

The earliest known sauropod dinosaur and the first steps towards sauropod locomotion

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A partial dinosaur skeleton from the Upper Triassic (Norian) sediments of South Africa is described and named *Antetonitrus ingenipes*. It provides the first informative look at a basal sauropod that was beginning to show adaptations towards graviportal quadrupedalism such as an elongated forelimb, a modified femoral architecture, a shortened metatarsus and a changed distribution of weight across the foot. These adaptations allowed the clade to produce the largest-ever terrestrial animals. However, *A. ingenipes* lacked specializations of the hand found in more derived sauropods that indicate it retained the ability to grasp. *Antetonitrus* is older than the recently described *Isanosaurus* from Thailand and is the oldest known definitive sauropod.

Keywords: dinosaur; sauropod; Triassic; phylogeny; quadrupedalism

1. INTRODUCTION

Sauropods are well known as the largest terrestrial animals to have ever existed and were the dominant large herbivores for most of the Mesozoic Era (McIntosh 1990). Eusauropods (a clade encompassing all but the most basal sauropods) share a suite of postcranial specializations, related to their gigantic size, obligate quadrupedalism and graviportal locomotion, which leave little doubt that the group is a monophyletic unit. These include: columnar limbs with reduced processes for muscle attachment; an elongated forelimb; a deep radial fossa on the proximal ulna; a radius with a flat, caudally facing ulnar facet at its distal end (forcing the manus into a partly pronated position); a ligament-bound semitubular metacarpus; an elliptical femoral cross-section; and a shortened, spreading pes (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Bonnan 2003). Eusauropods (Upchurch 1998) or a basal node within the clade (Wilson & Sereno 1998) are also characterized by exceptionally tall, broad dorsal neural spines that are constructed of bony laminae. Unfortunately, the early history of sauropods is poorly represented in the fossil record and the sequence in which these specializations were acquired has remained a mystery. A further area of uncertainty and disagreement is the nature of the relationship between sauropods and the assemblage of early dinosaurs known collectively as the 'prosauro-pods'. Prosauro-pods are frequently thought of as forming a sister clade to the Sauropoda that appears long before the oldest known sauropods (Sereno 1999; Benton *et al.* 2000), thus implying a long period of hidden evolution. However, some workers have suggested that certain 'prosauro-pods' are actually basal members of the Sauropoda (Yates 2003b), thus reducing the morphological and temporal gap between the two groups.

A new skeleton, from the Late Triassic (Norian) of South Africa (figure 1) and described herein, sheds some light on these questions.

2. MATERIAL AND METHODS

The specimen described here is housed in the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. The phylogenetic position of the new taxon was tested by scoring 19 sauropodomorph taxa (plus two outgroups) for 212 osteological characters (see electronic Appendix A available on the Royal Society's Publications Web site, for the character list and character–taxon matrix). The matrix was analysed with PAUP 4.0 (Swofford 1998) using the branch-and-bound search option. All characters were weighted equally. Bootstrap support and decay indices were calculated to determine the robustness of each node. A Templeton test was used to compare this hypothesis with a more traditional sauropodomorph phylogeny.

3. SYSTEMATIC PALAEOLOGY

Saurischia (Seeley 1888)
Sauropodomorpha (Von Huene 1932)
Sauropoda (Marsh 1878)
Antetonitrus ingenipes gen. et sp. nov.

(a) *Diagnosis*

A primitive sauropod with the following autapomorphies. Dorsal neural spines flared transversely at their distal end (present to a lesser extent in *Lessemsaurus sauro-podooides*). Dorsal vertebrae with broad, triangular hyposphenes (in caudal view). A ventral ridge on the hyposphenes of the caudal dorsal vertebrae. A deep sulcus adjacent to the lateral distal margin of the deltopectoral crest. An extremely short, broad metacarpal I.

Antetonitrus ingenipes most closely resembles *Blikanasaurus cromptoni* (Galton & Van Heerden 1985) and *Lessemsaurus sauro-podooides* (Bonaparte 1999), both of which are poorly known (a partial hindlimb and a dorsal series, respectively). It differs from *Blikanasaurus* in having a less robust metatarsus and lacking the marked cranial extension of the proximal articular surface of metatarsal II. It differs from *Lessemsaurus* in having triangular hyposphenes and incipient lamination of the dorsal neural spines.

