

## ANATOMY AND SYSTEMATICS OF THE PROSAUROPOD DINOSAUR *THECODONTOSAURUS ANTIQUUS* FROM THE UPPER TRIASSIC OF SOUTHWEST ENGLAND

MICHAEL J. BENTON<sup>1</sup>, LARS JUUL<sup>1,2</sup>, GLENN W. STORRS<sup>1,3</sup>, and PETER M. GALTON<sup>4</sup>

<sup>1</sup>Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, U.K.;

<sup>2</sup>Geologisk Centralinstitut, Københavns Universitet, Øster Voldgade 10, DK-1350 København K, Denmark;

<sup>3</sup>Cincinnati Museum Center, Museum of Natural History and Science, Geier Collections and Research Center, 1720 Gilbert Avenue, Cincinnati, Ohio 45202-1401;

<sup>4</sup>College of Naturopathic Medicine, University of Bridgeport, Bridgeport, Connecticut 06601-2449

**ABSTRACT**—Re-examination of the surviving specimens of *Thecodontosaurus antiquus* indicates that this plesiomorphic sauropodomorph can be diagnosed on the basis of elongate basiptyergoid processes, a relatively short dentary, and a squared posterior process of the ilium. Although much of the original topotype material found in the 1830s in Bristol, England, has now been lost, some 245 specimens remain. These indicate a small, gracile prosauropod, up to 2.5 m in length, distinguished primarily on the absence of derived characters seen in other prosauropods. Although attempts were formerly made to subdivide the Bristol specimens into several dinosaurian, and other, taxa, most appear to pertain to the prosauropod *Thecodontosaurus antiquus*. The specimens do indicate a clear separation into two morphs, a gracile and a robust form, presumably evidence of sexual dimorphism. A juvenile *Thecodontosaurus* sp. from South Wales may belong to the same species. A cladistic analysis indicates that Prosauropoda is probably a clade, rather than a series of outgroups to Sauropoda, but support for this conclusion is weak. Echoing other recent cladistic analyses, stronger support is found for the existence of a clade Sauropodomorpha, made up from Prosauropoda + Sauropoda, for the clade Sauropoda itself, and for the clade Eusauropoda within Sauropoda.

### INTRODUCTION

Recent cladistic analyses of Dinosauria have indicated that the genus *Thecodontosaurus* is the most primitive reasonably complete sauropodomorph (Gauthier, 1986; Benton, 1990; Galton, 1990). However, character scoring for the genus *Thecodontosaurus* Riley and Stutchbury, 1836 has not been based just on the material of *T. antiquus* Morris, 1843, the type species of the genus, from Durdham Down, Bristol, S.W. England. Instead, some of the characters are based on material of *Thecodontosaurus* sp. from south Wales that represents a much smaller, and probably juvenile, individual (Kermack, 1984).

The type specimen of *T. antiquus* is not now available for study, since it was lost in a bombing raid on Bristol in November, 1940 that destroyed the original geology gallery of Bristol City Museum. It has often been assumed that all the original material was lost at that time. However, several drawers of topotype material of *T. antiquus* still remain in the Bristol collection, including many figured specimens, and this material dates largely from the collecting efforts in the 1830s. The extant material consists of 184 specimens, many of them figured, and including some of the specimens figured by Riley and Stutchbury (1840). One specimen, the proximal end of a femur (BRSMG Ca7456), shows burn marks, and a note states that it was salvaged from the wreckage of the museum annex in May, 1941.

Additional topotype material of *Thecodontosaurus antiquus* is in the Natural History Museum, London, the Peabody Museum of Natural History, and the Academy of Natural Sciences, Philadelphia. These specimens were distributed by Edward Wilson (1848–1898), who was Curator at the Bristol Museum from 1884 until his death. Part of the Yale material was presented to O. C. Marsh during a visit to Bristol, and the remainder was acquired through exchange in 1888 and 1889. London was given its material by Bristol in 1888–1889, and the Philadelphia specimens were acquired through a local benefactor, T. B. Wilson, prior to 1865, possibly independently of the Bristol Institution. Huene (1908a, 1914) described some additional Durd-

ham Down specimens in the Geological Survey Museum, London, but after this institution's relocation to Keyworth, these cannot be found. A single bone was given by Bristol through exchange to Wells Museum, Somerset, in 1932. In total, some 245 original topotype specimens of *Thecodontosaurus* still survive.

The purpose of this paper is to re-describe the surviving material of *Thecodontosaurus antiquus*, to consider the relationships of this species to '*Thecodontosaurus* sp.,' described by Kermack (1984), and to elucidate the phylogenetic position of the genus. The significance of this study lies in the plesiomorphic position of *Thecodontosaurus* relative to other Sauropodomorpha. In addition, *Thecodontosaurus* is historically important as the first dinosaur to have been reported from the Triassic, and the sixth dinosaur to be named from anywhere in the world. The initial work reported here was carried out by LJ in 1992–1993 as part of his Candidatus Scientiae thesis for the University of Copenhagen, under the supervision of MJB. PMG studied much of the material, and particularly the braincase, dentary, and forelimb in the late 1960s, the early 1970s, and the early 1980s, and MJB and GWS added descriptions of the Yale and Philadelphia specimens, along with comparisons and phylogenetic discussion.

**Institutional Abbreviations**—ANSP, Academy of Natural Sciences, Philadelphia; BRSMG, Bristol City Museum and Art Galleries, Bristol; BMNH, Natural History Museum, London; YPM, Peabody Museum, Yale University, New Haven, Connecticut. BRSMG specimens bear old registration numbers, either written on a label glued to the specimen, painted on the specimen itself, or written on an accompanying card. It is not clear who first numbered the specimens. These old numbers are indicated in parentheses after the first mention of the current BRSMG registration numbers.

### HISTORY AND NOMENCLATURE

*Thecodontosaurus* Riley and Stutchbury, 1836 was the fourth dinosaur genus to be named from Britain, after *Megalosaurus*

(1824), *Iguanodon* (1825), and *Hylaeosaurus* (1833). It was only the sixth dinosaur named, if one includes the dubious genera *Streptospondylus* (1832) and *Macrodoniphion* (1834). *Thecodontosaurus* and *Paleosaurus* (*Palaeosaurus*) represent the first substantial reptiles to be described from the Triassic (Riley and Stutchbury, 1836, 1837, 1840). Because of the historical importance of these finds, and the convoluted vicissitudes of their nomenclature, further information is given.

Dr. Henry Riley and Mr. Samuel Stutchbury began to excavate specimens of 'saurian animals' in autumn, 1834 in the limestone quarries of Durdham Down, Clifton, Bristol. These quarries are now largely infilled or built over. Henry Riley (1797–1848) was a local surgeon and medical school teacher who had been trained in Paris. He gave a successful series of lectures in Bristol, emphasising the works of Lamarck, Cuvier, and Geoffroy, and was a member of the important group of gentleman naturalists who founded the Bristol Institution (Taylor and Torrens, 1987; Taylor, 1994). Samuel Stutchbury (1798–1859) began his professional career as an assistant at the Hunterian Museum of the Royal College of Surgeons in London (Crane, 1983; Taylor, 1994). Stutchbury was then employed as curator of the Bristol Institution in 1831, and served there until 1850 when he went to Australia as mineral surveyor for New South Wales.

The first accounts of the new saurian remains were short announcements in 1834 and 1835 (Anon., 1834, 1835; Williams, 1835). Riley and Stutchbury communicated a fuller account to the Geological Society of London in March, 1836 (Riley and Stutchbury, 1836), and to the British Association for the Advancement of Science, which met in Bristol later that year (Riley and Stutchbury, 1837). Riley and Stutchbury (1836), an abstract, is unillustrated, but it gives a full page of description of the new taxon *Thecodontosaurus*, and indicates the repository of the jaw bone and other elements, and can hence be regarded as an adequate characterization of the genus. Riley and Stutchbury (1836) also announced their new genus *Palaesaurus*, and the two species *P. cylindricum* [sic] and *P. platyodon* [sic], but here the characterization of the genus is minimal and, of the species, non-existent. The second paper (Riley and Stutchbury, 1837) concentrates mainly on the geology of the bone-bearing sediments, and adds nothing in the way of characterization of the taxa. The genus *Palaesaurus* is referred to in a footnote (p. 91), together with its two species *P. cylindrodon* and *P. platyodon* [both now spelled correctly], but the genus name is spelled *Paleosaurus* in a table on p. 94. The full descriptive memoir (Riley and Stutchbury, 1840) was published three years later. This confirms the indication in the 1836 paper that *Thecodontosaurus* was founded upon a right dentary with 21 teeth, while the two species of *Paleosaurus* [note spelling], *P. cylindrodon* and *P. platyodon*, are described and illustrated adequately, each on the basis of a single tooth (Riley and Stutchbury, 1840:pl. 29, figs. 4, 5). These authors also described a range of postcranial remains which were not clearly assigned to either of these taxa. Riley and Stutchbury (1836, 1837, 1840) named only the genus *Thecodontosaurus*; the specific name *antiquus* was added by Morris (1843:211) in his Catalogue of British Fossils.

When first described, *Thecodontosaurus* and *Paleosaurus* were not yet recognised as belonging to the Dinosauria, the group erected by Owen (1842) to include *Iguanodon*, *Megalosaurus*, and *Hylaeosaurus*. Owen (1842:153–155) redescribed *Thecodontosaurus* and *Paleosaurus* (now spelled by him *Palaesaurus*, the spelling generally used thereafter) in the same paper, and he attempted to divide the postcranial elements between the two taxa. Owen followed Riley and Stutchbury's (1840) interpretation that these were 'inferior or squamate saurians,' with some resemblances to crocodilians, lizards, rhynchosaurs, and dinosaurs, and he later (Owen, 1860:275) includ-

ed them among the Thecodontia, basal archosaurs. Owen (1842) may not have considered *Thecodontosaurus* to be dinosaurian as it was Triassic in age and of relatively small size; he regarded immense size as a diagnostic feature of Dinosauria. The dentary of *Thecodontosaurus* is only about 100 mm long—quite small when compared to *Iguanodon*, for example.

*Thecodontosaurus* was first recognised as a dinosaur by Huxley (1870) after his examination of the Durdham Down material. Huxley separated *Thecodontosaurus* and *Paleosaurus* into two different dinosaurian groups based on their teeth; he placed the former in his family Scelidosauridae, together with *Scelidosaurus* and the ankylosaurs *Hylaeosaurus*, *Polacanthus*, and *Acanthopholis* (although the last he regarded as megalosauroid). Marsh (1892) illustrated the braincase and the articulated forelimb, and he was the first to compare *Thecodontosaurus* to the American *Anchisaurus*. Seeley (1895) and Huene (1902, 1908a, b, 1914) re-described the Durdham Down specimens, and Huene's monograph (1908a:190–216) is especially valuable. Huene (1914) described several of the specimens at YPM, including the braincase and the articulated forelimb. Both Seeley and Huene divided the Durdham Down specimens between species of *Paleosaurus* and *Thecodontosaurus*.

A further small collection of *Thecodontosaurus antiquus* remains from Durdham Down has surfaced recently. The collection, a left tibia (Fig. 17), an ungual phalanx, a distal caudal vertebra, a partial right tibia, and a partial right radius (BMNH 49984) were named *Agrosaurus macgillivrayi* Seeley, 1891, one of the first dinosaurs to be reported from Australia. However, the origin of the materials had been confused, and the specimens are almost certainly from the Durdham Down locality (Vickers-Rich et al., 1999).

There have been a number of more recent studies of the topotype material of *Thecodontosaurus*. John Attridge of Birkbeck College, London, studied the Bristol specimens between 1959 and 1979, and had some of them prepared from the rock, but nothing was published (Anon., 1961). PMG examined most of the remains, and published preliminary accounts of the braincase (YPM 2192: Galton, 1973, 1976, 1990; Galton and Cluver, 1976; Galton and Bakker, 1985), the articulated forelimb (YPM 2192: Galton, 1973; Galton and Cluver, 1976), and the left dentary, which he designated as neotype of *Thecodontosaurus antiquus* Morris, 1843 (Galton, 1985a).

There has been continued and vigorous debate about the validity of the two species of *Paleosaurus*, *P. platyodon* and *P. cylindrodon*. Huxley (1870) assigned the *P. platyodon* holotype tooth to *Thecodontosaurus*, regarding it as having come from a larger species of that genus, while retaining *P. cylindrodon* (the holotypic tooth of which was destroyed in World War II) as a megalosauroid. Seeley (1895), on the other hand, retained *T. antiquus* and *P. platyodon*, but invalidated *P. cylindrodon*, and divided the postcranial remains from Durdham Down, on limited evidence, between the two species. Huene (1902:62–63) established the new phytosaur *Rileya bristolensis* on the basis of a humerus and two 'caudal vertebrae' from Durdham Down. Huene (1908a:240, b) identified *P. platyodon* as a phytosaur and, as the name *Palaesaurus* was preoccupied, renamed the Bristol phytosaur *Rileya platyodon* (Riley and Stutchbury, 1836) and assigned further teeth and postcranial elements to it. Huene (1908a:214–216) divided the postcranial material from Bristol between two species of *Thecodontosaurus*, assigning the commoner lightly-built elements to *T. antiquus*, and the rarer more robust elements to *T. cylindrodon*.

During much of the twentieth century, the concept of *Paleosaurus* led to extraordinary confusion in the understanding of early dinosaurian evolution and systematics. Huene (1908a, 1932) had established that *Paleosaurus*, as indicated by Riley and Stutchbury (1840), had classic carnivorous archosaur teeth, but apparently had the skeleton of a prosauropod. In the same

papers, Huene (1908a, 1932) had also associated a great deal of prosauropod postcranial remains with the jaw fragment that had been named *Teratosaurus*. Again, the teeth were those of a carnivore. This view strongly influenced Romer (1956), and it led Colbert (1964) to divide Late Triassic sauropodomorph dinosaurs into Palaeosauria (for *Paleosaurus* and *Teratosaurus*) and Plateosauria (for *Thecodontosaurus* and *Plateosaurus*). Charig et al. (1965) sank the Palaeosauridae into the Thecodontosauridae, assigned the postcranial material of '*Teratosaurus*' to the Plateosauridae, and separated the Teratosauridae, based on teeth and jaws, as *Saurischia incertae sedis*. Nonetheless, the view of prosauropods as a mixture of herbivorous and carnivorous prosauropods survived, and it was revived on different evidence by Cooper (1981). The astonishing fact is that Palaeosauria was an entire invention, an amalgam of generalized carnivorous archosaur teeth and prosauropod postcranial remains, as were the other apparent associations of carnivore teeth with prosauropod skeletons (Galton, 1985b; Benton, 1986; Storrs, 1994).

Here, it is assumed that all the Durdham Down dinosaur remains belong to a single species, *Thecodontosaurus antiquus*, and that shape variations are an expression of sexual dimorphism (see below). In addition, most of the postcranial remains assigned by Huene (1902, 1908b) to the purported phytosaur species, *Rileya platyodon*, are returned here to *T. antiquus*. These include a partial chevron (BRSMG C4534), a metacarpal (BRSMG Ca7505), a radius (BRSMG Ca7504), and the partial forelimb (YPM 2195) identified by Marsh (1892) as *T. platyodon*. Two vertebrae (YPM 2192) assigned by Huene (1908b) to the phytosaur *Rileya bristolensis* are dorsals of *T. antiquus*, as Huene (1914:figs. 55, 56) noted. Only the humerus (BRSMG Ca7461) is quite different from that of any prosauropod, and quite different from previously figured complete humeri of *T. antiquus* (e.g., Huene, 1908a:pls. 80, 81). However, the entepicondylar groove, a distinguishing feature of phytosaur humeri, is not preserved in this specimen. The shape of BRSMG Ca7461 is broadly phytosaurian, but the identification is uncertain (A. Hungerbühler, pers. comm., 1998). The name *Rileya* was also found to be preoccupied, and it was renamed *Rileyasuchus* by Kuhn (1961). Both generic names, and the specific name *bristolensis*, are *nomina dubia*, however, since the type specimen, the humerus BRSMG Ca7461, lacks diagnostic characters.

The taxonomic status of the teeth named by Riley and Stutchbury (1836, 1837, 1840) as *Paleosaurus cylindrodon* and *P. platyodon* must be considered. There is no evidence that the teeth named *P. platyodon* pertain to the taxon *Rileya* (= *Rileyasuchus*). Nonetheless, the type tooth of *P. platyodon*, from the illustration (Riley and Stutchbury, 1840:pl. 29, fig. 5), is almost certainly a posterior maxillary or dentary tooth of a heterodont phytosaur (A. Hungerbühler, pers. comm., 1998), but it lacks generic and specific diagnostic characters, and must be termed a *nomen dubium*. Steel (1970:25) was first to designate *P. platyodon* as type species of *Paleosaurus* (= *Palaeosaurus* pre-occupied; = *Palaeosauriscus* Kuhn, 1959), a surprising decision, since *P. cylindrodon* has page priority. Nonetheless, this decision makes *Paleosaurus* a phytosaurian taxon, albeit an invalid one. *Paleosaurus cylindrodon* was placed in *Palaeosauriscus* by Kuhn (1959), but the original figure of this tooth taxon (Riley and Stutchbury, 1840:pl. 29, fig. 4) suggests that it can be identified no more precisely than Archosauria incertae sedis. Hence, the species *P. cylindrodon* is also a *nomen dubium*. This confirms the view of Galton (1973:246) and Galton and Walker (1996a:732) that the generic names *Paleosaurus*, *Palaeosaurus*, *Palaeosauriscus*, *Rileya*, *Rileyasuchus*, and the species *P. cylindrodon* and *P. platyodon* are invalid, being based initially on single largely non-diagnostic teeth, together with later additions of generally non-diagnostic postcranial remains.

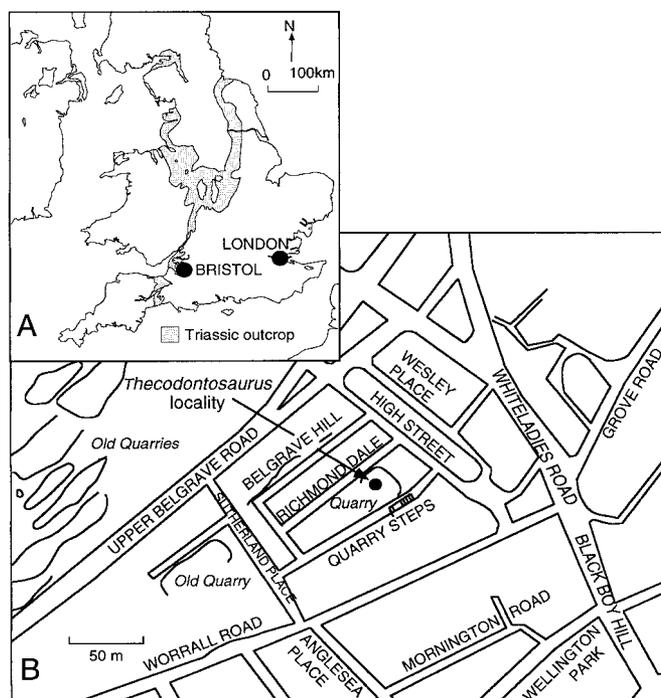


FIGURE 1. Map of the old quarries on Durdham Down, Bristol, showing the location of the *Thecodontosaurus* find in 1834. Key map shows the distribution of Triassic exposure in England and Wales, and the location of the Bristol deposit.

#### LOCALITY AND GEOLOGY

The specimens of *Thecodontosaurus*, and the associated reptilian taxa, were found in brecciated beds of apparently Late Triassic age (Storrs, 1994). The Bristol locality (Fig. 1; National Grid Reference, ST 572747) has been identified (Benton and Spencer, 1995:89) from information in papers by Etheridge (1870), Moore (1881), and Huene (1908c). Etheridge (1870: figs. 4, 5) gave two drawings showing the reptile deposit at about 320 ft above mean sea level and noted (Etheridge, 1870: 188) that 'the spot where these remains were found is no longer recognizable or determinable, having been many years ago quarried away, and the site built upon'. Moore (1881:72), however, mentioned specifically a place known as 'The Quarry and The Quarry Steps' and states 'Looking from it [the platform of Quarry Steps], along the Down escarpment to the west, the eye takes in Bellevue Terrace [Belgrave Terrace], on the edge of the Down; and it was between these houses and the quarry, a distance probably of 200 yards, along the same face of limestone, and on the same horizon, that the deposit containing the Thecodontosaurian remains was found. Unfortunately the precise spot is unknown . . . and built over'. Huene (1908a:191) seemingly misunderstood Moore, naming the site of discovery as Avenue Quarry at the end of Avenue Road, but Moore mentioned this quarry as a location 680 yards away from Quarry Steps and terminating a transect of workings which produced fissures of different ages. The discovery site may still be seen, largely overgrown, forming a cliff behind a block of flats, and with an old set of stone steps (Quarry Steps) descending beside it. The topotype quarry contains at least one fissure with a lithology similar to that of the bone-bearing matrix, but all bones appear to have been quarried away.

Durdham Down fissures take the form of cracks and natural caves formed in marine Lower Carboniferous limestone, and appear similar to other Late Triassic and Early Jurassic fossil-

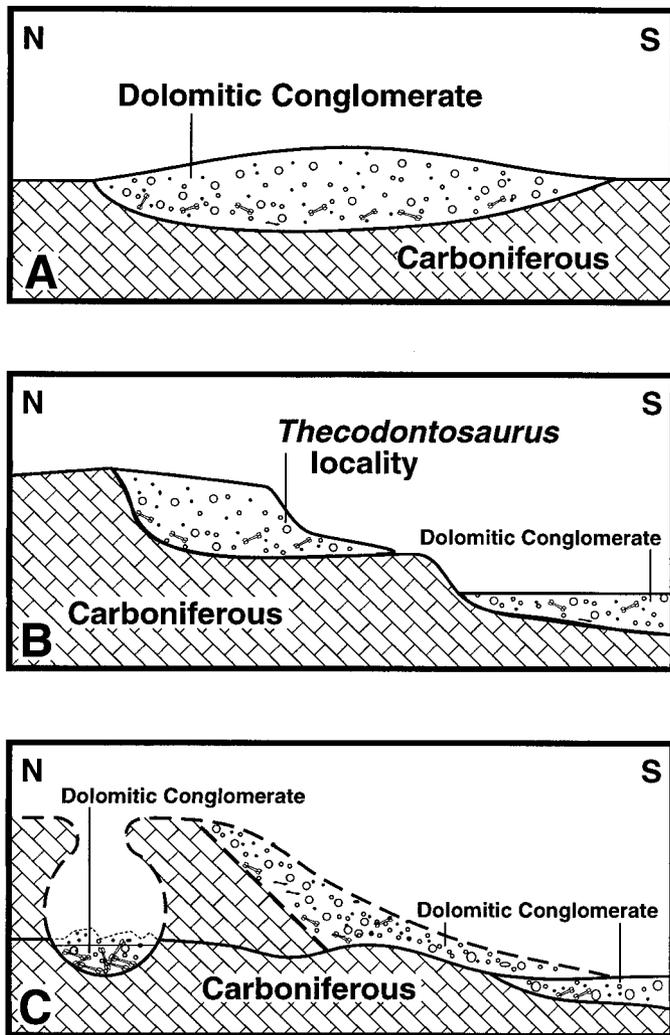


FIGURE 2. Sections through the Dolomitic Conglomerate deposit in which *Thecodontosaurus* bones were found. A, section by Samuel Stutchbury, reproduced by Etheridge (1870). B, section by W. Sanders, reproduced by Moore (1881). C, proposed model of the Durdham Down bone-bearing breccia as infill of a collapsed cavern, after Halstead and Nicoll (1971). The upper portions, indicated by dashed lines, have been eroded.

iferous fissure fills of the Mendip Archipelago in the Bristol and South Wales areas (Fraser, 1985, 1986, 1994; Savage, 1993; Storrs, 1994). Etheridge (1870:189, fig. 6) reproduced a sketch by Stutchbury of the occurrence of the Durdham Down bones, showing a saucer-shaped depression on top of steeply dipping Carboniferous Limestone (Fig. 2A). Disarticulated bones are indicated scattered throughout the conglomeratic infill, with some resting directly on the limestone. Moore (1881:73, fig. 2), however, gave a sketch surveyed by W. Sanders (Fig. 2B) which suggests that the fossiliferous sediment rested on a rather flat, eroded Carboniferous pavement. Halstead and Nicoll (1971) reinterpreted the Durdham Down deposit as a collapsed cavern (Fig. 2C), regarding the saucer-shaped depression indicated by Etheridge (1870) as its base, the rest having been eroded since Late Triassic times. The nature of the brecciated sediment lends support to this idea, consisting as it does of angular fragments of Carboniferous Limestone in a matrix of yellow marl.

