



# The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda

BLAIR W. MCPHEE<sup>1,2\*</sup>, ADAM M. YATES<sup>3</sup>, JONAH N. CHOINIERE<sup>1,2</sup> and FERNANDO ABDALA<sup>1,2</sup>

<sup>1</sup>Evolutionary Studies Institute, Centre of Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, Johannesburg, Gauteng, 2050, South Africa

<sup>2</sup>NRF/DST Centre of Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, Johannesburg, Gauteng, 2050, South Africa

<sup>3</sup>Museum of Central Australia, Araluen Cultural Precinct, P.O. Box 3521, Alice Springs, Northern Territory, 0871, Australia

Received 9 June 2013; revised 1 December 2013; accepted for publication 13 December 2013

We present a comprehensive description and phylogenetic analysis of the important transitional sauropodomorph *Antetonitrus ingenipes*. New information sheds light on the stepwise acquisition of sauropod-like traits just prior to the Triassic/Jurassic boundary. Although the forelimb of *Antetonitrus* and other closely related sauropodomorph taxa retains the plesiomorphic morphology typical of a mobile grasping structure, the changes in the weight-bearing dynamics of both the musculature and the architecture of the hindlimb document the progressive shift towards a sauropodan form of graviportal locomotion. Nonetheless, the presence of hypertrophied muscle attachment sites in the femur of *Antetonitrus* suggests the retention of an intermediary form of facultative bipedalism. The term Sauropodiformes is adopted here and given a novel definition intended to capture those transitional sauropodomorph taxa occupying a contiguous position on the pectinate line towards Sauropoda. A re-examination of the biased distribution of Sauropodomorpha in the earliest Jurassic suggests the presence of genuine palaeo-environmental processes that may have excluded the large-bodied, graviportal taxa from participating in a number of Early Jurassic ecosystems.

© 2014 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2014, 171, 151–205.  
doi: 10.1111/zoj.12127

ADDITIONAL KEYWORDS: late Triassic – locomotion – Lower Elliot Formation – Sauropodomorpha.

## INTRODUCTION

The late 20<sup>th</sup> and early 21<sup>st</sup> centuries witnessed an exponential increase in the study of sauropod dinosaurs (e.g. Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch, Barrett & Dodson, 2004; Yates, 2007b; Klein *et al.*, 2011). Consequently, the morphological complex of long neck, massive size, and columnar limbs that distinguishes Sauropoda as unique amongst dinosaur groups is now understood to have been well established by the Early Jurassic (e.g. Cooper, 1984; He *et al.*, 1998; Bandyopadhyay

*et al.*, 2010), and several important finds within the last two decades suggest a late Triassic origin for the clade (Buffetaut *et al.*, 2000; Yates & Kitching, 2003; Bonnan & Yates, 2007; Ezcurra & Apaldetti, 2012). In addition to yielding significant insight towards our understanding of the anatomy of the earliest sauropods, these finds have also contributed to a growing consensus that the traditional ‘prosauropod’ assemblage represents a paraphyletic grade of basal forms with respect to Sauropoda (Yates & Kitching, 2003; Pol, 2004; Smith & Pol, 2007; Upchurch, Barrett & Galton, 2007a; Yates, 2007a, b, 2010; Ezcurra, 2010; Novas *et al.*, 2010; Pol, Garrido & Cerda, 2011; Ezcurra & Apaldetti, 2012). It is a view

\*Corresponding author. E-mail: blair.mcphee@gmail.com

that has prompted a re-evaluation of the patterning and timing of the evolutionary changes within Sauropodomorpha at the Triassic–Jurassic boundary.

Nonetheless, although the evolutionary history of Sauropoda now extends much further into the Triassic than previously recognized, the origins of the derived bauplan of the Sauropoda remains poorly understood. This is because of an early sauropod record in which only fragmentary forms are known from rocks earlier than the Toarcian, as well the instability of several derived sauropodomorph taxa within a number of recent cladistic analyses (e.g. Upchurch, Barrett & Galton, 2007a; Pol *et al.*, 2011; Apaldetti, Pol & Yates, 2013). The large-bodied sauropodomorphs from the Lower Elliot Formation of South Africa (Norian/Rhaetian, Upper Triassic), with their unique combination of plesiomorphic and apomorphic traits, represent a significant addition to the sauropodomorph record, and a means of better unravelling the origins of the sauropod bauplan (Yates & Kitching, 2003; Bonnan & Yates, 2007; Pol & Powell, 2007; Yates, 2007a, b). In particular, the species *Antetonitrus ingenipes* Yates & Kitching, 2003, displays an intermediary collection of primitive and derived traits and is therefore ideally positioned – both temporally and morphologically – to inform on the acquisition of a number of distinctive sauropod adaptations.

This intermediate morphology helps eliminate a stratigraphical gap of some 20 000 000 years in which the sauropod bauplan was previously observed to appear suddenly at the outset of the Jurassic (Wilson & Sereno, 1998; Sereno, 1999; Wilson, 2002), and several recent topologies have recognized *Antetonitrus* as one of the basal-most sauropods known (Yates, 2007a, b; Allain & Aquesbi, 2008; Pol *et al.*, 2011; Apaldetti *et al.*, 2011). However, this position was based only on preliminary descriptive data, and a thorough comparative analysis of the *Antetonitrus* hypodigm remains to be undertaken. This study aimed to address the continued gaps in our knowledge of early sauropod evolution by providing a thorough description and phylogenetic analysis of the type material of *Antetonitrus*.

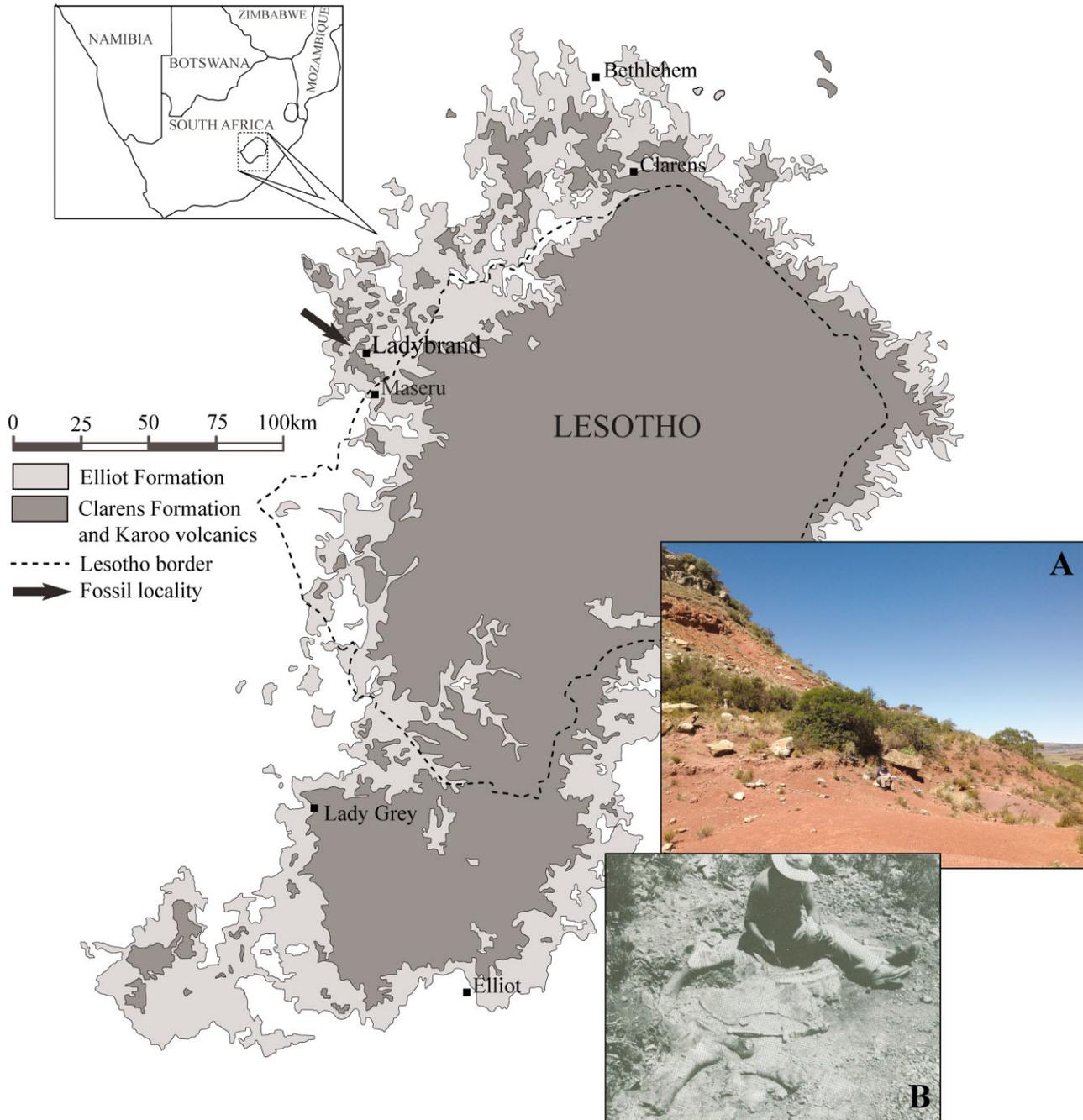
#### SAUROPODOMORPHA AND THE LOWER ELLIOT FORMATION

The Elliot Formation is an Upper Triassic ('Lower' Elliot Formation) to Lower Jurassic ('Upper' Elliot Formation) fluviolacustrine succession that skirts the western side of the Lesotho/Free State border before terminating at its thickest point (c. 300–400 m) near Jamestown in the Eastern Cape (Fig. 1). Together with the underlying Molteno and overlying Clarens formations, it forms part of the stratigraphical Stormberg Group and represents the final deposi-

tional stages of the Karoo Supergroup (Catuneanu, Hancox & Rubidge, 1998; Bordy, Hancox & Rubidge, 2004, 2005). In addition to *Antetonitrus*, there are four valid sauropodomorph taxa currently recognized within the Lower Elliot Formation (LEF). This follows a decade of intensive taxonomic revision by Yates & Kitching (2003) and Yates (2003b, 2004b, 2007a) in which a number of genera previously lumped within the ubiquitous 'waste-basket' taxon of *Euskelosaurus browni* Huxley, 1866 (see Van Heerden, 1979) were resurrected and rediagnosed.

*Plateosaurus cullingworthi* Houghton, 1924, possibly represents the most plesiomorphic species within the LEF sauropodomorph assemblage [having been recovered in a position basal to the Plateosauria in most recent analyses (e.g. Yates, 2007a, b; Apaldetti *et al.*, 2013)] and captures a substantial amount of material that had previously been referred to *Eus. browni* by Van Heerden (1979) (Yates, 2003b). Nonetheless, a formal diagnosis and comprehensive description of the material collected under *Plateosaurus* awaits publication, and future investigation may lead to a re-evaluation of its phylogenetic position. *Eucnemesaurus fortis* Van Hoepen, 1920, is the most problematic of the LEF sauropodomorphs. Diagnosed almost exclusively by its peculiar femur, *Euc. fortis* was, until recently, thought to represent the 'herrerasaurid' theropod *Aliwalia rex* Galton, 1985a. However, the discovery of a similarly diagnostic femur found in association with sauropodomorph vertebrae led Yates (2007a) to resurrect the long-forgotten *Euc. fortis*. Although based on exceedingly fragmentary material, *Eucnemesaurus* has been consistently recovered as the sister taxon to *Riojasaurus incertus* Bonaparte, 1972 within a monophyletic Riojasauridae in most recent phylogenetic analyses (e.g. Yates, 2007a, b; Apaldetti *et al.*, 2011, 2013).

*Melanorosaurus readi* Houghton, 1924, is the most well-known sauropodomorph within the LEF, and is often considered to represent one of the closest sister taxa to the sauropodan clade of obligate quadrupeds (e.g. Upchurch *et al.*, 2007a; Yates, 2007a, b, 2010). Originally based on a composite collection of postcranial bones (SAM-PK-K3449, 3450), *Melanorosaurus* later had the partial remains of two individuals (catalogued as NM QR1551: Galton, Van Heerden & Yates, 2005), as well as a largely complete and articulated skeleton with a complete skull (NM QR3314), referred to it. This latter individual was finally subjected to a systematic analysis and description by Yates (2007b) and Bonnan & Yates (2007). *Blikanasaurus cromptoni* Galton & Van Heerden, 1985, is based primarily on an articulated left epipodium, tarsus, and pes (SAM K403), with only a first metatarsal (BP/1/5271a) having been additionally referred to it (Yates, 2008). Galton & Van Heerden (1985, 1998) originally



**Figure 1.** The Elliot Formation of South Africa showing the type locality of the *Antetonitrus ingenipes* fossil assemblage (modified from Bordy *et al.* 2004). A, the lead author seated at the base of the saddle where *A. ingenipes* was discovered. B, the original excavation of *A. ingenipes* (from Kitching & Raath 1984).

suggested that the robust morphology evident in *Blikanasaurus* was convergent with respect to the heavily built, quadrupedal sauropod condition, and thus not on the evolutionary line that gave rise to it. However, although the remains suggest an unexpectedly small adult body size for a taxon of its robusticity, recent phylogenetic assessments argue for a close relationship between *Blikanasaurus* and Sauropoda

(Yates & Kitching, 2003; Galton & Upchurch, 2004; Yates, 2007b). *Blikanasaurus* is also of interest as the holotype was found at the very bottom of the southern section of the LEF where it meets the underlying Molteno Formation (Charig, Attridge & Crompton, 1965). The occurrence of another specimen (BP/1/5271a) in the upper 20 m of the LEF and located in the attenuated northern third of the basin (where it overlies the

Kaapval Craton), indicates that the northern section of the LEF probably represents a condensed deposit that is coeval and biostratigraphically homogenous with the thicker southern section (Yates, 2008).

### MATERIAL AND METHODS

The current work employs traditional anatomical and directional terms over veterinarian alternatives (e.g. 'anterior' and 'posterior' rather than 'cranial' and 'caudal'). For the sake of terminological simplicity, when describing directional orientations the bone is assumed to have been held along its closest horizontal or vertical axis (e.g. the scapular is presented as being completely vertically orientated).

Clade names used in the paper are outlined in Table 1. We favour the definition of Sauropoda *sensu* Salgado, Coria & Calvo (1997; see also Langer *et al.*, 2010) for reasons that will be outlined in the text. The anatomical descriptions are based on first-hand observation of the *Antetonitrus* holotype BP/1/4952 and other referred material. The comparisons with other members of Sauropodomorpha made in the following description were based on both the literature and on personal observation of specific taxa detailed in Table 2.

### INSTITUTIONAL ABBREVIATIONS

AMNH, American Natural History Museum, New York, USA; BPI, Bernard Price Institute, Johannesburg, South Africa; FMNH, Field Museum of Natural History, Chicago, Illinois; GPIT, Institute for Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany (formerly Geologisch-Paläontologisches Institut Tübingen); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; NM QR, National Museum, Bloemfontein, South Africa; PULR, Paleontologia, Universidad Nacional de La

Rioja, La Rioja, Argentina; PVL, Instituto Miguel Lillo, Tucuman, Argentina; SAM-K, Iziko-South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZDM T, The Chongqing Natural History Museum, Chongqing, People's Republic of China.

### CLADISTIC ANALYSIS

A cladistic analysis was conducted to investigate the phylogenetic implications of the new anatomical knowledge of the *Antetonitrus* material. This analysis was drawn from the data matrix initially employed by Yates (2007b) and subsequently modified (in terms of the revision and addition of both taxa and characters) by Smith & Pol (2007), Yates *et al.* (2010), Yates (2010), and Apaldetti *et al.* (2011) (see Supporting Information Appendix S1). The additional 17 characters suggested by Ezcurra (2010) were not employed because errors in the published data made it difficult to reconcile his data with other phylogenetic data sets. Nonetheless, a number of the modifications to *Guaibasaurus* Bonaparte, Ferigolo & Ribeiro, 1999, *Chindesaurus* Long & Murry, 1995, *Herrerasaurus* Reig, 1963, *Eoraptor* Sereno *et al.*, 1993, and *Saturnalia* Langer *et al.*, 1999 suggested by Ezcurra (2010) are incorporated here. *Ignavusaurus* Knoll, 2010 was deliberately excluded as its status as a valid taxon remains controversial with some authors suggesting that it is synonymous with *Massospondylus* Owen, 1854 (Yates, Bonnan & Neveling, 2011). *Saraksaurus* Rowe, Sues & Reisz, 2011, was also excluded because we considered its coding to be questionable (i.e. it presents a conspicuously high number of autapomorphic character states, many of which converge on the sauropodan condition) and were unable

**Table 1.** Clade names and their sources mentioned throughout the text

Clade	Definition	Source
Sauropodomorpha	The most inclusive clade including <i>Saltasaurus</i> but not <i>Tyrannosaurus rex</i>	Taylor <i>et al.</i> , in press
Massopoda	The most inclusive clade that contains <i>Saltasaurus</i> but not <i>Plateosaurus engelhardti</i>	Yates, 2007a, b
Massospondylidae	The most inclusive clade containing <i>Massospondylus</i> but not <i>Plateosaurus engelhardti</i> or <i>Saltasaurus</i>	Sereno, 2007
Sauropodiformes	The most inclusive clade containing <i>Saltasaurus</i> but not <i>Massospondylus</i>	Defined within
Sauropoda	The least inclusive clade containing <i>Vulcanodon</i> and Eusauropoda	Salgado <i>et al.</i> , 1997, Langer <i>et al.</i> , 2010
Eusauropoda	The least inclusive clade containing <i>Shunosaurus</i> and <i>Saltasaurus</i>	Upchurch <i>et al.</i> , 2004
Neosauropoda	The least inclusive clade containing <i>Diplodocus</i> and <i>Saltasaurus</i>	Wilson & Sereno, 1998

**Table 2.** List of comparative taxa used in present analysis. Specific accession numbers represent specimens viewed first-hand by the authors, whereas all other comparative data were drawn from the literature listed within the table

Taxon	Source(s)
<b>Sauropodomorpha</b>	
<i>Saturnalia tupiniquim</i>	Langer, 2003; Langer <i>et al.</i> , 2007
<i>Thecodontosaurus antiquus</i>	Benton <i>et al.</i> , 2000
<i>Pantyraco caducus</i>	Yates, 2003a
<i>Plateosauravus cullingworthi</i>	Van Heerden, 1979
<i>Plateosaurus engelhardti</i>	von Huene, 1926; Moser, 2003; Yates, 2003a, Mallison, 2010a, b
<i>Eucnemesaurus fortis</i>	BP/1/6107; Yates 2007a
<i>Riojasaurus incertus</i>	PVL 3808; Bonaparte, 1972
<i>Lamplughosaura dhamaramensis</i>	Kutty <i>et al.</i> , 2007
<i>Seitaad ruessi</i>	Sertich & Loewen, 2010
<i>Leoneosaurus taquetrensis</i>	Pol <i>et al.</i> , 2011
<i>Massospondylus carinatus</i>	BP/1/4377, 4693, 4924, 4934, 4998, 5000, 5241; Cooper, 1981
<i>Coloradisaurus brevis</i>	PVL 5904 (field no. 6); Apaldetti <i>et al.</i> , 2013
<i>Lufengosaurus hueni</i>	Young, 1941
<i>Adeopapposaurus mognai</i>	Martínez, 2009
<i>Glacialisaurus hammeri</i>	Smith & Pol, 2007
<b>Sauropodiformes</b>	
<i>Yunnanosaurus huangi</i>	Young, 1942
<i>Jingshanosaurus xinwaensis</i>	Zhang & Yang, 1994
<i>Aardonyx celestae</i>	BP/1/386; various elements catalogued BP/1/5379–6893
<i>Anchisaurus polyzelus</i>	Galton, 1976; Yates, 2004a, 2010
<i>Melanorosaurus readi</i>	NM QR1551, 3314; Galton <i>et al.</i> , 2005; Bonnan & Yates, 2007
<i>Blikanasaurus cromptoni</i>	Galton & Van Heerden, 1998; Yates, 2008
<i>Lessemsaurus sauropoides</i>	PVL 4822; Pol & Powell, 2007
<i>Gongxianosaurus shibeiensis</i>	He <i>et al.</i> , 1998
<b>Sauropoda</b>	
<i>Isanosaurus attavipachi</i>	Buffetaut <i>et al.</i> , 2000
<i>Vulcanodon karibaensis</i>	Cooper, 1984
<i>Tazoudasaurus naimi</i>	Allain & Aquesbi, 2008
<i>Spinophorosaurus nigerensis</i>	Remes <i>et al.</i> , 2009
<b>Eusauropoda</b>	
<i>Shunosaurus lii</i>	Zhang, 1988
<i>Barapasaurus tagorei</i>	Bandyopadhyay <i>et al.</i> , 2010
<i>Omeisaurus tianfuensis</i>	He <i>et al.</i> , 1988
<i>Mamenchisaurus</i>	Young & Zhao, 1972
<i>Cetiosaurus oxoniensis</i>	Upchurch & Martin, 2003

to examine the specimen directly. Modifications in the current analysis focused primarily on the scoring of characters in *Antetonitrus*. However, first-hand examination of the closely related *Lessemsaurus* Bonaparte, 1999 (PVL 4822) also allowed us to reassess a number of characters in that taxon (see Appendix S1). Any changes in broader sauropodomorph ingroup codings were made on an *ad hoc* basis. The phylogenetic matrix represented by 54 taxa and 361 characters was analysed using TNT 1.1 (Goloboff, Farris & Nixon, 2008) using a heuristic search of 1000 replicates of Wagner trees followed by tree bisection-reconnection branch swapping with ten trees saved per replication. All 36 multistate characters coded as ordered in Yates (2007a, b) and Yates

*et al.* (2010) were kept as such. Characters were equally weighted.

## RESULTS

### SYSTEMATIC PALAEOONTOLOGY

#### DINOSAURIA OWEN, 1842

#### SAURISCHIA SEELEY, 1888

#### SAUROPODOMORPHA HUENE, 1932

#### MASSOPODA YATES, 2007A

#### SAUROPODIFORMES SERENO, 2007

*Definition:* Sauropodiformes is allocated the stem-based definition of all taxa sharing a more recent

common ancestor with *Saltasaurus* Bonaparte & Powell, 1980, than with *Massospondylus*. Sereno (2007) had originally defined Sauropodiformes as ‘the least inclusive clade including *Mussaurus* Bonaparte & Vince, 1979 and *Saltasaurus*’. However, *Mussaurus* (at the point of writing) is still a relatively poorly known taxon, whereas the Massospondylidae has been consistently recovered and expanded upon in the majority of phylogenetic analyses since 2007 (Yates, 2007a, b; Apaldetti *et al.*, 2011; Novas *et al.*, 2010). Additionally, all the taxa positioned apically to the Massospondylidae in the current analysis were regarded as sauropodiforms in Langer *et al.*’s (2010) expansion of the label via the concurrent restriction of Sauropoda to the node-based definition initially proposed by Salgado *et al.* (1997) (in which *Vulcanodon* Raath, 1972 is the basal anchor taxon). As a number of basal sauropodiform taxa (e.g. *Yunannosaurus* Young, 1942; *Seitaad* Sertich & Loewen, 2010) exhibit regular phylogenetic instability, a stem-based definition that specifies the nodes above Massospondylidae without requiring tiresome future name changes is preferred.

**Diagnosis:** Sauropodiformes as defined here is diagnosed by: the lack of an elongate median nasal impression (autapomorphically present in *Melanorosaurus*); mesial and distal serrations on the carinae of the maxillary and dentary teeth; absence of laterally expanded tables at the mid-length of the dorsal surface of the dorsal neural spines; posterior margin of the middle dorsal neural spines straight in lateral view; sacral rib not significantly narrower than the transverse process of the first primordial sacral vertebra; length of the manus less than 38% of the humerus + radius (reversed in *Anchisaurus* Marsh, 1885); absence of a posteriorly projecting ‘heel’ at the end of ischial peduncle of the ilium (convergently absent in some specimens of *Massospondylus*); absence of a well-developed brevis fossa (also present in *Lufengosaurus* Young, 1941); rounded posteromedial process of distal tarsal IV in proximal aspect; and a first metatarsal that is at least the same width proximally as the second metatarsal (present also in *Lufengosaurus* and *Glacialisaurus* Smith & Pol, 2007).

#### ANTETONITRUS YATES & KITCHING, 2003

##### *ANTETONITRUS INGENIPES* YATES & KITCHING, 2003

**Locality and horizon:** The specimen was discovered in 1982 by James Kitching in the saddle between the farms Welbedacht 611 and Edelweiss 698, Ladybrand District, Free State, South Africa (now within the boundary of Broken Slopes; 29°06′24″S, 27°19′10″E). A recent visit to the type locality by B.W.M. and J.N.C. revealed that this saddle exposes a substantial

portion of the upper strata of the Lower Elliot Formation. Although the precise excavation site could not be located, there is little reason to doubt Kitching & Raath’s (1984) observation that the remains came from ‘low down in the Elliot Formation’. Traditionally, the Lower Elliot Formation has been assigned to the Carnian stage (Gauffre, 1993; Anderson, Anderson & Cruickshank, 1998; Galton & Van Heerden, 1998; Warren & Damiani, 1999). However, the current consensus places it within the Norian, with the possibility that its upper sediments may even be Rhaetian in age (Lucas & Hancox, 2001; Bordy *et al.*, 2004, 2005; Knoll, 2004; Irmis, 2010). Recently, the Norian age of the Lower Elliot was supported by Bordy *et al.* (2005) via their interpretation of the Molteno–Elliot contact as an abrupt unconformity, which differed from previous reconstructions in which the Lower Elliot was hypothesized as being the distal, coeval equivalent of the Molteno (e.g. Cole, 1992; Anderson *et al.*, 1998). As this unconformity is thought to be related to a minor loading event in the Cape Fold Belt, the end of which has been dated at  $215 \pm 3$  Mya (Halbich, Fitch & Miller, 1983), the earliest occurrence of the Lower Elliot Formation would therefore appear to reside comfortably within the middle Norian.

**Holotype:** Although the holotype as defined by Yates & Kitching (2003) is represented by disarticulated material, we can conservatively show that some of the holotype material pertains to at least one separate individual. Accordingly, we revise the holotype and referred material as listed below.

The updated holotype BP/1/4952 includes: a cervical centrum, three dorsal neural arches, four dorsal centra; a ?caudosacral neural arch, ?ten caudal vertebrae, two dorsal ribs, chevrons, left scapula, right humerus, both ulnae, right radius, right metacarpal 1, left metacarpal 2, right manual phalanx 1.1, left pubis, left femur, left tibia, left fibula, left metatarsal 1, right metatarsal 2, left metatarsal 3, right metatarsal 5, two pedal phalanges, right pedal ungual 1, right pedal ungual ?3. The monospecific status of BP/1/4952 is supported by the closely associated, *in situ* nature of the bones upon discovery (Kitching & Raath, 1984; see Fig. 1).

Duplicates of the left scapula and left metacarpal 2, assigned to the holotype by Yates & Kitching (2003), are from an animal of similarly large dimensions to the rest of the holotype material. We remove these from the holotype and assign them the new catalogue number BP/1/4952c.

BP/1/4952b: the remaining material from the primary *Antetonitrus* quarry is comprised of duplicate elements that, although measurably smaller than the holotype, display an identical morphology (with the exception of the fibulae, but see Description).

This duplicate material essentially comprises the 'paratype' individual of Yates & Kitching (2003), and on this basis we retain the catalogue number assigned in that paper (BP/1/4952b). Included is a posterior dorsal neural arch, ?two caudal vertebrae, a right scapulae, right humerus, right ulna, right radius, and right fibula.

*Referred material:* NM QR1545: an assemblage of approximately three individuals representing two distinct size classes recovered from the Excelsior District of the Free State. It consists of a large right humerus of similar relative proportions and absolute size to BP/1/4952; two small right ulnae (both missing the proximal and distal ends); left and right ilia (of slightly different size and markedly different preservation); two femora including a large left (heavily damaged) and large right that is once again of the same general relative and absolute proportions as BP/1/4952 (but missing the major portion of the femoral head); three tibia, a small (incomplete) right element, and two large, subequally sized left (complete) and right (incomplete) elements; three fibulae, a large right and two subequally sized, smaller elements of both sides.

Where observable (the condition of NM QR1545 is comparably poorer than that of BP/1/4952), the above bones display the same diagnostic criteria and basic morphology as that listed above for BP/1/4952. This provides a strong case for their referral to *A. ingenipes*. However, differential preservation (i.e. in colour, quality of preservation) amongst many of the elements suggests that NM QR1545 may not represent an associated assemblage of bones, but that fossilized 'float' from the surrounding area was collected alongside other, *in situ*, material.

BP/1/5091: recovered from the *Antetonitrus* type locality two years after the collection of BP/1/4952, BP/1/5091 represents sacral material from a juvenile specimen (as indicated by the unfused neuro-centro/sacrocostal juncture) and includes a sacral neural arch from either of the primordial sacral vertebrae, a partial ?caudosacral neural arch, and the centra from what was potentially the dorsosacral vertebra. The referral of these elements to *Antetonitrus* is based mainly on the transverse dorsal expansion of the neural spine of the primordial vertebrae as well as the wide, equilateral triangle-shaped hyposphene. Additionally, the partial caudosacral neural arch very closely resembles the same element in BP/1/4952.

The 'Bloem Dino': This material represents a large sauropodomorph that has, in turn, been referred to '*Euskelosaurus*' (Gauffre, 1993) as well as providing the basis for the erection of a novel taxon ('*Kholumulomosaurus*') in an unpublished PhD thesis (Gauffre, 1996). Now divided between the National

Museum in Bloemfontein, the University of Cape Town, and the Museum National d'Histoire Naturelle in Paris, no formal referral of this vast sum of material to *Antetonitrus* is offered here. Nonetheless, several analyses suggest that amongst this material is an animal very similar to *Antetonitrus* (Ellenberger & Ellenberger, 1956; Ellenberger & Ginsburg, 1966; Gauffre, 1993, 1996). Accordingly, some of this material is currently under study at the University of Cape Town.

*Diagnosis:* A robust, large-bodied transitional sauropodomorph. In addition to the features given in Yates & Kitching (2003), *A. ingenipes* can be further distinguished from most nonsauropodan sauropodomorphs by the following unique combination of characters (\* = autapomorphy): high dorsal neural spines comprising more than half the total height of the neural arch\*; dorsal neural arches more than twice as tall as associated centra\*; pneumatic subfossae in the posterior infradiapophyseal fossae of the mid-posterior dorsal neural arch; presence of a caudosacral vertebrae; single articular facet on proximal chevrons\*; broadly expanded dorsal scapular blade; head of humerus vaulted and expanded posteriorly; medial tuberosity of the humeral head reduced and slightly medially inturned\*; delicate, nonsinuuous deltopectoral crest; medial deflection of the anterior process of the proximal ulna\*; incipient radial fossa on the proximal ulna; distinct bifurcated tubercle on the ventrolateral edge of the shaft of metacarpal 2; femoral shaft elliptical in cross-section and reduced in lateral sinuosity; laterally displaced lesser trochanter of the femur visible in posterior view; fourth trochanter located on the medial edge of the mid-shaft of the femur; anteroposterior length of the proximal surface of the tibia over twice its transverse width and roughly level with the horizontal plane; descending process of the distal tibia compressed laterally so that the anterior ascending process is visible in posterior aspect; robust, entaxonically spreading pes; metatarsal 3 less than 40% length of tibia; length of pedal ungual 1 greater than metatarsal 1.

Additionally, *Antetonitrus* is plesiomorphic relative to more derived sauropodan taxa with respect to the following features: amphicoelous vertebral centra; deltopectoral crest that is orientated perpendicularly to the transverse axis of the distal condyles and represents at least half of the total length of the humerus; deep intercondylar depression (= cuboid fossa) on the distal humerus; large olecranon process of the ulna; short, robust antebrachium; shortened metacarpus with an axially twisted phalanx 1.1; iliac peduncle of the proximal pubis anteriorly subconfuent with the transversely orientated pubic apron; a hypertrophied *M. caudofemoralis brevis*

insertion\*; cnemial crest of the tibia transversely broad and anteriorly projecting; metatarsal V reduced in size relative to other metatarsals.