The holotype was initially identified as *Euskelosaurus* sp.

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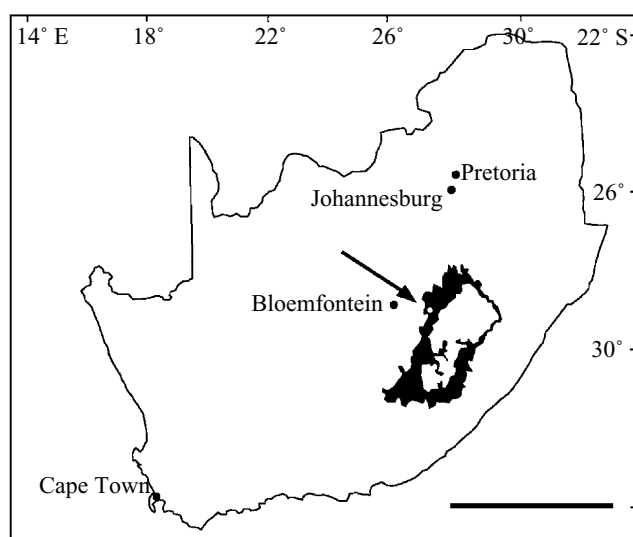


Figure 1. A sketch map of South Africa showing the extent of the Stormberg group (black area) and the locality from which *Antetonitrus ingenipes* gen. et sp. nov. was collected (arrowed). Scale bar, 500 km.

(Kitching & Raath 1984). *Euskelosaurus browni* (Huxley 1866) is almost certainly a *nomen dubium* because it has no derived characters or unique combination of characters that allow it to be distinguished from several early sauropodomorphs. Nevertheless, the holotype of *E. browni* displays a subcircular cross-section of the femoral midshaft, a proximally located fourth trochanter and a low ridge-like lesser trochanter that is not shifted towards the lateral margin of the femoral shaft (Van Heerden 1979) that distinguish it from *A. ingenipes*.

(b) *Holotype*

Partial disarticulated skeleton (BP/1/4952) including a cervical centrum, four dorsal vertebrae, sacral vertebra, caudal vertebrae, dorsal ribs, chevrons, scapulae, right humerus, both ulnae, left radius, left metacarpal I, both metacarpals II, left manual phalanx II, two ?manual unguals, left pubis, left femur, left tibia, left fibula, left metatarsal I, right metatarsal II, left metatarsal III, right metatarsal V, two pedal phalanges, right pedal ungual I, right pedal ungual ?III. The specimen was disarticulated but closely associated *in situ*. The fossils are thought to belong to a single individual because they are all from a large (for the Triassic), robust sauropodomorph representing most skeletal regions with no duplication of parts. A photograph of the excavation can be seen in Kitching & Raath (1984, fig. 4).

(c) *Referred specimens*

A right scapula, right humerus (with a deep sulcus on the lateral distal margin of the deltopectoral crest), left ulna, left fibula and a right metatarsal II that are smaller (*ca.* 80%) than their counterparts in the holotype. Found at the same site as the holotype and catalogued as (BP/1/4952b).

(d) *Locality and horizon*

The specimen was found in the saddle between the farms Welbedacht 611 and Edelweiss 698, Ladybrand

District, Free State, South Africa (29°06'24" S; 27°19'10" E). The strata in which the specimen was found belong to the Lower Elliot Formation, which is part of the informal 'Stormberg Group'. In the past, the Lower Elliot Formation has been assigned to the Carnian stage (Gauffre 1993a; Galton & Van Heerden 1998) but the current consensus places it in the Norian (Battail 1993; Lucas & Hancox 2001).

(e) *Etymology*

The generic name is from Latin, *ante* (before); *tonitrus* (thunder) and refers to the early occurrence of this sauropod relative to *Brontosaurus* (Greek, thunder lizard) one of the most familiar sauropod names. The species name is from Latin, *ingens* (massive) and *pes* (paw, or foot) and refers to its robust hands and feet.

