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RICHARD OWEN'S GIANT TRIASSIC FROGS: ARCHOSAURS FROM THE MIDDLE TRIASSIC OF ENGLAND

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ABSTRACT—The first archosaurs from the Middle Triassic were described unwittingly by Sir Richard Owen in the 1840s. He combined a variety of archosaurian postcranial elements with skull material of temnospondyls, thus producing his image of giant Triassic frogs. Archosaur bones have been collected from Middle Triassic (Anisian) sediments of Warwick and Bromsgrove in the West Midlands, and more recently, from south Devon. Some of the vertebrae and pelvic elements belong to the poposaurid *Bromsgroveia*, and other elements and teeth to unidentified archosaurs, one perhaps a dinosaur. The English faunas help fill a gap in knowledge of archosaurs in the early part of the Middle Triassic. If *Bromsgroveia* is a poposaurid, it is the oldest member of a family known otherwise from the Late Triassic of North America.

INTRODUCTION

Sir Richard Owen, the leading British paleontologist and anatomist of the early years of Queen Victoria's reign, was immensely active in describing new terrestrial fossil reptiles in the early 1840s. Not only did he name the Dinosauria in 1842 (Owen, 1842b; Torrens, 1992), but he also described the first Triassic amphibians and reptiles from England, including the first reported rhynchosaurs, and, as we now recognize, the first poposaurid archosaur, and indeed the first Middle Triassic terrestrial tetrapods from anywhere in the world (Owen, 1841a–c, 1842a–c). In these six papers, Owen reported new specimens he had been sent from Triassic rocks of central England, in the vicinities of Shrewsbury and Warwick. The Shrewsbury specimens consisted of nearly complete skeletons of a small rhynchosaur, which he named *Rhynchosaurus articeps* (Benton, 1990), and he ascribed all of the Warwick material, except some isolated teeth, to the temnospondyl amphibian *Mastodonsaurus*, reported first from the Keuper (Late Triassic) of Germany (Jaeger, 1828). Owen (1841a–c, 1842a, b) renamed *Mastodonsaurus* as *Labyrinthodon* since the former name was, in his view, 'objectionable.'

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 (Fig. 1) 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 3m, with short forelimbs, each equipped with a four-fingered hand, and long large-footed hindlimbs; clearly a frog from hell. This astonishing model was based on Owen's mistaken association of a number of beautiful undoubted temnospondyl jaws and partial skulls from Warwick (Paton, 1974; Milner et al., 1990), with isolated postcranial elements of archosaurs, to be described here, as well as rhynchosaurs (Benton, 1990) and the prolacertiform *Rhombopholis* (Benton and Walker, 1996). In the model, *Labyrinthodon* is equipped with archosaur-like teeth, found in association with the other bones at Warwick, but otherwise interpreted correctly by Owen as those of a flesh-eating archosaur. In addition, Owen argued that *Chirotherium* footprints from the Triassic of Germany, and from neighboring coeval sandstone beds in England, had probably been produced by *Labyrinthodon*, hence indicating that the animal had four- or five-fingered hands and large five-toed feet.

Owen classed all the Warwick material in the Order Batrachia, equivalent to the Class Amphibia, but regarded by him as an order of reptiles, just like the Order Dinosauria, or the Order Lacertilia. This combination of amphibians and reptiles into a larger Class Reptilia was typical at the time, and this was strengthened by Owen's mixing of temnospondyl bones with those of various reptiles. Indeed, he recognized the apparently compound nature of the batrachian *Labyrinthodon* when he described the ilium, which is now the holotype of the probable poposaurid archosaur *Bromsgroveia* (see below). Owen (1842a: 534–535) suggested that the ilium resembled that of modern amphibians (identifying the preacetabular process as a rudimentary homologue of the long anterior process in 'anourous Batrachians') and crocodiles, and he wrote:

> The cranial fragments correspond in size with those of the head of a Crocodile between six and seven feet in length, but the ilium supports an articular cavity for the reception of the head of the femur, somewhat greater than that exhibited by the same bone of a Crocodile twenty-five feet in length. If both belonged to the same individual, we should have an example of a reptile with hinder extremities of disproportionate magnitude as compared with those of existing Saurians, but which would approximate in this respect, as in many other particulars already pointed out, to some of the existing anourous Batrachians.

Hence, Owen sought to explain the apparent mismatch between head size and hip size by hinting that the Warwick bones came from some sort of giant extinct frog (see also Owen, 1842b:188).

The incorrectness of this association of temnospondyl skull and jaw bones with reptilian postcranial elements was pointed out by Meyer (1856), Huxley (1859, 1870), Miall (1874), Walker (1969), Paton (1974), Milner et al. (1990), and Benton et al. (1994). Thomas Henry Huxley, who rarely had a kind word to say about Owen, gleefully (Huxley, 1859:57) 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.'

Ironically, the *Chirotherium* footprints, attributed by Owen to his giant frog, are now interpreted (Krebs, 1965; Haubold, 1971; Tresise, 1989) as having been produced by rauisuchid archosaurs, possible close relatives of the poposaurids, such as *Bromsgroveia*, the true proprietor of the Warwick ilium and many of the other postcranial elements.

The purpose of this paper is to describe all the archosaur material from the English Middle Triassic, concentrating on the

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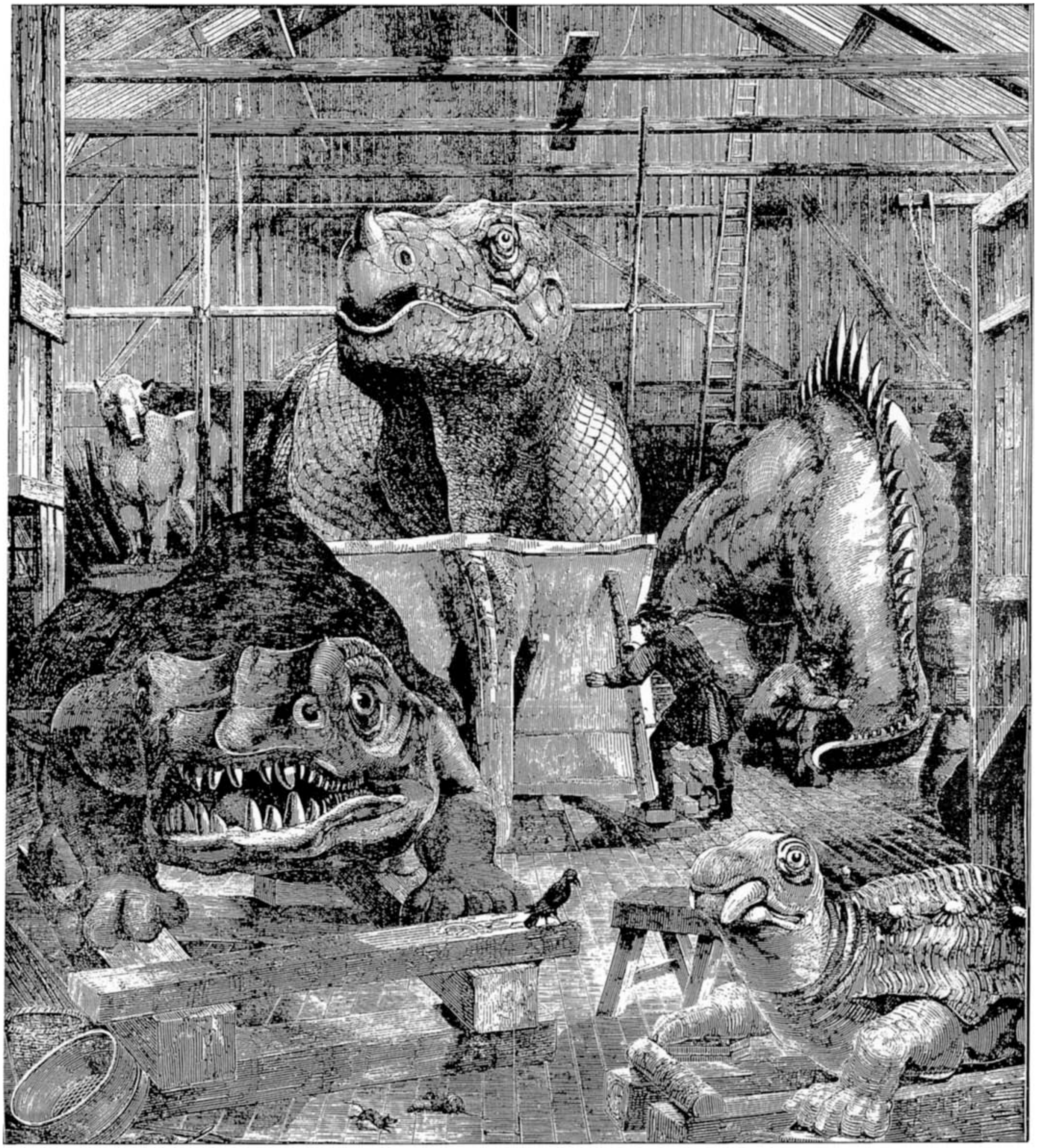

FIGURE 1. Sir Richard Owen's prehistoric menagerie taking shape in 1853 in the studio of Waterhouse Hawkins. The picture includes *Iguanodon* (center), *Palaeotherium* (top left), *Hylaeosaurus* (top right), *Dicynodon* (bottom right), and *Labyrinthodon* (bottom left). The latter was based on a combination of temnospondyl skull remains and reptilian postcranial elements.

classic specimens from Warwick, and presenting for the first time the new material from Devon. The English archosaur faunas, although consisting of isolated material, are important because of their Anisian age, a time when few such faunas are known. The faunas are unique in Europe, representing continental assemblages coeval with the extensive Muschelkalk Sea.

Repository abbreviations—BGS (GSM), British Geological Survey (Geological Survey Museum), Keyworth, Notting-

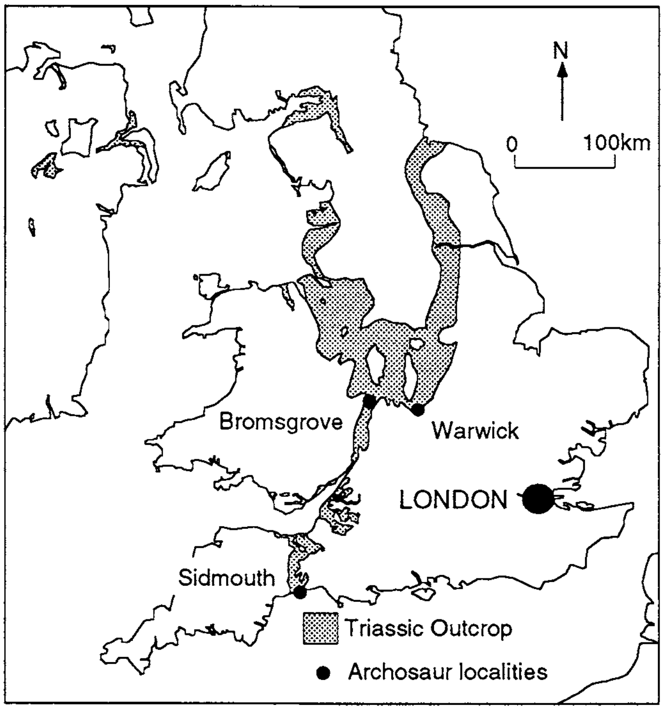

FIGURE 2. The Triassic outcrop of England, showing the localities in the English Midlands (Warwick, Bromsgrove) and Devon (Sidmouth) that have yielded archosaur remains.

ham; **BMNH**, British Museum (Natural History), London; **BRSUG**, Bristol University, Department of Geology Museum; **BU**, Department of Geology, University of Birmingham; **CAMSM**, Sedgwick Museum, Cambridge University; **WARMS**, Warwickshire Museum, Warwick.