#### ANATOMICAL DESCRIPTIONS

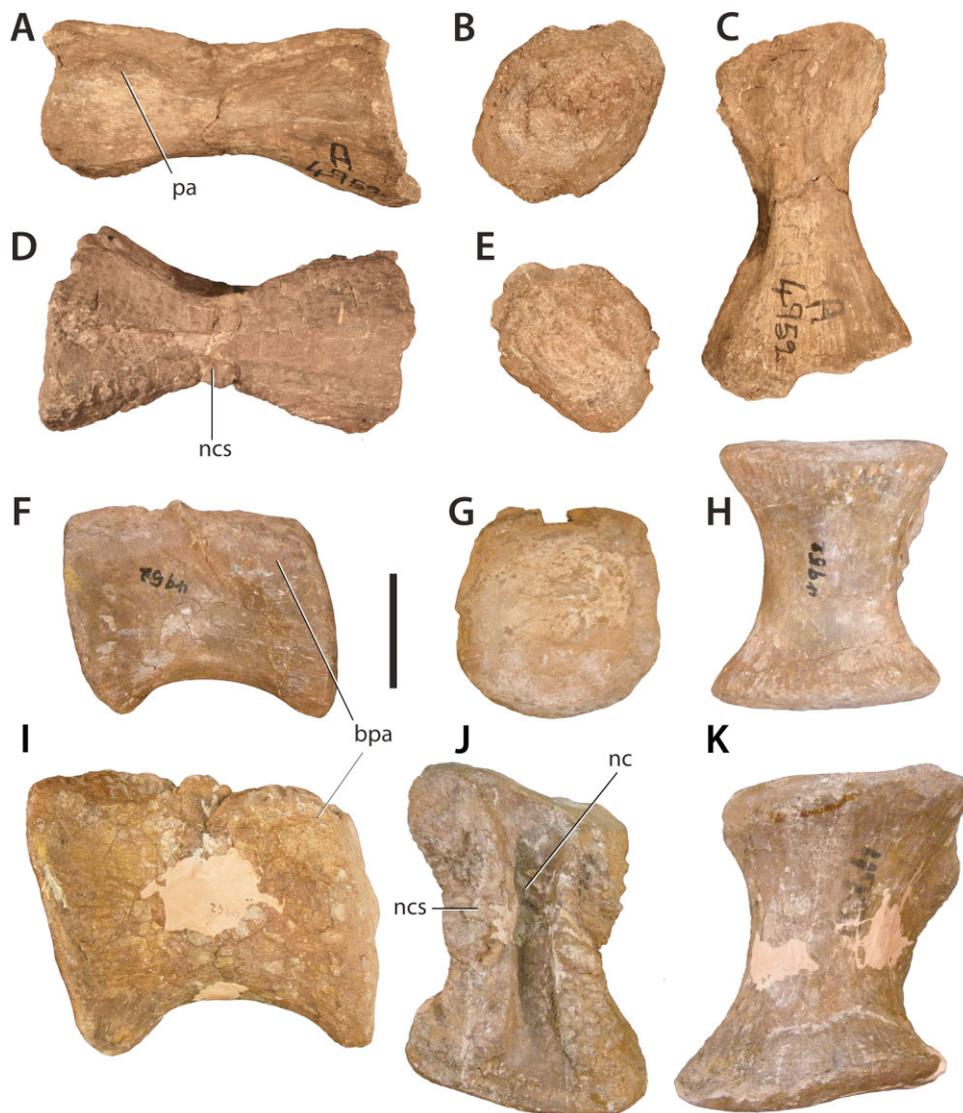
##### *Axial skeleton*

##### Cervical vertebrae

The neck of *Antetonitrus* is represented by a single cervical centrum (Fig. 2). A middle-to-posterior position in the cervical sequence for this centrum is likely because the parapophyses are clearly visible just above mid-height and set slightly back from the anterior margin of the centrum. The centrum has experi-

enced postdepositional compression so that the ventral surface has been obliquely displaced relative to the dorsal surface, deflecting the articular facets laterally. However, the basic morphology of the centrum remains preserved.

The centrum of is typical of those seen in all nonsauropodan sauropodomorphs, being both amphicoelous and acamerate. Given the postdepositional distortion of the bone, it is difficult to establish a precise measure of the relationships of the articular facets to both one another, and to the overall anteroposterior length of the bone. With this caveat in mind, the height of the anterior articular surface is approximately 0.85 times the height of the posterior



**Figure 2.** *Antetonitrus ingenipes* (BP/1/4952), isolated centra in A–E, middle/posterior cervical centrum in A, left lateral; B, posterior; C, ventral; D, dorsal; and E, anterior views. F–H: ?anterior dorsal centrum in F, right lateral; G, proximal; and H, ventral views. I–K: ?mid-posterior dorsal centrum in I, right lateral; J, dorsal; and K, ventral views. Abbreviations: bpa, base of parapophyses; nc, neural canal; ncs, neurocentro suture; pa, parapophyses. Scale bar = 5 cm.

surface, with the width of both articular facets being roughly subequal to their dorsoventral height. The anteroposterior length of the bone is approximately twice the dorsoventral height of the anterior surface and 1.82 times the height of the posterior end. Assuming that *Antetonitrus* displayed the same basic cervical proportions as most other non-eusauropodan sauropodomorphs (e.g. *Riojasaurus*; *Yunnanosaurus*; *Lessemsaurus*) then it is most likely that the centrum derives from somewhere towards the rear of the middle part of the neck.

The cervical centrum is strongly constricted mediolaterally, with its width at mid-length less than half the width of the articular surfaces, although it is possible that depositional flattening has exaggerated this degree of constriction. The parapophyses are rugose longitudinal crests positioned just above mid-height on the anterior margin of the centrum. Dorsally, the neural-arch sutures are represented by two heavily rugose, anteroposteriorly flared parasagittal ridges extending the entire anteroposterior length of the bone and separated by a relatively deep neural canal (at least where it is not obscured by remaining matrix). It is possible that a subtle ventral keel, observable in some non-eusauropodan taxa (e.g. *Massospondylus*; *Lamplughosaura* Kutty *et al.*, 2007; *Isanosaurus* Buffetaut *et al.*, 2000) was present on the anterior half of the ventral surface of the centrum, but it cannot be said with confidence whether or not this is an artefact of distortion.

#### Dorsal vertebrae

*General overview:* There are four disarticulated neural arches and four centra (Fig. 2) of the dorsal series present. Postdepositional distortion has warped most of the centra, thus making it difficult to establish whether they articulated with any of the preserved neural arches in life. This lack of dorsal fusion is indicative of an immature animal. All of the centra are amphicoelous and acamerate (solid). The anteroposterior length of the dorsal centra that have not experienced major dorsoventral compression is roughly subequal to the height of their posterior surfaces. This ratio is fairly typical for Sauropodomorpha whereas most massospondylids (e.g. *Massospondylus*; *Adeopapposaurus* Martínez, 2009) display an elongated length/height ratio of about 1.5 in the dorsal centra (Apaldetti *et al.*, 2013).

Based on the position of the parapophyses, the vertebral elements range from the middle-anterior to the posterior-most segments of the dorsal column. The anterior-most neural arch – possibly located somewhere between D4 and D6 – is the smallest of the dorsal neural arches, as is typical of anteriorly located dorsal vertebrae in sauropodomorphs. The next in the series probably represents a middle-to-

mid-posterior neural arch and is hypothesized as being located somewhere between D8 and D10. The final two dorsal arches probably represent an identical position in the vertebral series (based on equivalence in morphology) as the posterior-most dorsal neural arches. As one is clearly smaller (as well as being less well preserved), it is probable that at least two individuals are represented within the dorsal remains of the *Antetonitrus* vertebrae.

All of the disarticulated neural arches and centra interpreted as dorsal elements within the *Antetonitrus* assemblage display a similar relationship, with the former being roughly two to three times the dorsoventral height of the latter. This ratio, if it is correct, would represent a marked departure from the general nonsauropodan sauropodomorph condition, in which the neural arches of the dorsal series are subequal to slightly higher than the articular surfaces of the centra with which they connect (e.g. *Plateosaurus* Meyer, 1837; *Riojasaurus*; *Lufengosaurus*; *Yunnanosaurus*; *Leoneosaurus* Pol *et al.*, 2011). The putative ratio observed in *Antetonitrus* is closer to that of sauropodan taxa such as *Tazoudasaurus* Allain *et al.*, 2004, and *Shunosaurus* Dong, Zhou & Zhang, 1983, in which the dorsal arches are two to three times the height of their centra.

Much of the great dorsoventral height of the neural arches is conferred by especially tall neural spines, which in the anterior-most neural arch constitutes 0.56 in proportion of the total dorsoventral height of the bone. This represents another departure from the typical nonsauropodan sauropodomorph condition, in which the neural spine is half to less-than-half the total height of the anterior neural arches (e.g. *Plateosaurus*; *Massospondylus*; *Yunnanosaurus*; *Jingshanosaurus* Zhang & Yang, 1994). The only known non-eusauropodan sauropodomorphs to also display similarly high neural spines are *Lessemsaurus*, *Tazoudasaurus*, and *Isanosaurus*, although in *Lessemsaurus* the neural spines are slightly lower at approximately 0.52 the total height of the arch. As in *Lessemsaurus*, the neural spines in *Antetonitrus* are transversely widened at their dorsal margin compared to most nonsauropodan sauropodomorphs (e.g. *Massospondylus*; *Anchisaurus*), although not to the degree seen in *Tazoudasaurus* + Eusauropoda. The neural spines of all the dorsal elements are plesiomorphic insofar as they lack the pronounced anteroposterior constriction typical of *Tazoudasaurus* and eusauropodan genera, while also lacking the spinodiapophyseal laminae present in *Isanosaurus*, *Tazoudasaurus*, and more derived sauropods. Furthermore, none of the dorsal vertebrae of *Antetonitrus* has the anterior centroparapophyseal lamina, intraprezygapophyseal lamina, or the

prezygoparapophyseal lamina that are present in *Tazoudasaurus* and more derived taxa.

The articular facets of the zygapophyses in all the preserved dorsal neural arches of *Antetonitrus* are completely flat (irrespective of angled orientation), lacking the concave curvature observed in some of the dorsal neural arches of *Coloradisaurus* Bonaparte, 1978 (Apaldetti *et al.*, 2013). In the mid-anterior dorsal neural arch the prezygapophyses are especially large relative to the size of the neural arch, with their joint mediolateral width 0.5 times the maximum width of the neural arch (across the transverse processes). In the two posterior dorsal neural arches this metric is significantly reduced at about 0.39. Accordingly, throughout the dorsal vertebral sequence the transverse processes increase in relative width, being 0.73 times the total height of the neural spine in the mid-anterior neural arch and 1.04 in the posterior-most arch.

The neural canals of the dorsal neural arches are markedly high, slot-shaped channels with subvertical walls. This contrasts with the condition in most basal sauropodomorphs (e.g. *Plateosaurus*; *Eucnemesaurus*; *Massospondylus*; *Lamplughsaura*) that tend to have low, subcircular neural canals in the dorsal series. In posterior view, the hyposphenes of all the dorsal vertebrae of *Antetonitrus* are markedly well-developed equilateral triangles with ventral surfaces that are as mediolaterally broad (if not slightly more) as the neural canal. *Antetonitrus* was originally described as having hyposphenes as deep as the neural canals that they cap (Yates & Kitching, 2003). However, this is clearly not the case in both the mid-anterior and mid-posterior neural arches, where the hyposphenes constitute only approximately 0.65 and 0.68 to the total proportions of the canal height, respectively. Nonetheless, the hyposphenes in *Antetonitrus* appear to represent a particularly robust variant of the state typical to most derived basal sauropodomorphs (e.g. *Massospondylus*; *Aardonyx* Yates *et al.*, 2010), whereas the hyposphenes of *Tazoudasaurus* and most eusauropods are either mediolaterally attenuated or relatively reduced in sized. In accord with the high neural canal, the pedicles of the dorsal neural arches in *Antetonitrus* are also dorsoventrally elongate, meaning that the prezygapophyses would have been raised well above the anterodorsal lip of the centrum, further contributing to the great relative dorsoventral height of the element. In contrast, most other non-eusauropodan sauropodomorphs (e.g. *Massospondylus*; *Lessemisaurus*) tend to have considerably lower dorsal neural arch pedicles.

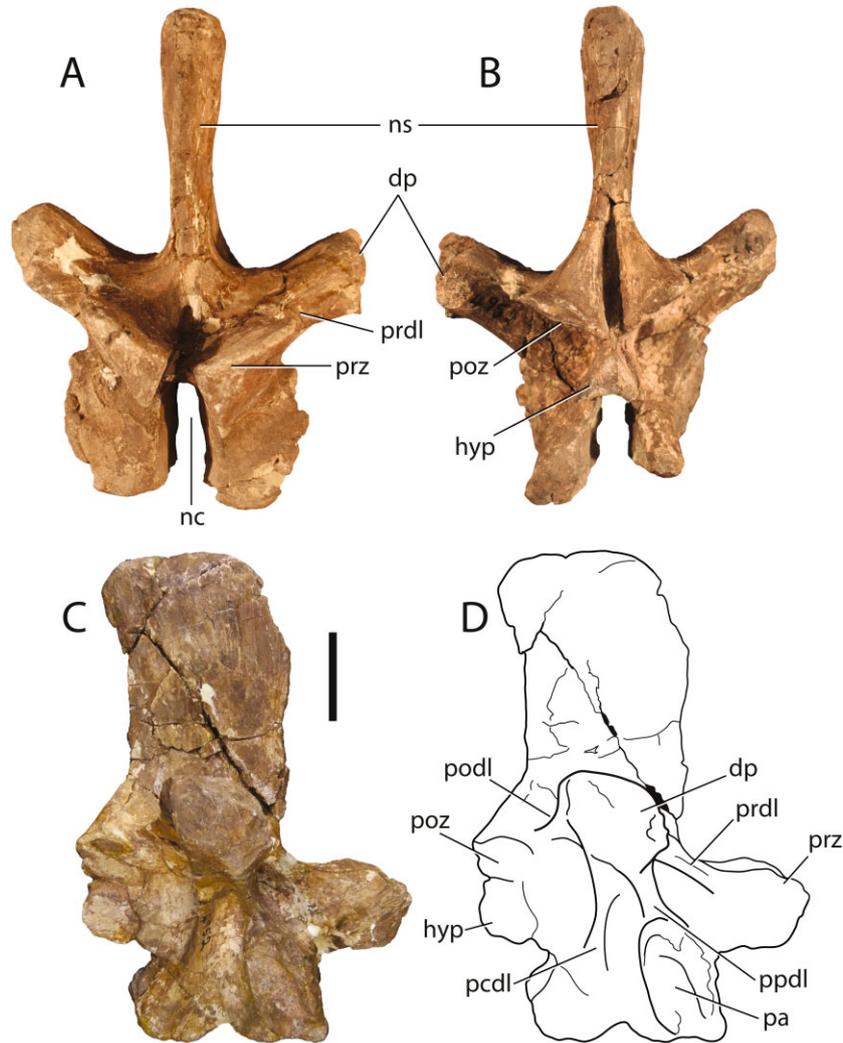
The following description focuses on the major distinguishing characteristics of the three largest, most complete neural arches. These are hypothesized to have derived from a single individual.

*Mid-anterior dorsal neural arch:* As in *Plateosaurus*, it is possible that the anterior margin of the neural spine of both the mid-anterior and mid-posterior neural arches possessed a 'keel' [possibly homologous to the prespinal laminae of later sauropods (Wilson, 1999)]; however, damage to both elements makes this difficult to verify and the process, if complete, is likely to have been relatively subtle. The neural spine of the mid-anterior neural arch is buttressed posteroventrally by incipient spinopostzygapophyseal laminae (spol) that exhibit a similar degree of development to that observed in derived basal sauropodomorphs (e.g. *Riojasaurus*; *Aardonyx*), but lack the flared, posterior expansion that braces most of the dorsoventral length of the neural spines in eusauropods (Fig. 3). Together, these bound a deep postspinal sulcus.

The postzygapophyseal facets are ovoid and directed medioventrally at an angle of about 40° where they meet the apex of the hyposphene ventrally. The prezygapophyses are large subcircular processes (in dorsal aspect) separated medially by a well-developed hypantrum and inclined at a similar angle as the postzygapophyses.

The transverse processes extend dorsolaterally and slightly posteriorly, rising above the level of both the posterior and anterior zygapophyses, as is typical of more anteriorly located dorsal vertebrae. The diapophyses are roughly pentagonal in lateral outline, mainly on account of the four primary saurischian vertebral laminae that radiate from their anterior, posterior, and ventral margins (Wilson, 1999). The postzygadiapophyseal lamina (podl) connects the diapophyses with the postzygapophyses via a stout, dorsally inclined strut. The posterior centrodiapophyseal lamina (pcdl) is the longest and thinnest of the laminae and extends from the diapophyses towards the posteroventral corner of the neural arch. The paradiapophyseal lamina (ppdl) is a short anteroventral extension linking the diapophyses with the parapophyses, the latter of which appear to have risen completely above the level of the centrum, thus occupying the entire anteroventral corner of the bone. The prezygadiapophyseal lamina (prdl) extends anteriorly at a slight ventral incline to connect the diapophyses with the prezygapophyses.

The neural arch of the mid-anterior dorsal vertebra in *Antetonitrus* is acamarate as in most non-eusauropodan sauropodomorphs. The fossa bounded by the podl and the pcdl (posterior infradiapophyseal fossa *sensu* Yates, Wedel & Bonnan, 2012) extends deeply into the arch, terminating roughly level with the anterior margin of the diapophyses, although without any bone invasion (or subfossae) being present.

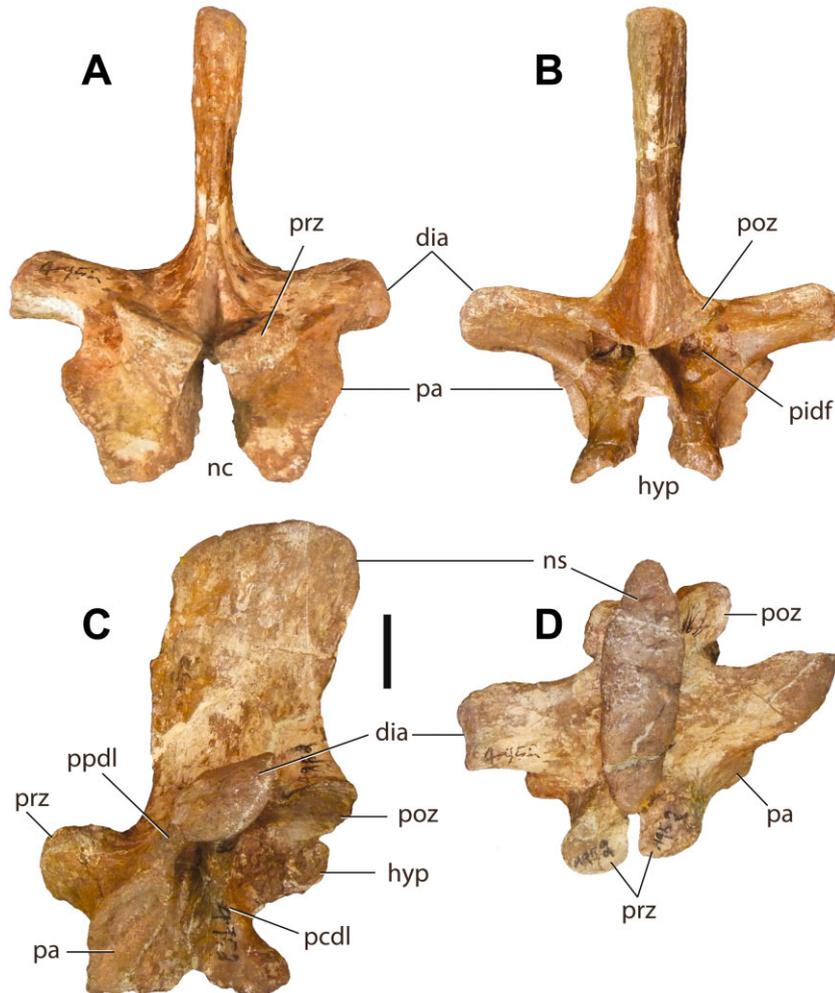


**Figure 3.** *Antetetonitrus ingenipes* (BP/1/4952), mid-anterior dorsal neural arch in A, anterior; B, posterior; and C, D, lateral views. Abbreviations: dp, diapophyses; hyp, hyposphene; nc, neural canal; ns, neural spine; pa, parapophyses; pcdl, posterior centrodiapophyseal lamina; podl, postzygodiapophyseal lamina; poz, postzygapophyses; ppdl, paradiapophyseal lamina; prdl, prezygodiapophyseal lamina; prz, prezygapophyses. Scale bar = 5 cm.

*Middle-posterior neural arch:* The neural spine of the mid-posterior dorsal arch presents the same basic proportions as in the more anterior dorsal neural arch (Fig. 4). The dorsoventral height of the neural spine is approximately 0.56 times the total height of the neural arch, whereas the height of the neural spine is roughly 1.5 times the anteroposterior length of its base. This latter ratio is relatively high for a non-sauropodan sauropodomorph, being greater than the same ratio in both *Melanorosaurus* and *Lessemsaurus* (1.3–1.47 in the mid-dorsals of PVL 4822). The condition in *Antetetonitrus* recalls that of derived sauropodan taxa (e.g. *Tazoudasaurus*; *Mamenchisaurus* Young, 1954) in which the middle dorsal neural spines are markedly dorsoventrally elongate. However, the neural spine in *Antetetonitrus*

retains the expansive anteroposterior length common to nonsauropodan sauropodomorphs. In both the mid-anterior and mid-posterior neural arches the neural spine is orientated somewhat posteriorly, with a subtle bow-like curvature of the anterior margin. This differs from the (more plesiomorphic) condition observed in *Lessemsaurus* in which the dorsal neural spines project anterodorsally along their anterior margin, so that the dorsal surfaces of the spines are anteroposteriorly expanded relative to their base. The spdl in the mid-posterior dorsal arch displays a similar degree of development as that observed in the mid-anterior dorsal arch.

Relative to the mid-anterior neural arch the zygapophyses are set at a slightly reduced angle of about 30° from the horizontal. As is typical of basal

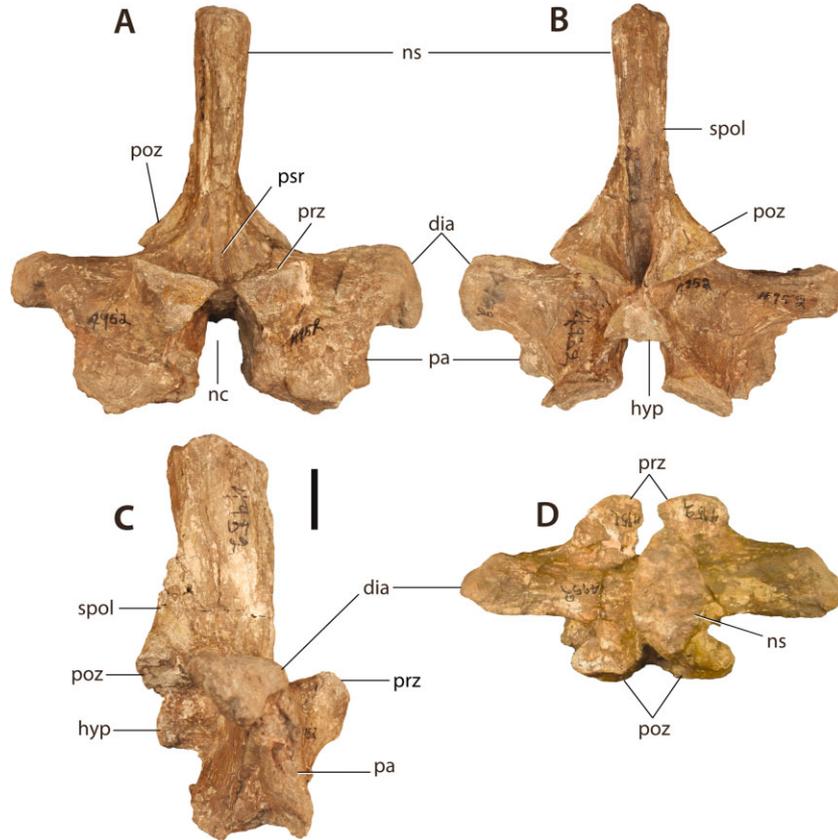


**Figure 4.** *Antetonitrus ingenipes*, mid-posterior dorsal neural arch (BP/1/4952) in A, anterior; B, posterior; C, lateral; and D, dorsal views. Abbreviations: dia, diapophyses; hyp, hyposphene; nc, neural canal; ns, neural spine; pa, parapophyses; pcdl, posterior centrodiapophyseal lamina; pidf, posterior infradiapophyseal subfossa; poz, postzygapophyses; ppdl, paradiapophyseal lamina; prz, prezygapophyses. Scale bar = 5 cm.

Sauropodomorpha, the prdl is no longer present by this point in the vertebral series, probably having been lost somewhere in the transition between the anterior-to-middle dorsal vertebrae. The ppdl and pcdl are still clearly expressed, being both shorter and more robust than in the mid-anterior dorsal arch. The mid-posterior neural arch also displays incipient spinoprezygapophyseal laminae, which bound a relatively deep prespinal sulcus, a feature shared with *Lessemsaurus*, but seen to a lesser degree in a number of nonsauropodan taxa (e.g. *Plateosaurus*; *Massospondylus*; *Aardonyx*).

The transverse processes of both posterior dorsal vertebrae of *Antetonitrus* are completely horizontal, as in all non-eusauropodan sauropodomorphs (Pol *et al.*, 2011). The orientation of the concave parapophyses in the mid-posterior neural arch is similar to that of the

mid-anterior arch, extending posterodorsally as oblique ellipsoid crests. Furthermore, as in the mid-anterior neural arch, the parapophyses are positioned only marginally anterior to the diapophyses. This condition is quite different from the morphology observed in the middle-to-posterior dorsal vertebrae of *Lessemsaurus* and most other nonsauropodan taxa (e.g. *Plateosaurus*; *Massospondylus*; *Yunnanosaurus*) where the parapophyses are set much further forward from the diapophyses than in *Antetonitrus*. In a number of basal sauropodomorph taxa (e.g. *Massospondylus*; *Lufengosaurus*; *Lessemsaurus*) this results in a pronounced, wing-like laminar shelf that runs almost horizontally between the parapophyses and the diapophyses (the ppdl), a condition that is absent in all known dorsal neural arches of *Antetonitrus*.



**Figure 5.** *Antetonitrus ingenipes*, posterior dorsal neural arch (BP/1/4952) in A, anterior; B, posterior; C, lateral; and D, dorsal views. Abbreviations: dia, diapophyses; hyp, hyposphene; nc, neural canal; ns, neural spine; pa, parapophyses; poz, postzygapophyses; prz, prezygapophyses; psr, prespinal ridge; spol, spinopostzygapophyseal lamina. Scale bar = 5 cm.

Perhaps the most important distinguishing feature of the mid-posterior neural arch in *Antetonitrus* is the presence of well-developed pneumatic subfossae that penetrate the posterior infradiapophyseal fossae on both sides. These were recently described in detail by Yates *et al.* (2012). Similar – albeit far less developed – pneumatic structures are only currently known from the dorsal vertebrae of *Eucenemsaurus* and *Aardonyx* outside of Eusauropoda [although it is possible that a posterior dorsal in *Tazoudasaurus* exhibited similar subfossae (Allain & Aquesbi, 2008: text fig. 14)].

*Posterior-most dorsal neural arch:* The neural spine of the posterior-most neural arch (possibly the last nonsacral vertebra) is straighter, shorter anteroposteriorly, and more expanded transversely than the two more anterior dorsal arches (Fig. 5). This element appears to have had relatively well-developed spinopostzygapophyseal laminae that extended for over half the dorsoventral height of the neural spine. However, as this element was damaged during a postpreparation casting attempt, the original figure from Yates & Kitching (2003: fig. 3) stands as the only

complete record. The spol frame an expansive area on the posterior surface of the neural spine that is both flatter and mediolaterally broader than the slit-shaped postspinal sulci of the two more anterior dorsal neural arches. Similarly, the anterior surface of the posterior-most neural spine is also mediolaterally expanded, lacking the incipient spinoprezygapophyseal laminae of the more anterior dorsal arches. This broad, flattened area dorsal to the base of the prezygapophyses is divided down the middle by a pronounced prespinal ridge (= ?lamina), as opposed to the more typical prespinal sulci of the more anterior neural arches. This ridge merges with the anterior margin of the neural spine as a broad keel that is less ambiguous in definition than in the two more anterior dorsal neural arches.

The prezygapophyses are smaller and less anteriorly projecting than in the two more anterior arches, with both the zygapophyseal articular facets reduced to an angle of  $< 30^\circ$ . Compared to the more anterior dorsal neural arches, the dorsoventral height of the transverse processes of the posterior-most neural arch is considerably greater than their anteroposterior

length. This is expressed throughout the element, with the vertebral arch anteroposteriorly compressed in such a fashion that no single lamina is particularly pronounced (with the exception of the spol). However, highly reduced pdcl can still be discerned, as can broad, shelf-like podl. This anteroposterior compression presages the condition common to sacral vertebrae.

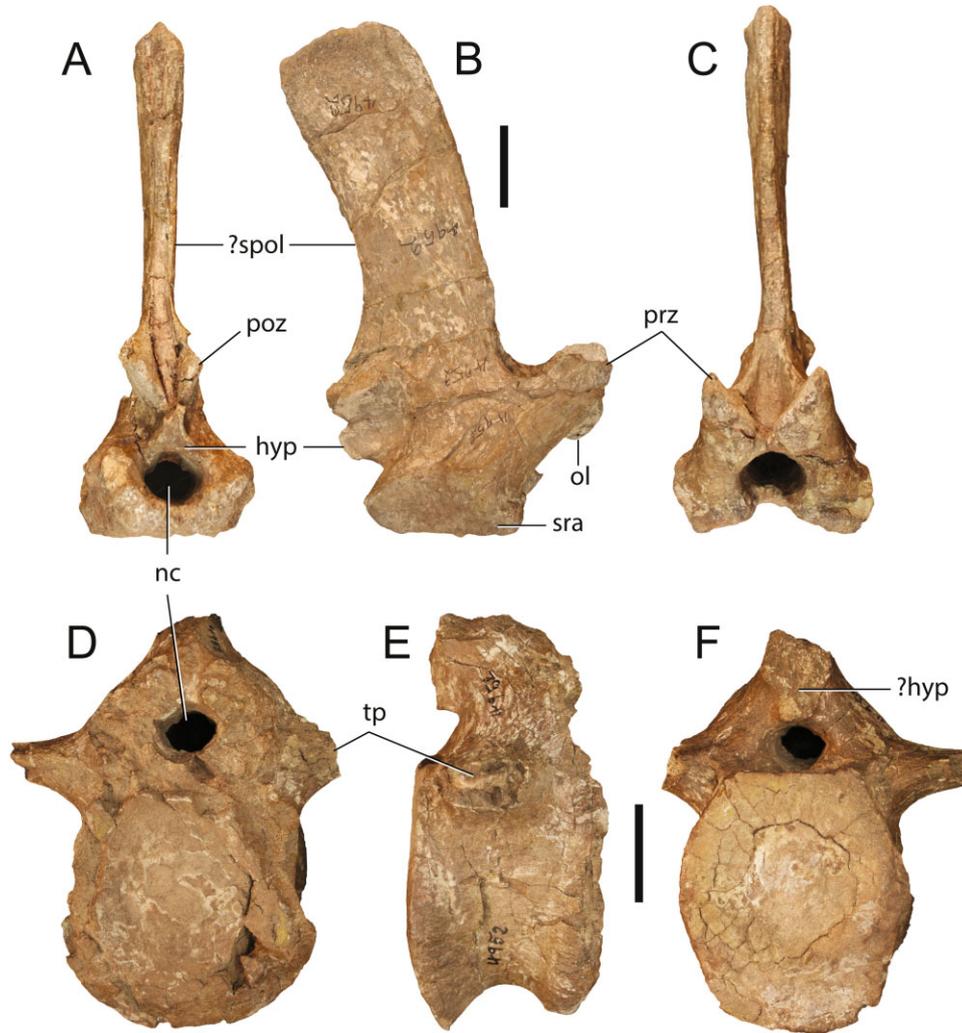
The parapophyses are present as ventrally directed ellipsoid concavities that essentially excavate the anteroventral surface of the diapophyses. The parapophyseal rim is emarginated to a similar – if not slightly more developed – degree as in the parapophyses of the mid-posterior dorsal vertebra. It is possible that this morphology presages the hollowed-out attachments for the ball-like sacral ribs

of the sacrum; however, as in vertebrae immediately anterior to the sacrum, this element may have been ribless (J. Nair, pers. comm.; see also von Huene, 1926: plate 2, fig. 3).

The hyposphene is subequal in depth to the neural canal only in the posterior-most arch. It also possesses a distinct medial ridge beginning in the middle of its posterior surface that extends along the ventral surface for most of its length. The mid-posterior arch displays a similar medial bump on the ventral surface of the hyposphene, but this is not as distinct a crest as in the more posterior arch.

#### ?Caudosacral/anterior caudal

There is an isolated neural arch (Fig. 6) that was originally allocated to the sacrum (Yates & Kitching,



**Figure 6.** *Antetonitrus ingenipes*. A–C, ?caudosacral neural arch (BP/1/4952) in A, posterior; B, lateral; C, anterior views. D–F, anterior caudal vertebra (?BP/1/4952b) in D, anterior; E, lateral; F, posterior views. Abbreviations: hyp, hyposphene; nc, neural canal; ol, ossified lip; poz, postzygapophyses; prz, prezygapophyses; spol, spinopostzygapophyseal lamina; sra, possible sacral rib articular surface; tp, transverse process. Scale bars = 5 cm.

2003). However, as both the centrum and the transverse processes/sacral ribs are missing, the possibility that it represents an anterior caudal neural arch cannot be discounted. Nonetheless, several features suggest that this neural arch belongs to the sacrum, possibly as a caudosacral, and these are discussed below.

The neural spine is remarkably tall and transversely thin, being 2.3 times higher than the length of its base and over two thirds of the height of the entire arch. The neural spine rises dorsally with a gentle posterior bowing that contrasts with the uniformly oblique angle observed in the caudal vertebrae. Where present, the caudosacrals of other sauropodomorph taxa [i.e. *Plateosaurus*; *Melanorosaurus* (NM QR1551)] are similarly arcuate, if lacking the marked dorsoventral height observed in *Antetonitrus*. The anterior margin of the neural spine appears to have had a subtle keel similar to that of the two more anterior dorsal neural arches. On the left side of the neural spine this anterior keel is demarcated by a distinct groove or sulcus that is visible along the entire dorsoventral extent of the neural spine. However, it is possible that this groove may have been exaggerated during preparation. The posterior surface of the neural spine is divided by thin, sheet-like spinopostzygapophyseal laminae that may have extended for most of the dorsoventral height of the spine, although poor preservation at the posterodorsal margin makes this difficult to confirm. This lamination is clearly absent from all the other caudal elements within the assemblage. In contrast, the postzygapophyses that form the base of the spool are reduced and steeply angled (*c.* 70°) as is typical of caudal vertebrae.