(f) *Description*

The skeleton is of a small, robustly built sauropod that is estimated to have a total length of 8–10 m and a hip height of 1.5–2 m (figure 2). The neurocentral sutures of the cervical and dorsal vertebrae are open, suggesting that the individual was immature at the time of death (Brochu 1996). None of the vertebral centra has pleurocoels. The cervical centrum is amphicoelous. The dorsal neural arches (figure 3) are tall, ranging from 2 to 2.4 times the height of the centrum and the neural spines are much higher than they are long at their base. Neural arch lamination consists of the usual four diapophyseal laminae that are present in most saurischians, although the prezygodiapophyseal lamina is absent from the mid-dorsal vertebrae. Dorsals from the caudal end of the series display incipient spinal lamination with tall, thin spinopostzygapophyseal laminae and broad, low prespinal, postspinal and spinoprezygapophyseal laminae. The hyposphenes are particularly well developed and are broad triangular structures that are as deep as the neural canal. The scapula has a broad blade (blade width 30% of the scapula length) and a flared distal end, but the acromion remained narrow as it is in prosauropods (Wilson & Sereno 1998). The humerus is long (90% of the femur) and has a tall, well-developed deltopectoral crest. Although large, the deltopectoral crest does not extend for half the length of the humerus as it does in prosauropods. It bears a deep sulcus along its distolateral margin. The proximal ulna combines a deep radial fossa on its cranio-lateral face, a long cranial proximal condylar process and a well-developed olecranon process. The radius is straight with an ovoid distal articular surface. Metacarpal I is a very short element (maximum length only 85% of the proximal width) with strongly asymmetrical distal condyles. Phalanx I.1 is short and blocky with the transverse axis of the distal end rotated *ca.* 40° ventrolaterally relative to the proximal end. The proximolateral fossa receives metacarpal II and when they are articulated it is clear that the proximolateral region of metacarpal I would have projected into the carpus as it does in prosauropods (Sereno 1999). The pubis is gracile compared to other sauropods and the pubic blades are oriented transversely to form a flat, plate-like pubic apron. The distal ends of the pubes bear a modest cranio-caudal swelling. The femur has an elliptical cross-section. It retains a sigmoid curvature in lateral view as well as a crest-like lesser trochanter (where the height is