LOCALITIES AND SPECIMENS

Middle Triassic amphibian and reptile remains have been reported from a number of localities in the English Midlands and in Devon (Fig. 2), from units dated as Anisian (Benton et al., 1994). Most of the material has been reviewed recently (Walker, 1969; Galton, 1985; Benton, 1990; Milner et al., 1990; Benton et al., 1993, 1994; Benton and Walker, 1996), but further work is in progress on the procolophonids (Spencer and Storrs, in prep.). The tetrapod faunas include a variety of temnospondyls, procolophonids, rhynchosaurs, a prolacertiform, and archosaurs, and these are associated, in some localities, with plant fossils, as well as arthropods and other invertebrates. The first tetrapod remains from these beds were found near Warwick in 1823, but most specimens came to light after 1836 (Buckland, 1837; Murchison and Strickland, 1840; Owen, 1841a–c, 1842a–c). Most of the teeth and bones described by Owen and Huxley from Warwick came from a small quarry within the town, Coten End Quarry, but others bear the names 'Emscote' and 'Leek Wootton,' small villages near Warwick (more details in Benton et al., 1994).

The first archosaur specimens from the English Anisian were collected in Warwick about 1835 by Dr G. Lloyd, three isolated teeth illustrated by Murchison and Strickland (1840:pl. 28, figs. 6, 7, 7a). Further similar teeth were sent to Owen, and he made these the types of the new genus and species *Cladyodon lloydii* (Owen, 1841b, 1842b:155). Owen compared the *Cladyodon* teeth with those of *Megalosaurus*, a genus assigned to the new Order Dinosauria in the same 1842 paper, but he did not then designate *Cladyodon* as a dinosaur. He allied it with the Late Triassic taxa *Thecodontosaurus* and *Palaeosaurus*, described earlier by Riley and Stutchbury (1840) from the Bristol area, and placed all three in the 'Thecodonts,' a branch of the Order Lacertilia, according to his classification.

Subsequently, a vertebra and a nearly complete left ilium were collected about 1840 by Dr G. Lloyd of Leamington, and transmitted to Owen, who described and figured the material (Owen, 1841a:582; 1842a:532–535, pl. 45, figs. 16, 17; 1842b: 187–188). Owen associated these specimens with cranial material he had referred, in the same papers, to *Labyrinthodon pachygnathus* Owen, 1842. This temnospondyl species was later (Paton, 1974) referred to *Cyclotosaurus*, but Milner et al. (1990) regard it as a nomen dubium, considering the jaw and skull fragments non-diagnostic.

Huxley (1870) assigned *Thecodontosaurus* and *Palaeosaurus* to the Dinosauria, a view maintained today, since most of the material is clearly that of a prosauropod. He stated that the *Cladyodon* teeth from Warwick were also those of dinosaurs, and he distinguished two forms, one assigned to the Bristol genus *Palaeosaurus*, and the other identified as 'megalosaurian.' Huxley (1870:46–47) described new archosaur specimens from Warwick, supplied to him by Mr J. W. Kirshaw: a partial sacrum consisting of three vertebrae, and a possible dorsal vertebra and another vertebra, all of which he ascribed to a dinosaur like *Thecodontosaurus*. Finally, Huxley (1870:47) made reference to the ilium described by Owen (1842a), and stated that it was 'intermediate in its characters between the ilium of a Teleosaurian and that of a Lizard.'

Little work has been done on the English Middle Triassic archosaurs this century. Huene (1908:figs. 214, 215, 228, 267) refigured the sacrum and tooth described by Huxley, the vertebra figured by Owen (1842a), and a left ischium, and he followed Huxley in assigning all the material to the dinosaur *Thecodontosaurus*. Huene (1908:242, fig. 269, 270) placed the *Cladyodon* teeth tentatively in the German genus *Teratosaurus*, interpreted by him as a dinosaur, but re-interpreted (Galton, 1985; Benton, 1986) as a rauisuchian archosaur. Walker (1969) re-identified the ilium as that of a poposaurid archosaur, and Galton (1985) made it the holotype of *Bromsgroveia walkeri*. Walker (1969) also included the three sacral vertebrae, a dorsal and a caudal vertebra, the ischium, and the *Cladyodon* teeth in the same taxon, a view followed by Galton (1985). Walker (1969) suggested that two further archosaurs might have been present at Warwick: a 'large thecodont' represented by a fragment of an ilium, and a possible prosauropod dinosaur, represented by a *Thecodontosaurus*-like tooth, and a cervical vertebra.

Later collections by Wills (1907, 1910) revealed a new fauna from the Hospital Quarries, Bromsgrove, West Midlands (SO 948698), also in the Bromsgrove Sandstone Formation, and comparable to the Warwick material. Further new archosaur material came to light in the 1980s and 1990s in the Otter Sandstone Formation of Devon, and this has been referred to briefly (Spencer and Isaacs, 1983; Benton, 1990; Milner et al., 1990; Benton et al., 1994), but not described or illustrated.

SYSTEMATIC PALEONTOLOGY

Attribution of the Warwick and Bromsgrove Archosaur Specimens

The archosaur specimens from Warwick and Bromsgrove are treated together because the two localities are close geographically, the tetrapod fossils come from the same stratigraphic unit (the Bromsgrove Sandstone Formation) and previous studies have shown that many taxa are shared (Walker, 1969; Benton, 1990; Benton et al., 1994).

The only specimen that belongs clearly to the poposaurid *Bromsgroveia walkeri* Galton, 1985 is the right ilium (WARMS G.3a, b). As for attribution of the remaining archosaur specimens from Warwick and Bromsgrove, two issues must be addressed: (1) could some, or all, of these other specimens be attributed to this taxon; and, (2) could some, or all, of these specimens be attributed to a poposaurid?

There are three arguments for attributing all the archosaur material from Warwick to *Bromsgroveia walkeri*: (1) evidence for association; (2) matching of material by size and fit; and, (3) evidence in some specimens for poposaurid affinity. First, the main specimens were found in close proximity, in the small Coten End Quarry, seemingly in two main tranches. The first batch of specimens, including the ilium, as well as several teeth (WARMS G.7, 8, 954, 969), a vertebra (WARMS G.5), and possibly an ilium fragment (WARMS G.4713), were found about 1840 by Dr G. Lloyd, and the second main batch, consisting of three sacral vertebrae (WARMS G.1, 2), two dorsal centra (WARMS G.121, 128), and a left ischium (WARMS G.970), and teeth (WARMS G.956.1, 2) were collected from Coten End Quarry about 1862-8 by J. W. Kirshaw. The other archosaur remains from Warwick and Bromsgrove include teeth and vertebrae that are indistinguishable from the specimens just noted. The proposal by Huene (1908) that the teeth belong to one archosaur taxon (*Teratosaurus*), and the postcranial elements to another (the dinosaur *Thecodontosaurus*) seems unlikely.

The second line of evidence for association of most of the archosaur material from Warwick and Bromsgrove comes from anatomical correspondence. The ilium shows sacral rib insertion regions on its medial face which correspond in size to those indicated by the three damaged sacral vertebrae. The ischium also corresponds in size and shape to the relevant faces of the ilium. The vertebrae and other postcranial elements, and the teeth, also correspond in size to the pelvic elements.

Thirdly, and with caution, poposaurid characters may be identified in some specimens. The caution derives from the fact that poposaurid definitions and diagnoses remain unclear (see below). The type genus *Poposaurus* (Colbert, 1961) is known only from fragmentary postcranial material. The more complete *Postosuchus* (Chatterjee, 1985) has been shown by Long and Murray (1995) to have been based on more than a single taxon, and these authors conclude that most of the material is rauisuchid rather than poposaurid. Nonetheless, the *Bromsgroveia* ilium is clearly rauisuchian in its morphology, and most similar to poposaurids, based on Long and Murray's (1995) criteria. Further resemblances between the vertebrae and ischia of *Bromsgroveia* and *Poposaurus* are consistent with poposaurid morphology without exhibiting any diagnostic characters.

The view that most of the significant archosaur specimens from Warwick and Bromsgrove come from a single taxon was adopted by previous authors. Galton (1985: 11) listed as paratypes the other specimens associated with the type ilium by Huxley (1870), Huene (1908), and Walker (1969), the sacrum (WARMS G.1, 2), the first caudal vertebra (WARMS G.5), and the ischium (WARMS G.970). These are also included here in *Bromsgroveia walkeri*, as well as the majority of the Warwick teeth, and the other archosaur bones. The ilium fragment (WARMS G.4713) cited by Walker (1969) as evidence of a 'large thecodont' is also retained with *Bromsgroveia*, because it shows no clear distinguishing characters. We reiterate, however, that evidence for identification of the bulk of the Bromsgrove and Warwick archosaur material as *Bromsgroveia* is circumstantial.

ARCHOSAURIA Cope, 1869
SUCHIA Krebs, 1974
Family POPOSAURIDAE Nopcsa, 1928
Genus *BROMSGROVEIA* Galton, 1985

BROMSGROVEIA WALKERI Galton, 1985
(Figs. 3–12)

Megalosaurus?, Murchison and Strickland 1840: pl. 28, fig. 6a, b, 7.
Labyrinthodon, Owen 1841a:582.
Labyrinthodon pachygnathus Owen 1842a:532–535; pl. 45, figs. 1–4, 16, 17.
Cladyodon lloydii Owen 1842b: 155.
Labyrinthodon pachygnathus Owen 1842b:187–188.
Labyrinthodon pachygnathus, Brodie *in* Hull 1869:121.
Cladydon lloydi, Brodie *in* Hull 1869:121.
Palaeosaurus (?), Huxley 1870:46, pl. 3, fig. 4.
Teratosaurus (?), Huxley 1870:46, pl. 3, fig. 11.
Thecodontosaurian, Huxley 1870:46–47; pl. 3, figs. 9, 10.
reptilian ilium, Miall 1874:431.
Thecodontosaurus antiquus, Huene 1908:200–201, 202, 208–209, 211, figs. 214, 215, 228, 233.
Teratosaurus (?) *lloydi*, Huene 1908:242, figs. 269, 270.
Thecodontosaurus, Allen 1909:276–277.
archosaur related to *Poposaurus*, Walker 1969:471.
(?) primitive prosauropod dinosaur, Walker 1969:473.
large thecodont, Walker 1969:473.
poposaurid, Galton 1977:fig. 6J.
Bromsgroveia walkeri Galton 1985:11–12, figs. 2E–I, 4H, I.
'poposaurid,' Benton 1986:298.

