptured scutes are typical of Crurotarsi, but not of certain rauisuchian groups, and Poposauroidae lack scutes (Benton, 1999; Nesbitt, 2005; Brusatte et al., 2010). The pointed, presumed anterior, end and the overall shape of the scute resembles that of the Middle Triassic 'rauisuchian' *Ticinosuchus* (Krebs, 1965). More widely, such dermal scutes with anteriorly pointing ends are also present in several non-avesuchian archosaurs, such as *Euparkeria* (holotype), *Vancleavea* (Nesbitt et al., 2009), and the enigmatic *Turfanosuchus* (Wu and Russell, 2001). Otherwise, dermal scutes (osteoderms) are a primitive feature of archosaurs (Benton and

Clark, 1988; Brusatte et al., 2010), and so these OSF specimens are at least archosaurian.

3.5. Large pubis

A large fragmentary bone (BRSUG 29009; Fig. 5), previously undescribed, probably also represents a medium-sized archosaur, and is tentatively identified (see below) as the distal end of a right pubis. The specimen was found by Mark Hounslow at the same time as a nearly complete skull of the rhynchosaur *Fodonyx spenceri* (BRSUG 27200), in spring 1999 at Pennington Point, source of the jaw described above. The skull was in situ, whereas this bone was in a fallen block, as is more commonly the case. Stratigraphically, the jawbone and other elements (SIDMM G42010) and the pubis distal end (BRSUG 29009) probably came from just below the top of Andy Newell's Unit C, the Pennington Point Member of Gallois, and layer 21 of Hounslow and McIntosh (2003).

The specimen is 90 mm long at most, and it consists of an element that broadens towards the proximal (upper) end, and with a roughly triangular, asymmetric cross section, and triangular distal (lower) end. If the concave side is assumed to face backwards, then the element can be oriented to show a series of faces (Fig. 5). The anterolateral face (Fig. 5A and F) shows the taper

of the whole element from the distal (lower) end; there is a broad ridge along the middle of this face, and a roughened bone surface around the end. Turning the bone on its long axis, the first side view (lateral; Fig. 5B and G) is flat, and relatively symmetrically tapering, with numerous elongate striations (? muscle attachment) near the distal end. A further 90° rotation shows the posteromedial face (Fig. 5C and H), which is broadly concave for its entire length; the right-hand edge has been worn down as a result of damage before collection. The final 90° rotation shows the medial face (Fig. 5D and I), emphasising the projecting, rather thin anterior face that obscures part of the concavity of the posterior face. The distal end (Fig. 5E and J) is triangular, shaped rather like the Nike trademark 'swoosh' or 'tick', with a broad, shorter process to the left as illustrated, the anterior face, and a longer, thinner process to the left, terminating in a rather sharp point, the lateral face. Note, however, that the broad process is incomplete, marked in the drawing by dashes (Fig. 5J), corresponding to the area of damage. The terminal facet is flat to slightly concave, extremely rough, and presumably unfinished, suggesting the element comes from a young animal. The broken end of the bone, opposite the distal end, is also triangular to 'tick'-shaped (Fig. 5K), but in this case, the bulkier branch leads to the narrower process at the dorsal end (anterior face), and the narrow process, shown to the right (lateral face), matches the broken piece of bone that extends down in Fig. 5A–I, and so runs into an initially thin process that becomes thicker towards the distal end.

The specimen is hard to identify because it is incomplete, even despite the presence of the terminal (distal) end (Fig. 5E and J). Among large tetrapods from the Anisian, it could be an archosaur, rhynchosaur, or a temnospondyl. In the latter two, limb elements are broader and more massive for the size, so it is most likely from an archosaur. An identification might have been as the distal end of an ischium. In many archosaurs, including 'rauisuchians' such as *Postosuchus* (Long and Murry, 1995, Figs. 138 and 165), the ischia run back as slender posterior processes, largely in contact along the midline. Each ischium is not, however, asymmetrically triangular in cross section, so this identification is unlikely. Other possible identifications include the distal end of an ulna or tibia, but the element is more triangular/crescent-shaped in section and in the shape of the articular end than those limb elements in typical archosaurs.

The specimen lacks any diagnostic characters and so cannot be determined closer than the distal end of the right pubis possibly from an archosaur. Comparisons show general resemblance to the distal pubis in a broad range of poposauroids, and perhaps raiuisuchians in general, but no diagnostic apomorphic characters. For example, *Arizonasaurus* shows the same kind of distal pubic process, and the gently expanding distal end on the lateral face as seen here (cf. Nesbitt, 2005, Fig. 24C, Fig. 5B and G here). In *Arizonasaurus*, the process is L-shaped in cross section, as here, with the heavier branch of the 'L' forming the lateral face, and the thinner branch the anterior pubic apron. If correct, then the slightly expanded posteriorly oriented 'pubic boot' can be identified here (pb, Fig. 5G), as in *Arizonasaurus* (Nesbitt, 2005, Fig. 24C). More broadly, however, the same structure is seen in the poposauroid *Sillosuchus* (Alcober and Parrish, 1997), as well as in the basal poposauroid *Qianosuchus* (Li et al., 2006), the raiuisuchoid *Batrachotomus* (Gower and Schoch, 2009), and the mysterious *Yarasuchus* (Sen, 2005). The distal end of the pubis in the poposauroids *Poposaurus* (Weinbaum and Hungerbühler, 2007), *Effigia* (Nesbitt, 2007), and *Shuvosaurus* (Long and Murry, 1995) ends in an elongate, thin 'boot-like' expansion, unlike the current specimen. The OSF distal pubis then shows only plesiomorphic characters, perhaps of Raiuisuchia in general, or even of a wider archosaurian clade. If this is a distal pubic element, then it comes from an animal the same size as *Arizonasaurus*: in both, the pubic