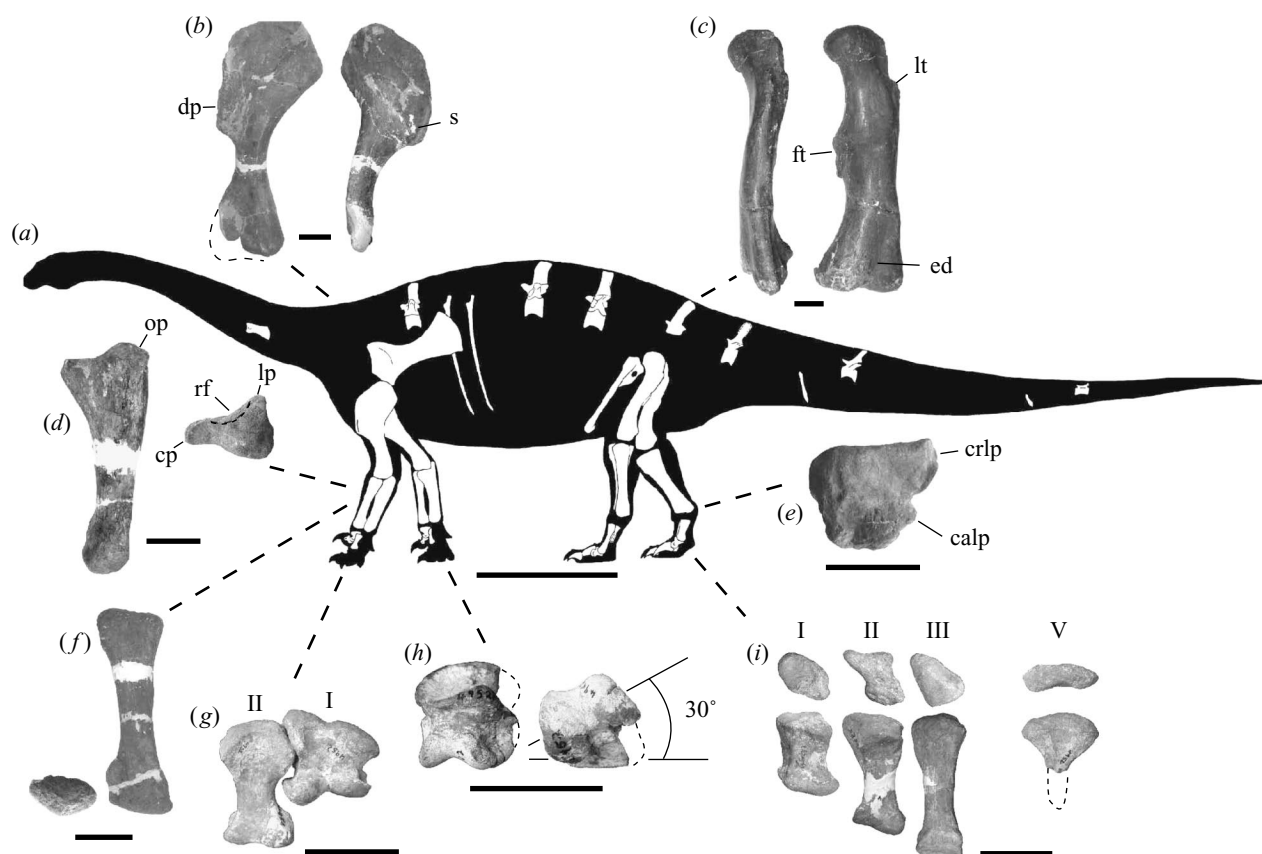


Figure 2. Skeletal reconstruction of *Antetonitrus ingenipes* showing (a) preserved bones. Individual bones: (b) right humerus in cranial and lateral views, (c) left femur in lateral and cranial views, (d) left ulna in medial and proximal views (dotted line represents limit of radial fossa that is obscured by a laterally projecting bulge on the proximolateral edge), (e) left tibia in distal view, (f) left radius in medial and distal views, (g) right metacarpals I and II in dorsal view, (h) right phalanx I.1 in dorsal and distal views (angle represents degree of ventrolateral rotation of the distal end relative to the proximal end), (i) left metatarsus in proximal and dorsal views (metatarsal II is a right element that has been reversed for comparison). Scale bars represent 100 mm, except in (a) where the scale bar represents 1 m. Abbreviations: calp, caudolateral process; cp, cranial process; crlp, craniolateral process; dp, deltopectoral crest; ed, extensor depression; ft, fourth trochanter; lp, lateral process of the proximal ulna; lt, lesser trochanter; op, olecranon process; rf, radial fossa; s, sulcus.

greater than its basal width). The tall fourth trochanter is situated halfway along the length of the femur. Its profile is subrectangular with a sharp caudodistal corner. The distal tibia is subtriangular with a reduced descending caudolateral flange that lies medial to the craniolateral corner. The metatarsus is short (length of metatarsal III is 38% of the tibia) and is similarly proportioned to *Vulcanodon* (table 1). Metatarsal I is shorter than metatarsals II–IV but has an elliptical cross-section where the maximum diameter is greater than that of any other metatarsal. Metatarsal V is incomplete but the midshaft is 65% of metatarsal III suggesting that it bore little, if any, weight. The first pedal ungual is longer than metatarsal I. It is moderately asymmetrical but does not form the flattened sickle-shaped, strongly asymmetrical claw seen in *Vulcanodon* and *Eusauropoda* (Wilson & Sereno 1998).