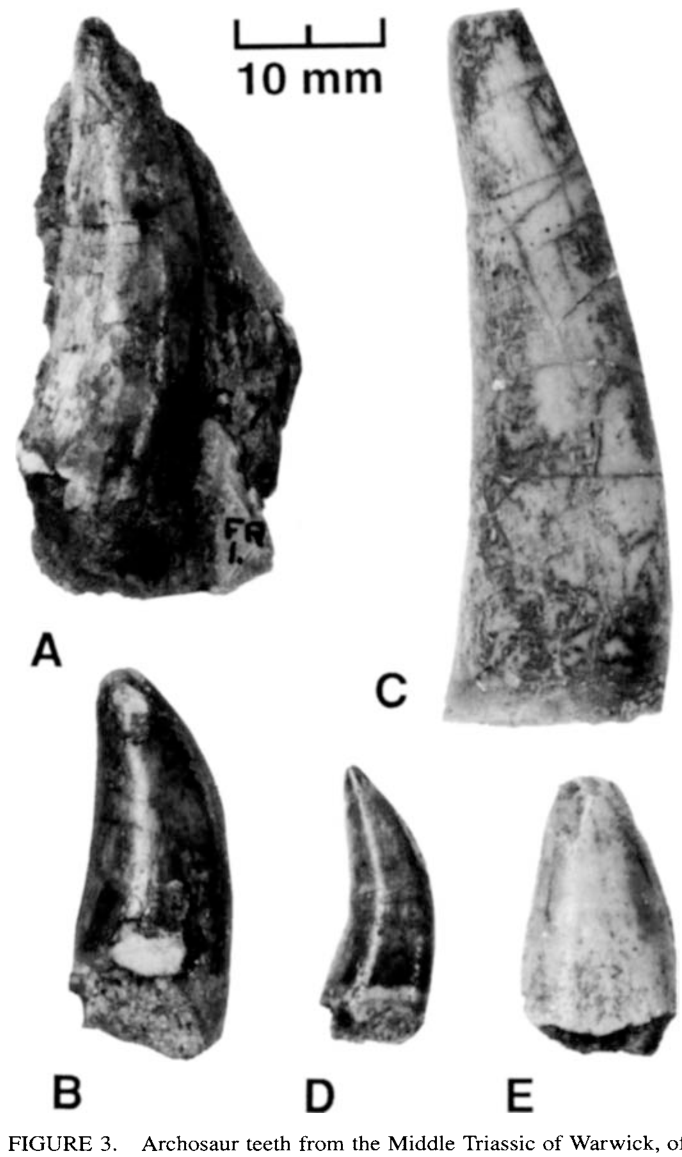

FIGURE 3. Archosaur teeth from the Middle Triassic of Warwick, of two types, long and recurved (**A–D**), and spatulate (**E**). **A**, WARMS G.7; **B**, WARMS G.8; **C**, WARMS G.956.2; **D**, WARMS G.969; **E**, WARMS G.954.

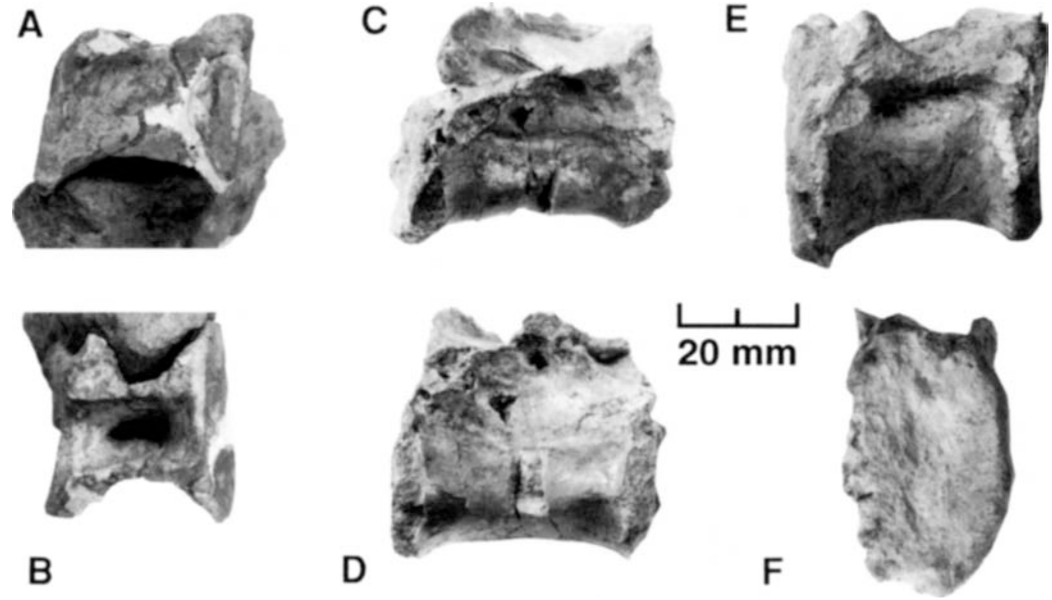

FIGURE 4. Dorsal vertebrae of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Warwick (**A**, **B**, **D**, **E**) and Bromsgrove (**C**). **A**, **B**, posterior dorsal centrum, WARMS G.121, in lateral (**A**) and dorsal (**B**) views. **C**, **D**, partial anterior dorsal vertebra, BU 2473, in lateral (**C**) and ventro-lateral (**D**) views. **E**, **F**, dorsal centrum, WARMS G.128, in lateral (**E**) and anterior (**F**) views.

Bromsgroveia walkeri, Benton 1990:288–289.
Bromsgroveia walkeri, Benton et al. 1994:140, fig. 9I.
Bromsgroveia walkeri, Long and Murray 1995:142–143, fig. 147.

Holotype—A right ilium (WARMS G.3a, b), collected by Dr G. Lloyd of Leamington about 1840.

Type Horizon and Locality—Upper part of the Bromsgrove Sandstone Formation of the Sherwood Sandstone Group (Anisian), Coten End Quarry, Warwick, Warwickshire, England (National Grid Reference, SP 289655).

Additional Material—The Warwick archosaur specimens are listed, with brief details of locality and collection data, extracted from old labels attached to the specimens, or associated with the specimens in their boxes. The labels were written at various times by curators of the different museums.

WARMS G.1, 2, a fused first and second sacral vertebra, and a separated third sacral vertebra, from Coten End, Warwick, presented by J. W. Kirshaw, 1867. Figured by Huxley (1870: pl. 3, figs. 9, 10) and Huene (1908:fig. 214).

WARMS G.3a, b, right ilium from Coten End, Warwick, presented by Dr G. Lloyd. Figured by Owen (1842a:533, pl. 45, figs. 16, 17), Galton (1977:fig. 6J), and Galton (1985:figs. 2E–I, 4H, I), and referred to by Huxley (1870:47), Miall (1874: 431), and Walker (1969:471).

WARMS G.5, fragmentary dorsal vertebra from Warwick, presented by Dr G. Lloyd. Figured by Owen (1842a:pl. 45, figs. 1–4) and Huene (1908:fig. 215), and referred to by Miall (1874: 431).

WARMS G.7, tooth of '*Cladyodon Lloydi*' from Coten End, Warwick, presented by Dr G. Lloyd. Figured by Murchison and Strickland (1840:pl. 28, fig. 6a, b).

WARMS G.8, tooth of '*Cladyodon Lloydi*' from Coten End, Warwick, presented by Dr G. Lloyd. Figured by Murchison and Strickland (1840:pl. 28, fig. 7).

WARMS G.121, centrum of a dorsal vertebra, from Coten End, Warwick, presented by J. W. Kirshaw, 1862. Figured by Huene (1908:fig. 210).

WARMS G.128, centrum of a mid-caudal vertebra, from Coten End, Warwick, presented by J. W. Kirshaw, 1867. Mentioned by Huxley (1870:47) and figured by Huene (1908:fig. 211), as a dorsal.

WARMS G.954, tooth of '*Cladyodon Lloydii*' from Coten End, Warwick, presented by Dr G. Lloyd. May be the holotype.

WARMS G.956.1, 2, two teeth of '*Cladydodon Lloydii*' from Leek Wootton, near Warwick, presented by J. W. Kirshaw. Perhaps G.956.2 is the large tooth figured by Huxley (1870:pl. 3, fig. 11).

WARMS G.957, archosaur tooth in matrix, from Coten End, Warwick. 'Presented Mr Allen.'

WARMS G.969, tooth of '*Cladyodon Lloydi*,' from Warwick, presented by Dr G. Lloyd.

WARMS G.970, left ischium from 'near Warwick.' Figured by Huene (1908:fig. 228).

WARMS G.981/982, partial right humerus from Leek Wootton, near Warwick, presented by J. W. Kirshaw. Originally catalogued as two separate specimens, 981 listed as from 'Coten End', and 982 from 'Wootton.'

WARMS G.1036, distal end of a (?) right humerus from Emscote, near Warwick, presented by Dr G. Lloyd. Figured by Huene (1908:fig. 233) as the distal end of a left femur.

WARMS G.4713, post-acetabular process of a left ilium, lacking collecting information.

CAMSM G.344a–f, sacral vertebra, from Bromsgrove quarries, L. J. Wills collection, collected about 1905.

CAMSM G.352, tooth of '*Teratosaurus*? *lloydii*,' from Bromsgrove quarries, L. J. Wills collection, collected about 1905. Figured by Huene (1908:fig. 273).

CAMSM G.353, posterior caudal vertebra, from Bromsgrove quarries, L. J. Wills collection, collected about 1905. Figured by Huene (1908:fig. 216).

CAMSM G.357, proximal end of an archosaur femur (?), from Bromsgrove quarries, L. J. Wills collection, collected about 1905.

BU 2473 (formerly 4410 (768)), incomplete dorsal vertebra from Griffin's S. Quarry, Bromsgrove. L. J. Wills collection.

BMNH R2645, a tooth of 'cf. *Cladyodon lloydi*, Keuper, Warwick'. P. B. Brodie Collection. Figured by Huene (1908: fig. 269).