Ventral to the postzygapophyses there is a thin but dorsoventrally tall hyposphene. The presence of hyposphenes on proximal caudals/caudosacrals is a complexly distributed character throughout Sauropodomorpha. The presence of a hyposphene has been regarded as a synapomorphy of *Vulcanodon* + Sauropoda in the past (Upchurch, 1998; Yates, Hancox & Rubidge, 2004). However, there is reason to suspect that the distribution of caudal hyposphenal ridges was not restricted to Sauropoda *sensu stricto*, as a number of undescribed (and unaccessioned) proximal caudal elements from the Los Colorados Formation housed in the collections of the Instituto Miguel Lillio display hyposphenal ridges. Additionally, a small hyposphene is observable in a partial ?anterior caudal/caudosacral neural arch located amongst material informally referred to *Aardonyx* (BP/1/386), and a hyposphenal ridge has also been cited in specimens of *Melanorosaurus* (Yates, 2007a, b). A hyposphene on either the caudosacral or anterior-most caudal vertebra is subsequently regarded as a tentative apomorphy of *Antetonitrus* here.

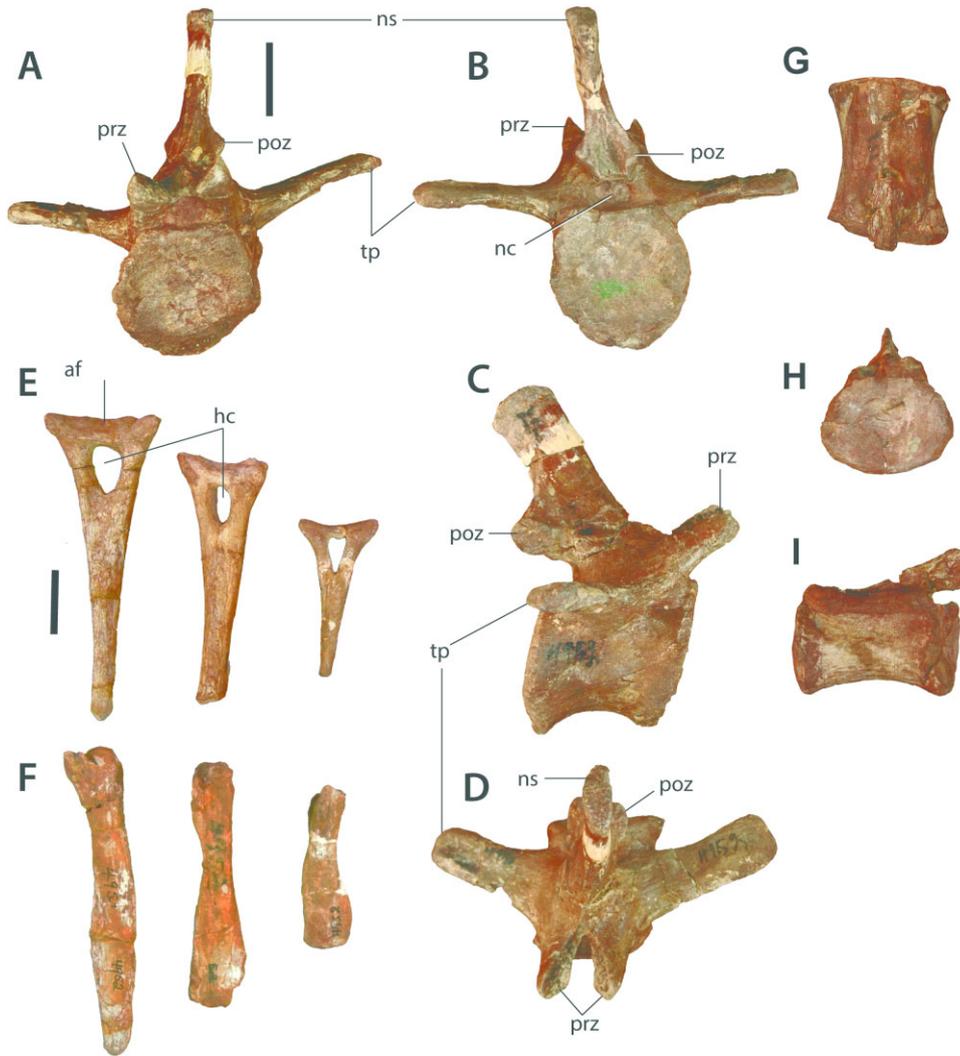
The prezygapophyses display the general caudal condition of being strongly anteriorly projected with elliptical facets set at an angle of about 70° from the horizontal (in anterior aspect). They are connected to the neural spine via well-developed spinoprezygapophyseal laminae. The prezygapophyseal facets have an ossified lip of bone that is clearly visible along their medioventral edge. This lip of bone would have provided an additional cradling mechanism for the hyposphene of the vertebra immediately anterior to it (= ?second primordial), and may potentially relate to the general strengthening of the sacral unit.

As in the rest of the caudal series the neural canal is short and circular in cross-section, lacking the pronounced dorsoventral expansion of the dorsal neural arches. Evidence that this neural arch articulated with the ilium as part of the sacral unit can be seen in the steeply inclined suture scars at the base of the arch. Many of the caudal vertebrae within the *Antetonitrus* assemblage are missing the transverse process; however, all are broken and/or snapped in a manner that one would expect from general postdepositional stresses, with no evidence of fusion lines. In contrast, the base of the neural arch described here displays the rugose, slightly concave surface reminiscent of the sacral rib articular surfaces seen in the disarticulated neural arches of other sauropodomorphs [e.g. *Lamplughosaura*; referred specimen of *Antetonitrus* (BP/1/5091)]. This unfused surface is much lower than the wing-like projections typical of the neural arches in primordial sacral vertebrae, being anteroposteriorly longer than high. The rugose concavity is bordered dorsally and posteriorly by a slight emargination.

In light of the above discussion this element is best interpreted as the posterior-most sacral vertebra or the anterior-most caudal vertebra, which may have joined the sacrum as a caudosacral. This raises the possibility that *Antetonitrus* displayed at least four sacral vertebrae (assuming the additional presence of the typical dorsosacral) as in *Leoneosaurus* and *Melanorosaurus* + Sauropoda and further corroborates the phylogenetic scenario outlined in Pol *et al.* (2011), in which a four-vertebrae sacrum represents a synapomorphy of the above taxa.

#### Caudal vertebrae

There are 12 caudal vertebrae present. Based on relative proportions it is likely that the majority (ten) belong to a larger individual, whereas at least two are from a smaller, possibly juvenile individual. A mid-anterior caudal (Fig. 7) from the smaller specimen is the only fully complete caudal vertebra present and therefore forms the main focus of the following description, although changes throughout the series are also be addressed.



**Figure 7.** *Antetonitrus ingeniipes*. A–D, mid-caudal vertebra (small individual: BP/1/4952b) in A, anterior; B, posterior; C, lateral; and D, dorsal views. E–F, chevrons (BP/1/4952) in E, posterior and F, lateral views. G–I, posterior caudal (BP/1/4952) in G, dorsal; H, anterior and I, lateral views. Abbreviations: af, articular facet; hc, haemal canal; nc, neural canal; ns, neural spine; poz, postzygapophyses; prz, prezygapophyses; tp, transverse process. Scale bar = 5 cm.

The caudal vertebrae of *Antetonitrus* are broadly typical all of non-eusauropodan sauropodomorphs. All of the caudal centra within the assemblage are shallowly amphicoelous and constricted mediolaterally with a deeply concave (when viewed laterally) ventral surface. As in all non-eusauropodan sauropodomorphs the neural arch (where preserved) occupies the majority of the anteroposterior length of the centrum, being generally confluent with the anterior face of the centrum, and set slightly forward from the posterior face. The ventral surfaces of the articular faces of all caudal centra display the characteristically thickened lip that represents the oblique articular facets for the chevrons. This is generally most developed on the posteroventral surface, which is interesting given

that none of the preserved chevrons display a clear proximo-anterior facet – the facet that would have articulated with the posteroventral surfaces of the caudal centra.

An anterior caudal vertebra (also possibly from the smaller individual) that is missing both its transverse processes and neural spine represents the most anterior caudal, although its precise position is unknown (Fig. 6). As is typical of anterior caudal vertebrae in derived sauropodomorphs (e.g. *Lufengosaurus*; *Aardonyx*) the centrum is much higher than long, with its anteroposterior length being 0.66 times its dorsoventral height. The articular faces are slightly ovoid, being higher than transversely wide, with neither surface offset relative to the other. This

element fails to display the ventral excavation of the anterior caudal centrum described for *Vulcanodon* and an unnamed sauropod from the Upper Elliot Formation (BP/1/6105: possibly referable to *Vulcanodon*; Yates *et al.*, 2004). As in those specimens it is possible that the anterior-most caudal vertebra of *Antetonitrus* may have possessed a hyposphenal ridge, although breakage to the neural arch prior to the level of the postzygapophyses makes this impossible to confirm.

In the fully complete mid-anterior caudal the transverse processes extend posterolaterally with a slight dorsal elevation, becoming increasingly posteriorly swept-back in more posterior vertebrae. The transverse processes in this element are long, being only slightly shorter than the neural spine (Fig. 7). There is a moderately deep fossa beneath the buttress connecting the transverse processes to the prezygapophyses, a feature that can also be seen in a mid-anterior caudal vertebra of *Aardonyx*, but cannot be distinguished in any other of the *Antetonitrus* caudals. The prezygapophyses project well forward from the anterodorsal margin of the centrum; their articular facets are elongate and set at an angle of about 50°. There are no spinoprezygapophyseal laminae present, although an incipient keel is visible on the ventral margin of the anterior surface of the neural spine. The postzygapophyses are set at a slightly steeper angle than the prezygapophyses, and also lack clear laminae. The neural spine is relatively deep, being approximately three-quarters of the anteroposterior length of the base of the neural arch. Neural spines of anterior caudal vertebrae that are greater than half the length of their associated neural arch has been cited on more than one occasion as a synapomorphy of sauropodomorphs basal to Sauropoda (i.e. 'Prosauropoda') (Yates, 2003a; Upchurch *et al.*, 2007a). However, the cogency of this character is questioned here because several basal (and not so basal) sauropods (e.g. *Tazoudasaurus*; *Shunosaurus*; *Barapasaurus* Jain *et al.*, 1975) display anterior neural spines that are clearly over half the anteroposterior length of the neural arch – although it is not clear if 'neural arch length' is intended as meaning between the zygapophyses or along the contact-line with the centrum (although it would appear that the above still applies even in the case of the former, see Zhang, 1988; Allain & Aquesbi, 2008: text-fig. 16). The neural spine of the complete mid-anterior caudal is minimally transversely expanded and directed posteriorly at an angle of about 50°.

The articular facets of the caudal centra become progressively more circular in posterior elements of the series. This differs from closely related taxa such as *Melanorosaurus* and *Aardonyx* that tend to display posterior caudals that are slightly square-shaped in

cross-section with flat, nonconvex ventral surfaces. This is accompanied by a general lengthening of the centrum relative to its height, with the neural arch positioned slightly more anteriorly from the mid-caudals onwards. Towards the posterior end of the series the transverse arches become progressively more posteriorly swept-back, being ultimately reduced to low ridges on the lateral sides of the centrum in the posterior-most caudals. Likewise, the neural spine becomes progressively more posteriorly located, disappearing entirely in the posterior-most elements (Fig. 7). These changes can be observed in the caudal series of most sauropodomorph taxa (e.g. *Lufengosaurus*, *Yunnanosaurus*).

#### Chevrons and ribs

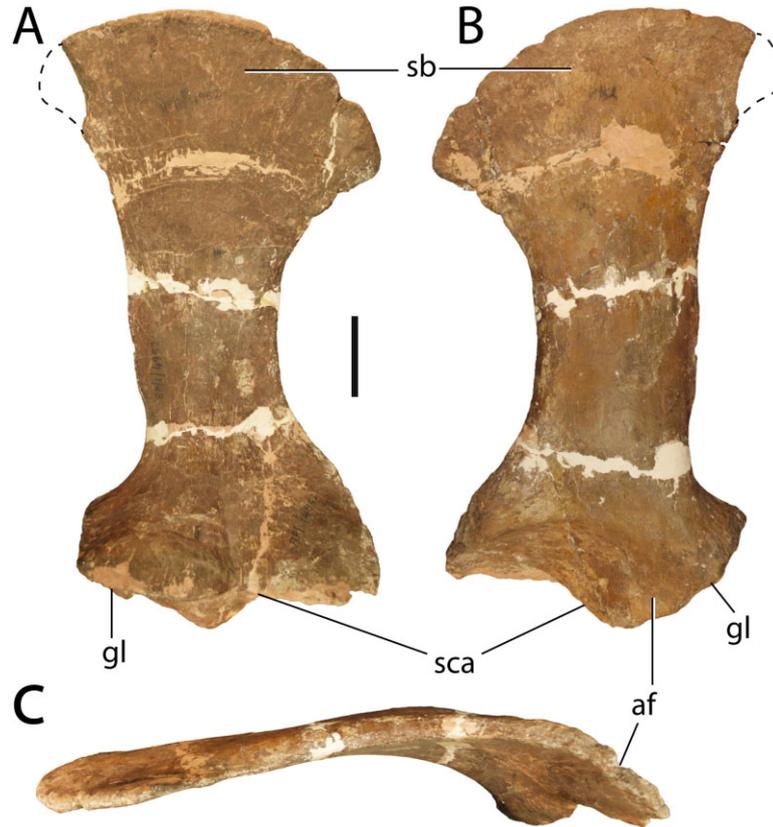
There are two dorsal ribs present. Although they are preserved together in close proximity and lying parallel to one another, their distal and proximal ends are juxtaposed – indicating the degree of taphonomic displacement that the *Antetonitrus* assemblage experienced prior to fossilization. Both ribs have long, curved shafts, although only one completely preserves the capitulum and tuberculum, which are typically diapsidan in appearance. There is the partial shaft of a third rib obliquely overlying these two elements.

There are several isolated chevrons of typical non-eusauropodan morphology (Fig. 7). The proximal end forms the distinctive Y shape whereupon it is transversely bridged by the posterodorsally concave inter-centrum facet. Unlike a number of derived sauropodomorphs that appear to have possessed an additional facet on the anterior margin of the proximal surface for articulation with the caudal centra (e.g. *Lamplughsaura*; *Aardonyx*; *Tazoudasaurus*), *Antetonitrus* presents but one large posterodorsal facet. Distal to this facet is the prominent, triangular foramen (= haemal canal) for the caudal blood vessels (Cooper, 1984). In all preserved chevrons the distal blade is mediolaterally compressed; however, the distal end of the blade in more posteriorly located chevrons becomes increasingly truncated and anteroposteriorly expanded, potentially presaging the distally forked chevrons of later sauropodan taxa [although a similar distal expansion is observable in other non-eusauropodan sauropodomorphs (e.g. *Plateosaurus*)].

#### Appendicular skeleton

##### Scapula

There are three scapulae present, all belonging to separate individuals. In accord with the revised diagnosis (see above), these scapulae are hereafter referred to as BP/1/4952 (a large left), BP/1/4952b (a small right), and BP/1/4952c (another left, slightly



**Figure 8.** *Antetonitrus ingenipes*, left scapula (BP/1/4952c) in A, medial; B, lateral; and C, anterior views. Abbreviations: af, acromion facet; gl, glenoid; sb, scapular blade; sca, scapular–coracoid articulation. Dashed line represents missing bone. Scale bar = 10 cm.

smaller in dimension than BP/1/4952). As BP/1/4952b is missing a portion of its anteroventral corner, BP/1/4952 and BP/1/4952c form the main focus of the following description (Fig. 8).

The scapula of *A. ingenipes* is notably similar to that of *Lessemsaurus sauropoides* (PVL 4822/51; Pol & Powell, 2007). As mentioned in the Material and methods, we assume an orientation where the distal end (free end) of the scapula is directed dorsally, where the acromial end of the scapula is directed ventrally, and where the surface of the scapula closest to the ribs is medial. As in *Lessemsaurus* both the ventral and dorsal ends are strongly expanded. The anteroposterior expansion of the dorsal end is 0.54 in proportion of total scapular length whereas the ventral end is slightly less expanded at 0.50. These proportions are almost identical to the same measurements in *Lessemsaurus*. As mentioned by Pol & Powell (2007: 27), the vast majority of basal sauropodomorphs (e.g. *Plateosaurus*; *Massospondylus*; *Lufengosaurus*; *Coloradisaurus*; *Anchisaurus*) lack this pronounced expansion of the dorsal end of the scapular blade, and certainly do not display scapulae in which the dorsal expansion is greater than that of the ventral. However,

species such as *Riojasaurus*, *Yunnanosaurus*, and (possibly) *Gongxianosaurus* He *et al.*, 1998, although presenting a ratio of dorsal expansion to total scapular length that is lower than that of *Antetonitrus* and *Lessemsaurus*, still exhibit a relatively strong dorsal expansion with respect to the ventral end of the scapula. Interestingly, the majority of sauropodan taxa (e.g. *Isanosaurus*; *Shunosaurus*) present relatively attenuated scapular blades when compared with the condition observed in *Antetonitrus* and *Lessemsaurus*.

The ventral portion of the lateral surface is concave because of the deep acromion facet. This process occupies most of the lateral surface of the anteroposteriorly expanded ventral portion of the scapula, stretching as an ovoid fossa from the broken clavicular facet [possibly present in the largest left scapula (BP/1/4952) as a slight widening of the anterodorsal margin of the acromion, but this is also obscured by poor preservation] to just anterior of the glenoid region. The acromion facet is not bounded anterodorsally by an acromial ridge, and in this respect the scapula of *Antetonitrus* is more similar to non-eusauropodan sauropodomorphs than to more derived neosauropods, which bear this feature

(Upchurch *et al.*, 2004). The anteroventral margin (= coracoidal suture) of the acromion facet is markedly thin whereas it thickens dramatically in the posterior half, being thickest at the distinct 'step' where the coracoidal articular surface meets the glenoid facet. As noted by Remes (2008), the scapulocoracoidal articular surface possesses a ventrally extending lateral lip. A similar ventrolateral lip can be seen in the scapula of *Melanorosaurus* (NM QR1551). Both the glenoid and the coracoidal articular surfaces are strongly rugose.

Anteriorly, the medial surface of the ventral scapula is gently convex, whereas the posterior side of the medial surface rises as a pronounced convex ridge that runs from the coracoidal articular suture to a point about a third of the way along the ventromedial length of the shaft. According to the myological reconstruction of Remes (2008), this ridge delimits the facet for the *M. subscapularis* anteriorly, and the smaller facet for the *M. serratus superficialis* posteriorly. A similar ridge can be seen in most sauropodomorph taxa. The long axis (anteroposterior) of the ventral expansion and the long axis of the scapular blade form an angle of about 70°, with the scapular blade angled slightly anteriorly relative to the ventral end. This angle is slightly reduced compared to the perpendicular angle present in most basal sauropodomorphs, but still shy of the substantially reduced angle (c. 40–50°) exhibited by some sauropodan taxa (e.g. *Spinophorosaurus* Remes *et al.*, 2009; *Barapasaurus*; *Omeisaurus* Young, 1939).

The minimum anteroposterior width at the mid-shaft of the scapular blade of *Antetonitrus* constitutes approximately 0.23 times the total length, extremely similar to that of *Lessemsaurus*. As mentioned by Pol & Powell (2007: 227), most sauropodomorphs have narrower scapular shafts with ratios varying between 0.15 and 0.17. This is true for both *Melanorosaurus* (0.17: NM QR1551) and for a number of basal sauropod taxa including *Isanosaurus* and *Shunosaurus*. It is possible that *Gonxianosaurus* may have displayed a broadened scapular shaft relative to total length, but an updated description of this poorly known taxon is required to confirm the presence or absence of this character. On the posterior margin of the scapular shaft there is a slight caudal flange that is associated with the facet for the *M. serratus superficialis* medially (Remes, 2008).

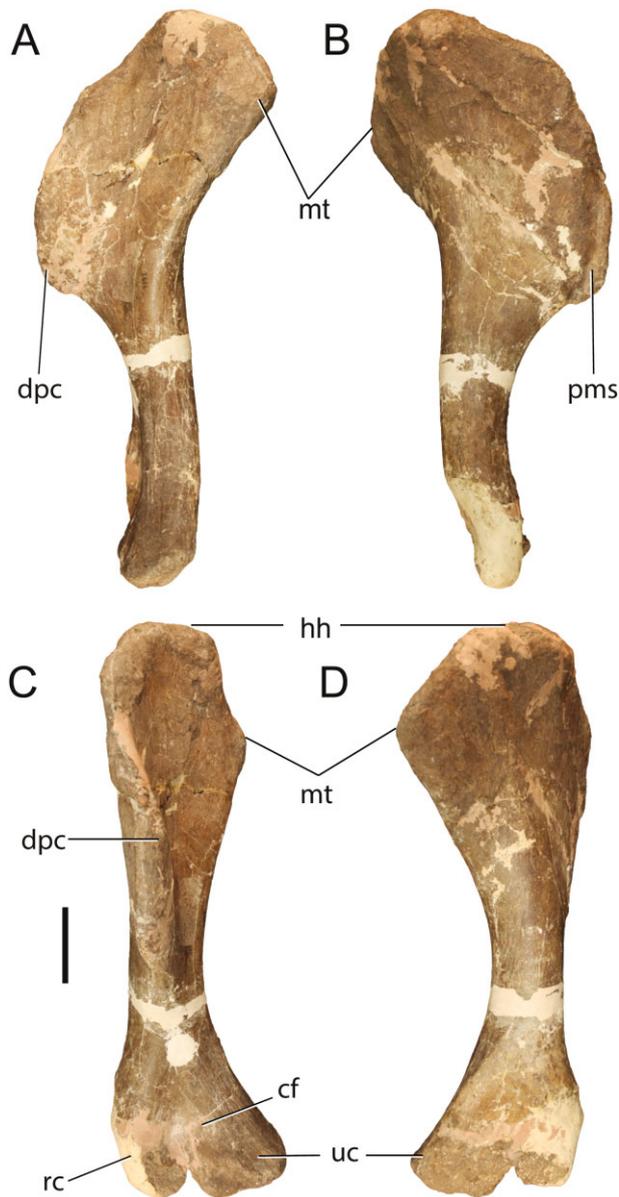
The dorsal surface of the scapular blade is thin, planar, and presents the typical convex outline in either medial or lateral view. As in *Lessemsaurus*, the largest scapula of *Antetonitrus* (BP/1/4952; broken in the other two elements) displays an acute flange on the posterior edge of the dorsal blade that exceeds the posteroventral corner of the ventral end in posterior expansion. This flange, along with the pronounced

general expansion of the dorsal blade, means that both the anterior and (to a lesser degree) the posterior margins of the scapular blade in *Antetonitrus* are strongly concave.

#### Humerus

There are two right humeri; the larger (BP/1/4952) is nearly complete but is missing most of the radial condyle. The proximal half of the deltopectoral crest of the smaller humerus (BP/1/4952b) is damaged and the distal condyles – although complete – are flattened in a manner similar to the humeral head. The resulting effect is that the axis of both the distal and proximal halves of the smaller humerus lie in much the same plane. It is difficult to confidently associate either humerus with any of the scapulae. The length of the largest humerus is approximately 0.93 times the length of the largest scapula (BP/1/4952). This ratio is relatively high for sauropodomorphs, although the authors' personal observation of postcranial material collected under *Melanorosaurus readi* (NM QR1551) suggests a similar relationship between scapula and humerus in that taxon, and the newly described *Seitaad ruessi* (UMNH VP, 18040: Sertich & Loewen, 2010) may also have potentially displayed similar proportions (however, UMNH VP, 18040 remains partially obscured by matrix). The length of the smaller right humerus is 0.78 times the length of the smallest scapula (also from the right side), a proportion comparable to most derived sauropodomorphs (i.e. *Lunfengosaurus*; *Yunnanosaurus*; *Shunosaurus*). The larger humerus provides the main focus for the following description (Fig. 9).

The proximal half of the bone is subrectangular in lateral view and is offset about 45° from the transverse axis of the distal condyles, although this approaches almost 90° at the apex of the deltopectoral crest. In this regard the humerus of *Antetonitrus* retains the plesiomorphic morphology of basal sauropodomorph taxa such as *Plateosaurus*, *Lufengosaurus*, and *Massospondylus*, which also display a similarly strong axial twist of the humeral shaft. In contrast, a number of other non-eusauropodan sauropodomorphs (i.e. *Lessemsaurus*; *Vulcanodon*; *Tazoudasaurus*) display a reduced axial twist; hence, the roughly symmetrical 'hourglass' morphology of the humerus of these taxa viewed in anterior aspect. However, Yates (2003a) and Remes (2008) have cautioned that the relative orientation of the deltopectoral crest (and hence the full degree of axial twist) is susceptible to geomorphological processes, and is therefore not a good indicator of either phylogeny or function. The markedly different orientation of the deltopectoral crests exhibited by the two humeri in the *Antetonitrus* assemblage is emblematic of this phenomenon.



**Figure 9.** *Antetonitrus ingenipes*, right humerus (BP/1/4952) in A, medial; B, lateral; C, anterior; and D, posterior views. Abbreviations: cf, cuboid fossa; dpc, deltopectoral crest; hh, humeral head; mt, medial tuberosity; pms, paramarginal sulcus; rc, radial condyle; uc, ulnar condyle. Scale bar = 10 cm.

The transverse width of the distal portion of the humerus is approximately 0.30 times the total length of the bone, whereas the oblique anteroposterior expansion of the proximal half is 0.46 times the total humeral length. These proportions are similar to most derived sauropodomorphs; however, *Lessem-saurus* and *Yunnanosaurus* are notable for having distally expanded condyles exceeding 0.4 times the total humeral length.

Proximally, the head of the humerus is strongly convex, displaying the vaulted morphology characteristic of all sauropodomorphs more derived than the Plateosauridae (= Massopoda *sensu* Yates, 2007a, b). The transverse width of the humeral head is thickest at the point where it would have articulated with the glenoid, after which it tapers posteromedially to form a sharp angle with the posteromedial corner (medial tuberosity) of the bone. As noted by Remes (2008) the mediolateral expansion of the head exceeds the borders of the humeral shaft, although it lacks the pronounced incursion onto the proximoposterior side of the shaft observed in *Riojasaurus* (and also to a lesser degree in *Massospondylus*, *Coloradisaurus*, and *Adeopapposaurus*). Although present, the medial tuberosity is less pronounced than in the humeral head of most nonsauropodan sauropodomorphs (e.g. *Massospondylus*; *Lufengosaurus*; *Yunnanosaurus*) and is deflected slightly medially, as opposed to the posterolateral deflection of basal sauropodomorph taxa such as *Massospondylus*, *Coloradisaurus*, and *Lufengosaurus* (= the Massospondylidae).

The medial surface of the proximal half is gently concave, whereas the lateral surface is almost entirely flat and is bordered anteriorly by the pronounced deltopectoral crest. This crest extends for roughly half of the length of the entire bone but is not as high and sharply demarcated as that of many nonsauropodan sauropodomorphs (e.g. *Plateosaurus*; *Riojasaurus*; *Lufengosaurus*). In the original description of *Antetonitrus* Yates & Kitching (2003: 1754) stated that ‘the deltopectoral crest does not extend for half the length of the humerus as it does in prosauropods’; however, the deltopectoral crest can be clearly shown to be at least half of the entire length of the humerus. In the smaller humerus, however, the deltopectoral crest is comfortably within the proximal half of the bone, possibly representing an effect of either ontogeny or variation. In lateral view, the profile of the deltopectoral crest of *Antetonitrus* is rounded and anteriorly convex as in *Lessem-saurus* and *Leonerasaurus*, but with a steeper distal margin than in those taxa. In contrast, other non-eusauropod sauropodomorphs have a sharply delineated, subrectangular profile with a straight and vertically orientated anterior margin (Pol *et al.*, 2011). On the laterodistal margin of the deltopectoral crest there is a clear paramarginal sulcus, a possible autapomorphy that is shared with the smaller humerus [although a similar sulcus can be seen on the anterolateral surface of the deltopectoral crest in *Riojasaurus* (PVL 3808) and *Melanorosaurus* (NM QR3314)]. However, with the exception of this sulcus the deltopectoral crest is relatively uniform, lacking both sinuosity and the raised, irregular topography seen in a number of

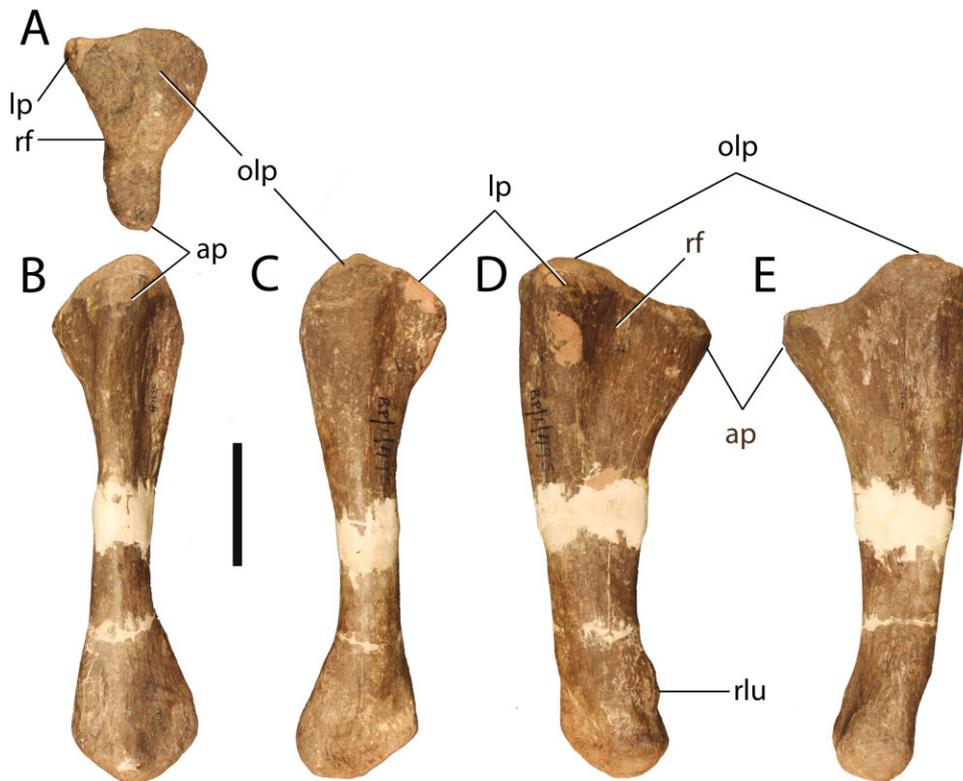
nonsauropodan sauropodomorphs (e.g. *Lufengosaurus*; *Riojasaurus*; *Massospondylus*).

The humeral shaft is short, robust, and subcircular in cross-section, with a slight anterior curvature when viewed laterally. There is a relatively deep cuboid fossa (= intercondylar cavity) on the anterior surface of the distal humerus. This is a plesiomorphic feature generally absent in Eusauropoda that has been hypothesized either as accepting the radius during flexion (Bonnar & Senter, 2007; Bonnar & Yates, 2007) or as a receptacle for synovial fluids (Remes, 2008: 251). The posterior surface of the distal condyles is flat and extensive. Slight erosional damage makes it difficult to discern the true extent of the olecranon fossa; however, this appears to have been only weakly developed. The distal condyles display a clear transverse expansion. However, damage to the lateral (radial) condyle makes it difficult to know the exact proportion and delimitation of each respective condyle, although extrapolating from the complete medial condyle gives a total mediolateral width of only 0.33 times total bone length for the distal end. This is a similar ratio to that is observed in the more distally complete smaller humerus and is within the lower value-range for basal sauropodomorphs.

#### Ulna

There are three well-preserved ulnae; a large left and right (BP/1/4952) of equal size probably belonging to the same individual; and a smaller right (BP/1/4952b) element. The distal end of the smaller ulna is slightly medially deflected compared to the larger elements. This may be the result of differences in variation, ontogeny, or diagenesis. However, at this point it is impossible to distinguish amongst any of the above processes. The complete larger right element (BPI/4952) is the best preserved and forms the focus of the following description (Fig. 10). This ulna is 0.6 times the length of the humerus (identical to that of *Melanorosaurus*: NM QR3314 and *Lessemsaurus*) and therefore possibly belongs to the same individual.

The ulna is a solid, robust bone that is most similar in general appearance to the ulna of *Plateosauravus* (SAM 3351: Van Heerden, 1979; Remes, 2008). Proximally, the ulna of *Antetonitrus* possesses both the standard anterior process typical of saurischians and an additional lateral process characteristic of Sauropoda (Bonnar & Yates, 2007: 161). Although not as distinctly triradiate as the Y-shaped proximal ulnae of the more derived eusauropods, the enlarged lateral process delimits a moderately deep radial



**Figure 10.** *Antetonitrus ingenipes*, right ulna (BP/1/4952) in A, proximal; B, anterior; C, posterior; D, lateral; and E, medial views. Abbreviations: ap, anterior process; lp, lateral process; olp, olecranon process; rf, radial fossa; rlu, radial ligament of the ulna. Scale bar = 10 cm.