4. DISCUSSION

Phylogenetic analysis of the matrix finds five most-parsimonious trees (see electronic Appendix A available on The Royal Society's Publications Web site for a synapomorphy list). The strict consensus places *Antetonitrus* near the base of the Sauropoda, in a polytomy with *Isanosaurus*,

Blikanasaurus and a clade containing *Kotasaurus*, *Vulcanodon* and *Eusauropoda*. When the poorly represented *Blikanasaurus* is pruned from the trees, *Antetonitrus* is resolved as the sister taxon to the clade containing *Isanosaurus* and remaining sauropods (figure 4). The decay index of the node connecting *Antetonitrus* to more derived sauropods is just one but this is due to the incomplete knowledge of basal sauropods above *Anchisaurus*. When *Melanorosaurus*, *Blikanasaurus* and *Isanosaurus* are excluded from the analysis, the decay index for this node climbs to seven. A Templeton test shows that the shortest tree with a traditional content of the Sauropoda (i.e. one that excludes *Anchisaurus*, *Melanorosaurus* and *Antetonitrus*) is significantly longer than the most-parsimonious trees ($p = 0.0041$). The immaturity of the holotype of *A. ingenipes* is not likely to seriously affect these results. As far as is known the appendicular skeleton of sauropodomorphs experiences little, if any, allometric change with growth (Bonnan 2003). The sauropod-like lamination of the neural spines is only likely to have become more pronounced, not less so, with maturity (Carpenter & McIntosh 1994).

Antetonitrus ingenipes represents an important intermediate between the gracile basal sauropodomorphs with an