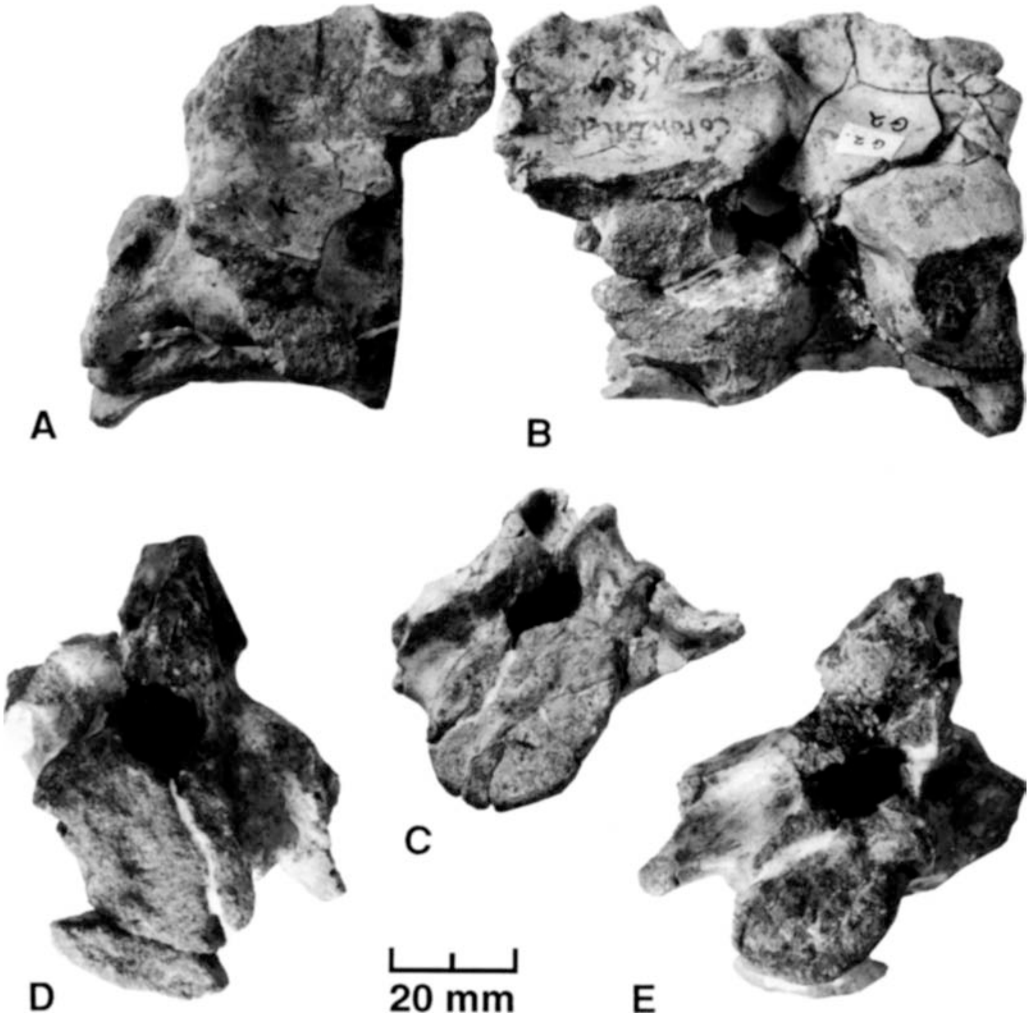

FIGURE 5. Set of three sacral vertebrae of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Warwick. **A**, **B**, right lateral view of sacral vertebrae 3 (**A**) and 2 and 1 (**B**) arranged in contact. **C**, anterior view of sacral vertebra 1. **D**, **E**, sacral vertebra 3, in posterior (**D**) and anterior (**E**) views.

BMNH R4847-48. Two teeth of *Cladyodon lloydi*, labelled in the handwriting of Sir Richard Owen, from the 'New Red Sandstone of Warwickshire'. 'Purchased F. H. Butler, March 1922'.

DESCRIPTION

Teeth

Two forms of teeth have been identified. The first, represented by WARMS G.7, 8, 956.1, 956.2, 957, and 969, BMNH R2645, R4847, and R4848, and CAMSM G.352, is slender and recurved, while the second, represented by WARMS G.954, is somewhat broader, more symmetrical in lateral view, and not curved.

The first tooth form (Fig. 3A–D) includes crowns ranging in length from 18 mm (WARMS G.969) to 47 mm (WARMS G.956.2). Height to width ratios range between 2.4 and 3.1. Serrations are spaced 16 per 5 mm, both fore and aft, in the larger teeth, and 19 per 5 mm in the smaller WARMS G.969 (Fig. 3D). The second tooth form, WARMS G.954 (Fig. 3E), measures 18 mm long and is 10 mm broad at the base (height to width ratio of 1.8). Serrations are spaced 16 per 5 mm over most of the edges, but are much smaller, 22 per 5 mm, near the bases of the anterior and posterior series. The shape of the serrations is similar to that in tooth type 1, but the grooves between serrations are longer.

These teeth fall well within the range of variation in shape seen in the jaws of *Postosuchus* (Chatterjee, 1985:fig. 10) which has recurved teeth ranging in length from 8 to 58 mm. Serration density in *Postosuchus* (12 per 5 mm) is less than in *Bromsgroveia* (16–22 per 5 mm).

Vertebrae

A number of archosaur vertebrae from Coten End Quarry clearly resemble those of many archosaurs, including rauisuchians, and are probably referable to *Bromsgroveia*. There are three isolated dorsal vertebrae, three fused sacrals, an isolated sacral, and two caudals.

Dorsal Vertebrae—WARMS G.121 (Fig. 4A, B) consists of a nearly complete centrum that lacks most of the neural arch. The centrum is strongly constricted, and there is no ventral ridge/keel. It matches in size and form the first of the sacral vertebrae described below (WARMS G.1, 2), as noted by Huene (1908: 198), and it is therefore interpreted as a posterior dorsal.

A further dorsal vertebra from Bromsgrove (BU 2473) is slightly more complete, especially on the left-hand side (Fig.

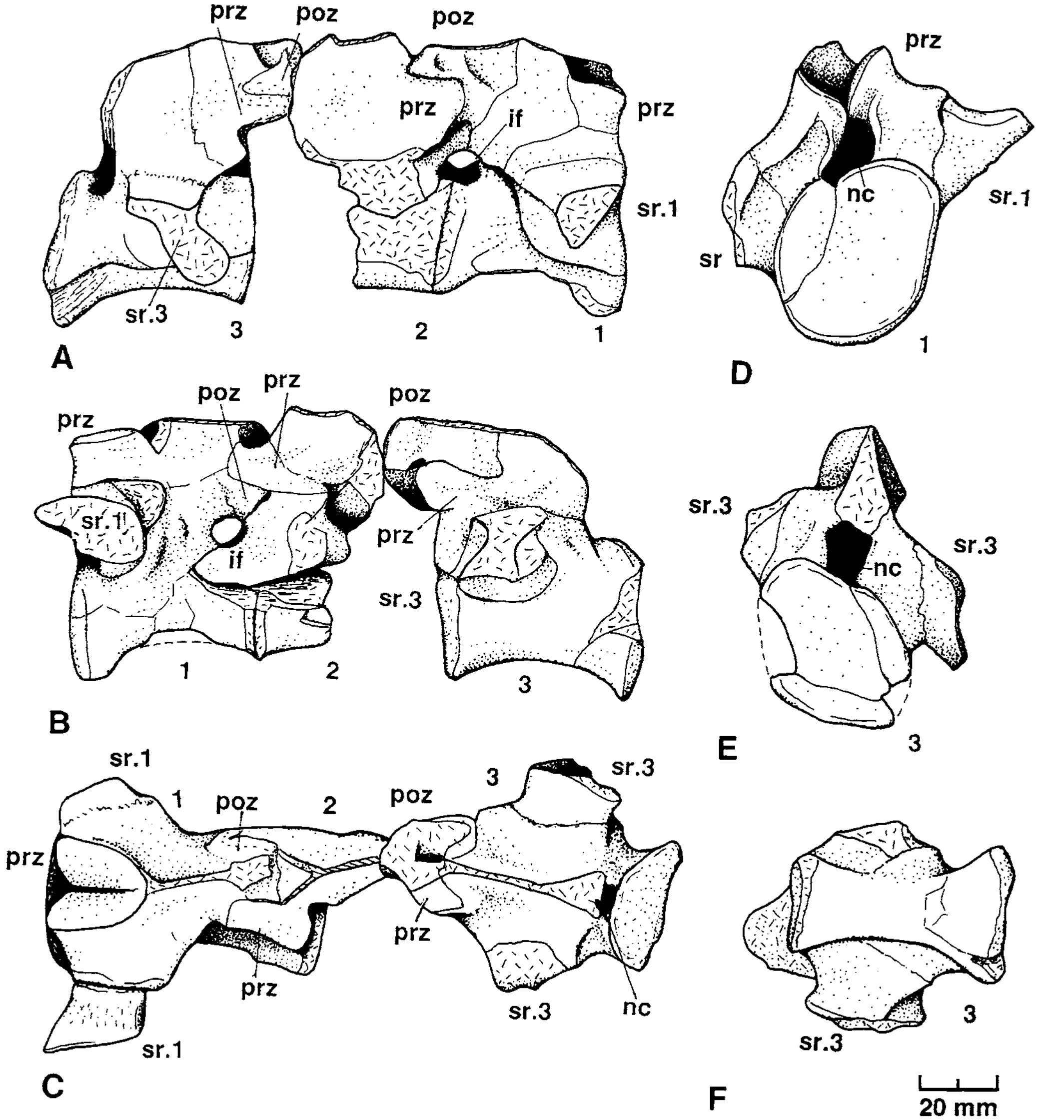

FIGURE 6. Set of three sacral vertebrae of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Warwick. **A–C**, all three sacral vertebrae, in right lateral (**A**), left lateral (**B**), and dorsal (**C**) views. **D**, sacral vertebra 1, in anterior view. **E**, **F**, sacral vertebra 3, in posterior (**E**) and ventral (**F**) views. **Abbreviations: if**, intervertebral foramen; **nc**, neural canal; **poz**, postzygapophysis, **prz**, prezygapophysis; **sr**, sacral rib.

4C, D). Facets for a two-headed rib are worn, but visible. An incised paired opening deep beneath the transverse process is probably equivalent to a similar feature seen in dorsal vertebra 4 of *Postosuchus* (Chatterjee, 1985:fig. 12). There are additional pits at the anterior, posterior, and possibly dorsal edges of the transverse process. Chatterjee (1985:418) considers that this opening might be for a pectoral ganglion or brachial plexus. Similar pits are seen in at least the dorsal part of the column of many archosaurs, and might be pneumatic in nature. The overall shape of this vertebra also resembles the anterior dorsal vertebra of *Poposaurus* (Colbert, 1961:fig. 32A).

A further centrum (WARMS G.128) was identified by Huene (1908:198, fig. 211) as a dorsal. It is deep and narrow-sided, and slightly constricted from the sides and from below (Fig. 4E, F).

Sacral Vertebrae—A set of three sacral vertebrae, preserved as one isolated vertebra (WARMS G.1) and a pair of fused vertebrae (WARMS G.2), were originally associated (Huxley, 1870:46, pl. 3, fig. 9), but have since lost clear evidence of their precise contact. When restored to the arrangement indicated by Huxley (1870), the three vertebrae are complete except for the posterior portion of the centrum of the second, the distal parts of the neural spines, and the sacral ribs (Fig. 5, 6). All three sacrals have been distorted, presumably by compression, so that the left side has rolled higher than the right.

Sacrals 1 and 2 are firmly fused from top to bottom, and the line of fusion is hard to follow (Fig. 6A, B). The contact of sacral centra 2 and 3 was probably not looser, as suggested by Huxley (1870), although the vertebrae have broken apart down this line, because the anterior articular face of centrum 3 shows signs of fracture. All three sacral centra are elongate, increasing slightly in length from sacral 1 (40 mm) to 2 (est. 40 mm), to 3 (44 mm). The centra are moderately constricted. Sutures between centra and neural arches cannot be seen. The prezygapophyseal facets are set at an angle of about 45° above horizontal (prz, Fig. 6D), and those of sacral 1 form a deep socket for reception of the postzygapophyseal unit of the last dorsal vertebra. The prezygapophyses of sacrals 2 and 3 can only be seen in general outline because the postzygapophyses of sacrals 1 and 2 are firmly fused in place (poz, Fig. 6A–C). The post-

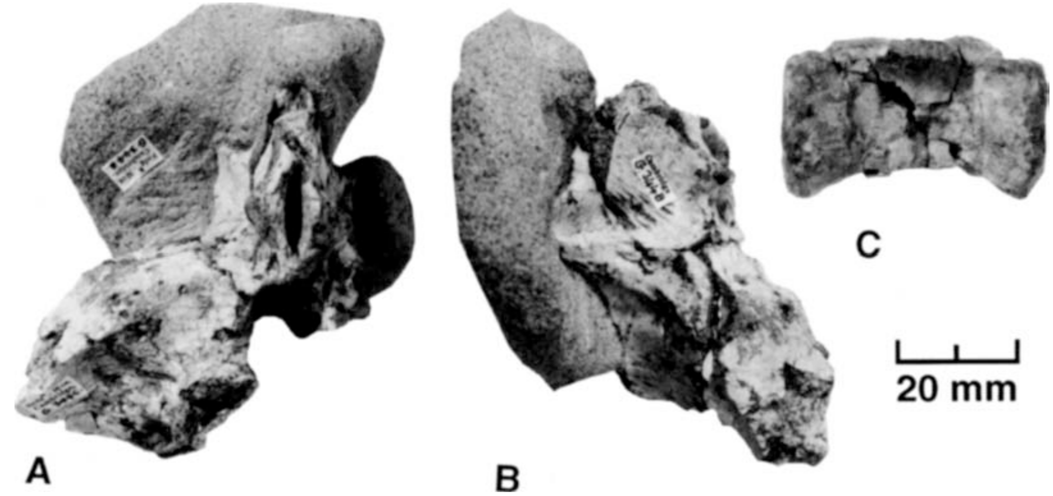

FIGURE 7. Vertebrae of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Bromsgrove. **A**, **B**, sacral vertebra, CAMSM G.344a–f, in posterior (**A**) and left lateral (**B**) views. **C**, caudal centrum, CAMSM G.353, in lateral view.

zygapophyses of sacral 3 are absent (Fig. 6E), but the triangular posterior margin of the neural spine shows that they must have been narrow and set close to the midline.

Sacral ribs are indicated for all three vertebrae, but none is complete. The best examples are seen in sacral vertebra 1 where the right-hand sacral rib is firmly attached to the neural arch, but a raised suture zone is evident. The second sacral vertebra is so damaged that the bases of the sacral ribs have been broken off. The third sacral rib may be seen best on the right side (sr.3, Fig. 6A, C, E, F).

In addition, a much decayed specimen of a sacral vertebra (Fig. 7A, B) from Bromsgrove (CAMSM G.344a–f), appears to be that of an archosaur. The left sacral rib is reasonably well preserved. The neural arch expands dramatically ventrally into

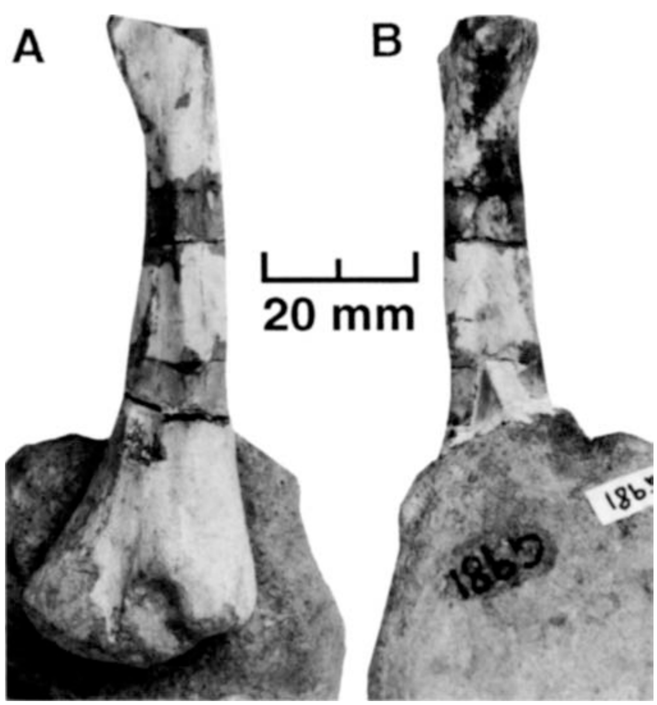

FIGURE 8. Right humerus of *Bromsgroveia walkeri* Galton, 1985, WARMS G.981/982, from the Middle Triassic of Warwick, in posterior (**A**) and anterior (**B**) views.

the left-hand sacral rib. As preserved, all this area of the neural spine, centrum, and sacral rib are hollow, presumably following the loss of cancellous bone during preservation or preparation. There are a small number of long and narrow parallel pits positioned at the dorsal, and possibly anterior, edges of the base of the transverse process. The sacral rib projects down, when seen in lateral view (Fig. 7B), but the distal termination is absent. Comparison with WARMS G.1, 2 shows that this specimen is very similar in size and shape, but it is not clear whether CAMSM G.344 is a first, second, or third sacral.

The sacral vertebrae of *Bromsgroveia* are comparable to those of other rauisuchians. Chatterjee (1985) described *Postosuchus* as having four sacral vertebrae, but Long and Murray (1995) have shown that only two were present. *Bromsgroveia* almost certainly has three, as is also found in some rauisuchids. It might be noted that the *Postosuchus* vertebra identified by Chatterjee (1985:fig. 13) as the first sacral is likely to be the last. This same vertebra is figured by Long and Murray (1995: fig. 129), and the split articular surfaces of the sacral ribs fit against the medial ridge towards the posterior part of the ilium, an arrangement also seen in the 'Kupferzell rauisuchid' (D.J.G., pers. obs.). The sacrals of *Bromsgroveia* resemble those of poposaurids (sensu Long and Murray), in being fused and having relatively short ribs, although the ribs appear to be more downturned than in *Poposaurus*.

Caudal Vertebrae—One of the vertebrae from Warwick (WARMS G.5) consists of the top of a centrum and the lower part of a neural arch. The specimen cannot be located, but it was described by Huene (1908:202, fig. 215) as an anterior caudal. A further caudal vertebra (CAMSM G.353), this time from Bromsgrove, probably comes from the middle or posterior part of the tail (Fig. 7C). The centrally positioned 'transverse process' probably includes the proximal part of a small fused caudal rib.

Forelimb Elements

Humerus—A postulated right humerus, WARMS G.981/982 (Fig. 8A, B), consists of part of the proximal end, the shaft, and the distal end of an 83 mm long element. Two broad ridges run longitudinally towards the distal end, surrounding a midline concavity. The articular faces of the bone are abraded. The ectepicondyle expands over a recess on the lateral side of the distal end that is identified as the supinator groove. Proximally, the medial ridge extends right up the length of the shaft, while

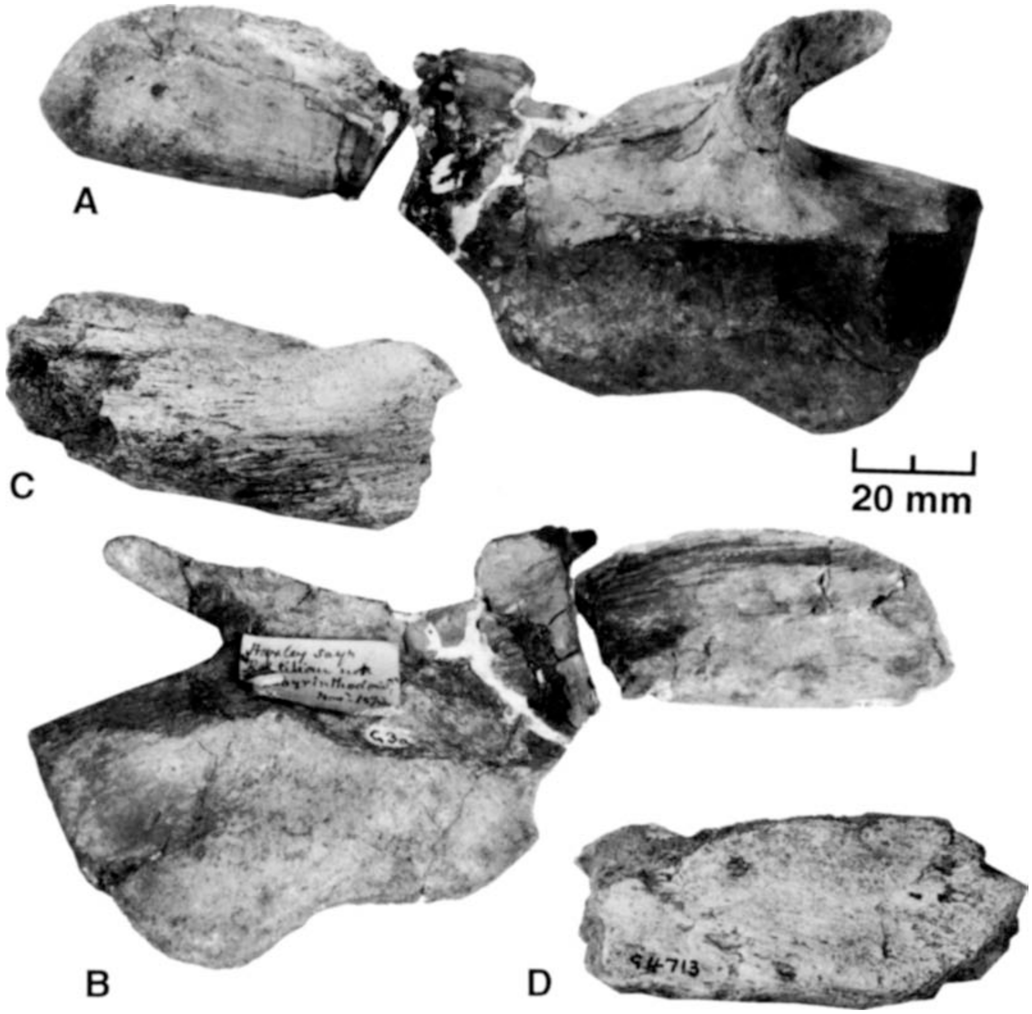

FIGURE 9. Ilia of *Bromsgroveia walkeri* Galton, 1985, from the Middle Triassic of Warwick. **A**, **B**, right ilium, WARMS G.3, the holotype of the species, in lateral (**A**) and medial (**B**) views. **C**, **D**, isolated postacetabular process from a right ilium, WARMS G.4713, from a larger animal, in lateral (**C**) and medial (**D**) views.

the lateral ridge is less marked. This gives the shaft a triangular cross section. At the most proximal part preserved, a lateral process begins to expand from the side, presumably the base of the deltopectoral crest. The proximal broken face of the bone shows a circular hollow core.

A fragment, WARMS G.1036, is a heavily abraded distal end from a rather larger individual: the specimen is 31 mm broad, but this is probably an underestimate. The specimen could be the distal end of a right humerus of an animal that was perhaps 25% larger than that represented by WARMS G.981/982, based on a comparison of shaft widths (18 mm, compared to 14 mm). Huene (1908:211) identified this element as a possible distal end of a left femur.

Pelvic Girdle Elements

Ilium—A more or less complete right ilium, WARMS G.3 (Figs. 9A, B, 10), has been designated the holotype of *Bromsgroveia walkeri* Galton, 1985. The lower margin of the acetabulum is divided into an anterior pubic process and a posterior ischiadic process. The pubic process (pp, Fig. 10) is much thickened anteriorly, where a certain amount of damage has occurred, but the bone is thinner posteriorly and ventrally. The acetabulum is deep, and is surrounded by a heavy preacetabular pillar that sweeps into a deep supra-acetabular shelf (prp, sas, Fig. 10).

The supra-acetabular buttress or rugosity resembles that of poposaurids (sensu Long and Murray) in that it curves anterodorsally along the dorsolateral edge of the anterior process. The anterior process of the iliac blade is shorter and less robust than in *Poposaurus* and *Postosuchus*. The concave upper margin of the ilium reproduced in Galton (1977:fig. 6J; 1985:fig. 4H, I) and Chatterjee (1985:fig. 26f) is based on figures in Owen (1842a), but there has been damage and originally the margin was straighter.

The medial surface of the ilium bears facets for three sacral ribs (1, 2, 3, Fig. 10B). The distribution and relative sizes of these sacral rib insertion sites matches the pattern suggested by the sacral vertebrae (WARMS G.1, 2), but an exact fit cannot be attempted since the distal parts of those sacral ribs are missing. Based on the available evidence from both the sacral vertebrae and ilium, it is unclear whether the ilium of *Bromsgroveia* was downturned or not.

The isolated postacetabular process, WARMS G.4713 (Fig. 9C, D), comes from a different individual, perhaps 25% larger than that represented by WARMS G.3. Comparison with WARMS G.3 shows that it comes from the left-hand side of the body. Walker (1969:473) suggested that this fragment came from a 'large thecodont,' presumably a different taxon from *Bromsgroveia walkeri*, but this view is not supported here, be-

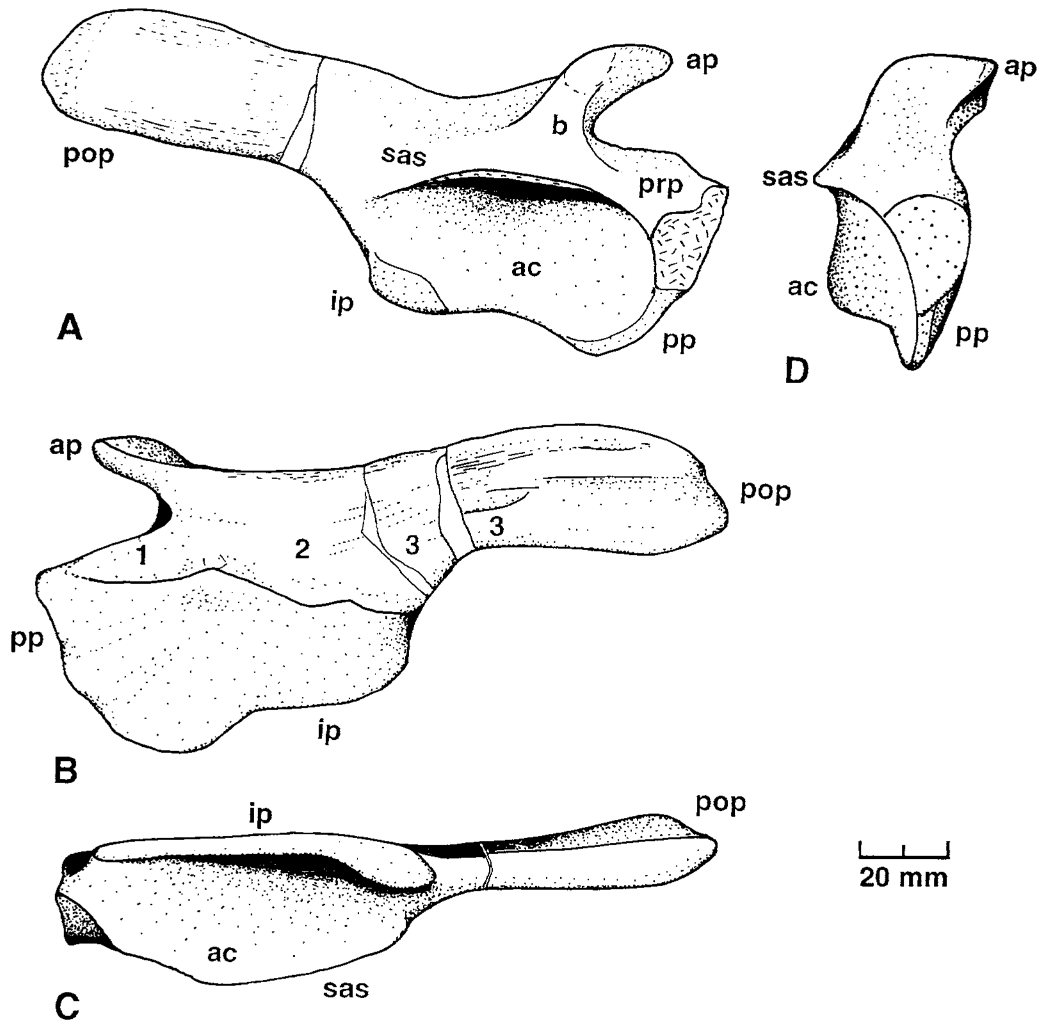

FIGURE 10. Right ilium of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Warwick, the holotype, in lateral (**A**), medial (**B**), ventral (**C**), and anterior (**D**) views. **Abbreviations: ac**, acetabulum; **ap**, anterior process; **b**, buttress; **ip**, ischiadic process; **pop**, postacetabular process; **pp**, pubic process; **prp**, preacetabular process; **sas**, supra-acetabular shelf.

cause of the morphological similarity of the two, and because the fragment lacks any diagnostic features.

The ilium of *Bromsgroveia* is most similar to that of poposaurids (sensu Long and Murray), although it is less robust than the ilia of *Poposaurus* and *Lythrosuchus* (Long and Murray, 1995). The strongest similarities lie in the right-angled preacetabular/pubic process and the nature of the supra-acetabular thickening. Although Parrish (1993:301) hypothesizes an independent origin of the three thecodontian taxa that possess a supra-acetabular thickening (poposaurids, rauisuchids, prestosuchids), he still considers that this feature might be 'homologous' in rauisuchids and poposaurids. The suggestion of a narrow slit between ilium and ischium in *Bromsgroveia* could possibly be the result of damage, although this slit is seen in some rauisuchids as well as poposaurids (Long and Murray, 1995).

Ischium—An isolated left ischium (WARMS G.970) is incomplete distally, and lacks some of the proximal termination (Fig. 11). In medial view (Fig. 11A), the broad dorsal articular face for contact with the ilium is incomplete. The dorsal margin of the ischium bears a shallow groove (dg, Fig. 11B), possibly accommodating femoral adductor muscles. The element as a whole is quite strongly laterally compressed.

Long and Murray (1995) consider rauisuchids to be characterized by rodlike ischia, while poposaurids have more laterally compressed, platelike ischia. In this respect, the ischium of *Bromsgroveia* is poposauridlike (Long and Murray, 1995), although this morphology is also seen in the 'Kupferzell rauisuchid' (D.J.G., pers. obs.), which is not thought to be a poposaurid.

Hindlimb Element

Femur—A poorly preserved specimen from Bromsgrove (CAMSM G.357) is interpreted as the proximal end of a right femur (Fig. 12). The specimen is merely a shell of the outer bone surface which was broken before burial and filled by sand. The element is seen in posterior view, and this surface is broad and flat. Part of the medial face of the bone may be seen, and it shows the slightly inturned proximal articular face. The lateral face is incomplete and trochanters cannot be seen.

ARCHOSAUR INDET. FROM WARWICK

Walker (1969) identified one of the Warwick teeth, and a cervical vertebra, as belonging perhaps to a prosauropod dinosaur. If the identification is correct, this would be the oldest dinosaur in the world, since the oldest skeletal (Benton, 1986) and footprint (King and Benton, 1996) records otherwise are Carnian (Late Triassic) in age.

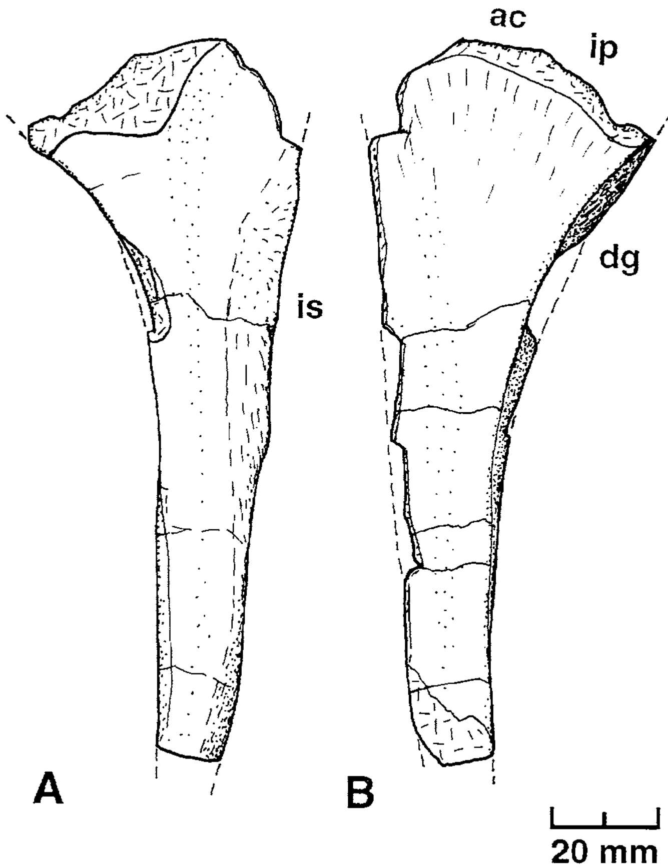

FIGURE 11. Left ischium of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Warwick, in medial (**A**) and lateral (**B**) views. **Abbreviations: ac**, acetabulum; **dg**, dorsal groove; **ip**, iliac process; **is**, ischiadic symphysis.

Tooth—The small tooth (BGS(GSM) 4873; Fig. 13), figured by Murchison and Strickland (1840:pl. 28, fig. 7a; copy in Huene, 1908:fig. 265), is quite different from the other Warwick teeth (Fig. 3). The crown measures only 5 mm in length, and it is virtually symmetrical in lateral view; most typical Triassic archosaur teeth are obviously recurved. The tooth bears fine serrations on both carinae, spaced at 26 per 5 mm. Walker (1969:473) compared the tooth with those of the Late Triassic prosauropod *Thecodontosaurus*, and indeed Huene (1908:241) ascribed it to the species *T. antiquus* Morris, 1843. The teeth of *Thecodontosaurus* from the Late Triassic of Bristol are comparable: they are nearly symmetrical and leaf-shaped, 5–6 mm tall, and with 25 serrations per 5 mm (Huene, 1908:196; Juul et al., 1996). However, a single tooth such as this is slender evidence to indicate the oldest dinosaur in the world, and it is best identified as 'archosaur *incertae sedis*'.

Vertebra—An anterior fragment of a cervical vertebra (BMNH R2628) was also identified by Walker (1969:473) as possibly that of a prosauropod. He interpreted the vertebra as perhaps the third, fourth, or fifth cervical, by comparison with vertebrae of *Plateosaurus*. The specimen could not be found in the BMNH during a recent search.