Most of the dinosaur bones were not found in articulation and many seem to show signs of transport, perhaps as a result

of having been washed by flood water into the cave. Other specimens, however, are articulated—most notably the forelimb of YPM 2195. Several individuals are represented: Huene (1908a) counted 20 femora and fragments, indicating the presence of at least ten individuals, but it is unclear whether or not he included some Middle Triassic material from Warwick that was also used by him in his description of *Thecodontosaurus*. The material from the Midlands is now known to be largely non-dinosaurian, and comes mainly from the poposaurid *Bromsgroveia walkeri* (Galton, 1985b; Galton and Walker, 1996b; Benton and Gower, 1997).

Other fossils from the Durdham Down site are rare. There is the phytosaur *Paleosaurus platyodon*, based on a tooth (Riley and Stutchbury (1840:pl. 29, fig. 5), as well as other similar teeth in the BMNH (hitherto unfigured), with, perhaps, a putative phytosaur humerus named *Rileya bristolensis* Huene, 1902. In addition, two specimens of the sphenodontid *Diphydontosaurus avonis* were noted as the partial skeleton of a 'lizard' (BRSMG Cb4715) and a small jaw of the sphenodontid *Clevosaurus* (BRSMG Cb4714) by Halstead and Nicoll (1971: pl. 23B).

#### AGE

The Durdham Down fissure fillings, for which there is no independent age evidence, are now known to be genetically distinct from the nearby Dolomitic or Magnesian Conglomerate (Storrs, 1994). Riley and Stutchbury (1840:349) mistakenly regarded the two sets of sediments as equivalent and representing the 'lower divisions of the new red sandstone series,' hence Permian. On the other hand, Etheridge (1870) treated both as equivalent to the German Muschelkalk or Lower Keuper (Middle Triassic), while Huene (1908a, b, c) preferred a lower assignment, equivalent to the German Muschelkalk or Buntsandstein, based on the assumption that the Bristol reptiles were very like some archosaurs reported from the Middle Triassic of the English Midlands, now dated as Anisian (Benton et al., 1994).

Moore (1867, 1881) ascribed a Rhaetian age to the Dolomitic Conglomerate, on the basis of its topographic position and on similarities of several fissure faunas to those of unequivocal Rhaetian bone bed deposits of the region (Storrs, 1994). Moore (1867) described 'the tableland of Durdham Down, where numerous veins, one of them 18 ft. in thickness, traversed the Carboniferous Limestone. One of these, near the Zoological Gardens, was proved to be of the age of the Lower Lias,—Ammonites, Echini, Foraminifera and the other remains of that age being exhibited by the author, taken from between the walk of the Carboniferous Limestone 30 feet from the surface. In another vein near the Suspension Bridge he had found numerous scattered fish-remains of Rhaetic age, including Saurichthys and Achrodus [sic], mentioned above, found also with the *Thecodontosaurus* and *Palaeosaurus* on the Mendips; and he could therefore come to no other conclusion than that the deposits were equivalents in time, and that the Durdham Down reptilia must be referred to the Rhaetic age.'

The fissures in the Bristol area appear to have been formed by a major pluvial episode during the Carnian (Simms, 1994), and the infilling sediments range in age from Late Triassic (?Carnian) to Early Jurassic (Hettangian). The presence of the primitive prosauropod *Thecodontosaurus* suggests a Late Triassic age, perhaps late Carnian or early Norian for the Durdham Down deposit. *Diphydontosaurus avonis*, known also from Tytherington and Slickstones (Cromhall) quarries (Fraser and Walkden, 1983; Whiteside, 1986), might indicate a younger age: some of the Tytherington deposits at least are dated palynologically as Rhaetian (Marshall and Whiteside, 1980), and they have also yielded abundant dinosaur bones, probably *The-*

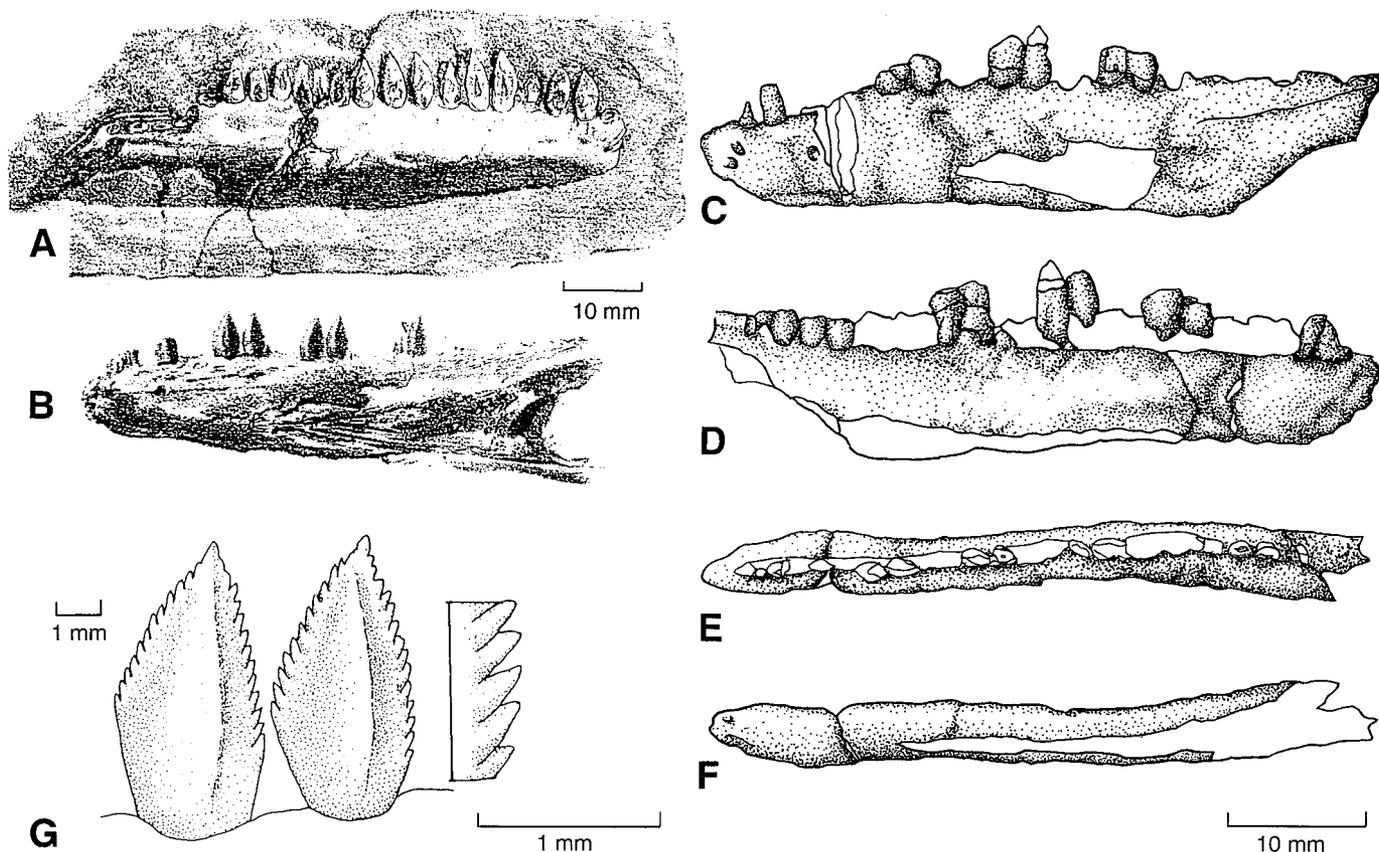


FIGURE 3. The dentary of *Thecodontosaurus antiquus* Morris, 1843. **A**, the holotype, 'BCM 1', now lost, from Riley and Stutchbury (1840: pl. 29, fig. 1); **B–G**, left dentary, BRSMG C4529, selected by Galton (1985a) as neotype, (**B**) from an early illustration by Huxley (1870:pl. 3, fig. 1), and in lateral (**C**), medial (**D**), dorsal (**E**), and ventral (**F**) views; (**G**) mid-series dentary teeth, about 14th and 15th, in labial aspect, with an enlarged drawing of the marginal serration (after Huene, 1908a:fig. 207a, b).

*codontosaurus*. The presence of a phytosaur, *Paleosaurus platyodon*, at Durdham Down at least guarantees a Late Triassic age, since phytosaurs are not known after the end of the Triassic, and pre-Carnian records are equivocal.

#### SYSTEMATIC PALEONTOLOGY

Superorder DINOSAURIA Owen, 1842

Order SAURISCHIA Seeley, 1887

Suborder SAUROPODOMORPHA Huene, 1932

Family THECODONTOSAURIDAE Lydekker, 1890

*THECODONTOSAURUS* Riley and Stutchbury, 1836

*THECODONTOSAURUS ANTIQUUS* Morris, 1843

*Thecodontosaurus* Riley and Stutchbury, 1836:398

*Thecodontosaurus* Riley and Stutchbury; Riley and Stutchbury, 1837:91, 94

*Thecodontosaurus* Riley and Stutchbury; Riley and Stutchbury, 1840:352, pl. 29, 30

*Thecodontosaurus* Riley and Stutchbury; Owen, 1842:153–155

*Palaeosaurus* Riley and Stutchbury; Owen, 1842:154–155 (pars)

*Thecodontosaurus antiquus* Morris, 1843:211

*Thecodontosaurus*; Huxley, 1870:43–45, pl. 3, figs. 1, 2, 5–8

*Agrosaurus macgillivrayi* Seeley, 1891:161, figs. 1–6

*Thecodontosaurus platyodon* (Riley and Stutchbury); Marsh, 1892:546, pl. 16, fig. 5; pl. 17, figs. 1, 2

*Thecodontosaurus* Riley and Stutchbury; Seeley, 1895

*Palaeosaurus* Riley and Stutchbury; Seeley, 1895 (pars)

*Rileyia bristolensis* Huene, 1902: 62–63 (pars)

*Thecodontosaurus macgillivrayi* (Seeley); Huene, 1906:147, figs. 86–90

*Thecodontosaurus antiquus* Morris; Huene, 1908a:190–216, 241, pl. 76–90

*Thecodontosaurus cylindrodon* (Riley and Stutchbury); Huene, 1908a:190–216, 241, pl. 76–90 (pars)

*Rileyia platyodon* (Riley and Stutchbury); Huene, 1908b (pars)

*Thecodontosaurus antiquus* Morris; Huene, 1932:116, pl. 54, fig. 1

*Thecodontosaurus antiquus* Morris; Galton, 1973:248, fig. 1G, J, L, N, T, U

*Thecodontosaurus antiquus* Morris; Galton and Cluver, 1976: 139, figs. 7D, 8F, 9B, F, S, 10F, 11A–G

*Thecodontosaurus antiquus* Morris; Galton, 1984a:10, fig. 4F

*Thecodontosaurus antiquus* Morris; Galton and Bakker, 1985: 9, fig. 4J, K

*Thecodontosaurus* Riley and Stutchbury; Galton, 1985a:15–16

*Thecodontosaurus* Riley and Stutchbury; Galton, 1990:323–344, figs. 15.4B, D, 15.6O

*Thecodontosaurus antiquus* Morris; Galton and Walker, 1996: 1, fig. 3A

**Neotype**—The holotype, a right dentary with 21 teeth in place (Riley and Stutchbury, 1840:pl. 29, fig. 1; Fig. 3A), was destroyed during a bombing raid on BRSMG in November, 1940. A left dentary, BRSMG C4529, is present among the topotype material in Bristol and was designated (as BCM 2) the neotype by Galton (1985a:pl. 9, figs. 6, 7). This specimen

(Fig. 3B-G) is the sole survivor of the four dentaries originally excavated at Durdham Down. The morphology of dentary BRSMG C4529, and the teeth it contains, are very like the type specimen, judging from a comparison with published descriptions and figures (Galton, 1985a; Huene, 1908a; Huxley, 1870; Riley and Stutchbury, 1840). Indeed, Huene (1908a) confused the two specimens in his figure caption, presumably following the hand-written label attached to the specimen, which states 'Figured f. 1. 2' (see Huene, 1908a:pl. 76, fig. 2). This label may have also confused Huxley, who referred to the type specimen in the text, but figured the dentary now considered to be the neotype (1870:pl. 3, fig.1; Fig. 3B).

**Hypodigm**—In addition to the neotype dentary, surviving skull material consists of a partial occiput and braincase (YPM 2192). Postcranial remains include four cervical vertebrae (BRSMG Ca7467; YPM 2192, 2195), 19 partial dorsal vertebrae (ANSP 9861, 9865; BRSMG C4533, Cb4153–Cb4156, Cb4163a, b, Cb4171, Cb4174a, b, Cb4182, Cb4197, Cb4221, Cb4293, Cb4714; YPM 2192), two sacral vertebrae (YPM 2192), 19 caudal vertebrae (ANSP 9854, 9875; BMNH 49984, R1534, R1550; BRSMG C4532a, b, Ca7473–Ca7475, Ca 7507, Ca7510, Cb4164a, b, Cb4166, Cb4276; YPM 2192, 2193), 16 unidentified vertebrae (ANSP 9855, 9858; BMNH R1533, R1535; BRSMG C4301, Ca7475, Cb4157, Cb4167, Cb4171, Cb4174a, b, Cb4178, Cb4280, Cb4283, Cb4151, Cb4152, Cb4301), a neural spine (ANSP 9857), three chevrons (BRSMG C4532c, C4534, Ca7510), at least 43 ribs and rib fragments (BMNH R1536a, b, R1537a–c, R1538; BRSMG C4528, Ca7466, Cb4168a, b, Cb4169, Cb4170, Cb4172–Cb4174, Cb4194–Cb4196a, b, Cb4200a–e, Cb4206, Cb4212, Cb4213, Cb4218, Cb4227, Cb4234, Cb4255, Cb4256, Cb4285, Cb4286, Cb4297, Cb4298, Cb4300, Cb4528, Cb4714; YPM 2192, 2195), both scapulae and an articulated forelimb (YPM 2195); a right scapular blade (BRSMG Ca7481) and three possible scapula fragments (ANSP 9865, 9876; BRSMG Cb4216), 13 partial humeri (ANSP 9871, 9880; BMNH R1541–R1543; BRSMG Cb4189, Cb4201, Cb4209, Cb4219, Cb4265, Cb4266, Cb4284; YPM 2192), a radius (BRSMG Ca7504), a right ulna (BRSMG Ca7486) and possible fragmentary ulna (ANSP 9860), four possible metacarpals (BRSMG Ca7482, Cb4174, Cb4179), two possible manual phalanges (BRSMG Ca7485, Cb4187), two right ilia (ANSP 9870; BMNH R1539) and three fragmentary ilia (BMNH R1540; BRSMG Cb4180, Cb4181), a left pubis (BRSMG Cb4267), two distal fragments of ischia (YPM 2192) and a probable proximal end of an ischium (ANSP 9870), 23 partial femora (ANSP 9854, 9874; BMNH R1544, R1545; BRSMG C4530, Ca7456, Ca7481, Ca7490, Ca7494, Ca7495, Cb4176, Cb4177, Cb4183, Cb4184, Cb4190, Cb4207, Cb4228, Cb4243, Cb4259, Cb4266, Cb4269, Cb4281; YPM 2192), 12 partial tibiae (BMNH 49984, R1546; BRSMG C4531, Ca7495, Cb4185, Cb4186, Cb4188, Cb4289; YPM 2192), a right fibula (BRSMG Ca7497) and five partial fibulae (ANSP 9863, 9867, 9869, 9872; YPM 2192), three unidentified limb bones (BMNH R1547–R1549), a right metatarsal III (BRSMG Ca7451a), an indeterminate metatarsal (BRSMG Ca7499), six possible pedal phalanges (BMNH R1552, R1553; BRSMG Ca7501, YPM 2192), and three ungual phalanges (BMNH 49984; ANSP 9861; BRSMG Ca7451b). Additional catalogued and uncatalogued fragments and blocks of matrix are contained in these collections. Some Bristol specimens described or figured by Huene (1908a) retain his identification numbers in addition to BRSMG catalogue numbers. In order to facilitate comparisons with older works, and to document for the first time the extant materials of *T. antiquus*, a listing of all specimens, together with former illustrations by Huene (1908a, 1914), is given (Appendix 1).

**Locality and Horizon**—All materials are from the Durdham Down locality at Quarry Steps, off Belgrave Terrace, Clifton,

Bristol, England (ST 572747). Specimens were found in fissure fills of Late Triassic age contained within Early Carboniferous (Dinantian) marine limestones.

**Diagnosis**—Small, gracile prosauropod (up to 2 m), distinguished primarily on the absence of derived characters seen in other prosauropods. Autapomorphies:

1. Elongate basiptyergoid processes in the braincase. The height measured from the top of the parasphenoid to the distal tip of the basiptyergoid process is equal to the height of the braincase measured from the top of the parasphenoid to the top of the supraoccipital (Fig. 6B), whereas other prosauropods for which braincases are known share the primitive character of considerably shorter basiptyergoid processes. This character is seen also in sauropods (J. Wilson, pers. comm., 1999), but its homology has to be assessed.

2. Dentary less than half length of mandible. The dentary, though damaged (Figs. 3, 4), appears to be relatively complete, and it is short compared to that of other early dinosaurs. If the juvenile specimens from South Wales ascribed to *Thecodontosaurus* sp. are correctly identified, then the relative shortness of the dentary is confirmed.

3. Posterior process of iliac blade subquadratic. The posterior process of the iliac blade in several specimens of *T. antiquus* has a distinctly squared termination (Fig. 15A, B), whereas other prosauropods, and other early dinosaurs, have a rounded termination to the posterior process.

## DESCRIPTION

### Lower Jaw

**Dentary**—Huene (1908a:195–196) described three partial dentaries, a right (No. 1; Huene, 1908a:figs. 206, 208, pl. 76, fig. 3; 50 mm long), a left (No. 2; Huene, 1908a:fig. 207, pl. 76, fig. 3; 71 mm long), and a possible right (No. 85; Huene, 1908a:pl. 76, fig. 2), of which only one survives, the left dentary, BRSMG C4529. The fate of the fragment of jaw, exhibiting the alveolar septa and a young tooth (Riley and Stutchbury, 1840:351, pl. 29, fig. 3, in the collection of the Rev. David Williams of Bleaden) is not known. It is tempting to identify BRSMG C4529 as the type dentary element figured by Riley and Stutchbury (1840:pl. 29, figs. 1, 2). Indeed, Huene did this in his figure caption (see above). Riley and Stutchbury (1840:350) identify 21 teeth in their specimen, which approaches our estimate for BRSMG C4529, and both are the same size. Huene (1908a:195) counted 16 tooth positions for BRSMG C4529, but he illustrated only the front part of this dentary (Huene, 1908a:pl. 76, fig. 3) and this agrees with the measured length of 50 mm (Huene, 1908a:195). However, this jaw originally measured close to 80 mm, and Riley and Stutchbury (1840:350, pl. 29, fig. 1), who mentioned that the jaw was fractured into three pieces, show a substantial crack running obliquely anterodorsally to tooth positions 11–12. The original authors are clear that the jaw is a right ramus, as is also indicated in their figure. The orientation of specimens in early lithographs is often reversed, but this seems not to be the case in Riley and Stutchbury's (1840) plates, as indicated by the orientation of their other specimens. There is also no sign in BRSMG C4529 of a substantial crack involving tooth positions 11–12. Hence, the type dentary, and another figured by Huene (1908a) are now lost, presumably destroyed during World War II.

BRSMG C4529 is eroded to some extent, but is in relatively good condition, and it appears to be relatively complete from snout tip to the posterior termination of the tooth row (Figs. 3, 4). In 1992, Bristol Museum staff removed the matrix from the specimen in order to expose its lingual face. Although the teeth were damaged during this preparation, a cast of the entire specimen is preserved (BMNH R1108), and figures of the original

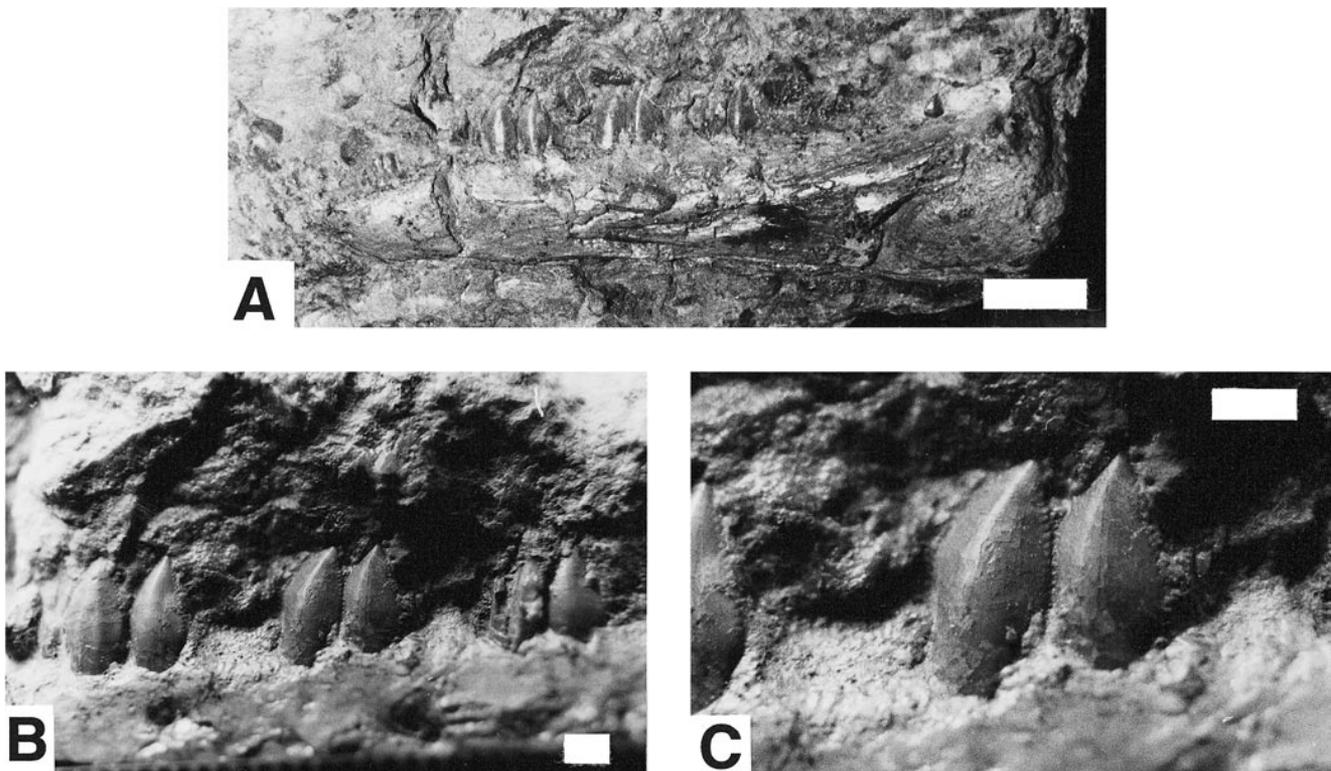


FIGURE 4. Left dentary of *Thecodontosaurus antiquus* Morris, 1843, BRSMG C4529, selected by Galton (1985a) as neotype, photographed before preparation out of the matrix. All views are lateral. **A**, photograph of the whole specimen, **B**, close-up of teeth in positions 9–19, and **C**, close-up of teeth in positions 12–15. Scale bar equals 10 mm in **A**, and 2 mm in **B** and **C**.

appear in Huxley (1870:pl. 3, fig. 1; Fig. 3B), Huene (1908a: pl. 76, fig. 2), and Galton (1985a:pl. 9, fig. 6).

In lateral aspect (Figs. 3C, 4A), the anterior tip of the jaw is slightly downcurved, as is seen to some extent in other prosauropods. The dentary is fractured approximately 15 mm from the tip and the root of an anterior tooth is visible. Anterior to this, three shallow foramina are present, two opening anterodorsally at the tip of the jaw, and another located close to the fracture. A further shallow depression lies near the fifth or sixth tooth. A weakly developed shelf on the posterior third of the bone might indicate the former presence of a muscular cheek, as noted in other basal sauropodomorphs and in ornithischians (Galton, 1990).