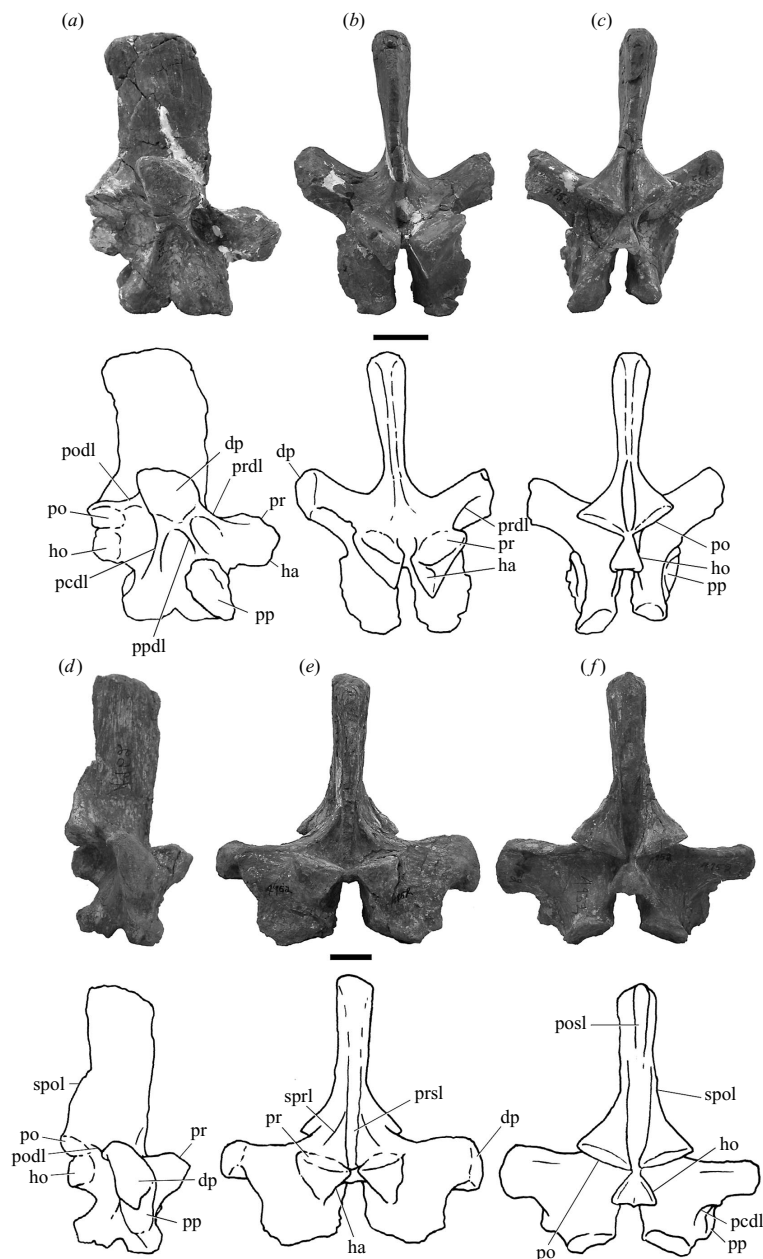


Figure 3. Dorsal neural arches of *Antetonitrus ingenipes* gen. et sp. nov. Cranial dorsal neural arch in (a) cranial, (b) left lateral and (c) caudal views. Caudal dorsal neural arch in (d) cranial, (e) left lateral and (f) caudal views. Abbreviations: dp, diapophysis; ha, hypantrum; ho, hyposphene; pcdl, posterior centrodiapophyseal lamina; po, postzygopophysis; podl, postzygodiapophyseal lamina; posl, postspinal lamina; pp, parapophysis; prdl, prezygodiapophyseal lamina; pr, prezygopophysis; prsl, prespinal lamina; sprl, spinoprezygopophyseal lamina; spol, spinopostzygopophyseal lamina.

inferred facultative bipedal gait (Van Heerden 1997) and the specialized graviportal, obligate quadrupeds that characterize Eusauropoda and related taxa. It is interesting to note that the basal sister group to all other sauropods, *Anchisaurus* (Yates 2003b), retains the primitive body form. Therefore, the characteristic body form of eusauropods must have started to evolve some time after the initial diversification of the Sauropoda. Given the early occurrence of *Antetonitrus* this early evolution must have been quite rapid. The synapomorphies that unite *Antetonitrus* with more derived sauropods are: suprapostzygopophyseal laminae on the dorsal vertebrae; a humerus that is greater than 80% of the femur; a long cranial process on the proximal ulna; an elliptical cross-section of the femur; the

third metatarsal is less than 40% of the tibia; the midshaft of metatarsal 1 is broader than all other metatarsals; pedal ungual I is longer than metatarsal I. The presence of suprapostzygopophyseal laminae indicates that the evolution of laminated dorsal neural spines may have begun earlier in sauropod phylogeny than previously recognized. The exceptionally long forelimbs imply that *Antetonitrus* was a habitual quadruped. Quadrupedal walking requires a pronated manus so that it may swing in a parasagittal plane. The distinctive triradiate proximal ulna of *Antetonitrus* and derived sauropods may be linked to a medial shift in the position of the radius that brought about this pronation (Bonnan 2003). The flat caudal face of the distal radius of *Vulcanodon* and Eusauropoda would lock the manus

Table 1. Skeletal dimensions and proportions of the prosauropod *Plateosaurus engelhardti* (Von Huene 1926) and the basal sauropods *Antetonitrus ingenipes*, *Vulcanodon karibaensis* (Raath 1972), *Shunosaurus lii* (Zhang 1988) and *Omeisaurus tianfuensis* (He et al. 1988).

(Institutional abbreviations: NMZ, National Museum of Zimbabwe, Bulawayo; SMNS, Staatliches Museum für Naturkunde, Stuttgart; ZDM, Zigong Dinosaur Museum, Zigong. All measurements are in millimetres and are maximum lengths unless otherwise stated.)

measurement	<i>Plateosaurus</i> SMNS 13200	<i>Antetonitrus</i> BP/1/4952	<i>Vulcanodon</i> NMZ QG24	<i>Shunosaurus</i> ZDM T5401	<i>Omeisaurus</i> ZDM T5701
humerus	400	717	ca. 700	670	1080
radius	240	376	647	480	755
ulna	270	419	660	438	—
metacarpal I	80	92	—	116	210
metacarpal I (proximal width)	54	109	—	92	94
metacarpal II	100	132	—	160	280
femur	680	794	ca. 1100	1200	1310
tibia	500	512	634	680	820
metatarsal I	135	122	159	110	192
metatarsal I (mid-width)	39	64	50	46	72
metatarsal II	200	170	204	150	202
metatarsal II (mid-width)	37	45	40	42	53
metatarsal III	240	197	236	175	229
metatarsal III (mid-width)	38	43	40	40	45
humerus/femur	0.58	0.90	ca. 0.64	0.56	0.82
metatarsal III/tibia	0.49	0.38	0.37	0.26	0.28