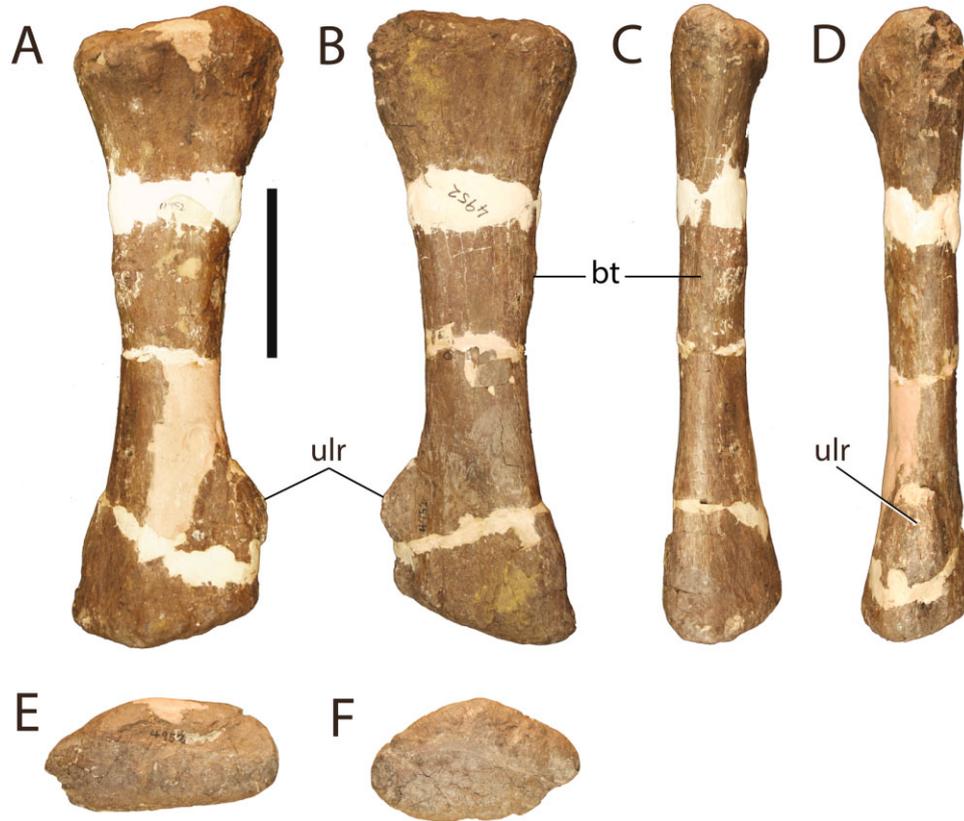
fossa that is similar in appearance – albeit less developed – than the same process in *Vulcanodon*. This fossa may have been instrumental in facilitating the anteromedial rotation of the proximal radius around the ulna, a shift in forearm orientation now generally associated with the pronation of the manus (Bonnar, 2003; Bonnar & Yates, 2007). The possession of a distinct radial fossa distinguishes *Antetonitrus* from most basal sauropodomorph species, which possess a more triangular proximal ulna with a blunt, rounded, and short lateral process. A similarly developed lateral process is seen in *Melanorosaurus*, *Lessemsaurus*, and the recently described *Aardonyx celestae* (Yates *et al.*, 2010). However, *Melanorosaurus* (NM QR3314; SAM PK 3532) can be distinguished from most other closely related taxa on account of its acutely developed medial process, which is almost equivalent to that of the lateral process. As in *Melanorosaurus*, the anterior process of *Antetonitrus* is slightly concave proximally whereas the lateral process is strongly convex. A curious medially directed extension of the anterior process, especially marked in the larger right ulna, possibly represents an additional autapomorphy of *Antetonitrus*. Unfortunately, most of the anterior process appears to have been eroded prior to discovery in the companion left ulna, but a distinct medial deflection can still be seen. As in sauropodomorphs basal to the ‘*Vulcanodontidae*’ (*Vulcanodon* + *Tazoudasaurus*) there is a strongly convex olecranon process that occupies the majority of the proximal surface.

If the ulna is positioned so that the anterior and lateral processes transversely frame an anteriorly facing radial fossa, then the mediolateral expanse of the proximal surface constitutes 0.38 in proportion of total ulna length, whereas the anteroposterior expanse of the distal bone is only 0.25 in proportion of the total ulna length. However, as there still appears to be some confusion regarding the precise life orientation of the ulna in most large sauropodomorph taxa (Bonnar & Yates, 2007 *contra* Pol & Powell, 2007), the mediolateral expansion of the proximal end would only be 0.26 in proportion of the total length if positioned so that the anterior process faces directly forward. In this case both proximal and distal ends display proportionately less mediolateral expansion than in *Lessemsaurus* (Pol & Powell, 2007). Just distal to the radial fossa is a small, slightly rugose tubercle that most likely provided ligamentous attachments for the posterior edge of the proximal radius. On account of the autapomorphic deflection of the anteromedial process the medial surface is equally as concave as the lateral surface, where the radial fossa is located. The posterior surface is gently convex and only about 0.66 times the proximal expansion of the other two surfaces.

The shaft is strongly elliptical and runs in the same plane as the anteromedial process before shifting to a transverse expansion in the distal third of the bone. The distal end is twisted about 15° medially relative to the anteroposterior axis of the proximal surface. On the anterolateral corner of the distal end there is a pronounced tuberosity that corresponds with a similarly rugose bump on the posterior edge of the radius. These are the attachments for the radio-ulna ligament and can be seen in most basal sauropodomorph taxa (Cooper, 1981). This condition appears to be the opposite of that in derived sauropods in which the distal radial fossa of the ulna cradles the radius distally [hypothesized as restricting movement at the wrist during quadrupedal locomotion (Bonnar, 2003)]. However, as a distinct bump is still present in the distal ulna of the basal sauropod *Tazoudasaurus* (Allain & Aquesbi, 2008: fig. 22), this condition is therefore not seen as precluding the possibility of manual pronation. As mentioned by Remes (2008), the posterior side of the distal expansion is characterized by a large, pitted depression that merges with the transversely expanded distal articular surface. The distal surface is ovoid in shape, and bears the same rugose texture as the proximal end.

#### Radius

There is a single complete radius (BP/1/4952) that articulates well with the right ulna. The radius is a straight, morphologically simple element with the proximal and distal expansion of both ends roughly equivalent and in the same plane (Fig. 11). This is in contrast to the morphology of basal sauropodomorph taxa such as *Massospondylus*, *Lufengosaurus*, and *Seitaad*, in which the ends exhibit a modest axial twist with respect to one another. The proximal surface is subovoid with a simple planar articular surface that rises slightly posterolaterally. The long, elliptical proximal surface indicates the absence of a mobile rotary elbow joint, and hence ‘active’ manual pronation in *Antetonitrus* would have probably been rather limited. The shaft is elliptical in cross-section, being substantially wider anteroposteriorly than mediolaterally. The lack of anteroposterior constriction of this bone contrasts with the slender, rod-like shape of the radial shaft in a number of nonsauropodan sauropodomorphs (e.g. *Thecodontosaurus* Riley & Stutchbury, 1836; *Plateosaurus*; *Lufengosaurus*; *Riojasaurus*). In medial and lateral views the radius is markedly similar to that of *Melanorosaurus* (SAM-PK-K3532) and *Lessemsaurus* (‘lateral’ view in Pol & Powell, 2007: fig. 4c). The stout radius (and ulna) of *Melanorosaurus*, *Lessemsaurus*, and *Antetonitrus* is also distinct from the markedly more elongate and slender radii of *Vulcanodon* and *Tazoudasaurus*. *Antetonitrus* also lacks the distinct medial bowing



**Figure 11.** *Antetonitrus ingenipes*, right radius (BP/1/4952) in A, medial; B, lateral; C, anterior; D, posterior; E, proximal; and F, distal views. Abbreviations: bt, biceps tubercle; ulr, attachment for ulnar ligament of the radius. Scale bar = 10 cm.

seen in more derived sauropods (e.g. *Vulcanodon*; *Camarasaurus* Cope, 1877).

Immediately proximal to the midshaft on the anterior edge there is a clear rugose tubercle for the attachment of the *M. biceps* (clearly present also in *Aardonyx*). The posterodistal edge displays a pronounced tuberosity that participates with a similar rugosity on the anteromedial corner of the ulna. This represents the attachment sites for ligamentous tissues that Bonnan (2003) and Bonnan & Yates (2007) hypothesized as a supportive mechanism that limited the movement of the radius at the wrist. The distal articular surface is similar in size but slightly more ovoid than the proximal surface. It is gently convex and slopes upwards towards the posterior corner at a slightly greater angle than the similarly orientated proximal surface. A distal end that is proximally offset from the perpendicular angle formed with the long axis of the radial shaft has been hypothesized as further assisting in manual pronation by Remes (2008).

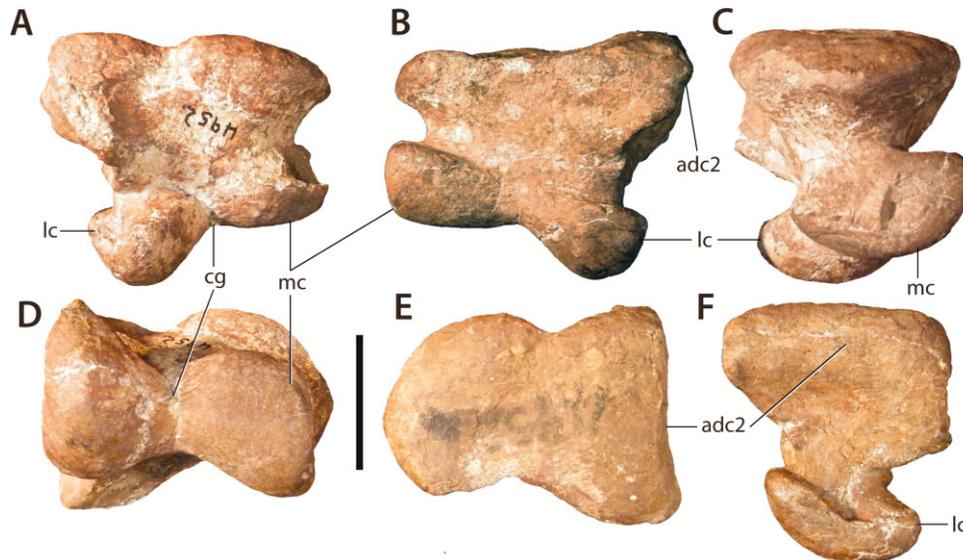
#### Manus

The manus of *A. ingenipes*, as preserved, is restricted to a right metacarpal 1, its companion phalanx 1.1,

and two second metacarpals. In the original description of *Antetonitrus* (Yates & Kitching, 2003) both second metacarpals were assigned to the holotype. However, although the second metacarpals are of equivalent size, both elements are from the same side, and therefore do not belong to a single individual. Previous reconstructions of the *Antetonitrus* hand (Yates & Kitching, 2003; Remes, 2008) have figured the second metacarpal as articulating with the lateral side of the first metacarpal, and therefore constituting the medial half of the metacarpus of a right hand. However, comparison with a fully articulated and fused inner carpus and metacarpus (BP/1/386) found amongst material referred to *Aardonyx* clearly indicates that both the second metacarpals of *Antetonitrus* belong to the left side; therefore showing that the figured articulation in Yates & Kitching (2003) and Remes (2008) could not be correct (see Fig. 13). Unfortunately, this reduces the scope of inference regarding the functional manoeuvrability and locomotory limitations of the *Antetonitrus* hand.

#### Metacarpal 1

The first metacarpal in *Antetonitrus* is markedly stout and wide, with the mediolateral width of the flat



**Figure 12.** *Antetonitrus ingenipes*, right metacarpal 1 (BP/1/4952) in A, dorsal; B, ventral; C, medial; D, distal; E, proximal; and F, lateral views. Abbreviations: adc2, articular surface for distal carpal 2; cg, central ginglymus; lc, lateral condyle; mc, medial condyle. Scale bar = 5 cm.

proximal surface exceeding the proximodistal length of the bone (Fig. 12). The mediolateral width of the proximal end is 1.18 times the total length of the bone. *Aardonyx* (1.12: BP/1/5379) and *Melanorosaurus* (NM QR3314) exhibit similarly short and broad first metacarpals, whereas *Lessemsaurus* is stouter still with a ratio of about 1.26. In contrast, all other derived nonsauropodan sauropodomorphs display proportionally longer first metacarpals with values ranging from the 0.65 and 0.7 seen in *Anchisaurus* and *Plateosaurus*, respectively, to the subequal ratios of *Yunnanosaurus*, *Lufengosaurus*, and *Seिताad*. Eusauropodan taxa also display elongated first metacarpals, although the width/length ratio of *Shunosaurus* remains relatively stout at 0.94 (Zhang, 1988: fig. 49). The first metacarpal tends to lengthen closer to Neosauropoda, where the manus adopts the characteristic semitubular colonnade interpreted to be mechanically advantageous in supporting graviportal locomotion (Bonnan, 2003). The proximal articular surface is constricted at the midpoint of the transverse plane, mainly on account of a proximomedial articular surface that is almost as expanded dorsoventrally as the proximolateral surface. Most other basal sauropodomorphs (e.g. *Plateosaurus*; *Massospondylus*) have a proximomedial articular surface that tapers to a clear point, hence the subtriangular proximal outline of their first metacarpals. In comparison, the proximal outline of the first metacarpal of *Antetonitrus* is keyhole in shape.

The lateral margin of the proximal surface of the first metacarpal exceeds the lateral extent of the

lateral distal condyle. This feature is not commonly displayed in basal sauropodomorphs, although *Seिताad* and potentially *Lufengosaurus* show a similar proximolateral expansion (Young, 1941; Sertich & Loewen, 2010). The lateral margin of the proximal end is proximodistally broad and dorsoventrally extensive, possibly delimiting the synovial joint against which the second distal carpal would have rested—effectively precluding distal carpal 1 from articulating with the proximal surface of metacarpal 2 (Serenó, 1999, 2007). The first metacarpal of *Lessemsaurus* also displays this proximolateral flattening, indicating that it may have been inset into the carpus in a similar fashion; a configuration clearly visible in the similarly proportioned manus of BP/1/386 (= *Aardonyx*). This configuration of carpus and metacarpus has been cited on numerous occasions (Serenó, 1999; Galton & Upchurch, 2004) as synapomorphic evidence uniting a monophyletic ‘Prosauropoda’. However, although distal carpal 2 appears to have been lost by that point of sauropodomorph evolution, an intermediate morphology is potentially observable in the articulated manus of a juvenile individual of *Tazoudasaurus* (Allain & Aquesbi, 2008: fig. 23).

Distal to the synovial joint the proximolateral fossa (where the second metacarpal would have articulated) is large and dorsoventrally extensive, occupying the majority of the lateral surface. The medial surface, on account of the limited proximodistal extension of the shaft, is reduced to a short concave ridge between the proximal surface and the medial condyle. As in all

nonsauropodan sauropodomorphs, the distal articular condyles are strongly asymmetrical, with the medial condyle expanded mainly ventrally and the lateral condyle expanded mainly dorsally. The mediolateral width of the medial condyle exceeds that of the lateral condyle, a configuration also present (although to a slightly greater degree) in the first metacarpal of *Lessemsaurus* (PVL 4822). The opposite condition is observed in most nonsauropodan sauropodomorphs (e.g. *Plateosaurus*; *Massospondylus*; *Riojasaurus*; *Anchisaurus*). As in all non-eusauropodan sauropodomorphs the lateral condyle is much more distally expanded than the medial condyle, owing mainly to the oblique orientation of the condyles. In *Lessemsaurus* this distal expansion of the lateral condyle appears to have been somewhat reduced compared to the condition observed in *Antetonitrus*. The articular surfaces of the distal condyles presents a ginglymoidal joint of approximately 180° that is directed slightly more ventrally than dorsally, observable also in *Lessemsaurus*, *Aardonyx*, and most basal sauropodomorphs. The collateral ligament pit on the lateral condyle is slightly more excavated than on the medial.

#### Metacarpal 2

The second metacarpal in *Antetonitrus* is 1.43 times the length of metacarpal 1. This is within the general range of most nonsauropodan sauropodomorphs (e.g. *Thecodontosaurus*; *Anchisaurus*; *Riojasaurus*; *Plateosaurus*; *Massospondylus*) but proportionally longer than that of *Jingshanosaurus* (1.15) and the newly described basal sauropodomorph *Seitaad ruessi* from the early Jurassic of Utah, which appears to have had subequally sized first and second metacarpals (Sertich & Loewen, 2010). Interestingly, the second metacarpal of *Lessemsaurus* is conspicuously elongated at 1.78 times the length of the first metacarpal, but it is highly probable that both elements belong to different individuals (although a similar relationship cannot be discounted in *Antetonitrus*).

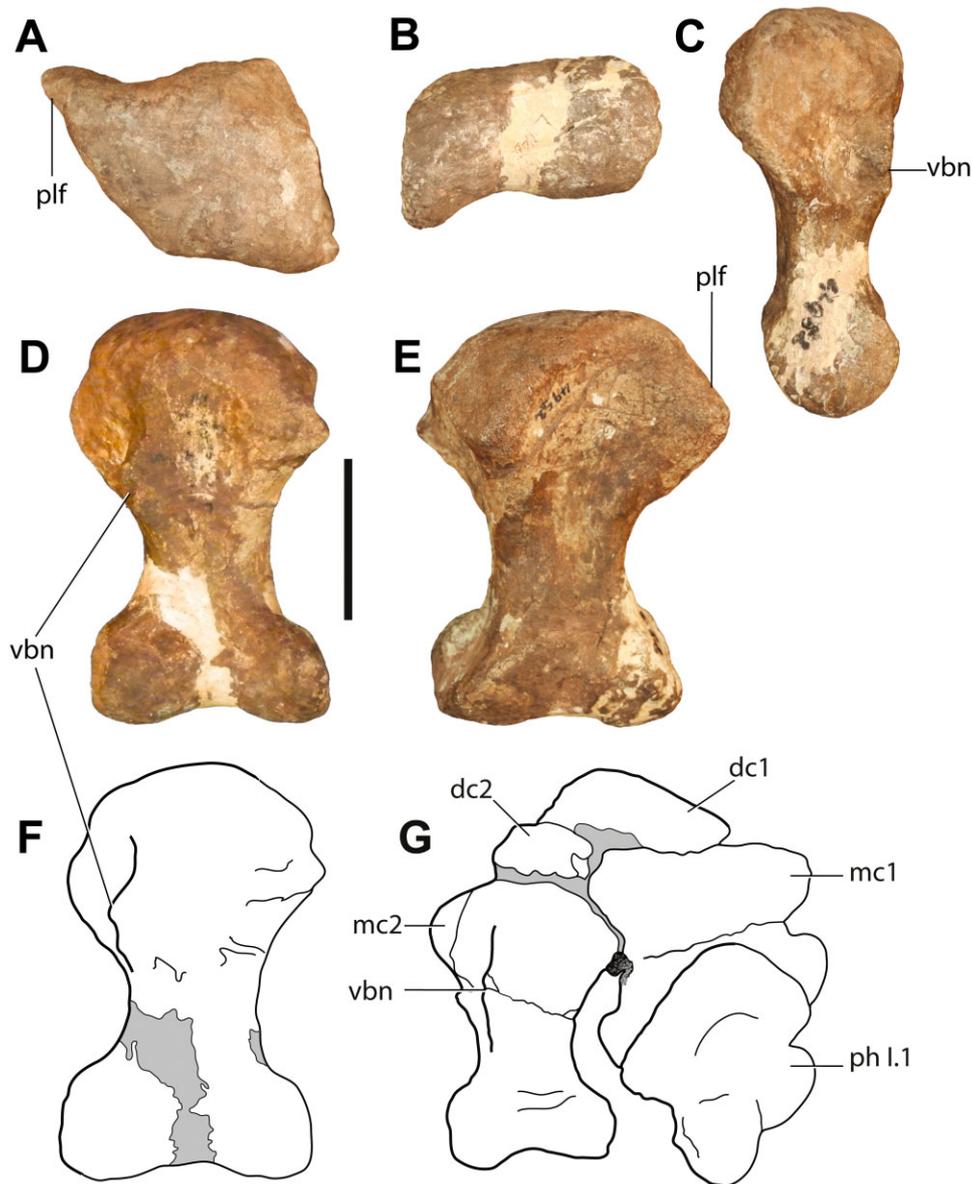
The proximal articular surface of the second metacarpal in *Antetonitrus* is strongly convex and rhomboidal in general outline (Fig. 13). There is a distinct dorsolateral flange that begins proximally and extends for half the length of the bone that may have abutted with the third metacarpal proximomedially. This acute lateral flange of bone is common in a number of non-eusauropodan sauropodomorph taxa, including *Lessemsaurus*, *Plateosaurus*, *Massospondylus*, and BP/1/386 (*contra* Pol & Powell, 2007), but absent in other non-eusauropodan taxa (e.g. *Yunnanosaurus*; *Tazoudasaurus*). The dorsomedial corner of the proximal surface also displays an incipient swelling, although this is considerably less developed than on the dorsolateral corner. Together the dorsolateral

flange and dorsomedial swelling delimit a distinctly concave proximodorsal surface. The medioventral corner of the proximal surface houses a small tubercle that probably cradled the first metacarpal ventrally. Just proximal to the mid-point on the ventrolateral margin of the shaft there is a distinct bifurcated tuberosity that is similar to that seen on the ventrolateral margin of the shaft in BP/1/386 (provisionally referred here to *Aardonyx celestae*; Fig. 13). This process is present in both of the *Antetonitrus* second metacarpals and potentially represents an apomorphy of both *Antetonitrus* and *Aardonyx* as a similar process is observed nowhere else within the sauropodomorph record. The functional significance of this process is difficult to speculate upon, although it may indicate that the manus in *Antetonitrus* was relatively tightly bound, potentially representing an additional supporting mechanism during regular or sporadic quadrupedal motion.

The shaft is notably short and stout, with its minimum transverse width 0.35 times the total proximodistal length of the bone. This contrasts with a ratio of 0.2 to 0.25 in most derived sauropodomorphs (e.g. *Plateosaurus*; *Riojasaurus*; *Yunnanosaurus*; *Tazoudasaurus*), although the eusauropodan taxon *Shunosaurus lii* displays the exact same ratio as *Antetonitrus* (Zhang, 1988). The distal articular condyles are symmetrically developed and minimally differentiated from one another, although the ventral corner of the medial condyle is slightly more acute and ventrally expanded than in the lateral condyle. There is no evidence of a collateral ligament fossa on either condyle.

#### Manual phalanx 1.1

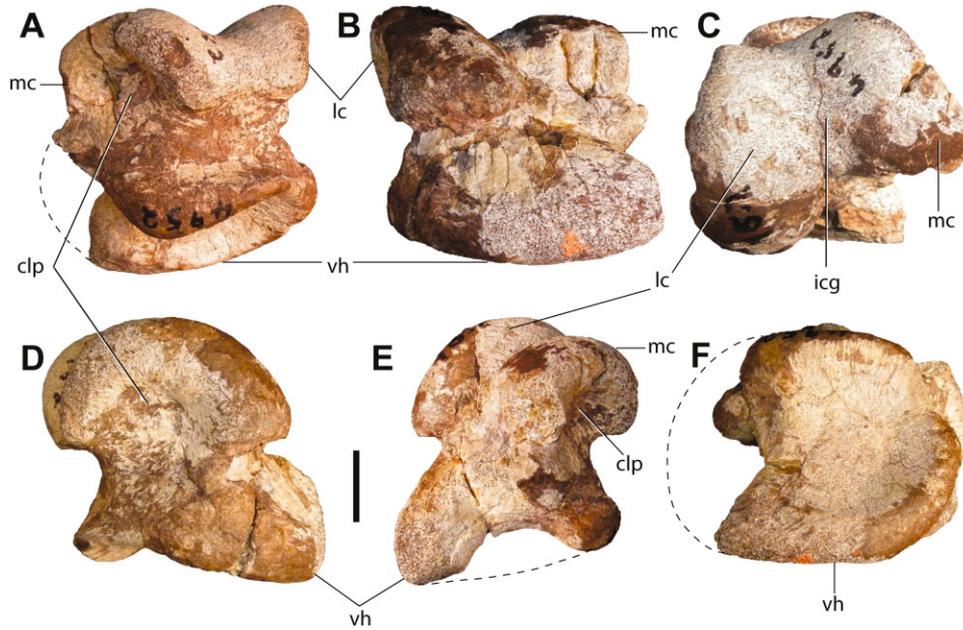
The manual phalanx 1.1 of *Antetonitrus* is a short and robust element with a proximal articular surface that is mediolaterally wider than the total proximodistal length of the bone (Fig. 14). These same proportions are seen in *Lessemsaurus* (although this is only true when measured from the dorsal surface), whereas most other nonsauropodan sauropodomorphs tend to have a manual phalanx 1.1 that is slightly longer than wide (e.g. *Plateosaurus*; *Riojasaurus*; *Seitaad*). Although the proximal medial articular facet is missing, it is clear that it would have been much reduced compared to the extensively subcircular lateral articular facet, as in all sauropodomorphs. The proximoventral heel of manual phalanx 1.1 is deeper proximally than the proximodorsal lip, as is common to all non-eusauropodan sauropodomorphs. The shaft, being extremely short, is represented by no more than a subtle mediolateral constriction between the proximal and distal articular surfaces. However, the damage sustained by the proximomedial corner of the bone makes it difficult to confirm the precise degree of



**Figure 13.** *Antetonitrus ingenipes*, left metacarpal 2 (BP/1/4952) in A, proximal; B, distal; C, lateral; D, ventral; and E, dorsal views. F, G, line drawings of F, *A. ingenipes* second metacarpal in ventral view and G, referred *Aardonyx celestae* (BP/1/386) left carpus and metacarpus in ventral view. Abbreviations: dc1, distal carpal 1; dc2, distal carpal 2; mc1, metacarpal 1; mc2, metacarpal 2; ph I.1, manual phalanx 1.1; plf, proximolateral flange; vbn, ventral bifurcated notch. Scale bar = 5 cm.

transverse constriction in the shaft. As is typical of all non-eusauropodan sauropodomorphs, the distal condyles are twisted laterally along the proximodistal axis in relation to the proximal surface. In *Antetonitrus* this degree of axial torsion is approximately 30°, similar to the low degree of torsion seen in *Lessemsaurus* and a number of basal sauropodomorphs (e.g. *Thecodontosaurus*; *Plateosaurus*; *Riojasaurus*), but contrasting with species such as *Massospondylus*, *Lufengosaurus*; and *Yunnanosaurus*

that exhibit a highly twisted phalanx 1.1 of about 45°. The distally twisted phalanx 1.1 of nonsauropodan sauropodomorphs, coupled with the asymmetrically developed lateral condyle of metacarpal 1, would have exerted a strong medial cant to the ungual phalanx of manual digit 1 during flexion (Cooper, 1981; Galton & Upchurch, 2004). The ability of sauropodomorph dinosaurs to hyperextend the first digit dorsally is well known (Galton & Upchurch, 2004), and was facilitated by a distal ginglymus of the first manual



**Figure 14.** *Antetonitrus ingenipes*, right manual phalanx 1.1 (BP/1/4952) in A, dorsal; B, ventral; C, distal; D, lateral; E, medial; and F, proximal views. Abbreviations: clp, collateral ligament pit; icg, intercondylar groove; lc, lateral condyle; mc, medial condyle; vh, ventral heel. Dashed line represents missing bone. Scale bar = 2 cm.

phalanx that extended along the dorsoventral curvature of the bone at an angle of  $180^\circ$ . This morphology is well recorded in phalanx 1.1 of *Antetonitrus*, in which the distal articular surface extends well above the dorsal surface of the shaft. It is possible that hyperextension of the first manual digit represents an adaptive response to the need to raise the thumb above the substrate while walking or standing quadrupedally/tripedally (Galton & Upchurch, 2004), although it is possible that it simply represents an augmentation of the dexterity required for efficient grasping and feeding (Remes, 2008; Mallison, 2010b).

The distal articular condyles extend further ventrally than dorsally, and are also mediolaterally wider and more divergent ventrally than dorsally, as is common to most nonsauropodan sauropodomorphs. The collateral ligament pit appears to have been much more deeply developed on the medial condyle than on the lateral. This same relationship is described for *Lessemsaurus* (Pol & Powell, 2007).

#### Ilium

Amongst the referred material of *Antetonitrus* (NM QR1545) housed in the collections of the National Museum there are two large ilia, a left and a right. Given the close morphological similarity of the appendicular elements to the BPI material (see above: Referred material) it is assumed that the ilium described herein also belongs to *Antetonitrus* (or a taxon of extremely close taxonomic affinity). Both



**Figure 15.** *Antetonitrus ingenipes*, right ilium (NM QR1545) in lateral view. Abbreviations: acc, acetabular crest; pap, preacetabular process; pop, postacetabular process; ip, ischial peduncle. Mesh pattern indicates areas that have been replaced with plaster. Maximum length (anteroposteriorly) = 565 mm.

elements are tentatively referred to different individuals as the left is both slightly smaller and of dissimilar preservation to the right. The right, although missing the pubic peduncle, is also considerably better preserved, and forms the main focus of the following description (Fig. 15).

The ilium of *Antetonitrus* retains the plesiomorphic condition seen in most nonsauropodan sauropodomorphs: the iliac blade is anteroposteriorly elongate and dorsoventrally low; the preacetabular process is

short, pointed, and does not appear to have exceeded the anterior extent of the pubic peduncle (although as the latter is broken, this cannot be said with certainty). This morphology is present in most basal sauropodomorph taxa (e.g. *Plateosaurus*; *Riojasaurus*; *Massospondylus*), although some species are exceptional in having preacetabular processes that extend beyond the anterior margin of the pubic peduncle (*Anchisaurus*; *Leoneosaurus*). This latter condition is also typical of *Tazoudasaurus* + Eusauropoda, although in that group the preacetabular process is greatly expanded dorsoventrally and the apex is proportionally blunter compared to non-eusauropodan sauropodomorphs. The preacetabular process of *Antetonitrus* appears to have exhibited/retained a slight ventral deflection, in contrast to the anteriorly directed preacetabular process seen in *Lessemsaurus*, although this deflection is very subtle.

The mediolaterally thin anterodorsal margin of the iliac blade is missing in the better preserved ilium, making it difficult to distinguish if a similar ‘step’ between the preacetabular process and the dorsal margin of the iliac blade (as seen in *Riojasaurus* and some specimens of *Massospondylus*) was present. The left ilium of NM QR1545 does preserve this area, however, whereupon the preacetabular process appears to have presented a continuum with the shallowly convex dorsal margin of the blade. Compared to most basal sauropodomorphs (e.g. *Massospondylus*; *Melanorosaurus*) and more derived taxa (i.e. eusauropods) the acetabular region is anteroposteriorly, dorsoventrally, and mediolaterally massive. The supracetabular crest appears to have been well developed on the lateral surface of the pubic peduncle and rises as a pronounced lateral flange along the anterodorsal margin of the acetabulum. Derived sauropodan taxa (e.g. *Tazoudasaurus*; *Shunosaurus*) lack such extensive development of the supracetabular crest, although it is worth noting that the sharp, laterally flared morphology of this process in *Antetonitrus* appears to have been historically augmented with plaster. This augmentation makes it difficult to determine if the laterally ‘overhung’ rim of the supracetabular crest (i.e. in lateral view the lateral margin of the supracetabular crest is deflected ventrally so as to obscure the dorsal apex of the acetabulum from view) is a true autapomorphy of *Antetonitrus*, or if this is simply an artefact of the reconstruction of the supracetabular crest in NM QR1545.

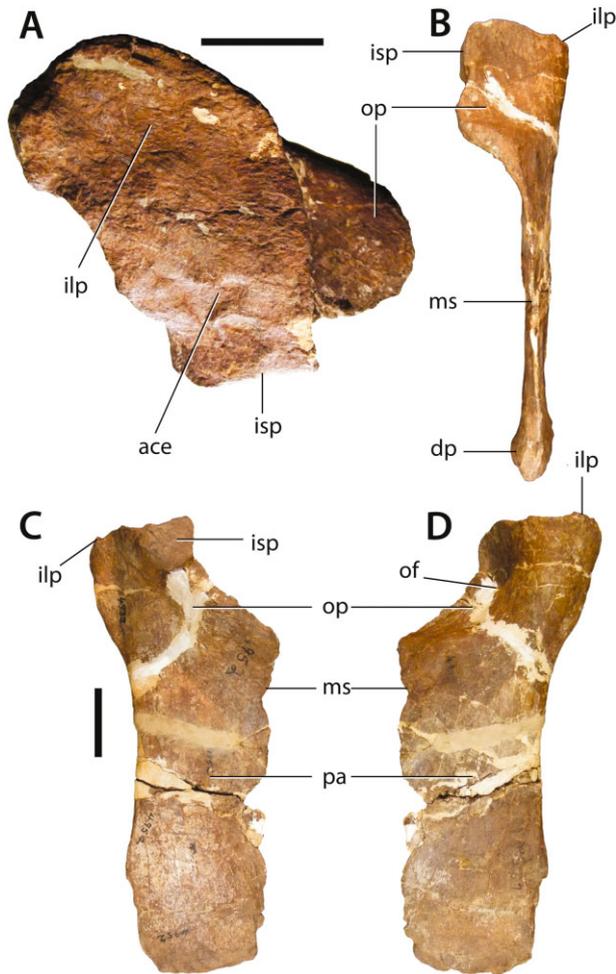
Anteriorly, the acetabulum is markedly concave and mediolaterally extensive, being almost hemispherical at its anterodorsal margin. As the pubic peduncle is missing it is difficult to ascertain whether the same anteromedial wall of the acetabulum observed in *Lessemsaurus* (Pol & Powell, 2007) was present in *Antetonitrus*. The ischial peduncle also appears to have

been ‘repaired’ with plaster, but it is nonetheless evident that the ischial peduncle was ventrally extensive as in most non-eusauropodan sauropodomorphs. In contrast, Sauropoda + Eusauropoda have highly reduced or entirely absent ischial peduncles. It is also possible that the ischial peduncle of *Antetonitrus* exhibited an incipient heel on its posteroventral corner, although this was probably less developed than in a number of other sauropodomorph taxa (i.e. *Plateosaurus*; *Plateosaurus*; *Riojasaurus*).