ARCHOSAUR REMAINS FROM DEVON

Materials

Isolated archosaur teeth and bones have been reported from the Otter Sandstone Formation of the Devon coast near Sidmouth (Spencer and Isaacs, 1983; Milner et al., 1990; Benton et al., 1994). There is nothing to suggest that these archosaur specimens do not belong to *Bromsgroveia*, but diagnostic materials are lacking. All the Devon specimens could come from a single taxon, but that is not certain, especially because of the diversity of tooth forms. Archosaur specimens from Devon were all collected by Patrick Spencer, and they include:

EXEMS 60/1985.6, a broken tooth from SY 0907 8395.

EXEMS 60/1985.27, a tooth from SY 1010 8555, mentioned by Spencer and Isaac (1983: 269).

EXEMS 60/1985.28, a tooth from SY 1010 8555.

EXEMS 60/1985.51, a tiny fragment of a tooth from SY 1022 8567.

EXEMS 60/1985.76, a tooth from SY 1042 8582.

EXEMS 60/1985.84, midline skull roof elements, from SY 1050 8592, mentioned by Spencer and Isaac (1983:269).

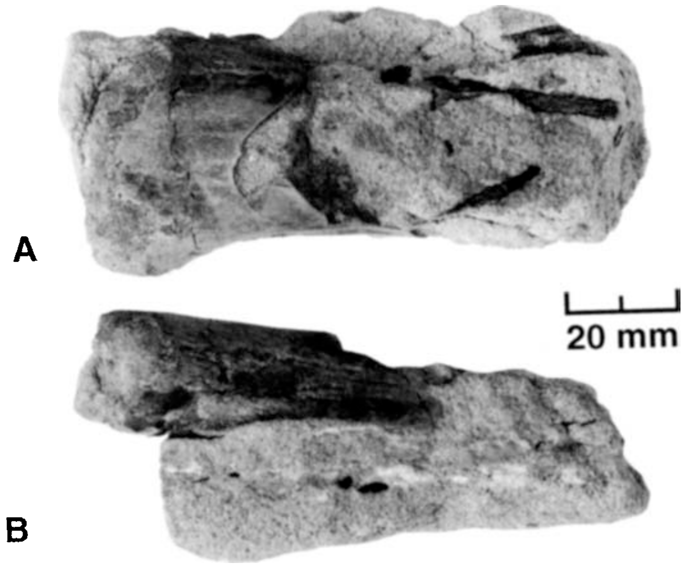

FIGURE 12. Proximal end of a right femur of *Bromsgroveia walkeri* Galton, 1985 from the Middle Triassic of Bromsgrove, CAMSM G.357, in ventral (**A**) and medial (**B**) views. The strap-like remains in the sandstone are leaves of a horsetail-like plant.

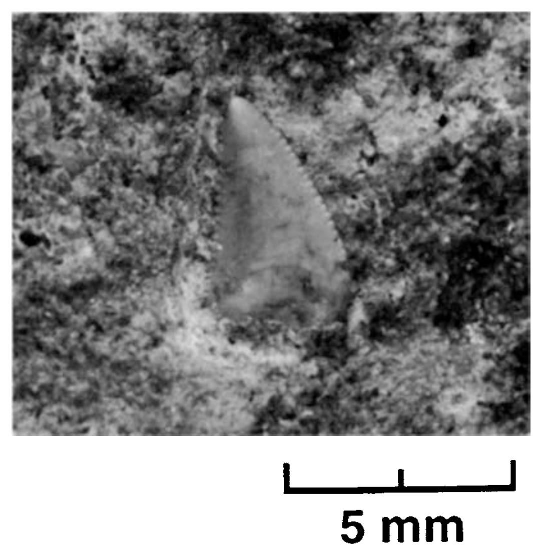

FIGURE 13. Tooth of an archosaur, BGS(GSM) 4873, formerly identified as that of a prosauropod dinosaur.

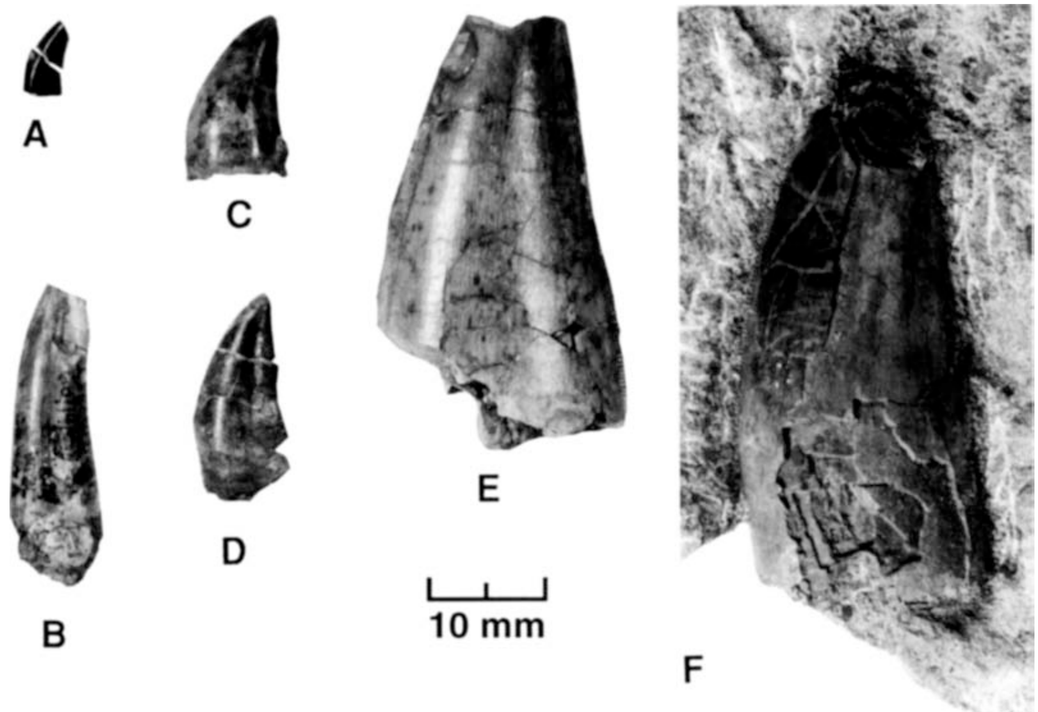

FIGURE 14. Archosaur teeth from the Middle Triassic of Devon, of five types, tiny and elongate (**A**), small and broad (not illustrated), long and slender (**C**), short and broad (**C**, **D**), and large (**E**, **F**). **A**, type-1 tooth, EXEMS 60/1985.115. **B**, type-3 tooth, EXEMS 60/1985.28. **C**, **D**, type-4 teeth, EXEMS 60/1985 (**C**) and EXEMS 60/1985.76 (**D**). **E**, **F**, type-5 teeth, EXEMS 60/1985.177 (**E**) and BRSUG 26212 (**F**).

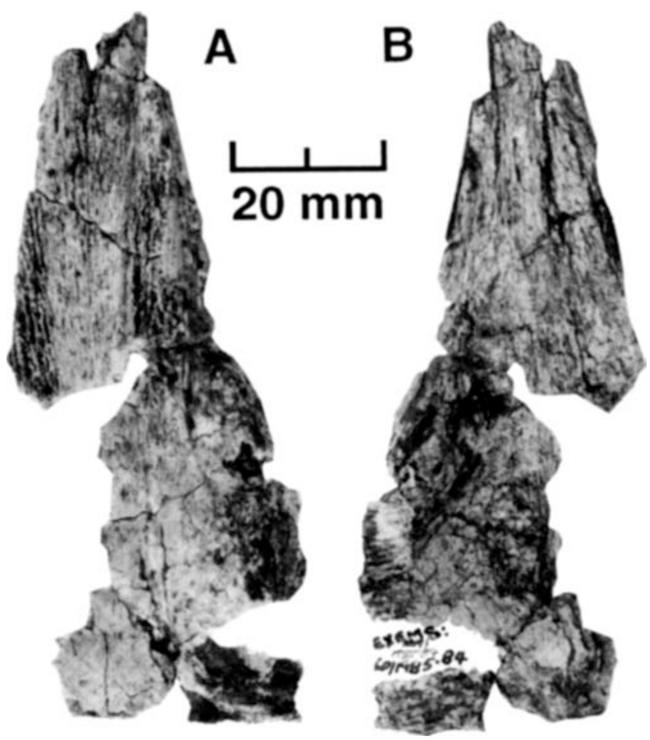

FIGURE 15. Archosaur (?) skull roof elements from the Middle Triassic of Devon, in dorsal (**A**) and ventral (**B**) views.

EXEMS 60/1985.115, a tooth from Windgate (SY 1072 8644), mentioned by Spencer and Isaac (1983:269).

EXEMS 60/1985.133, a tooth from Chit Rocks (SY 1208 8737), mentioned by Spencer and Isaac (1983:269).

EXEMS 60/1985.150, a partial right ischium from Port Royal (SY 1293 8733).

EXEMS 60/1985.165, a fragment of a large tooth, from SY 1297 8731.

EXEMS 60/1985.177, a large tooth from Port Royal (SY 1297 8731), mentioned by Spencer and Isaac (1983:269).

EXEMS 60/1985.291, a broken tooth.

EXEMS 60/1985.320, a tiny tooth.

EXEMS 7/1986.7, a partial neural spine of an anterior caudal vertebra, from SY 1051 8598

EXEMS 7/1986.8, a tooth from SY 1057 8641.

EXEMS 7/1986.8, an anterior dorsal vertebral centrum.

BRSUG 26206, dorsal vertebra.

BRSUG 26207, tooth.

BRSUG 26212, a large tooth.

Teeth

The fourteen archosaur teeth include two damaged specimens (EXEMS 60/1985.6, 165) that offer little information. The remainder fall into five morphological categories (Fig. 14), some of which may belong to different taxa, but it is worth recalling that in many Triassic archosaurs, not least rauisuchians (e.g., Chatterjee, 1985), individuals possessed teeth of different shapes and sizes in their jaws. Even the range of sizes shown by the Devon teeth could be accommodated within one archosaur species, when one takes account of adults and juveniles as well as developing teeth. None of the Devon teeth matches those from Warwick and Bromsgrove precisely, but many of them are broadly comparable in shape and in serration pattern.

The smallest Devon teeth (EXEMS 60/1985.51, 113, 115, 320) are about 7 mm long and 2–4 mm broad at the base (Fig.