The medial face of the dentary (Fig. 3D) is largely smooth. Unfortunately, the symphyseal area is somewhat weathered and not clearly distinguishable. The anterior tip is deflected laterally and slightly ventrally; a long foramen opens ventrally here. A depression halfway along the bone could be original or the result of post-mortem compression. Posteriorly, a weak crest overhangs the ventral part of the bone. In dorsal aspect (Fig. 3E) the dentary displays a weak sigmoid curvature followed broadly by the tooth row, but the latter is somewhat recessed from the labial margin in the region of the postulated cheek. The labial edge of the dentary is higher than the lingual, and the former bears concavities at each tooth position. The ventral edge of the dentary (Fig. 3F) is slightly concave and smooth.

There are 20 or 21 thecodont alveoli preserved. The teeth are separated by bony projections, possibly interdental plates, that are more or less confluent with the alveolar borders. The mid-dentary teeth are the largest; the anterior and posterior teeth are subequal in size, with crowns 3.5–4.0 mm high. The crowns are leaf-shaped, with slightly recurved tips, and they are constricted at their bases. They overlap to form a continuous

shearing edge; the primary orientation of the crowns does not parallel that of the tooth row, but rather each crown is twisted just below mid height, allowing its posterior edge to overlap laterally the anterior edge of the following crown to give an *en echelon* arrangement (Fig. 3E).

A typical dentary tooth from the middle third of the tooth row (Figs. 3G, 4B, C; see also Huene, 1908a: fig. 207; Galton, 1985a:pl. 9, fig. 7) is convex on its labial side, and is partitioned into an anterior concave and a posterior flat surface on its lingual face. Both the anterior and posterior edges are sharp, and bear denticles. The denticles become smaller towards the tip of the tooth and extend nearer to the root on the posterior edge of the crown. In the 14th or 15th tooth there are 3.8 denticles per mm that are subrectangular (Fig. 3G) and end in a modest dorsal point. Individual denticles are 1.8 mm high. The teeth of *Thecodontosaurus* are smaller versions of those of *Sellosaurus* (Galton, 1985a), but are far more delicate, more acutely pointed, and bear finer denticles than those of *Plateosaurus*.

### Skull

**Occiput**—A partial occiput and braincase, YPM 2192, preserves the complete basioccipital, basisphenoid with sella turcica, paroccipital processes, supraoccipital, and parietals (Figs. 5, 6). The specimen was originally figured without description by Marsh (1892:pl. 17, figs. 1, 2). Huene (1908a:192–195, pl. 76, figs. 1a–d) provided a description on the basis of photographs and casts, and later (Huene, 1914:figs. 35a–c) based on the original specimen. A preliminary reconstruction was provided by Galton (1973:fig. 1G) and Galton and Bakker (1985: fig. 4J, K). Preparation of a latex endocranial cast has provided details of part of the midbrain and all of the hindbrain. *The-*

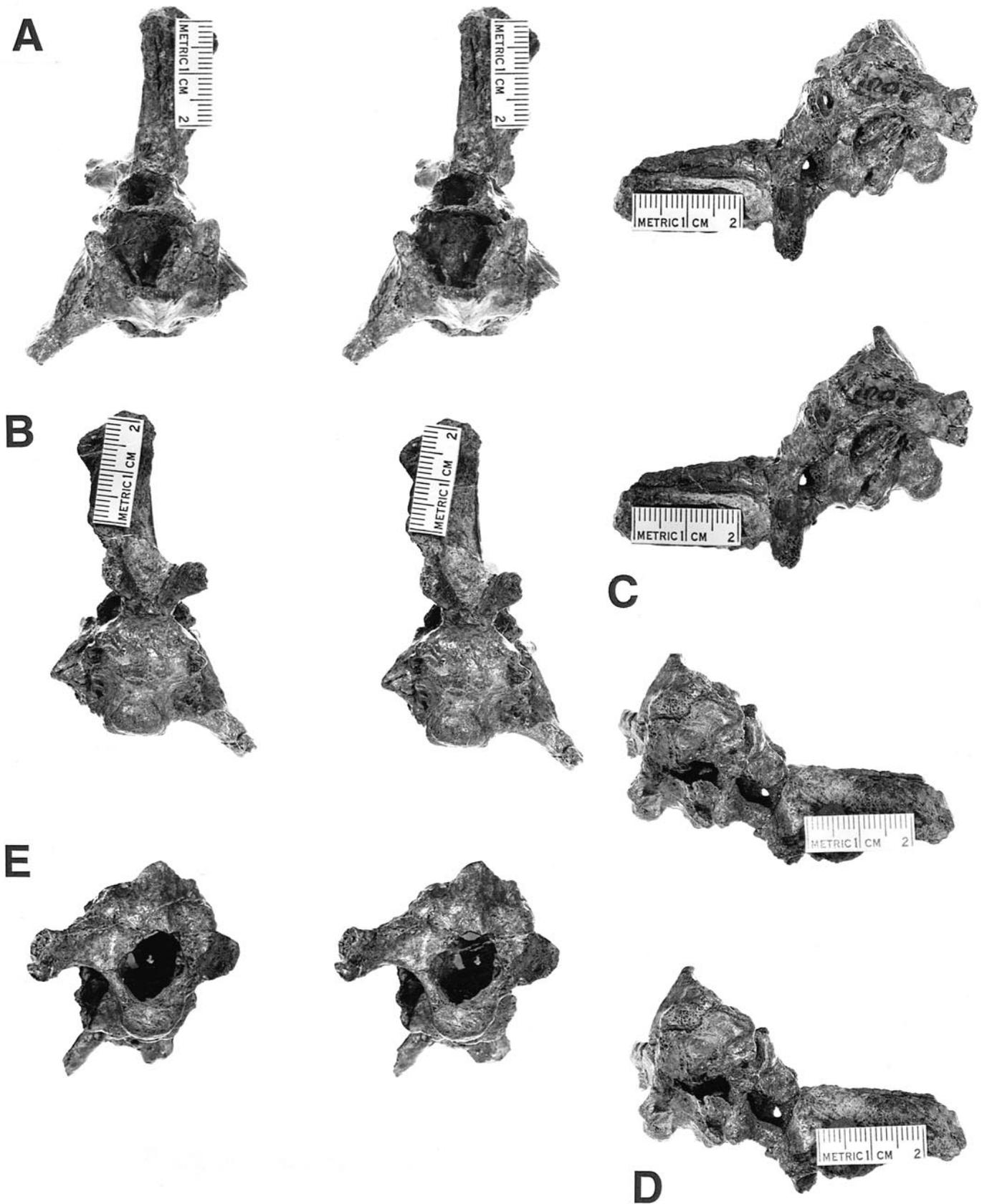


FIGURE 5. Occiput and braincase of *Thecodontosaurus antiquus* Morris, 1843, YPM 2192, shown as stereoscopic pairs in dorsal (A), ventral (B), left lateral (C), right lateral (D), and occipital (E) views. Compare with Figure 6.

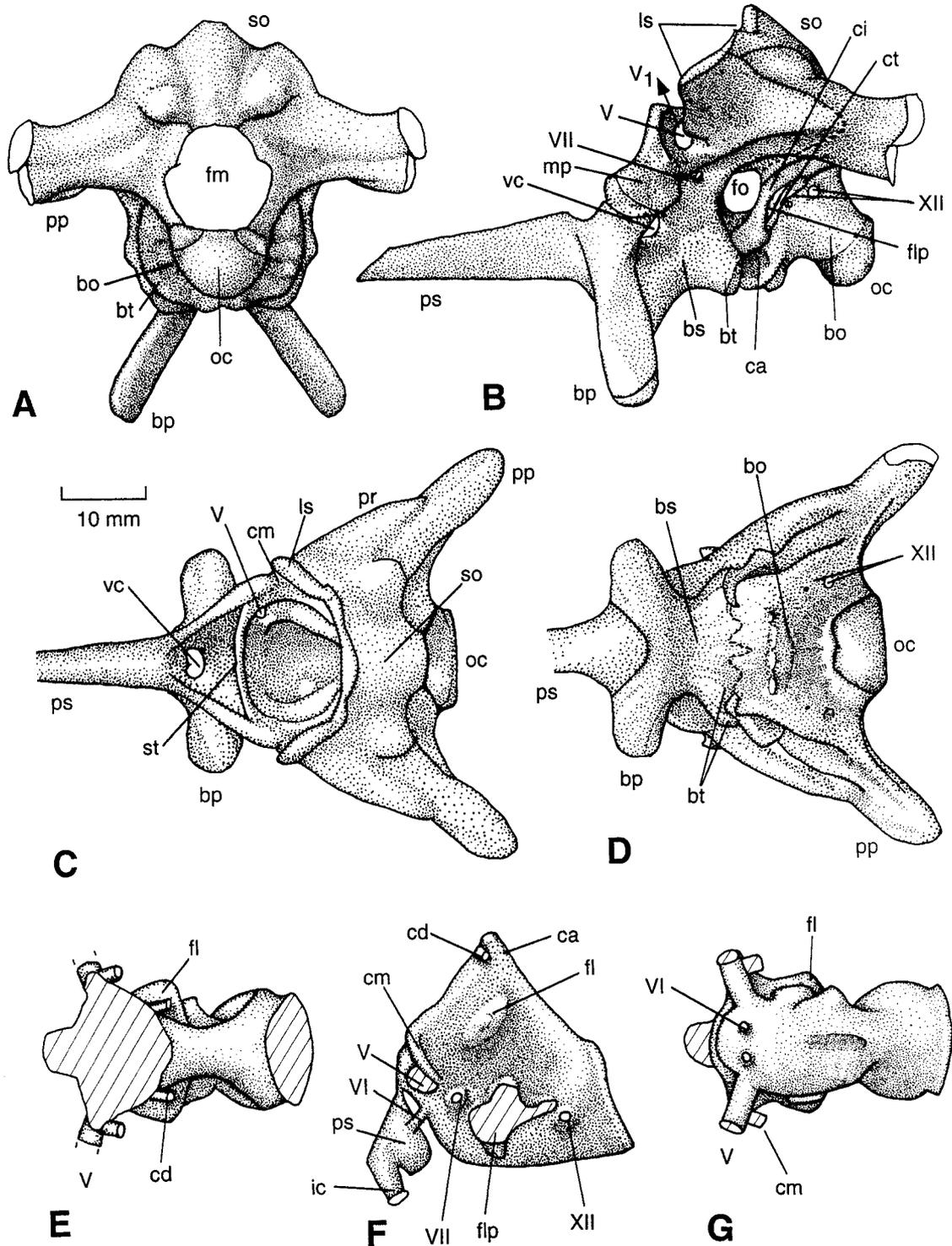


FIGURE 6. Interpretive drawings of occiput, braincase, and endocast of *Thecodontosaurus antiquus* Morris, 1843. **A–D**, occiput and braincase in posterior (**A**), right lateral (**B**), dorsal (**C**), and ventral (**D**) views, based on YPM 2192, (compare with Fig. 5); **E–G**, reconstructed endocast from YPM 2192, in dorsal (**E**), left lateral (**F**), and ventral (**G**) views. **Abbreviations:** **bo**, basioccipital; **bp**, basipterygoid processes; **bs**, basisphenoid; **bt**, basisphenoid tubera; **ca**, cartilage; **cd**, vena capitis dorsalis; **ci**, crista interfenestralis; **cm**, vena cerebialis medius (groove); **ct**, crista tuberalis; **fl**, floccular lobe of the cerebellum; **flp**, foramen lacerum posterior; **fm**, foramen magnum; **fo**, fenestra ovalis; **ic**, internal carotid artery; **ls**, laterosphenoid (attachment site); **mp**, attachment site for *M. protractor pterygoideus*; **oc**, occipital condyle; **pp**, paroccipital process; **pr**, prootic; **ps**, parasphenoid; **so**, supraoccipital; **st**, sella turcica; **vc**, Vidian canal; **V**, trigeminal nerve (foramen); **V<sub>1</sub>**, ophthalmic division of trigeminal nerve (groove); **VI**, abducens nerve (foramen); **VII**, facial nerve (foramen); **XII**, hypoglossal nerve (foramina).

*codontosaurus* is only the second prosauropod genus, after *Plateosaurus* (see Galton, 1985c), for which the endocast is known.

The basioccipital (bo, Fig. 6A, B, D) forms the posterior part of the floor of the braincase and the major part of the occipital condyle, the articular surface of which is equally developed ventrally and posteriorly. Anterior to the occipital condyle, the external surfaces of the basioccipital are concave up to the irregular suture with the low and rugose basisphenoid tubera (bt, Fig. 6A, B, D). The deep depression in the ventrolateral part of this suture may have been filled with cartilage in life (ca, Fig. 6B); it was not the point of entry of the internal carotid artery as suggested by Huene (1914). The basisphenoid is constricted mediolaterally anterior to the basioccipital suture and posterior to the Vidian canal (vc, Fig. 6B, C) through which the internal carotid artery reached the sella turcica. The posterior and lateral walls of the sella turcica, enclosing the pituitary space, are formed entirely by the basisphenoid (bs, Fig. 6B, D). The posterior wall of the sella turcica (st, Fig. 6C) is pierced by two foramina; the smaller foramen on the right side was presumably for the abducens (VI) nerve. Huene (1914) believed that the vertebral arteries passed through these foramina. The larger left foramen seemingly represents both the abducens foramen and the median foramen for passage of the basilar artery. This may be an artifact of preparation. In *Plateosaurus* the abducens foramina and the basilar foramen are either three separate openings or are combined into a single passage (Galton, 1985c).

The basisphenoid is excavated dorsal to the Vidian canal and is slightly overhung by part of an anterolaterally facing surface that was the origin site of the *M. protractor pterygoideus* (mp, Fig. 6B). This surface is traversed by traces of the prootic suture; inferior to it, the basisphenoid forms the divergent and ventrally-directed basiptyergoid processes (bp, Fig. 6A–D). The anterior wall of the sella turcica is formed by the parasphenoid (ps, Fig. 6B–D); the parasphenoid merges imperceptibly with the base of the pterygoid processes and forms the anteriorly-directed cultriform process, only the lateral surface of which is visible.

The only indications of the anterior part of the braincase side wall are the sutural surfaces for the laterosphenoid on the supraoccipital and prootic (ls, Fig. 6B, C). The sutures between the preserved side wall bones are clearly visible (posterior part of prootic-opisthotic suture only on left side). However, the sutures with the bones of the floor are less obvious. The prootic completely encloses the oval-shaped foramen prooticum that transmitted the trigeminal (V) nerve (V, V<sub>1</sub>, Fig. 6B, C) and housed the trigeminal ganglion. The ophthalmic division (V<sub>1</sub>) of the trigeminal nerve exited across the dorsal margin of the prootic in a prominent groove; this latter merges with the partially overhung vena cerebialis medius groove (cm, Fig. 6C). Traces of the groove for the connection of the vena capitis dorsalis are visible on the medial surface of the prootic and supraoccipital (cd, Fig. 6E, F; cf. Galton, 1985c:figs. 7C, 8A, pl. 6, fig. 4). The adjacent medial surfaces on either side of the prootic-supraoccipital suture are excavated by a large depression, the fossa subarcuata, that in life was occupied by the floccular lobes of the cerebellum (fl, Fig. 6E–G). The fossa subarcuata was misidentified by Huene (1914:78; Se, fig. 35b) as the 'groove-shaped depression for the saccus endolymphaticus.' The internal opening for the facial nerve is clear (VII, Fig. 6F), but the external opening has been reconstructed (VII, Fig. 6B).

The sharp-edged crista prootica borders the recessed area containing the fenestra ovalis (fo, Fig. 6B), the exact form of which is unknown because of missing bone on the right side and a bone/matrix contact that is difficult to discern on the left. The right crista interfenestralis (ci, Fig. 6B) of the opisthotic is complete; it is a large, obliquely inclined sheet passing anterolaterally from the base of the paroccipital process to suture with the adjacent part of the basisphenoid.

The recessed area between the crista interfenestralis and the more posterior crista tuberalis (ct, Fig. 6B) is incompletely preserved on the left side and is obscured by matrix on the right. However, it is clearly similar to those of *Massospondylus* (Gow, 1990) and *Plateosaurus* (Galton, 1985c) in having a fissura metotica that consists of two connected parts. The foramen lacerum posterior (flp, Fig. 6B; foramen lacertericum of Gow, 1990), a parallel-sided, narrow (1–1.2 mm) opening superior to the fissura metotica, is oriented at about 45° to the basicranial axis; it merges inferiorly with the slightly more vertically aligned and wider foramen jugularis. Posterior to these foramina lie another two for passage of the hypoglossal nerve (XII, Fig. 6B, D), but only the larger is evident on the prepared endocast (XII, Fig. 6F).

As there is no trace of the suture between the opisthotic and exoccipital, their relative contributions to the posterior part of the side wall cannot be determined. In posterior aspect, the supraoccipital is low and broad, separating the opisthotics at the dorsal margin of the foramen magnum (fm, so, Fig. 6A–C).

### Axial Skeleton

Numerous isolated vertebrae were found in the fissure. Many specimens may be assigned to their original region of the vertebral column, but a number of vertebrae are so incomplete that they are unidentified.

**Cervical Vertebrae**—One partial cervical vertebra, BRSMG Ca7467, consists of the neural arch, lacking the neural spine and parts of the zygapophyses (Fig. 7A, B). This specimen probably corresponds to cervical 3 to 6, because of its long low profile, as in *Plateosaurus* (cf. Galton, 1990:fig. 15.5B). The neural arch is narrow, the broad zygapophyses diverge only modestly from the midline, and the neural spine is anteroposteriorly long (approximately 17 mm), with no sign of neural arch laminae. An anterior cervical vertebra, YPM 2195 (Fig. 7C), shows a similar long low neural arch, low neural spine, and a centrum that is deeper posteriorly than anteriorly. YPM 2192 comprises two cervicals, figured by Huene (1908a:pl. 77, fig. 1). One is badly preserved, but the other has a 28 mm long centrum, sharply constricted mediolaterally in the middle. The posterior articular surface is deeply concave, and the anterior half of the centrum bears a sharp midline keel on its ventral surface.

**Dorsal Vertebrae**—Numerous presumed dorsal vertebrae are present, but are partial or are partly buried in matrix. A large fragmentary arch, BRSMG Cb4153, has powerful transverse processes, 14 mm high measured at their bases, exposed in cross-sectional view (Fig. 7D). It has short thick diapophyses, and is hence an anterior dorsal.

A large fragmentary neural arch, BRSMG Cb4155 (Fig. 7E, F), at least 56 mm long, lacks the zygapophyses, but preserves the upper surfaces of the transverse processes and possibly the neural spine, which is still embedded in the matrix. The transverse processes are each supported by a pair of strong buttresses which arise on the lateral surface of the arch and project vertically. In front of the anterior buttress, on the lateral surface of the arch, lies a shallow circular depression, and between the buttresses is a distinct hollow, 7 mm deep. Huene (1908a:197) claimed that such hollows are characteristic of all *Thecodontosaurus* dorsals, and he used this character, and the relatively greater length of the centra, to distinguish them from dorsals of *Plateosaurus*. The same deep hollows are seen in two mid dorsals in YPM 2192 (Fig. 7G–K). Similar vertical laminae buttressing the transverse process are seen in *Anchisaurus* (Galton, 1976:37), *Plateosaurus* (Huene, 1926:pl. 2), *Massospondylus* (Cooper, 1981:figs. 9, 10), and in most sauropods and theropods. The elongate posterior portion of BRSMG Cb4155 bears a horizontal face in front of the postzygapophyses, which

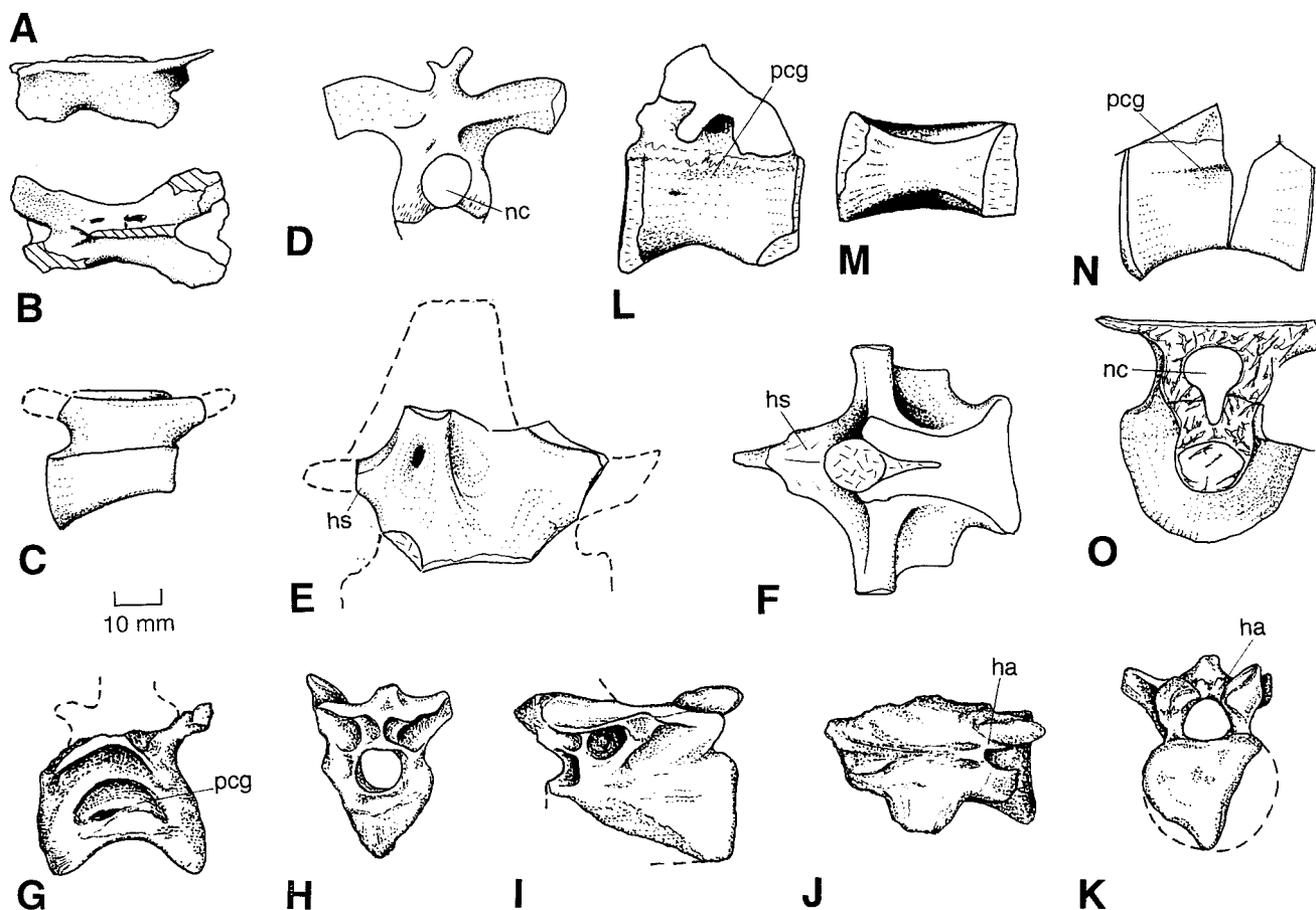


FIGURE 7. Cervical (A–C) and dorsal (D–O) vertebrae of *Thecodontosaurus antiquus* Morris, 1843. A, left lateral and B, dorsal views of cervical neural arch, BRSMG Ca7467; C, left lateral view of anterior cervical, YPM 2195; D, anterior view of the neural arch of an anterior dorsal, BRSMG Cb4153; E, right lateral and F, ventral views of the neural arch of a dorsal, BRSMG Cb4155; G, left lateral view of a dorsal vertebra, YPM 2192; H, posterior, I, right lateral, J, dorsal, and K, anterior views of a second dorsal vertebra, YPM 2192; L, left lateral and M, ventral views of the neural arch of a dorsal, BRSMG Cb4182; N, left lateral and O, cross-sectional views of the neural arch of a posterior dorsal, BRSMG Cb4154. **Abbreviations:** ha, hypantrum, hs, hyposphene; nc, neural canal; pcg, pleurocentral groove.

are absent. This face represents additional articulating surfaces, the hyposphene (hs, Fig. 7E, F), a saurischian synapomorphy (Gauthier, 1986). Small accessory articulation surfaces between the prezygapophyses in one of the dorsals in YPM 2192 may be the matching hypantra (ha, Fig. 7J, K).

Another centrum, with a fragment of the middle part of the pedicel in place, BRSMG Cb4182 (Fig. 7L, M), 36 mm long, shows the same pattern of buttresses and hollows beneath the transverse processes as in BRSMG Cb4153, although the hollows are not so deep. The centrum flares significantly towards the articular ends and is amphicoelous.

Several of the *Thecodontosaurus* vertebrae are almost certainly posterior dorsals because of their large size, the absence of the parapophysis, and a depression on the side of the centrum, the pleurocentral groove (pcg, Fig. 7G, L, N), as in *Anchisaurus* (Galton, 1976:fig. 5G), *Plateosaurus* (Huene, 1908a: 197–8), many basal archosaurs, and most theropods. Galton (1976) termed this depression a pleurocoel, but it is very different from the true pleurocoels of sauropods. A large centrum with part of its neural arch, BRSMG Cb4154, a posterior dorsal 35 mm long (Fig. 7N, O), is platycoelous. The centrum flares from 16 mm in the middle to 38 mm at the posterior articular surface, which is circular in outline. Although the rim of the anterior face is eroded, it is about the same width as the posterior face. In cross-section, the vertebra is highly cancellous,

with a virtually hollow centrum and a keyhole-shaped neural canal (nc, Fig. 7O). The division between neural arch and centrum is marked by a suture through the bone, just below the widest part of the neural canal whose lower narrow part is accommodated entirely in the upper surface of the centrum. BRSMG Cb4174 is a block containing two posterior dorsals similar to BRSMG Cb4182, except that the centra are pinched transversely, as in posterior dorsals of *Plateosaurus* (Huene, 1908a:pl. 2, fig. 7). BRSMG C4533, one of the first-figured remains of *Thecodontosaurus* (Riley and Stutchbury, 1840:pl. 29, fig. 7), is a waisted dorsal centrum with broad horizontal transverse processes, as well as the keyhole-shaped neural canal on the broken face.

**Sacral Vertebrae**—Two articulated sacrals, YPM 2192, show broad ribs for attachment to the ilium (Fig. 8). These are interpreted as sacrals 1 and 2 on the basis of their shape, the orientation of the ribs, and their relative sizes, the posterior one being 43 mm long and the anterior 37 mm long. The prezygapophyses of the first sacral are well preserved, but the zygapophyses between the two sacrals are modest in size. The postzygapophyses of the second sacral are small. The neural spines are missing. The left sacral rib of the first sacral is present, as is the left, and part of the right, sacral rib of the second sacral. These ribs are tightly fused to the vertebrae and their distal ends are as broad as the centra are long; the first rib is

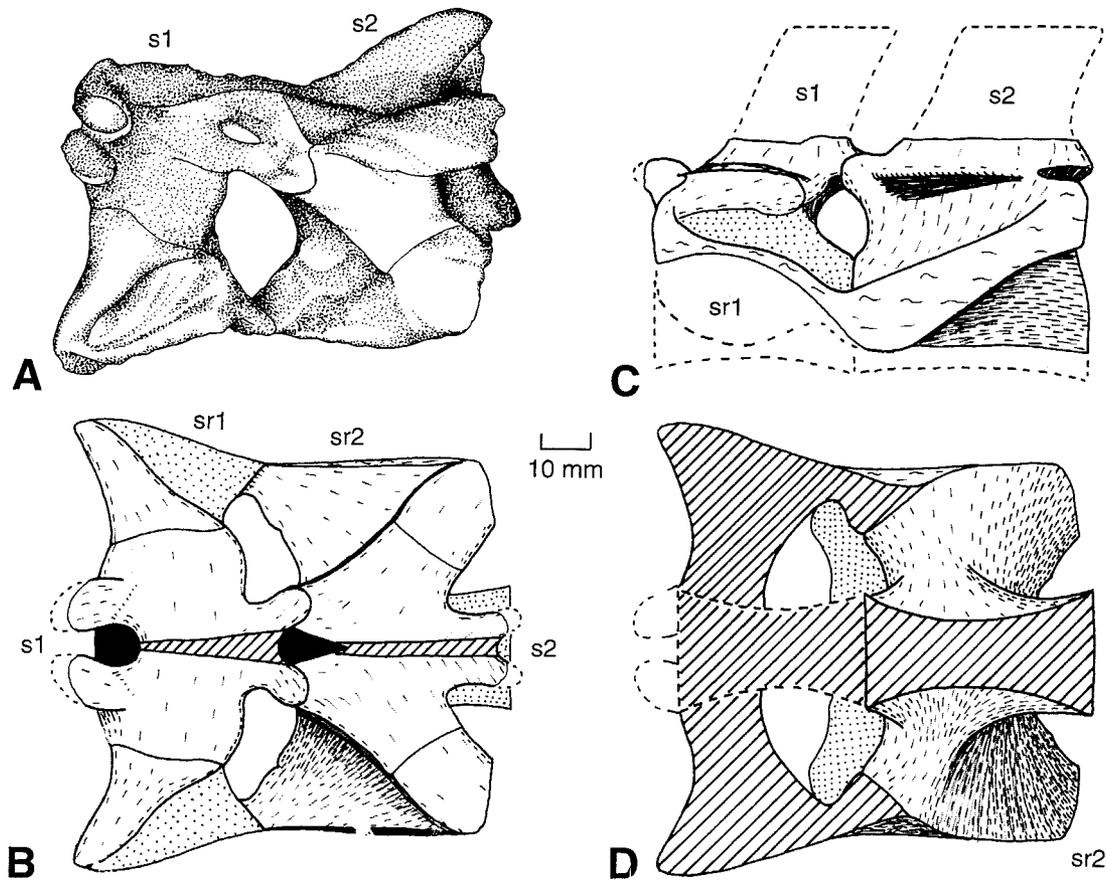


FIGURE 8. Sacral vertebrae of *Thecodontosaurus antiquus* Morris, 1843. Fused sacral vertebrae 1 and 2, with sacral ribs on the left side, in dorsal (A) view; B–D, reconstructed sacral vertebrae 1 and 2, and sacral ribs 1 and 2, in dorsal (B), lateral (C), and ventral (D) views. **Abbreviations:** s1, s2, sacral vertebrae 1 and 2; sr1, sr2, sacral ribs 1 and 2.

36 mm long at the distal end, the second, 48 mm. The first sacral rib is directed slightly forwards, and the second backwards. The distal articular contacts for the ilium are not preserved. Huene (1914:79) estimated the total breadth of the sacrum as 102 mm, based on the width of the left-hand side of the first sacral vertebra and rib, perpendicular to the midline (51 mm). The sacrum is similar to that of *Massospondylus* (Cooper, 1981:fig. 12), but the sacral ribs, especially the first, are broader than those of *Anchisaurus* (Galton, 1976:fig. 15K).

*Thecodontosaurus* probably had three sacral vertebrae. The posterior margin of sacral 2, both vertebra and ribs, shows an articular facet for at least a third sacral (Fig. 8). None of the surviving ilia is complete, nor are any exposed in medial view. One specimen figured by Huene (1908a:pl. 82, fig. 4; Fig. 15D) shows a complete medial view, and the articular facets for the distal ends of the sacral ribs extend for about 85 mm, although the extreme distal end of the iliac blade is broken off. The anteroposterior length of the articular faces of sacral ribs 1 and 2 (Fig. 8C) is 78 mm, so *Thecodontosaurus* probably had only three sacrals in all. Huene (1908a:199–200, fig. 213) described a second or third sacral vertebra, BMNH R1532, a specimen that cannot now be located.

**Caudal Vertebrae**—An anterior caudal, BRSMG Ca7474 (Fig. 9A–D), has a notably platycoelous, spool-shaped centrum (note that Huene, 1908a:pl. 78, fig. 7 orients the specimen in reverse). The anteroventral articular margin lies slightly lower than the posterior, giving the centrum a profile very similar to that of the first caudal of *Massospondylus* (Cooper, 1981:fig.

13). The centrum is short, 23 mm, relative to its width, 22 mm at the articular ends, it is pinched transversely at mid-length, narrowing to 14 mm, and it flares towards the articular surfaces. The ends are almost circular in outline and of equal width. No chevron facet is evident. Chevron facets are seen in another, relatively longer (32 mm), centrum, BRSMG Ca7473 (Fig. 9E–G), in which three ridges run along the ventral surface. This ridge structure is unusual for a dinosaurian caudal vertebra, and the specimen might belong to another taxon. A further anterior caudal, YPM 2192 (Fig. 9H–K), 40 mm long, also shows caudal facets, as well as a transverse process, and it was estimated to be the second or third caudal by Huene (1908a:pl. 77, fig. 7a). The transverse process is very thick, and sweeps posteriorly. It arises at the posterior end of the neural arch, about two-thirds of the way along the centrum. The prezygapophyses have steep facets, angled at some 50° above horizontal.

One small block, BRSMG C4532, contains a posterior caudal vertebra, a mid-series caudal, an impression of the ventral surface of a ?caudal centrum, a portion of a caudal with a chevron still in articulation, and other fragments. The mid-series caudal (here designated C4532a; first figured by Riley and Stutchbury, 1840:pl. 29, fig. 8) is embedded in matrix and shows little more than its right side, the posterior half of which is badly weathered (Fig. 9L). The platycoelous centrum has a deeper anterior articular surface than the posterior, as in a mid-series caudal vertebra of *Massospondylus* (Cooper, 1981:fig. 15). On the ventral surface, a small furrow runs from the back for about one quarter of the centrum length, tapering from a width of 25 mm

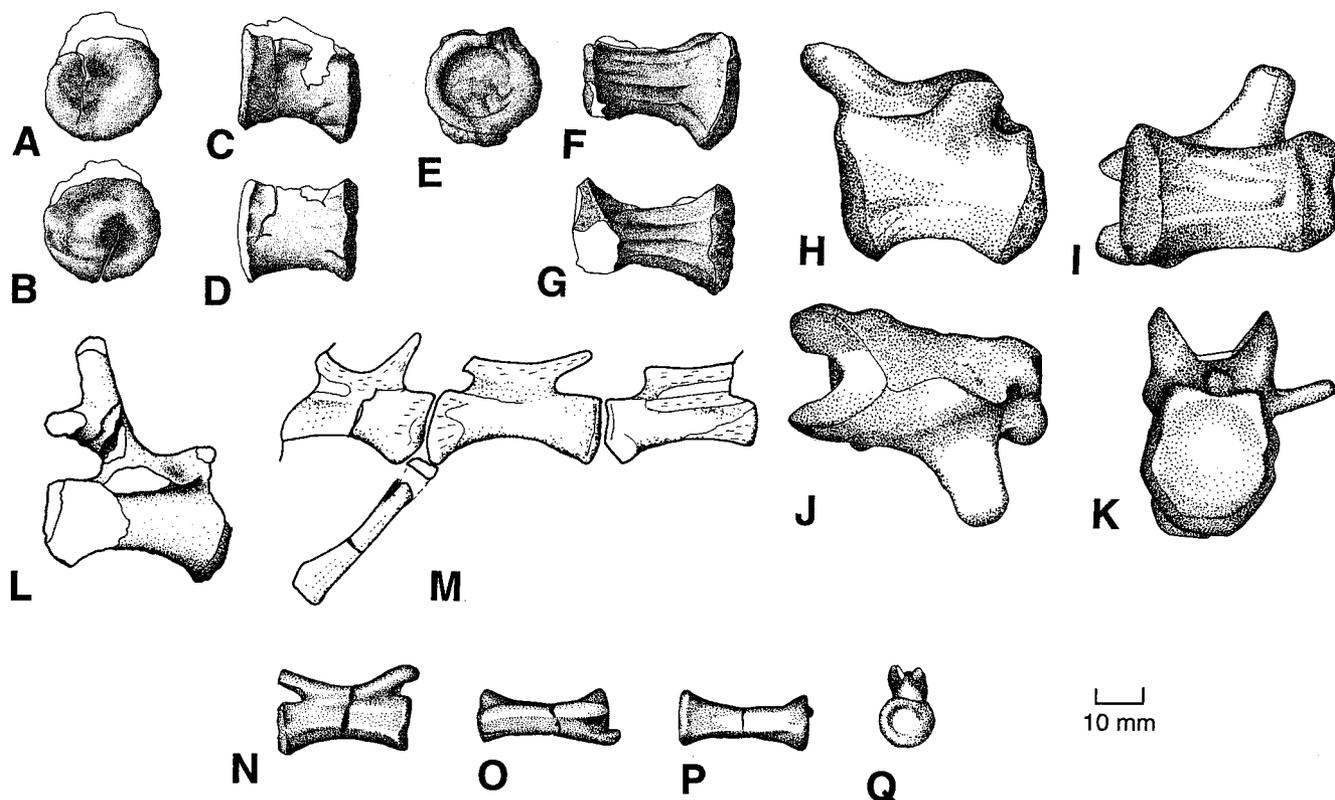


FIGURE 9. Caudal vertebrae of *Thecodontosaurus antiquus* Morris, 1843. A–D, anterior caudal centrum, BRSMG Ca7474, in (A) anterior, (B) posterior, (C) right lateral, and (D) ventral views; E–G, anterior caudal centrum, BRSMG Ca7473, in (E) posterior, (F) left lateral, and (G) ventral views; H–K, mid caudal, YPM 2192, in left lateral (H), ventral (I), dorsal (J), and anterior (K) views; L, mid caudal, BRSMG Ca4532a, in right lateral view; M, mid caudals, BRSMG Ca7510, in right lateral view, with chevrons in place; N–Q, posterior caudal, YPM 2193, in left lateral (N), dorsal (O), ventral (P), and anterior (Q) views.

to 18 mm, where it is succeeded by several tiny longitudinal ridges extending to mid-length of the ventral surface, possible muscle attachment sites. The neural arch of BRSMG C4532a is saddle-shaped, as is typical of prosauropod mid-series caudals, but with a deeper 'saddle' than in caudal 13 of *Plateosaurus* (Huene, 1908a:pl. 3). The 'saddle' curvature is smoother than in either *Plateosaurus* or *Massospondylus* (Cooper, 1981: fig. 15). The neural arch extends laterally as a narrow ledge joining the base of the incomplete transverse process, the base of which is long and relatively high compared to that of *Plateosaurus* (Huene, 1908a) and *Massospondylus* (Cooper, 1981). The neural spine has a straight anterior margin and slopes posteriorly at  $17^\circ$ . It is 23 mm long, but lacks the extreme tip. The prezygapophyses are small, and the postzygapophyses are positioned high on the neural spine.

Three somewhat more posterior caudals, BRSMG Ca7510 (Fig. 9M), preserved in association, show elongate low centra, each 28–30 mm long, with expanded articular ends. The neural arch is a low narrow saddle-shaped structure, with no vertical neural spine. A chevron is in place between the second and third vertebrae in the series.

The best preserved posterior caudal, YPM 2193 (Fig. 9N–Q) has a low neural spine and prominent zygapophyses with facets angled steeply. As in all posterior caudals, there is no transverse process. Other posterior caudals include BRSMG C4532b, Ca7507, Cb4166, Cb4276, and BMNH R1550, and these range in centrum length from 27 to 34 mm.

**Ribs**—At least 42 partial ribs survive among the Durham Down material. Most are isolated specimens, but five blocks, BRSMG Cb4168, Cb4196; BMNH R1536, R1537; YPM 2192,

contain two ribs, a number of partial ribs are associated in YPM 2195 (Fig. 12), and another, BRSMG Cb4200, preserves five. Two slender rib shafts and a rib impression on one such block, BRSMG Cb4196 (Fig. 10A), may represent cervicals because of their delicate construction, small size, and limited curvature. The longer specimen, 90 mm in length, has very little curvature, as in posterior cervical ribs of *Massospondylus*. The shafts are uniform in diameter throughout their length. Other possible cervical rib fragments are BRSMG Cb4195, Cb4206, Cb4212, and Cb4256.

Another rib missing its articular and distal ends, BRSMG Cb4169 (Fig. 10B), is probably a dorsal, by comparison with *Massospondylus* (Cooper, 1981:fig. 19). Proximally, there is a sharp ridge between the anterior and lateral surfaces, but this ridge degenerates distally, and the anterior and lateral surface meet at an angle of about  $90^\circ$ . A proximal fragment, BRSMG C4528 (Fig. 10C), 93 mm long, and preserving parts of the capitulum and tuberculum, is a left dorsal rib, possibly from the anterior chest region (Huene, 1908a:204, pl. 77, fig. 3). The capitulum is 20 mm long, the tuberculum 7 mm, and the two processes diverge from one and other at an angle of  $62^\circ$ . A shallow wide groove on the posterior surface of the rib extends from between the diverging articular heads at least 30 mm distally, as in *Massospondylus* (Cooper, 1981). A small foramen is present on the mid-posterior surface, 12 mm beneath the bases of the articular heads. An association of very fragmentary splint-like bones in YPM 2195 may represent the remains of gastralia (g?, Fig. 12). YPM 2192 also includes some thin gastralia in association with a dorsal vertebra.

**Chevrons**—A partial chevron, BRSMG Ca4532c (Fig. 10D),

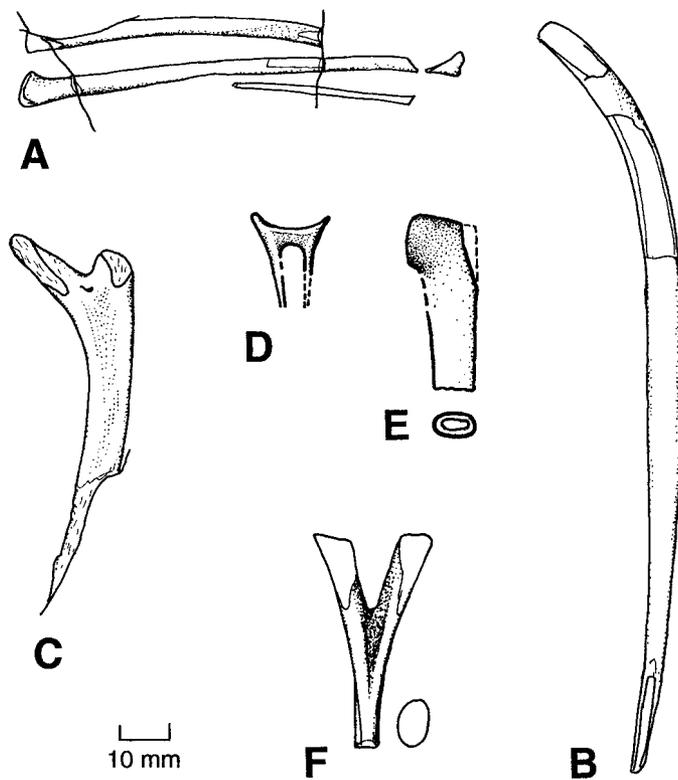


FIGURE 10. Ribs and chevrons of *Thecodontosaurus antiquus* Morris, 1843. **A**, cervical ribs, BRSMG Cb4196; **B**, dorsal rib, BRSMG Cb4169; **C**, proximal end of dorsal rib, BRSMG C4528; **D**, **E**, proximal end of chevron, BRSMG Ca4532c, in anterior (**D**) and right lateral (**E**) views, with a distal cross-section profile indicated; **F**, chevron, BRSMG Ca7510, in anterior view, showing deepened distal end in distal cross section. **Abbreviations:** c, capitulum; t, tuberculum.

E), is represented by the proximal end and part of the shaft, 24 mm long in all. The bone is Y-shaped, with a proximal crescentic cross-piece, typical of basal archosaurs and saurischians (Romer 1956). This chevron is shown by Huxley (1870:pl. 3, fig. 5, 6) and Huene (1908a:pl. 78, fig. 11) in articulation with the mid-series caudal vertebra BRSMG Ca4532a. Another partial chevron, BRSMG Ca7510 (Fig. 9M), in association with two of a set of three caudal vertebrae (Huene, 1908a:fig. 220) has a shaft that expands in depth from 54 mm to 84 mm towards its distal end. Distal expansion of chevrons is widespread among Diapsida, including dinosaurs. Another large chevron, BRSMG C4534 (Fig. 10F), originally figured by Riley and Stutchbury (1840, pl. 29, fig. 9), is larger. The proximal branches are up to 22 mm apart, and the distal shaft is 6 mm broad and 10 mm deep. This chevron was ascribed to the phytosaur *Rileya platyodon* by Huene (1908b:pl. 6, fig. 3), but it is just as likely from an anterior caudal of *Thecodontosaurus*.

#### Appendicular Skeleton

**Pectoral Girdle**—Seven incomplete scapulae are the only elements of the pectoral girdle surviving. In one, BRSMG Ca7481 (Fig. 11A), the distal end is absent, as is the proximal portion with acromion and glenoid facet; the element is broken across about mid-length. This bone is curved and plate-like, 172 mm long as preserved, widest near the proximal end and convex laterally; this convexity is most pronounced distally. The medial margin appears straight in cross-section. The dorsal blade as seen in several specimens, notably ANSP 9876, 9865,

and YPM 2195. In the last, both scapulae are present (Fig. 12C), but the blades are straight and symmetrical in lateral aspect, and left and right cannot be distinguished (Galton and Cluver, 1976:fig. 11b; Huene, 1908a:pls. 79, 80). The distal tip of the blade is only slightly expanded relative to its shaft, measuring 40 mm wide in the better preserved scapula in YPM 2195 (Fig. 11B) in an overall preserved length of 130 mm in the other.

Huene (1908a:204–205, pls. 79–81) described five scapulae, including two, BRSMG Ca7478, Ca7479, both now lost, with associated coracoid impressions. These were relatively well-preserved specimens, and Huene's (1908a:pl. 79) drawings permit a reconstruction (Fig. 11C), which suggests typical features seen in other prosauropods, such as *Anchisaurus* (Galton, 1976) and *Sellosaurus* (Galton, 1984a), although the distal end of the scapular blade is less expanded than in *Plateosaurus* (Galton, 1990).

**Humerus**—At least 13 partial humeri survive. The best surviving example, YPM 2195 (Fig. 12C, 13A, B), is 160 mm long, preserving much of the shaft and proximal end. It is slightly abraded. The prominent deltopectoral crest is broadly convex and is shorter and positioned more proximally than in other prosauropods (Galton, 1973, 1990). The proximal end of this humerus is 60 mm wide, compared to a shaft width of about 10 mm. The oval shaft has the classic twist which offsets the proximal and distal ends by about 60°. The distal end of the shaft is flattened anteroventrally, and it is even slightly dished laterally. A second complete deltopectoral crest, YPM 2192 (Fig. 11D, E) confirms this condition; a broad depression occupies the medial face of the humerus at the base of the crest.

Huene (1908a:205, pl. 80, 81, 83) described seven humeri from 160 to 190 mm long, two of which, BRSMG Ca7477, Ca7512, now lost, showed substantial detail of the proximal and distal ends; these more complete specimens permit a reconstruction (Fig. 11F). The overall shape of the humerus is clearly dinosaurian, with a distinct twist to the shaft, seen in ANSP 9880, and a subrectangular deltopectoral crest, seen in BMNH R1541. Other extant humeri, BRSMG Cb4189 and BMNH R1542, confirm the overall shape. The lateral margin of the shaft, where it meets the humeral head, describes a shallower concave curve, extending further proximally, than in *Plateosaurus* (Galton, 1990), and is more like that of *Anchisaurus* (Galton, 1976). The shaft region is relatively narrow, giving the bone a more gracile appearance than humeri of *Plateosaurus* and *Massospondylus*, but this could be a simple allometric difference, a result of the smaller size of *Thecodontosaurus*.

**Forearm**—The ulna is best represented by a specimen from the articulated left forelimb YPM 2195 (Fig. 12C, 13C–E), 95 mm long, 23 mm wide proximally and 18 mm distally, and a possible right ulna, BRSMG Ca7486 (Fig. 14A, B), 110 mm long. They are similar to other prosauropod ulnae in being roughly triangular in cross section proximally, and in flaring at the distal end, creating an anteromedially-oriented surface. Longitudinally, the ulna is slightly bowed. Because of abrasion, in neither case can the presence of a tubercle for attachment of the radio-ulnar ligament, as in *Massospondylus*, be demonstrated. The proximal and distal ends are twisted with respect to each other to about the same degree as in *Massospondylus* (Cooper, 1981:fig. 31) and, like the ulna of *Plateosaurus* (Galton, 1990), the bone has a straight long axis, in contrast to the curved ulna of *Anchisaurus* (Galton, 1976).