On the ventral surface of the posterior blade a thin brevis crest extends from the posterodorsal margin of the ischial peduncle to the ventral surface of the postacetabular process. As in most derived sauropodomorphs the posterior iliac blade is relatively flat and featureless, and the absence of a brevis shelf results in the concomitant absence of a brevis fossa. The postacetabular process is not entirely preserved but appears to have been bluntly rounded to subrectangular in shape with a distinct posteroventral corner, as in a number of other non-eusauropodan sauropodomorphs (e.g. *Riojasaurus*; *Yunnanosaurus*; *Massospondylus* BP/1/4693). In contrast, taxa such as *Plateosaurus* and *Plateosaurus* display much sharper, square-ended postacetabular process. Consistent with the basal sauropodomorph condition the postacetabular process is anteroposteriorly extensive, lacking the extreme reduction of the postacetabular region seen in Sauropoda + Eusauropoda. On the anterodorsal surface of the postacetabular process there is a pronounced striated swelling. This represents the thickest point of the dorsal margin of the ilium in NM QR1545 and is possibly related to the attachment for the *M. iliobtibialis* (Langer, 2003).

#### Pubis

A single large left pubis is preserved (Fig. 16). The pubis is similar in overall proportions to most non-eusauropodan sauropodomorphs being relatively long and slender. The maximum mediolateral width of the pubis (measured where the obturator plate meets the pubic apron) is approximately 0.37 times the total proximodistal length. This is slightly more squat but in the same basic range as other non-eusauropodan sauropodomorphs (e.g. *Plateosaurus*; *Riojasaurus*; *Massospondylus*; *Aardonyx*; *Lessemsaurus*; *Tazoudasaurus*), being closest to the condition observed in *Vulcanodon* (Cooper, 1984). In contrast, *Spinophorosaurus* + Eusauropoda display proportionally shorter and wider pubes (Remes *et al.*, 2009). The obturator plate (= proximal plate *sensu* Pol & Powell, 2007) is reduced in much the same manner as in most nonsauropodan sauropodomorphs, representing only approximately 0.30 in proportion of the total proximodistal length. This contrasts with the condition present in *Vulcanodon*, *Tazoudasaurus*,



**Figure 16.** *Antetonitrus ingenipes*, left pubis (BP/1/4952) in A, proximal (anterior is up); B, medial; C, posterior; and D, anterior views. Abbreviations: ace, acetabulum; dp, distal expansion; ilp, iliac peduncle; isp, ischial peduncle; ms, medial symphysis; of, obturator foramen; op, obturator plate; pa, pubic apron. Scale bars = 10 cm.

*Spinophorosaurus*, and basal eusauropods in which the proximal plate generally occupies at least 0.40–0.50 as a proportion of the total pubic length. Interestingly, the pubis of *Lessemsaurus* is described as presenting the latter condition (Pol & Powell, 2007: text-fig. 7); however, close examination of PVL 4822/61 yields a more conservative ratio of approximately 0.37 for that taxon.

The iliac peduncle is flat proximally and markedly thick anteroposteriorly, being proportionately thicker than the same process in a number of basal sauropodomorph taxa (e.g. *Massospondylus*; *Aardonyx*; *Yunnanosaurus*). The acetabular portion of the pubis is equally broad but very short, lying posteromedial to the iliac peduncle and proximal to the

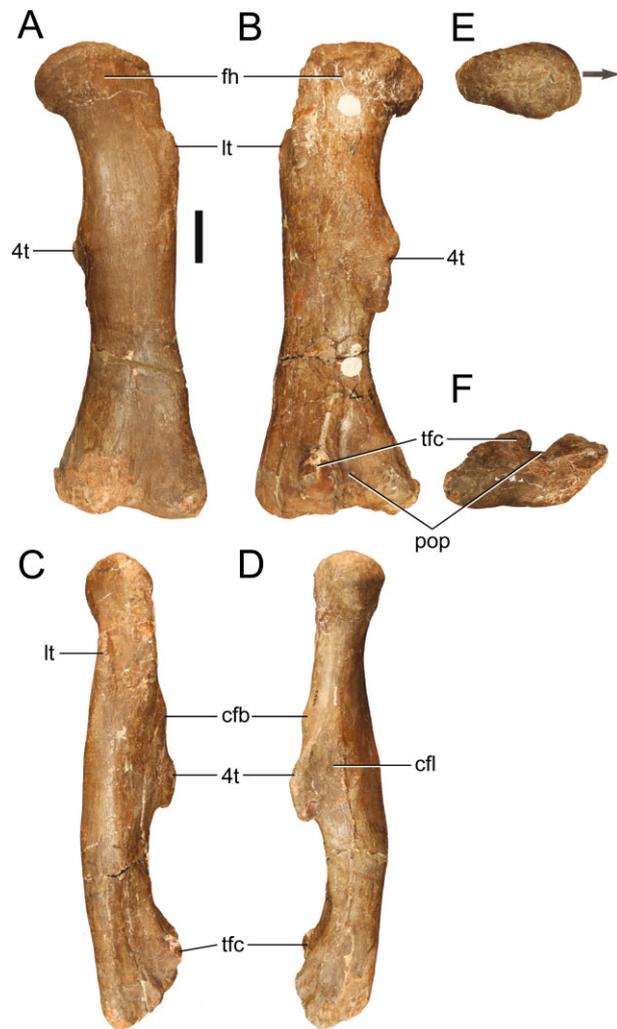
anteriorly directed puboischial symphysis. The latter is broad proximally but tapers distally, becoming thin and sinuous for the majority of its length. The obturator foramen is obscured by both plaster and matrix, but its dimensions appear to have been reduced as in derived sauropodomorphs and certainly would not have exceeded those of *Vulcanodon*. Distal to the obturator plate the pubic apron is flat, proximodistally straight, lateromedially wide, and orientated transversely. This condition is plesiomorphic amongst basal saurischians including all non-eusauropodan sauropodomorphs (e.g. *Vulcanodon*; *Tazoudasaurus*); although the recently described *Spinophorosaurus*, which is hypothesized to be the sister taxon to Eusauropoda (Remes *et al.*, 2009), appears to represent an exception. The anterior margin of the pubic apron is roughly confluent with the anterior margin of the iliac pedicle in mediolateral view. This appears to have been the primitive condition for Dinosauria but was independently gained several times in Sauropodomorpha (e.g. *Antetonitrus*; *Saturnalia*; *Efraasia*; *Cetiosaurus* Owen, 1841), whereas most sauropodomorphs/sauropods (e.g. *Massospondylus*; *Coloradisaurus*; *Lessemsaurus*; *Omeisaurus*) present proximal plates that are anteriorly expanded beyond the anterior margin of the pubic apron.

The lateral margin of the apron is thick, rounded, and has a similar degree of lateral concavity (when viewed in anterior aspect) as that evinced by *Lufengosaurus*, *Lessemsaurus*, and *Tazoudasaurus* (and possibly *Vulcanodon*). In contrast, the medial edge (= the symphyseal connecting suture with the right pubic blade) is much thinner and irregularly preserved. The transverse width of the pubic apron is approximately 0.44 times its proximodistal length. This is a slightly higher ratio than a number of basal sauropodomorphs (e.g. *Massospondylus*; *Plateosaurus*; *Aardonyx*), which generally display a ratio of around 0.27–0.38, approaching instead the ~0.50 observed in *Vulcanodon* and *Tazoudasaurus*. It is possible that the general pubic proportions of *Antetonitrus* were very similar to that of *Lessemsaurus*, but the medial edge of the pubic apron in PVL 4822/61 has sustained significant damage, rendering estimates of the transverse dimensions of the pubic apron in *Lessemsaurus* problematic.

As in *Lessemsaurus*, the distal end of the pubis is slightly expanded anteroposteriorly, but less so than in other non-eusauropodan sauropodomorphs such as *Massospondylus*, *Plateosaurus*, *Vulcanodon*, and *Tazoudasaurus*.

#### Femur

There is a single large left femur (BPI/1/4952) (Fig. 17). Although well preserved, it appears to have undergone a modest degree of post-mortem distortion,



**Figure 17.** *Antetonitrus ingenipes*, left femur (BP/1/4952) in A, anterior; B, posterior; C, lateral; D, medial; E, proximal (arrow directed medially); and F, distal views. Abbreviations: 4t, fourth trochanter; cfb, M. caudofemoralis brevis insertion site; cfl, M. caudofemoralis longus insertion site; fh, femoral head; lt, lesser trochanter; pop, popliteal fossa; tfc, tibiofibular crest. Scale bar = 10 cm.

so that the distal condyles are slightly flattened anteroposteriorly and deflected anterolaterally with respect to the anterior surface of the femoral shaft. The resulting effect is subtle, however, and although there is the possibility that this distortion might be exaggerating the placement of certain femoral processes (such as the acute medial position of the fourth trochanter), the uniform and undamaged contours of the bone suggest that its essential morphology remains intact.

The femur is a stout, robust element, that, although large (780 mm), is not significantly more so than the larger humerus, with the resulting humeral/femoral

ratio slightly higher than 0.90. The implications of this relatively elevated humerus/femur ratio are treated at length in the Discussion. The head of the femur is directed perpendicular to the proximodistal axis of the shaft and in dorsal view is deflected slightly anterior to the mediolateral plane, although significantly less so than the approximately 45° seen in basal sauropodomorph taxa such as *Plateosaurus*. The posterolateral corner of the femoral head is slightly damaged, such that most of the greater trochanter is missing; however, its distal segment can be seen terminating adjacent to the lesser trochanter and was possibly separated from the latter via a shallow trochanteric ridge. In lateral view the sigmoid curvature of the femoral shaft is highly reduced compared to most nonsauropodan sauropodomorphs, being similar in appearance to that of *Melanorosaurus* (NM QR1551), *Riojasaurus*, and *Camelotia* Galton, 1985b (Galton, 1998). However, it is possible that the anteroposterior flattening of the distal condyles means that the lateral curvature of the distal half is less than it would have been in life. The femur is straight in anterior or posterior view, as is typical of most saurischians and all derived sauropodomorphs (Rauhut *et al.*, 2011). The femoral shaft is strongly elliptical throughout its length, with the anteroposterior width approximately 0.66 times the transverse width. This marks a departure from the subcircular femoral shafts of most nonsauropodan sauropodomorphs and places the basic femoral morphology of *Antetonitrus* intermediate between that of *Melanorosaurus* and *Isanosaurus* + Sauropoda.

The lesser trochanter is a well-developed ridge that is similar in relative size to most basal sauropodomorphs (e.g. *Melanorosaurus*; *Riojasaurus*; *Eucnemesaurus*). It rises steeply with its proximal termination distal to the distal margin of the femoral head. The sheet-like distal end merges gradually with the femoral shaft, terminating roughly parallel to the proximal margin of the fourth trochanter. The lesser trochanter in *Antetonitrus* is axially straight, lacking the subtle oblique orientation observed in a number of nonsauropodan taxa [e.g. *Plateosaurus*; specimens of *Massospondylus*; material referred to *Aardonyx* (BP/1/386)]. Of special note is the prominent lateral placement of the lesser trochanter, being partially visible in posterior view. Although the lateral migration of this process presages the condition in Sauropoda, in that group the lesser trochanter is reduced to a negligible bump on the lateroproximal corner of the shaft (Carrano, 2005).

The fourth trochanter is an especially well-developed crest located halfway down the medial side of the femoral shaft. By all indications this process and the adjacent bone surface is hypertrophied to an autapomorphic extent within Sauropodomorpha. In

most basal sauropodomorph taxa (e.g. *Saturnalia*; *Plateosaurus*; *Jingshanosaurus*) the fourth trochanter projects as a pronounced flange from the posterior surface of the femoral shaft. Although the degree of trochanteric projection in these taxa is similar to that of *Antetonitrus*, the area of bone immediately surrounding the fourth trochanter is relatively smooth and flat (with the exception of the medial fossa where the *M. caudofemoralis longus* inserts). In contrast, the fourth trochanter in *Antetonitrus* is bordered posteriorly by an elevated surface scored with extensive striations. This begins proximal to the fourth trochanter in the middle of the posterior femoral shaft, where it descends mediolaterally to meet the top of the fourth trochanter on the medial surface of the shaft. This surface is hypothesized as the insertion area for the *M. caudofemoralis brevis*, which has been reconstructed in a similar position in a number of dinosaurian taxa (Dilkes, 2000; Carrano & Hutchinson, 2002; Dilkes *et al.*, 2012). The apical surface of the fourth trochanter is crescent-shaped with the proximal half deflected anteriorly and the distal half in line with the proximodistal orientation of the shaft. This orientation of the fourth trochanter, along with its steep distal termination, is similar to that seen in *Lessemsaurus* [Pol & Powell, 2007; although a curved fourth trochanter with steep 'semi-pendent' distal margin has also been described for specimens of *Eucnemesaurus* (Yates, 2007a)]. The fourth trochanter of *Antetonitrus* is subrectangular in profile, similar to most nonsauropodan sauropodomorphs, but different to the more rounded profile described for *Eucnemesaurus* and *Riojasaurus* (Bonaparte, 1972; Yates, 2007a). The medial surface of the fourth trochanter bears a shallow depression and is markedly rugose, housing as it would have the insertion of the *M. caudofemoralis longus* (Langer, 2003). The medial placement of the fourth trochanter at mid-shaft distinguishes *Antetonitrus* from most basal sauropodomorphs, which tend to have a more posteriorly positioned fourth trochanter located in the proximal half of the bone. Instead, the placement is similar to that of *Melanorosaurus* + Sauropoda (*sensu* Yates, 2007a, b). However, all derived sauropods beginning with *Isanosaurus* and *Vulcanodon* have reduced muscle attachment sites on the femur. The opposite condition is seen in *Antetonitrus*, where the rugose raised and pitted areas surrounding the fourth trochanter account for approximately 0.43 in proportion of the total circumference of the femoral shaft (measured just proximal to fourth trochanter). The functional significance of these muscular proxies is addressed in the Discussion.

Despite the distortion of the distal end of the femur it is still possible to observe the mediolateral expansion of the distal condyles and the deep,

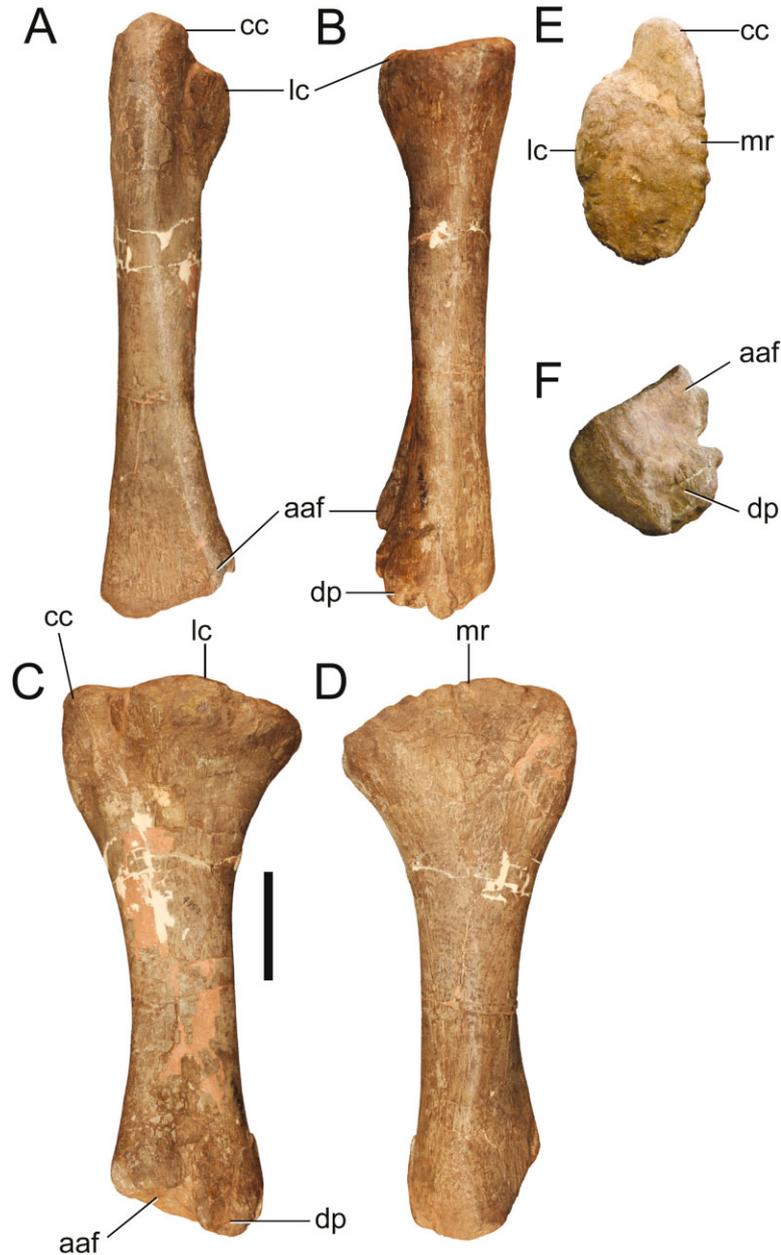
proximodistally extensive popliteal fossa on the posterior surface. The tibiofibular crest appears (it has been partially repaired with plaster) to have been reduced compared with the posteriorly projecting flange of bone seen in most basal sauropodomorphs (e.g. *Plateosaurus*, *Plateosaurus*, *Massospondylus*, and *Aardonyx*) and is wider mediolaterally than it is proximodistally high, as in *Glacialisaurus*, *Melanorosaurus*, and possibly *Jingshanosaurus*. It is possible that this represents a secondary reduction in the development of the tibiofibular crest that *Antetonitrus* shares with more derived sauropodan taxa (e.g. *Tazoudasaurus*; *Shunosaurus*).

#### Tibia

The single preserved left tibia is 0.64 times the length of the single preserved femur (Fig. 18). As this is within the range of both derived nonsauropodan sauropodomorphs [e.g. *Anchisaurus*; *Lufengosaurus*; *Melanorosaurus* (NM QR3314)] and sauropod taxa such as *Vulcanodon*, *Mamenchisaurus*, and *Apatosaurus*, we consider it highly probable that they belonged to the same individual. The tibia is well preserved and does not appear to have suffered much (if any) postdepositional distortion.

The tibia is a relatively stout element, being comparable in robustness to those of *Blikanasaurus*, *Lessemsaurus*, and the newly described PULR 136 from the Los Colorados formation of Argentina (Ezcurra & Apaldetti, 2012), whereas the proximal articular surface is notably similar to that of *Vulcanodon*. As in a number of derived sauropodomorphs [e.g. *Tazoudasaurus*; '*Kotasaurus*' (115/S1Y/76: Yadagiri, 2001); *Blikanasaurus*], the anteroposterior length of the proximal end of the tibia of *Antetonitrus* is approximately half the total length of the bone. The proximal articular surface is strongly expanded anteroposteriorly, being over twice the transverse width and thus rendering the proximal surface distinctly elliptical in outline. This feature was described by Allain & Aquesbi (2008) as a synapomorphy shared exclusively with *Tazoudasaurus* and *Vulcanodon*, but also appears to have been present in *Antetonitrus*. Most other non-eusauropod sauropodomorphs (e.g. *Lessemsaurus*; *Melanorosaurus*; *Yunnanosaurus*; PULR 136) have a proximal tibia that is subtriangular in outline, with the transverse width at least 0.60 times the anterolateral depth.

The cnemial crest is a stout flange of bone that accounts for 0.25 times the total anteroposterior length of the proximal surface and is as mediolaterally wide as it is long. This differs from the mediolaterally broad cnemial crest of *Lessemsaurus* (although it is possible that the flattened morphology observed in *Lessemsaurus* is the result of taphonomic



**Figure 18.** *Antetonitrus ingenipes*, left tibia (BP/1/4952) in A, anterior; B, posterior; C, lateral; D, medial; E, proximal; and F, distal views. Abbreviations: aaf, astragalar articular facet (=ascending process); cc, cnemial crest; dp, descending process; lc, lateral condyle; mr, medial ridge. Scale bar = 10 cm.

stresses). The degree of lateral deflection of the cnemial crest is very slight, being similar to that seen in *Vulcanodon*. As in *Lessemsaurus* and Sauropoda the cnemial crest does not project dorsally, resulting in a relatively flat proximal articular surface. However, a subtle, posteriorly directed incline can be discerned in the proximal surface of the tibia when viewed laterally in *Antetonitrus*, but this is still considerably less than in *Blikanasaurus* and PULR 136 (Ezcurra & Apaldetti, 2012). The proximity of the

cnemial crest to the lateral condyle creates a distinct notch (the 'lateral sulcus') that communicates with the anterolateral fossa just below the proximal surface. The anterolateral fossa is irregularly convex and rugose, facilitating the proximal articulation of the tibia with the fibula. The lateral condyle is a large, rounded protuberance that is situated just posterior to the cnemial crest on the proximal surface of the bone, and is therefore much more anteriorly positioned than the lateral condyle of PULR 136.

However, this may be an artefact of the pronounced posterior expansion of the proximal articular surface in *Antetonitrus*. The medial condyle is slightly more posteriorly placed than the lateral condyle and separated from the latter via a very shallow median depression. Although a much subtler protuberance than the lateral condyle, the medial condyle nonetheless possesses approximately four distinctly rounded tubercles along its proximomedial margin.

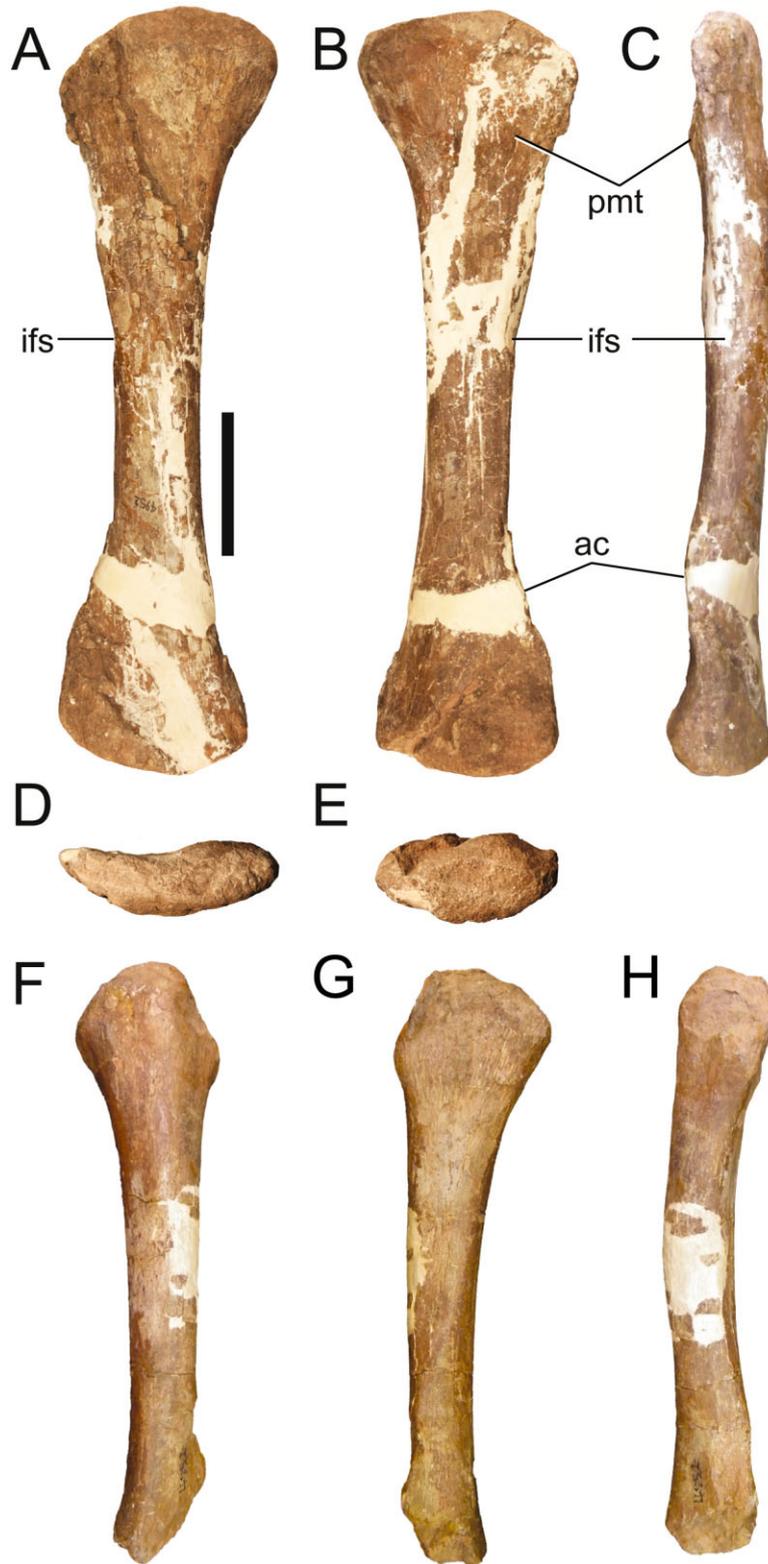
The proximomedial surface of the tibial shaft is generally flat and devoid of distinct features. However, a slight concavity, bounded anteriorly by an equally slight rugosity, suggests a site for anchoring musculature [possibly representing the attachment site for the *M. gastrocnemius pars medialis* (Carrano & Hutchinson, 2002)]. Distal to the proximal third of the tibia the medial and lateral surfaces of the shaft are relatively flat, the lateral surface lacking the vertical tuberosity in other basal sauropodomorph taxa (Ezcurra & Apaldetti, 2012). The shaft is subelliptical in cross-section with the transverse width 0.73 times that of the anteroposterior depth, a substantially greater value than that presented by the mediolaterally constricted tibial shafts of *Vulcanodon* and *Tazoudasaurus*. The distal end of the shaft displays a strong mediolateral expansion, being greater than the transverse width of the proximal end. This condition is observed in a number of derived forms (e.g. *Tazoudasaurus*; *Vulcanodon*; *Lessemsaurus*) but is also seen, to a lesser degree, in more basal forms such as *Massospondylus*, *Lufengosaurus*, and *Yunnanosaurus*. In contrast, the anteroposterior length of the distal end is less pronounced, being only 0.59 times the anteroposterior length of the proximal end. *Antetonitrus* therefore lacks the pronounced anteroposterior expansion of the distal tibia seen in one of the specimens referred to *Lessemsaurus* [although the tibiae of *Lessemsaurus* appear to have experienced extreme postdepositional distortion, given their rather compacted appearance and the lack of concordance exhibited between the distal ends of both specimens (B. W. M. and F. A. pers. observ. PVL 4822/66–67)].

The proportional relationships of the distal tibia of *Antetonitrus* are difficult to explicitly define because of the anterolaterally oblique orientation of the astragalar ascending facet. This differs from the more mediolaterally orientated distal articular surfaces of most basal sauropodomorph tibiae (i.e. *Massospondylus*; *Lufengosaurus*; *Aardonyx*), and renders the anteroposterior and mediolateral dimensions of the distal tibia in *Antetonitrus* roughly subequal to one another. Nonetheless, the distal surface of the tibia can probably be said to be slightly more expanded mediolaterally than anteroposteriorly – as is generally typical of Sauropodomorpha.

The distal articular surface of the tibia is subtriangular in shape, with the tip of the facet for the ascending process of the astragalus (FAA) providing the anterolaterally directed apex of this triangle. As in PULR 136 the (antero)medial and lateral sides of the distal articular surface are subequal in length. The FAA is an oblique facet that occupies the anterolateral third of the distal articular surface before gradually sloping distally to meet the posterolateral process and the gently convex mediolateral surface. There is a distinct notch on the lateral surface separating the FAA from the posterolateral process, but this is greatly reduced compared to most nonsauropodan sauropodomorphs (i.e. *Riojasaurus*; *Coloradosaurus*; *Massospondylus*). As in PULR 136, this notch communicates with a very shallow concavity on the distal articular surface, further separating the FAA and the posterolateral process laterally. As opposed to most basal sauropodomorphs, the posterolateral process is transversely compressed and therefore does not exceed the lateral extent of the FAA, rendering the astragalar articular socket visible in posterior view. In recent years this has become an accepted synapomorphy of Sauropoda (Yates, 2004a; Pol & Powell, 2007), being present in *Lessemsaurus*, PULR 136 and more derived sauropod taxa (also apparent in the gracile early Jurassic sauropodomorph *Anchisaurus polyzelus* and the recently named *Aardonyx celestae*: Yates, 2004a; Yates *et al.*, 2010). There is no clear notch on the posteriomedial corner (described as the articular facet for reception of the posteromedial dorsal expansion of the astragalar body) as in PULR 136 and *Riojasaurus*, and also usually present in basal theropods and sauropodomorphs (Ezcurra & Apaldetti, 2012). However, a distinct convex notch is present on the posterior corner of the posterolateral process but this is assumed to represent damage to the bone. The anteromedial and posteromedial borders of the distal end are gently concave and gently convex, respectively, the resultant angle between them is acute.

#### Fibula

There are two fibulae (Fig. 19). The largest, a left, is subequal in size to the tibia and possibly belongs to the same individual (BP/1/4952). The smaller right fibula (BP/1/4952b), although similarly robust, displays some noticeable differences when compared to the larger fibula. The shaft is bowed and subcircular in the smaller specimen, as opposed to the straight and elliptical shaft of the larger specimen. Another potential difference is that the distal end is twisted and less expanded relative to the proximal end in the smaller specimen. However, as the distal end is damaged and incomplete in the smaller fibula, this interpretation should be treated with caution. These



**Figure 19.** *Antetonitrus ingenipes*. A–E, left fibula (BP/1/4952) in A, lateral; B, medial; C, anterior; D, proximal (medial is up); and E, distal (medial is up) views. F–H, right fibula (BP/1/4952b) in F, lateral; G, medial; and H, anterior views. Abbreviations: ac, anterior crest; ifs, iliofibularis scar; pmt, proximomedial tubercle. Scale bar = 10 cm.

differences may be attributable to intraspecific variation, taphonomic influences, and/or differential ontogenetic development, but the possibility that these fibulae represent different taxa cannot be ruled out. Interestingly, a similar relationship is seen between two similarly proportioned fibulae (BP/1/6316 and an uncatalogued element) recovered from the *Aardonyx* type locality, as well as the partial fibulae contained within the NM QR1545 *Antetonitrus* assemblage, adding some weight to the suggestion that the differences between the two fibulae of *Antetonitrus* are attributable to ontogeny or individual variation.

The following description focuses on the larger, more complete fibula. As in practically all sauropodomorphs the proximal head of the fibula in *Antetonitrus* is considerably longer anteroposteriorly than mediolaterally wide, with a convex proximal outline. The posterior expansion of the proximal head is slightly greater than that of the anterior margin, giving the proximal end a vague hatchet shape in lateral view. However, this could be the result of damage sustained by the anteroproximal margin of the bone. The same damage makes it difficult to confirm if *Antetonitrus* displayed a similar anterior trochanter to that seen in the fibulae of *Vulcanodon* and *Tazoudasaurus*. There is a slight depression on the anterior face of the bone just proximal to mid-shaft, a feature that is also clearly present in both the NM QR1545 *Antetonitrus* fibulae and *Plateosaurus* (von Huene, 1926) and probably related to the insertion of *M. iliofibularis* (one of the major flexors of the knee). However, it is unknown whether this process is homologous with the much more proximally placed anterior trochanters of the basal sauropods *Vulcanodon* and *Tazoudasaurus*.

The relatively flat proximal end of the medial surface of the fibula in *Antetonitrus* is marked by the same broad, triangular arrangement of striations – for articulation with the proximal tibia – common to all sauropodomorphs. Anteriorly, the proximal end of the medial surface houses a distinct rugose boss that can also be seen in the smaller fibula (as well as in *Melanorosaurus readi* and *Aardonyx celestae*). The shaft tapers softly from the proximal end with a barely perceptible rise present just above mid-shaft on the lateral side. This is substantially subtler than the distinct trochanter visible on the lateral shaft of the fibula in *Tazoudasaurus* and more derived sauropods (hypothesized as the origin of the *M. flexor digitorum longus*: Borsuk-Bialynicka, 1977; Wilson & Sereno, 1998). The fibular shaft in *Antetonitrus* is straight and elliptical in cross-section, with the lateral side softly convex and the medial side softly concave. This contrasts with the condition in a number of nonsauropodan sauropodomorphs (e.g. *Blikanasaurus*;

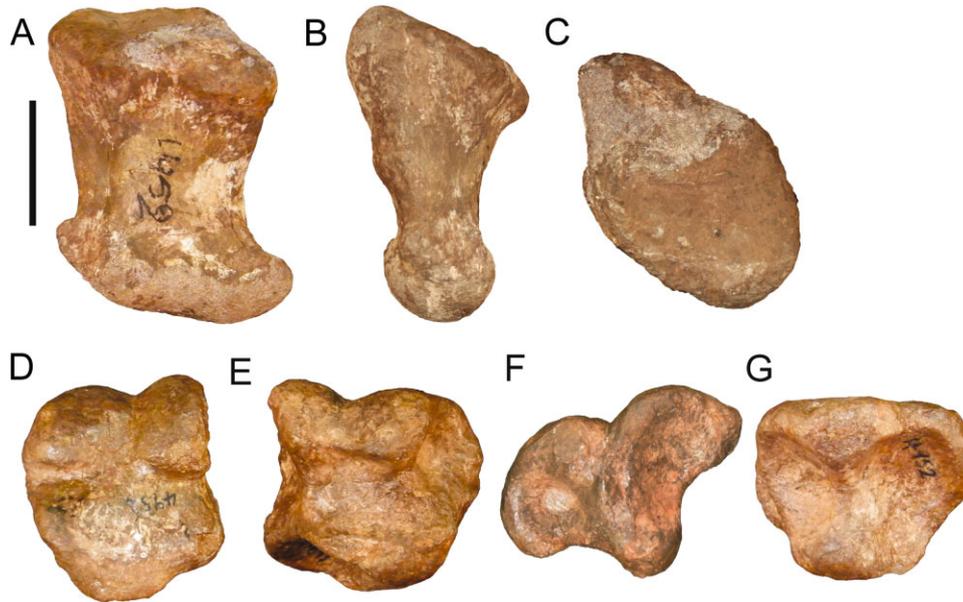
*Aardonyx*; *Massospondylus*; *Riojasaurus*) that tend to have medially bowed, subcircular shafts, and is more similar to the derived sauropodan condition (Upchurch *et al.*, 2004). Towards the distal end the anterior margin of the shaft thins, forming a low, axially orientated ridge that is possibly homologous to the vertical crest described for *Tazoudasaurus*. A similar vertical ridge can be seen in the fibula of *Plateosaurus* (von Huene, 1926). The distal end expands in the same anteroposterior plane as the proximal end, failing to display the 40–50° axial twist of most nonsauropodan sauropodomorph taxa (e.g. *Plateosaurus*; *Yunnanosaurus*; *Massospondylus*). The lack of axial twisting, as well as a distal end that displays a similar degree of expansion as the proximal end, is similar to that of most sauropod taxa (e.g. *Tazoudasaurus*; *Spinophorosaurus*; *Barapasaurus*). As in *Melanorosaurus* (Galton *et al.*, 2005) there is an anteromedial sulcus proximal to the distal articular surface that is confluent with an oblique groove that rises from the posteromedial corner of the distal surface. However, as the majority of the distal condyle appears to have been displaced laterally because of taphonomic deformation, it is possible that the extent of this rather deep groove may be artificially exaggerated. The distal condyle is flat-to-convex throughout its length and lacks the pronounced posteroventral extension visible in *Blikanasaurus* (Galton & Van Heerden, 1998).