distal end is 45–40 mm wide on the lateral face, corresponding to a 3 m-long animal, three or four times the size of the animal represented by the Otter Sandstone jaw (Fig. 3).

4. Discussion

Archosaurs from the Middle Triassic of England are still enigmatic, not least because the remains are fragmentary and usually found isolated. Galton and Walker (1996) and Benton and Gower (1997) identified the poposauroid *Bromsgroveia* from the English Midlands, and some of the Devon material could belong to this taxon, or something like it. Walker (1969) identified a tooth and a cervical vertebra from Warwick as possibly from a basal sauropodomorph dinosaur, but the identifications are uncertain (Benton and Gower, 1997). No other archosaur bones from the Anisian of the English Midlands, or from Devon, have shown convincing diagnostic characters of any other clade.

The English Anisian archosaur remains could then all pertain to a poposauroid, perhaps all *Bromsgroveia*, perhaps all similar to the coeval *Arizonasaurus* from the Moenkopi Formation of Arizona, USA. Equally, and probably more likely, the English Middle Triassic archosaur remains likely pertain to several taxa, but they are currently so incomplete that this cannot be determined.

Isolated archosaur teeth are the most evocative and commonest fossils of archosaurs in the OSF, and they range in length from 7 to 60 mm (Benton and Gower, 1997). The larger teeth, those ranging in length from 13 to 60 mm, all match the teeth from the English Midlands ascribed to *Bromsgroveia*. The new mandible (SIDMM G42010) confirms that assertion, showing teeth with crowns typically 16–24 mm long from jaw margin to tip, and 6–10 mm wide, measured antero-posteriorly at the jaw socket margin. Whether the smaller teeth are all archosaurian, or some possibly prolacertiform, as suggested for the small tooth described above (t, Fig. 4A and B), is not clear. Equally, it cannot be said for sure whether larger isolated teeth, some 50–60 mm long, described by Benton and Gower (1997, Fig. 14) could be poposauroid or could come from another archosaurian taxon.

The combination of temnospondyls, procolophonids, rhynchosaurs, and a putative poposauroid in the OSF is comparable to the faunas of the Bromsgrove Sandstone Formation in the English Midlands (Benton et al., 1994; Benton and Gower, 1997), and possibly those of the slightly older Holbrook/Anton Chico Member of the Moenkopi Formation, source of the rhynchosaur *Ammorhynchus*, the poposauroid *Arizonasaurus*, as well as other archosaurs, temnospondyls, and possible parareptiles (Nesbitt, 2005; Schoch et al., 2010).

There are further similarities also with the coeval, late Anisian Donguz Svita in Russia (Tverdokhlebov et al., 2003), which has produced remains of numerous temnospondyls (five species), the procolophonid *Kapes*, shared with the OSF, archosaurs (five species), as well as theriodonts and dicynodonts. Among the five Donguz Svita archosaurs (Gower and Sennikov, 2000), two forms appear to belong to basal archosaurian clades, *Sarmatosuchus*, represented by isolated skull and postcranial remains, appears to be a proterosuchid, and *Uralosaurus*, known from isolated pieces, a possible erythrosuchid. The small *Dorosuchus*, often called a euparkeriid, might belong to some other derived archosaurian clade, and *Vjushkovisaurus* might be a 'rauisuchian' (Gower and Sennikov, 2000). *Dongusia* is based on a single vertebra, and so is generally considered a nomen dubium. However, all the Donguz archosaurs are based on isolated, although often well preserved, elements, and so they are still somewhat enigmatic.

The Donguz Svita differs from the English and North American units in having yielded synapsid specimens. The OSF, and the Moenkopi, seem to lack synapsids, which are common enough in Anisian faunas of Gondwana, such as the *Cynognathus* Zone B and C

of the Karoo in South Africa, the Manda Formation of Tanzania, the Ehrmayung Formation of China, and others. In his study of Triassic tetrapod provinciality, Ezcurra (2010) found an enigmatic signal for the Middle Triassic, with many groups existing worldwide, and no clear separation of northern and southern hemisphere faunas (Laurasia; Gondwana). Nonetheless, his broad-brush analysis for the whole Middle Triassic perhaps could not detect subtler signals, including the apparent absence of synapsids from Laurasia until the Late Triassic, and the varying dominance of the key herbivores, the rhynchosaurs and dicynodonts, from continent to continent (e.g. rhynchosaurs in Gondwana and England, rare or absent in the Germanic Basin, North America, and Russia).

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