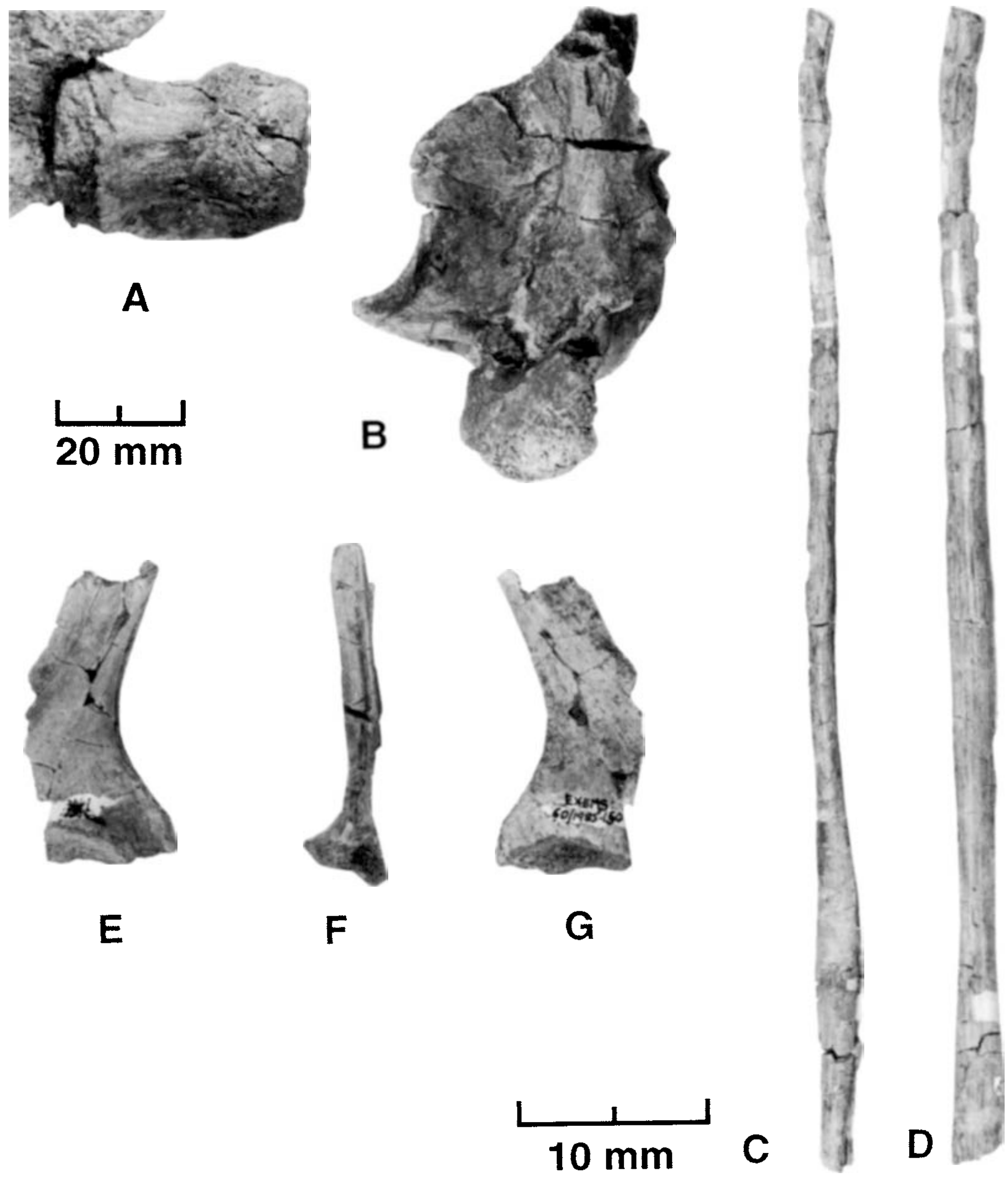

FIGURE 16. Archosaur postcranial elements from the Middle Triassic of Devon. **A**, dorsal centrum, EXEMS 7/1986.8, in ventral view. **B**, partial neural arch of an anterior caudal vertebra, EXEMS 7/1986.7, in left lateral view, showing the broad neural arch, tiny pointed prezygapophysis to the left, and projecting transverse process at bottom right. **C**, **D**, neural spine (?) of a ctenosauriscid archosaur, in two views. **E-G**, partial right ischium, in lateral (**E**), ventral (**F**), and medial (**G**) views.

14A). A second, unusual tooth shape is represented by the long and slender EXEMS 60/1985.28 (Fig. 14B). In this specimen, serrations may be seen on the posterior keel, and only at the distalmost tip of the anterior keel, and they are spaced about 20 per 5 mm.

The commonest teeth are small and large examples that approximate the commonest tooth type ascribed to *Bromsgroveia*. Type-4 teeth (EXEMS 60/1985.27, 76, 291 (?); 7/1986.8; BRSUG 26207) are short and broad, and markedly recurved (Fig. 14C, D). They measure 13–18 mm long and about 8 mm broad at the base, giving a length/breadth ratio of 1.6–2.2. Serrations are spaced about 20 per 5 mm. The larger type-5 teeth (EXEMS 60/1985.177 and BRSUG 26212) are 50–60 mm long and 20–22 mm broad, giving a ratio of 2.5–2.7 (Fig. 14E, F). Serrations are spaced 14–15 per 5 mm, close to the spacing seen in teeth ascribed to *Bromsgroveia*.

Skull Roof Elements

One specimen (EXEMS 60/1985.84) preserves a number of possibly midline skull roof elements (Fig. 15) from an archosaur. The specimen can be identified thus far by its general shape and by the paired ridges on the underside which appear to be the structures that typically bound the olfactory lobes of the brain in the midline, and which mark the medial margins of the orbit laterally. If this interpretation is correct, the element represents largely the paired frontals of a long-snouted archosaur.

Apart from the ridges, the bone is thin, and lightly sculpted. A midline suture cannot be made out between the paired ridges on the underside. Any other suture lines are also hard to discern, and there is only an indication, above and below, of a short stretch of suture that may mark the line between the right frontal and the right postfrontal.

Vertebrae

Three archosaur vertebrae have been identified from Devon. EXEMS 7/1986.8 (Fig. 16A) is a dorsal centrum, identified as such because of its overall shape, lack of rib apophyses, and by a slight ventral keel. The centrum is 37 mm long, and the heavily abraded articular surfaces are roughly 20 mm broad by 30 mm high.

The second specimen (BRSUG 26206) is represented by a centrum and partial neural arch identified as an anterior dorsal. The ventral 'keel' is present as a low and narrow ridge. The suture between the neural arch and centrum is not visible. The centrum is about 50 mm long, and the articular faces, one of which is eroded, are approximately 27 mm broad and 31 mm high.

The third archosaur vertebra from Devon, EXEMS 7/1986.7, is a partial neural arch of an anterior caudal. The specimen (Fig. 16B) shows the left side of the neural arch. There is a broad transverse process, whose distal end and posterior margin are damaged, which tilts at 45° and faces anterodorsally. Below it is a deep pit beneath a ridge that runs to the small prezygapophysis. In anterior view, the articular face of the prezygapophysis is set at an angle of 45° above horizontal. The neural spine consists mainly of a thin sheet of bone, with a broader column of bone at the posterior margin, similar to caudal vertebra '32' of *Postosuchus* (Chatterjee, 1985: fig. 13).

A further specimen possibly from an archosaur consists of a long element, some 550 mm long, of varying cross section (Fig. 16C, D). This bone is straplike in shape, with narrow and bulbous segments when viewed on the narrow side (Fig. 16C), and of nearly equal width from end to end in broad view (Fig. 16D). The element is incomplete, terminating at both ends in a broken face. The bone has been examined by many paleontologists, as noted by Milner et al. (1990) and Benton et al. (1994), and one possibility is that it is a dorsal neural spine of a ctenosauriscid archosaur, although it is narrower than in described forms.

Ischium

The specimen EXEMS 60/1985.150 (Fig. 16E–G) is a partial right ischium of a 'rauisuchian' archosaur. It is comparable in morphology to the Warwick ischium described above, to the ischia of known 'rauisuchians', and particularly poposaurids (sensu Long and Murray, 1995). It is relatively long and slender, although the distal end is missing. The dorsal edge bears a well-defined groove, while the ventral edge is narrow. Medially, a small part of the area that articulated with the opposite ischium along the midline is preserved. This Devon specimen is much smaller than that from Warwick.

DISCUSSION

Archosaurs are known only patchily from Middle Triassic rocks. Anisian archosaurs include the last proterosuchids and erythrosuchids, as well as the first proterochampsids, rauisuchids, and poposaurids. During the Ladinian, further new archosaur groups appeared, lagosuchids, as represented by specimens, and ornithosuchids, dinosaurs, and pterosaurs, as inferred from minimum ages of nodes in cladograms.

Knowledge of Anisian archosaurs is limited for two reasons. First, most continental formations of that age (e.g., Yerrapalli Formation, India; Manda Formation, Tanzania; Obere Buntsandstein, Germany and Poland; Grès à *Voltzia*, France; Donguz and Bukobay Svitas, Russia; Ehrmaying Formation, China) have produced only sparse remains. Secondly, in central Europe, most of Anisian time is represented by the marine beds of the Muschelkalk. These have produced few archosaur specimens, although the Grenzbitumenzone of Switzerland (conventionally dated at the Anisian/Ladinian boundary), is famous for specimens of the rauisuchid *Ticinosuchus*.

A critical review of the morphology and relationships of 'rauisuchian' archosaurs is beyond the scope of this work, but it is necessary to consider the affinities of the material described here. The ilium of *Bromsgroveia* resembles the ilia of *Poposaurus*, particularly in the prominent, anterodorsally inclined supra-acetabular buttress, considered a poposaurid synapomorphy by Parrish (1993), and thick preacetabular process. *Bromsgroveia* was first identified as a poposaurid by Walker (1969), an interpretation followed by Chatterjee (1985), Galton (1985), Parrish (1993), Benton et al. (1994), and Long and Murray (1995). The ischia from Devon and Warwick also resemble those of poposaurids. The remaining material, particularly the teeth and vertebrae, while consistent with 'rauisuchian' morphology, is not diagnostic.

'Rauisuchians' are currently known from an assortment of fragmentary specimens and more nearly complete material that is largely inadequately described. As a result, there are problems in assessing relationships. The 'rauisuchians' fall within the Suchia (sensu Krebs, 1974, 1976; Benton and Clark, 1988; Sereno, 1991; Parrish, 1993), together with aetosaurs and crocodylomorphs, but their position within this clade is far from clear. Earlier studies (e.g., Chatterjee, 1982, 1985; Benton, 1984, 1986; Gauthier and Padian, 1985; Gauthier, 1986) indicated two families, Rauisuchidae and Poposauridae, that together constituted a natural group, the Rauisuchia. Benton and Clark (1988) considered this grouping to be paraphyletic, hypothesizing that the poposaurids are the sister group of the crocodylomorphs. Parrish (1993) supported Benton and Clark's (1988) conclusions about the positions of crocodylomorphs, poposaurids, and rauisuchids, but suggested that the Aetosauria are more closely related to these taxa than are a small group of taxa formerly considered to be rauisuchids (Parrish's Prestosuchidae). However, some aspects of Parrish's (1993) analysis are problematic (Juul, 1994; Long and Murray, 1995; Gower, 1996; Gower and Wilkinson, 1966), and subsequent work on rauisuchian morphology (Long and Murray, 1995) has reasserted monophyly of the group. Long and Murray (1995) have also claimed that the taxon usually used to represent the Poposauridae in phylogenetic analyses, *Postosuchus*, was founded on composite material, the majority of which appears to be rauisuchid, although some is poposaurid. Long and Murray (1995) did not present a cladogram of rauisuchians, but their work, and study of more complete specimens such as the 'Kupferzell rauisuchid,' should permit a clearer phylogenetic analysis.

ACKNOWLEDGMENTS

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Notes added in Proof

Galton and Walker (1996a, b) also review the Middle Triassic archosaur material from Warwick. While agreeing with us on the referral of most of this material to the poposaurid *Bromsgroveia*, they refer some of the isolated teeth and the ilial fragment WARMS G.4713 to Parasuchia, and the vertebra BMNH R2628 to Dinosauriformes.

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