#### Pes

The pedal elements are represented by a left metatarsal 1, a right metatarsal 2, a left metatarsal 3, a right(?) metatarsal 5, two nonterminal pedal phalanges, a right pedal ungual 1, and a smaller pedal ungual from possibly the second or third digit. Nearly all the elements are complete, although the distal end of the fifth metatarsal is missing. The metatarsals are also in general proportion (for non-eusauropodan sauropodomorphs) to one another so it is therefore possible they all derive from a single individual. In the original *Antetonitrus* study (Yates & Kitching, 2003) a second, smaller metatarsal 2 was attributed to the ‘paratype individual’, but this bone cannot currently be located.

The pes is of special interest as it documents the general shortening of the individual elements and, perhaps more importantly, the reduction of the third metatarsal in relation to the first as the weight-bearing axis of the foot shifts from mesaxonic to entaxonic at the base of Sauropoda (Carrano, 2005).

*First metatarsal:* The first metatarsal is a squat, robust element most similar in basic morphology to that of *Blikanasaurus* (BPI/1/527/a: Yates, 2008),



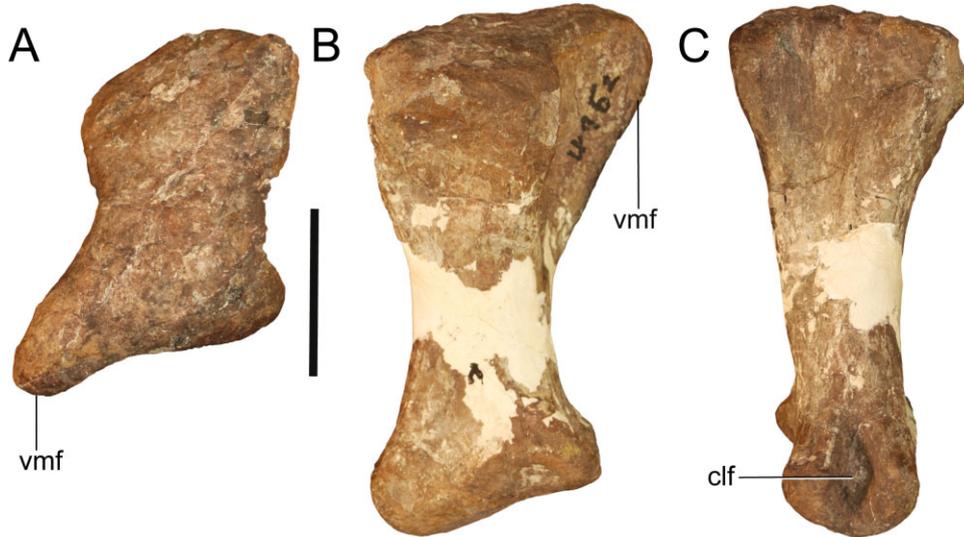
**Figure 20.** *Antetonitrus ingenipes* (BP/1/4952). A–C, left metatarsal 1 in A, dorsal; B, medial; and C, proximal views. D–G, ?right nonterminal pedal phalanx in D, dorsal; E, ventral; F, medial; and G, proximal views. Scale bar = 5 cm.

although it is volumetrically larger than the first metatarsal in that species (Fig. 20). The maximum transverse width (measured as the maximum width of proximal articular surface) of metatarsal 1 is 0.77 times the total proximodistal length of the bone. This ratio is similar to that of other sauropodiform taxa such as *Blikanasaurus* (0.80), *Aardonyx* (0.74), and *Jingshanosaurus* (Yates, 2008). In contrast, most basal sauropodomorph taxa (e.g. *Massospondylus*; *Plateosaurus*; *Leoneosaurus*) display a proportionally longer, more slender first metatarsal with a width/length ratio of around 0.35–0.44. An interesting phenomenon, rarely noted upon within the literature, is the tendency for metatarsal 1 to lengthen again within basal Sauropoda, with the proximal width/total length ratio of the first metatarsal in *Vulcanodon* and *Tazoudasaurus* approximately 0.62 and 0.52, respectively. In eusauropod taxa such as *Shunosaurus lii* and *Omeisaurus* the first metatarsal has reassumed a squat and robust morphology similar to the proportions observed in *Antetonitrus* and *Blikanasaurus*. This pattern implies a complicated series of evolutionary reversals, the adaptive function/significance of which is unknown. Curiously, the elongated metatarsal 1 of *Lessemsaurus* appears to present a ratio closer to ‘core prosauropods’ than that of *Antetonitrus* and *Blikanasaurus*, but examination of text-figure 12 in Pol & Powell (2007) reveals a first metatarsal that is distinctly atypical in appearance, suggesting either erroneous assignment or diagnosis. Unfortunately, this element could not be located during a trip to the collections at the Instituto Miguel Lillo (PVL), so

the curious morphology of the first metatarsal in *Lessemsaurus* could not be investigated further.

The proximal surface of the first metatarsal in *Antetonitrus* is flat, dorsoventrally deep, and ovoid in shape, being subequal in size to the proximal surface of the only preserved metatarsal 2. There is a narrow, rounded, protrusion extending from the lateral side of the dorsal surface where it would have overlapped the second metatarsal. This morphology is extremely similar to the proximal articular surface of the first metatarsal in both *Blikanasaurus* and *Vulcanodon*. In contrast, most nonsauropodan sauropodomorphs (e.g. *Massospondylus*; *Plateosaurus*; *Lufengosaurus*; *Aardonyx*) have much narrower proximal heads that are substantially smaller relative to the proximal articular surface of the second metacarpal. The proximal surface is twisted about 40° relative to the transverse axis of the shaft (seen also in *Blikanasaurus* and *Vulcanodon*) and angled so that the articular facet can be seen in anterior view. As noted by Pol *et al.* (2011), an obliquely orientated articular facet (when viewed either anteriorly or laterally) has been regarded as a synapomorphy of Eusauropoda (Wilson, 2002), but is also clearly observable in *Antetonitrus* and *Tazoudasaurus*. In contrast, the proximal articular surface of metatarsal 1 in most nonsauropodan sauropodomorphs is orthogonal with respect to the proximodistal axis of the metatarsal shaft.

The shaft is markedly short, with its minimum transverse width 0.53 times the total bone length. This differs from most basal sauropodomorphs [e.g. *Anchisaurus polyzelus*, YPM, 208; *Lufengosaurus*



**Figure 21.** *Antetonitrus ingenipes*, right metatarsal 2 (BP/1/4952) in A, proximal; B, dorsal; and C, lateral views. Abbreviations: clf, collateral fossa; vmf, ventromedial flange. Scale bar = 5 cm.

*huenei*, LV 003; *Plateosaurus* (von Huene, 1926)] that display a minimum mid-shaft width of between 0.21 and 0.31 times the total length, and is almost identical to the same ratio in the first metatarsal of *Blikanasaurus* and *Omeisaurus tianfuensis* (He *et al.*, 1998). However, it is again stouter than the 0.32–0.35 ratio observed within ‘Vulcanodontidae’. As in most derived sauropodomorphs the shaft of metatarsal 1 is significantly thicker than the shaft of metatarsal 3, a feature for which *Lessemsaurus* appears to represent a curious exception (but see above). The distal condyles conform to the typical asymmetrical morphology of derived sauropodomorphs in which the lateral condyle is substantially more developed both dorsoventrally and distally than the medial condyle. There is a well-developed and deep ligament pit on the lateral side of the lateral condyle.

**Second metatarsal:** The second metatarsal is 1.47 times the length of the first metatarsal. Provided that both the elements derive from a single individual then this ratio is similar, if not slightly reduced, to that of most nonsauropodan sauropodomorphs. In accord with all the other bones of the pes, the second metatarsal records the shift towards a shorter, more robust foot architecture in sauropod (or near-sauropod) dinosaurs. The maximum transverse width of the proximal surface of the second metatarsal (Fig. 21) in *Antetonitrus* (measured as total proximal surface visible when viewed anteriorly) is approximately half the proximodistal length of the bone. This proportion most closely matches the second metatarsals of derived sauropodomorphs like *Aardonyx* and *Tazoudasaurus* (Allain & Aquesbi, 2008; Yates *et al.*,

2010). In contrast, most basal sauropodomorphs (e.g. *Massospondylus*, BP/1/4377; *Plateosaurus*: von Huene, 1926; *Lufengosaurus*; *Anchisaurus*) have a much more slender second metatarsal, with a maximum width approximately 0.29–0.43 times the total length (interestingly, the most basal ‘true’ sauropod, *Vulcanodon*, has a second metatarsal width/length value that falls between these two groups). In Eusauropoda the second metatarsal becomes squatter still, with species such as *Omeisaurus tianfuensis* exhibiting a ratio of about 0.73 (He, Kui & Cai, 1988).

Proximally, the articular surface of metatarsal 2 in *Antetonitrus* adheres to the well-known biconcave (or ‘hour-glass’) morphology recognized in all basal sauropodomorphs (e.g. *Pantyraco* Galton, Yates & Kermack, 2007; *Massospondylus*; *Lufengosaurus*), although the medial surface is considerably deeper than the lateral. This morphology reflects the tight articulation of the second metatarsal with the first (medially) and the second (laterally) and appears to have been reduced in *Vulcanodon* and lost in more derived sauropods, although *Tazoudasaurus* appears to have retained the plesiomorphic condition (Allain & Aquesbi, 2008: text-fig. 32h). The proximal surface is deeper dorsoventrally than transversely wide and distinctly asymmetrical, mainly on account of the marked expansion of the medioventral corner of the proximal surface (incorrectly described as a ‘ventrolateral wing’ in Smith & Pol, 2007). This ventromedial flange of bone probably buttressed the first metatarsal ventrally (possibly reflecting the increased weight-supporting function of that element) and can also be seen in the second metatarsals of other derived sauropodomorphs (e.g. *Aardonyx*;

*Vulcanodon*; *Tazoudasaurus*). In contrast, several other non-eusauropod sauropodomorphs have a more developed ventrolateral flange of the proximal surface of metatarsal 2 (e.g. *Massospondylus*; *Glacialisaurus*; *Lufengosaurus*).

The shaft of metatarsal 2 is short and straight with a rhomboidal cross-section. The distal condyles are more equally developed than in metatarsal 1, although the lateral condyle is still more distally and mediolaterally expanded than the medial condyle, as in most non-eusauropod sauropodomorphs. There is a deep collateral fossa on the lateral surface of the lateral condyle, as on metatarsal 1.

**Third metatarsal:** As in all non-neosauropodan sauropodomorphs the third metatarsal (Fig. 22) is the longest element of the pes (although metatarsal 4 is not represented here in *Antetonitrus*). The ratio of the length of metatarsal 1 to metatarsal 3 in *Antetonitrus* is 0.58, which is within the immediate range of most other non-eusauropodan sauropodomorphs (e.g. *Plateosaurus*; *Riojasaurus*; *Massospondylus*, BP/1/4377; *Aardonyx*; *Blikanasaurus*). *Vulcanodon*, with its secondarily elongated first metatarsal, displays a higher ratio of ~0.65 (Cooper, 1984), and *Lessemsaurus*

is more atypical yet, with a ratio of 0.79 (Pol & Powell, 2007). Pol & Powell (2007: 237) stated that although the ratio of metatarsal 1 to metatarsal 3 in *Lessemsaurus* has no non-eusauropodan correlate, derived forms such as *Omeisaurus maoianus* Tang *et al.*, 2001, 'have a metatarsal 1 that is enlarged and similar to that of *Lessemsaurus*'. However, examination of the *Omeisaurus maoianus* metatarsus (Tang *et al.*, 2001: fig. 42a) yields a ratio of only about 0.6. Furthermore, although other derived eusauropod forms such as *Shunosaurus lii* and *Omeisaurus tianfuensis* may have had first metatarsals that were proportionately longer when compared to metatarsal 3, it is more likely that this is the result of reduction in metatarsal 3 than enlargement in metatarsal 1. This is evidenced by a metatarsal 1 in *Antetonitrus* that is of similarly squat proportions to those of *Shunosaurus* and *Omeisaurus* and a metatarsal 3 that displays proportionally shorter (0.43; measured as maximum width of the proximal surface over total proximodistal length) dimensions than those of most nonsauropodan sauropodomorphs in which a ratio of around 0.24–0.33 is observed (*Anchisaurus*; *Massospondylus*; *Riojasaurus*; *Plateosaurus*). Derived sauropods such as *Shunosaurus lii* and *Omeisaurus tianfuensis* therefore



**Figure 22.** *Antetonitrus ingenipes* (BP/1/4952). A–D, left metatarsal 3 in A, proximal; B, dorsal; C, ventral; and D, medial views. E, F, ?right metatarsal 5 in E, dorsal; and F, proximal views. Scale bar = 5 cm.

record the further reduction of relative metatarsal 3 length with proximal width/total length values of around 0.6 (Zhang, 1988) and 0.53, respectively.

As is typical of most derived sauropodomorphs (including *Vulcanodon* and *Tazoudasaurus*), the convex proximal surface of the third metatarsal is triangular in outline, with a broad ventrolateral surface and an acute dorsomedial apex. This differs from most massospondylid sauropodomorphs (i.e. *Glacialisaurus*; *Lufengosaurus*; *Coloradisaurus*), which have subtrapezoidal proximal outlines in which the posteromedial edge is expanded into a discrete surface (Smith & Pol, 2007). Proximally, on the anterolateral surface of the shaft, there is a faintly striated shallow concavity, which potentially represents the insertion area of the M. tibialis anterior (Carrano & Hutchinson, 2002; Smith & Pol, 2007).

The shaft is straight and subtriangular in cross-section, tapering gently towards the distal condyles which, as in most non-eusauropodan sauropodomorphs, are deflected slightly medially (e.g. *Massospondylus*; *Aardonyx*; *Lessemsaurus*; *Vulcanodon*). On the distal end of the dorsal surface there is another shallow, striated depression, which is interpreted as the attachment site for the extensor ligament. The distal condyles are roughly symmetrically developed but the medial condyle is slightly deeper dorsoventrally. On neither the lateral nor medial surfaces of the distal condyles can obvious collateral ligament fossae be observed, but it is possible that the lateral surface still has some adherent matrix obscuring the full dimensions of the fossa.

*Fifth metatarsal:* Metatarsal 5 is complete proximally but is missing its distal portion (Fig. 22). Although incomplete, it is clear that metatarsal 5 would have been reduced in much the same manner as in all non-eusauropodan sauropodomorphs. The reduction of the fifth metatarsal in relation to the rest of the pes was traditionally one of the major synapomorphies hypothesized to link a monophyletic 'Prosauropoda' (Cruickshank, 1975); however, the transitional state of the fifth metatarsal in derived taxa like *Vulcanodon* and *Omeisaurus* has been pointed out in recent years (Serenó, 2007).

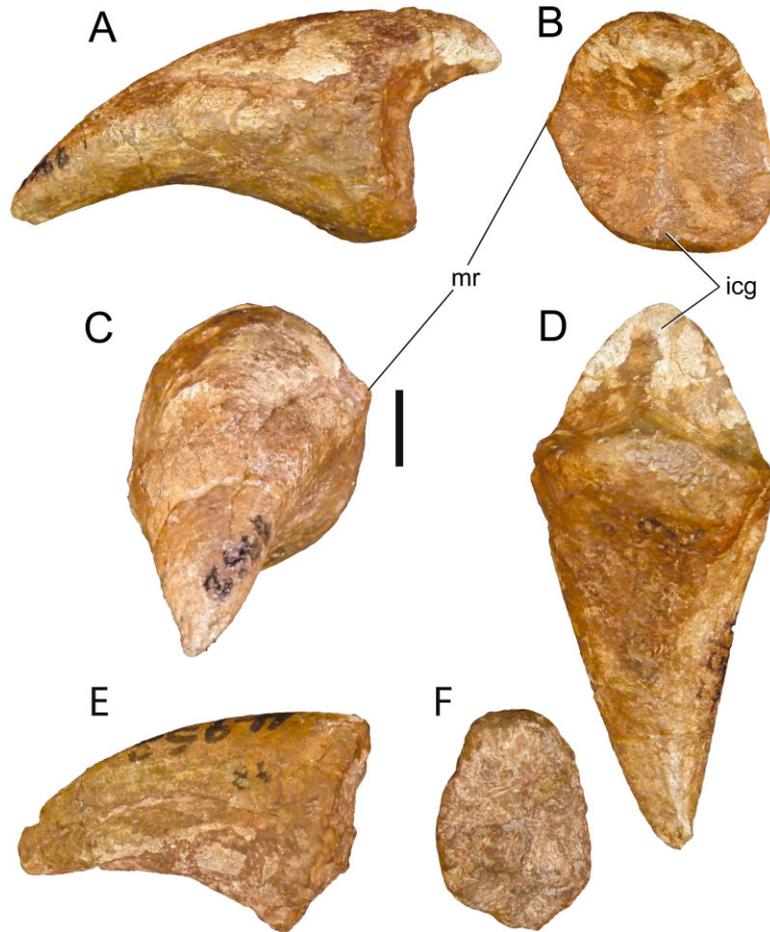
As in all nonsauropodan sauropodomorphs metatarsal 5 in *Antetonitrus* is relatively flat and triangular, displaying the characteristic 'paddle' shape common to all basal sauropodomorphs. The convex proximal surface is mediolaterally wide and dorsoventrally shallow, its maximum depth 0.32 times its total transverse width. This is a somewhat smaller ratio than most nonsauropodan sauropodomorphs (e.g. *Massospondylus*; *Plateosaurus engelhardti*; *Lufengosaurus*), which have comparatively less transversely expanded fifth metatarsals, displaying values of

around 0.42 to 0.45. *Antetonitrus* is therefore closer to the ratios exhibited by *Vulcanodon* (0.36: Cooper, 1984) and *Tazoudasaurus* (0.38: Allain & Aquesbi, 2008: text-fig. 33d). The dorsal surface is slightly concave and the medial margin is thinner than the lateral margin; this is to be expected as the fourth metatarsal would have overlapped the fifth dorsomedially. However, the fifth metatarsal in *Antetonitrus* lacks the pronounced medial flange evident in metatarsal 5 of *Lessemsaurus*. The bone tapers strongly mediolaterally from the proximal surface but, unfortunately, the distal extent of the fifth metatarsal is unknown because of breakage. It is therefore impossible to say if the distal condyle was weakly developed as in all known nonsauropodan sauropodomorphs, or approached the comparatively robust architecture observed in basal sauropods like *Vulcanodon*, *Tazoudasaurus*, and *Shunosaurus*.

*Pedal phalanges:* There are two nonterminal pedal phalanges present (Fig. 20). Both are markedly robust, with the width of one subequal to its total length and the width of the other rather greater than its length. Given their lack of mid-point constriction and squat morphology, it is likely that they are distal elements, although this represents no more than an educated guess. Given their relatively large size with respect to the metatarsals it is possible that they derive from the inner digits (potentially 2 or 3), in which case the foot of *Antetonitrus* can be seen as approaching the short and broad condition seen in eusauropods. However, the pedal phalanges of *Antetonitrus* are plesiomorphic in still retaining strongly developed ginglymoidal articular surfaces and deep collateral fossa (seen also in *Vulcanodon*, *Tazoudasaurus*, and all non-eusauropodan sauropodomorphs).

*Pedal unguals:* There are two pedal unguals present in the *Antetonitrus* assemblage. One is a large, well-preserved ungual from the ?right pedal digit 1. The other is substantially smaller, less well preserved, and probably belongs to either pedal digit 2 or 3 (Fig. 23).

Pedal ungual 1 is longer proximodistally than metatarsal 1. Provided that both elements belong to the same individual this would differentiate *Antetonitrus* from the majority of non-eusauropodan sauropodomorphs (e.g. *Lamplughsaura*; *Massospondylus*; *Anchisaurus*; *Vulcanodon*), which exhibit a proportionally shorter pedal ungual 1 than metatarsal 1. Although there is a tendency in derived nonsauropodan sauropodomorphs [e.g. *Melanorosaurus* (NM QR3314); *Jingshanosaurus*; *Blikanasaurus*] for the first pedal ungual to exceed the length of metatarsal 1, *Vulcanodon* is again notable



**Figure 23.** *Antetonitrus ingenipes* (BP/1/4952). A–D, right pedal ungual 1, in A, medial; B, posterior; C, anterior; and D, ventral views. E, F, pedal ungual ?3 in E, side; and F, proximal views. Abbreviations: icg, intercondylar groove; mr, medial ridge. Scale bar = 2 cm.

in exhibiting the reverse condition (possibly explainable via its secondarily elongate first metatarsal). Whether this is because of homoplastic convergence with respect to Eusauropoda [e.g. *Shunosaurus*; *Omeisaurus maoianus* (Tang *et al.*, 2001)] in the case of the former, or character reversal in the latter, remains to be established. The dorsoventral height of pedal ungual 1 in *Antetonitrus* is 0.60 times the proximodistal length of metatarsal 1, very similar to the same ratio in *Lessemsaurus* (Pol & Powell, 2007).

In contrast to *Vulcanodon* and most derived sauropods, the first pedal ungual of *Antetonitrus* is not particularly sickle-shaped or recurved (Bonnar, 2005). The proximal articular surface of pedal ungual 1 is as transversely wide as it is dorsoventrally deep. This contrasts with most sauropodomorph taxa that tend to have more mediolaterally compressed first unguals (e.g. *Pantydraco*; *Massospondylus*;

*Aardonyx*; *Camarasaurus grandis*: Wilson & Sereno, 1998), but is similar to the closely related non-eusauropodan taxa *Melanorosaurus* (NM QR3314) and *Blikanasaurus*. The two concave proximal articular facets are roughly symmetrical, although the longitudinal intercondylar ridge is directed obliquely mediodorsally, rendering the medial articular facet somewhat smaller. The proximodorsal lip extends further than the proximoventral base, upon which there is no easily distinguishable flexor tubercle. Pedal ungual 1 of *Antetonitrus* is laterally deflected along its proximodistal axis so that the convex dorsal surface faces slightly medially and the flatter ventral surface is directed laterally – an orientation further developed in eusauropods (Bonnar, 2005). The angle between the dorsal and ventral surfaces is more acute medially than laterally. The lateral and medial nail grooves are shallowly represented and lack the proximal bifurcation of a number of other basal

sauropodomorphs [e.g. *Massospondylus* (BP/1/4377); *Aardonyx* (BP/1/7044)], a feature also seen in the largest pedal ungual of *Lessemsaurus* (PVL 4822/78). The tip, although broken at its distal extreme, appears to have tapered to a relatively sharp apex.

Pedal ungual ?3 is a smaller, morphologically simpler element that lacks the degree of preservation seen in pedal ungual 1. It is mediolaterally narrow, at least relative to the first pedal ungual, lacking the distinctive dorsoventral flattening seen in pedal unguals 1 and 2 of *Vulcanodon*. The proximal articular surface is poorly preserved and therefore unable to provide any diagnostic information. There appear to have been very shallow keratin grooves on the mediolateral surfaces. The distal tip is bluntly rounded.

#### RESULTS OF CLADISTIC ANALYSIS

The initial cladistic analysis (see Material and methods) produced 160 most parsimonious trees (MPTs) with a shortest length of 1206 steps. In the strict consensus of this analysis, taxa more derived than *Aardonyx* are grouped as successively unresolved polytomies [i.e. (*Melanorosaurus*, *Blikanasaurus*, *Gongxianosaurus*, *Camelotia*, *Lessemsaurus*, *Antetonitrus*) (*Isanosaurus*, *Vulcanodon*, *Tazoudasaurus*)]. a posteriori examination of the MPTs revealed that the position of *Camelotia* (in either lacking apomorphies that would place it with higher taxa or possessing conflicting character data) is wildly unstable. The a posteriori exclusion of *Camelotia* from the consensus, although confirming the position of *Antetonitrus* as more derived than *Melanorosaurus* and *Blikanasaurus*, failed however to resolve the relationships of *Antetonitrus* to *Lessemsaurus* and *Gongxianosaurus*. This uncertainty, along with the paucity of figured information with which to corroborate the character scoring of *Camelotia* (cf. Galton, 1998), argued in favour of an a priori exclusion of *Camelotia* from the analysis. This final investigation, along with the deletion of character 184 (see Description: caudal vertebrae), produced 16 MPTs of 1194 steps (Fig. 24). This tree provides the main focus for the following phylogenetic discussion.

The overall topology of the strict consensus tree at nodes basal to *Melanorosaurus* is much the same as in the topologies produced by Yates (2007a, b, 2010) and Apaldetti *et al.* (2011), in which a monophyletic Plateosauridae and Massospondylidae is recovered. Taxa more derived than *Melanorosaurus* adhere to the 'classic' topology in which *Antetonitrus* and *Lessemsaurus* are sister taxa at the base of Sauropoda *sensu* Yates (2007a,b). Similar to the results published in Apaldetti *et al.* (2011), the newly described North American form *Seitaad* (Sertich &

Loewen, 2010) is a sister taxon to *Jingshanosaurus* in a relatively derived position between *Yunnanosaurus* and *Anchisaurus*. *Isanosaurus* is recovered as more derived than *Vulcanodon*, separating the latter from its 'vulcanodontid' (*sensu* Allain & Aquesbi, 2008) sister taxon, *Tazoudasaurus*. This topology would require a redefinition of 'Gravisauria' *sensu* Allain & Aquesbi (2008) if *Vulcanodon* were to remain within that taxonomic unit (but see Yates *et al.*, 2012); however, as 'Gravisauria' is a subjective junior synonym with the traditional Sauropoda *sensu* Salgado *et al.* (1997), no redefinition is attempted here. The position of *Isanosaurus* as more derived than *Vulcanodon* is suspicious, given the putative Rhaetian age of the former, and the ?Toarcian age of the latter, and is potentially an artefact of the considerable sum of missing information on both taxa [it is also possible that the derived position of *Isanosaurus* results from its having preserved elements with highly derived, diagnostic features that are unknown in *Vulcanodon* (i.e. opisthocoeleous cervical vertebrae; dorsal neural arches with spinodiapophyseal laminae)].

The *Lessemsaurus*/*Antetonitrus* clade is supported by a number of unambiguous synapomorphies, including: slit-shaped neural canals on the dorsal neural arches; dorsal neural spines that are transversely expanded towards their dorsal end; a minimum width of the scapula that is greater than 20 per cent of its length; the dorsal expansion of the scapula blade equal to the width of the scapular head; and a first metacarpal the proximal width of which is greater than its length. The only unambiguous synapomorphies linking the common ancestor of *Lessemsaurus* and *Antetonitrus* with more advanced sauropodomorphs (*Gongxianosaurus* + Sauropoda) are two features of the astragalus – an element that remains unknown in *Antetonitrus*. A further possible synapomorphy linking *Antetonitrus* and *Lessemsaurus* to later sauropods relates to the length of the deltopectoral crest (no more than 50% of the length of the humerus), but this is rendered ambiguous because of the unknown condition of *Blikanasaurus*.

Bremer support for nodes within Sauropodomorpha is generally no higher than 2 (Fig. 25), although some groups have relatively high bootstrap values (e.g. Sauropoda *sensu* Salgado *et al.*, 1997 = 68%). Although the grouping of *Antetonitrus* and *Lessemsaurus* is consistently recovered in the final analysis, support for this clade (bootstrap = < 50%) is nonetheless reduced compared to previous analyses (Yates, 2007a, b). This is probably related to changes in the scoring of *Lessemsaurus* in the current analysis that generally tended towards the more conservative, plesiomorphic condition (see Appendix S1).

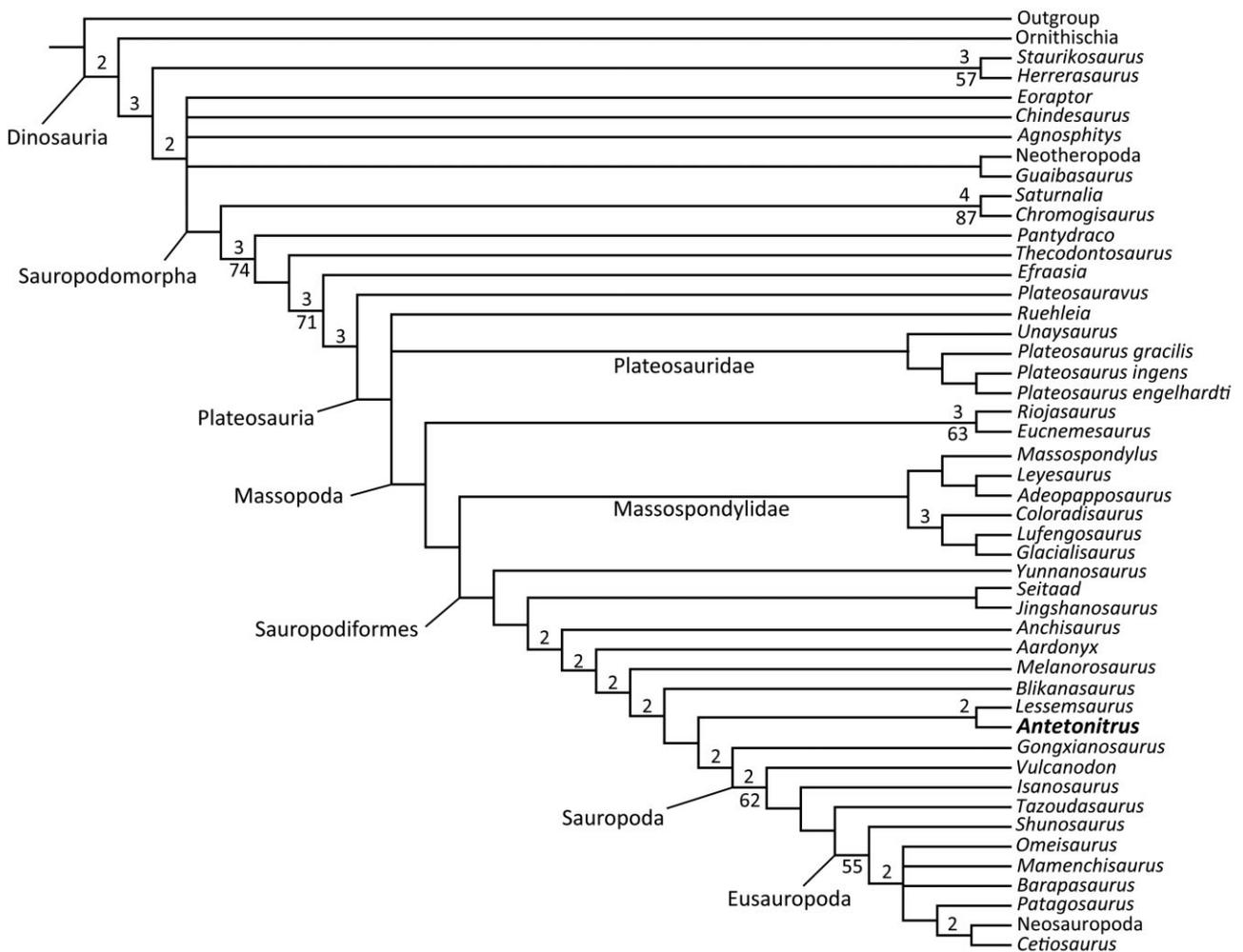
## DISCUSSION

PHYLOGENETIC POSITION OF *Antetonitrus*

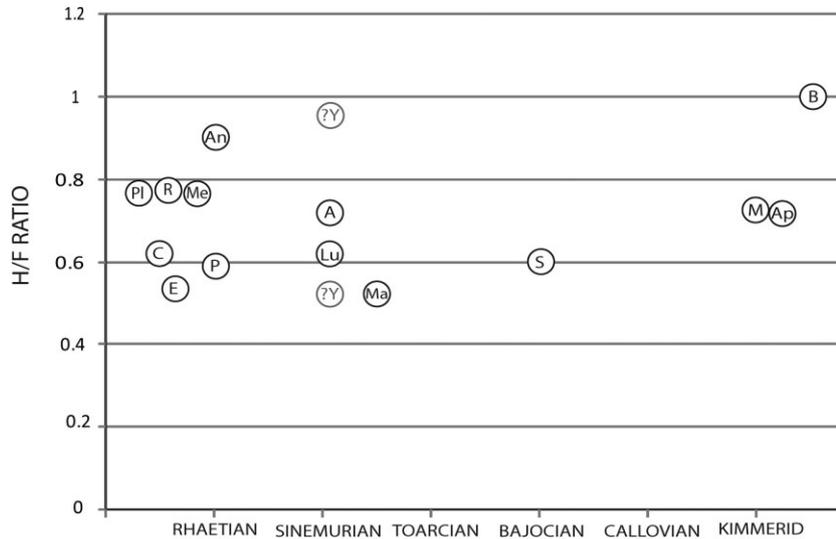
Our analysis corroborates the position of *Antetonitrus* as a transitional taxon positioned intermediately between a pectinate array of (?mostly) bipedal basal sauropodomorph taxa and the clade of large quadrupedal herbivores of the Jurassic. In the phylogenetic definition of Sauropoda favoured by Yates (2007a, b), the poorly known *Blikanasaurus* is the only sauropodan taxa more basal than the clade formed by *Lessemsaurus* and *Antetonitrus*, suggesting that these species are of particular significance in reconstructing the rate and nature of character change at this critical juncture in sauropodomorph evolution.