The radius in YPM 2195 is merely a sliver crossing the shaft of the ulna (ra, Fig. 12C). A radius, BRSMG Ca7504, assigned by Huene (1908a:206) to the phytosaur *Rileya platyodon*, is more likely from *Thecodontosaurus*. This bone (Fig. 14C–F), with a length of 130 mm, is longer than the ulna BRSMG Ca7486, although the latter lacks the proximal end. The radius, presumably from the right side, is a straight element, with a

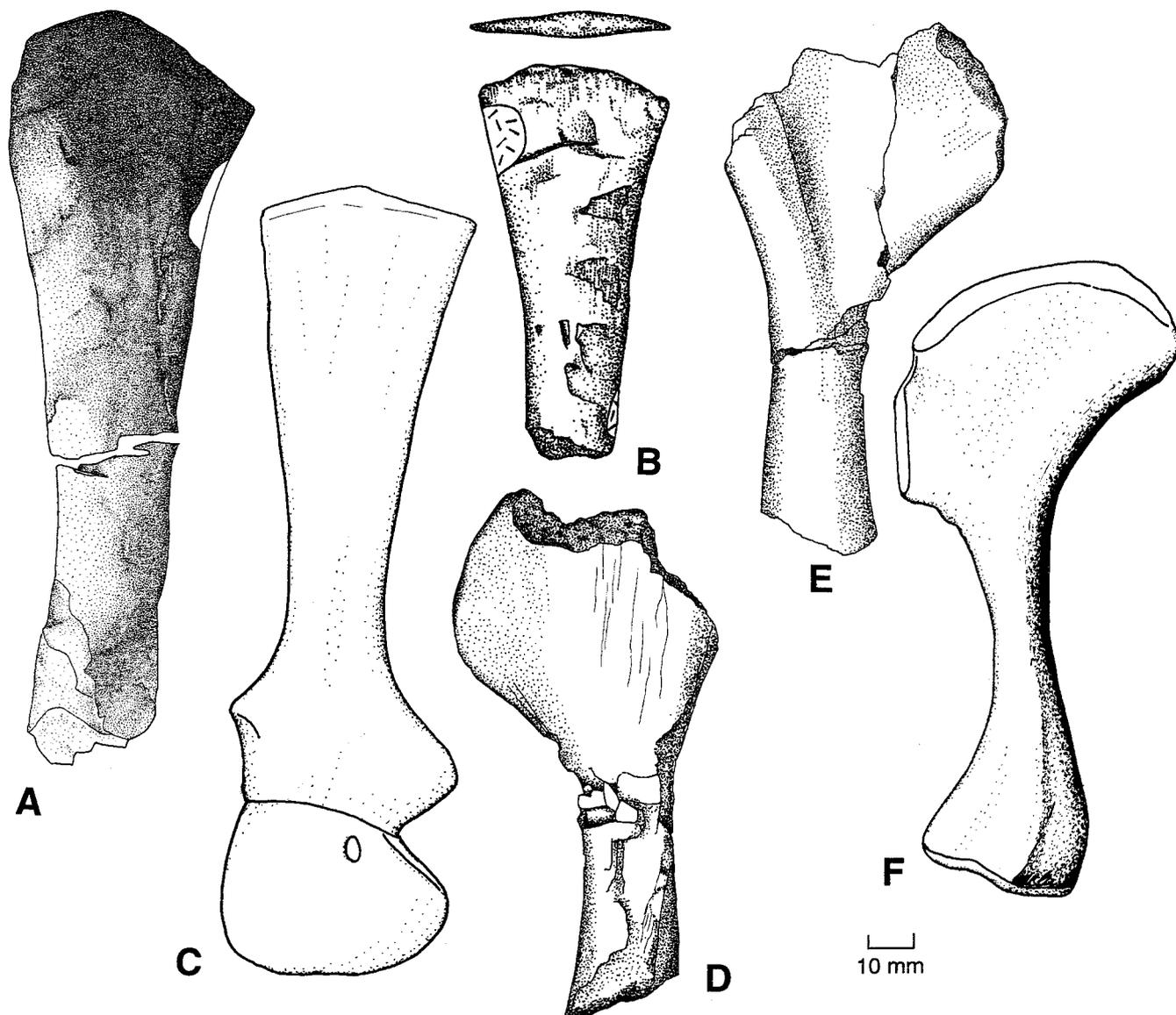


FIGURE 11. Elements of the shoulder girdle and forelimb. **A**, partial right scapular dorsal blade, BRSMG Ca7481, in right lateral view; **B**, partial scapular blade (right or left?) of YPM 2195 in lateral and dorsal views; **C**, reconstructed left scapula and coracoid, based on BRSMG 89 and 92 (both now lost, from Huene, 1908a:pl. 79); the distal scapular blade and the ventral margin of the coracoid are unknown; **D**, **E**, partial proximal right humerus, YPM 2192, in posterior (**D**) and anterior (**E**) views; **F**, reconstructed right humerus in anterolateral view, based on BRSMG Ca7477 (37), now lost, from Huene (1908a:pl. 81, fig. 2).

shaft 9–10 mm in diameter, and somewhat elliptical in cross section. The ends of the bone are expanded, and both measure at most 25 mm across. The proximal expansion is triangular in cross section, with a flat anterior face (Fig. 14C) and a rounded ridge on the posterior face (Fig. 14E).

**Carpus and Manus**—The hand is well known from the articulated forelimb, YPM 2195 (Fig. 12A, 13G). This is a left arm with the humerus, partial epipodium, and manus doubled back upon themselves. The limb appears largely complete and is the best example of articulated dinosaur material from the Durdham Down fissures. Three small disc-like carpals are present, the largest being distal carpal I (dcI, Fig. 12A). No proximal carpals are evident. Digit I consists of a robust metacarpal and two stout phalanges, including a large scythe-like ungual 35 mm long, which is incompletely preserved (I, Fig. 12A). Digit III is approximately 110 mm long, including the meta-

carpal, and the hand measures 45 mm wide across the proximal ends of the metacarpals. Digits II and III in YPM 2195 are more or less complete (II, III, Fig. 12A), missing only the proximal part of the metacarpal of digit II. These two digits are more slender and longer than digit I, but equal to each other in size. Digit II contains three phalanges, and digit III four. The unguals are smaller and straighter than in digit I, and the ungual of digit II is considerably longer than that of digit III. The slender metacarpal of digit IV is capped by two poorly preserved nubbin-like phalanges; no phalanges are preserved in association with the short metacarpal V (IV, V, Fig. 12A). This specimen allows a confident reconstruction of the hand of *Thecodontosaurus* (Fig. 13G). The phalangeal formula is 1-2-3-1-0. The entire hand, and digit I in particular, are more slender than in *Anchisaurus*, whose hand is also more slender than those of plateosaurids (Galton, 1973; Galton and Cluver, 1976).

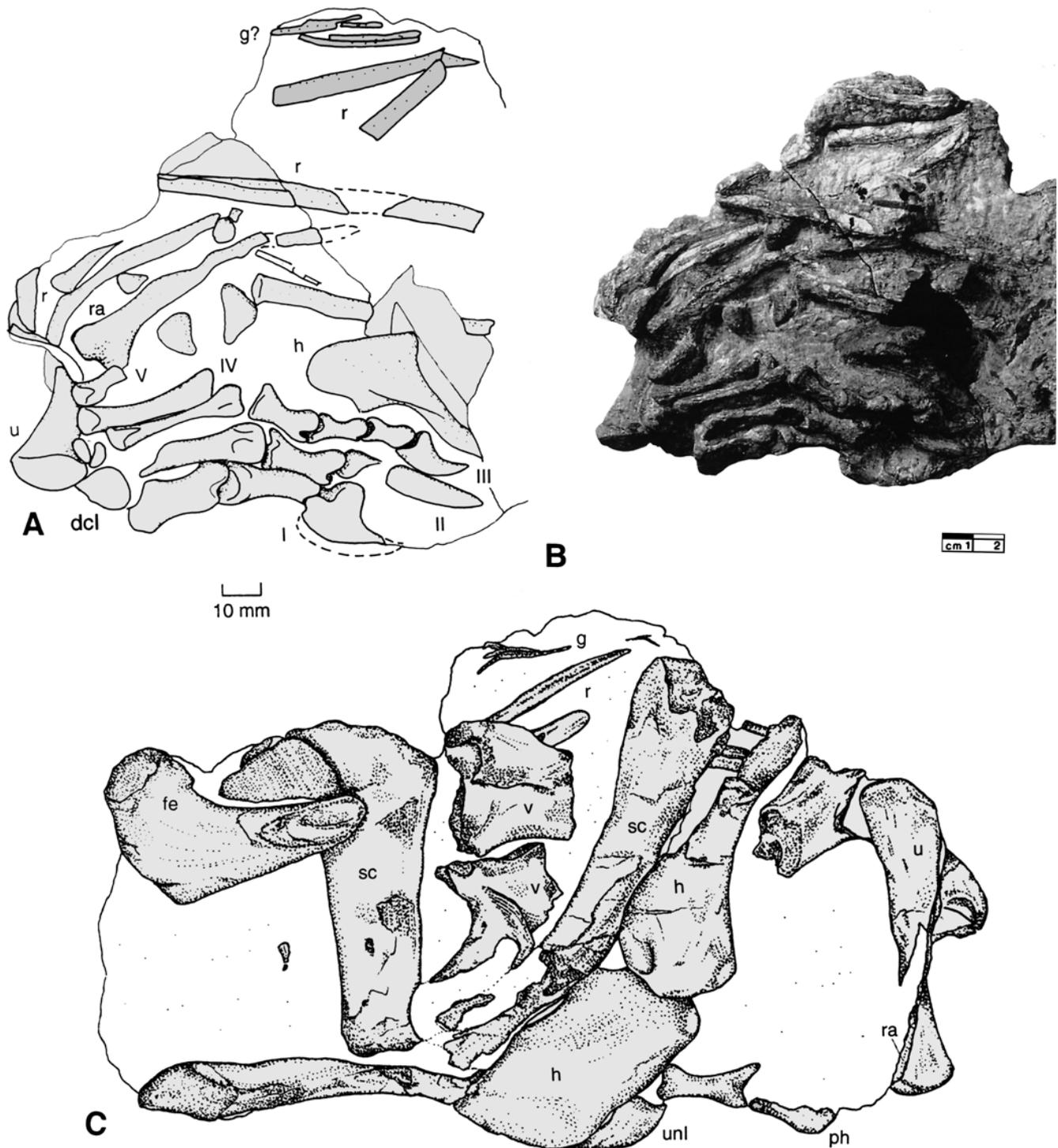


FIGURE 12. Articulated left arm and hand bones of *Thecodontosaurus antiquus* Morris, 1843, YPM 2195. **A, B**, interpretive drawing and photograph of the block from one side, and **C**, from the other. **Abbreviations:** **dcl, dc3, 4**, distal carpals 1, 2, 3; **fe**, femur; **g**, gastralgia; **h**, humerus; **ph**, phalanx; **r**, rib; **ra**, radius; **sc**, scapula; **u**, ulna; **un**, ungual; **v**, vertebra; **I–V**, digits I–V.

Several additional metacarpal and phalangeal elements exist in the Bristol collection. Carpal elements have not been identified here, but there are several putative metacarpals and phalanges. One slender metacarpal, BRSMG Cb4174 (Fig. 14G), must be from digit II, III or IV because of its length (at least 57 mm), although most of the proximal end is missing and the distal end badly eroded. The bone shows the normal twisting

of prosauropod metacarpals. A second abraded bone, BRSMG Ca7482 (Fig. 14H), described by Huene (1908a:207, pl. 81, fig. 4) as a third metacarpal, is associated with a fragment of metacarpal II or IV. The ends of this 56 mm long element appear to be twisted relative to each other, but the state of preservation of the bone does not allow detailed comparisons. The impression of BRSMG Cb4179 is at least 43 mm long and 17 mm

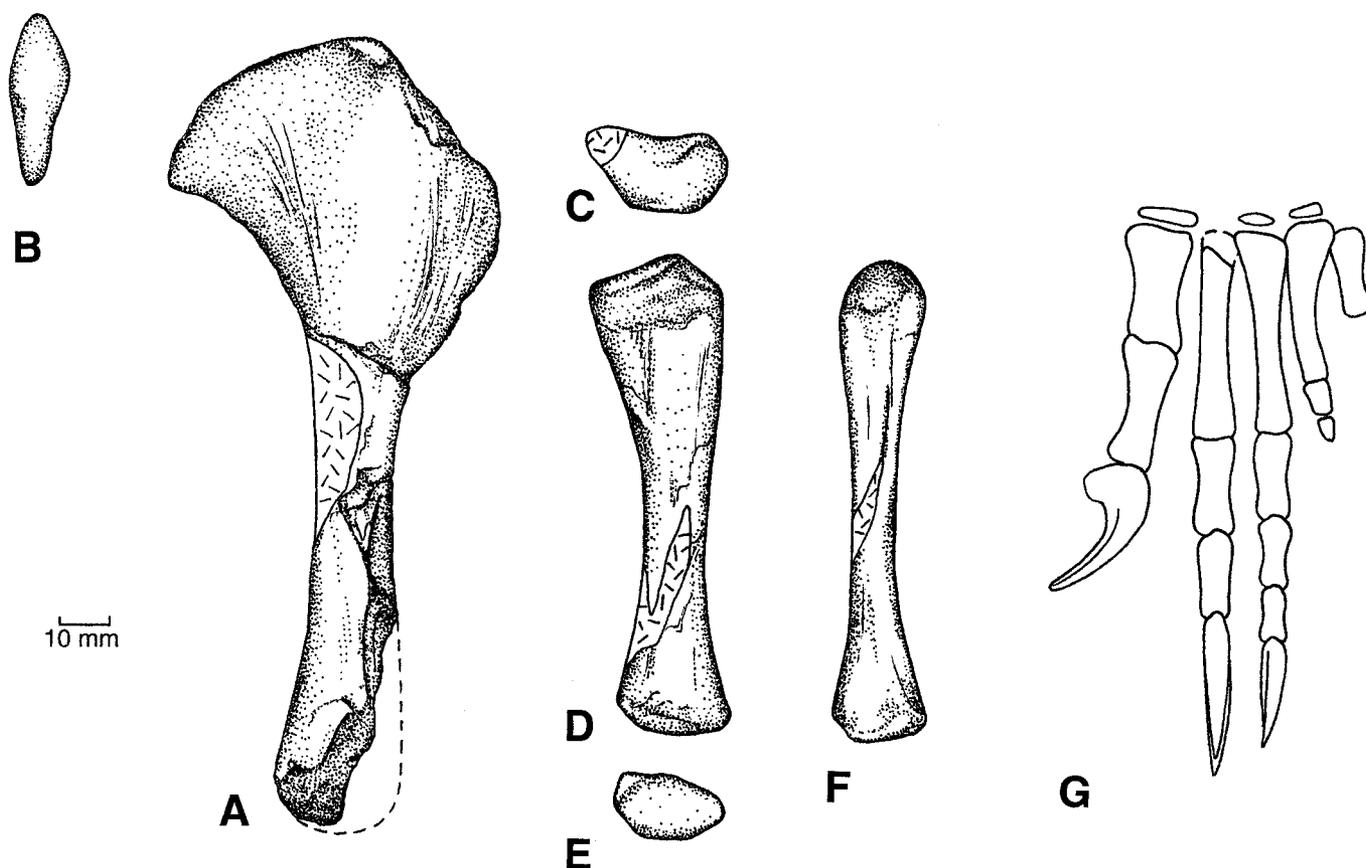


FIGURE 13. Forelimb elements of *Thecodontosaurus antiquus* Morris, 1843, YPM 2195. A, B, left humerus in dorsolateral (A) and posterior (B) views; C–F, left ulna in proximal (C), lateral (D), distal (E) anterior (F) views; G, left manus in dorsal view.

wide; the fact that it is curved, makes it probable that it is a second metacarpal. The shaft is uniformly wide, about 7 mm.

Several isolated phalanges may have come from the hand. BRSMG Ca7485, 29 mm long, is relatively slender compared to those of *Plateosaurus* and *Massospondylus* (Fig. 14I, J). The proximal articular surface is subquadrangular in outline. The bone shaft is triangular in transverse section at mid-length; its ventral face arches dorsally. This is probably the phalanx figured by Riley and Stutchbury (1840:pl. 30, fig. 8) and Huene (1908a:pl. 81, fig. 7), and because of its great width, interpreted by the latter as pertaining to digit I. However, phalanx I of digit I is rotated in YPM 2195, as in all other prosauropods, so Ca7485 is presumably from another digit. A phalanx of YPM 2192, probably phalanx II of digit II or III, is triangular at its proximal end, 32 mm long by 11 mm wide minimum. BRSMG Cb4187 could be the unguis phalanx of digit I (Fig. 14K). It is a large claw, 50 mm long and strongly curved, though not so extremely as in *Massospondylus*, nor quite so robust in appearance. The proximal half is deep, and the distal half of the bone is slender, terminating in a sharp point.

**Pelvic Girdle**—The pelvic girdle is represented by a right ilium, four fragmentary ilia and a pubis, although Huene (1908a:207–210, pl. 82, 84, 85) described eight ilia, two partial ischia, and two proximal parts of the pubis. The surviving ilia include one from the right side, BMNH R1539, and three badly preserved specimens, BRSMG Cb4180, Cb4181, and BMNH R1540. Unknown to Huene, a good ilium was present in the Philadelphia collection, ANSP 9870, with a broad shelf-like iliac blade, about 27 mm broad (Fig. 15A, B). This is the posterior ramus, some 65 mm long, measured from the middle of

the acetabulum, the anterior part being broken off. BMNH R1539 (Fig. 15C), an incomplete specimen, shows an out-turned anterior ramus of the iliac blade, a widespread condition in Dinosauromorpha. This ramus is relatively small, indicating the brachyiliac condition characterizing Sauropodomorpha, but relatively smaller than in *Anchisaurus* (Galton, 1976). The posterior iliac blade ramus in both BMNH R1539 and ANSP 9870 is proportionally large and is rectangular in lateral aspect, instead of rounded, as in other sauropodomorphs. The ischiadic peduncle is a slim process, and the acetabulum is deep and fully perforated, although the iliac border of the acetabulum is not deeply concave. The pubic peduncle is delicate and slender in relation to those of other prosauropods. The iliac blade of BMNH R1539 is 39 mm high, measured from the dorsal margin of the acetabulum, and 80 mm long, as preserved. The acetabulum is 34 mm wide.

The medial view of the ilium is best seen in BRSMG Ca7460, now lost (Huene, 1908a:pl. 82, fig. 4). This showed a flat-faced articular facet for the distal ends of the sacral ribs, the brevis shelf (brs, Fig. 15D) running diagonally from behind the anterior part of the acetabulum to, presumably, the distal-most tip of the posterior process of the iliac blade. It is hard to distinguish separate facets, but measurements of the sacral ribs of YPM 2192 (Fig. 8) suggest that *Thecodontosaurus* had three sacral vertebrae (see above).

A left pubis, BRSMG Cb4267, shows only its anterodorsal surface, missing the distal end (Fig. 15E). The bone is long, plate-like and wedge-shaped in transverse section (Fig. 15F). Proximally the bone is badly preserved, but shows the beginning of the narrowing and twisting seen in, for example, *Lu-*

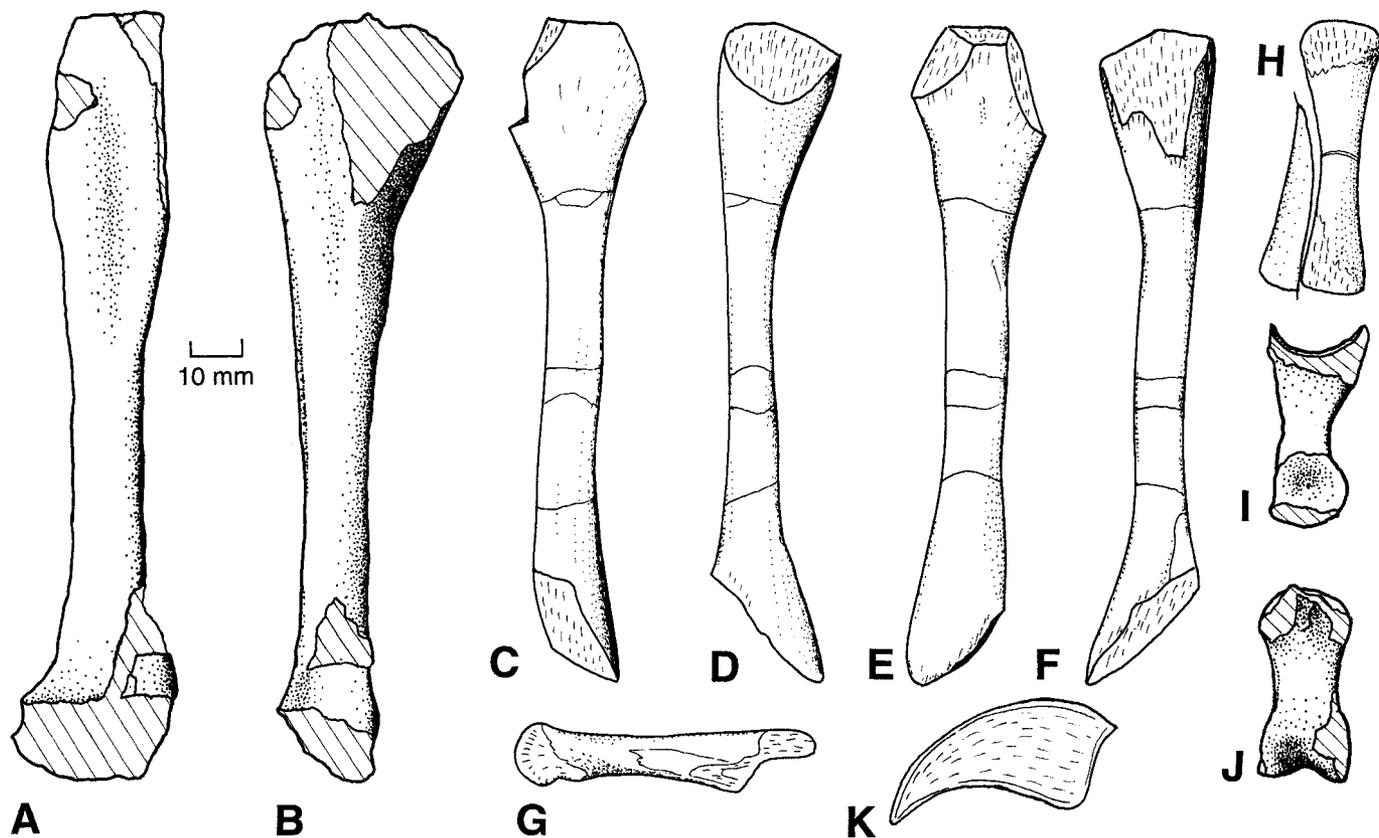


FIGURE 14. Arm and hand bones of *Thecodontosaurus antiquus* Morris, 1843. **A, B**, right ulna, BRSMG Ca7486, in medial (**A**), and posterior (**B**) views; **C–F**, right radius in anterior (**C**), medial (**D**), posterior (**E**), and lateral (**F**) views; **G**, metacarpal, BRSMG Cb4174, in lateral view. **H**, metacarpal III, in dorsal view, with parts of II and IV, BRSMG Ca7482; **I, J**, manual phalanx, BRSMG Ca7485, in medial (**I**), and ventral (**J**) views; **K**, claw, BRSMG Cb4187, possibly from manual digit I, preserved as a broken bone outline.

*fengosaurus* (Galton and Cluver, 1976). The medial margin curves laterally and dorsally, as in many other prosauropods (Galton and Cluver, 1976). Because of poor preservation, it is not possible to establish whether the obturator foramen was open or closed. Total length of the specimen is 135 mm, and distal width is 30 mm.

The ischium is poorly represented. Two putative distal parts, YPM 2192, are straight rod-like elements (Huene, 1908a:pl. 83), the best preserved being 120 mm long by 20 mm wide at a minimum. The distal tip is strongly thickened. The anterior edge of the shaft is sharp relative to the posterior. A small portion of what appears to be the proximal end of the ischium remains articulated to the ilium/acetabulum of ANSP 9870. The ischium head is small and the shaft narrow, and otherwise similar to that of anchisaurids.

**Femur**—Huene (1908a:210–211, pl. 85–88) described 20 femora, of which some were virtually complete. Although 23 partial femora still exist from Durham Down, there is now no complete specimen. The most promising for reconstruction is BRSMG Ca7456, the proximal end of a left femur, including the head and most of the shaft, although the latter is largely preserved as an impression in the underlying matrix (Fig. 16A). This specimen was formerly complete (Huene, 1908a:pl. 87), and it can be used for a reconstruction (Fig. 16B). The femoral head is inturned, a typical feature of dinosaurs, and well known in *Plateosaurus* (Huene, 1908a:pl. 14) and *Massospondylus* (Cooper, 1981:fig. 54). The shaft is weakly sigmoid in posterior view, uniformly wide throughout its length, and curves laterally

towards the distal end. The rectangular fourth trochanter is seen now as an impression (tr4, Fig. 16A, B).

A partial left femur, BRSMG Ca7490 (Fig. 16C–H) has a rather crushed shaft, but the distal condyles are in good condition, except for the tip of the fibular condyle. The anterior face of the femur is flat, but the fibular and tibial condyles are separated by a deep intercondylar groove on the posterior face (Fig. 16E). The articular facets are subrectangular in outline and wrap around from the distal end of the bone on to its posterior face (Fig. 16E, G). The fibular flange does not project posteriorly beyond the medial condyle in distal view, in contrast with the condition in *Anchisaurus* (Galton and Cluver, 1976:fig. 8), *Massospondylus* (Cooper, 1981:fig. 60), and *Plateosaurus* (Galton, 1990:fig. 15.7). Further femora include a distal part of a large right femur (BRSMG C4530), and a proximal right femur (BRSMG Cb4183). In this, a few muscle scars are visible on the lateral surface of the fourth trochanter, which is seen as a prominent flange-like process.

**Tibia**—Twelve specimens of tibiae survive, of which only one, the mistakenly localised type specimen of *Agrosaurus macgillivrayi* Seeley, 1891 (BMNH 49984), is complete (Vickers-Rich et al., 1999). This tibia (Fig. 17), 205 mm long, has an expanded proximal end, a slightly bowed shaft, and a slightly expanded distal end. The proximal end is triangular and flat, measuring approximately 50 × 40 mm, and it slopes down posteriorly. The articular end bears two faces, divided by a shallow groove, and corresponding to the two distal condyles of the femur. A strong cnemial crest marks the anterior face of the

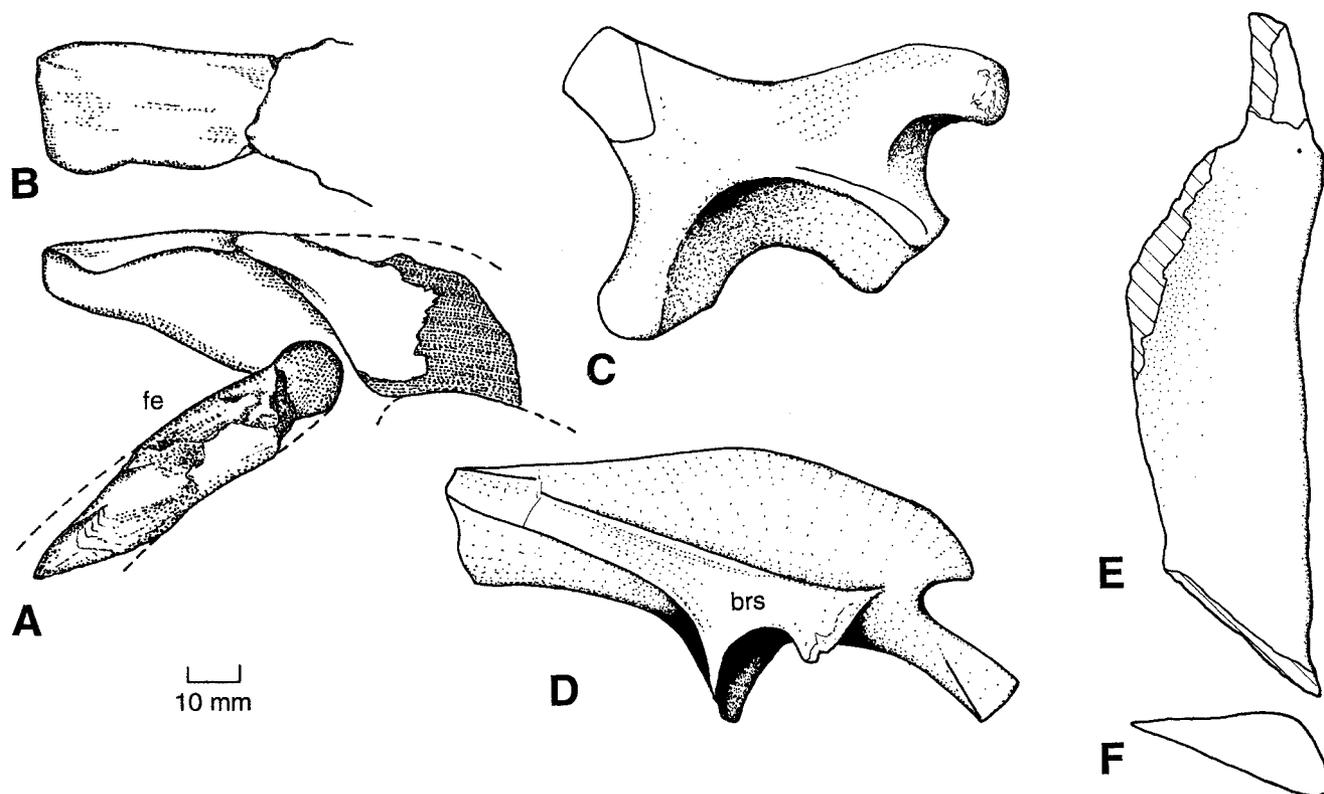


FIGURE 15. Pelvic bones of *Thecodontosaurus antiquus* Morris, 1843. **A, B**, posterior ramus of right ilium, ANSP 9870, in lateral (**A**) and dorsal (**B**) views, the lateral with the femur associated; **C**, right ilium, BMNH R1539, in lateral view; **D**, left ilium, BRSMG Ca7460 (57), in medial view (specimen now lost; from Huene, 1908a:pl. 82, fig. 4); **E, F**, left pubis, BRSMG Cb4267, in (**E**) anterodorsal, and (**F**) distal cross-sectional views; the proximal end is to the top of the figure. **Abbreviations:** brs, brevis shelf; fe, femur.

proximal portion of the bone. The shaft contracts to a diameter of 12 mm, and it is straight on the posterior margin, somewhat bowed on the anterior. The shaft expands gradually distally to a width of 30 mm. The distal articular face shows two flat facets for attachment of the astragalus, and a deep groove above these in the midline of the medial face (Fig. 17C). This, and other tibiae of *Thecodontosaurus* are more gracile than those of *Plateosaurus* (Galton, 1990) and *Massospondylus* (LJ, pers. obs.). One of the best proximal portions of a tibia, a right, BRSMG C4531 (Fig. 18A–E), lacks part of the medial edge of the proximal surface, and is eroded on its lateral face. The anterior aspect is dominated by a strong cnemial crest (cn, Fig. 18A, B). On the proximal surface, the cnemial crest projects anteriorly (cn, Fig. 18E), with two short grooves close to the posterolateral edge of the bone. The medial surface is flat with a possible ligament scar near the cnemial crest. The shaft is oval to subquadrangular in cross-section. A left tibia, YPM 2192, figured by Huene (1908a:pl. 89, fig. 3) is similar.

A distal right tibial fragment, BRSMG Ca7495 (Fig. 18F–J), matches BRSMG C4531 in size. It is slender relative to that of *Plateosaurus*, which flares distally. The anterior surface is slightly rounded proximally, but less so distally. The medial surface (Fig. 18I) is flat, with a distinct, heavily scarred, distal depression near the posterior margin. The shaft is twisted, as in all dinosaur tibiae. The posterior malleolus is incomplete distally and laterally, but appears to have been prominent; enough remains to show that it had a flange-like appearance with a laterodistal outer margin. In distal view (Fig. 18J), the posterior and medial margins of the tibia are straight and meet at an angle of about 105°.

One distal portion of a left tibia, YPM 2192 (Fig. 18K–O),

retains the astragalus in contact with its distal articular surface. The two elements fit firmly, and the ascending process of the astragalus keys into a groove in the lateral edge of the distal end of the tibia, as is usual. The transverse width of the distal end of the tibia is 25 mm.

**Fibula**—Six fibulae survive, one, BRSMG Ca7497 (Fig. 18P), comprising the proximal end and most of the shaft. This is a right fibula, not left as stated by Huene (1908a:212). The bone is slender, as seen in gracile prosauropods such as anchisaurids; its preserved length is 129 mm, the diameter of the rounded shaft 9 mm. The proximal end is divided by a low ridge into an anterior and a posterior face that merge distally into the rounded shaft. A large nutritive foramen on the medial surface (nf, Fig. 18P) is comparable to one found in *Plateosaurus* (Galton, 1990) and *Massospondylus* (Cooper, 1981, fig 68c). ANSP 9867 is a similar proximal end of a fibula.

**Tarsus and Pes**—The astragalus in YPM 2192 (Fig. 18K–O) is approximately 35 mm long by 11 mm high in anterior view in the middle of its width. The height at the ascending process is about 20 mm. The process itself is broad and bulbous; the dorsal tip is rounded but directed slightly anteriorly. In distal aspect (Fig. 18O), the astragalus is trapezoidal, the medial edge being broader (22 mm) than the lateral (13 mm). The lateral edge with the ascending process lies well beyond that of the naturally articulated tibia, and it bears a shallow fibular facet (ff, Fig. 18L) to accommodate part of the distal end of the fibula, as in *Plateosaurus*. Huene (1914:82, fig. 52) described the calcaneum belonging to the distal tibia and astragalus just described (Fig. 18K–O), a tiny element with a flat proximal face, a convex distal face, and pointed laterally. The specimen cannot be located now.

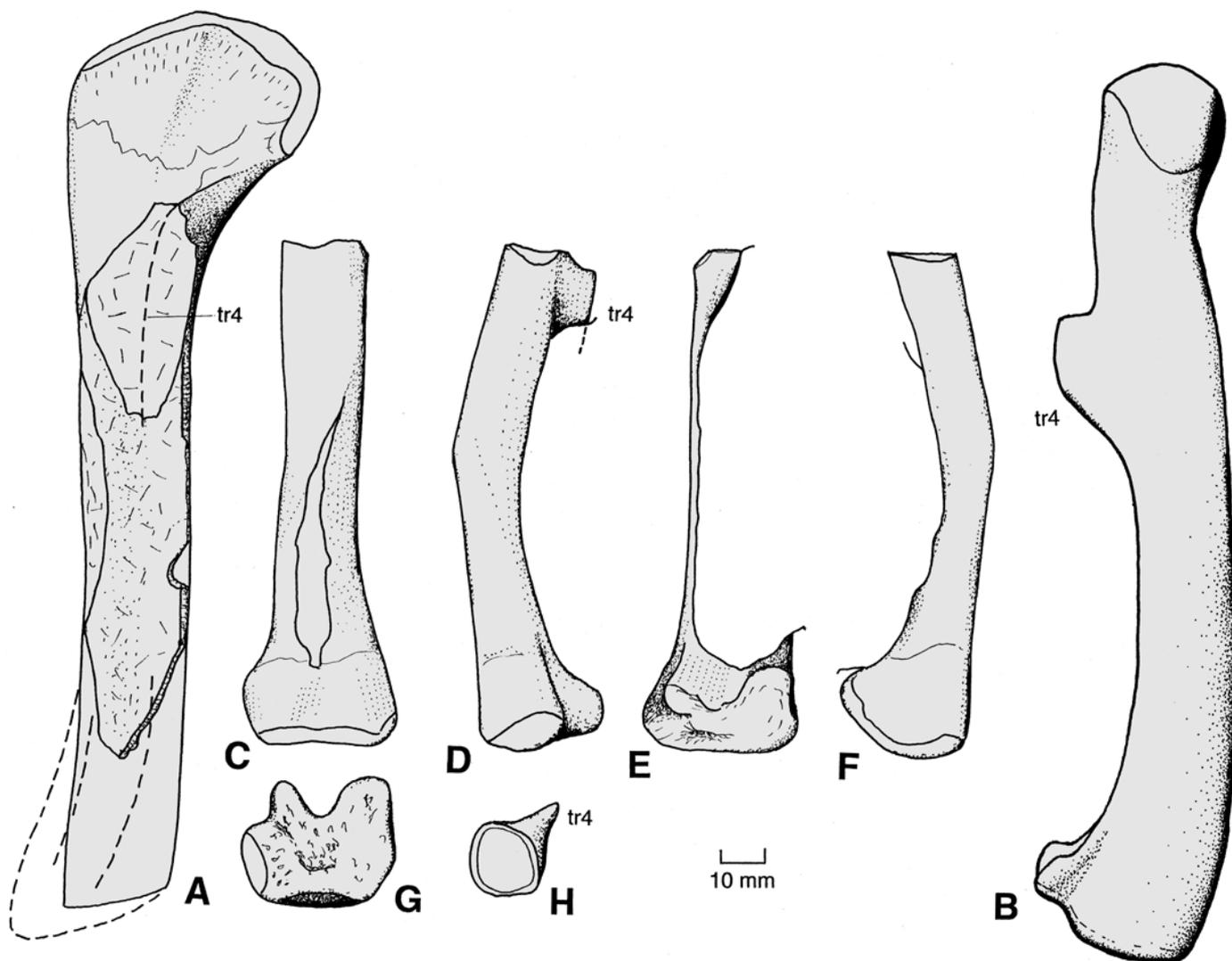


FIGURE 16. Femora of *Thecodontosaurus antiquus* Morris, 1843. **A, B**, formerly complete left femur, BRSMG Ca7456, as preserved now, in posterior view (**A**), and restored version, in medial view (**B**), with information from Huene (1908a:pl. 87, fig. 2); **C–H**, distal left femur, BRSMG Ca7490, in anterior (**C**), lateral (**D**), posterior (**E**), medial (**F**), distal (**G**), and proximal cross-sectional (**H**) views. **Abbreviation:** tr4, fourth trochanter.

The only metatarsal surviving, assuming the metacarpals described above have been correctly identified, is a right metatarsal III, BRSMG Ca7451a (Fig. 18Q). The palmar, or ventral, surface is embedded in matrix, as is the distal part of the medial surface. It is 90 mm long, 17 mm wide at the distal end, and 24 mm at the proximal. The bone is twisted at the proximal end to provide a flat surface against which metatarsal II would have pressed closely. The dorsal and medial surfaces are heavily scarred proximally. Matrix covers the lateral collateral fossa and most of the medial collateral fossa. The proximal articular end is wider than the distal, as in *Plateosaurus*, but the reverse of the condition in *Massospondylus* (LJ, pers. obs.). The distal end bears a symmetrical articular face, surmounted by a triangular depression on the dorsal surface. The proximal articular end has a subtriangular outline, as seen in *Massospondylus* (Cooper, 1981:fig. 75), but BRSMG Ca7451a is more slender than metatarsal III of that genus. A second preserved metatarsal, BRSMG Ca7499, has an undetermined pedal position.

Several pedal phalanges exist but most do not vary markedly from those of the manus. A possible pedal ungual phalanx

(BRSMG Ca7451b) occurs in the same block as the above-mentioned metatarsal III (Fig. 18Q). This ungual is strongly curved, but smaller than the manual ungual, BRSMG Cb4187. Several possible pedal phalanges exist in the collections: BRSMG C7499 (Fig. 18R, S) shows the broad roller-like distal end, and a laterally-placed ligament pit. ANSP 9861 (Fig. 18T) represents an additional ungual phalanx, approximately 23 mm long and most likely from the pes. There is a marked lateral groove for the claw sheath.

#### VARIATION

##### Sexual Dimorphism in the Durdham Down Sample

In their extensive reviews of *Thecodontosaurus* material, both Seeley (1895) and Huene (1908a) suggested that there were at least two species, based on variations in the material. Huene (1908a:214–216) assigned some elements to *T. antiquus*, and others to *T. cylindrodon*. The need for such a distinction was based on the differentiation of the teeth from Durdham Down, the leaf-shaped teeth of *Thecodontosaurus antiquus*



FIGURE 17. Left tibia of *Thecodontosaurus antiquus* Morris, 1843, named mistakenly as type specimen of *Agrosaurus macgillivrayi* Seeley, 1891, BMNH 49984, in lateral (A), anterior (B), medial (C), and posterior (D) views. Scale bar equals 10 mm.

Morris, 1843, the cylindrical pointed teeth of *Paleosaurus cylindrodon* Riley and Stutchbury, 1836, and the broad teeth of *P. platyodon* Riley and Stutchbury, 1836. This last species is based on teeth of a phytosaur (see above).

Huene (1908a:214–216) ascribed the two dinosaurian tooth types to *Thecodontosaurus*, and he associated with them the postcranial remains from Durdham Down by analogy with the dentition and skeletons of the more complete Late Triassic dinosaurs *Plateosaurus poligniensis* from France and *P. reinigeri* from Germany. He argued that the *T. antiquus* teeth were very like those of *P. poligniensis*, and those of *T. cylindrodon* like those of *P. reinigeri*. Since *P. poligniensis* had a more gracile skeleton than *P. reinigeri*, so *T. antiquus* presumably had a more gracile skeleton than *T. cylindrodon*. Huene's criteria for differentiation of the postcranial remains were: (1) *T. antiquus* has more 'lightly built' limb bones than *T. cylindrodon*, which are 'more plumply built'; and, (2) limb bones of *T. antiquus* are commoner than those of *T. cylindrodon*.

In his overview, Huene (1908a:215–216) ascribed 44 appendicular elements to *T. antiquus* and nine to *T. cylindrodon*. Many of these elements were lost in the World War II bombing, and only two robust elements, BRSMG Ca7481, a scapula, and BRSMG Ca7456, a femur (now incomplete), survive, together with rather more of the gracile specimens.

The robust bones described by Huene (1908a:215–216) include a scapula, a humerus, three femora, a tibia, and a fibula. The scapula (BRSMG Ca7481) is larger, stouter, and less curved, and its narrowest part is relatively more distal in position than in the scapulae of the gracile form. The humerus of the robust form has a relatively broader proximal part, a thicker shaft, and the deltopectoral crest extends further distally, but projected less anteriorly, than in the humeri attributed to the gracile form. The femora, including BRSMG Ca7456, have a somewhat smaller lesser trochanter, a larger and stronger fourth

trochanter, the distal part of the shaft is straighter, and the distal end is transversely broader compared to the other femora. The tibia has a somewhat stronger shaft, but the proximal end is transversely narrower and the condyles are shaped differently compared to the other tibiae. The proximal end of an associated fibula has no distinguishing characters.

The variation in the postcranial bones from Durdham Down could be ascribed to specific differences, as Seeley (1895) and Huene (1908a) argued, but the variation could also be a result of sexual dimorphism (Galton, 1997), allometry (growth-related shape change), or individual variation. Allometric variation is ruled out because the gracile and robust forms are of essentially the same size. The shape differences could represent individual variation, but this idea is also hard to sustain in the face of evidence that there were two morphs of *Thecodontosaurus*, and not a continuum of forms. The two morphs could then represent different species, or they could be males and females. Among vertebrates, a distinction into gracile and robust forms is often an indication of sexual dimorphism. By analogy with *Plateosaurus* (Weishampel and Chapman, 1990; Galton, 1997), the variation seen in *Thecodontosaurus* is probably sexual dimorphism. It is debatable whether the more robust animal was a male or female (males are often larger, for reasons of display and fighting, but female reptiles may be larger because of the rigors of egg production).

The possibility of two species of *Thecodontosaurus* cannot be excluded, but, in the absence of any distinguishing character, other than relative proportions, all material from Durdham Down is referred to one species, *T. antiquus*. The only evidence in favor of two species, and against sexual dimorphism, is that robust individuals appear to be much rarer than gracile: 9 elements to 44, according to Huene (1908a). If two species were present, it is unlikely that Huene's (1908a:214–215) argument that the robust one should be called *T. cylindrodon* can be sustained. *Paleosaurus cylindrodon* Riley and Stutchbury, 1836, was based on a tooth, and the name should be restricted to that specimen (see above).

#### Juvenile Specimen from South Wales

Kermack (1984) reported a small prosauropod dinosaur from Pant-y-ffynnon Quarry, South Glamorgan, South Wales, as a possible juvenile *Thecodontosaurus* sp. The remains allowed her to reconstruct the skull and skeleton, and her account has been used as indicative of the anatomy of *Thecodontosaurus*. The assignment to this genus, and the assumption that the Welsh specimen is equivalent to *T. antiquus* must be tested. The juvenile came from a fissure deposit dated as tentatively Norian (Benton and Spencer, 1995:82), and most likely Late Triassic. It is not possible at present to date the fissure fills at Pant-y-ffynnon or Durdham Down more precisely.

Kermack's (1984) conclusion that the specimen is a juvenile seems justified. The centra and neural arches of the cervical vertebrae are not fused, and some of the long bones show rugose articular surfaces, evidence that the cartilage had not entirely turned to bone. The skull and orbit are relatively large in comparison to other prosauropods. When restored, the Welsh prosauropod is about 1 m long, as compared to a length of about 2.5 m for a typical (adult) *T. antiquus*. (The Durdham Down material is treated as belonging to adult animals since neural arches are fused to centra with no obvious joint, and there are no limb bones with unfused articular ends. Among the surviving material, and that described by Huene [1908a] and others, there were no unusually larger specimens. This precludes the possibility that the Durdham Down *Thecodontosaurus* material could consist of juveniles of a larger prosauropod such as *Sellosaurus* from the Norian of Germany.)

There are some difficulties in comparing the Welsh prosau-

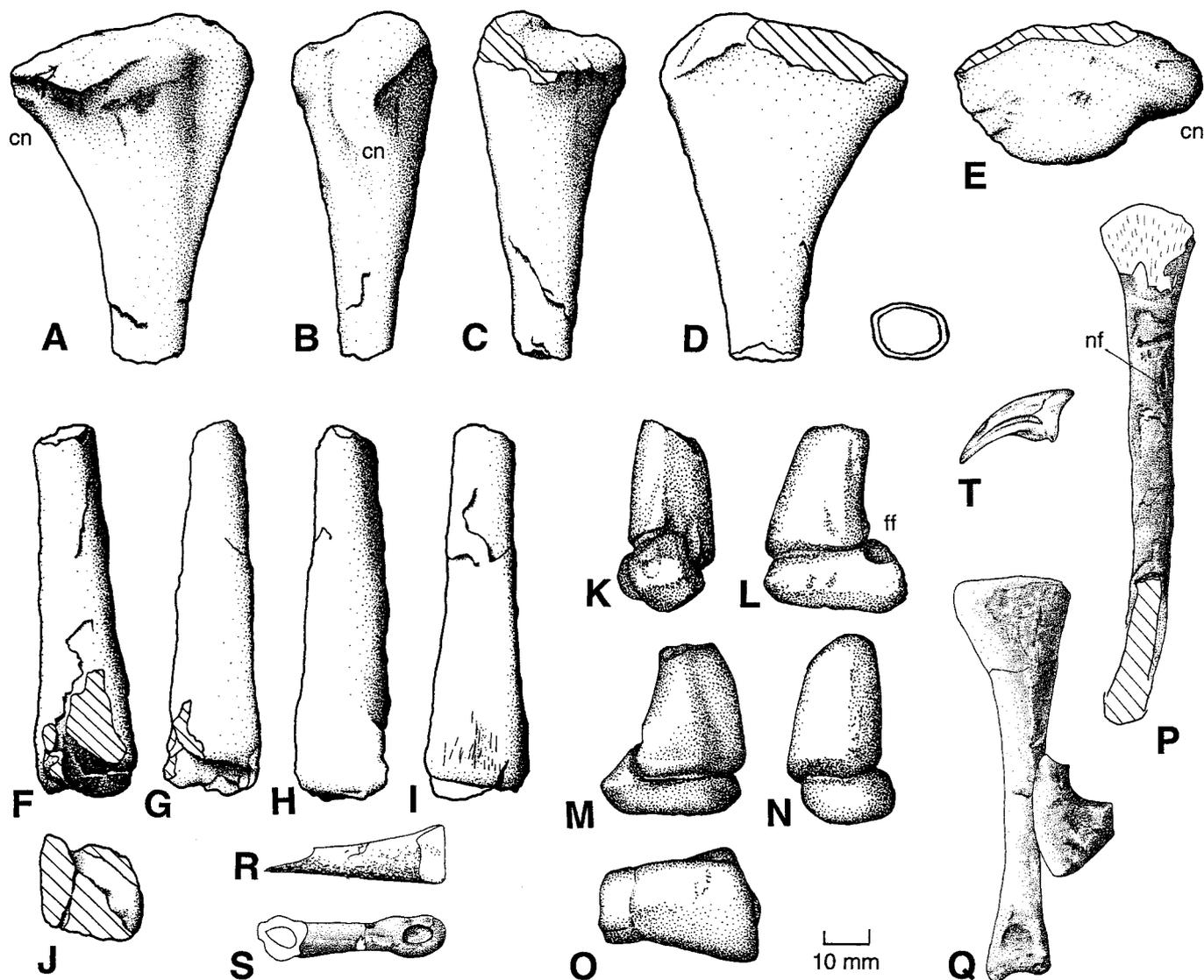


FIGURE 18. Hindlimb bones of *Thecodontosaurus antiquus* Morris, 1843. A–E, proximal end of right tibia, BRSMG C4531, in medial (A), anterior (B), posterior (C), lateral and cross-sectional (D), and proximal (E) views; F–J, distal end of right tibia, BRSMG Ca7495, in lateral (F), anterior (G), posterior (H), medial (I), and distal (J) views; K–O, distal end of tibia with astragalus in place, YPM 2192, in lateral (K), anterior (L), posterior (M), medial (N), and distal (O) views; P, right fibula, BRSMG Ca7497, in medial view; Q, third right metatarsal, in dorsal view, and isolated pedal claw, BRSMG Ca7451; R, S, possible pedal phalanx, in ventral (R) and lateral (S) views; T, isolated pedal claw, ANSP 9861. **Abbreviations:** cn, cnemial crest; ff, fibular facet on astragalus; nf, nutritive foramen.

ropod and *T. antiquus*. The juvenile specimen shows some parts not seen in the Durdham Down *T. antiquus*, such as much of the skull and the foot, while other parts are missing, such as the forearm and hand, the dorsal vertebrae, and parts of the pelvis and femur. The braincases are comparable, both showing the primitive high position of the parasphenoid, in line with the base of the occipital condyle, unlike in other prosauropods. The dentary and its teeth also appear to be nearly identical. The cervical and caudal vertebrae appear comparable. According to the restorations, both the Welsh juvenile and *T. antiquus* apparently share the primitive long hindlimb (clearly longer than the trunk), a feature lost in other prosauropods, where the hindlimb is relatively shorter. However, note that the trunk length in the juvenile *Thecodontosaurus* is estimated since dorsal vertebrae are absent. So far as can be seen, the scapula, humerus, ilium, femur, and lower limb elements are all comparable.

The Welsh juvenile shows all three diagnostic characters of

*T. antiquus*: the elongate basiptyergoid processes, the relatively short dentary, and the squared posterior process of the ilium. We accept, therefore, that the Welsh specimens are correctly assignable to *Thecodontosaurus*, but comparative materials are insufficient to decide whether they belong to *T. antiquus* or to another species.

#### RECONSTRUCTION

*Thecodontosaurus antiquus* from Durdham Down was reconstructed by Huene (1932:pl. 54, fig. 1) on the basis of the extensive collections available to him. Kermack (1984) was also able to reconstruct the juvenile *Thecodontosaurus*, and her illustration has been used recently as an indication of the appearance of *Thecodontosaurus* (e.g., Galton, 1990).

We felt that the surviving specimens of *Thecodontosaurus antiquus*, together with earlier descriptions of specimens now

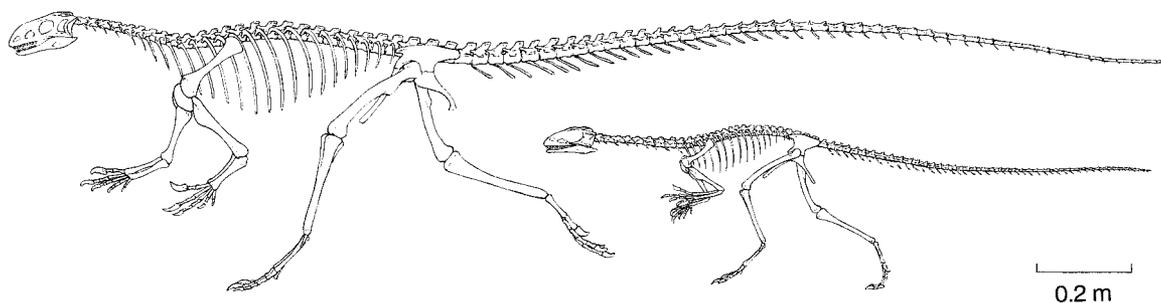


FIGURE 19. Reconstruction of the skeleton of an adult and juvenile *Thecodontosaurus antiquus*. The adult is based on the Durdham Down material, and on a reconstruction by Huene (1932:pl. 54, fig. 1), based on much more extensive material. The juvenile is taken from Kermack (1984). Drawing by John Sibbick.

lost (especially Huene, 1908), would provide adequate material for a new reconstruction of the adult skeleton. The surviving specimens, described here, include some associated material, a relatively complete arm (Figs. 12, 13), some associated vertebrae (Figs. 8, 9M), and associated ilium and femur (Fig. 14A, B). The scapulocoracoid has been restored (Fig. 10C), and much of the sacrum, pelvis, and hindlimb are available. Huene (1932) showed *Thecodontosaurus* in a low walking pose, with all four limbs on the ground. Careful study of his reconstruction, and measurement of surviving specimens, and of those he described earlier (Huene, 1908a) has shown the general accuracy of his reconstruction.

In our reconstruction (Fig. 19), the skull, foot, and tail are largely conjectural. In reconstructing the skull, *Plateosaurus* has been used as a general model. The neotype dentary (Fig. 3) formerly extended to the anterior margin of the mandibular fenestra (Fig. 3B), which probably lay in the posterior third of the mandible. The length of the dentary is about 70 mm, hence giving a total mandible length of perhaps 140 mm. The vertebral column in *Plateosaurus* consists of the proatlas plus 10 cervicals, 15 dorsals, 3 sacrals, and about 50 caudals, and similar figures are found in other prosauropods (Galton, 1990). These figures are assumed for *Thecodontosaurus*. Cervicals measure 17–28 mm long (herein; Huene, 1908a:197), so the neck is reconstructed as 220 mm long in all, with vertebral length increasing to cervicals 7–8, and then declining slightly to the shoulder region. Dorsal centra are 28–40 mm long, but normally 35 mm or less (herein; Huene, 1908a:197–199), with the anterior five or six dorsals and the last one or two presumably shorter than the others, as in *Plateosaurus*. This gives a dorsal column length of about 500 mm. Sacrals 1 and 2 measure 37 and 43 mm long respectively, and the missing sacral 3 is estimated at 40 mm, giving a total sacrum length of 120 mm. Anterior caudals vary from 23–40 mm in length, and mid-series and more posterior caudals, 28–35 mm (herein; Huene, 1908a: 201–203). With an assumed total of some 50 caudal vertebrae, the tail of adult *Thecodontosaurus* must have been about 1.5 m long. This gives a total body length of 2,450 mm, hence about 2.5 m, of which 1.5 m is tail.

The limbs can be reconstructed with some confidence. Measurements of the shoulder girdle and forelimb, taken from various specimens, including the articulated forelimb, YPM 2195 (Figs. 11–14) indicate a scapulocoracoid 180 mm deep, a humerus 160 mm long, an ulna 95 mm long, and a hand 110 mm long. The pelvis is based on isolated remains. Estimated length of the dorsal iliac blade is 100 mm, and pubis length 135 mm. The femur is 210 mm long (Fig. 16B), and the tibia 205 mm (Fig. 17). The length of the foot is estimated at 190 mm, based on other prosauropods.

## RELATIONSHIPS

### *Thecodontosaurus* as a prosauropod

The Durdham Down material of *T. antiquus* is clearly saurischian. It shows diagnostic characters of inclusive clades (Gauthier, 1986; Benton, 1990; Sereno, 1991; Juul, 1994; Novas, 1996) (Characters indicated with an asterisk [\*] are unknown in the topotype *T. antiquus*, but are seen in the juvenile *Thecodontosaurus* sp.; Kermack, 1984.):

1. Dinosauromorpha: femoral proximal head subrectangular and distinctly offset, astragalar ascending flange on anterior face of tibia, astragalar anteromedial corner acute, midshaft diameters of metatarsals I and V less than II–IV\*.

2. Dinosauriformes: centra of cervical vertebrae parallelogram-shaped, femoral head articular surface extends under head, femoral lesser (anterior) trochanter weakly developed.

3. Dinosauria: quadrate head exposed in lateral aspect\*, deltopectoral crest elongate and with apex situated at a point corresponding to more than 38% down the length of the humerus, brevis shelf on ventral surface of postacetabular part of ilium, acetabulum extensively perforated, tibia with posterolateral flange and receiving depression on dorsal aspect of astragalus, astragalar ascending flange on anterior face of tibia.

4. Saurischia: jugal overlaps lacrimal\*, presence of hyposphene–hypantrum articulations in dorsal vertebrae, robust saurischian thumb (metacarpal I robust and half or less the length of metacarpal II, first phalanx longer than metacarpal I or any other phalanx in the hand, ungual phalanx I much larger than other unguals).

*Thecodontosaurus* has generally been identified as a prosauropod, and it has been compared with other prosauropods such as *Anchisaurus* and *Plateosaurus*. In cladistic analyses, *Thecodontosaurus* has occupied a basal position among prosauropods (Gauthier, 1986; Galton, 1990). However, in assessing the relationships of *Thecodontosaurus*, it is necessary to widen the ingroup to include all sauropodomorphs (i.e., prosauropods plus sauropods), since the nature of the ‘Prosauropoda’ is disputed.

### The Prosauropoda

Prosauropods are either a paraphyletic group forming a stem group to Sauropoda (Colbert, 1964; Charig et al., 1965; Gauthier, 1986; Benton, 1990), or a monophyletic group forming a sister clade to Sauropoda (Sereno, 1989, 1997, 1998; Galton, 1990; Gauffre, 1995; Upchurch, 1995, 1998; Wilson and Sereno, 1998). So far, a full cladistic analysis of basal sauropodomorphs has not been published, although Sereno (1989, 1997, 1998; Wilson and Sereno, 1998) and Gauffre (1995) report their unpublished results.

In the cladistic analysis, a number of reasonably completely

TABLE 1. Prosauropod taxa considered in the cladistic analysis. Main synonyms are indicated, from Van Heerden (1979), Cooper (1981), and Galton (1990), and the main references for anatomical data are given. In addition, the authors have studied all the named taxa first hand. Taxa are listed in order of establishment.

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<i>Thecodontosaurus</i> Riley and Stutchbury, 1836 (Huene, 1908a; this paper) (= <i>Palaeosauriscus</i> (pars), <i>Palaeosaurus</i> (pars), <i>Rileya</i> (pars), <i>Rileyasuchus</i> (pars))
<i>Plateosaurus</i> Meyer, 1837 (Huene, 1926; Galton, 1984b, 1985c, 1990) (= <i>Dimodosaurus</i> , <i>Dinosaurius</i> , <i>Gresslyosaurus</i> , <i>Pachysauriscus</i> , <i>Pachysaurops</i> , <i>Pachysaurus</i> )
<i>Massospondylus</i> Owen, 1854 (Cooper, 1981; Attridge et al., 1985; Gow, 1990; Gow et al., 1990) (= <i>Aetonyx</i> , <i>Aristosaurus</i> , <i>Dromicosaurus</i> , ? <i>Gryponyx</i> , <i>Gyposaurus</i> , ? <i>Hortalotarsus</i> , ? <i>Leptospondylus</i> , ? <i>Pachospondylus</i> )
<i>Euskelosaurus</i> Huxley, 1866 (Van Heerden, 1979) (=? <i>Eucnemesaurus</i> , ? <i>Orinosaurus</i> , <i>Orosaurus</i> , <i>Plateosauravus</i> )
<i>Anchisaurus</i> Marsh, 1885 (Galton, 1976; Galton and Cluver, 1976) (= <i>Amphisaurus</i> , <i>Gyposaurus</i> , <i>Megadactylus</i> , <i>Yaleosaurus</i> )
<i>Sellosaurus</i> Huene, 1908 (Galton, 1973, 1984a, 1985a; Galton and Bakker, 1985) (= <i>Efraasia</i> )
<i>Melanorosaurus</i> Houghton, 1924 (Houghton, 1924; Heerden and Galton, 1997)
<i>Lufengosaurus</i> Young, 1941 (Young, 1941, 1951) (= <i>Fulengia</i> , <i>Tawasaurus</i> )
<i>Yunnanosaurus</i> Young, 1942 (Young, 1942, 1951)
<i>Riojasaurus</i> Bonaparte, 1969 (Bonaparte, 1972) (= <i>Strenusaurus</i> )
<i>Coloradisaurus</i> Lambert, 1983 (Bonaparte, 1978) (= <i>Coloradia</i> )

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known prosauropod taxa were considered (Table 1). Over the years, dozens of genera and species have been named, most based on entirely inadequate material, and these have been heavily synonymised (Galton, 1990). In the end, *Lufengosaurus* and *Yunnanosaurus* had to be omitted from the analysis since it is not clear whether the two genera are truly distinct or not, nor which of the material from the Lufeng Formation belongs to which of the two taxa (cf. Young, 1941, 1942, 1951).

In the present analysis, two outgroups were selected, the basal avemetatarsalian *Scleromochlus*, sister group to Ornithodira (Benton, 1999), and the early non-sauropodomorph dinosaur *Herrerasaurus* (Serenó and Novas, 1992, 1993; Novas, 1993; Sereno, 1993). Sauropods included were *Vulcanodon* (Raath, 1972; Cooper, 1984), *Barapasaurus* (Jain et al., 1975, 1979), *Shunosaurus* (Zhang, 1988), and *Brachiosaurus* (Riggs, 1904; Janensch, 1935, 1936, 1950). The four sauropod genera are included simply to represent the crown clade Sauropoda, and not to test the monophyly of that group, nor of Eusauropoda, which has been demonstrated unequivocally elsewhere (Upchurch, 1995, 1998; Salgado et al., 1997; Wilson and Sereno, 1998).

### Characters

Some previous publications (e.g., Gauthier, 1986; Dodson, 1990; Galton, 1990) list various supposedly diagnostic characters of Sauropodomorpha and Prosauropoda. However, some of these characters, such as proportions of limb bones and girdles, are probably size-related, and such attributes have been omitted here as far as possible. This is important especially in trying to resolve the relationships of the large prosauropods, such as *Riojasaurus* and *Melanorosaurus*, to other, smaller, prosauropods, and to the sauropods. In addition, Galton (1990) lists some characters for Prosauropoda, and clades within Prosauropoda, which are present in the outgroup, such as losses and reductions of digits, and other characters with imprecise definitions. These are either omitted or reformulated here.

The characters are listed (Appendix 2) in anatomical order, from the premaxilla to the toes, rather than according to their placement as synapomorphies in the cladistic hierarchy. This anatomical sequence makes it easier to find specific characters, and it implies no expected phylogenetic solution. Characters were scored for the 15 selected taxa based on original specimens and on published descriptions of *Herrerasaurus* and *Shunosaurus*, which we have not seen. Inevitably, many of the characters used here are modified from anatomical work by

previous authors, including Charig et al. (1965), Gauthier (1986), Sereno (1989), and Upchurch (1995). As the data matrix (Appendix 3) indicates, some taxa could be coded completely, while others (*Euskelosaurus*, *Coloradisaurus*, *Vulcanodon*, *Barapasaurus*) lacked significant portions of their skeletons. Codings for *Thecodontosaurus* come from the Durham Down material described here, except for characters 1–7, 9–11, 16, 35, and 49, which were coded from the South Wales juvenile of *Thecodontosaurus* sp.

### Phylogenetic Analysis

The data matrix (Appendix 3) was analysed with PAUP 3.1.1 (Swofford, 1993), using the branch-and-bound search option. The first run of all the data yielded 42 equally most parsimonious trees (15 taxa, 49 characters, tree length 83, consistency index 0.651, homoplasy index 0.349, rescaled consistency index 0.484). The strict and Adams consensus solutions from these 42 trees showed a number of poorly resolved nodes. In the strict consensus, all prosauropods formed an unresolved multitomy. The Adams consensus sorted out an unresolved basal grouping of *Euskelosaurus* and *Coloradisaurus*, with the other prosauropod taxa, and these remaining prosauropod taxa were sorted into a subgroup consisting of *Massospondylus*, *Melanorosaurus*, and *Riojasaurus*, and a pairing of *Plateosaurus* and *Sellosaurus*, with *Anchisaurus* and *Thecodontosaurus* as successive outgroups.

The trees were then assessed according to Wilkinson's 'safe deletion rules' (Wilkinson, 1992; Wilkinson and Benton, 1996). The data matrix (Appendix 3) showed no autapomorphies, nor were any taxa redundant. The Adams consensus tree was then examined, and taxa contributing to multitomies were experimentally deleted in order to produce a reduced Adams consensus tree (Wilkinson, 1994), a tree with the advantages of being fully resolved, of being a 'real' tree and not a construct which contains information from a variety of solutions, and of minimising the number of deletions. After some manipulations, it turned out that only *Riojasaurus* had to be deleted. On re-running the data matrix without *Riojasaurus*, a single most parsimonious tree (Fig. 20A) was found (14 taxa, 49 characters, tree length 77, consistency index 0.701, homoplasy index 0.299, rescaled consistency index 0.549).

This tree was assessed using bootstrapping (1000 replicates), and most of the nodes collapsed at this point (Fig. 20B), since few of them were supported in more than 50% of bootstrap

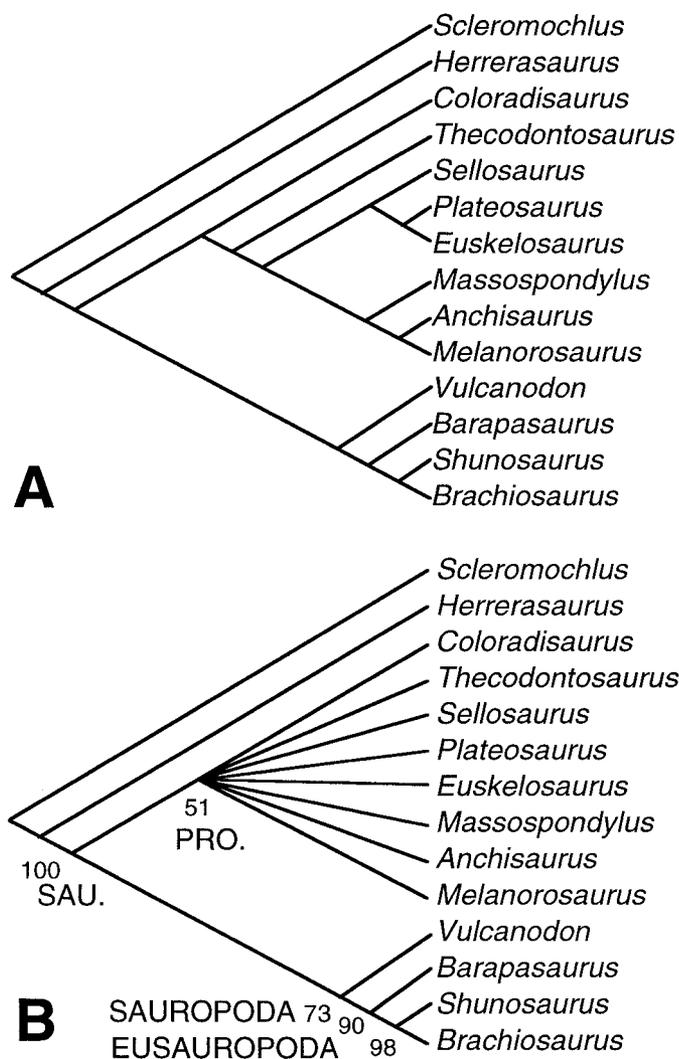


FIGURE 20. Cladograms showing the relationships of *Thecodontosaurus* and other basal sauropodomorphs. **A**, the single most parsimonious cladogram based on an analysis of 14 taxa and 49 characters (tree length 77, consistency index 0.701, homoplasy index 0.299, rescaled consistency index 0.549). **B**, bootstrapping (1,000 replicates) shows, however, that most of the nodes are poorly resolved, and only Sauropodomorpha, Prosauropoda, Sauropoda, an unnamed taxon consisting of *Barapasaurus* + Eusauropoda, and Eusauropoda, achieve bootstrap support of close to, or more than, 50%. **Abbreviations:** PRO, Prosauropoda, SAU, Sauropodomorpha.

replicates. The best-supported node was Sauropodomorpha, with 100% support, followed by Eusauropoda (*Shunosaurus* + *Brachiosaurus*), with 98% support, the unnamed clade (*Barapasaurus* + Eusauropoda), with 90% support, Sauropoda, with 73% support, and Prosauropoda, with 51% support. The conclusions are summarized in Appendix 4, only so far as the nodes with more than 50% bootstrap support are concerned.

#### DISCUSSION

The proposition that Prosauropoda is monophyletic, recently accepted by most workers (Serenó, 1989, 1997, 1998; Galton, 1990; Gauffre, 1995; Wilson and Sereno, 1998) rests on rather weak ground according to the current study. Sereno (1989) noted only two characters diagnostic of Prosauropoda, marked torsion in the first phalanx of manual digit I (character 27 here)

and an unusual carpal–metacarpal articulation that involves inset of the base of metacarpal I into the carpus. The latter character was not used since we could not determine it in the taxa under study. More characters diagnostic of Prosauropoda are required to confirm the proposition of unequivocal monophyly.

In the past, the Prosauropoda has been divided into a number of families, and Galton (1990:336–337) presented a listing in which he accepts seven: Thecodontosauridae, Anchisauridae, Massospondylidae, Yunnanosauridae, Plateosauridae, Melanorosauridae, and Blikanasauridae. Most of these families contain one genus only, except Plateosauridae (*Ammosaurus*, *Mussaurus*, *Plateosaurus*, *Sellosaurus*, *Coloradisaurus*, *Euskelosaurus*, *Lufengosaurus*) and Melanorosauridae (*Camelotia*, *Melanorosaurus*, *Riojasaurus*). Gauffre (1995) reported a different result, with two major prosauropod clades, (*Euskelosaurus* (*Massospondylus* (*Sellosaurus* (*Plateosaurus* + *Coloradisaurus*))), and (*Lufengosaurus* (*Yunnanosaurus* (*Riojasaurus* (*Anchisaurus* + *Ammosaurus*)))) Sereno (1997, 1998), reporting his unpublished cladogram, divides prosauropods into two main families, Massospondylidae (*Massospondylus*, *Yunnanosaurus*), with low skulls, and Plateosauridae (*Plateosaurus*, *Sellosaurus*, *Lufengosaurus*), with dropped jaw joints, and with *Riojasaurus* as outgroup to those two.

Unfortunately, the cladistic analysis carried out here does not resolve relationships within Prosauropoda. None of the previous proposals for subdivision of Prosauropoda gains adequate support in the present analysis. For example, the proposition that *Thecodontosaurus* is plesiomorphic to all other sauropodomorphs (Gauthier, 1986; Benton, 1990) is supported by only 22% of bootstrap replicates. The Family Plateosauridae of Galton (1990) is also poorly supported: *Plateosaurus* and *Euskelosaurus* are paired in 38% of bootstrap replicates, and those two with *Sellosaurus* in 20% of replicates. Sereno's two families cannot be assessed here since neither of the Chinese genera, *Lufengosaurus* or *Yunnanosaurus*, was included in the current analysis because of extreme ambiguity about the composition of each taxon. Galton's (1990) other prosauropod families cannot be assessed, since they either consist of single genera, or they include only one codable genus together with other more poorly known forms.

The results of Gauffre (1995) and Sereno (1997) are presented without character data, or measures of homoplasy or robustness, and so they cannot be assessed. Our study, and the difficulties we had in establishing any strong pattern of character distribution among prosauropod taxa, suggests that the unpublished cladograms by Gauffre (1995) and Sereno (1997) are probably far from robust.

Experiments were made with the present data set in an attempt to find some robust nodes among the prosauropod taxa. If the four sauropod taxa are excluded, and the PAUP analyses re-run, three clades emerge in the Reduced Adams Consensus (RAC) tree: *Thecodontosaurus* is outgroup to all other prosauropods, whose relationships are unresolved, except for a strong pairing of *Plateosaurus* and *Euskelosaurus*. *Thecodontosaurus* is strongly indicated as the basal taxon (in 99% of 1,000 bootstrap replicates). *Plateosaurus* and *Euskelosaurus* pair off in 51% of bootstrap replicates, but no other phylogenetic arrangement achieves a bootstrap score of over 50%.

A standard view of prosauropod evolution was that the melanorosaurids, like *Melanorosaurus* and *Riojasaurus* were a well defined clade close to Sauropoda (e.g., Gauthier, 1986; Benton, 1990). However, none of the recent cladistic studies supports this view. The RAC study shows that *Riojasaurus* is a 'rogue' taxon in certain ways; at least, it was the single taxon which, when excluded, allowed the cladogram to resolve fully from 42 trees to one tree. Perhaps if *Melanorosaurus* were better known, a Family Melanorosauridae might be established. Character codings for *Riojasaurus* do not show any close alli-

ance with any of the other prosauropods; its large size may be a confusing factor, but purely size-related and proportional characters were excluded from consideration in the present study specifically in order to avoid confusions of this kind.

#### ACKNOWLEDGMENTS

We thank Roger Clark and Roger Vaughan at Bristol City Museum for access to specimens, and for their patience over several years of our studies. We are grateful to former curators at Bristol City Museum, Peter Crane and Peter Crowther, for help in earlier years. We also thank J. H. Ostrom, M. A. Turner, and C. L. Chandler at the Peabody Museum and Ted Daeschler at the Academy of Natural Sciences, Philadelphia for their help. The drawings were made by MJB, LJ, PMG, and Richard Dury (Bristol specimens), Mary Beth Danielak (Fig. 6) and Pam Bal-daro and Emma Koch (other Peabody Museum specimens). Michael Quinn and Simon Powell printed the photographs. We especially thank John Sibbick for the reconstruction drawing. We thank the Department of Earth Sciences, University of Bristol and Cincinnati Museum of Natural History for funding artwork, the Dinosaur Society for funding preparation of ANSP and YPM specimens, YPM (1969) and NSF grant DEB 81-01969 for funding travel by PMG, and the Danish Academy for funding work by LJ. We thank Peter Dodson, Axel Hungerbühler, Ollie Rauhut, Paul Upchurch, and especially Jeffrey Wilson, for helpful comments on the MS.

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Received 29 June 1998; accepted 10 May 1999.

APPENDIX 1. Listing of the specimens of *Thecodontosaurus antiquus* at Bristol City Museum (formerly BCM; now BRSMG), indicating their original numbers, their identity, their status (lost in World War II or extant), their current register numbers, as used in this paper, and figures by Huene (1908a), the most comprehensive earlier description. Paralectotype materials, those figured by Riley and Stutchbury, 1840) are indicated with an asterisk (\*). Figures in Seeley (1895) and Huene (1914) are also noted. In addition, the collections in the Natural History Museum, London (BMNH), the Peabody Museum, New Haven (YPM), and the Academy of Natural Sciences, Philadelphia (ANSP) are given. The YPM specimens were originally given accession numbers 1979, 2001, and 2105, but have been renumbered.

Original BCM number	BRSMG number and current status	Identity	Figure in Huene (1908a)	Other figures—Seeley (1895), Huene (1914)
1	*Ca7465 (lost)	Right lower jaw	Fig. 206, 208; Pl. 76, fig. 3	
2	C4529	Left lower jaw	Fig. 207; Pl. 76, fig. 2	
4	*Ca7449 (lost)	Tooth	Fig. 266	
5	Ca7496	Distal fibula	Pl. 88, fig. 5	
8	*C4533	Anterior caudal vertebra		
9	Ca7470 (lost)	Dorsal vertebra	Pl. 78, fig. 4	
11	Cb4153	Dorsal vertebra		
12	Cb4154	Dorsal vertebra		
13	Ca7469 (lost)	Dorsal vertebra	Pl. 78, fig. 2	
14	Ca7468 (lost)	Dorsal vertebra	Pl. 78, fig. 1	
15	Cb4155	Dorsal vertebra		
15a	Cb4156	Dorsal vertebra		
16	Ca7472 (lost)	Cervical vertebra	Pl. 78, fig. 5	
16	Ca7473	Caudal vertebra	Pl. 78, fig. 6	
16	Ca7474	Caudal vertebra	Pl. 78, fig. 7	
17	*Ca4532a	Caudal vertebra	Pl. 78, fig. 10	
17	Ca4532b	Caudal vertebra		
17	C4532c	Chevron	Pl. 78, fig. 11	
18	Ca7510	Three caudal vertebrae	Fig. 220	
20	Ca7471 (lost)	Dorsal vertebra	Pl. 78, fig. 3	
20	Ca7509 (lost)	Distal caudal vertebrae	Fig. 218a	
21	Ca7508 (lost)	Distal caudal vertebrae	Fig. 218b	
22	Ca7475	Caudal vertebra	Pl. 78, fig. 8	
23	Ca7507	Caudal vertebra	Fig. 217	
25	Cb4163a, b	Two dorsal vertebrae		
26	*Ca7452 (lost)	Vertebral centrum	Fig. 212	
27	Cb4164a, b	Two caudal vertebrae		
29	Cb4166	Caudal vertebra		
30	*C4534	Proximal chevron	Formerly <i>T. platyodon</i>	
32	*C4528	Proximal rib	Pl. 77, fig. 3	
34	Cb4169	Rib		
35	Ca7466	?Distal chevron	Pl. 77, fig. 5	
37	Ca7477 (lost)	Proximal rib, humerus, femur	Pl. 78, fig. 12	1895:fig. 9
37	Ca7477 (lost)	Right humerus	Pl. 81, fig. 2	
37	Ca7477 (lost)	Proximal right femur	Pl. 85, fig. 3	

## APPENDIX 1. (Continued.)

Original BCM number	BRSMG number and current status	Identity	Figure in Huene (1908a)	Other figures—Seeley (1895), Huene (1914)
38	Ca7503 (lost)	Proximal metatarsal, ribs	Fig. 234	
41	Cb4174a, b	Two caudal vertebrae		
42	Ca7502 (lost)	Left fibula (?)		1895:fig. 6
44	Lost	Femur		
46	*Ca7459 (lost)	Left ulna	Fig. 223; Pl. 82, fig. 3	1895:fig. 10
46b	*Ca7485	Phalanx	Fig. 224; Pl. 81, fig. 7	
47	Ca7497	Right fibula	Pl. 88, fig. 6	
49	Cb4177	Proximal left femur		
52	Ca7504	Radius	Formerly <i>T. platyodon</i>	
53	Ca7495	Distal right tibia	Pl. 88, fig. 4	1895:fig. 5
54	Cb4179	Metacarpal impression		
55	Ca7499	Distal metatarsal	Pl. 90, fig. 3	
56	Ca7484 (lost)	Metacarpal	Pl. 81, fig. 6	
57	Ca7460 (lost)	Left ilium	Fig. 225; Pl. 82, fig. 4	
58	Cb4180	?Partial right ilium		
59	Ca7476 (lost)	Caudal vertebra, pubis	Pl. 78, fig. 9	
59	Ca7476 (lost)	Claw phalanx, ilium, vertebra	Pl. 90, fig. 5	
60	Ca7506 (lost)	Damaged right ilium	Fig. 227	
61	*Ca7450 (lost)	Damaged left ilium	Fig. 226	
63	Ca7457 (lost)	Two ilia, fibula, left tibia, rib, caudal vertebra	Pl. 84	1895:figs. 1–3
66	*Ca7453 (lost)	Right humerus	Pl. 81, fig. 1	
67	*Ca7456 (damaged)	Left femur	Pl. 87	
68	Ca7491 (lost)	Proximal left femur	Fig. 231; Pl. 86, fig. 1	1895:fig. 4
69 I	*Ca7492 (lost)	Distal left femur	Fig. 232; Pl. 86, fig. 2	
69a	Ca7494	Distal right femur	Pl. 88, fig. 1	
70	Ca7493 (lost)	Distal left femur	Pl. 86, fig. 3	
71	Ca7490 (lost)	Distal right femur	Pl. 85, fig. 5	
72	Cb4183	Distal left femur		
73	C4530	Distal right femur	Pl. 85, fig. 4	
76	*Ca7462 (lost)	Right tibia	Pl. 88, fig. 2	
77a	C4531	Proximal right tibia	Pl. 88, fig. 3	
77b	Ca7513 (lost)	?Distal ischium	Fig. 229	
79	Ca7486	Right ulna	Pl. 82, fig. 1	
80	Ca7482	Three metacarpals	Pl. 81, fig. 4	
81	*Ca7451	Metatarsal and claw	Pl. 90, fig. 1	
82	Ca7483 (lost)	Metacarpal	Pl. 81, fig. 5	
83	Ca7498 (lost)	Metatarsal	Pl. 90, fig. 2	
84	Cb4187	Ungual phalanx		
85	Ca7487 (lost)	Radius, jaw, claw	Pl. 82, fig. 2	
86	*Ca7455 (lost)	Claw phalanx	Pl. 90, fig. 7	
87	*Ca7454 (lost)	Claw phalanx	Fig. 235	
88	*Ca7463 (lost)	Phalanx	Pl. 90, fig. 4	
89	Ca7479 (lost)	Left scapula and coracoid	Fig. 221; Pl. 79, fig. 2	
90	Ca7480 (lost)	Left scapula	Pl. 79, fig. 3	
91	Ca7481	Right scapula	Pl. 80, fig. 1	
92	Ca7478 (lost)	Left scapula and coracoid	Pl. 79, fig. 1	
93	Ca7512 (lost)	Left humerus	Fig. 222	
94	Cb4188	Proximal tibia		
95, 96	Ca7461 (lost)	Humerus		
97	Ca7458 (lost)	Left scapula	Pl. 81, fig. 3	1895: fig. 7
99	Cb4190	Proximal right femur		
100	Ca7489 (lost)	Proximal left pubis	Pl. 85, fig. 2	
101	Ca7488 (lost)	Proximal right pubis	Fig. 230; Pl. 85, fig. 1	
102	Ca7505	Metacarpal	Formerly <i>T. platyodon</i>	
116	Cb4195	?Cervical rib fragment		
118	Ca7464 (lost)	Right humerus	Pl. 80, fig. 2	1895:fig. 8
Unnumbered	Ca7511 (lost)	Three chevrons	Fig. 219	
Unnumbered	Ca7467	Cervical neural arch	Pl. 77, fig. 2	
Unnumbered	Ca7500 (lost)	Proximal metatarsal	Pl. 90, fig. 6	
Unnumbered	Ca7501	Phalanx	Pl. 90, fig. 8	

The BRSMG collection includes many more specimens, including many which are unidentified, a total of 184 in all, under registration numbers BRSMG C4528–34, Ca7451, Ca7456, Ca7466–7, Ca7473–5, Ca7481–2, Ca7485–6, Ca7490, Ca7494–7, Ca7499, Ca7501, Ca7504, Ca7507, Ca7510, Cb4151–4282, Cb4284–4305, Cb4714–5.

Repository number	Identity	Figure in Huene (1908a)	Figure in Huene (1914)
BMNH 49984	Left tibia, and other limb elements		
BMNH R1531	?Skull roof element		
BMNH R1532	Sacral vertebra	Fig. 213	
BMNH R1533	Unidentified vertebra		
BMNH R1534	Caudal vertebra		
BMNH R1535	Unidentified vertebrae		

## APPENDIX 1. (Continued.)

Repository number	Identity	Figure in Huene (1908a)	Figure in Huene (1914)
BMNH R1536a, b	Rib fragments		
BMNH R1537a-c	Rib fragments		
BMNH R1538	Rib fragment		
'old '106'			
BMNH R1539	Right ilium		
BMNH R1540	Partial ilium		
BMNH R1541	Partial humerus		
BMNH R1542	Proximal left humerus	Pl. 80, fig. 4	
BMNH R1543	Partial humerus		
BMNH R1544	Distal end of femur		
BMNH R1545	Partial femur		
BMNH R1546	Partial tibia		
BMNH R1547	Unidentified limb bone		
BMNH R1548	Unidentified limb bone		
BMNH R1549	Unidentified limb bone		
BMNH R1550	Partial humerus; caudal vertebra		
BMNH R1552	Phalanges		
BMNH R1553	Phalanx		
YPM 2192 (accession 2001)	Braincase	Pl. 76, fig. 1	Fig. 35
YPM 2192	Two cervical vertebrae	Pl. 77, fig. 1	Fig. 36
YPM 2192	Dorsal vertebra	Pl. 77, fig. 7	Fig. 37
YPM 2192	Two sacral vertebrae		Fig. 39
YPM 2192	Caudal vertebra		Fig. 40
YPM 2192	Dorsal ribs	Pl. 77, fig. 6	
YPM 2192	Left humerus	Pl. 83, fig. 1	Fig. 48
YPM 2192	Proximal right ulna		Fig. 49
YPM 2192	Two distal ischia	Pl. 83, figs. 2, 3	
YPM 2192	Distal right femur	Pl. 89, fig. 1	
YPM 2192	Distal tibia and astragalus	Pl. 89, fig. 2	Figs. 51—53
YPM 2192	Proximal left tibia	Pl. 89, fig. 3	Fig. 50
YPM 2192	Distal right tibia	Pl. 89, fig. 4	
YPM 2192	Proximal left tibia	Pl. 89, fig. 5	
YPM 2192	Partial fibula		
YPM 2192	Three phalanges	Pl. 80, fig. 3	
YPM 2193	Caudal vertebra		Fig. 43
YPM 2195 (accession 2001)	Caudal vertebra	Pl. 77, fig. 4	
YPM 2195 (accession 1979)	Scapula, forelimb, ribs		Figs. 44-47, 54
ANSP 9854	Caudal vertebra; partial femur		
ANSP 9855	Unidentified vertebra		
ANSP 9857	Neural spine		
ANSP 9858	Unidentified vertebra		
ANSP 9860	?Partial ulna		
ANSP 9861	Dorsal vertebra; ungual phalanx		
ANSP 9863	Partial fibula		
ANSP 9865	Dorsal vertebra; ?scapula fragment		
ANSP 9867	Partial fibula		
ANSP 9869	Partial fibula		
ANSP 9870	Right ilium; proximal femur		
ANSP 9871	Partial humerus		
ANSP 9872	Partial fibula		
ANSP 9874	Partial femur		
ANSP 9875	Caudal vertebra		
ANSP 9876	?Scapula fragment		
ANSP 9880	Partial humerus		

## APPENDIX 2

Characters used in the analysis of relationships of Sauropodomorpha, and the placement of *Thecodontosaurus*. Most of the characters are binary (0, 1), but some are three-state (0, 1, 2). The plesiomorphic state (0) was obtained by outgroup comparison with a wider group of basal dinosaurs and dinosauromorphs, but there is no implied transition from state 1 to 2 (*characters run as unordered*).

**Skull and Lower Jaw**

1. Skull length: more than (0) or less than (1) one-half the length of the femur.
2. External naris: smaller than (0), similar in antero-posterior length to (1), or larger than (2) the antorbital fenestra.
3. External naris: located in front of (0), or above (1) the antorbital fenestra.
4. Posteroventral border of external naris: composed largely of the premaxilla and nasal (0), or of the maxilla (1).
5. Maxilla-lacrimal contact above the antorbital fenestra: present (0), or absent, excluded by lateral portion of nasal (1).
6. Prefrontal: narrow and short (0), or broad and elongate, about as long as the frontal (1).
7. Lower temporal fenestra: located entirely behind (0), or partly below (1) the orbit.
8. Braincase in lateral view: parasphenoid in line with (0), or set well below (1) the occipital condyle.
9. Dentary anterior tip: straight (0), or curves down (1).
10. External mandibular fenestra: large (0) or reduced or absent (1).
11. Jaw articulation: roughly in line with the dentary tooth row (0), or set well below the tooth row, and in line with the ventral margin of the dentary (1).
12. Tooth crowns: recurved or triangular (0), lanceolate (1), or spatulate (2).
13. Marginal serrations on teeth: absent, or laterally-directed (0), coarse, obliquely-angled upwards at about 45°, and pointed (1).
14. Tooth crowns: stand vertically (0) or slope forwards (1).
15. Tooth rows: end behind (0), or below or in front of (1) the antorbital fenestra.

**Vertebral Column**

16. Number of cervical vertebrae: fewer than ten (0), or ten or more (1).
17. Mid-series cervical centra: similar in length to (0), or at least 25% longer than (1) mid-series dorsal centra.
18. Cervical centra: amphicoelous (0) or opisthocelous (1).
19. Anterior and middle cervical neural arches: smooth-sided (0), or bearing complex laminations (1).
20. Dorsal neural spines: smooth-sided and solid (0), or laminated and bearing deep lateral pockets (1).
21. Mid-series dorsal neural arches: lower (0) or higher (1) than the centra.
22. Number of sacral vertebrae: two (0), three (1), or four or more (2), by addition of caudals.
23. First caudal centrum length: longer than high (0), higher than long (1).

**Forelimb**

24. Deltpectoral crest on humerus: distal margin of the crest is located less than one-third (0), or halfway (1) along the length of the humerus.
25. Distal carpal 1: similar in size to (0), or at least twice the size of (1) the other distal carpals.
26. Digit I of the manus: similar in width to the other digits (0), or broader than all other digits (1).
27. First phalanx of digit I of the manus: straight (0) or twisted so that the proximal and distal condyles are set at 45° to each other (1).
28. Digit I ungual of manus: similar in size to the unguals of other digits (0), or much longer than any other manual phalanges (1).
29. Metacarpals II to V: more than (0), or less than (1) three times as long as wide.
30. Phalangeal formula of the hand: 2-3-4-1/2-0/1 (0) or 2-2-2-2-1 (1).

**Hindlimb**

31. Iliac blade length: approximately equal to (0), or more than 30% longer than (1), full depth of ilium from dorsal margin of the blade to ventral margin of ischiadic peduncle.
32. Anterior process of iliac blade: deep or narrow and long, and square-ended (0), narrow and short and pointed (1).
33. Acetabulum: partly closed by iliac wall (0), fully open (1).
34. Acetabulum shape: broader than high (0), higher than broad (1).
35. Ischium relative length: shorter (0) or longer (1) than pubis.
36. Obturator foramen of the pubis: absent or tiny (0), or large, being half the width of the acetabulum or more (1).
37. Pubes: do not form an 'apron', or form a distal apron without straight lateral margins (0), or form a broad straight-sided 'apron' by fusion of laterally expanded distal portions of both pubes (1).
38. Distal part of pubis: rod-like or flattened distally (0); flattened for the entire distal portion and forming a broad sheet-like 'apron' (1); robust and thickened antero-posteriorly (2).
39. Hindlimb (femur + tibia + metatarsal 3): much longer than (0), or subequal to (1) the length of the dorsal vertebral column.
40. Femur: sigmoidal (0) or straight (1) in posterior view.
41. Fourth trochanter of the femur: distal margin is within the proximal half (0) or in the distal half (1) of the length of the femur.
42. Lesser trochanter of the femur: absent or insignificant (0), or large and sheet-like (1).
43. Tibia length: tibia longer or equal (0), slightly shorter (75–90%) (1), or much shorter (50–60%) than femur (2).
44. Ascending process of astragalus: absent (0), runs up the anterior face of the tibia (1), or keys into a slot formed by a descending process of the tibia (2).
45. Calcaneum proximo-distal height: more than one quarter (0), or less than one-fifth (1) of the medio-lateral width of the astragalus.
46. Distal tarsals: present (0) or absent (1).
47. Ungual of digit I of the pes: shorter than other phalanges (0); equal in length to, or longer than, all other pedal phalanges (1).
48. Metatarsals I–IV: more than (0), or less than (1) four times as long as the maximum width at the proximal end.
49. Pes digit IV: four or five (0) or three (1) phalanges.

APPENDIX 3. Matrix of character codings used in the analysis of relationships of sauropodomorph dinosaurs, and the placement of *Thecodontosaurus*. Characters are listed in Appendix 2. A hypothetical ancestor is not used, but two taxa, *Scleromochlus* and *Herrerasaurus*, are included as postulated outgroups of the crown-group clade. Three sauropod taxa, *Vulcanodon*, *Shunosaurus*, and *Brachiosaurus*, are also included in order to assess the relationships of prosauropods and sauropods. Character codings: 0, postulated plesiomorphic condition of character; 1–2, postulated derived conditions of character; N, character state uncertain; X, character uncodable because of transformation. The matrix can be copied electronically from <<http://palaeo.gly.bris.ac.uk/cladestore/Archosauria/Archosauria5.htm1>>

Taxa	Character									
	10	20	30	40	49					
<i>Scleromochlus</i>	00000	00000	00N00	00000	0200N	0NN0N	0N000	0NN00	00000	0N00
<i>Herrerasaurus</i>	00000	00000	00000	00000	00000	00000	00000	00100	00010	0000
<i>Thecodontosaurus</i>	11011	00010	01100	10000	0100N	11100	01101	N1100	00120	1100
<i>Plateosaurus</i>	11001	10110	11100	11000	0111N	11110	11100	11101	00120	1101
<i>Massospondylus</i>	12010	00110	01100	11000	01N11	11110	11100	11100	11120	1101
<i>Euskelosaurus</i>	NNNNN	NNNNN	NNNNN	N1000	0110N	NNNNN	1110N	NNN01	0012N	NNN1
<i>Anchisaurus</i>	11001	00110	01110	N1000	01000	11100	11100	11110	11120	1101
<i>Sellosaurus</i>	11001	01N10	11100	11000	0101N	11100	11100	11100	00120	1101
<i>Melanorosaurus</i>	NNNNN	NNNNN	NNNNN	NN000	0NN1N	NNNNN	0110N	NNN11	1112N	NNN1
<i>Riojasaurus</i>	11010	00010	01100	11000	01111	11110	11110	01110	11120	01N1
<i>Coloradisaurus</i>	N2010	00010	11100	NNNNN	NNNNN	NNNNN	NNNNN	NNNNN	NNNNN	NNNN
<i>Vulcanodon</i>	NNNNN	NNNNN	NNNNN	N100N	N210N	NNN1N	NN101	01111	00221	11N1
<i>Barapasaurus</i>	NNNNN	NNNNN	N20NN	N1111	12NNN	NNNNN	10101	00210	0022N	NNN1
<i>Shunosaurus</i>	12110	01011	02011	11111	1211X	00111	10111	00210	00221	1111
<i>Brachiosaurus</i>	12110	01011	12011	11111	1210X	00111	10111	00210	00221	1111

#### APPENDIX 4

Characters defining the clades in the cladogram shown in Figure 20B. The apomorphic condition (1) is normally not indicated, but in the case of multistate characters (numbers 2, 12, 22, 38, 43, 44), the condition (1, 2) is shown. Character state reversals are indicated by a negative sign. Equivocal character placements are indicated with an asterisk (\*) at each possible node. The clade diagnoses include only the unequivocal characters.

Sauropodomorpha: 1, 2(1), 9, 12(1), 16, 17, 22(1), 28, 33, 43(1), 44(2), 46, 47

Skull less than half length of femur, external naris enlarged, dentary tip curves down, tooth crowns lanceolate or spatulate, ten or more cervical vertebrae, mid-series cervical centra longer than dorsals, three or more sacral vertebrae, unguis of digit I of manus much longer than other manual phalanges, acetabulum fully open, tibia longer than femur, ascending process of astragalus keys into a slot formed by descending process of tibia, distal tarsals absent, unguis of digit I of pes equal to or longer than other pedal phalanges.

Prosauropoda: 5\*, 12(1), 13, 22(1), 26, 27, 32, 36

Tooth crowns lanceolate, marginal serrations on teeth coarse and obliquely angled upwards, three sacral vertebrae by addition of caudals, digit I of manus broader than other digits, first phalanx of digit I of manus twisted, anterior process of iliac blade narrow and short and pointed, obturator foramen in pubis enlarged.

Sauropoda: 2(2)\*, 3\*, 10\*, 14\*, 15\*, 22(2), 35\*, 39\*, 43(2), 45, 48\*

Four or more sacral vertebrae, tibia much shorter (50–60%) than femur, calcaneum proximo-distal height less than one-fifth of the medio-lateral width of the astragalus.

Unnamed clade: 2(2)\*, 3\*, 10\*, 12(2), 14\*, 15\*, 18, 19, 20, 21, 48\*

Tooth crowns spatulate, cervical centra opisthocoeleous, anterior and middle cervical neural arches laminated and bearing pleurocoels, dorsal neural spines laminated and bearing pleurocoels, mid-series dorsal neural arches higher than the centra.

Eusauropoda: 2(2)\*, 3\*, 10\*, 14\*, 15\*, 30, 34, –37\*, 38(2), 48\*

Phalangeal formula of the hand reduced to 2-2-2-1, acetabulum higher than broad, distal part of pubis robust and thickened antero-posteriorly.

#### NOTE ADDED IN PROOF

A stereophotograph of the manus of YPM 2195 (Fig. 12B) is given in Galton (in press a). Photographs of the holotype of *Agrosaurus macgillivrayi* Seeley, 1891 (BMNH 49984, tibiae, left and proximal end of right, distal end of left radius, sectioned unguis phalanx manus digit 1, distal caudal vertebra) are given by Vickers-Rich et al. (1999) and Galton (in press b). Based on the proportions of the distal end of the tibia, *Agrosaurus* is referred to *Thecodontosaurus antiquus* by Galton (in press b), rather than to the theropod family Herrerasauridae, as suggested by Sereno (1997).