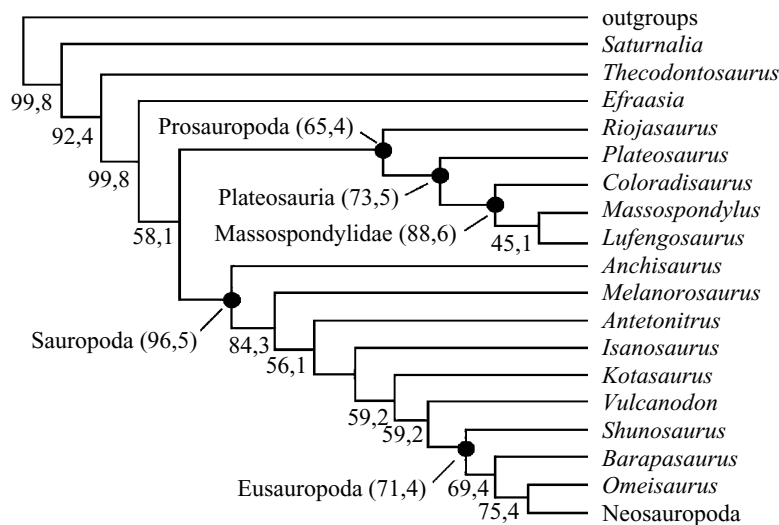


Figure 4. Simplified cladogram of sauropodomorph relationships based on an analysis of 20 taxa (including two outgroups) and 212 osteological characters. This fully resolved tree represents the topology of the five most-parsimonious trees (tree length of 449 steps, consistency index of 0.5434, retention index of 0.7288) after the unstable *Blikanasaurus* has been pruned. Numbers given at each node represent bootstrap frequency (left) and decay index (right).

into this position (Wilson & Sereno 1998). If so, then *Antetonitrus* would have been able to pronate its manus during locomotion but the ovoid shape of its distal radius suggests that it was not locked into this position. Thus, the manus probably had other functions. The manus retained a strongly twisted and mobile pollex that maintained the grasping ability seen in prosauropods (Galton 1971). The retention of a large deltopectoral crest and olecranon process also suggests a greater range of forelimb movement than in more derived sauropods. In the hindlimb the short metatarsus implies a loss of agility; however, it was neither as short nor as splayed as in Eusauropoda. The robustness of metatarsal I suggests that the distribution of weight across the metatarsus was begin-

ning to become biased towards the medial side but it was not as extreme as in derived eusauropods, where the lateral metatarsals (III–V) are 65% of the width of the medial metatarsals (I and II) (Wilson & Sereno 1998).

Antetonitrus and its less well-represented contemporaries, *Blikanasaurus cromptoni* and *Melanorosaurus readi* (Haughton 1924), are the oldest known sauropods. The only other accepted Triassic sauropod, *Isanosaurus attavipachi* (Buffetaut et al. 2000) from Thailand, is Rhaetian in age and therefore postdates *Antetonitrus*. The Lower Elliot Formation sauropods are contemporary with the oldest known true prosauropods: an undescribed taxon from the same formation (BP/1/4953, personal observation) and *Plateosaurus* (= *Sellosaurus*) *gracilis* (Von Huene 1908;

Yates 2003a) from the middle Norian of Germany. Claims of older, Carnian prosauropods cannot be substantiated. *Saturnalia tupiniquim* is a stem sauropodomorph (Langer *et al.* 1999; this analysis), while *Azendohsaurus laarousii* (Gauffre 1993b) and two unnamed forms from Madagascar (Flynn *et al.* 1999) represent fragmentary basal sauropodomorphs of an indeterminate systematic position. Thus, the stratigraphic gap between the first appearances of Sauropoda and Prosauropoda no longer exists.

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