*Blikanasaurus* + (*Antetonitrus* + *Lessemsaurus*) are linked with more derived sauropods (in Yates' preferred terminology) via two unambiguous synapomorphies: the reduction in the length of the

third metatarsal relative to the tibia (character 336), and the asymmetrically flared ventral surface of the proximal second metatarsal (character 354). The former is undoubtedly correlated with the move towards a more graviportal, less cursorial form of locomotion, whereas the latter also suggests a change in the weight-bearing dynamics of the foot. *Antetonitrus* also shares a number of derived characters with Sauropoda that are either non-unique (i.e. appear at nodes basal to *Antetonitrus*) or are rendered as local autapomorphies because of absences in taxa immediately apical to it (although it should be noted that the majority of these 'absences' are exclusive to *Gongxianosaurus*, a taxon for which the available figured information is comparably poor). These include: relatively deep hyposphenes (present from *Melanorosaurus* onwards); invasion of dorsal neural arches by pneumatic diverticula (present to a lesser degree in *Aardonyx* and *Eucnemesaurus*, absent in



**Figure 24.** Strict consensus tree of final cladistic analysis (16 most parsimonious trees). Numbers above branches represent Bremer support (> 1) and those below represent bootstrap values (> 50%).



**Figure 25.** Sauropodomorph humerus-to-femur (H/F) ratios by geological age. The dual placement of Y: *Yunnanosaurus* (IVPP V20) reflects the discrepancy in measurements given in Young (1942) and Rauhut *et al.* (2011). Taxa: A, *Anchisaurus* YPM 1883 (Rauhut *et al.*, 2011); An, *Antetonitrus* BP/1/4952; Ap, *Apatosaurus* (Rauhut *et al.*, 2011); B, *Brachiosaurus altithorax* FMNH P 25107 (Taylor, 2009); C, *Coloradisaurus* PVL 5904; E, *Efraasia* SMNS 12667 (Rauhut *et al.*, 2011); Lu, *Lufengosaurus* IVPP V20 (Young, 1941); M, *Memenchisaurus* ZDM 0083 (Rauhut *et al.*, 2011); Ma, *Massospondylus* SAM-K-5135 (Bonnar & Senter, 2007); Me, *Melanorosaurus* NM QR3314; P, *Plateosaurus* SMNS13200 (Rauhut *et al.*, 2011); Pl, *Plateosaurus* SAM-K-3342, 3602 (Van Heerden, 1979); R, *Riojasaurus* PVL 380; S, *Shunosaurus* ZDM T 5402 (Rauhut *et al.*, 2011).

*Gongxianosaurus* and *Lessemsaurus*); concurrently high neural arches and spines in the dorsal vertebrae (present to a lesser degree from *Aardonyx* onwards, absent in *Gongxianosaurus*); well-developed spinopostzygapophyseal laminae (absent in *Gongxianosaurus*); acquisition of a caudosacral vertebra and hypospheneal ridge on anterior caudals (present from *Melanorosaurus* onwards); anteroposteriorly shortened anterior caudal vertebrae (present from *Aardonyx* onwards); a (possibly) elongated humerus (present from *Anchisaurus* onwards); radial fossa on the proximal ulna (also in *Melanorosaurus*); femoral shaft elliptical with reduced sinuosity in lateral view (present to lesser degree from *Aardonyx* onwards); relocation of both the lesser and fourth trochanters (present in varying degrees in both *Aardonyx* and *Melanorosaurus*); a tibia that is approximately 0.6 times the length of the femur; an ascending process of the distal tibia that is visible in posterior aspect (present from *Anchisaurus* onwards); and a sloped orientation of the proximal surface of the first metatarsal (absent in *Gongxianosaurus*). From the above it is clear that the paucity of available information on important transitional Laurasian taxa like *Gongxianosaurus* (cf. He *et al.*, 1998) obscures a detailed reading of the relationships between *Antetonitrus* and taxa immediately apical to it. A comprehensive treatment of this poorly known taxon

(and the more robust character data that would result from it) could potentially demonstrate that many of the classically ‘sauropodan’ characters seen in *Antetonitrus* and more advanced taxa may in fact be synapomorphies of a more inclusive group that includes not only Sauropoda, but more transitional forms like *Melanorosaurus* and *Aardonyx*.

Nonetheless, *Antetonitrus* retains a number of plesiomorphies relative to Sauropoda (*sensu* this study). These include: fully acamerate vertebral centra; absence of prezygaparapophyseal and spinodiapophyseal laminae in dorsal vertebra (unknown in *Vulcanodon*); shallow caudal transverse processes; presence of cuboid fossa on humerus; retention of an olecranon process (?absent in *Gongxianosaurus*); length of radius less than 80% of the length of the humerus; manual phalanx 1.1 twisted along proximodistal axis and with an embayment on the medial side (unknown in *Vulcanodon* and *Isanosaurus*); ilium with a straight dorsal margin and a dorsoventrally shallow preacetabular process that does not project beyond the anterior margin of the pubic peduncle [inferred from referred material (NM QR1545); unknown in *Vulcanodon* and *Isanosaurus*]; pubic apron medioventrally extensive; fourth trochanter present as a tall crest (?absent in *Gongxianosaurus*); proximal surface of metatarsal 2 biconcave; a (possibly) reduced pedal digit 5

(?enlarged in *Gongxianosaurus*); a subcircular, mediolaterally wide pedal ungual 1; and a femur that is less than 1000 mm in length. It is also possible that *Antetonitrus* can be further distinguished from Sauropoda because of the 'plesiomorphic' position of its primary fibula trochanter (anterior as opposed to lateral). However, as there appears to be some confusion regarding both the homology and myological associations of these fibular processes (see Description), this distinction should be treated with caution.

#### DEFINITION OF SAUROPODIFORMES

From the above it is clear that *Antetonitrus* retained a suite of morphological features that have more in common with the unspecialized form of facultative quadrupedality/bipedality of taxa immediately basal to it than they do to the specialized, columnar forelimbs characteristic of Sauropoda. Although *Antetonitrus* presages many of the changes associated with the sauropod bauplan (especially those related to shifts in the weight-bearing architecture), many of these traits – especially of the hindlimb – were already present (if only incipiently) in several taxa basal to *Antetonitrus* (e.g. *Anchisaurus*; *Aardonyx*; *Melanorosaurus*). The name Sauropodiformes is elected here in order to group these 'transitional' forms occupying a contiguous phylogenetic position near the base of Sauropoda. Of particular interest is the observation that all of the Sauropodiformes taxa (as defined here) that share a shortened manus (character 222) roughly correspond with the genera that Remes (2008) described as exhibiting 'manus type 2' (wide metacarpal 1, robust metacarpals 2–4, and block-like phalanges) in his comprehensive study of the evolutionary development of the sauropodomorph forelimb. Furthermore, Remes (2008: 252) stated that the forms sharing this modified manual type typically display (to varying degrees) adaptations for manus pronation in the antebrachium. This suggests that the basal sauropodiform hand represents a functional trade-off between the need to retain manual dexterity and mobility whilst providing an important auxiliary role in resisting large loading stresses during contact with the substrate. The bifurcated tubercle observed on the ventrolateral corner of the second metacarpal in both *Aardonyx* (BP/1/386) and *Antetonitrus* may relate – as a potential additional supporting mechanism – to this specific locomotory strategy. A further exploration of the hypothesized range of motion in both *Antetonitrus* and similarly derived sauropodomorph taxa is given in the discussion below.

#### THE DEGREE OF QUADRUPEDALITY IN *ANTETONITRUS*

The primitive dinosauromorphs/dinosauriforms of the Middle Triassic (e.g. *Marasuchus* Sereno &

Arcucci, 1994) are generally reconstructed as small, habitual bipeds with cursorial limbs (Sereno *et al.*, 1993; Sereno & Arcucci, 1994; Langer *et al.*, 2010). Although the earliest sauropodomorphs (e.g. *Panphagia* Martinez & Alcober, 2009; *Saturnalia*, *Thecodontosaurus*) appear to have retained a similar body plan, it took as little as 10 000 000 years for the first multi-tonne herbivores of the Late Triassic to appear (Bonaparte, 1972; Langer *et al.*, 2010; Rauhut *et al.*, 2011). Given that *Antetonitrus* – with its early stratigraphical age and great size – has obvious bearing on this transition, it is unfortunate that continued uncertainty in regards to its appendicular proportions renders its full relevance to the acquisition of obligate quadrupedalism in sauropod dinosaurs contentious.

When *Antetonitrus* was originally described (Yates & Kitching, 2003), the elongate length of the forelimb was listed as one of the principal diagnostic features linking *Antetonitrus* with the obligatory quadrupedal sauropods of the Early Jurassic. Explicit in this view was the understanding that the fossil assemblage BP/1/4952 represented no more than two individuals; a subadult holotype that constituted the majority of the remains and a smaller, more juvenile paratype (Yates & Kitching, 2003). It is clear that such a division no longer accurately reflects the *Antetonitrus* fossil assemblage. A simple Minimum Number of Individuals count of the entire BPI assemblage reveals that the scapulae alone account for three different individuals (two subequally sized left-sided elements and a substantially smaller right).

As reconstructed in Remes (2008), it is likely that the larger humerus, ulnae, radius, and manus (at least metacarpal 1) (BP/1/4952) represent an individual forelimb. This is supported by agreement in the inter-relationships of each element with the general proportions observed within the majority of derived Sauropodomorpha genera. However, the smaller duplicate elements of the forelimb (humerus and ulna: BP/1/4952b) are harder to configure, and it is less likely that the ulna belongs with the humerus given that the former is 0.7 times the length of the latter (which would be unusually high for a Triassic sauropodomorph) compared to the ratio of 0.59 observed in the larger elements (although it is possible that this reflects allometric growth of the forelimbs). If the large, duplicate left-sided metacarpal 2 and scapula are then considered, the number of individuals represented by the pectoral girdle and forelimb alone rises to potentially as many as four (see Table 3).

The relationship of the major collection of the forelimb material to the hindlimb material is harder to determine, and is essentially contingent on the relationship of the larger humerus to the femur. If, as originally hypothesized (Yates & Kitching, 2003), both

**Table 3.** Appendicular bones present in the *Antetonitrus* type quarry and their hypothesized relationships

ID	Scapula	Humerus	Ulna	Radius	McI	McII	Pubis	Femur	Tibia	Fibula	Pes
1	L	R	*	R	R	L					
2	L					L					
3	R	R									
4			R								
5							L	L	L	L	

Light grey = BP/1/4952, which is split to convey uncertainty in inter-relatedness. Dark grey = BP/1/4952c and mid-tone = BP/1/4952b. Dashed lines also represent uncertainty in hypothesized 'individuality' (ID).

\*Both elements present.

L, left; McI and II, metacarpal 1 and 2; R, right.

elements are collected under the holotype BPI/1/4952 as belonging to a single individual, a dramatic increase in relative humerus-to-femur length (= 0.9) within a relatively limited temporal span must ultimately be postulated. All other sauropodomorphs from the late Triassic for whom the relative humerus-to-femur lengths are known have a humeral/femoral ratio of between approximately 0.53 and 0.78 (e.g. *Plateosaurus*; *Anchisaurus*; *Lufengosaurus*; *Riojasaurus*; *Melanorosaurus*). In fact, it is not until the advent of later Jurassic species such as *Brachiosaurus* Riggs, 1903 (Taylor, 2009) that sauropods begin to display a humeral/femoral ratio of over 0.9 (Fig. 25). One curious exception may be that of *Yunnanosaurus*, which in a recent analysis of sauropodomorph morphometrics (Rauhut *et al.*, 2011) was described as having a humeral/femoral ratio of 0.96. However, in the original description (Young, 1942) this same individual (IVPP V, 20) has a humeral/femoral ratio of only 0.53. Unfortunately, the reasons for this rather marked discrepancy are unknown.

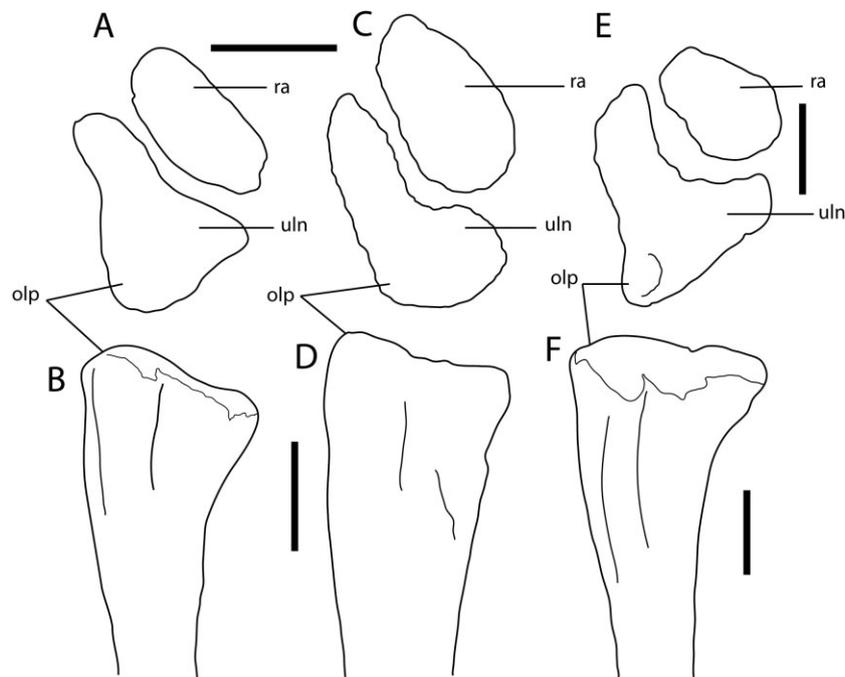
The referred assemblage NM QR1545 lends modest support for an elongate humerus in *Antetonitrus* as the assemblage contains a solitary humerus and (mostly) complete femur of almost identical relative (and absolute) lengths to that of the holotypic material. However, as the National Museum assemblage also preserves the remains of at least three differently sized individuals, any supporting evidence has to be regarded with this caveat in mind. Anecdotal evidence for elongation of the humerus was also offered by Gauffre (1993) in his referral of the 'Bloem dino' to '*Euskelosaurus*' (later renamed '*Kholumolumosaurus*' Gauffre, 1996). This material was excavated from Maphutseng in Lesotho between 1955 and 1970 by Ellenberger and represents a massive, potentially monospecific dinosaur bone-bed that is now divided between Cape Town and Paris (see Material and methods). According to Gauffre (1993) this material conforms to the diagnostic criterion of '*Euskelosaurus*'

(Van Heerden, 1979) in which the length of the humerus approaches 80% of that of the femur. However, it is near-impossible to gauge the individuality of various limb bones within a very large quarry of dissociated sauropodomorph material, and any assumptions of association of elements should be treated with caution.

It should be noted, also, that if the total length of the forelimb (i.e. humerus + radius + metacarpal 2) is compared to the total length of the hindlimb (i.e. femur + tibia + metatarsal 3) the resulting metric is slightly less extreme, with a forelimb/hindlimb ratio of around 0.81. Although this metric is similar to a greater variety of taxa than that of the humerus/femur ratio, it is again shared exclusively with sauropods of the late Jurassic (e.g. *Mamenchisaurus*; *Camarasaurus*) while being significantly greater than that of the basal sauropod *Shunosaurus* (0.66; see Rauhut *et al.*, 2011: 125). This implies an appendicular specialization in *Antetonitrus* that is in marked distinction with the observed phylogenetic trend of Triassic–Jurassic sauropodomorphs. There is an additional danger in extrapolating the length of entire limbs from multiple-individual assemblages as the reliance on a greater number of elements (i.e. three for each limb) can conflate any inaccuracies that may arise in the erroneous assignment of particular limb segments. It is clear, therefore, that the implementation of ratio data from *Antetonitrus* will probably have to await the discovery of more complete, semi-articulated specimens.

BEYOND RATIOS: THE RANGE OF MOVEMENT IN  
*ANTETONITRUS* AS INFERRED FROM PREVIOUS  
STUDIES INTO SAUROPODOMORPH  
FUNCTIONAL MORPHOLOGY

Sauropodomorph variation, when presented as a reductive collection of differential ratios (i.e. hindlimb/trunk; forelimb/hindlimb), tends to occupy the full spectrum of values between those 'expected' of



**Figure 26.** Changes in radius and ulna morphology throughout Sauropodomorpha. A, B, *Antetonitrus ingenipes*: A, right ulna and radius in proximal view; B, right ulna in lateral view. C, D, *Vulcanodon karibaensis* (modified from Cooper, 1984): C, right ulna and radius in proximal view; D, right ulna in ?lateral view. E, F, *Camarasaurus grandis* (modified from Wilson & Sereno, 1998): E, left (reversed) ulna and radius in proximal view; F, left (reversed) ulna in lateral view. Abbreviations: olp, olecranon process; ra, radius; uln, ulna. Scale bars = 10 cm.

obligate bipeds and those 'expected' of obligate quadrupeds (see Galton, 1976, 1990; Galton & Upchurch, 2004; Bonnan & Senter, 2007; Rauhut *et al.*, 2011). Owing to this ambiguity, recent studies have tended to focus instead on functional and phylogenetic data in elucidating the habitual posture and locomotion of sauropodomorph dinosaurs (Bonnan & Senter, 2007; Remes, 2008; Mallison, 2010a, b). Bonnan & Senter (2007) reconstructed the well-known 'prosauropods' *Plateosaurus* and *Massospondylus* as obligate bipeds primarily because of the plesiomorphic morphology of the antebrachium (which prohibited the anterior rotation of the radius about the ulna, precluding the use of the manus as a pronated support/propulsive structure), a reconstruction corroborated by Mallison's (2010a, b) analysis of a complete virtual skeleton of *Plateosaurus*. A slightly more complex picture of the range of motion in the sauropodomorph forelimb was presented by Remes (2008). With the possible exception of *Plateosaurus*, he found no major modifications in the basal sauropodomorph (and basal dinosaur) forelimb that indicated obligate bipedalism, suggesting instead that the convexly expanded humeral head and hypertrophied forearm flexor (*M. biceps brachii*) of most basal sauropodomorph taxa are primarily related to the increased mobility of a semi-abducted grasping apparatus.

This morphology is still very much evident in the forelimb of *Antetonitrus*, in which the presence of a deep intercondylar cavity (= cuboid fossa) on the distal humerus, along with the pronounced olecranon process on the proximal ulna, suggests a degree of compression-resistant flexion consistent with the partially abducted forelimb posture plesiomorphic to archosaurs (Remes, 2008). Although it is possible that the reduced medial tuberosity of the proximally vaulted, dome-like humeral head allowed for a more vertical, parasagittal inclination of the humerus, the plesiomorphic subperpendicular angle between the long axes of the scapular blade and head argues against a sauropod-like anteroventral rotation of the glenoid in *Antetonitrus* (unfortunately, the lack of a preserved coracoid makes the full range of movement at the glenoid impossible to determine) (Remes, 2008; see also Bonnan & Senter, 2007; Mallison, 2010a, b). Nonetheless, other features observed in *Antetonitrus* can be viewed as a potential shift towards a more sauropodan orientation of the anterior limb. The incipient radial fossa of the proximal ulna, although not as developed as in later sauropod taxa (Fig. 26), may have facilitated manual pronation by supporting the radius in a derived position anterior to the ulna (see Bonnan, 2003; Yates & Kitching, 2003; Bonnan & Senter, 2007; Bonnan & Yates, 2007).

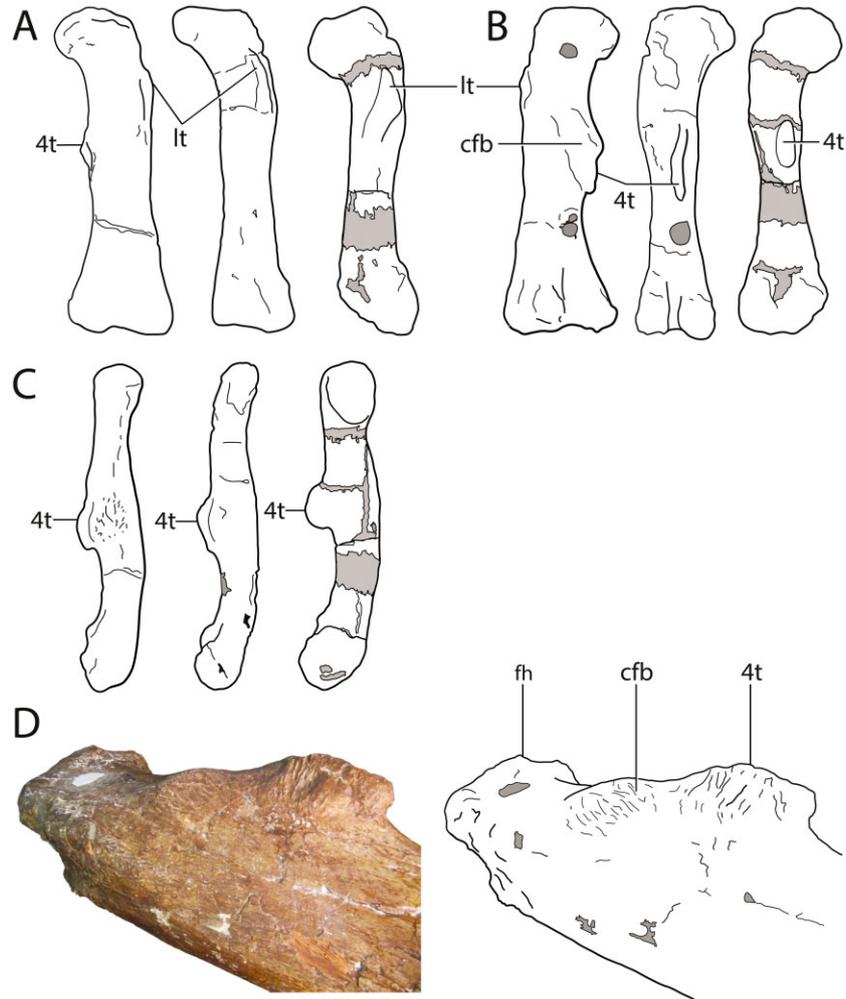
This morphology, in concert with a semi-abducted forelimb, probably represents an important intermediary point whereby the manus of *Antetonitrus* and other closely related sauropodiform taxa (e.g. *Melanorosaurus*; *Aardonyx*) could be manipulated for a variety of tasks in either a bipedal or quadrupedal context. As the fully pronated, tubular manus of derived sauropods was primarily an immobile support structure [with the majority of propulsive force being generated by the hindlimb (Bonnan, 2003; Carrano, 2005)], the semisupinated manus of a number of 'prosauropods' is therefore probably more indicative of a retained grasping ability than it is a lack of supportive/propulsive potential.

The hindlimb in both stem (e.g. *Marasuchus*) and basal (e.g. *Eoraptor*; *Herrerasaurus*) dinosaurs has traditionally been characterized as the cursorial extension of an obligate biped (e.g. Charig, 1972; Sereno & Arcucci, 1994; Novas, 1996; Benton *et al.*, 2000). Langer (2003) was the first to comprehensively explore the locomotor posture of a (very) basal sauropodomorph (*Saturnalia*) with reference to the functional morphology of the hindlimb. Although *Saturnalia* shared the disparate limb proportions and elongated epipodium of nondinosaurian dinosauromorphs, the degree of lateral movement inferred from the reconstructed hindlimb (along with the potentially heightened trunk/hindlimb ratio) led Langer (2003) to suggest that quadrupedality constituted an important part of the *Saturnalia* behavioural suite. This superficially agreed with Christian, Koberg & Preuschoft's (1996; see also Christian & Preuschoft, 1996) reconstruction of the hindlimb posture of *Plateosaurus* as a more erect version of the sprawling gait of lizards [as previously suggested by Van Heerden (1979, 1997)], whereby the powerful adductor muscles observed in the pelvic girdle of *Plateosaurus* are hypothesized as counteracting the abducting forces inherent in a semi-erect hindlimb. However, Mallison (2010a) has shown that in order to avoid toppling, large adductor forces in *Plateosaurus* would have been necessary to steady the feet directly beneath the centre of mass (the pelvis) whilst walking bipedally.

*Antetonitrus* (along with most sauropodomorphs) shares with *Plateosaurus* a suite of features related to a fully erect hindlimb posture [e.g. a fully perforate acetabulum with a transversely broadened dorsal margin (= supra-acetabular crest); a medially orientated femoral head; and distal condyles roughly perpendicular to the long axis of the femoral shaft]. However, the hindlimb of *Antetonitrus* departs from *Plateosaurus* in a number of respects that could be broadly deemed 'sauropodan'. These include: an eccentric (transversely widened) femoral shaft in which the lesser trochanter is displaced laterally and

the fourth trochanter migrated disto-medially (see Fig. 27); a robust tibia that is reduced in length relative to the femur and with a anteroposteriorly levelled proximal surface; and a stout, subplantigrade metatarsus with the main weight-bearing axis shifted medially (see Carrano, 1999, 2001, 2005; Wilson, 2005). Nonetheless, a notable difference between the hindlimb of *Antetonitrus* and 'true' sauropods can be observed in the major sites of muscle attachment. Owing to the need to diffuse points of peak stress across a wider area of bone, along with a concurrent reduction in the flexion/extension movements of the lower limb, the osteological correlates of the musculature system are significantly reduced in fully graviportal, columnar-limbed sauropods (Carrano, 2005; Wilson, 2005). In contrast, *Antetonitrus* continues to display many of the associate pits, ridges, and striations of an extensive muscular complex built to withstand large loading forces and facilitate efficient flexion/extension (e.g. the cnemial crest).

Of particular interest is the prominent muscle scar posterior and slightly proximal to the plesiomorphically massive fourth trochanter, which, including the trochanter and its associated muscle scars, accounts for approximately 40% of the total circumference of the femoral shaft at that point (Fig. 27). We hypothesize that this rugose area of bone represents the lateral incursion of the *M. caudofemoralis brevis* onto the posterior side of the femoral shaft. Exercising the primary femoral retraction forces, the caudofemoralis group of muscles are recognized as the key propulsive agents during dinosaur locomotion (Gatesy, 1990; Hutchinson & Gatesy, 2000), and Bates & Schachner (2012) have recently demonstrated the ability of *M. caudofemoralis brevis* to exert an additional adducting force on the femur in a number of dinosaurian taxa. In progressively more derived, wider-gaited sauropodomorphs the fourth trochanter moves from a proximal position on the posterior side of the femur to a position mid-way down the medial edge of the femoral shaft (e.g. *Melanorosaurus*; *Vulcanodon*; *Barapasaurus*). Although possibly conserving the optimum line of action for the major femoral retractor (*M. caudofemoralis longus*), a more medially orientated fourth trochanter would have located the *M. caudofemoralis brevis* directly beneath the iliac postacetabular process, limiting the degree to which this muscle could exert adductor forces upon the femur. Therefore, a lateral expansion of the *M. caudofemoralis brevis* onto the posterior side of the femoral shaft potentially represents an intensification of its adductor-based properties during hindlimb retraction. It is unlikely that *Antetonitrus* would have required the additional power (or support) of a specialized adduction/retraction mechanism if its weight was distributed across at least three limbs at



**Figure 27.** A–C, femoral variation in selected sauropodomorph taxa from the Elliot Formation of South Africa. A, (from left to right) *Antetonitrus ingenipes* (BP/1/4952 = 775 mm), *Aardonyx celestae* (BP/1/6510 = 681 mm), and an unnamed sauropodomorph (BP/1/4910 = 564 mm) in anterior view. B, *An. ingenipes*, *Aa. celestae*, and BP/1/4910 in posterior view. C, *An. ingenipes*, *Aa. celestae*, and BP/1/4910 in medial view. Note the plesiomorphic position of the major trochanters in BP/1/4910. D, femur of *An. ingenipes* (BP/1/4952) in posterolateral view emphasizing the hypertrophied attachment site for the *M. caudofemoralis brevis*. Abbreviations: 4t, fourth trochanter; cfb, *M. caudofemoralis brevis* insertion site; fh, femoral head; lt, lesser trochanter.

all times (i.e. while walking quadrupedally). Therefore, it is possible that the posterolateral expansion of the *M. caudofemoralis brevis* represents an amplification of the forces required to facilitate a degree of facultative bipedality in a large animal that may have also exhibited an elongate forelimb – a reconstruction consistent with Mallison's (2010a, b) observations on the adduction forces present in *Plateosaurus*. The retention (albeit rather reduced) of subcursorial locomotor abilities in *Antetonitrus* may have presented a considerable advantage in a Late Triassic ecosystem in which the faster predatory cursors were of considerably smaller size (e.g. *Coelophysis*), but in which large ambush predators (e.g. the 'Rausuchidae') were still

active. Bipedality, in association with efficient flexion/extension motions at the elbow and knee would have also been of obvious utility during feeding (i.e. when rearing to reach high vegetation), while possibly playing an additional role in inter- and intraspecific aggression displays and mating.

#### PALAEOECOLOGY OF BASAL SAUROPODA

The early record of the diversification and evolution of Sauropoda is extremely poorly known. Although the Late Triassic is represented by a number of taxa that provide insight into the ancestral suite of sauropod features [e.g. *Blikanasaurus* (Galton & Van

Heerden, 1998); *Lessemsaurus* (Pol & Powell, 2007); *Antetonitrus* (Yates & Kitching, 2003; present study); *Isanosaurus* (Buffetaut *et al.*, 2000)], the Early Jurassic has currently only a handful of fragmentary genera of equivocal sauropod affinity (He *et al.*, 1998; Yates *et al.*, 2004, 2012; Upchurch & Barrett, 2005; Upchurch *et al.*, 2007b). In fact, most of the genera often presented as exemplars of Early Jurassic basal Sauropoda (e.g., *Vulcanodon*; *Tazoudasaurus*; *Gongxianasaurus*; *Barapasaurus*) do not enter the record until at least the early Toarcian [c.f. Bandyopadhyay *et al.*, 2010: age estimates for the Early/Middle Jurassic Kota formation of India are poorly constrained and wide ranging, with the majority of evidence favouring at least a late Early Jurassic depositional onset (e.g. Parmar, Prasad & Kumar, 2013)]. In contrast, a multitude of basal sauropodomorph dinosaurs are present in the Early Jurassic that are unambiguously nonsauropodan in both taxonomy and morphology (Young, 1951; Galton, 1976; Cooper, 1981; Gow, Kitching & Raath, 1990; Zhang & Yang, 1994; Yates, 2004a, 2010; Barrett, Upchurch & Xiao-Lin, 2005; Barrett *et al.*, 2007; Smith & Pol, 2007; Martínez, 2009; Sertich & Loewen, 2010; Yates *et al.*, 2010; Pol *et al.*, 2011; Rowe *et al.*, 2011). This invites the question: is the biased distribution of Early Jurassic sauropodomorph taxa merely an artefact of inadequate sampling of Early Jurassic rocks, or is there another – possibly ecological – explanation for the scarcity of sauropod-grade animals from these deposits?

The end of the Triassic has long been recognized as a period of dramatic geological, environmental, and ecological upheaval (e.g. Raup & Sepkoski, 1982; Benton, 1991; Hallum, 2002; see Sues & Fraser, 2010). Mass faunal turn-over was accompanied by the general aridification of many of the major terrestrial fossil-bearing deposits of the early Jurassic (e.g. the Upper Elliot, Clarens, and Navajo formations). Recently, Irmis (2010) identified a general dinosaur-wide drop in diversity beginning at the Sinemurian, citing as a probable explanation the increasingly arid conditions of some areas that created unfavourable conditions for body-fossil preservation. Although Mannion *et al.* (2011) observed a relatively high sauropodomorph diversity from the Norian through to the later Early Jurassic, what both of these studies fail to explain is the paucity of sauropod-grade animals in deposits where more basal taxa are comparatively common, especially following the Late Triassic peak in diversity of the large-bodied transitional forms.

We hypothesize that the widespread prevalence of arid conditions in the Early Jurassic initiated an era of environmental hardship that precluded the large-bodied, transitional taxa from participating in many

early Jurassic ecosystems. The Late Triassic deposits where these forms are found (e.g. the Lower Elliot Formation; the Los Colorados Formation) are generally characterized by thick alluvial plain sediment suggestive of a humid or subhumid depositional environment (Anderson *et al.*, 1998; Caselli, Marsicano & Arcucci, 2001; Arcucci, Marsicano & Caselli, 2004; Bordy *et al.*, 2004; Bordy, Prevec & Makhwelo, 2006). The low-lying marshes and riparian forests thought to predominate in such a landscape would have provided ample plant matter to support a large, bulk-browsing dinosaur equivalent in size to *Antetonitrus* (Anderson *et al.*, 1998). In comparison, the drier, ephemeral-fluvial and aeolian conditions of formations like the Upper Elliot, Clarens, and Navajo appear to have favoured smaller, generalized feeders such as *Seitaad* and *Massospondylus* (e.g. Bordy & Catuneanu, 2002; Sertich & Loewen, 2010). Although the onset of these arid conditions clearly failed to extinguish the sauropod line completely, the fringe refugia that sustained them [possibly within the warm-temperate high latitudes of northern Laurasia and southern Gondwana (see Hallam, 1994; Sellwood & Valdes, 2008)] are yet to be recovered in the fossil record. Towards the Middle Jurassic the adaptations that had facilitated increased size and a move towards graviportal locomotion in several sauropodomorph lineages in the Late Triassic suddenly proved universally advantageous, with Sauropoda ultimately displacing their more gracile cousins entirely (cf. Allain & Aquesbi, 2008). Although evidence remains too sparse to meaningfully test the degree to which direct competition from sauropod dinosaurs may have led to the demise of the prosauropod grade, it appears that scenarios that posit a superior feeding apparatus in basal Sauropoda can be eliminated because of the relatively plesiomorphic morphology of the dentition of the basal sauropod taxa *Chinshakiangosaurus* and *Tazoudasaurus* (see Barrett & Upchurch, 2005). More probably, it was the result of a confluence of factors centring on the acquisition of large size, a quadrupedal gait, an elongate neck, and what may have been a novel mode of in-gut food processing (see Klein *et al.*, 2011; Sander *et al.*, 2011).

Testing the above hypothesis will require intensive fieldwork in the sauropodomorph-bearing beds of the Lower Jurassic, and it is likely that the fossiliferous deposits of southern Africa (e.g., the Upper Elliot Formation) and Laurasia (e.g. the Lufeng and Dashanpu formations, and the Junggar Basin of China) will play a significant role. However, the paucity of early Jurassic terrestrial sediments from the more northern and southern latitudes of Pangaea will probably continue to obscure a detailed reading of this pivotal period in sauropodomorph evolution.

## CONCLUSION

*Antetonitrus* is perhaps the best exemplar we currently have of the morphological halfway point between the generalized locomotor strategy of 'prosauropods' and the columnar graviportalism of sauropods. Evidence from *Antetonitrus* and other closely related taxa suggests that the forelimb accrued changes more slowly than the hindlimb on the line leading to Sauropoda, probably expressing the retained mobility of the former (as an effective grasping apparatus), and the reorganization of mass-reaction forces (at increased body sizes) in the latter. In *Antetonitrus* a marked size increase, in conjunction with a possibly elongate forelimb, may have led to the development of a unique form of facultative bipedalism. Presently, the phylogenetic inter-relationships of Sauropodomorpha are derived from cladistic analyses that fail to consider the full spectrum of data relating to functional myology and its osteological proxies, with future character formulations needing to draw on our improved understanding of the differential range of motion evident across Sauropodomorpha (e.g. Remes, 2008; Mallison, 2010a, b). Finally, the comprehensive analysis of poorly known – yet highly significant – transitional taxa such as *Jingshanosaurus* and *Gongxianasaurus* is also required in order to strengthen our inferences of both the convoluted relationships of sauropodomorph dinosaurs, and the origin of Sauropoda.

## ACKNOWLEDGEMENTS

B. W. M. would like to thank Bernard Zipfel, Jennifer Botha, Sheena Kaal, and Jamie Powell for access to specimens in their care, and Jay Nair for helpful conversations. He would also like to thank Dr Peter Hayward for his patience and assistance in bringing the current study to press. The authors would like to thank an anonymous reviewer for comments that improved the strength of this manuscript. Funding for B. W. M. to visit collections in Argentina was provided by the Bi-national Cooperation project between South Africa (DST to Bruce Rubidge) and Argentina (MINCYT to Claudia Marsicano).

## REFERENCES

- Allain R, Aquesbi N. 2008. Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas* **30**: 345–424.
- Allain R, Aquesbi N, Dejax J, Meyer C, Monbaron M, Montenat C, Richir P, Rochdy M, Russell D, Taquet P. 2004. A basal sauropod dinosaur from the Early Jurassic of Morocco. *Comptes Rendus Palevol* **3**: 199–208.
- Anderson JM, Anderson HM, Cruickshank AR. 1998. Late Triassic ecosystems of the Molteno/Lower Elliot biome of southern Africa. *Palaeontology* **41**: 387–412.
- Apaldetti C, Martinez RN, Alcober OA, Pol D. 2011. A new basal sauropodomorph (Dinosauria: Saurischia) from Quebrada del Barro Formation (Marayes-El Carrizal Basin), northwestern Argentina. *PLoS ONE* **6**: e26964.
- Apaldetti C, Pol D, Yates A. 2013. The postcranial anatomy of *Coloradisaurus brevis* (Dinosauria: Sauropodomorpha) from the late Triassic of Argentina and its phylogenetic implications. *Palaeontology* **56**: 277–301.
- Arcucci AB, Marsicano CA, Caselli AT. 2004. Tetrapod association and palaeoenvironment of the Los Colorados Formation (Argentina): a significant sample from Western Gondwana at the end of the Triassic. *Geobios* **37**: 557–568.
- Bandyopadhyay S, Gillette DD, Ray S, Sengupta DP. 2010. Osteology of *Barapasaurus tagorei* (Dinosauria: Sauropoda) from the Early Jurassic of India. *Palaeontology* **53**: 533–569.
- Barrett PM, Upchurch P. 2005. Sauropodomorph diversity through time: paleoecological and macroevolutionary implications. In: Curry Rogers KA, Wilson JA, eds. *The sauropods: evolution and paleobiology*. Berkeley, CA: University of California Press, 125–126.
- Barrett PM, Upchurch P, Xiao-Lin W. 2005. Cranial osteology of *Lufengosaurus huenei* Young (Dinosauria: Prosauropoda) from the Lower Jurassic of Yunnan, People's Republic of China. *Journal of Vertebrate Paleontology* **25**: 806–822.
- Barrett PM, Upchurch P, Zhou XD, Wang XL. 2007. The skull of *Yunnanosaurus huangi* Young, 1942 (Dinosauria: Prosauropoda) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. *Zoological Journal of the Linnean Society* **150**: 319–341.
- Bates KT, Schachner ER. 2012. Disparity and convergence in bipedal archosaur locomotion. *Journal of The Royal Society Interface* **9**: 1339–1353.
- Benton MJ. 1991. What really happened in the Late Triassic? *Historical Biology* **5**: 263–278.
- Benton MJ, Juul L, Storrs GW, Galton PM. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the upper Triassic of southwest England. *Journal of Vertebrate Paleontology* **20**: 77–108.
- Bonaparte JF. 1972. Los tetrapodos del sector superior de la formacion los colorados, La Rioja, Argentina (Triasico Superior). *Opera Lilloana* **22**: 1–183.
- Bonaparte JF. 1978. *Coloradia brevis* n. g. et n. sp. (Saurischia, Prosauropoda), dinosaurio Plateosauridae superior de la Formacion Los Colorados, Triasico Superior de La Rioja, Argentina. *Ameghiniana* **15**: 327–332.
- Bonaparte JF. 1999. Evolucion de las vertebras presacras en Sauropodomorpha. *Ameghiniana* **36**: 115–187.
- Bonaparte JF, Ferigolo J, Ribeiro AM. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sol state, Brazil. *Proceedings of the Second Gondwanan Dinosaur Symposium, National Science Museum Monographs* **15**: 89–109.

- Bonaparte JF, Powell J. 1980.** A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Mémoires de la Société Géologique de France (Nouvelle Série)* **139**: 19–28.
- Bonaparte JF, Vince M. 1979.** El hallazgo del primer nido de dinosaurio Triásicos, (Saurischia, Prosauropoda), Triásico superior de Patagonia, Argentina. *Ameghiniana* **16**: 173–182.
- Bonnan MF. 2003.** The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. *Journal of Vertebrate Paleontology* **23**: 595–613.
- Bonnan MF. 2005.** Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny. In: Tidwell V, Carpenter K, eds. *Thunder-lizards: the sauropodomorph dinosaurs*. Bloomington, IN: Indiana University Press, 346–379.
- Bonnan MF, Senter P. 2007.** Were the basal sauropodomorph dinosaurs *Plateosaurus* and *Massospondylus* habitual quadrupeds? *Special Papers in Palaeontology* **77**: 139–155.
- Bonnan MF, Yates AM. 2007.** A new description of the forelimb of the basal sauropodomorph *Melanorosaurus*: implications for the evolution of pronation, manus shape and quadrupedalism in sauropod dinosaurs. *Special Papers in Palaeontology* **77**: 157–168.
- Bordy EM, Catuneanu O. 2002.** Sedimentology and palaeontology of upper Karoo aeolian strata (Early Jurassic) in the Tuli Basin, South Africa. *Journal of African Earth Sciences* **35**: 301–314.
- Bordy EM, Hancox PJ, Rubidge BS. 2004.** Basin development during the deposition of the Elliot Formation (Late Triassic – Early Jurassic), Karoo Supergroup, South Africa. *South African Journal of Geology* **107**: 397–412.
- Bordy EM, Hancox PJ, Rubidge BS. 2005.** The contact of the Molteno and Elliot formations through the main Karoo Basin, South Africa: a second-order sequence boundary. *South African Journal of Geology* **108**: 351–364.
- Bordy EM, Prevec R, Makhwelo C. 2006.** Late Triassic (Norian) palaeoecosystem of the lowermost Elliot Formation (Salpeterberg, Eastern Cape, South Africa). In: Parker WG, Ash SR, Irmis RB, eds. *A century of research at Petrified Forest National Park: geology and paleontology*. Flagstaff, AZ: Museum of Northern Arizona Bulletin, 169–170.
- Borsuk-Bialynicka M. 1977.** A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica* **37**: 1–64.
- Buffetaut E, Suteethorn V, Cuny G, Tong H, Le Loeuff J, Khansubha S, Jongautchariyakul S. 2000.** The earliest known sauropod dinosaur. *Nature* **407**: 72–74.
- Carrano MT. 1999.** What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. *Journal of Zoology* **247**: 29–42.
- Carrano MT. 2001.** Implications of limb bone scaling, curvature and eccentricity in mammals and non-avian dinosaurs. *Journal of Zoology* **254**: 41–55.
- Carrano MT. 2005.** The evolution of sauropod locomotion. In: Curry Rogers KA, Wilson JA, eds. *The sauropods: evolution and paleobiology*. Berkeley, CA: University of California Press, 229–250.
- Carrano MT, Hutchinson JR. 2002.** Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology* **253**: 207–228.
- Caselli A, Marsicano C, Arcucci A. 2001.** Sedimentología y paleontología de la Formación Los Colorados, Triásico superior (provincias de La Rioja y San Juan, Argentina). *Revista de la Asociación Geológica Argentina* **56**: 173–188.
- Catuneanu O, Hancox JP, Rubidge BS. 1998.** Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. *Basin Research* **10**: 417–439.
- Charig AJ. 1972.** The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. In: Josey KA, Kemp TS, eds. *Studies in vertebrate evolution*. Edinburgh: Oliver and Boyd, 121–155.
- Charig AJ, Attridge J, Crompton AW. 1965.** On the origin of the sauropods and the classification of the Saurischia. *Proceedings of the Linnean Society of London* **176**: 197–221.
- Christian A, Koberg D, Preuschoft H. 1996.** Shape of the pelvis and posture of the hindlimbs in *Plateosaurus*. *Paläontologische Zeitschrift* **70**: 591–601.
- Christian A, Preuschoft H. 1996.** Deducing the body posture of extinct large vertebrates from the shape of the vertebral column. *Palaeontology* **39**: 801–812.
- Cole DI. 1992.** Evolution and development of the Karoo Basin. In: de Witt MJ, Ransome IGD, eds. *Inversion tectonics of the Cape Fold Belt, Karoo and Cretaceous basins of Southern Africa*. Rotterdam, the Netherlands: A. A. Balkema, 87–99.
- Cooper MR. 1981.** The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers, National Museums and Monuments of Rhodesia, Series B* **6**: 689–840.
- Cooper MR. 1984.** A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. *Palaeontologia Africana* **25**: 203–231.
- Cope ED. 1877.** On a gigantic saurian from the Dakota epoch of Colorado. *Palaeontological Bulletin* **25**: 5–10.
- Cruickshank AR. 1975.** The origin of sauropod dinosaurs. *South African Journal of Science* **71**: 89–90.
- Dilkes DW. 2000.** Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Transactions of the Royal Society of Edinburgh* **90**: 87–125.
- Dilkes DW, Hutchinson JR, Holliday CM, Witmer LM. 2012.** Reconstructing the musculature of dinosaurs. In: Brett-Surman MK, Holtz TR, Farlow JO, eds. *The complete dinosaur*, 2nd edition. Bloomington, IN: Indiana University Press, 151–190.
- Dong Z, Zhou S, Zhang Y. 1983.** Dinosaurs from the Jurassic of Sichuan. *Palaeontologica Sinica* **162**: 1–151.
- Ellenberger F, Ellenberger P. 1956.** Le gisement de dinosauriens de Maphutseng (Basutoland, Afrique du sud).

- Comptes Rendus Sommaires de la Societe Geologique de France* **8**: 99–101.
- Ellenberger F, Ginsburg L. 1966.** Le gisement de dinosauriens de Maphutseng (Basutoland, Afrique du sud) et l'origine des sauropodes. *Comptes Rendus de l'Académie des Sciences, Paris* **262**: 444–447.
- Ezcurra MD. 2010.** A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. *Journal of Systematic Palaeontology* **8**: 371–425.
- Ezcurra MD, Apaldetti C. 2012.** A robust sauropodomorph specimen from the Upper Triassic of Argentina and insights on the diversity of the Los Colorados Formation. *Proceedings of the Geologists' Association* **123**: 155–164.
- Galton PM. 1976.** Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla* **169**: 1–98.
- Galton PM. 1985a.** The poposaurid thecodontian *Teratosaurus suevicus* v. Meyer, plus referred specimens mostly based on prosauropod dinosaurs, from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg. *Stuttgart Beiträge zur Naturkunde (B)* **116**: 1–29.
- Galton PM. 1985b.** Notes on the Melanorosauridae, a family of large Prosauropod Dinosaurs (Saurischia: Sauropodomorpha). *Geobios* **18**: 671–676.
- Galton PM. 1990.** Basal Sauropodomorpha–Prosauropoda. In: Weishampel DB, Dodson P, Osmolska H, eds. *The Dinosauria*. Berkeley, CA: University of California Press, 733.
- Galton PM. 1998.** Saurischian dinosaurs from the Upper Triassic of England: *Camelotia* (Prosauropoda, Melanorosauridae) and *Avalonianus* (Theropoda, ?Carnosauria). *Palaeontographica Abteilung A*: 155–172.
- Galton PM, Upchurch P. 2004.** Prosauropoda. In: Weishampel DB, Dodson P, Osmolska H, eds. *The Dinosauria*. 2nd edition. Berkeley, CA: The University of California Press, 232–258.
- Galton PM, Van Heerden J. 1985.** Partial hindlimb of *Blikanasaurus cromptoni* n. gen. and n. sp., representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. *Geobios* **18**: 509–516.
- Galton PM, Van Heerden J. 1998.** Anatomy of the prosauropod dinosaur *Blikanasaurus cromptoni* (Upper Triassic, South Africa), with notes on the other tetrapods from the lower Elliot Formation. *Paläontologische Zeitschrift* **72**: 163–177.
- Galton PM, Van Heerden J, Yates AM. 2005.** Postcranial anatomy of referred specimens of the sauropodomorph dinosaur *Melanorosaurus* from the Upper Triassic of South Africa. In: Tidwell V, Carpenter K, eds. *Thunder-lizards: the sauropodomorph dinosaurs*. Bloomington, IN: Indiana University Press, 1–37.
- Galton PM, Yates AM, Kermack D. 2007.** *Pantydraco* n. gen. for *Thecodontosaurus caducus* Yates, 2003, a basal sauropodomorph dinosaur from the Upper Triassic or Lower Jurassic of South Wales, UK. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* **243**: 119–125.
- Gatesy SM. 1990.** Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* **16**: 170–186.
- Gauffre F-X. 1993.** Biochronostratigraphy of the Lower Elliot Formation (Southern Africa) and preliminary results on the Maphutseng dinosaur (Saurischia: Prosauropoda) from the same formation of Lesotho. *New Mexico Museum Of Natural History & Science Bulletin* **3**: 147–149.
- Gauffre F-X. 1996.** Phylogénie des dinosaures prosauropodes et étude d'un prosauropode du trias supérieur d'Afrique Australe. PhD Thesis. Museum national d'histoire naturelle, Paris.
- Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Gow CE, Kitching JW, Raath MA. 1990.** Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for Palaeontological Research. *Palaeontologia Africana* **27**: 45–58.
- Halbich IW, Fitch FJ, Miller JA. 1983.** Dating the Cape orogeny. *Special Publication Geological Society of South Africa* **12**: 149–164.
- Hallam A. 1994.** Jurassic climates as inferred from the sedimentary and fossil record. In: Allen JRL, Hoskins BJ, Sellwood BW, Spicer RA, Valdes PJ, eds. *Palaeoclimates and their modelling: with special reference to the Mesozoic Era*. London: Chapman and Hall, 79–88.
- Hallum A. 2002.** How catastrophic was the end-Triassic mass extinction? *Lethaia* **35**: 147–157.
- Haughton SH. 1924.** The fauna and stratigraphy of the Stormberg Series. *Annals of the South African Museum* **12**: 323–497.
- He X, Wang C, Liu S, Zhou F, Lui T, Cai K, Dai B. 1998.** A new species of sauropod from the Early Jurassic of Gongxian Co., Sichuan. *Acta Geologica Sichuan* **18**: 1–7.
- He X-L, Kui L, Cai K. 1988.** *The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan. IV. Sauropod dinosaurs (2) Omeisaurus tianfuensis*. Chengdu: Sichuan Publishing House of Science and Technology.
- von Huene F. 1926.** Vollständige Osteologie eines Plateosauriden aus dem schwabischen Keuper. *Geologische und Palaontologische Abhandlungen* **15**: 129–179.
- von Huene F. 1932.** Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaontologie* **4**: 1–361.
- Hutchinson JR, Gatesy SM. 2000.** Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology* **26**: 734–751.
- Huxley TH. 1866.** On the remains of large dinosaurian reptiles from the Stormberg Mountains, South Africa. *Geological Magazine* **3**: 563.
- Irmis RB. 2010.** Evaluating hypotheses for the early diversification of dinosaurs. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101**: 397–426.
- Jain SL, Kutty TS, Roy-Chowdhury T, Chatterjee S. 1975.** The sauropod dinosaur from the Lower Jurassic Kota Formation of India. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **188**: 221–228.
- Kitching JW, Raath MA. 1984.** Fossils from the Elliot and Clarens formations (Karoo sequence) of the northeastern

- Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia Africana* **25**: 111–125.
- Klein N, Remes K, Gee CT, Sander PM, eds. 2011.** *Biology of the sauropod dinosaurs: understanding the life of giants*. Bloomington, IN: Indiana University Press.
- Knoll F. 2004.** Review of the tetrapod fauna of the 'Lower Stormberg Group' of the main Karoo Basin (southern Africa) : implication for the age of the Lower Elliot Formation. *Bulletin de la Societe Geologique de France* **175**: 73–83.
- Knoll F. 2010.** A primitive sauropodomorph from the upper Elliot Formation of Lesotho. *Geological Magazine* **147**: 814–829.
- Kutty TS, Chatterjee S, Galton PM, Upchurch P. 2007.** Basal sauropodomorphs (Dinosauria: Saurischia) from the Lower Jurassic of India: their anatomy and relationships. *Journal of Paleontology* **81**: 1218–1240.
- Langer MC. 2003.** The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *Paleo Bios* **23**: 1–30.
- Langer MC, Abdala F, Richter M, Benton MJ. 1999.** A sauropodomorph dinosaur from the Upper Triassic (Carman) of southern Brazil. *Comptes Rendus de l'Académie des Sciences – Series IIA – Earth and Planetary Science* **329**: 511–517.
- Langer MC, Ezcurra MD, Bittencourt JS, Novas FE. 2010.** The origin and early evolution of dinosaurs. *Biological Reviews* **85**: 55–110.
- Langer MC, Franca MAG, Gabriel S. 2007.** The pectoral girdle and forelimb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Upper Triassic, Brazil). *Special Papers in Palaeontology* **77**: 113–137.
- Long RA, Murry PA. 1995.** Late Triassic (Carnian and Norian) tetrapods from the Southwestern United States. *New Mexico Museum of Natural History & Science Bulletin* **4**: 1–254.
- Lucas SG, Hancox JP. 2001.** Tetrapod-based correlation of the nonmarine Upper Triassic of southern Africa. *Albertiana* **25**: 5–9.
- Mallison H. 2010a.** The digital *Plateosaurus* I: body mass, mass distribution, and posture assessed using CAD and CAE on a digitally mounted complete skeleton. *Palaeontologia Electronica* **13**: 1–26.
- Mallison H. 2010b.** The digital *Plateosaurus* II: an assessment of the range of motion of the limbs and vertebral column and of previous reconstructions using a digital skeletal mount. *Acta Palaeontologica Polonica* **55**: 433–458.
- Mannion PD, Upchurch P, Carrano MT, Barrett PM. 2011.** Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* **86**: 157–181.
- Marsh O. 1885.** Names of extinct reptiles. *American Journal of Science* **29**: 169.
- Martínez RN, Alcober OA. 2009.** A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS ONE* **4**: e4397.
- Martínez RN. 2009.** *Adeopapposaurus mognai*, gen. et sp. nov. (Dinosauria: Sauropodomorpha), with comments on adaptations of basal Sauropodomorpha. *Journal of Vertebrate Paleontology* **29**: 142–164.
- Meyer H. 1837.** Briefliche Mitteilung an Professor Bronn gerichtet (*Plateosaurus engelhardti*). *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Paläontologie* **1837**: 316.
- Moser M. 2003.** *Plateosaurus engelhardti* Meyer, 1837 (Dinosauria: Sauropodomorpha) aus dem Feuerletten (Mittelkeuper; Obertrias) von Bayern. *Zitteliana* **24**: 3–186.
- Novas FE. 1996.** Dinosaur monophyly. *Journal of Vertebrate Paleontology* **16**: 723–741.
- Novas FE, Ezcurra MD, Chatterjee S, Kutty TS. 2010.** New dinosaur species from the Upper Triassic Upper Maleri and Lower Dharmaram formations of Central India. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101**: 333–349.
- Owen R. 1842.** Report on British fossil reptiles. *Part II. Report of the Eleventh Meeting of the British Association for the Advancement of Science; Held at Plymouth in July 1841* **11**: 60–204.
- Owen R. 1854.** *Descriptive catalogue of the fossil organic remains of Reptilia and Pisces contained in the Museum of the Royal College of Surgeons of England*. London: British Museum of Natural History.
- Parmar V, Prasad GR, Kumar D. 2013.** The first multituberculate mammal from India. *Die Naturwissenschaften* **100**: 515–523.
- Pol D. 2004.** Phylogenetic relationships of basal Sauropodomorpha. PhD Thesis, Columbia University, USA.
- Pol D, Garrido A, Cerda IA. 2011.** A new sauropodomorph dinosaur from the Early Jurassic of Patagonia and the origin and evolution of the sauropod-type sacrum. *PLoS ONE* **6**: e14572.
- Pol D, Powell JE. 2007.** New information on *Lessemsaurus sauropoides* (Dinosauria: Sauropodomorpha) from the Upper Triassic of Argentina. *Special Papers in Palaeontology* **77**: 223–243.
- Raath M. 1972.** Fossil vertebrate studies in Rhodesia: a new dinosaur (Reptilia: Saurischia) from near the Trias-Jurassic boundary. *Arnoldia* **30**: 1–37.
- Rauhut OWM, Fechner R, Remes K, Reis K. 2011.** How to get big in the mesozoic: the evolution of the sauropodomorph body plan. In: Klein N, Remes K, Gee CT, Sander PM, eds. *Biology of the sauropod dinosaurs: understanding the life of giants*. Bloomfield, IN: Indiana University Press, 119–149.
- Raup DM, Sepkoski JJJ. 1982.** Mass extinctions in the fossil record. *Science* **215**: 1501–1503.
- Reig OA. 1963.** La presencia de dinosaurios saurisquios en los 'Estratos de Ischigualasto' (Mesotriásico Superior) de las provincias de San Juan y La Rioja (República Argentina). *Ameghiniana* **3**: 3–20.
- Remes K. 2008.** Evolution of the pectoral girdle and forelimb in Sauropodomorpha (Dinosauria, Saurischia): osteology, myology and function. PhD Thesis, Ludwig-Maximilians-Universität München.

- Remes K, Ortega F, Fierro I, Joger U, Kosma R, Marín Ferrer JM, Ide OA, Maga A, for the Project P, for the Niger Project S. 2009.** A new basal sauropod dinosaur from the middle Jurassic of Niger and the early evolution of Sauropoda. *PLoS ONE* **4**: e6924.
- Riggs ES. 1903.** *Brachiosaurus altithorax*, the largest known dinosaur. *American Journal of Science Series 4* **15**: 299–306.
- Riley H, Stutchbury S. 1836.** A description of various fossil remains of three distinct saurian animals, recently discovered in the Magnesian Conglomerate near Bristol. *Proceedings of the Geological Society of London* **2**: 397–399.
- Rowe TB, Sues H-D, Reisz RR. 2011.** Dispersal and diversity in the earliest North American sauropodomorph dinosaurs, with a description of a new taxon. *Proceedings of the Royal Society B: Biological Sciences* **278**: 1044–1053.
- Salgado L, Coria RA, Calvo JO. 1997.** Evolution of titanosaurid sauropods. I. Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* **34**: 3–32.
- Sander PM, Christian A, Clauss M, Fechner R, Gee CT, Griebeler E-M, Gunga H-C, Hummel J, Mallison H, Perry SF, Preuschoft H, Rauhut OWM, Remes K, Tütken T, Wings O, Witzel U. 2011.** Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews* **86**: 117–155.
- Seeley HG. 1888.** On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* **43**: 165–171.
- Sellwood BW, Valdes PJ. 2008.** Jurassic climates. *Proceedings of the Geologists' Association* **119**: 5–17.
- Sereno PC. 1999.** The evolution of dinosaurs. *Science* **284**: 2137–2147.
- Sereno PC. 2007.** Basal Sauropodomorpha: historical and recent phylogenetic hypotheses, with comments on *Ammosaurus major* (Marsh, 1889). *Special Papers in Palaeontology* **77**: 261–289.
- Sereno PC, Arcucci AB. 1994.** Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology* **14**: 53–73.
- Sereno PC, Forster CA, Rogers RR, Monetta AM. 1993.** Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* **361**: 64–66.
- Sertich JJW, Loewen MA. 2010.** A new basal sauropodomorph dinosaur from the Lower Jurassic Navajo Sandstone of Southern Utah. *PLoS ONE* **5**: e9789.
- Smith ND, Pol D. 2007.** Anatomy of a basal sauropodomorph from the Early Jurassic Hanson Formation of Antarctica. *Acta Palaeontologica Polonica* **52**: 657–674.
- Sues H-D, Fraser NC. 2010.** *Triassic life on land: the great transition*. New York: Columbia University Press.
- Tang F, Jin X-S, Kang X-M, Zhang G-J. 2001.** *Omeisaurus maoianus. A complete Sauropoda from Jingyan, Sichuan*. Beijing: China Ocean Press.
- Taylor MP. 2009.** A re-evaluation of *Brachiosaurus altithorax* Riggs 1903 (Dinosauria, Sauropoda) and its generic separation from *Giraffatitan brancai* (Janensch 1914). *Journal of Vertebrate Paleontology* **29**: 787–806.
- Taylor MP, Upchurch P, Yates AM, Wedel MJ, Naish D. In press.** Sauropodomorpha. In: Queiroz K, Cantino PD, Gauthier JA, eds. *Phylonyms: a companion to the PhyloCode*. Berkeley, CA: University of California Press.
- Upchurch P. 1998.** The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* **124**: 43–103.
- Upchurch P, Barrett PM. 2005.** A phylogenetic perspective on sauropod diversity. In: Curry Rogers KA, Wilson JA, eds. *The sauropods: evolution and paleobiology*. Berkeley, CA: University of California Press, 104–124.
- Upchurch P, Barrett PM, Dodson P. 2004.** Sauropoda. In: Weishampel DB, Dodson P, Osmolska H, eds. *The Dinosauria*, 2nd edition. Berkeley, CA: University of California Press, 259–322.
- Upchurch P, Barrett PM, Galton P. 2007a.** A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. *Special Papers in Palaeontology* **77**: 57–90.
- Upchurch P, Barrett PM, Xijin Z, Xing X. 2007b.** A re-evaluation of *Chinshakiangosaurus chunghoensis* Ye vide Dong 1992 (Dinosauria, Sauropodomorpha): implications for cranial evolution in basal sauropod dinosaurs. *Geological Magazine* **144**: 247–262.
- Upchurch P, Martin J. 2003.** The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology* **23**: 208–231.
- Van Heerden J. 1979.** The morphology and taxonomy of *Euskelosaurus* (Reptilia: Saurischia: Late Triassic) from South Africa. *Navorsinge van die Nasionale Museum* **4**: 21–84.
- Van Heerden J. 1997.** Prosauropods. In: Farlow JO, Brett-Surman MK, eds. *The complete dinosaur*. Bloomington, IN: Indiana University Press, 216–233.
- Van Hoepen ECN. 1920.** Contributions to the knowledge of the reptiles of the Karoo Formation. 6. Further dinosaurian material in the Transvaal Museum. *Annals of the Transvaal Museum* **7**: 93–140.
- Warren AA, Damiani RJ. 1999.** Stereospondyl amphibians from the Elliot Formation of South Africa. *Palaeontologia Africana* **35**: 45–54.
- Wilson JA. 1999.** A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* **19**: 639–653.
- Wilson JA. 2002.** Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* **136**: 215–275.
- Wilson JA. 2005.** Overview of sauropod phylogeny and evolution. In: Curry Rogers KA, Wilson JA, eds. *The sauropods: evolution and paleobiology*. Berkeley, CA: University of California Press, 15–49.
- Wilson JA, Sereno PC. 1998.** Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoir (Society of Vertebrate Paleontology)* **5**: 1–68.
- Yadagiri P. 2001.** The osteology of *Kotasaurus yamanpalliensis*, a sauropod dinosaur from the Early Jurassic Kota Formation of India. *Journal of Vertebrate Paleontology* **21**: 242–252.

- Yates AM. 2003a.** A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* **1**: 1–42.
- Yates AM. 2003b.** A definite prosauropod dinosaur from the lower Elliot Formation (Norian: Upper Triassic) of South Africa. *Palaeontologia Africana* **39**: 63–68.
- Yates AM. 2004a.** *Anchisaurus polyzelus* (Hitchcock): the smallest known sauropod dinosaur and the evolution of gigantism among sauropodomorph dinosaurs. *Postilla* **230**: 1–58.
- Yates AM. 2004b.** The death of a dinosaur: dismembering *Euskelosaurus*. *Geoscience Africa* **2004**: 715.
- Yates AM. 2007a.** Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. *Historical Biology* **19**: 93–123.
- Yates AM. 2007b.** The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). *Special Papers in Paleontology* **77**: 9–55.
- Yates AM. 2008.** A second specimen of *Blikanasaurus* (Dinosauria: Sauropoda) and the biostratigraphy of the lower Elliot Formation. *Palaeontologia Africana* **43**: 39–43.
- Yates AM. 2010.** A revision of the problematic sauropodomorph dinosaurs from Manchester, Connecticut and the status of *Anchisaurus* Marsh. *Palaeontology* **53**: 739–752.
- Yates AM, Bonnan MF, Neveling J. 2011.** A new basal sauropodomorph dinosaur from the Early Jurassic of South Africa. *Journal of Vertebrate Paleontology* **31**: 610–625.
- Yates AM, Bonnan MF, Neveling J, Chinsamy A, Blackbeard MG. 2010.** A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism. *Proceedings of the Royal Society B: Biological Sciences* **277**: 787–794.
- Yates AM, Hancox JP, Rubidge BS. 2004.** First record of a sauropod dinosaur from the Upper Elliot Formation (Early Jurassic) of South Africa. *South African Journal of Science* **100**: 504–506.
- Yates AM, Kitching JW. 2003.** The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**: 1753–1758.
- Yates AM, Wedel MJ, Bonnan MF. 2012.** The early evolution of postcranial skeletal pneumaticity in sauropodomorph dinosaurs. *Acta Palaeontologica Polonica* **57**: 85–100.
- Young C-C. 1939.** On a new Sauropoda, with notes on other fragmentary reptiles from Szechuan. *Bulletin of the Geological Society of China* **19**: 279–315.
- Young C-C. 1941.** A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.). *Palaeontologica Sinica, Series C* **7**: 1–53.
- Young C-C. 1942.** *Yunnanosaurus huangi* Young (gen. et sp. nov.), a new Prosauropoda from the Red Beds at Lufeng, Yunnan. *Bulletin of the Geological Society of China* **22**: 63–104.
- Young C-C. 1951.** The Lufeng saurischian fauna in China. *Palaeontologica Sinica, Series C* **13**: 1–96.
- Young C-C. 1954.** On a new sauropod from Yiping, Szechuan, China. *Acta Scientia Sinica* **3**: 491–504.
- Young C-C, Zhao X. 1972.** *Mamenchisaurus*. *Institute of Vertebrate Paleontology and Paleoanthropology Monograph Series I* **8**: 1–30.
- Zhang YH. 1988.** *The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan: sauropod dinosaurs (1)*. *Shunosaurus*. Chengdu: Sichuan Publishing House of Science and Technology [in Chinese with English summary].
- Zhang YH, Yang Z. 1994.** *A new complete osteology of Prosauropoda in Lufeng Basin, Yunnan, China: Jingshanosaurus*. Kunming: Yunnan Publishing House of Science and Technology.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda.