

# A new basal sauropodiform from South Africa and the phylogenetic relationships of basal sauropodomorphs

ALEJANDRO OTERO<sup>1,2\*</sup>, EMIL KRUPANDAN<sup>3</sup>, DIEGO POL<sup>4</sup>, ANUSUYA CHINSAMY<sup>3</sup>  
and JONAH CHOINIERE<sup>2,5</sup>

<sup>1</sup>*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900, La Plata, Argentina*

<sup>2</sup>*Evolutionary Studies Institute, Centre of Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, Johannesburg, Gauteng, 2050, South Africa*

<sup>3</sup>*Biological Sciences Department, University of Cape Town, Private Bag, Rondebosch, Cape Town, South Africa*

<sup>4</sup>*CONICET, Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100, Trelew, Argentina*

<sup>5</sup>*NRF/Centre of Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, Johannesburg, Gauteng, 2050, South Africa*

*Received 8 September 2014; revised 20 January 2015; accepted for publication 20 January 2015*

We present a new medium-sized basal sauropodomorph, *Sefapanosaurus zastronensis* gen. et sp. nov., from the Upper Triassic–Lower Jurassic Elliot Formation of South Africa. It is represented by parts of the postcranial skeleton of at least four individuals, including: cervical, dorsal, sacral and caudal vertebrae, most of the forelimb, and part of the hindlimb. *Sefapanosaurus* bears several autapomorphies of the astragalus, and referred material also shows autapomorphic features. The inclusion of *Sefapanosaurus* in a phylogenetic analysis places it within the group of sauropodomorphs more closely related to sauropods than to *Massospondylus* (i.e. Sauropodiformes), increasing the currently known diversity of the so-called ‘transitional forms’ leading to Sauropoda. Character optimization revealed the presence of several features that are common for taxa placed within the transitional branches basal to Sauropoda. *Sefapanosaurus*, together with other transitional sauropodomorphs reported during the last decade, highlights the importance of Gondwanan taxa for understanding the palaeobiodiversity, global distribution, and macroevolutionary changes in the group related to the rise of sauropods.

© 2015 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2015, **174**, 589–634.  
doi: 10.1111/zoj.12247

ADDITIONAL KEYWORDS: Anchisauria – Elliot Formation – Gondwana – Sauropoda – Sauropodiformes.

## INTRODUCTION

The rise of sauropod dinosaurs from the primitive paraphyletic assemblage commonly called ‘prosauropod’ was one of the most dramatic transformations in the evolutionary history of dinosaurs. The evolution of Sauropoda entailed a reorganization of the body plan, from moderately cursorial habitual bipedality to graviportal obligate quadrupedality, an increase in

maximum body size of up to two orders of magnitude, and major changes in the structure of the vertebral column and the appendicular skeleton as well (Wilson & Sereno, 1998; Yates, 2007a). Our current understanding of this event is that it took place between the Late Triassic and Early Jurassic in Gondwana (Yates & Kitching, 2003; Galton & Upchurch, 2004; Yates *et al.*, 2010).

During the last decade our understanding of nonsauropod sauropodomorph anatomy and phylogenetic relationships has markedly increased (Leal *et al.*, 2004; Pol & Powell, 2007a, b; Yates, 2007a; Upchurch, Barrett

---

\*Corresponding author. E-mail: alexandros.otero@gmail.com

& Galton, 2007; Ezcurra, 2010; Sertich & Loewen, 2010; Yates *et al.*, 2010; Apaldetti *et al.*, 2011; Martínez *et al.*, 2011; Apaldetti, Pol & Yates, 2012; Otero & Pol, 2013; McPhee *et al.*, 2014, amongst others). This host of new information is based partly on new discoveries, as well as on redescription of previously known basal sauropodomorph taxa, including basalmost forms (e.g. *Eoraptor*, *Panphagia*, *Chromogisaurus*), plateosaurids (*Unaysaurus*), and massospondylids (e.g. *Adeppapposaurus*, *Leyesaurus*, *Coloradisaurus*, *Lufengosaurus*, *Glacialisaurus*). This has modified our understanding of the anatomy (Kutty *et al.*, 2007; Pol & Powell, 2007a, b; Martínez, 2009; Lu *et al.*, 2010; McPhee *et al.*, 2014), phylogenetic relationships (Smith & Pol, 2007; Upchurch *et al.*, 2007; Yates, 2007a; Ezcurra, 2010; Apaldetti *et al.*, 2011, 2012; Pol, Garrido & Cerda, 2011; Otero & Pol, 2013), and biology (Bonnar & Yates, 2007; Bonnar & Senter, 2007; Cerda *et al.*, 2013) of the successive outgroups of the clade Sauropoda. However, a large amount of this new information has derived from basal sauropodiforms, which are commonly denoted as ‘transitional forms’ (Pol & Powell, 2007a, b; Yates *et al.*, 2010; Pol *et al.*, 2011; Otero & Pol, 2013; McPhee *et al.*, 2014).

Here we describe a new basal sauropodomorph from the Upper Triassic–Lower Jurassic Elliot Formation of South Africa. The remains were collected by A. W. Keyser near the locality of Zastron during the period 1936–1946 and consist of at least four individuals that are now housed in the Institute for Evolutionary Studies at the University of the Witwatersrand in Johannesburg, South Africa. This new taxon preserves part of the postcranial skeleton, which displays a unique combination of characters, including several autapomorphic features that place it close to the origin of sauropods.

## MATERIAL AND METHODS

### TERMINOLOGY AND SOURCE OF COMPARATIVE DATA

Anatomical terminology used herein follows traditional or ‘Romerian’ directional terms (e.g. anterior, posterior) (Wilson, 2006) for composite structures of the

skeleton (e.g. anterior/posterior caudal vertebrae). Veterinarian terms (e.g. caudal, cranial) are used to refer to parts of a single bone (e.g. cranial face of the femur) (NAV, 2005). The schemes of Wilson (1999) and Wilson *et al.* (2011) were followed for the laminae and fossae nomenclature, respectively. The phylogenetic nomenclature used for the clades in this paper is presented in Table 1. The comparisons made with other saurischian dinosaurs in this contribution were based on personal observations and on the literature specified in Table 2.

### PHYLOGENETIC ANALYSIS

A phylogenetic analysis using parsimony as an optimality criterion was conducted in order to test the phylogenetic relationships of the new taxon within Sauropodomorpha. The analysis was based on a modified version of the data matrix published by Otero & Pol (2013), which in turn was based on a modified version of Yates (2007a) (see Supporting Information File S1). The data set was modified by the addition of two characters proposed by Apaldetti *et al.* (2012) and four new characters proposed in this study, for a total of 370 characters scored across 56 taxa. Outgroup taxa included some nonsauropodomorphs (e.g. theropods, ornithischians, dinosauriforms, and basal archosaurs) and ingroup taxa comprised a broad sampling of basal sauropodomorphs, basal sauropods, and some members of Eusauropoda as well. The basal sauropodomorph *Ignavusaurus* was eliminated from the data matrix as it was recently regarded as a junior synonym of *Massospondylus* (Yates, Bonnar & Neveling, 2011).

Thirty-seven characters are multistate and were treated as ordered (following the original analysis of Yates, 2007a; see also Appendix). The equally weighted parsimony analysis was carried out using TNT v. 1.1 (Goloboff, Farris & Nixon, 2008a, b). A heuristic tree search was performed consisting of 1000 replicates of Wagner trees (with random addition sequence of taxa) followed by branch swapping (tree bisection-reconnection; saving ten trees per replicate).

**Table 1.** Phylogenetic nomenclature used in this study

| Clade           | Definition   | Source                        |
|-----------------|--|-------------------------------|
| Sauropodomorpha | The most inclusive clade containing <i>Saltasaurus</i> but not <i>Passer</i> or <i>Triceratops</i> | Sereno, 2007                  |
| Massopoda       | The most inclusive clade that contains <i>Saltasaurus</i> but not <i>Plateosaurus</i>              | Yates, 2007a, b               |
| Anchisauria     | <i>Anchisaurus</i> and <i>Melanorosaurus</i> , their common ancestor, and all its descendants      | Galton & Upchurch, 2004       |
| Sauropodiformes | The least inclusive clade containing <i>Mussaurus</i> and <i>Saltasaurus</i>                       | Sereno, 2007                  |
| Sauropoda       | The most inclusive clade containing <i>Saltasaurus</i> but not <i>Melanorosaurus</i>               | Yates, 2007b                  |
| Eusauropoda     | The least inclusive clade containing <i>Shunosaurus</i> and <i>Saltasaurus</i>                     | Upchurch <i>et al.</i> , 2004 |

**Table 2.** Source of comparative data used in this study

| Taxon                                  | Source   |
|--|--|
| <i>Aardonyx celestae</i>               | Yates <i>et al.</i> , 2010, and specimens referred therein                 |
| <i>Adeopapposaurus magnai</i>          | PVSJ 610   |
| <i>Anchisaurus polyzelus</i>           | YPM 1883/ACM 41109   |
| <i>Antetonitrus ingenipes</i>          | BPI/1/4952/4956/4957/5091/5339   |
| <i>Blikanasaurus cromptoni</i>         | SAM-K403   |
| <i>Camelotia borelais</i>              | BMNH R2870   |
| <i>Coloradisaurus brevis</i>           | PVL 5904; Apaldetti <i>et al.</i> , 2012                                   |
| <i>Efraasia minor</i>                  | SMNS 12354/12667/12668/12684   |
| <i>Euskelosaurus browni</i>            | BMNH R1625   |
| <i>Guaibasaurus candelariensis</i>     | Bonaparte, Ferigolo & Ribeiro, 1999; Bonaparte <i>et al.</i> , 2007        |
| <i>Herrerasaurus ischigualastensis</i> | PVSJ 373   |
| <i>Leoneriasaurus taquetrensis</i>     | MPEF-PV 1663   |
| <i>Lessemsaurus sauropoides</i>        | PVL 4822   |
| <i>Lufengosaurus huenei</i>            | Galton & Upchurch, 2004  |
| <i>Massospondylus carinatus</i>        | BPI/1/4934/5421/4693/4377  |
| <i>Melanorosaurus readi</i>            | NM QR3314/1551, SAM-K3449  |
| <i>Mussaurus patagonicus</i>           | MLP 68-II-27-1/60-III-20-22, MACN-SC 3379                                  |
| <i>Plateosaurus engelhardti</i>        | SMNS 13200, MB Skelett 1, 25, 42, 45, C, D                                 |
| 'Plateosaurus' <i>gracilis</i>         | GPIT 18392, SMNS 5715  |
| <i>Riojasaurus incertus</i>            | PVL 3526/3663/3808   |
| <i>Ruhelia bedheimensis</i>            | MB.R. 4718   |
| <i>Sarhsaurus aurifontanalisi</i>      | TMM 43646-2/43646-3  |
| <i>Saturnalia tupiniquim</i>           | Langer, 2003; Langer <i>et al.</i> , 1999; Langer, Franca & Gabriel, 2007. |
| <i>Seitaad ruessi</i>                  | UMNH VP 18040  |
| 'Sellosaurus' <i>gracilis</i>          | SMNS 17928   |
| <i>Tazoudasaurus naimi</i>             | Allain & Aquesbi, 2008   |
| <i>Thecodontosaurus antiquus</i>       | YPM 2195   |
| <i>Pantyraco caducus</i>               | BMNH P77/1   |
| <i>Unaysaurus toletinoi</i>            | Leal <i>et al.</i> , 2004  |
| <i>Vulcanodon karibaensis</i>          | Cooper, 1984   |
| <i>Yunnanosaurus huangi</i>            | Galton & Upchurch, 2004  |

## INSTITUTIONAL ABBREVIATIONS

ACM, Beneski Museum of Natural History; BMNH, The Natural History Museum, London, UK; BPI, Evolutionary Studies Institute, Johannesburg, South Africa (formerly Bernard Price Institute); GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MB, Institut für Palaontologie, Museum für Naturkunde, Humbolt-Universität, Berlin, Germany; MLP, Museo de La Plata, La Plata, Argentina; MPEF-PV, Museo Paleontológico 'Egidio Feruglio', Trelew, Chubut, Argentina; NMQR, National Museum, Bloemfontein, South Africa; PVL, Instituto 'Miguel Lillo', Tucumán, Argentina; PVSJ-UNSJ, Paleontología de Vertebrados – Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; SAM, Iziko – South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; TMM, Texas Memo-

rial Museum, Austin, USA; UMNH, Utah Museum of Natural History, Salt Lake City, USA; YPM, Yale Peabody Museum, New Haven, USA.

## SYSTEMATIC PALAEOLOGY

DINOSAURIA OWEN, 1842

SAURISCHIA SEELEY, 1887

SAUROPODOMORPHA HUENE, 1932

MASSOPODA YATES, 2007B

ANCHISAURIA GALTON &amp; UPCHURCH, 2004

SAUROPODIFORMES SERENO, 2007

***SEFAPANOSAURUS ZASTRONENSIS* GEN. ET SP. NOV.***Holotype*

BP/1/386, incomplete articulated left pes including astragalus, calcaneum, a putative distal tarsal IV, proximal portions of metatarsals III and IV, and almost complete metatarsal V.

*Referred material*

BP/1/7409–7455. Partial skeletons of at least four individuals comprising: BP/1/7409, a cervical vertebra; BP/1/7410, 7411, 7412, cervical centra; BP/1/7413, a partial cervical centrum?; BP/1/7414, middle dorsal vertebra; BP/1/7415–7417, three partially preserved dorsal vertebrae; BP/1/7418, a dorsal transverse process; BP/1/7419, a dorsal centrum; BP/1/7421, a posterior dorsal centrum; BP/1/7423, a posterior partial dorsal vertebra; BP/1/7431, an isolated dorsal neural arch; BP/1/7420, a dorsosacral centrum; BP/1/7422, a putative caudosacral vertebra; BP/1/7424–7429, six caudal vertebrae; BP/1/7430, an haemal arch; BP/1/7432, left coracoid; BP/1/7433, right scapula; BP/1/7434, proximal half of right humerus; BP/1/7435, right radius; BP/1/7436, right (?) radius; BP/1/7437, left ulna; BP/1/7438, incomplete articulated left manus consisting of distal carpals I and II, metacarpals I and II and phalanx I.1, and isolated manual digit V; BP/1/7439, proximal end of pubis (?); BP/1/7440–7443, proximal end of four femora; BP/1/7444, distal portion of femur; BP/1/7445, proximal end of right tibia; BP/1/7446, distal end of right fibula (?); BP/1/7447, left fibula; BP/1/7448, isolated proximal end of right metatarsal II; BP/1/7449, distal end of metatarsal III; and BP/1/7450, proximal end of ischium.

Information available at the Evolutionary Studies Institute (Johannesburg) collection database indicates that all the material described here (the holotype BP/1/386 as well as all the referred material) was ‘collected from the same locality’. These materials were catalogued as *Euskelosaurus* by James W. Kitching, and subsequently referred to *Aardonyx* by Adam Yates (a referral recently followed by McPhee *et al.*, 2014). The referred material includes repeated elements, such as four partial femora of different sizes, indicating that this assemblage contains a minimum of four individuals. Despite the size differences, there are several autapomorphic features amongst the referred material that distinguish this assemblage from other sauropodomorphs (see Diagnosis). The available remains also lack autapomorphic features of other known basal sauropodomorphs and share characters typical of Anchisauria. Therefore, based on these features we deduce that there is no evidence to support the presence of more than one taxon amongst the material collected at this locality. The holotype is nonetheless restricted to the articulated remains of the tarsus and pes (BP/1/386), which were chosen based on the presence of autapomorphic traits that distinguish these elements from all other sauropodomorphs for which the tarsus and pes is known. The remaining material is catalogued under different collection numbers (BP/1/7409–7455) and referred here to the same taxon.

*Type locality and horizon*

The remains were collected by A. W. Keyser near the town of Zastron, in the Free State Province of South Africa, about 30 km west of the Lesotho border. There is no precise information about the exact stratigraphical level where the remains were found. However, around Zastron both lower and upper Elliot Formations crop out (Bordy, Hancox & Rubidge, 2004); hence, we assign *S. zastronensis* to the Upper Triassic–Lower Jurassic Elliot Formation (Fig. 1).

*Diagnosis*

*Sefapanosaurus zastronensis* is a medium-sized basal sauropodomorph distinguished from other nonsauropod sauropodomorphs by the following autapomorphies present in the holotype: tall ascending process of the astragalus, being 35% of the mediolateral length of the astragalus body; T-shaped, triradiate cross-section of ascending process of the astragalus; and ascending process of the astragalus framed medially and caudally by well-developed, straight, thick ridges, which have subcircular cross-sections.

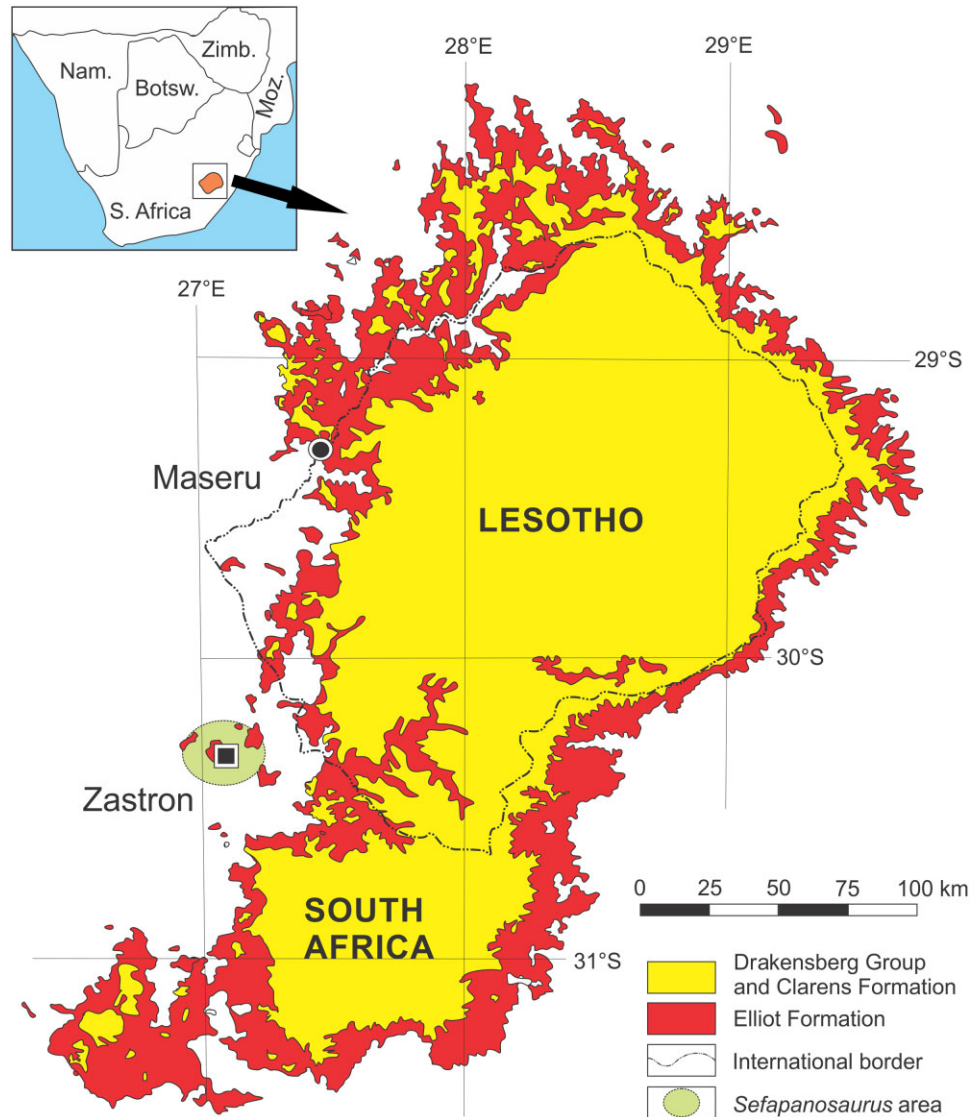
Additionally, the material referred to *S. zastronensis* (BP/1/7409–7455) differs from other nonsauropod sauropodomorphs by the following unique combination of characters (autapomorphies denoted with an asterisk): slit-shaped posterior dorsal neural canal; length of the base of the proximal neural spine greater than half the length of the neural arch; cross-sectional shape of distal caudal centra square-shaped; long ridge extending from the craniodorsal margin of the coracoid to the coracoid foramen\*; craniomedial process of the ulna twice as long as the craniolateral process and distally tapered\*; presence of biceps tubercle and caudodistal tubercles of the radius; distal carpal I with proximally pointing tip on the palmar surface, giving a triangular shape in palmar view\*; strongly concave medial margin of metacarpal I; ventral margin of phalanx I.1 well developed with a proximally pointing tip; metacarpal V longer than wide with flat proximal surface; first metacarpal short and wide (proximal width is more than 100% of the total length of the bone); craniomedial projection on the distal end of the fibula\*.

*Description**Etymology*

From the Sesotho language *sefapano*, meaning ‘cross’, and from the Greek *saurus*, meaning ‘lizard’, in reference to the cross T-shaped ascending process of the astragalus. The specific name makes reference to Zastron, the type locality.

*Axial skeleton*

The major components of the entire axial column are all represented by at least one vertebra, although some



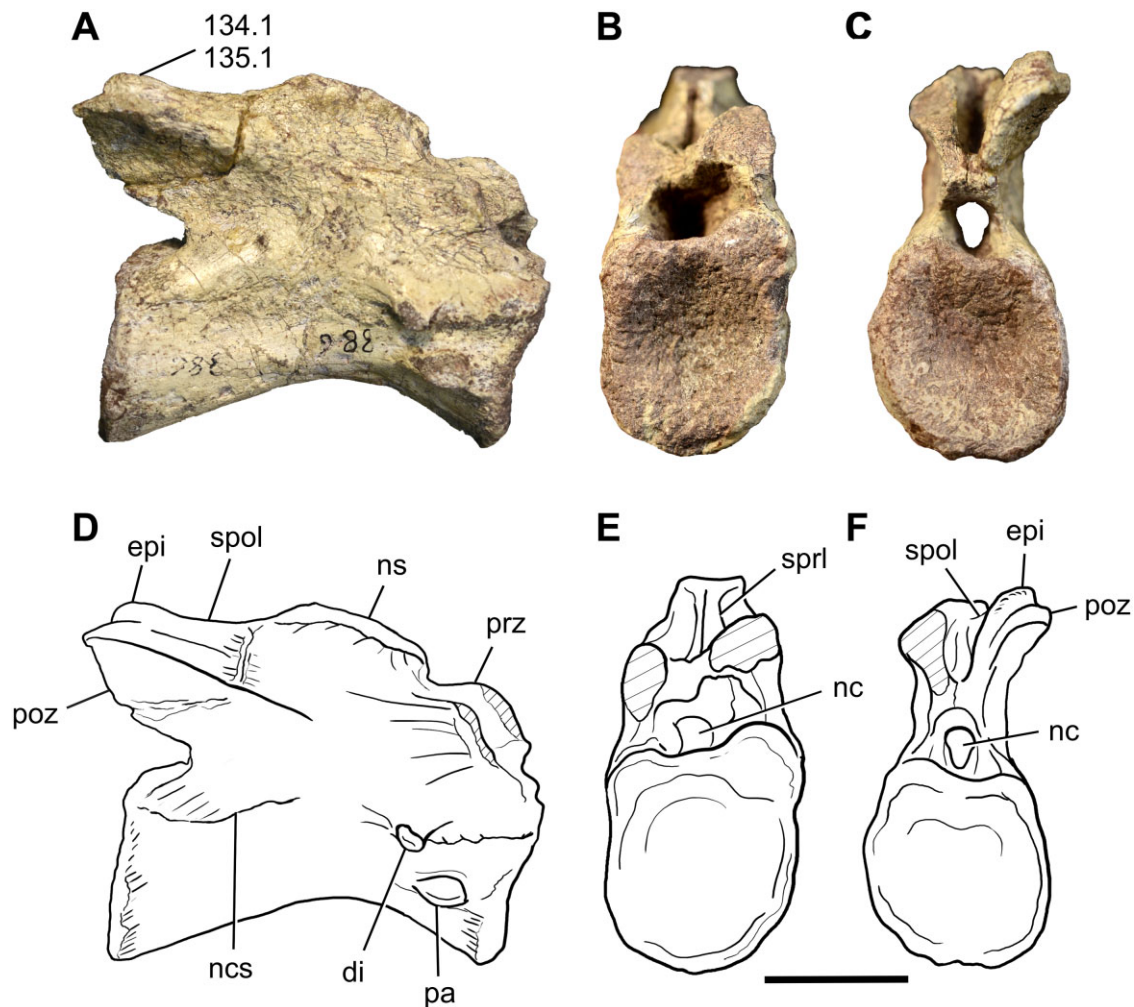
**Figure 1.** *Sefapanosaurus zastronensis* gen. et sp. nov. occurrence. Map showing the area where *Sefapanosaurus* was collected, close to the locality of Zastron, in the Free State of South Africa. Abbreviations: Botsw., Botswana; Moz., Mozambique; Nam., Namibia; Zimb., Zimbabwe.

elements have only preserved the centrum or the neural arch. There are 12 presacral vertebrae, an isolated neural arch, an isolated transverse process, a dorsosacral vertebra, a putative caudosacral vertebra, and six caudal vertebrae. The descriptions below were based mainly on the best-preserved elements, which present the neural arch.

*Cervical vertebrae:* A nearly complete cervical vertebra (BP/1/7409) is preserved in *Sefapanosaurus*, plus four isolated cervical centra (BP/1/7410, 7411, 7412, 7413). The former is probably the fifth or sixth cervical vertebra (Fig. 2). The general morphology of the nearly complete vertebra is typical for a non-sauropodan

sauropodomorph cervical element: it is elongate and low, the height of the neural arch is less than the height of the centrum, and there are no depressions on the lateral surface of the centrum (Galton & Upchurch, 2004). The length of the centrum is 2.25 times the height of the cranial surface of the centrum, and the latter is 1.2 times the cranial face width (see Table S2 for measurements). A neurocentral suture is clearly visible, although obliterated in BP/1/7409. The presence of an isolated cervical centrum suggests that this element may belong to an immature individual (Brochu, 1996; Irmis, 2007).

The articular facets of the centra are amphicoelous, the cranial surface being shallowly concave and the caudal face deeply excavated, as is the generalized



**Figure 2.** *Sefapanosaurus zastronensis* gen. et sp. nov., cervical vertebra (BP/1/7409), photographs and interpretative drawings. Right lateral (A, D); cranial (B, E), and caudal (C, F) views. Numbers indicate character state, respectively. Abbreviations: di, diapophysis; epi, epiphysis; nc, neural canal; ncs, neurocentral suture; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. Scale bar = 5 cm.

condition for basal sauropodomorphs, and both the cranial and caudal articular facets are subequal in size. The ventral and lateral margins are concave. The ventral surfaces of the centra lack a keel, having only a low ridge on the cranial portion. Immediately caudal to this low ridge, several small foramina are present on BP/1/7409, but these foramina are not present in BP/1/7410. However, the ventral keel is a feature that is not always well developed along the cervical series amongst basal sauropodomorphs, being commonly present and more developed in the posterior cervical vertebrae (cervical eight to ten) and anterior dorsal vertebrae (dorsals one and two). This pattern is noticeable in the complete axial series of *Plateosaurus longiceps* (MB.R. 4404) and *Ruehleia bedheimensis* (MB.R. 4718). Other basal sauropodomorphs, however,

have well-developed ventral keels along the entire cervical series (e.g. *Leoneosaurus taquetrensis*).

The parapophyses are well developed and located at the midheight region of the lateral surface of the centrum. In lateral view the parapophyses are lacrimiform in shape, with a tapering posterior end and a rounded anterior end. This shape can only be seen on the right side of BP/1/7409, and the left side of BP/1/7410. Ventrally they have a sharply defined margin, visible in ventral view. The diapophyses are present, projecting lateroventrally in a pendant fashion, and are situated on the cranioventral corner of the bases of the neural arches. This contrasts with the condition present in *Aardonyx*, in which the diapophyses are extremely reduced (Yates *et al.*, 2010). No diapophyseal laminae are present, as is common for midcervical vertebrae

of sauropodomorphs more basal than *Tazoudasaurus* (Galton & Upchurch, 2004).

The prezygapophyses are not preserved in BP/1/7409, although both spinoprezygapophyseal laminae (SPRL) are present. Only the right cervical postzygapophysis is complete. In posterior view, its mediolateral axis is orientated laterodorsally at an angle of approximately 30°, as commonly found in middle cervical vertebrae of most basal sauropodomorphs (Galton & Upchurch, 2004). The caudal-most extent of the postzygapophysis exceeds the level of the caudal margin of the centrum. An epiphysis is present and well developed, extending along the entire length of the postzygapophysis and grading into the spinopostzygapophyseal lamina (SPOL), as in *Sarhsaurus*, *Lufengosaurus*, and most sauropodiforms. The epiphysis does not reach the level of the caudal margin of the postzygapophysis, a condition also present in *Pantydraco*, *Thecodontosaurus*, *Sarhsaurus*, *Leyesaurus*, and *Adeopapposaurus*.

Only the base of the neural spine is preserved. The base of the spine is craniocaudally developed, as in the middle cervical vertebrae of most basal sauropodomorphs.

The isolated cervical centrum, BP/1/7010, is approximately the same length as that of BP/1/7409, but its rostral and caudal articular surfaces are about 10% mediolaterally wider and dorsoventrally taller. The parapophysis is of a similar shape and is in a topologically similar position to BP/1/7409. Comparisons with other basal sauropodomorphs (e.g. *Adeopapposaurus*, *Plateosaurus engelhardti*, *Ruehleia*) suggest that it probably represents a middle cervical vertebra.

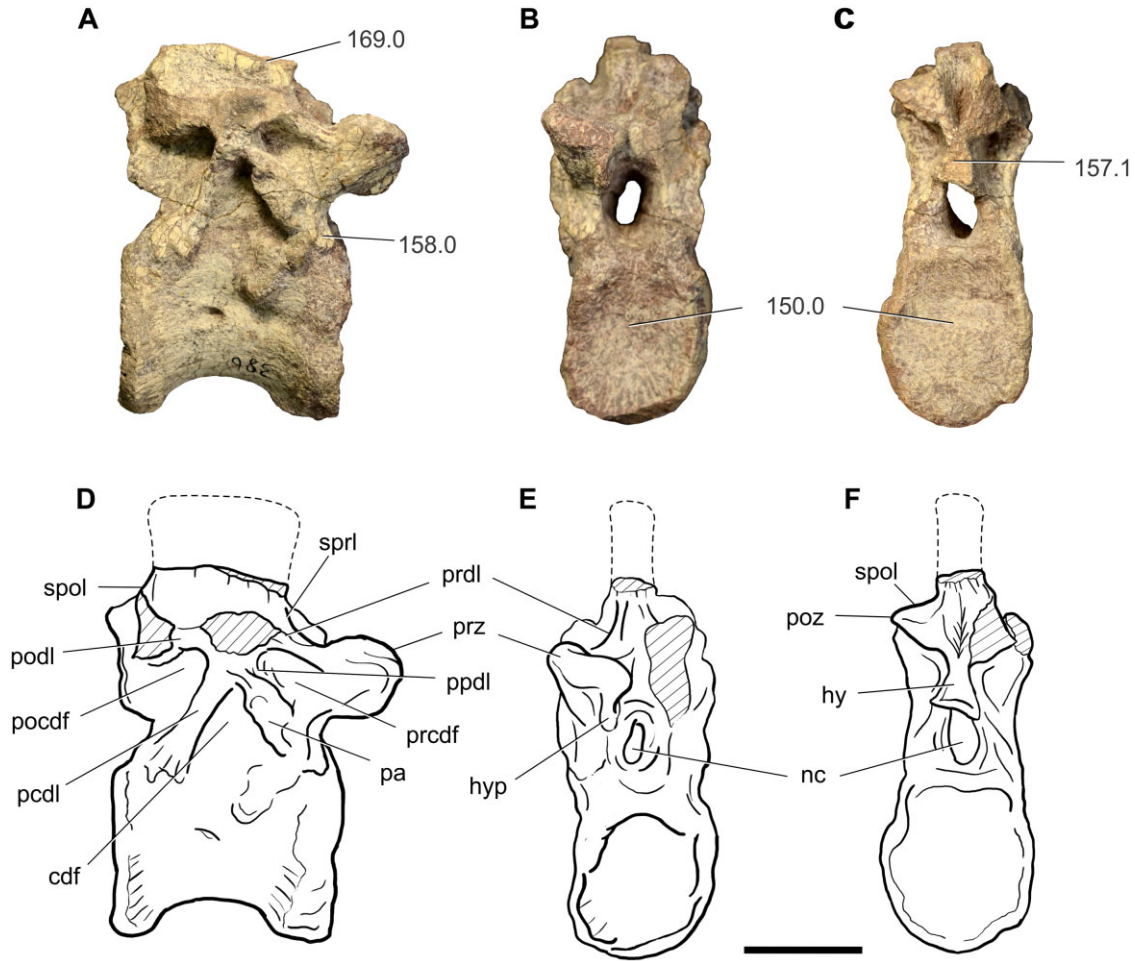
*Dorsal vertebrae:* Seven dorsal vertebrae are present in *Sefapanosaurus*, together with an isolated transverse process, and an isolated neural arch. Five elements (BP/1/7414, 7415, 7416, 7417, 7423) preserve partial or complete neural arches, two posterior elements lack neural arches (BP/1/7419, 7421), and there is also an isolated neural arch (BP/1/7431). The description is focused mainly upon the two better-preserved elements, which probably represent dorsal vertebrae five and ten. The isolated neural arch corresponds to the middle or midposterior region of the dorsal column series.

The anterior dorsal vertebra (BP/1/7415; probably the fifth dorsal) is almost completely preserved, in which the neural arch lamination and fossae are clearly visible (Fig. 3).

The centrum length is 1.2 times the cranial centrum height, and the latter is 1.3 times the width of the cranial facet (see Table S2 for measurements). Overall, the centrum is spool-shaped, with a constricted mesial region and expanded cranial and caudal ends. The cranial face is flat and caudal articular facets are shallowly concave, as is common for most basal sauropodomorphs. The facets

are subcircular, being slightly taller than they are wide. The lateral surface bears a shallow fossa at approximately midheight immediately ventral to the neurocentral suture. The ventral surface is flat and lacks any sign of a ridge or keel, unlike the condition present in the last cervical and the anterior-most dorsals of most basal sauropodomorphs. The lateral surfaces of the centrum are also flat and no depressions are present. The centrum and neural arch are fused to each other, although a remnant line demarcating the neurocentral suture can be seen. Lateral surfaces of the centrum bear shallow foramina in their middle portions. The foramen on the right side opens caudally and is developed at the midheight of the centrum and slightly caudal to the anterior–posterior midline. The foramen on the left side is very weakly developed, and is located on the anterior–posterior midline but dorsally, close to the neurocentral suture.

The neural arch is low, not exceeding the centrum height, measured from the neurocentral suture up to the level of the zygapophyseal facets, a feature present in most nonsauropod sauropodomorphs. The neural spine is not completely preserved, but a craniocaudally elongated base can be seen. The distal ends of the parapophyses are eroded, but the preserved bases suggest that they are relatively large and ovoid in cross-section, with the long axis orientated caudodorsally. On the right side of the neural arch, a dorsoventrally elongated parapophysis defines most of the caudal boundary of the prezygapophyseal centrodiapophyseal fossa (PRCDF) and the cranial boundary of the centrodiapophyseal fossa (CDF) and is developed entirely on the neural arch. The PRCDF is also delimited by the prezygodiapophyseal lamina (PRDL) and the paradiapophyseal lamina (PPDL) and centrodiapophyseal lamina (ACDL). The diapophyses are not completely preserved, but the proximal portion of the left diapophysis is present. Apart from the PRCDF and CDF, a postzygapophyseal centrodiapophyseal fossa (POCDF) is also present. The CDF is delimited by the PPDL and the parapophysis cranially, and the posterior centrodiapophyseal lamina (PCDL) caudally, whereas the POCDF is bounded by the postzygodiapophyseal lamina (PODL) and the PCDL. Above the zygodiapophyseal table (ZDT) only the spinodiapophyseal fossa (SDF) can be recognized framed by the PRDL, SPRL, SPOL, and PODL. The preserved right prezygapophysis extends anterior to the level of the cranial margin of the centrum. The articular facet of the prezygapophysis has a slight dorsomedial inclination and bears a well-developed hypantrium on its ventromedial margin. The postzygapophyses bear SPOL dorsally, and a well-developed triangular hyposphene ventromedially, which does not exceed the dorsoventral height of the neural canal, as is common for all sauropodomorphs more



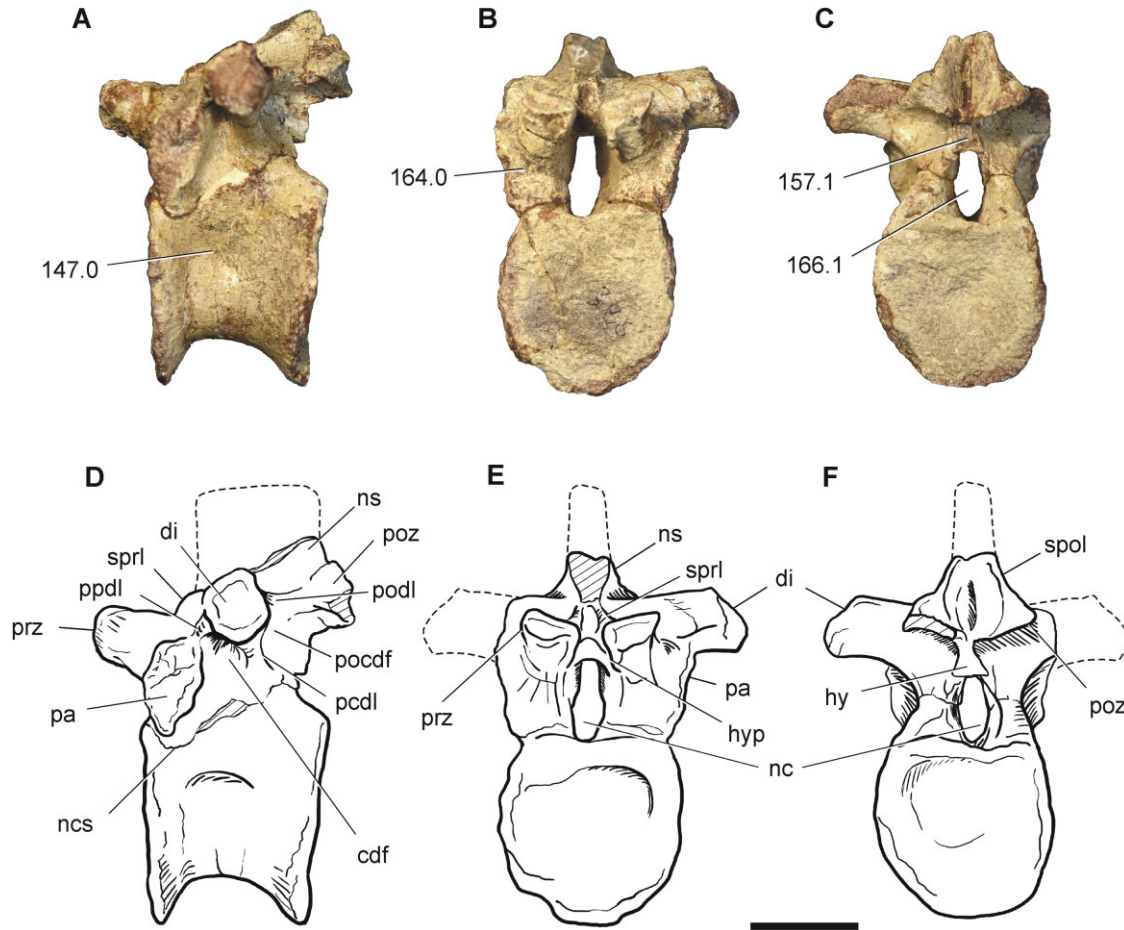
**Figure 3.** *Sefapanosaurus zastronensis* gen. et sp. nov., dorsal vertebra (BP/1/7415), photographs and interpretative drawings. Right lateral (A, D); cranial (B, E), and caudal (C, F) views. Numbers indicate character character state, respectively. Abbreviations: cdf, centrodiapophyseal fossa; hy, hyposphene; hyp, hypantrium; nc, neural canal; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophysis; ppdl, pardiapophyseal lamina; prcdf, prezygapophyseal centrodiapophyseal fossa; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. Scale bar = 5 cm.

primitive than *Melanorosaurus* (Yates, 2007a). The neural canal is dorsoventrally elongate, more than twice as tall as it is wide. It deeply excavates the dorsal surface of the centrum as a V-shaped furrow. Within this furrow, on the dorsal surface of the centrum, two shallow, lenticular foramina are present.

The middle dorsal vertebra (BP/1/7416, tenth or eleventh) is almost complete, lacking the right diapophysis and the neural spine (Fig. 4). The centrum is relatively short, with a length that is 0.85 times the cranial centrum height, and the latter being equal to the width of the cranial articular surface. The cranial and caudal articular facets are amphiplatyan to slightly amphicoelous, and the lateral surface of the centrum bears a shallow depression on its middle portion.

The presence of dorsal vertebrae with vague or shallow depressions is a common feature amongst sauropodomorphs more basal than *Isanosaurus*, unlike the condition of sauropods, in which deep fossae or invasive pleurocoels are present (Upchurch *et al.*, 2007; Yates, 2007a). The contact between the centrum and the neural arch shows the trace of a neurocentral suture, although both structures are fused to each other.

As for the anterior dorsal vertebra, the neural arch is low, with a height that is less than that of the centrum. The parapophyses are well developed and entirely situated on the neural arch. The left diapophysis is preserved and is well developed laterally and almost horizontally orientated. A CDF is present below the latter lamina. The PCDL projects caudoventrally from

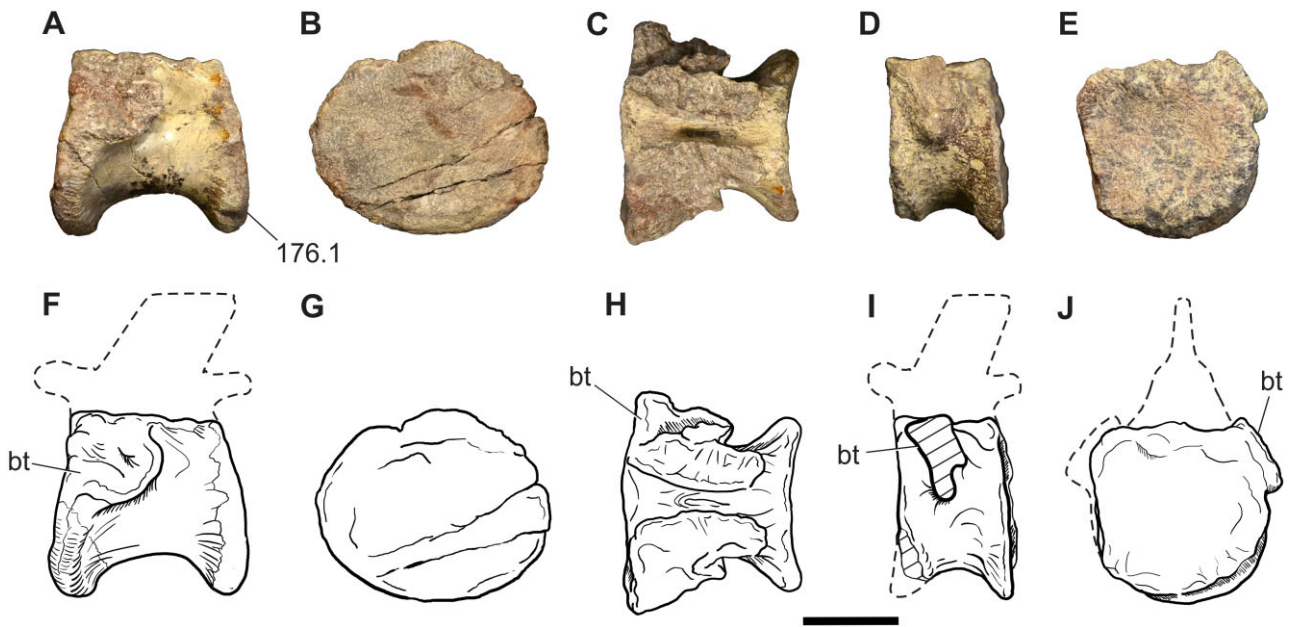


**Figure 4.** *Sefapanosaurus zastronensis* gen. et sp. nov., dorsal vertebra (BP/1/7416), photographs and interpretative drawings. Left lateral (A, D); cranial (B, E), and caudal (C, F) views. Numbers indicate character.state, respectively. Abbreviations: cdf, centrodiapophyseal fossa; di, diapophysis; hy, hyposphene; hyp, hypantrum; nc, neural canal; ncs, neurocentral suture; ns, neural spine; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophysis; ppdl, pardiapophyseal lamina; prz, prezygapophysis; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. Scale bar = 5 cm.

the diapophysis and the PODL extends caudally, delimiting a POCDF. The PPDL extends cranioventrally. At this point of the axial column, no PRDL are present, a common feature of the middle dorsals of most basal sauropodomorphs (Upchurch *et al.*, 2007; Yates, 2007a; Pol *et al.*, 2011). As a result, no PRCDF is present. The prezygapophyses exceed the cranial centrum margin and the angle between the two articular facets is approximately 165°. Hypantrum articulations are present and diverge from each other at an angle of approximately 35°. The postzygapophyses are situated almost at the same level as the prezygapophyses, have subcircular articular facets, and slightly exceed the caudal margin of the centrum. Dorsally, the postzygapophyses are framed by SPOL. The hyposphenes are noticeable, although they are dorsoventrally shorter than the neural canal, as in nonsauropod sauropodomorphs.

Posterior dorsal vertebrae are represented by four centra (BP/1/7417, 7419, 7421, 7423), two of them (BP/1/7417, 7423) including the base of the neural arch. These elements present expanded cranial and caudal faces, which are circular in shape, and amphiplatyan to slightly amphicoelous. Shallow depressions are present on the lateral faces, close to the neurocentral suture, a feature common to most basal sauropodomorphs (Galton & Upchurch, 2004). The element BP/1/7417 presents part of the ACDL and PCDL, which delimit the CDF.

*Sacral vertebrae:* Only one of the preserved vertebra can convincingly be attributed to a sacral element and corresponds to an isolated centrum that can be identified as a dorsosacral vertebra (Fig. 5). Besides this, a putative caudosacral vertebra is preserved.



**Figure 5.** *Sefapanosaurus zastronensis* gen. et sp. nov., sacral vertebrae, photographs and interpretative drawings. Dorsosacral vertebra (BP/1/7420) in left lateral (A, F), cranial (B, G), and dorsal (C, H) views. Caudosacral vertebra (BP/1/7422) in left lateral (D, I) and cranial (E, J) views. Numbers indicate character.character state, respectively. Abbreviation: bt, base of the transverse process. Scale bar = 5 cm.

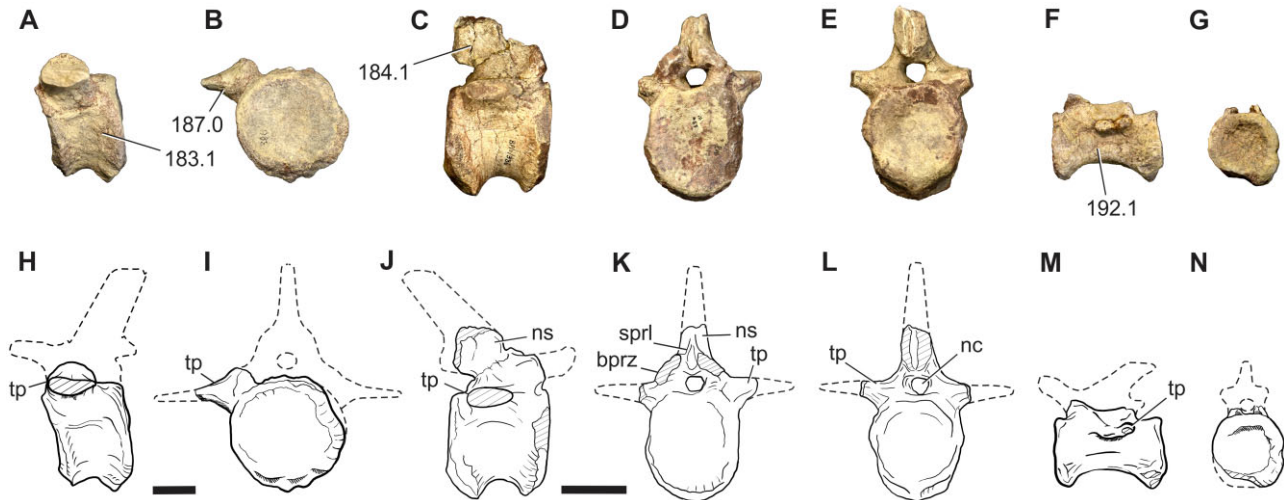
The dorsosacral vertebra (BP/1/7420) has a centrum that is 0.95 times the cranial centrum height and the latter is 0.8 times the cranial centrum width. The centrum is constricted and bears a shallow depression at its middle region. The cranial portion of the centrum has the transverse process with the articulation for the sacral rib and extends from the neurocentral suture to the cranioventral margin. A similar pattern is present in the dorsosacral vertebra of *Leoneriasaurus* (Pol et al., 2011; fig. 8E) and in *Melanorosaurus* (NMQR 1551).

The putative caudosacral vertebra (BP/1/7422), represented by an isolated centrum, is a robust element, with a centrum length that is 0.65 times the centrum height. The articular faces are amphiplatyan to slightly amphicoelous. Although the neural arch is not preserved, the base of the left transverse process does, showing a dorsoventral elongation, originating also from part of the centrum, as present in caudosacral vertebra of *Plateosaurus engelhardti* (SMNS 91269).

**Caudal vertebrae:** Six caudal vertebrae are preserved, representing the anterior, middle, and posterior region of the tail (Fig. 6). The anterior-most caudal vertebra (BP/1/7424, probably the first) lacks the neural arch, only preserving part of the left transverse process. The centrum length is about 0.65 times the cranial centrum height, and the latter is almost the same length as the cranial centrum width. A short anterior caudal centrum is a feature present in Sauropodiformes.

The articular facets are amphiplatyan to slightly amphicoelous. The lateral surface lacks depressions and the ventral surface has only traces of the chevron articular facets. There is no ventral longitudinal hollow. The transverse process preserved is not positioned on the neural arch, but in the dorsal region of the centrum, over its cranial half.

A second anterior caudal vertebra (BP/1/7425) is better preserved, with most of the neural arch, but preserving only the base of the neural spine. The cranial and caudal articular facets are slightly amphicoelous. The centrum length is 0.85 times the cranial centrum height, and the latter is 1.2 times its width. The ventral margin is strongly concave and the ventral surface bears a shallow longitudinal groove, which ends at the chevron articular facets. The centrum lateral surface lacks a depression. The transverse processes are dorsoventrally compressed, horizontally directed, and situated on the dorsal margin of the centrum, at the level of the neurocentral suture, as in most basal sauropodomorphs (except for *Anchisaurus*). The neural arch lacks zygapophyses and the neural spine, preserving only the base of the latter, from which can be seen a portion of the SPRL. The length of the base of the neural spine is greater than half of the length of the neural arch, a feature unusual in most basal sauropodomorphs, except for basal-most forms (i.e. *Chromogisaurus*, *Saturnalia*, *Thecodontosaurus*, *Efrassia*), *'Plateosaurus' gracilis*, and the basal sauropod *Tazoudasaurus*.



**Figure 6.** *Sefapanosaurus zastronensis* gen. et sp. nov., caudal vertebrae, photographs and interpretative drawings. First caudal centrum (BP/1/7424) in left lateral (A, H) and caudal (B, I) views. Anterior caudal vertebra (BP/1/7425) in right lateral (C, J), cranial (D, K), and caudal (E, L) views. Posterior caudal centrum (BP/1/7429) in left lateral (F, M) and caudal (G, N) views. Numbers indicate character character state, respectively. Abbreviations: bprz, base of the prezygapophysis; nc, neural canal; ns, neural spine; sprl, spinoprezygapophyseal lamina; tp, transverse process. Scale bars = 5 cm.

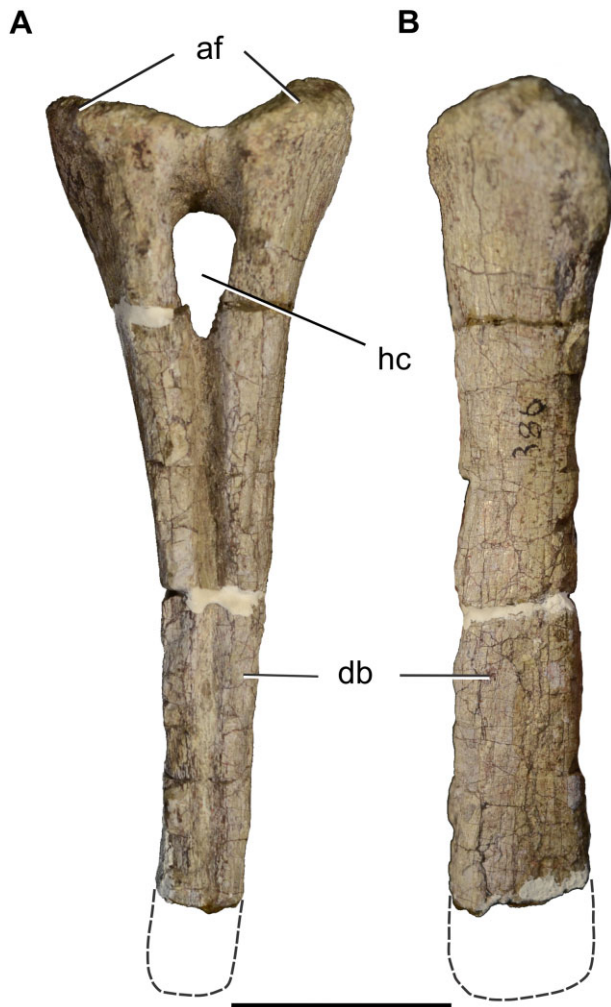
A posterior caudal centrum has also been preserved (BP/1/7429). It is elongate, its centrum length being 1.5 times the cranial centrum height. The cranial and caudal articular facets are rounded and amphicoelous. The ventral and lateral surfaces are almost flat, giving the centrum a square-shaped cross-section, a character present in *Adeopapposaurus* and common for most transitional forms leading to Sauropoda (i.e. *Anchisaurus*, *Mussaurus*, *Aardonyx*, *Melanorosaurus*, and *Camelotia*). The neural arch is missing, except for its base, which is situated cranially on the centrum. The transverse processes are broken.

**Chevron:** An isolated anterior chevron is preserved (BP/1/7430), lacking only the distal-most tip of the blade (Fig. 7). As is common for most basal sauropodomorphs, the chevron morphology closely resembles the closed 'Y-shaped' morphotype described by Otero *et al.* (2012) for sauropods.

#### Pectoral girdle and forelimbs

The preserved elements of the pectoral girdle include an almost complete right scapula (BP/1/7433) and left coracoid (BP/1/7432), whereas the forelimb bones are represented by a proximal portion of a right humerus (BP/1/7434), two radii (BP/1/7435 and 7436) and an ulna (BP/1/7437), and a partially articulated left manus (BP/1/7438), including distal carpals 1 and 2, metacarpals I, II, and V, and phalanges I-1, V-1, and V-2.

**Pectoral girdle:** The right scapula (BP/1/7433) preserves most of its proximal portion, including part of the acromion process, as well as the majority of the blade (Fig. 8A, B, E, F). Despite the fact that the acromion process is not complete, it can be determined that it rises from the scapular blade at an angle smaller than 65°, as in nonsauropod sauropodomorphs (with the exception of *Saturnalia*, *Lufengosaurus*, *Jingshanosaurus*, and *Mussaurus*). The glenoid region is the thickest part of the scapula and the glenoid articular facet is subcircular. The ventral margin of the blade and the caudal margin of the glenoid project at an angle close to 90°, as in *Coloradisaurus* but differing from *Plateosaurus*, *Adeopapposaurus*, *Mussaurus*, and *Euskelosaurus*, which have an angle more than 90°. The medial surface of the scapula has a ventromedial ridge, a feature also present in *Unaysaurus*, *Adeopapposaurus*, *Plateosaurus*, *Mussaurus*, and *Euskelosaurus*, although only in *Mussaurus* is this feature extremely developed and reaches the distal third of the distal blade (Otero & Pol, 2013). The minimum blade width is approximately 0.47 times the ventral expansion of the scapula. The general appearance of the scapula of *Sefapanosaurus* is similar to that of SAM-K386 assigned to *Euskelosaurus*; however, the latter taxon differs from *Sefapanosaurus* by the presence of a more robust morphology, a stouter ventromedial ridge, and an angle between the ventral margin of the blade and the caudal margin of the glenoid close to 120°.



**Figure 7.** *Sefapanosaurus zastronensis* gen. et sp. nov., anterior haemal arch (BP/1/7430), photographs and interpretative drawings. Cranial (A) and lateral (B) views. Abbreviations: af, articular facets for the vertebra; db, distal blade; hc, haemal canal. Scale bar = 5 cm.

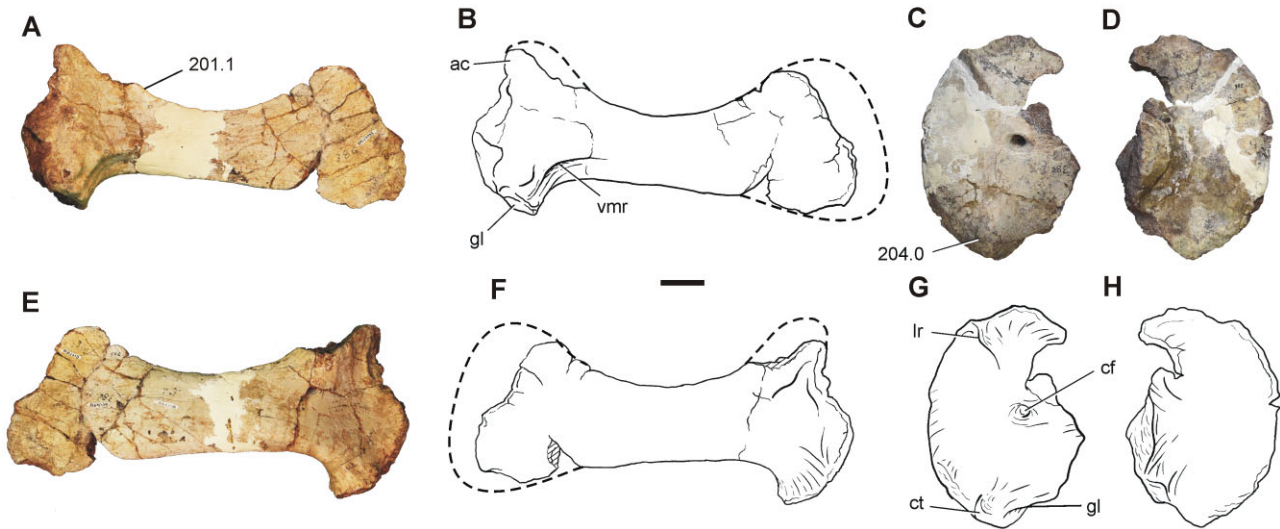
The left coracoid (BP/1/7432) is almost completely preserved, lacking only its caudodorsal portion (Fig. 8C, D, G, H). The overall morphology is congruent with the generalized condition of most basal sauropodomorphs in being an ovoid bone with its major axis parallel to the suture with the scapula. The coracoid foramen is situated close to the caudal margin at the midlength of the coracoid. The ventral margin is the thickest and this thickness is given by the presence of a coracoid tubercle, a feature also present in *Sarhsaurus*, *Adeopapposaurus*, *Coloradisaurus*, and sauropods more derived than *Tazoudasaurus*. There is a noticeable long ridge extending from the craniodorsal margin of the coracoid to the coracoid foramen, although not reaching it. This feature has not been reported in other basal sauropodomorphs and so is

regarded here as an autapomorphic feature of *Sefapanosaurus*.

**Humerus:** Only the proximal portion of the humerus (BP/1/7434) is preserved (Fig. 9). This portion is mediolaterally expanded, as in all basal sauropodomorphs. Proximal abrasion of the bone precludes the identification of the internal tuberosity. The deltopectoral crest is subrectangular and rises from the proximal portion of the humerus and projects cranio-laterally, as in most basal sauropodomorphs. The cranio-lateral margin is straight, as seen in most basal sauropodomorphs, with the exception of *Coloradisaurus*, *Riojasaurus*, *Sarhsaurus*, *Plateosaurus*, and *Lessemsaurus*, in which the crest is strongly sinuous in cranio-lateral view.

**Ulna:** An almost complete left ulna (BP/1/7437) has been preserved (Fig. 10). The proximal end of the ulna is expanded both mediolaterally and cranio-caudally, and has a triradiate profile in proximal view, given the development of the cranio-lateral and cranio-medial processes. A triradiate proximal surface of the ulna is present in all sauropodomorphs more derived than *Aardonyx*. The cranio-lateral and cranio-medial processes delimit a radial fossa, which is more developed in *Sefapanosaurus* than in *Aardonyx*, *Mussaurus*, and *Melanorosaurus*. The cranio-medial process of the ulna is extremely developed, a condition also reported in *Antetonitrus* and *Vulcanodon*. Moreover, the cranio-medial process of *Sefapanosaurus* tapers distally, unlike the condition in *Mussaurus*, *Aardonyx*, *Melanorosaurus*, and *Antetonitrus*. In the latter taxa, the cranio-medial process of the ulna terminates in a more rounded fashion. The maximum proximal length (measured along the cranio-medial process) is 0.42 times the total length of the ulna, whereas the minimum proximal length (measured along the cranio-lateral process) is 0.32 times the total ulnar length. The opposite margin (medial) of the radial fossa is also concave, a condition also present in other basal sauropodomorphs such as *Melanorosaurus readi* (SAM-PK-K3449) and the basal sauropods *Lessemsaurus sauropoides* (Pol & Powell, 2007b) and *Antetonitrus ingenipes* (BPI/1/4952), but absent in other sauropodomorphs (e.g. *Vulcanodon*, *Yunnanosaurus*, *Tehuelchesaurus*). As in all nonsauropod sauropodomorphs the ulnar proximal end bears a well-developed olecranon process that extends above the proximal articular surface.

The ulnar shaft is cranio-caudally expanded proximally and becomes constricted distally. The cranial margin of the shaft is concave as in *Adeopapposaurus*, *Mussaurus*, *Aardonyx*, *Melanorosaurus*, and *Antetonitrus*. The shaft is mediolaterally compressed and triangular in cross-section (with one tip pointing laterally at its proximal third), but becomes elliptical in cross-section along the distal two thirds.



**Figure 8.** *Sefapanosaurus zastronensis* gen. et sp. nov., pectoral girdle, photographs and interpretative drawings. Right scapula (BP/1/7433) in medial (A, B) and lateral (E, F) views. Right coracoid (BP/1/7434) in lateral (C, G) and medial (D, H) views. Numbers indicate character.state, respectively. Abbreviations: ac, acromion process; cf, coracoid foramen; ct, coracoid tubercle; gl, glenoid; lr, long ridge; vmr, ventromedial ridge. Scale bar = 5 cm.

The distal end of the ulna is mediolaterally expanded, its maximum dimension being 0.27 times the ulnar length. This condition is similar to that of other basal sauropodomorphs (e.g. *Adeopapposaurus*, *Massospondylus*, *Aardonyx*, *Mussaurus*, *Melanorosaurus*, and *Lessemsaurus*). More derived taxa, such as eusauropod outgroups (e.g. *Vulcanodon* and *Tazoudasaurus*), however, have the ulnar distal end much less expanded. The long axis of the distal articular surface is parallel to the craniolateral proximal process and perpendicular to the craniomedial process. The distal articular surface is convex.

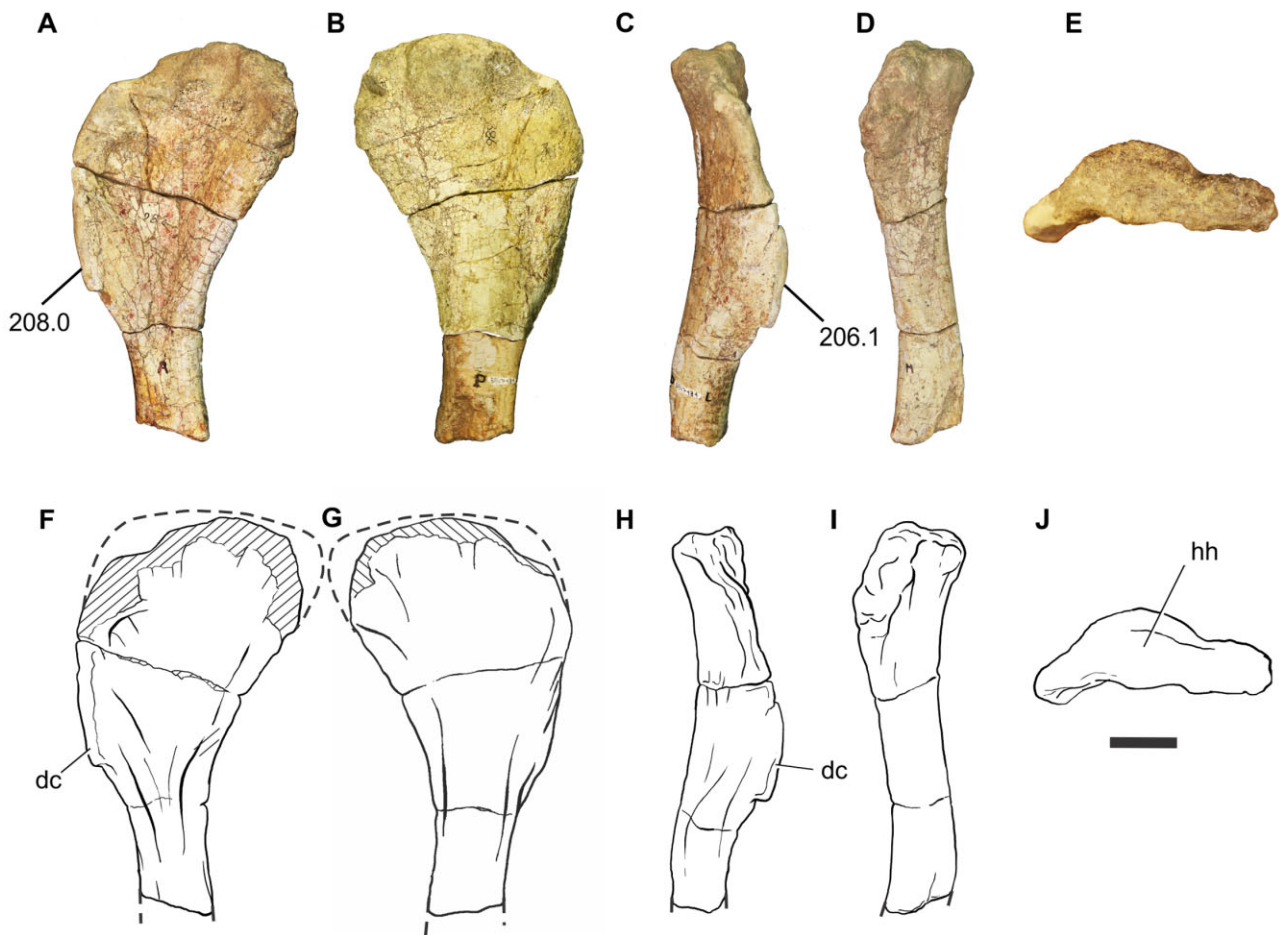
**Radius:** Two radii are preserved, with slightly different sizes (BP/1/7135 and 7436). The description is based on BP/1/7435, which presents fewer reconstructed portions with plaster.

The radius is a gracile bone, with the proximal end slightly more expanded than the distal end (maximum mediolateral width of the proximal end is 1.32 times the maximum width of the distal end) (Fig. 11). The proximal end is subrectangular to suboval, a condition also reported in *Plateosaurus*, *Adeopapposaurus*, *Massospondylus*, *Aardonyx*, and *Melanorosaurus*, but unlike the triangular shape present in *Mussaurus*. The shaft of the radius is rather straight, as in most basal sauropodomorphs, and its cross-section is subcircular. In the proximal half of the radius, over the craniomedial surface and close to the midshaft, there is a noticeable bulge ('biceps scar': Yates *et al.*, 2010; fig. 3h, i), also present in *Mussaurus*, *Aardonyx*, *Melanorosaurus*, and *Antetonitrus*, although in *Sefapanosaurus* it is much

more developed. The distal end of the radius is subovoid, as in other sauropodomorphs. The caudal margin of the distal end has a well-developed, proximodistally orientated ridge and groove, a feature also present in *Mussaurus*, *Aardonyx*, *Melanorosaurus*, *Antetonitrus*, and *Tazoudasaurus*. In *Aardonyx*, however, it is more elongated than in *Sefapanosaurus*. This structure was regarded as a 'radial ulnar process' by Remes (2008) and as a 'ligament scar' by Yates *et al.* (2010). The long axis of the distal articular surface is set at 45° with respect to the long axis of the proximal articular surface, as in most basal sauropodomorphs.

**Manus:** The preserved elements of the left manus correspond to the distal carpal I and II, metacarpal I, phalanx I.1, and metacarpal II, all of which were preserved in articulation. Additionally, digit five, consisting of a metacarpal, a nonterminal phalanx, and the ungual, is also present amongst the available material (BP/1/7438; Fig. 12).

Distal carpal I is the larger of the two carpal elements preserved. It is suboval in proximal view, with its dorsopalmar length 0.65 times its mediolateral width. Distal carpal I in basal sauropodomorphs is usually the largest of the distal carpals, and varies in shape from suboval (e.g. *Adeopapposaurus*) to subcircular (e.g. *Massospondylus*), except for *Mussaurus* in which distal carpal I is notably small (equal in size to distal carpal II) and is subtriangular in proximal view (Otero & Pol, 2013). Distal carpal I is proximodistally low and subtriangular shaped in dorsal and palmar views. It is mediolaterally narrower than the proximal



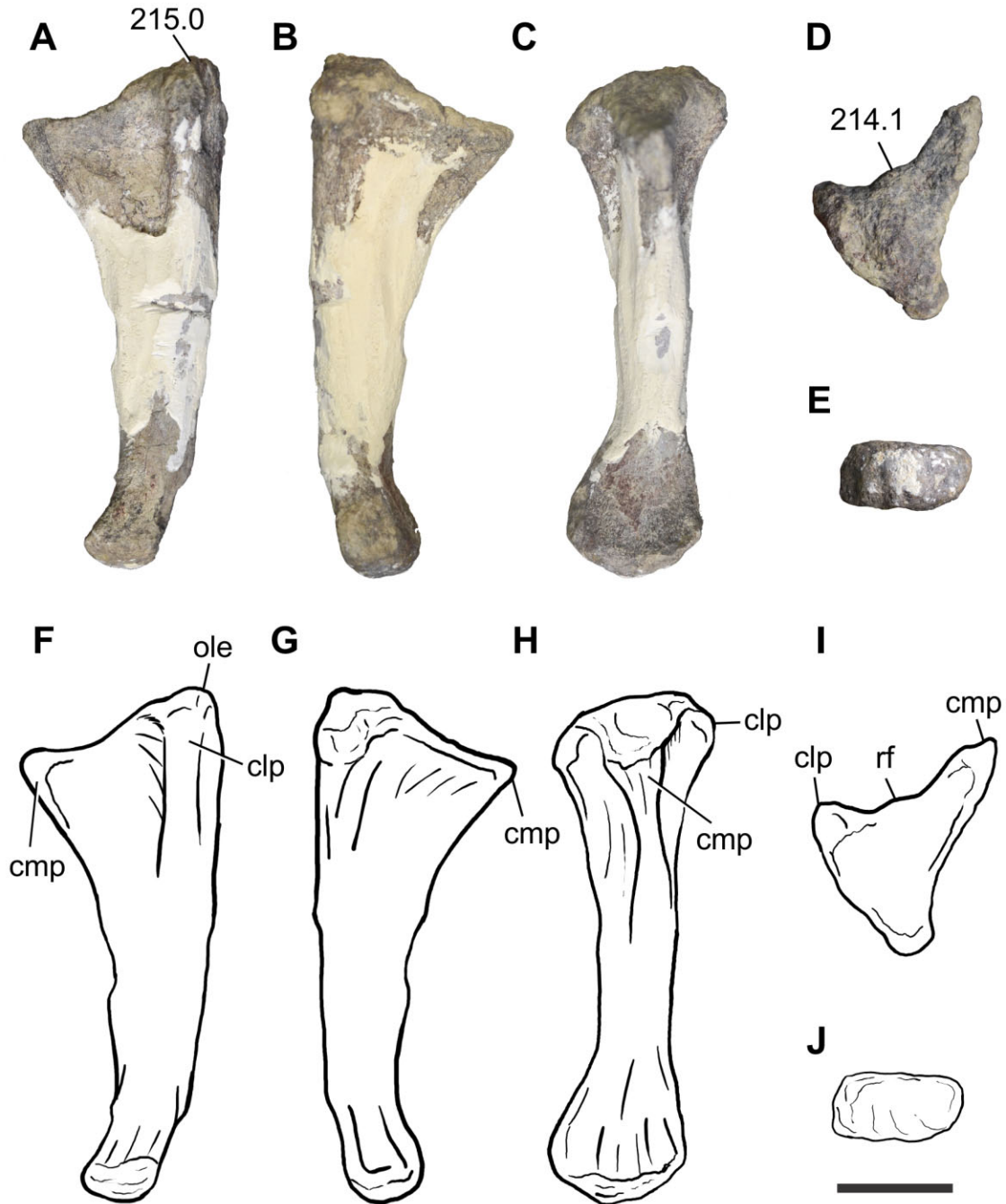
**Figure 9.** *Sefapanosaurus zastronensis* gen. et sp. nov., right humerus (BP/1/7434), photographs and interpretative drawings. Cranial (A, F), caudal (B, G), lateral (C, H), medial (D, I), and proximal (E, J, posterior towards top) views. Numbers indicate character:character state, respectively. Abbreviations: dc, deltopectoral crest; hh, humeral head. Scale bar = 5 cm.

mediolateral width of metacarpal I, differing from the condition of most basal sauropodomorphs (Upchurch *et al.*, 2007; Yates *et al.*, 2010) in which distal carpal I covers almost the entire proximal surface of metacarpal I. In this sense, the condition present in *Sefapanosaurus* resembles that of the most basal sauropodomorphs (e.g. *Efraasia*, *Ruehleia*; Upchurch *et al.*, 2007) and outgroups (*Heterodontosaurus*, *Herrerasaurus*). As noted above, the basal sauropodiform *Mussaurus patagonicus* (Otero & Pol, 2013) also has a small distal carpal I, resembling in this aspect the condition of *Sefapanosaurus*. As in most basal sauropodomorphs with known carpal elements, distal carpal I of *Sefapanosaurus* does not present the sulcus across the medial side, and partially overlaps distal carpal II.

Distal carpal II is smaller than distal carpal I, is subcircular in proximal view, and does not completely cover the proximal surface of metacarpal II, as in most basal sauropodomorphs, except for *Mussaurus*

(MLP 68-II-27-1 specimen A), in which distal carpal II is subtriangular in proximal view and the dorsal portion is thicker than the palmar margin.

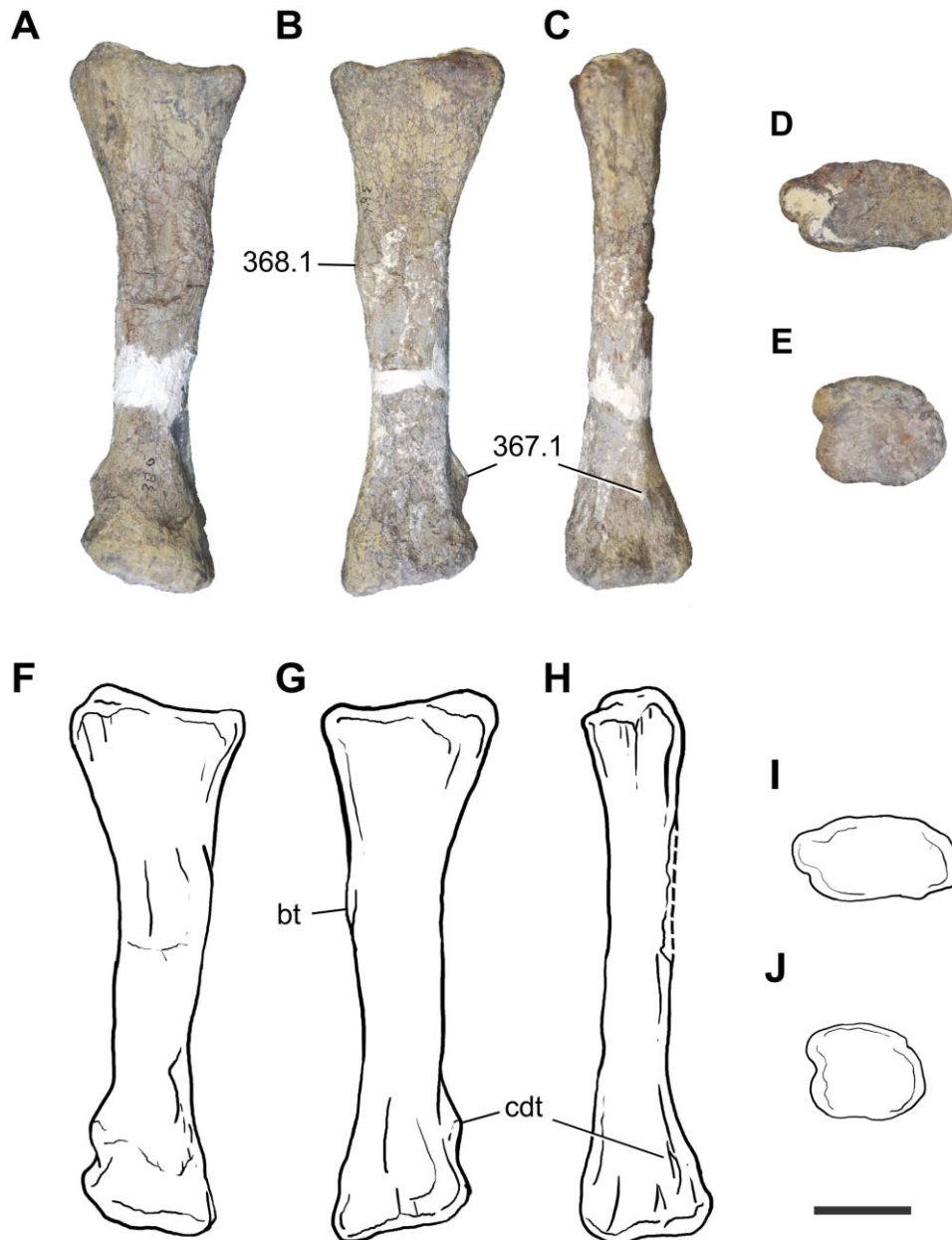
Metacarpal I is broad and much shorter than the other metacarpals, as in most basal sauropodomorphs. The overall shape of the proximal end is partially obscured by distal carpal I. However, it can be noted that the proximal end is mediolaterally well developed, as in most basal sauropodomorphs. The dorsoplantar height is 0.65 times its mediolateral width, whereas the proximodistal length is 1.2 times the proximodistal length of metacarpal II. The mediolateral width is 0.8 times its proximodistal length, an intermediate ratio between more primitive forms (e.g. *Adeopapposaurus*, 0.77) and more derived taxa (e.g. *Antetonitrus*, 1.12, McPhee *et al.*, 2014). The mediolateral length of the proximal end of metacarpal I is 1.5 times the mediolateral width of the proximal end of metacarpal II. A broad proximal end of metacarpal I with respect



**Figure 10.** *Sefapanosaurus zastronensis* gen. et sp. nov., left ulna (BP/1/7437), photographs and interpretative drawings. Craniolateral (A, F), caudomedial (B, G), craniomedial (C, H), proximal (D, I, anterior towards top), and distal (E, J, anterior towards top) views. Numbers indicate character.character state, respectively. Abbreviations: clp, craniolateral process; cmp, craniomedial process; ole, olecranon process; rf, radial fossa. Scale bar = 5 cm.

to metacarpal II is common for non-neosauropod sauropodomorphs (with the exception of *Omeisaurus*, which has the neosauropod condition). The dorsal and plantar margins of the proximal surface are subparallel to each other and concave, whereas the medial margin is convex and the lateral margin is concave

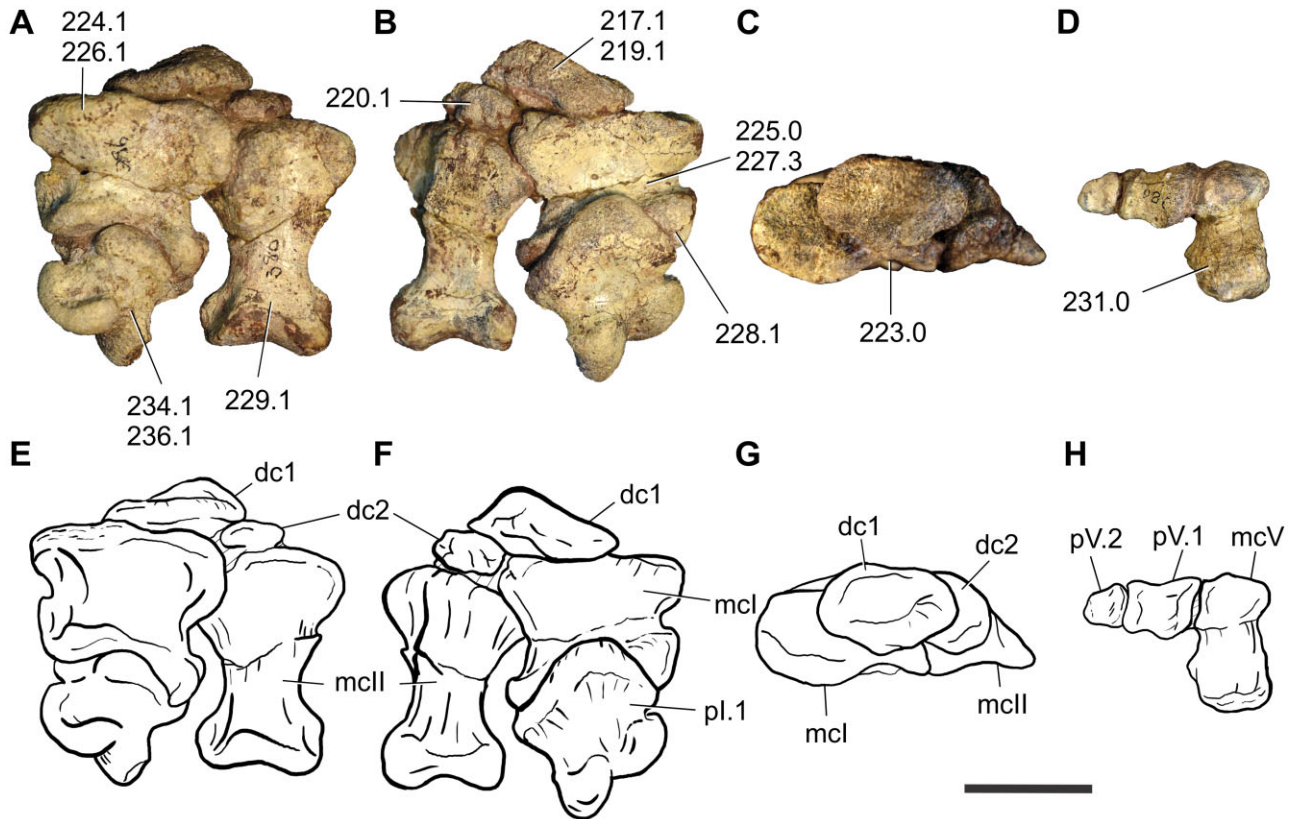
and receives the medial surface of metacarpal II. Metacarpal I is inset into the carpus, as is common for most basal sauropodomorphs except for *Sarhsaurus* and *Thecodontosaurus*. The proximal surface is flat and is twisted approximately 45° medially with respect to the distal articular surface.



**Figure 11.** *Sefapanosaurus zastronensis* gen. et sp. nov., right radius (BP/1/7435), photographs and interpretative drawings. Craniolateral (A, F), caudomedial (B, G), caudolateral (C, H), proximal (D, I, posterior towards top), and distal (E, J, anterior towards top) views. Numbers indicate character.character state, respectively. Abbreviations: bt, biceps tubercle; cdt, caudodistal process. Scale bar = 5 cm.

The shaft of metacarpal I of *Sefapanosaurus* is reduced, mediolaterally wide, and dorsoplantarly compressed, which is the general shape reported in other transitional sauropodomorphs leading to Sauropoda, such as *Aardonyx* and the basal sauropods *Antetonitrus* and *Lessemsaurus*. The lateral and medial margins are concave, with the latter extremely concave on its ventral margin. A metacarpal I with a notably concave ventromedial margin is present in *Lufengosaurus*,

*Aardonyx*, *Lessemsaurus*, and *Antetonitrus*; however, the condition present in *Sefapanosaurus* is much more pronounced than in these taxa. The minimum transverse width of the shaft of metacarpal I is 1.75 times that of the minimum transverse shaft of metacarpal II. This ratio exceeds the value of 2 that characterizes massospondylids and other basal sauropodomorphs (*Riojasaurus*, *Saraksaurus*, *Jingshanosaurus*, and *Yunnanosaurus*).



**Figure 12.** *Sefapanosaurus zastronensis* gen. et sp. nov., incomplete left manus (BP/1/7438), photographs and interpretative drawings. Incomplete digits one and two in dorsal (A, E), palmar (B, F), and proximal (C, G, palmar towards top) views. Digit five in medial (D, H) view. Numbers indicate character.character state, respectively. Abbreviations: dc1, distal carpal 1; dc2, distal carpal 2; mcl, metacarpal I; mcll, metacarpal II; mcV, metacarpal V; pl.1, phalanx I.1; pv.1, phalanx V.1; pv.2, phalanx V.2. Scale bar = 5 cm.

The distal articular condyles of metacarpal I are highly asymmetrical, as is common for basal saurischians (Gauthier, 1986). The lateral condyle is more distally located than the medial condyle; hence, the first manual phalanx of digit I is slightly deflected medially with respect to the rest of the manus. Collateral ligament pits are present and well developed on both distal condyles.

Manual phalanx I.1 is a robust bone with an expanded proximal end and is extremely short so that the shaft is virtually undifferentiated. The proximal articular surface's mediolateral width is subequal to its dorsoplantar length and is 0.85 times its proximodistal length. Although the proximal end is covered by the distal condyles of Metacarpal I, it can be noticed that it has two distinct articular facets for the articulation of the distal condyles of metacarpal I, as in most basal sauropodomorphs. The ventral margin has an extremely well-developed lip that tapers proximally and covers almost the entire surface of the ventral condyles of metacarpal I when articulated. A well-developed, proximally pointed ventral margin of

phalanx I.1 is present in *Mussaurus patagonicus* (MLP 68-II-27-1 specimen A), although is less developed than in *Sefapanosaurus*. The distal articular surface is trapezoidal and twisted medially approximately 60° with respect to the proximal end, a condition also present in some basal forms (e.g. *Thecodontosaurus*, *Efrasia*), some 'core prosauropods' (e.g. *Sarhsaurus*, *Riojasaurus*, *Adeopapposaurus*), basal sauropodiforms (e.g. *Aardonyx*), and basal sauropods (e.g. *Antetonitrus*). The condyles are well developed and separated by a well-defined intercondylar groove. The lateral and medial margins are set obliquely to each other. Collateral ligament pits are well developed and delimited by sharp margins.

Metacarpal II is a robust element with expanded proximal and distal ends. The proximal articular surface is subtriangular with the mediolateral width being 1.2 times the dorsoplantar length and 0.6 times the proximodistal length. The shaft of metacarpal II differs from that of other basal sauropodomorphs in having the lateral and medial margins not parallel to each other. This condition is also present in *Lessemsaurus*

and *Antetonitrus*. The lateroventral surface presents a bifurcated notch, similar to that reported in *Antetonitrus* (McPhee *et al.*, 2014). The distal articular surface has well-defined condyles, with a slightly developed intercondylar groove, denoting a ginglymoid shape.

Metacarpal V is robust and constitutes the smallest of the preserved elements of the metacarpus, as in most basal sauropodomorphs. The proximal end is almost rounded with its mediolateral width being 0.66 times its proximodistal length. The proximal surface is flat, as in some basalmost sauropodomorphs, such as *Thecodontosaurus* and *Efraasia*, but also as in sauropods more derived than *Tazoudasaurus*. The shaft is short, with a subcircular cross-section. The distal end is subtrapezoidal and lacks differentiation of the distal condyles.

Digit V has a nonterminal phalanx and an ungual. The shape and proportions are similar to those of other basal sauropodomorphs, such as *Plateosaurus engelhardti* (MB.R. 4430), *Massospondylus carinatus* (BP/1/4934), *Adeopapposaurus mognai* (PVSJ 610), and *Mussaurus patagonicus* (MLP68-II-27-1 specimen A). The nonterminal phalanx has expanded proximal and distal ends. The mediolateral length of the proximal end is 1.5 times the dorsoplantar length, and is similar to the proximodistal length. As in most basal sauropodomorphs in which phalanx V.1 is preserved, the shaft of this element has its lateral and medial margins not parallel to each other, tapering distally. The distal end is differentiated from the shaft but lacks discrete and differentiated condyles.

The ungual phalanx of digit V is also preserved in articulation. This is the smallest element preserved, with an expanded proximal end and a tapering distally rounded end, which lacks differentiated distal condyles.

#### Hindlimbs

*Femur*: Four proximal femora are preserved (BP/1/7440, 7441, 7442, 7443), which probably correspond to different individuals, all of them of different sizes (Fig. 13). The proximal region has a well-developed head, the major axis of which is orientated perpendicular to the longitudinal axis of the femoral shaft. The femoral head is roughly hemispherical in profile, having the same condition as in *Riojasaurus*, *Eucnemesaurus*, basal sauropods (e.g. *Isanosaurus*), and basal eusauropods (e.g. *Patagosaurus*, *Shunosaurus*). The greater trochanter is well developed and is situated at approximately the same level as the femoral head. The lesser trochanter is evident, corresponding to a proximodistally orientated ridge extending onto the cranial surface of the proximal end of the femoral shaft, below the level of the femoral head. A proximodistally elongated lesser trochanter is the generalized condition for most basal

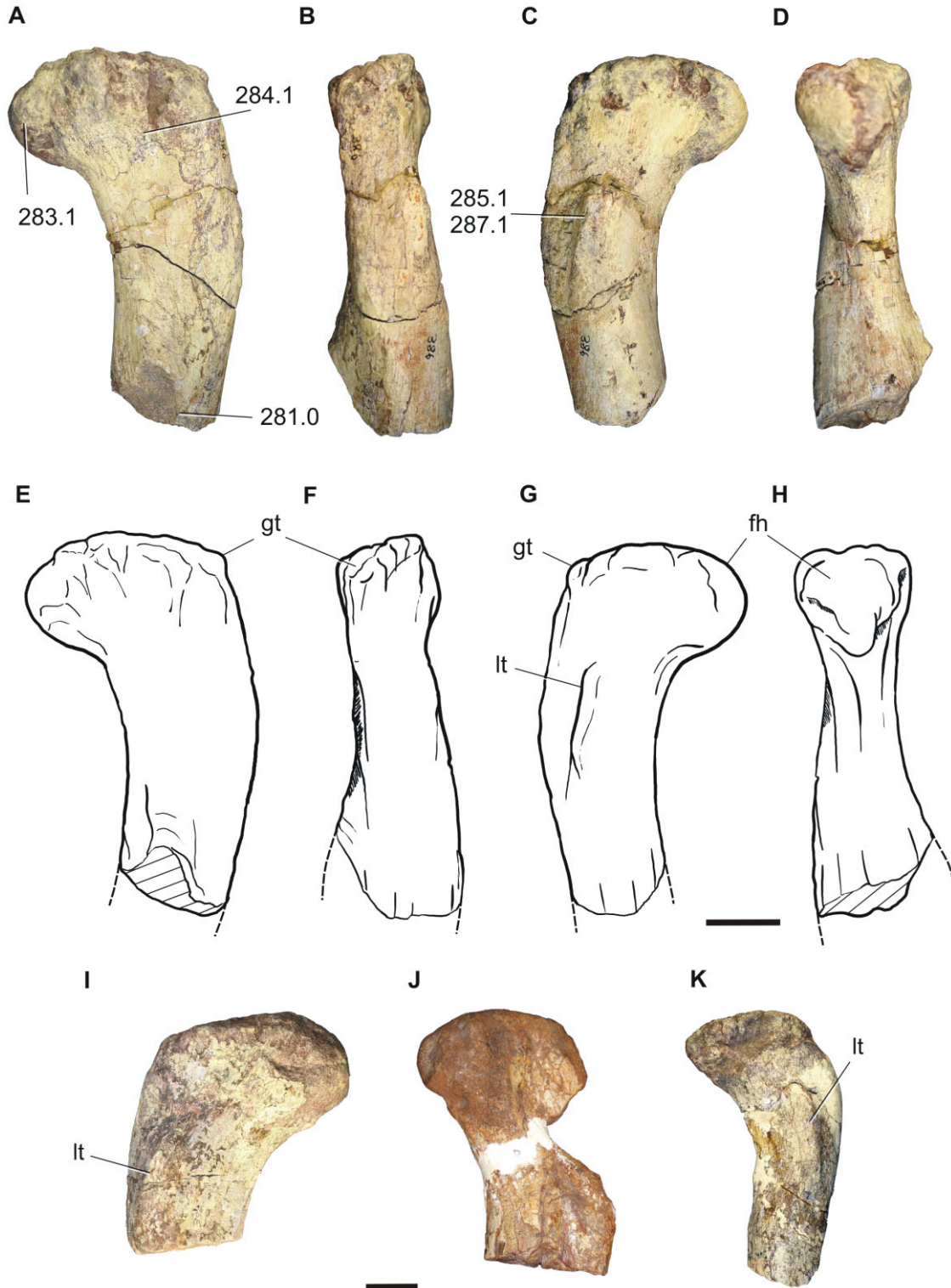
sauropodomorphs (except for *Saturnalia*, which has a rounded tubercle), and basal sauropods (e.g. vulcanodontids). The fourth trochanter is not preserved in any of the specimens.

*Tibia*: A proximal right tibia is preserved (BP/1/7445) (Fig. 14). The proximal end is well expanded as in all basal sauropodomorphs. The craniocaudal length of the proximal portion is 1.85 times its mediolateral length, giving the proximal end an ovoid shape, with the cnemial crest orientated cranially. The presence of a cranially orientated cnemial crest is characteristic of non-eusauropod sauropodomorphs, whereas the presence of ovoid proximal tibia is a feature present in all non-neosauropod sauropodomorphs (with the exception of *Omeisaurus* and *Mamenchisaurus*, which have the derived state; Wilson & Sereno, 1998). The tallest point of the cnemial crest is located close to the proximal end of the crest, as in most nonsauropod sauropodomorphs. The general robustness (maximum craniocaudal length/maximum mediolateral length) of the proximal portion of the tibia of *Sefapanosaurus* resembles that of *Ruehleia* (MB.R.4718.40), *Plateosaurus longiceps* (MB.R.4405.57.1, Skelett 1), *Mussaurus* (MLP 68-II-27-1 specimen A), and *Melanorosaurus* (NMQR 1551), but it is not as robust as that of *Antetonitrus* (BP/1/4952).

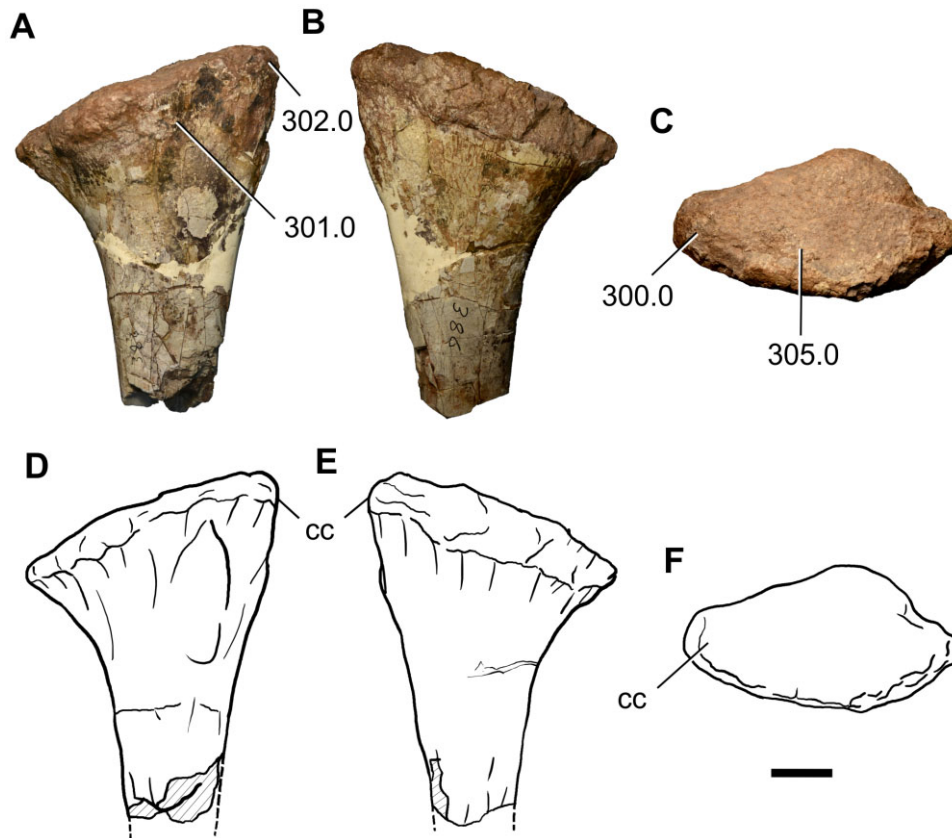
*Fibula*: A complete left fibula is preserved (BP/1/7447) (Fig. 15). The proximal end is craniocaudally expanded, its craniocaudal length being 2.95 times its mediolateral width. The cranial margin of the proximal end is rounded whereas the caudal margin tapers caudally. The lateral surface of the proximal end is convex and the medial surface is flat. The preserved shaft of the fibula is almost straight in lateral view and subcircular in cross-section. The lateral surface of the shaft bears a tenuous lateral tuberosity located close to the proximal end. The distal end is teardrop-shaped and bears a prominent projection on the craniomedial surface, which represents a unique feature amongst basal sauropodomorphs.

*Tarsals and pes*: A partially articulated left pes is preserved, including the astragalus, calcaneum, a putative distal tarsal IV, and proximal shafts of metatarsals III, IV, and V, which correspond to the holotype (BP/1/386). Additionally, an isolated proximal end of metatarsal II (BP/1/7448) and a distal end of metatarsal III (BP/1/7449) are preserved (Fig. 16).

The astragalus of *Sefapanosaurus* has the generalized condition of most basal sauropodomorphs in being subrectangular in proximal view, with a craniocaudally rounded medial margin and with the lateral surface slightly concave for its articulation with the calcaneum. The lateral and medial margins are almost



**Figure 13.** *Sefapanosaurus zastronensis* gen. et sp. nov., femora. Incomplete right femur (BP/1/7441), photographs and interpretative drawings. Caudal (A, E), lateral (B, F), cranial (C, G), and medial (D, H) views. Incomplete right femur (BP/1/7440) in cranial view (I). Incomplete right femur (BP/1/7443) in caudal view (J). Incomplete left femur (BP/1/7442) in cranial view (K). Numbers indicate character.state, respectively. Abbreviations: fh, femoral head; gt, greater trochanter, lt, lesser trochanter. Scale bars = 5 cm.



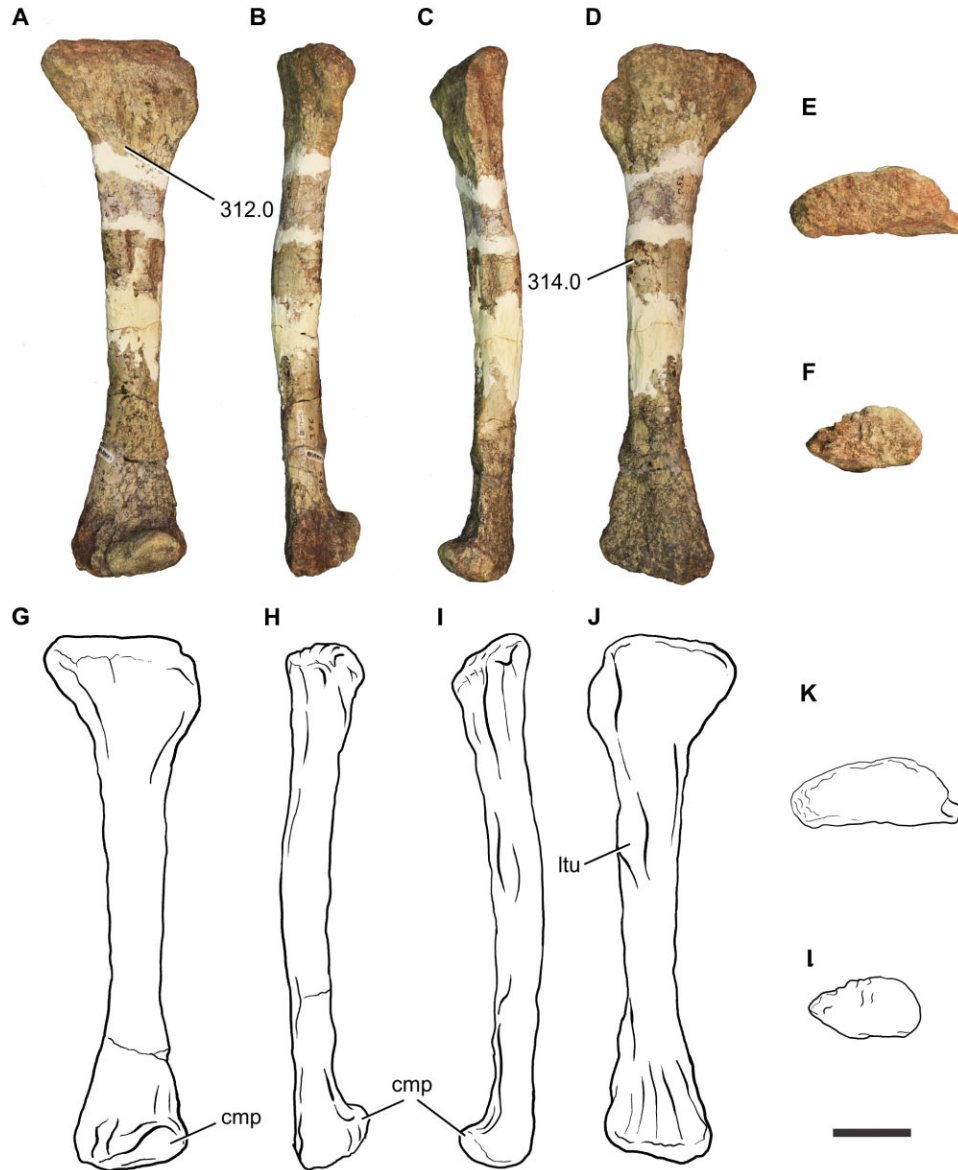
**Figure 14.** *Sefapanosaurus zastronensis* gen. et sp. nov., incomplete right tibia (BP/1/7445), photographs and interpretative drawings. Lateral (A, D), medial (B, E), and proximal (C, F, lateral towards top), views. Numbers indicate character character state, respectively. Abbreviation: cc, cnemial crest. Scale bar = 5 cm.

equally developed craniocaudally, as in *Plateosaurus*, but unlike other sauropodomorphs (e.g. massospondylids, *Blikanasaurus*, *Mussaurus*, Sauropoda), in which the medial margin is craniocaudally narrower than the lateral margin. In cranial view the astragalus has approximately the same depth both laterally and medially. The caudal margin is concave and lacks the caudomedial convexity reported for *Plateosaurus*, *Mussaurus*, and *Blikanasaurus* (Otero & Pol, 2013). The proximal surface of the astragalus is composed by cranial and caudal concave surfaces, which are divided from each other by the ascending process. Both surfaces are approximately equal in size given that the ascending process is placed close to the midpoint of the astragalus proximal surface. Nonetheless, the caudal surface is slightly larger than the cranial one.

The ascending process of *Sefapanosaurus* has a unique morphology that differentiates it from all other sauropodomorphs. As in all sauropodomorphs, the ascending process is mediolaterally wide and its lateral margin is proximodistally taller than its medial margin. However, in *Sefapanosaurus* the astragalus is notably tall and its lateral surface is much broader

(anteroposteriorly) than the medial surface, and these surfaces are delimited by well-developed ridges that run proximodistally along the entire ascending process. These ridges are unique amongst basal sauropodomorphs because they are notably thick, clearly framing the ascending process, are also straight, and present a subcircular cross-section. This morphology contrasts with the widespread condition amongst basal sauropodomorphs in which the ascending process presents thin framing ridges with convex margins (e.g. *Glacialisaurus*, *Massospondylus*, *Mussaurus*, *Blikanasaurus*). The ascending process presents a triradiate ‘T’-shaped cross-section when viewed proximally, representing a unique feature amongst sauropodomorphs, and is regarded here as an autapomorphy of this taxon.

This unusual morphology of the ascending process was probably not caused by injury or disease. Bones affected by traumatic or physiological stress often present characteristic features that are usually preserved in the fossil process (e.g. Gilmore, 1920; Molnar & Farlow, 1990; Farke & O’Connor, 2007; Tanke & Rothschild, 2010). The external surfaces of affected bones

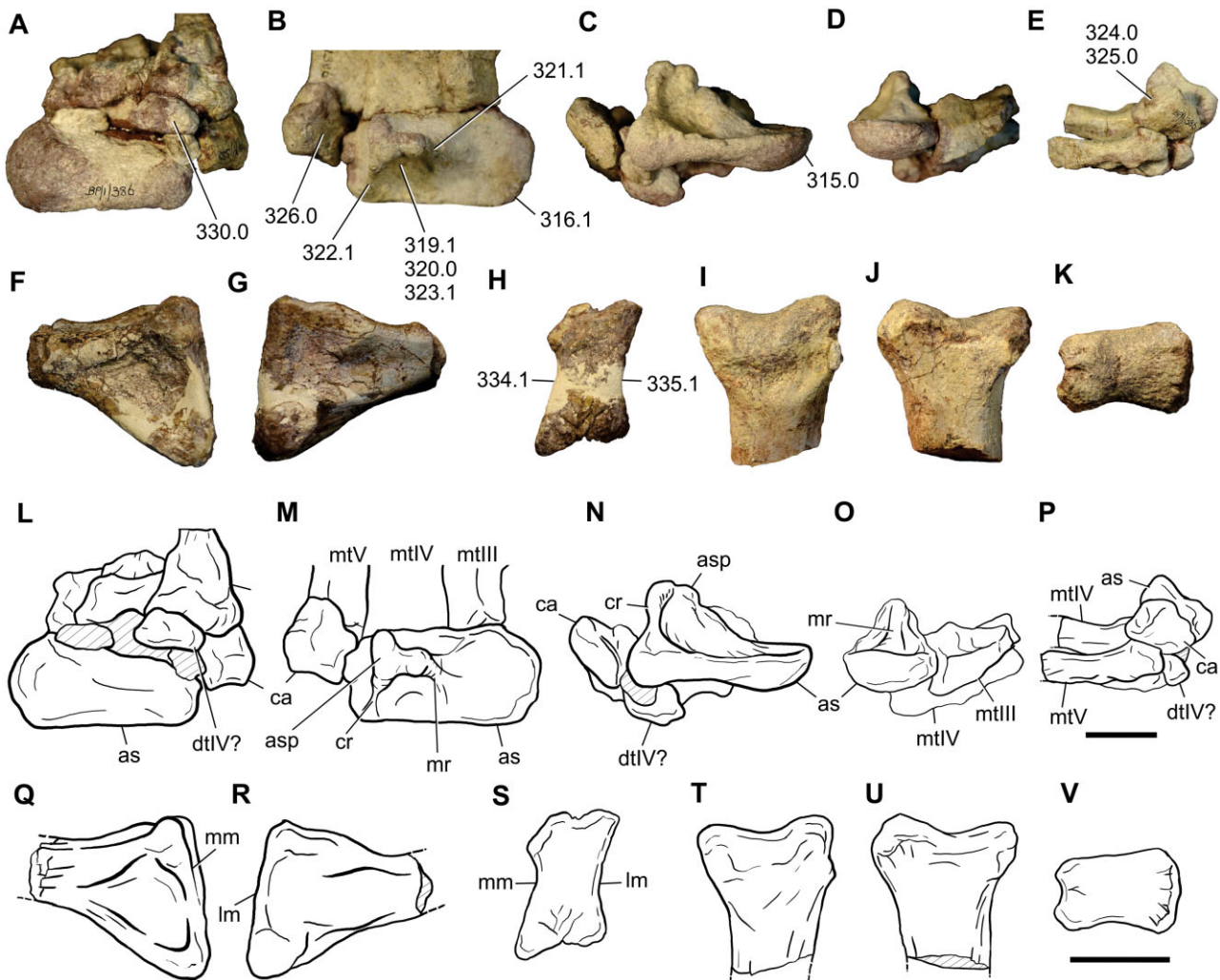


**Figure 15.** *Sefapanosaurus zastronensis* gen. et sp. nov., incomplete left fibula (BP/1/7447), photographs and interpretative drawings. Medial (A, G), caudal (B, H), cranial (C, I), lateral (D, J), proximal (E, K, lateral towards top), and distal (F, L, medial towards top) views. Abbreviations: cmp, craniomedial projection; ltu, lateral tuberosity. Numbers indicate character character state, respectively. Scale bar = 5 cm.

are often characterized by a differential texture and/or bone overgrowth in the surrounding area affected by the disorder, which may allow inference of particular pathologies (see Hanna, 2002 and references therein). Such abnormalities are absent in the astragalus of *Sefapanosaurus*, which casts doubt on a pathological origin for its unique morphology.

Vascular foramina are absent. The distal surface of the astragalus is craniocaudally convex and mediolaterally concave, as in other basal sauropodomorphs (e.g. *Massospondylus*, *Coloradisaurus*, *Mussaurus*).

The calcaneum is preserved associated (although not articulated) to the astragalus. It has the generalized proportions of most basal sauropodomorphs, with a transverse width greater than 0.3 times the transverse width of the astragalus (Yates & Kitching, 2003). The lateral surface is subrectangular, unlike the subtriangular condition present in basal forms such as *Herrerasaurus* (PVSJ-373), *Saturnalia* (Langer, 2003), and *Plateosaurus engelhardti* (GPIT Skelett 1), or the suboval shape present in *Blikanasaurus*. The lateral surface is convex and lacks the fossa or groove present



**Figure 16.** *Sefapanosaurus zastronensis* gen. et sp. nov., pes elements (BP/1/386, 7448, 7449), photographs and interpretive drawings. Incomplete left pes (BP/1/386) in distal (A, L), proximal (B, M), caudal (C, N), medial (D, O), and lateral (E, P) views. Proximal end of metatarsal II (BP/1/7448) in medial (F, Q), lateral (G, R), and proximal (H, S) views. Distal end of metatarsal III (BP/1/7449) in dorsal (I, T), ventral (J, U), and distal (K, V) views. Numbers indicate character.character state, respectively. Abbreviations: as, astragalus; asp, ascending process; ca, calcaneum; cr, caudal ridge; dtIV?, distal tarsal IV?; lm, lateral margin; mm, medial margin; mr, medial ridge; mtIII, metatarsal III; mtIV, metatarsal IV; mtV, metatarsal V. Scale bar = 5 cm.

in other basal sauropodomorphs (e.g. *Saturnalia*, *Anchisaurus*, *Blikanasaurus*, *Melanorosaurus*) and sauropods. The proximal surface is concave for the articulation with the distal end of the fibula.

A distal tarsal element is represented by a putative distal tarsal IV, articulated with metatarsal V. Its morphology is mostly obscured by its articulation with other bones, although it can be seen that its mediolateral width is greater than its dorsoplantar depth.

The pes includes partially preserved metatarsals II to V. Metatarsal II only has its proximal end preserved, which has the typical hourglass shape of most basal sauropodomorphs, in which the medial and lateral

margins are concave for the articulation with metatarsals I and III, respectively. Conversely, *Plateosaurus* and *Unaysaurus* display straight lateral margins. The proximal end is dorsoplantarly expanded, with its maximum mediolateral width 0.67 times the maximum dorsoplantar height.

Metatarsals III to V are preserved associated to the tarsus and to each other; hence, their proximal morphology cannot be observed. Metatarsal III and IV morphology is mostly obscured by the articulation and incompleteness. However, metatarsal IV presents a mediolaterally expanded proximal end, as in most basal sauropodomorphs.

Metatarsal V is almost complete, lacking only its distal end. This element is flat, has an expanded proximal end, and tapers distally, resulting in a triangular shape as in all basal sauropodomorphs. The proximal end is obscured by the presence of a distal tarsal and the calcaneum.

## DISCUSSION

We discuss in this section four different topics based on the observations made on the materials studied and the comparative analysis based upon them. First, we present the results of a cladistics analysis, in which *Sefapanosaurus* was included, as well as the new characters proposed herein. Second, we discuss the autapomorphic features of *S. zastronensis* that distinguishes it from other basal sauropodomorphs, particularly focusing on the differences between *Sefapanosaurus* and the closely related *Aardonyx celestae*. Third, we point out and describe in a phylogenetic context the features that distinguished *Sefapanosaurus* as a nonsauropod sauropodiform. Finally, we discuss the significance of *Sefapanosaurus* and other Late Triassic–Early Jurassic sauropodomorphs from Gondwana that help understanding the evolutionary origins of Sauropoda.

### PHYLOGENETIC RELATIONSHIPS

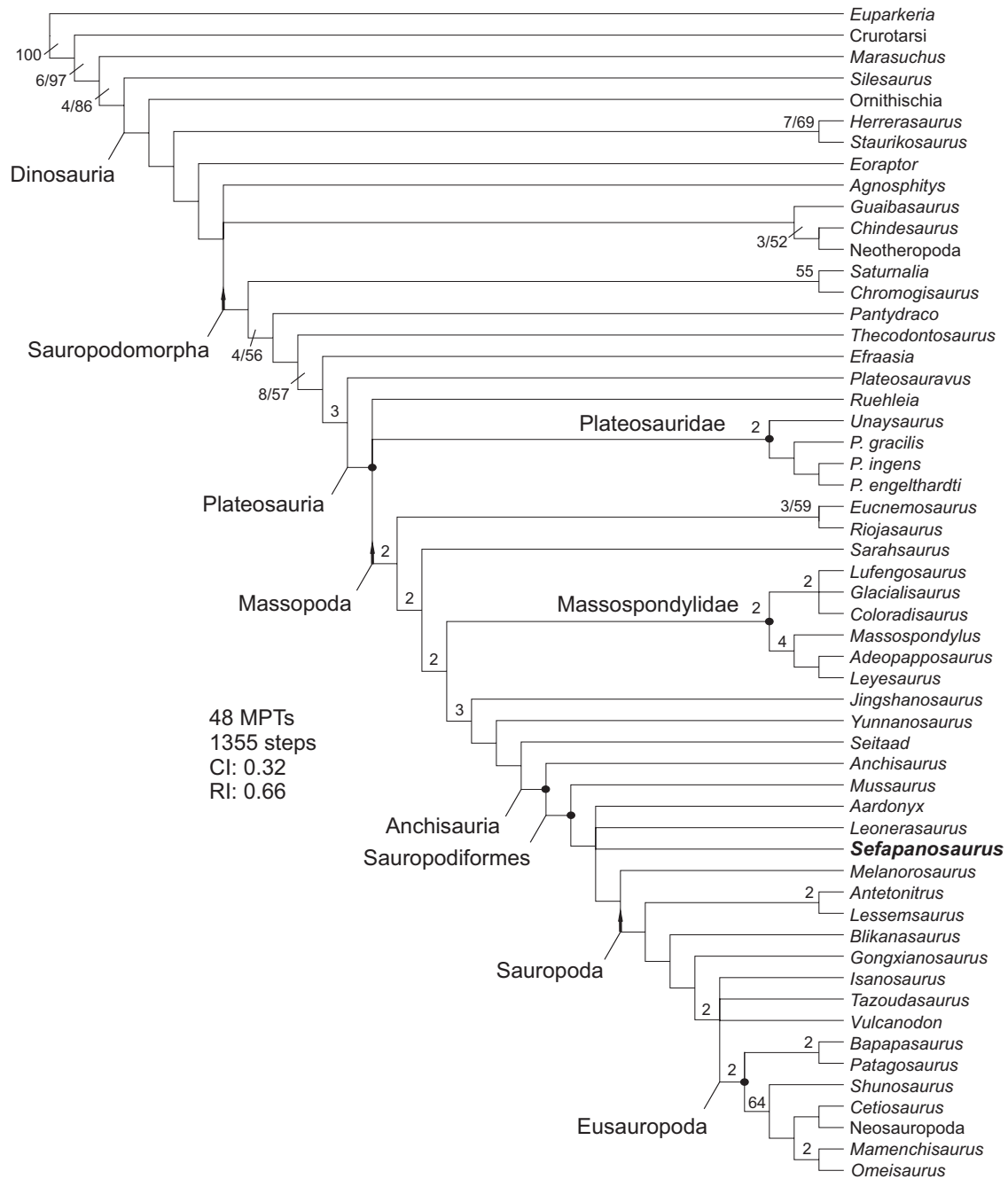
The postcranial remains of *Sefapanosaurus* described herein provide anatomical information to test the phylogenetic relationships of basal sauropodomorphs close to the origins of Sauropoda. The phylogenetic analysis retrieved 48 most parsimonious trees (MPTs) of 1355 steps (consistency index = 0.32; retention index = 0.66), found in 442 out of the 1000 replicates.

The strict consensus tree of the 48 MPTs (see Supporting Information File S1) is fairly well resolved, but small polytomies are present at various levels within Sauropodomorpha. As in most recent cladistic analyses (Yates, 2007a; Apaldetti *et al.*, 2011, 2012; Pol *et al.*, 2011; Otero & Pol, 2013; McPhee *et al.*, 2014), ‘prosauropods’ are depicted here as a paraphyletic group within Sauropodomorpha, retrieving two basal monophyletic clades, Plateosauridae and Massospondylidae, the internal relationships of which are unresolved. Amongst more advanced taxa there is a polytomy formed by *Sefapanosaurus*, *Leoneasaurus*, *Aardonyx*, and more derived sauropodomorphs, and a polytomy composed by *Melanorosaurus*, *Camelotia*, *Blikanasaurus*, (*Antetonitrus* + *Lessemsaurus*), plus more derived sauropodomorphs, and finally a polytomy formed by *Vulcanodon*, *Tazoudasaurus*, *Isanosaurus*, plus Eusauropoda. However, when the very fragmentary

*Camelotia* was pruned from the MPTs, the reduced consensus showed a good resolution of these derived sauropodomorphs, showing the clade constituted by *Blikanasaurus* plus more derived sauropodomorphs, with two successive sister groups: the clade formed by (*Lessemsaurus* + *Antetonitrus*) and the taxon *Melanorosaurus* (Fig. 17).

As stated above, *Sefapanosaurus* is retrieved within a polytomy along with *Leoneasaurus*, *Aardonyx*, and more derived sauropodomorphs. This clade is diagnosed by the following unambiguous synapomorphies: ventrolateral twisting of the transversal axis of the distal end of manual phalanx I.1 relative to its proximal end less than 60° (character 234.1, see Appendix) and the lesser trochanter positioned distal to the level of the femoral head (character 286.1). This clade and *Mussaurus patagonicus* are included within Sauropodiformes (*sensu* Sereno, 2007; see Otero & Pol, 2013), a group diagnosed in this analysis by the following unambiguous synapomorphies: concave posterior margin of middle neural spines in lateral view (character 173.1), length of manual digit one greater than length of manual digit two (character 233.1), longitudinal axis of the femur in lateral view weakly bent with an offset of less than 10° (character 280.1), length of the ungual of pedal digit one longer than all nonterminal phalanges (character 344.1), femoral length between 600 and 799 mm (character 353.3), and presence of a biceps tubercle on the radius (character 367.1). Anchisauria (*sensu* Galton & Upchurch, 2004) is a slightly more inclusive clade that clusters *Anchisaurus* with the above-mentioned clade, and is diagnosed in this analysis by a single unambiguous synapomorphy: lateral margin of descending caudoventral process of the distal end of the tibia positioned set well back from the cranioventral corner of the distal tibia (character 311.1).

To evaluate the robustness of the phylogenetic position retrieved for *Sefapanosaurus* within Sauropodomorpha, support measures were calculated (see Supporting Information File S1). Bremer support values within Sauropodomorpha vary from 1 to 8, but only a few nodes have values above 4. Similarly, bootstrap and jackknife frequency values are mostly below 50%. Alternative positions of *Sefapanosaurus* were tested to evaluate how suboptimal the topologies are when this taxon is positioned more basally or in a more derived position. Placing *Sefapanosaurus* more basally than *Mussaurus* implies two extra steps, whereas forcing its placement below *Anchisaurus* implies a minimum of three extra steps. Finally, placing *Sefapanosaurus* as more derived than in its optimal positions implies a suboptimal topology of five extra steps. This constrains the plausible positions of *Sefapanosaurus* within the transition from basal sauropodomorphs to sauropods.



**Figure 17.** Reduced strict consensus of the phylogenetic analysis depicting the position of *Sefapanosaurus zastronensis* gen. et sp. nov. Numbers at the nodes represent Bremer support values > 1 (left) and bootstrap values > 50% (right). The complete support values are presented in Supporting Information File S1. Abbreviations: CI, consistency index; MPTs, most parsimonious trees; RI, retention index.

DIAGNOSTIC FEATURES OF *SEFAPANOSAURUS*  
*ZASTRONENSIS* AND COMPARISONS WITH  
*AARDONYX CELESTAE*

The morphology of *Sefapanosaurus* resembles in general terms that of other sauropodomorphs placed

basally to Sauropoda. The diagnostic characters of *Sefapanosaurus* are discussed here and comparisons with other sauropod outgroups are conducted, with particular emphasis on the features that distinguish the new taxon from *Aardonyx*, which is also known from the Elliot Formation (Yates *et al.*, 2010) and to which

the specimens described here were referred by McPhee *et al.* (2014).

*Astragalus with triradiate cross-section*

The ascending process of the astragalus in basal sauropodomorphs is quite distinctive in being mediolaterally broad. There is some variation within the group in the mediolateral width of the ascending process, and forms closely related to Sauropoda usually have a comparatively narrower process at its proximal end (e.g. *Lessemsaurus*, *Blikanasaurus*). The ascending process of *Sefapanosaurus* becomes narrow proximally, resembling the condition in *Blikanasaurus* and the basal sauropods *Vulcanodon* and *Tazoudasaurus*. However, a unique feature of the new taxon amongst Sauropodomorpha is that this process has a triradiate cross-section, which extends from the base up to its distal end. When viewed proximally, the proximal tip of the ascending process displays a “T”-shape.

*Tall ascending process of the astragalus*

The ascending process of the astragalus amongst Sauropodomorpha is characterized by being mediolaterally wider than craniocaudally deep. However, its proximodistal height varies, being very low in some taxa (e.g. *Massospondylus*, *Glacialisaurus*) to moderately tall in others (e.g. *Coloradisaurus*, *Euskelosaurus*, *Blikanasaurus*). *Sefapanosaurus* has a proximodistally tall ascending process that exceeds in height the range of variation seen amongst basal sauropodomorphs. In this sense, the height of the ascending process is 35% of the mediolateral width of the main body of the astragalus. By contrast, other basal sauropodomorphs consistently have lower values, which range between 25–27% (e.g. *Plateosaurus*, *Coloradisaurus*, *Adeopapposaurus*, *Massospondylus*, *Glacialisaurus*, *Mussaurus*, *Blikanasaurus*).

*Ascending process of the astragalus framed medially and caudally by thick ridges*

The ascending process of most basal sauropodomorphs presents thin medial and lateral margins (e.g. plateosaurids, massospondylids, *Sarhsaurus*, *Mussaurus*). In *Sefapanosaurus* two noticeable ridges frame the medial and lateral margins of the ascending process of the astragalus. The lateral margin, placed caudally, rises from the caudal margin of the main body of the astragalus and continues through the proximal end of the ascending process. The medial margin rises near the medial end of the astragalus body and suddenly slopes towards the proximal tip of the ascending process. Both structures delimit a caudal fossa of the astragalus. This kind of framing of the ascending process is not reported in any other basal sauropodomorph.

In addition to the autapomorphies present in the astragalus (holotype), four autapomorphies are present in the appendicular material associated with the holotype, which are referred here to *S. zastronensis*. They are discussed below.

*Long ridge extending from the craniodorsal margin of the coracoid to the coracoid foramen*

The coracoid of basal sauropodomorphs is quite conservative in terms of general shape and features, as corroborated by the fact that only two phylogenetically informative characters were used in recent phylogenetic analyses on basal sauropodomorphs (e.g. Upchurch *et al.*, 2007; Yates, 2007a). The general shape of the basal sauropodomorph coracoid is traditionally subovoid, and such morphology is maintained without drastic modifications until Titanosauria, in which the proximodistally length exceeds the length of the scapular articulation and the cranioventral margins become rectangular (Carballido *et al.*, 2012). In terms of features, the coracoid tubercle, placed cranially to the glenoid region, on the lateral surface, is the only noticeable structure that can be distinguished in several basal sauropodomorph coracoids (i.e. *Sarhsaurus*, *Adeopapposaurus*, *Coloradisaurus*, and sauropods more derived than *Tazoudasaurus*), apart from the coracoid foramen.

*Sefapanosaurus* presents a novel structure, a long ridge on the craniodorsal margin of the coracoid, which points toward the coracoid foramen although it does not reach it. This structure is not reported in other basal sauropodomorphs and is regarded here as an autapomorphy of this taxon. The long ridge of the coracoids is probably the osteological correlate of the muscle biceps brachii, as extant crocodylians display a similar ridge running along the long axis of the coracoids, on the cranioventral surface close to the coracoid foramen (Meers, 2003).

*Distal carpal I with proximally pointing tip on the palmar surface, giving a triangular shape in palmar or dorsal view*

Distal carpal elements within basal sauropodomorphs share the same basic morphology: distal carpal I is the largest element (except in *Mussaurus*, which is subequal to distal carpal II), is subdiscoidal in shape, and covers totally or partially the proximal surface of the first metacarpal. Distal carpal I of *Sefapanosaurus* shares this general morphology, except for the presence of a notable pointed tip on the palmar margin of the bone, which gives the distal carpal a triangular shape when viewed in dorsal or palmar views. This contrast with the widespread condition amongst most basal sauropodomorphs in which the proximal surface of distal carpal I is uniformly convex to slightly flat (e.g. *Plateosaurus*, *Massospondylus*, *Adeopapposaurus*). A similar pattern

has been reported in *Lufengosaurus* (Young, 1941), although less pronounced than in *Sefapanosaurus*.

*Craniomedial process of the ulna distally tapered and twice as long as the craniolateral process*

One of the features that characterizes sauropodomorphs closely related to Sauropoda is the morphology of the proximal ulna, which has an incipient craniolateral process that allows the recognition of a shallow concavity on the ulna for the radius (Yates & Kitching, 2003; Bonnan & Yates, 2007; Yates *et al.*, 2010; Otero & Pol, 2013). The general morphology of the craniomedial and craniolateral processes amongst sauropod outgroups is relatively uniform, with the former much more developed with a wide proximal base and rounded distal tip, and the latter much less developed with a more acute tip. Although in *Sefapanosaurus* the craniomedial process is still much more developed than the craniolateral, the shape and development of the processes differ from those of other sauropod outgroups. In this sense, the proximal depth/maximum length ratio of the craniomedial process in *Sefapanosaurus* is 0.6, whereas this ratio is much higher in other sauropod outgroups (e.g. 1.1 in *Mussaurus*, 1.2 in *Aardonyx*, 1 in *Melanorosaurus*) and basal sauropods (e.g. 1 in *Lessemsaurus*, 1.6 in *Antetonitrus*). Additionally, the shape of the tip of the craniomedial process in *Sefapanosaurus* tapers distally, whereas in the rest of the taxa it terminates in a rounded surface. These proportions and shape show that the craniomedial process is long and gracile in *Sefapanosaurus*, in comparison with a shorter and stouter process in other taxa.

*Prominent projection on the craniomedial surface of the distal end of the fibula*

With the exception of the lateral tuberosity, present in most basal sauropodomorphs, and the anterior crest present in the fibula of *Antetonitrus* (McPhee *et al.*, 2014), the fibula of basal sauropodomorphs is a gracile, almost featureless bone. The latter is reflected in the scarcity of phylogenetic characters that describe its morphology (only three in the most recent phylogenetic analyses, Otero & Pol, 2013; McPhee *et al.*, 2014). The fibula of *Sefapanosaurus* displays a medial projection placed at the distal end, a unique feature amongst basal sauropodomorphs, which gives a stout appearance and might be related to the articulation to the distal end of the tibia.

*Comparisons with Aardonyx celestae*

Although the above-mentioned autapomorphic features allow the recognition of *Sefapanosaurus* as a distinct species of basal sauropodomorph, in a recent paper (McPhee *et al.*, 2014), the specimen BP/1/386 was tentatively referred to *A. celestae*, but without detailed jus-

tification being provided. This referral, albeit tentative, prompts a clear justification of the distinction between *A. celestae* and *S. zastronensis*. In this regard, *Sefapanosaurus* can be distinguished from *Aardonyx* by several features of different skeletal elements, which are discussed below (Fig. 18).

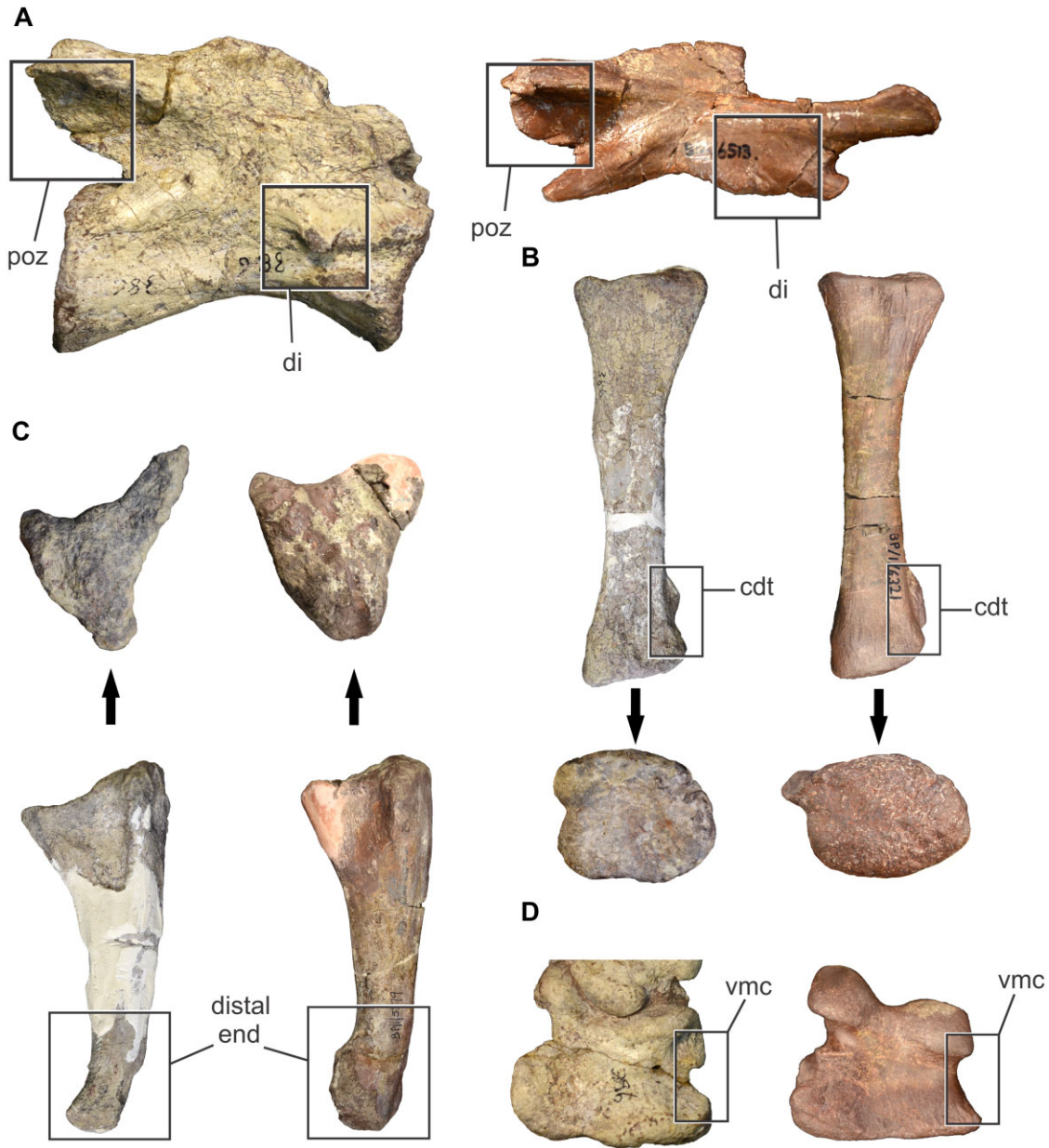
The presence of low, almost inexistent cervical diapophyses, with the concomitant absence of diapophyseal laminae, was regarded as an autapomorphy of *Aardonyx* (Yates *et al.*, 2010). Comparing equivalent elements of both taxa (middle cervicals, considering the height of the neural arches), it can be seen that *Sefapanosaurus* has a well-developed cervical diapophysis, which extends ventrally and exceeds the limit of the neurocentral suture, as in most basal sauropodomorphs. Comparing the same middle elements, the medial wall of the postzygapophysis is almost vertical and extends caudally with a strong convex margin in *Aardonyx* but in *Sefapanosaurus* the medial wall is medially slanted and the caudal margin is slightly convex.

The limb bones of the two taxa can also be differentiated. The caudodistal tubercle of the radius (also present in other sauropod outgroups), is less developed in *Sefapanosaurus* than in *Aardonyx*, and is proximodistally elongated in the latter. Additionally, the distal articular surface of the radius of *Sefapanosaurus* is more rounded than in *Aardonyx*. The ulna is more gracile in *Sefapanosaurus*, with a proximal surface bearing a craniomedial process that is much longer than the craniolateral process, whereas in *Aardonyx* the latter is much shorter. The distal end of the ulna is more robust in *Aardonyx* when viewed in lateral or medial views. Finally, the medial margin of metacarpal I is markedly concave in *Sefapanosaurus*, whereas only a mild concavity is present in *Aardonyx* (as well as in *Antetonitrus* and *Lessemsaurus*).

COMMON FEATURES OF *SEFAPANOSAURUS* AND OTHER SAUROPOD OUTGROUPS

The phylogenetic position of *Sefapanosaurus* places it within the group of sauropodomorphs closely related to sauropods. *Sefapanosaurus*, together with the pectinate array of nonsauropod sauropodiforms known from the Upper Triassic–Lower Jurassic, underlines the growing assemblage of taxa that reveal the transition from basal sauropodomorphs to Sauropoda. In this regard, we discuss here the features that characterize *Sefapanosaurus* as a ‘transitional’ form.

Although nonsauropod sauropodiforms share character states with plateosaurids, massospondylids, and Sauropoda, character optimization on the MPTs revealed a series of features that are common for the taxa placed within the transitional branches of the



**Figure 18.** Comparisons between *Sefapanosaurus zastronensis* gen. et sp. nov. and *Aardonyx celestae*. A, middle cervical vertebrae of *Sefapanosaurus* (BP/1/7409) and *Aardonyx* (BP/1/6513) in right lateral view depicting diapophysis and postzygapophysis. B, right radius of *Sefapanosaurus* (BP/1/7435) and *Aardonyx* (BP/1/6321) depicting the caudodistal tubercle (top) and the distal articular surface (bottom). C, left ulna of *Sefapanosaurus* (BP/1/7437) and *Aardonyx* (BP/1/5379) depicting the proximal articular surface (top) and the distal end robusticity (bottom). D, left metacarpal I of *Sefapanosaurus* (BP/1/7438) and *Aardonyx* (BP/1/5379) depicting the ventromedial concavity. *Sefapanosaurus* is placed on the left in (A) to (D). Abbreviations: cdt, caudodistal tubercle; di, diapophysis; poz, postzygapophysis; vmc, ventromedial concavity. Not to scale.

cladogram. The above-discussed autapomorphic characters depict *Sefapanosaurus* as a taxonomically distinct form within basal sauropodomorphs. *Sefapanosaurus* shares with nonsauropod

sauropodiforms a set of features that distinguishes them from basal forms and which demonstrates a common ‘transitional’ morphology within Sauropodomorpha. These characters are discussed below.

*Square-shaped cross-section of the distal caudal centra with flattened lateral and ventral sides (character 192.1)*

Most sauropodomorphs and also basal saurischians present distal caudal centra with lateral and ventral surfaces that are slightly convex rather than flat, giving the centra a subcylindrical shape. *Sefapanosaurus* and other nonsauropod sauropodiforms (i.e. *Mussaurus*, *Aardonyx*, *Melanorosaurus*, and *Camelotia*) display posterior caudal centra with flattened lateral and ventral surfaces, resulting in a square shape in cross-section. This character is convergently present in *Adeopapposaurus*.

*Presence of a caudodistal tubercle of the radius (character 367.1)*

A prominent tubercle is present on the caudodistal surface of the radius of *Sefapanosaurus*, most probably for the attachment of the radioulnar ligament, as also interpreted by other authors (Remes, 2008; Yates *et al.*, 2010; Otero & Pol, 2013; McPhee *et al.*, 2014). This feature is characteristic of basal sauropodiforms (*Mussaurus*, *Aardonyx*, *Melanorosaurus*) and is also present in the basal sauropods *Antetonitrus* and *Tazoudasaurus*.

*Presence of a biceps tubercle of the radius (character 368.1)*

As in the previous character, the biceps tubercle of the radius is another feature present in *Sefapanosaurus*. The biceps tubercle is a rounded tubercle situated on the cranial surface of the radius, close to the proximal end. As its name implies, the biceps tubercle is the osteological correlate of the muscle biceps brachii (Meers, 2003), and has also been reported in other basal sauropodiforms (i.e. *Mussaurus*, *Aardonyx*, *Melanorosaurus*) and the basal sauropod *Antetonitrus*, and is occasionally present in some basal sauropodomorphs (e.g. *Efraasia*, *Ruehleia*).

*Strongly concave ventromedial margin of metacarpal I (character 369.1)*

The first metacarpal of basal sauropodomorphs is characteristic because of its reduced size and robustness compared with metacarpals II–IV. Such general morphology of the first metacarpal is maintained without drastic modifications throughout the basal sauropodomorphs. Nonetheless, in *Sefapanosaurus* the first metacarpal is not only short and wide but also bears an extremely concave ventromedial margin. Within related sauropodiforms, only *Antetonitrus* displays a similar pattern to that observed in *Sefapanosaurus*, whereas in *Aardonyx* and *Lessemsaurus* the ventromedial margin is less concave. With the exception of *Mussaurus*, which displays a less concave medial margin of metacarpal I, this is a nonsauropod

sauropodiform feature, being absent in more primitive (basal-most sauropodomorphs, plateosaurids, massospondylids) and more derived (*Tazoudasaurus* and Eusauropoda) sauropodomorphs.

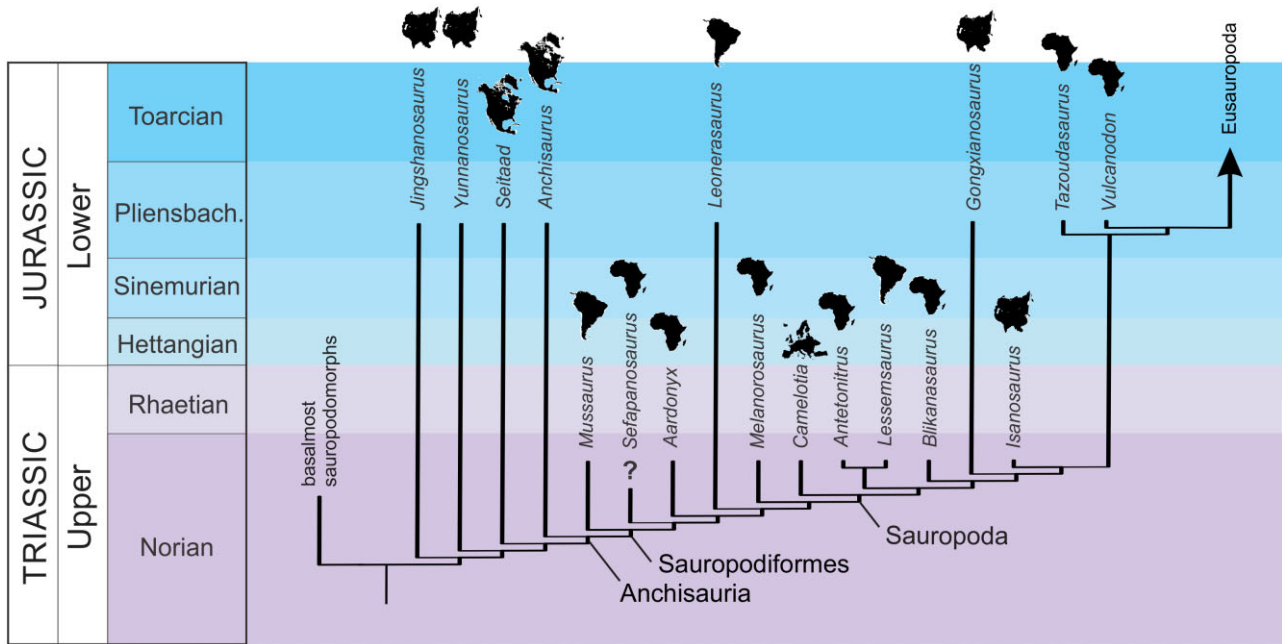
BASAL SAUROPODIFORMS AND THE SCENARIO OF THE LATE TRIASSIC–EARLY JURASSIC OF GONDWANA

A particularly interesting fact, critical to understanding the basal sauropodomorph–sauropod transition, is that the most basal sauropodiforms are mostly known from the Late Triassic and Early Jurassic of Gondwana, in particular from South America and South Africa (Galton & Van Heerden, 1985; Yates & Kitching, 2003; Yates, 2007a; Pol & Powell, 2007b; Yates *et al.*, 2010; Pol *et al.*, 2011; Otero & Pol, 2013). All nonsauropod sauropodiforms known to date, the closest outgroups to Sauropoda, are from Gondwana, with only the possible exception of the highly fragmentary *Camelotia* from the Late Triassic of Europe. This highlights the importance of the Late Triassic–Early Jurassic Gondwanan taxa for understanding the evolutionary steps toward the Sauropoda.

The poor geochronological constraints on most sauropodomorph-bearing units from this time in Gondwana prompts caution when analysing the timing of these evolutionary events. However, some comments are included below based on the current knowledge of the diversity of sauropodiforms (Fig. 19).

The oldest record of nonsauropod sauropodiforms is from the Late Triassic Norian of South Africa: *Melanorosaurus readi* from the Lower Elliot Formation (Haughton, 1924; Galton & Van Heerden, 1985; Yates & Kitching, 2003). More recent records of basal sauropodiforms include *Aardonyx* from South Africa and *Mussaurus* and *Leoneosaurus* from Argentina. Additionally, the most informative remains of basal sauropods are also found in the Late Triassic–Early Jurassic of Gondwana, including *Antetonitrus*, *Lessemsaurus*, *Tazoudasaurus*, and *Vulcanodon*.

These taxa share with Eusauropoda a large number of features, including cranial characters such as knob-like basal tuberae (character 82.0) separated by a deep, caudally open U-shaped fossa (character 84.2, present in *Melanorosaurus*); vertebral characters include the hyposphenes in dorsal vertebrae equal to the height of the neural canal (character 157.2, present in *Melanorosaurus*, *Camelotia*, *Lessemsaurus*, and *Antetonitrus*), middle dorsal neural spines greater than 1.5 times the length of the base (character 167.2, present in *Lessemsaurus* and *Antetonitrus*), two dorsosacral vertebrae (character 177.2, present in *Melanorosaurus*), and the length of first caudal centrum less than its height (character 183.1). Most notably, appendicular characters present in taxa from the Upper Triassic are:



**Figure 19.** Simplified reduced consensus tree showing the calibrated phylogeny of basal sauropodomorphs close to Sauropoda with their respective distributions on the continents where they were found. Abbreviation: Pliensbach., Pliensbachian.

caudal margin of the acromion process of the scapula greater than 65° from the long axis of the scapula at its steepest point (character 201.1, present in *Mussaurus*, *Antetonitrus*), length of the deltopectoral crest of the humerus 30–50% of the length of the humerus (character 207.1), presence of radial fossa and craniolateral process developed (character 214.1), length of the manus is less than 38% of humerus plus radius length (character 222.0, present in *Mussaurus*, *Lessemsaurus*, and *Antetonitrus*), elliptical cross-section of femoral shaft (character 281.1, present in *Melanorosaurus*, *Camelotia*, *Lessemsaurus*, and *Antetonitrus*), lateral margin of descending caudoventral process of the distal end of the tibia set well back from the craniomedial corner of the distal tibia (character 311.1, present in *Mussaurus*, *Lessemsaurus*, *Antetonitrus*, and *Blikanasaurus*), and length of the third metatarsal is less than 40% of the length of the tibia (character 336.1, present in *Antetonitrus*, *Blikanasaurus*). Many of these features optimize on different nodes along the basal nodes of Sauropodiformes before the origin of Sauropoda and Eusauropoda.

Therefore, although the eusauropod body plan (gigantic size, herbivorous diet, columnar limbs and graviportal locomotion, complex vertebral laminae) was fully established by the Early Jurassic, the records of such nonsauropod sauropodiforms indicate that many of the features that have traditionally been used to characterize eusauropods were already established by the Late Triassic.

## CONCLUSIONS

*Sefapanosaurus zastronensis* increases our knowledge on the diversity of basal sauropodiforms (sauropod outgroups) in the Triassic–Jurassic of Gondwana. It displays a set of characters in the ulna, manus, fibula, and ankle that identifies it as a distinct taxon within Sauropodomorpha, corroborating its taxonomic separation from *Aardonyx*, contrary to previous hypotheses/assumptions (McPhee *et al.*, 2014).

The new taxon also adds significant anatomical and phylogenetic information about the transition of basal sauropodomorphs to Sauropoda, especially with regard to characters of the manus and the pes. The identification of *Sefapanosaurus* as a taxon closely related to Sauropoda, together with other taxa discussed here, highlights the importance of Gondwanan taxa for understanding the evolutionary origin of sauropods.

## ACKNOWLEDGEMENTS

We thank all the people that allowed us access to collections as well as for their assistance and hospitality: K. Wellspring (ACM), J. Botha and E. Butler (BMQR), B. Rubidge and B. Zipfel (BPI), Philippe Havlik and Manuela Aiglstorfer (GPIT), S. M. Alvarez and A. Kramarz (MACN), J. Cundiff (MCZ), E. Ruigomez (MEF), M. Reguero (MLP), J. Powell (PVL), A. Marsh, J. Sagebiel, and T. Rowe (TMM), S. Kaal and R. Smith (SAM), Rainer Schoch (SMNS), M. Getty and R. Irmis

(UMNH), D. Abelín and R. Martínez (UNSJ), D. Brinkman and C. Norris (YPM). The version of TNT 1.1 is freely available thanks to a subsidy of the Willi Henning Society. The present study was developed with the following financial support: Agencia Nacional de Promoción Científica y Tecnológica (PICT 2011-2482), Subsidio para Viajes y Estadías (La Plata University), Whittington Award (The Palaeontological Association), Ostrom Fund (Yale University), and Deutscher Akademischer Austausch Dienst (DAAD) to A.O., and Programa de Cooperación Científico-Tecnológica MINCyT (Argentina) and DST (South Africa), to D.P. and A.C. Comments of Nat Smith and an anonymous reviewer greatly improved this paper.

## 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.
- Apaldetti C, Martinez RN, Alcober OA, Pol D. 2011.** A new basal sauropodomorph (Dinosauria: Saurischia) from Quebrada del Barro Formation (Marayes-El Carrizal Basin), north-western Argentina. *PLoS ONE* **6**: e26964. doi:10.1371/journal.pone.0026964.
- Apaldetti CG, Pol D, Yates A. 2012.** The postcranial anatomy of *Coloradisaurus brevis* (Dinosauria: Sauropodomorpha) from the Late Triassic of Argentina and its phylogenetic implications. *Palaeontology* **56**: 277–301.
- Barrett PM, Upchurch P, Wang XL. 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.
- Benton MJ, Juul L, Storrs GW, Galton PM. 2000.** Anatomy and systematic of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *Journal of Vertebrate Paleontology* **20**: 71–102.
- Bonaparte JF. 1986.** The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. In: Padian K, ed. *The beginning of The Age of Dinosaurs*. Cambridge: Cambridge University Press, 247–258.
- Bonaparte JF. 1999.** Evolución de las vértebras presacras en Sauropodomorpha. *Ameghiniana* **36**: 115–187.
- Bonaparte JF, Brea G, Schultz CL, Martinelli AG. 2007.** A new specimen of *Guaibasaurus candelariensis* (basal Saurischia) from the Late Triassic Caturrita Formation of southern Brazil. *Historical Biology* **19**: 73–82.
- Bonaparte JF, Ferigolo J, Ribeiro AM. 1999.** A new Early Triassic saurischian dinosaur from Rio Grande Do Sul State, Brazil. *National Science Museum Monographs* **15**: 89–109.
- 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, 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.
- Brochu CA. 1996.** Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* **16**: 49–62.
- Carballido JL, Rauhut OWM, Pol D, Salgado L. 2012.** Osteology and phylogenetic relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. *Zoological Journal of the Linnean Society* **163**: 605–662.
- Carrano MT. 2000.** Homoplasy and the evolution of dinosaur locomotion. *Paleobiology* **26**: 489–512.
- Cerda I, Pol D, Chinsamy A. 2013.** Osteohistological insight into the early stages of growth in *Mussaurus patagonicus* (Dinosauria, Sauropodomorpha). *Historical Biology* **26**: 110–121.
- Cooper MRA. 1984.** A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. *Palaeontologia Africana* **25**: 203–231.
- 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.
- Farke AA, O'Connor PM. 2007.** Pathology in *Majungatholus crenatissimus* (Theropoda, Abelisauridae) from the Late Cretaceous of Madagascar. *Memoir of the Society of Vertebrate Paleontology* **8**: 180–184.
- Galton PM. 1985.** Cranial anatomy of the prosauropod dinosaur *Sellosaurus gracilis* from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg, West Germany. *Stuttgarter Beiträge zur Naturkunde, Series B* **118**: 1–39.
- Galton PM. 1990.** Basal Sauropodomorpha – Prosauropoda. In: Weishampel D, Dodson P, Osmólska H, eds. *The Dinosauria*. Berkeley, CA: University of California Press, 320–344.
- Galton PM, Upchurch P. 2004.** Prosauropoda. In: Weishampel D, Dodson P, Osmólska H, eds. *The Dinosauria*, 2nd edn. Berkeley, CA: 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.
- Gauthier JA. 1986.** Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* **8**: 1–55.
- Gilmore CW. 1920.** Osteology of the carnivorous Dinosauria in the United States National Museum, with special mention to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum* **110**: 1–159.

- Goloboff PA, Farris JS, Nixon K. 2008a.** TNT: tree analysis using new technology, v. 1.1 (Willi Hennig Society Edition). Available at: <http://www.zmuc.dk/public/phylogeny/tnt>.
- Goloboff PA, Farris JS, Nixon K. 2008b.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Hanna RR. 2002.** Multiple injury and infection in a sub-adult theropod dinosaur *Allosaurus fragilis* with comparisons to allosaur pathology in the Cleveland-Lloyd Dinosaur Quarry Collection. *Journal of Vertebrate Paleontology* **22**: 76–90.
- Haughton SH. 1924.** The fauna and stratigraphy of the Stormberg Series. *Annals of the South African Museum* **12**: 323–497.
- Holtz TR Jr. 1994.** The phylogenetic position of Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* **68**: 1100–1117.
- Huene F von. 1932.** Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Paläontologie* **4**: 1–361.
- Irmis RB. 2007.** Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology* **27**: 350–361.
- 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). *Paleobios* **23**: 1–40.
- Langer MC. 2004.** Basal Saurischia. In: Weishampel D, Dodson P, Osmolska H, eds. *The Dinosauria*, 2nd edn. Berkeley, CA: University of California Press, 25–46.
- Langer MC, Abdala F, Richter M, Benton MJ. 1999.** A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Académie des Sciences IIA* **329**: 511–517.
- Langer MC, Franca MAG, Gabriel S. 2007.** The pectoral girdle and forelimb anatomy of the stem sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *Special Papers in Palaeontology* **77**: 113–137.
- Leal LA, Azevedo SAK, Kellner AWA, Rosa ÁAS D. 2004.** A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Parana Basin, Brazil. *Zootaxa* **690**: 1–24.
- Lu J, Kobayashi Y, Li T, Zhong S. 2010.** A new basal sauropod dinosaur from the Lufeng Basin, Yunnan Province, Southwestern China. *Acta Geologica Sinica* **84**: 1336–1342.
- 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.
- Martínez RN, Sereno PC, Alcober OA, Colombi CE, Renne PR, Montañez IP, Currie BS. 2011.** A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science* **331**: 206–210.
- McPhee BW, Yates AM, Choiniere JN, Abdala F. 2014.** The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda. *Zoological Journal of the Linnean Society* **171**: 151–205.
- Meers MB. 2003.** Crocodylian forelimb musculature and its relevance to Archosauria. *The Anatomical Record Part A* **274 A**: 892–916.
- Molnar RE, Farlow JO. 1990.** Carnosaur paleobiology. In: Weishampel D, Dodson P, Osmolska H, eds. *The Dinosauria*. Berkeley, CA: University of California Press, 210–224.
- Molnar RE, Kurzanov SM, Dong Z. 1990.** Carnosauria. In: Weishampel D, Dodson P, Osmolska H, eds. *The Dinosauria*. Berkeley, CA: University of California Press, 169–209.
- Nomina Anatomica Veterinaria. 2005.** *Fifth Edition. International Committee on Veterinary Gross Anatomical Nomenclature*. Columbia: Hannover.
- Novas FE. 1992.** Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* **35**: 51–62.
- Novas FE. 1993.** New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* **13**: 400–423.
- Novas FE. 1996.** Dinosaur monophyly. *Journal of Vertebrate Paleontology* **16**: 723–741.
- Otero A, Gallina PA, Canale JI, Haluza A. 2012.** Sauropod haemal arches: morphotypes, new classification and phylogenetic aspects. *Historical Biology* **24**: 243–256.
- Otero A, Pol D. 2013.** Postcranial anatomy and phylogenetic relationships of *Mussaurus patagonicus* (Dinosauria, Sauropodomorpha). *Journal of Vertebrate Paleontology* **33**: 1138–1168.
- Owen R. 1842.** Report on British fossil reptiles. Part II. *Report of the British Association for the Advancement of Science* **1841**: 60–204.
- Pérez-Moreno BP, Sanz JL, Buscalioni AD, Moratalla JJ, Ortega F, Rasskingutman D. 1994.** A unique multi-toothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* **370**: 363–367.
- 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. doi:10.1371/journal.pone.0014572.
- Pol D, Powell JE. 2005.** Anatomy and phylogenetic relationships of *Mussaurus patagonicus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Patagonia. *2 Congreso Latinoamericano de Paleontología de Vertebrados*, Río de Janeiro: 208–209.
- Pol D, Powell JE. 2007a.** Skull anatomy of *Mussaurus patagonicus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Patagonia. *Historical Biology* **19**: 125–144.
- Pol D, Powell JE. 2007b.** New information on *Lessemsaurus sauropoides* (Dinosauria: Sauropodomorpha) from the Upper Triassic of Argentina. *Special Papers in Palaeontology* **77**: 223–243.
- Rauhut OWM. 2003.** The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**: 1–213.

- Remes K. 2008.** Evolution of the pectoral girdle and forelimb in Sauropodomorpha (Dinosauria, Saurischia): osteology, myology and function. DPhil Thesis, Universität München.
- Rowe T. 1989.** A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology* **9**: 125–136.
- Salgado L, Coria RA, Calvo JO. 1997.** Evolution of the titanosaurid sauropods. 1. Phylogenetic analysis based on postcranial evidence. *Ameghiniana* **34**: 3–32.
- Seeley HG. 1887.** On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* **43**: 165–171.
- 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, Dutheil DB, Iarochene M, Larsson HCE, Lyon GH, Magwene PM, Sidor CA, Varricchio DJ, Wilson JA. 1996.** Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* **272**: 986–991.
- 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. doi:10.1371/journal.pone.0009789.
- Smith ND, Pol D. 2007.** Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica. *Acta Palaeontologica Polonica* **52**: 657–674.
- Tanke DH, Rothschild BM. 2010.** Paleopathologies in Albian ceratopsids and their behavioral significance. In: Ryan MJ, Chinnery-Allgeier BJ, Eberth DA, eds. *New perspectives on horned dinosaurs*. Bloomington and Indianapolis: Indiana University Press, 355–384.
- Upchurch P. 1995.** Evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London B* **349**: 365–390.
- Upchurch P. 1998.** The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* **124**: 43–103.
- 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 PM. 2007.** A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. *Special Papers in Palaeontology* **77**: 57–90.
- 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**: 217–276.
- Wilson JA. 2006.** Anatomical nomenclature of fossil vertebrates: standardized terms or lingua franca. *Journal of Vertebrate Paleontology* **26**: 511–518.
- Wilson JA, D’Emic MD, Ikejiri T, Moacdieh EM, Whitlock JA. 2011.** A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS ONE* **6**: e17114. doi:10.1371/journal.pone.0017114.
- Wilson JA, Sereno PC. 1998.** Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology, Memoir* **5**: 1–68.
- 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.** The species taxonomy of the sauropodomorph dinosaurs from the Löwenstein Formation (Norian, Late Triassic) of Germany. *Palaeontology* **46**: 317–337.
- Yates AM. 2004.** *Anchisaurus polyzelus* Hitchcock: the smallest known sauropod dinosaur and the evolution of gigantism amongst sauropodomorph dinosaurs. *Postilla* **230**: 1–58.
- Yates AM. 2007a.** The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). *Special Papers in Palaeontology* **77**: 9–55.
- Yates AM. 2007b.** Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. *Historical Biology* **19**: 93–123.
- 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 of London* **277**: 787–794.
- Yates AM, Kitching JW. 2003.** The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London B* **270**: 1753–1758.
- Young C-C. 1941.** A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.). *Palaeontologica Sinica, Series C* **7**: 1–53.

## APPENDIX

## CHARACTER LIST

The complete list of characters used in the phylogenetic analysis is provided here. The following multistate characters were treated as ordered, summing to a total of 37: 8, 13, 19, 23, 40, 57, 69, 92, 102, 108, 117, 121, 134, 144, 147, 149, 150, 157, 167, 170, 171, 177, 205, 207, 222, 227, 242, 251, 254, 277, 294, 299, 336, 342, 349, 353, and 370.

This character list include the characters listed by Yates (2007a), the characters added by Smith & Pol (2007), those added by Apaldetti *et al.* (2012), and Otero & Pol (2013). Finally, four new characters were added in this contribution.

## SKULL

1. Skull to femur ratio: greater than (0), or less than (1), 0.6 (modified from Gauthier, 1986).
2. Lateral plates appressed to the labial side of the premaxillary, maxillary, and dentary teeth: absent (0) or present (1) (Upchurch, 1995).
3. Relative height of the rostrum at the posterior margin of the naris: more than (0), or less than (1), 0.6 times the height of the skull at the middle of the orbit (Langer, 2004).
4. Foramen on the lateral surface of the premaxillary body: absent (0) or present (1) Yates (2007a).
5. Distal end of the dorsal premaxillary process: tapered (0) or transversely expanded (1) (Sereno, 1999).
6. Profile of premaxilla: convex (0) or with an inflection at the base of the dorsal process (1) (Upchurch, 1995).
7. Size and position of the posterolateral process of premaxilla: large and lateral to the anterior process of the maxilla (0) or small and medial to the anterior process of the maxilla (1) Yates (2007a).
8. Relationship between posterolateral process of the premaxilla and the anteroventral process of the nasal: broad sutured contact (0), point contact (1), or separated by maxilla (2) (modified from Gauthier, 1986). Ordered.
9. Posteromedial process of the premaxilla: absent (0) or present (1) (Rauhut, 2003).
10. Shape of the anteromedial process of the maxilla: narrow, elongated, and projecting anterior to lateral premaxilla–maxilla suture (0) or short, broad, and level with lateral premaxilla–maxilla suture (1) Yates (2007a).
11. Development of external narial fossa: absent to weak (0) or well developed with sharp posterior and anteroventral rims (1) Yates (2007a).
12. Development of narial fossa on the anterior ramus of the maxilla: weak and orientated laterally to dorsolaterally (0) or well developed and forming a horizontal shelf (1) (modified from Upchurch, 1995).
13. Size and position of subnarial foramen: absent (0), small (no larger than adjacent maxillary neurovascular foramina) and positioned outside of narial fossa (1), or large and on the rim of, or inside, the narial fossa (2) (modified from Sereno *et al.*, 1993). Ordered.
14. Shape of subnarial foramen: rounded (0) or slot-shaped (1) Yates (2007a).
15. Maxillary contribution to the margin of the narial fossa: absent (0) or present (1) Yates (2007a).
16. Diameter of external naris: less than (0), or greater than (1), 0.5 times the orbital diameter (Wilson & Sereno, 1998).
17. Shape of the external naris (in adults): rounded (0) or subtriangular with an acute posteroventral corner (1) (Galton & Upchurch, 2004).
18. Level of the anterior margin of the external naris: anterior to (0) or posterior to (1) the midlength of the premaxillary body (Rauhut, 2003).
19. Level of the posterior margin of external naris: anterior to, or level with, the premaxilla–maxilla suture (0), posterior to the first maxillary alveolus (1), or posterior to the midlength of the maxillary tooth row and the anterior margin of the antorbital fenestra (2) (modified from Wilson & Sereno, 1998). Ordered.
20. Dorsal profile of the snout: straight to gently convex (0) or with a depression behind the naris (1) Yates (2007a).
21. Elongate median nasal depression: absent (0) or present (1) (Sereno, 1999).
22. Width of anteroventral process of nasal at its base: less than (0) or greater than (1) width of anterodorsal process at its base (modified from Sereno, 1999).
23. Nasal relationship with dorsal margin of antorbital fossa: not contributing to the margin of the antorbital fossa (0), lateral margin overhangs the antorbital fossa and forms its dorsal margin (1), overhang extensive, obscuring the dorsal lachrymal–maxilla contact in lateral view (2) (modified from Sereno, 1999).
24. Pointed caudolateral process of the nasal overlapping the lachrymal: absent (0) or present (1) (Sereno, 1999).
25. Anterior profile of the maxilla: slopes continuously towards the rostral tip (0) or with a strong inflection at the base of the ascending ramus, creating a rostral ramus with parallel dorsal and ventral margins (1) (Sereno *et al.*, 1996).
26. Length of rostral ramus of the maxilla: less than (0), or greater than (1), its dorsoventral depth (Sereno *et al.*, 1996).
27. Shape of the main body of the maxilla: tapering posteriorly (0) or dorsal and ventral margins parallel for most of their length (1) Yates (2007a).
28. Shape of the ascending ramus of the maxilla in lateral view: tapering dorsally (0) or with an anteroposterior expansion at the dorsal end (1) Yates (2007a).
29. Rostrocaudal length of the antorbital fossa: greater (0), or less (1), than that of the orbit (Yates, 2003a).
30. Posteroventral extent of medial wall of antorbital fossa: reaching (0), or terminating anterior to (1), the anterior tip of the jugal (modified from Galton & Upchurch, 2004).
31. Development of the antorbital fossa on the ascending ramus of the maxilla: deeply impressed and delimited by a sharp, scarp-like rim (0) or

- weakly impressed and delimited by a rounded rim or a change in slope (1) Yates (2007a).
32. Shape of the antorbital fossa: crescentic with a strongly concave posterior margin that is roughly parallel to the rostral margin of the antorbital fossa (0), subtriangular with a straight to gently concave posterior margin (1), or antorbital fossa absent (2) (modified from Galton, 1985).
  33. Size of the neurovascular foramen at the caudal end of the lateral maxillary row: not larger than the others (0) or distinctly larger than the others in the row (1) (Yates, 2003a).
  34. Direction that the neurovascular foramen at the caudal end of the lateral maxillary row opens: caudally (0) or rostrally, ventrally, or laterally (1) (modified from Sereno, 1999).
  35. Arrangement of lateral maxillary neurovascular foramina: linear (0) or irregular (1) (modified from Sereno, 1999).
  36. Longitudinal ridge on the posterior lateral surface of the maxilla: absent (0) or present (1) (Barrett, Upchurch & Wang, 2005).
  37. Dorsal exposure of the lachrymal: present (0) or absent (1) (Gauthier, 1986).
  38. Shape of the lachrymal: dorsoventrally short and block-shaped (0) or dorsoventrally elongate and shaped like an inverted L (1) (Rauhut, 2003).
  39. Orientation of the lachrymal orbital margin: strongly sloping anterodorsally (0) or erect and close to vertical (1) Yates (2007a).
  40. Length of the anterior ramus of the lachrymal: greater than (0), or less than (1), half the length of the ventral ramus, or absent altogether (2) (modified from Galton, 1990). Ordered.
  41. Web of bone spanning junction between anterior and ventral rami of lachrymal: absent and antorbital fossa laterally exposed (0) or present, obscuring posterodorsal corner of antorbital fossa (1) Yates (2007a).
  42. Extension of the antorbital fossa onto the ventral end of the lachrymal: present (0) or absent (1) (modified from Wilson & Sereno, 1998).
  43. Length of the caudal process of the prefrontal: short (0), or elongated (1), so that total prefrontal length is equal to the rostrocaudal diameter of the orbit (Galton, 1985).
  44. Ventral process of prefrontal extending down the posteromedial side of the lachrymal: present (0) or absent (1) (Wilson & Sereno, 1998).
  45. Maximum transverse width of the prefrontal: less than (0), or more than (1), 0.25 times the skull width at that level (modified from Galton, 1990).
  46. Shape of the orbit: subcircular (0) or ventrally constricted, making the orbit subtriangular (1) (Wilson & Sereno, 1998).
  47. Slender anterior process of the frontal intruding between the prefrontal and the nasal: absent (0) or present (1) (modified from Sereno, 1999).
  48. Jugal–lachrymal relationship: lachrymal overlapping lateral surface of jugal or abutting it dorsally (0), or jugal overlapping lachrymal laterally (1) (Sereno *et al.*, 1993).
  49. Shape of the suborbital region of the jugal: an anteroposteriorly elongate bar (0) or an anteroposteriorly shortened plate (1) Yates (2007a).
  50. Jugal contribution to the antorbital fenestra: absent (0) or present (1) (Holtz, 1994).
  51. Dorsal process of the anterior jugal: present (0) or absent (1) (modified from Rauhut, 2003).
  52. Ratio of the minimum depth of the jugal below the orbit to the distance between the rostral end of the jugal and the rostroventral corner of the infratemporal fenestra: less than (0), or greater than (1), 0.2 (modified from Galton, 1985).
  53. Transverse width of the ventral ramus of the postorbital: less than (0), or greater than (1), its rostrocaudal width at midshaft (Wilson & Sereno, 1998).
  54. Shape of the dorsal margin of postorbital in lateral view: straight to gently curved (0) or with a distinct embayment between the anterior and posterior dorsal processes (1) Yates (2007a).
  55. Height of the postorbital rim of the orbit: flush with the posterior lateral process of the postorbital (0) or raised so that it projects laterally to the posterior dorsal process (1) Yates (2007a).
  56. Postfrontal bone: present (0) or absent (1) (Sereno *et al.*, 1993).
  57. Position of the rostral margin of the infratemporal fenestra: behind the orbit (0), extends under the rear half of the orbit (1), or extends as far forward as the midlength of the orbit (2) (modified from Upchurch, 1995). Ordered.
  58. Frontal contribution to the supratemporal fenestra: present (0) or absent (1) (modified from Gauthier, 1986).
  59. Orientation of the long axis of the supratemporal fenestra: longitudinal (0) or transverse (1) (Wilson & Sereno, 1998).
  60. Medial margin of supratemporal fossa: simple smooth curve (0) or with a projection at the frontal/postorbital–parietal suture producing a scalloped margin (1) (Leal *et al.*, 2004).
  61. Length of the quadratojugal ramus of the squamosal relative to the width at its base: less than (0), or greater than (1), four times its width (Sereno, 1999).
  62. Proportion of infratemporal fenestra bordered by squamosal: more than (0), or less than (1), 0.5 times the depth of the infratemporal fenestra.

63. Squamosal–quadratojugal contact: present (0) or absent (1) (Gauthier, 1986).
64. Angle of divergence between jugal and squamosal rami of quadratojugal: close to 90° (0) or close to parallel (1) Yates (2007a).
65. Length of jugal ramus of quadratojugal: no longer than (0), or longer than (1), the squamosal ramus (Wilson & Sereno, 1998).
66. Shape of the rostral end of the jugal ramus of the quadratojugal: tapered (0) or dorsoventrally expanded (1) (Wilson & Sereno, 1998).
67. Relationship of quadratojugal to jugal: jugal overlaps the lateral surface of the quadratojugal (0), quadratojugal overlaps the lateral surface of the jugal (1), or quadratojugal sutures along the ventrolateral margin of the jugal (2). Unordered.
68. Position of the quadrate foramen: on the quadrate–quadratojugal suture (0), deeply incised into, and partly encircled by, the quadrate (1), or on the quadrate–squamosal suture, just below the quadrate head (2) (modified from Rauhut, 2003). Unordered.
69. Shape of posterolateral margin of quadrate: sloping anterolaterally from posteromedial ridge (0), everted posteriorly creating a posteriorly facing fossa (1), posterior fossa deeply excavated, invading quadrate body (2) (Wilson & Sereno, 1998). Ordered.
70. Exposure of the lateral surface of the quadrate head: absent, covered by lateral sheet of the squamosal (0) or present (1) (Sereno *et al.*, 1993).
71. Percentage of the length of the quadrate that is occupied by the pterygoid wing: at least 70% (0) or greater than 70% (1) (Yates, 2003a).
72. Depth of the occipital wing of the parietal: less than (0), or more than (1), 1.5 times the depth of the foramen magnum (Wilson & Sereno, 1998).
73. Position of foramina for midcerebral vein on occiput: between supraoccipital and parietal (0) or on the supraoccipital (1) (modified from Yates, 2003a).
74. Postparietal fenestra between supraoccipital and parietals: absent (0) or present (1) Yates (2007a).
75. Shape of the supraoccipital: diamond-shaped, at least as high as wide (0), or semilunate and wider than high (1) (Yates, 2003b).
76. Orientation of the supraoccipital plate: erect to gently sloping (0) or strongly sloping forward so that the dorsal tip lies level with the basiptyergoid processes (1) (Galton & Upchurch, 2004).
77. Orientation of the paroccipital processes in occipital view: slightly dorsolaterally directed to horizontal (0) or ventrolaterally directed (1) (Rauhut, 2003).
78. Orientation of the paroccipital processes in dorsal view: posterolateral forming a V-shaped occiput (0) or lateral forming a flat occiput (1) (Wilson, 2002).
79. Size of the post-temporal fenestra: large fenestra (0) or a small hole that is much less than half the depth of the paroccipital process (1) Yates (2007a).
80. Exit of the midcerebral vein: through trigeminal foramen (0) or through a separate foramen anterodorsal to trigeminal foramen (1) (Rauhut, 2003).
81. Shape of the floor of the braincase in lateral view: relatively straight with the basal tuberae, basiptyergoid processes, and parasphenoid rostrum roughly aligned (0), bent with the basiptyergoid processes and the parasphenoid rostrum below the level of the basioccipital condyle and the basal tuberae (1), or bent with the basal tuberae lowered below the level of the basioccipital and the parasphenoid rostrum raised above it (2) (modified from Galton, 1990). Unordered.
82. Shape of basal tuberae: knob-like, with basisphenoidal component rostral to basioccipital component (0), or forming a transverse ridge with the basisphenoidal component lateral to the basioccipital component (1) Yates (2007a).
83. Length of the basiptyergoid processes (from the top of the parasphenoid to the tip of the process): less than (0), or greater than (1), the height of the braincase (from the top of the parasphenoid to the top of the supraoccipital) (Benton *et al.*, 2000).
84. Ridge formed along the junction of the parabasisphenoid and the basioccipital, between the basal tuberae: present with a smooth rostral face (0), present with a median fossa on the rostral face (1), or absent with the basal tuberae being separated by a deep, caudally opening U-shaped fossa (2) Yates (2007a). Unordered.
85. Deep septum spanning the interbasiptyergoid space: absent (0) or present (1) (Galton, 1990).
86. Dorsoventral depth of the parasphenoid rostrum: much less than (0), or about equal to (1), the transverse width (Yates, 2003a).
87. Shape of jugal process of ectopterygoid: gently curved (0) or strongly recurved and hook-like (1) (Yates, 2003a).
88. Pneumatic fossa on the ventral surface of the ectopterygoid: present (0) or absent (1) (Sereno *et al.*, 1996).
89. Relationship of the ectopterygoid to the pterygoid: ectopterygoid overlapping the ventral (0), or dorsal (1), surface of the pterygoid (Sereno *et al.*, 1993).
90. Position of the maxillary articular surface of the palatine: along the lateral margin of the bone (0) or at the end of a narrow anterolateral process

- owing to the absence of the posterolateral process (1) (Wilson & Sereno, 1998).
91. Centrally located tubercle on the ventral surface of palatine: absent (0) or present (1) Yates (2007a).
  92. Medial process of the pterygoid forming a hook around the basiptyergoid process: absent (0), flat and blunt-ended (1), or bent upward and pointed (2) (modified from Wilson & Sereno, 1998). Ordered.
  93. Length of the vomers: less than (0), or more than (1), 0.25 times the total skull length Yates (2007a).
  94. Position of jaw joint: no lower than the level of the dorsal margin of the dentary (0) or depressed well below this level (1) (Sereno, 1999).
  95. Shape of upper jaws in ventral view: narrow with an acute rostral apex (0) or broad and U-shaped (1) (Wilson & Sereno, 1998).
  96. Length of the external mandibular fenestra: more than (0), or less than (1), 0.1 times the length of the mandible (modified from Upchurch, 1995).
  97. Caudal end of dentary tooth row medially inset with a thick lateral ridge on the dentary forming a buccal emargination: absent (0) or present (1) (Gauthier, 1986).
  98. Height : length ratio of the dentary: less than (0), or greater than (1), 0.2 (modified from Benton *et al.*, 2000).
  99. Orientation of the symphyseal end of the dentary: in line with the long axis of the dentary (0) or strongly curved ventrally (1) (Sereno, 1999).
  100. Position of first dentary tooth: adjacent to symphysis (0) or inset one tooth's width from the symphysis (1) (Sereno, 1999).
  101. Dorsoventral expansion at the symphyseal end of the dentary: absent (0) or present (1) (Wilson & Sereno, 1998).
  102. Splenial foramen: absent (0), present and enclosed (1), or present and open anteriorly (2) (Rauhut, 2003). Ordered.
  103. Splenial–angular joint: flattened sutured contact (0), synovial joint surface between tongue-like processes of angular, fitting in groove of the splenial (1) (Sereno *et al.*, 1993).
  104. A stout, triangular, medial process of the articular, behind the glenoid: present (0) or absent (1) (Yates, 2003a).
  105. Length of the retroarticular process: less than (0), or greater than (1), than the depth of the mandible below the glenoid (Yates, 2003a).
  106. Strong medial embayment behind glenoid of the articular in dorsal view: absent (0), or present (1) (Yates & Kitching, 2003).
  107. Number of premaxillary teeth: four (0) or more than four (1) (Galton, 1990).
  108. Number of dentary teeth (in adults): fewer than 18 (0) or 18 or more (1) (modified from Wilson & Sereno, 1998).
  109. Arrangement of teeth within the jaws: linearly placed, crowns not overlapping (0) or imbricated with distal side of tooth overlapping mesial side of the succeeding tooth (1) Yates (2007a).
  110. Orientation of the maxillary tooth crowns: erect (0) or procumbent (1) (modified from Gauthier, 1986).
  111. Orientation of the dentary tooth crowns: erect (0) or procumbent (1) (modified from Gauthier, 1986).
  112. Teeth with basally constricted crowns: absent (0) or present (1) (Gauthier, 1986).
  113. Tooth–tooth occlusal wear facets: absent (0) or present (1) (Wilson & Sereno, 1998).
  114. Mesial and distal serrations of the teeth: fine and set at right angles to the margin of the tooth (0) or coarse and angled upwards at an angle of 45° to the margin of the tooth (1) (Benton *et al.*, 2000).
  115. Distribution of serrations on the maxillary and dentary teeth: present on both the mesial and distal carinae (0), absent on the posterior carinae (1), or absent on both carinae (2) (Wilson, 2002). Unordered.
  116. Long axis of the tooth crowns distally recurved: present (0) or absent (1) (Gauthier, 1986).
  117. Texture of the enamel surface: entirely smooth (0), finely wrinkled in some patches (1), or extensively and coarsely wrinkled (2) (modified from Wilson & Sereno, 1998).
  118. Lingual concavities of the teeth: absent (0) or present (1) (Upchurch, 1995).
  119. Longitudinal labial grooves on the teeth: absent (0) or present (1) (Upchurch, 1998).
  120. Distribution of the serrations along the mesial and distal carinae of the tooth: extend along most of the length of the crown (0) or are restricted to the upper half of the crown (1) (Yates, 2003a).

## VERTEBRAE

121. Number of cervical vertebrae: eight or fewer (0), nine to ten (1), 12–13 (2), or more than 13 (3) (modified from Wilson & Sereno, 1998). Ordered.
122. Shallow, dorsally facing fossa on the atlantal neurapophysis bordered by a dorsally everted lateral margin: absent (0) or present (1) (Yates & Kitching, 2003).
123. Width of axial intercentrum: less than (0), or greater than (1), width of axial centrum (Sereno, 1999).
124. Position of axial prezygapophyses: on the anterolateral surface of the neural arch (0) or mounted on anteriorly projecting pedicels (1) Yates (2007a).
125. Posterior margins of the axial postzygapophyses: overhang the axial centrum (0) or are flush with

- the caudal face of the axial centrum (1) (Serenó, 1999).
126. Length of the axial centrum: less than (0), or at least (1), three times the height of the centrum Yates (2007a).
  127. Length of the anterior cervical centra (cervicals 3–5): no more than (0), or greater than (1), the length of the axial centrum Yates (2007a).
  128. Length of middle to posterior cervical centra (cervicals 6–8): no more than (0), or greater than (1), the length of the axial centrum Yates (2007a).
  129. Dorsal excavation of the cervical parapophyses: absent (0) or present (1) (Upchurch, 1998).
  130. Lateral compression of the anterior cervical vertebrae: centra are no higher than they are wide (0) or are approximately 1.25 times higher than wide (1) (Upchurch, 1998).
  131. Relative elongation of the anterior cervical centra (cervicals 3–5): lengths of the centra are less than 2.5 times the height of their anterior faces (0), lengths are 2.5–4 times the height of their anterior faces (1) or the length of at least cervicals 4 or 5 exceeds four times the anterior centrum height (2) (modified from Sereno, 1999). Ordered.
  132. Ventral keels on cranial cervical centra: present (0) or absent (1) (modified from Upchurch, 1998).
  133. Height of the midcervical neural arches: no more than (0), or greater than (1), height of the posterior centrum face Yates (2007a).
  134. Cervical epipophyses on the dorsal surface of the postzygapophyses: absent (0), or present on at least some cervical vertebrae (1).
  135. Caudal ends of cranial, postaxial epipophyses: with a free pointed tip (0) or joined to the postzygapophysis along their entire length (1) Yates (2007a).
  136. Shape of the epipophyses: tall ridges (0) or flattened, horizontal plates (1) (Yates, 2003a).
  137. Epipophyses overhanging the rear margin of the postzygapophyses: absent (0), or present in at least some postaxial cervical vertebrae (1) (Serenó *et al.*, 1993).
  138. Anterior spur-like projections on midcervical neural spines: absent (0) or present (1) Yates (2007a).
  139. Shape of midcervical neural spines: less than (0), or at least (1), twice as long as high Yates (2007a).
  140. Shape of cervical rib shafts: short and posteroventrally directed (0) or longer than the length of their centra and extending parallel to cervical column (1) (Serenó, 1999).
  141. Position of the base of the cervical rib shaft: level with, or higher than, the ventral margin of the cervical centrum (0) or located below the ventral margin because of a ventrally extended parapophysis (1) (Wilson & Sereno, 1998).
  142. Postzygodiapophyseal lamina in cervical neural arches 4–8: present (0) or absent (1) (Yates, 2003a).
  143. Laminae of the cervical neural arches 4–8: well-developed tall laminae (0) or weakly developed low ridges (1) (Wilson & Sereno, 1998).
  144. Shape of anterior centrum face in cervical centra: concave (0), flat (1), or convex (2) (modified from Gauthier, 1986). Ordered.
  145. Ventral surface of the centra in the cervicodorsal transition: transversely rounded (0) or with longitudinal keels (1) (Rauhut, 2003).
  146. Number of vertebrae between cervicodorsal transition and primordial sacral vertebrae: 15–16 (0) or no more than 14 (1) (modified from Wilson & Sereno, 1998).
  147. Lateral surfaces of the dorsal centra: with at most vague, shallow depressions (0), with deep fossae that approach the midline (1), or with invasive, sharp-rimmed pleurocoels (2) (Gauthier, 1986). Ordered.
  148. Oblique ridge dividing pleural fossa of cervical vertebrae: absent (0) or present (1) (Wilson & Sereno, 1998).
  149. Laterally expanded tables at the midlength of the dorsal surface of the neural spines: absent in all vertebrae (0), present on the pectoral vertebrae (1) or present on the pectoral and cervical vertebrae (2) (Yates & Kitching, 2003). Ordered.
  150. Dorsal centra: entirely amphicoelous to amphiplatyan (0), first two dorsals are opisthocelous (1), or cranial half of dorsal column is opisthocelous (2) (Wilson & Sereno, 1998). Ordered.
  151. Shape of the posterior dorsal centra: relatively elongated for their size (0) strongly axially compressed for their size (1) (modified from Novas, 1993).
  152. Laminae bounding triangular infradiapophyseal fossae (chonae) on dorsal neural arches: absent (0) or present (1) (Wilson, 1999).
  153. Location of parapophysis in first two dorsals: at the anterior end of the centrum (0), or located at the midlength of the centrum, within the middle chonos (1) Yates (2007a).
  154. Parapophyses of the dorsal column completely shift from the centrum to the neural arch: anterior (0), or posterior (1), to the thirteenth presacral vertebra (Langer, 2004).
  155. Orientation of the transverse processes of the dorsal vertebrae: most horizontally directed (0) or all upwardly directed (1) (Upchurch, 1998).
  156. Contribution of the paradiapophyseal lamina to the margin of the anterior chonos in mid-dorsal vertebrae: present (0) or prevented by high placement of parapophysis (1) Yates (2007a).

157. Hyposphenes in the dorsal vertebrae: absent (0), present but less than the height of the neural canal (1), or present and equal to the height of the neural canal (2) (modified from Gauthier, 1986). Ordered.
158. Prezygodiapophyseal lamina and associated anterior triangular fossa (chonos): present on all dorsals (0) or absent in mid-dorsals (1) (Yates, 2003a).
159. Anterior centroparapophyseal lamina in dorsal vertebrae: absent (0) or present (1) (Wilson, 2002).
160. Prezygoparapophyseal lamina in dorsal vertebrae: absent (0) or present (1) Yates (2007a).
161. Accessory lamina dividing posterior chonos from postzygapophysis: absent (0) or present (1) Yates (2007a).
162. Lateral pneumatic fenestra in middle chonos of middle and posterior dorsal vertebrae opening into neural cavity: absent (0) or present (1) (Wilson & Sereno, 1998).
163. Separation of lateral surfaces of anterior dorsal neural arches under transverse processes: widely spaced (0) or only separated by a thin midline septum (1) (Upchurch *et al.* 2004).
164. Height of dorsal neural arches, from neurocentral suture to level of zygapophyseal facets: much less than (0), or subequal to or greater than (1), height of centrum Yates (2007a).
165. Form of anterior surface of neural arch: simple centroprezygopophyseal ridge (0) or broad anteriorly facing surface bounded laterally by centroprezygopophyseal lamina (1) (Bonaparte, 1999).
166. Shape of posterior dorsal neural canal: subcircular (0) or slit-shaped (1) (Wilson & Sereno, 1998).
167. Height of middle dorsal neural spines: less than the length of the base (0), higher than the length of the base but less than 1.5 times the length of the base (1) or greater than 1.5 times the length of the base (2) (modified from Bonaparte, 1986). Ordered.
168. Shape of anterior dorsal neural spines: lateral margins parallel in anterior view (0) or transversely expanding towards dorsal end (1) Yates (2007a).
169. Cross-sectional shape of dorsal neural spines: transversely compressed (0), broad and triangular (1), or square-shaped in posterior vertebrae (2) (modified from Bonaparte, 1986).
170. Spinodiapophyseal lamina on dorsal vertebrae: absent (0), present and separated from spinopostzygapophyseal lamina (1) or present and joining spinopostzygapophyseal lamina to create a composite posterolateral spinal lamina (Wilson & Sereno, 1998).
171. Well-developed, sheet-like suprapostzygapophyseal laminae: absent (0), present on at least the caudal dorsal vertebrae (1) (Bonaparte, 1986).
172. Shape of the spinopostzygapophyseal lamina in middle and posterior dorsal vertebrae: singular (0) or bifurcated at its distal end (1) (Wilson, 2002).
173. Shape of posterior margin of middle dorsal neural spines in lateral view: approximately straight (0) or concave with a projecting posterodorsal corner (1) (Yates, 2003b).
174. Transversely expanded plate-like summits of posterior dorsal neural spines: absent (0) or present (1) (Novas, 1993).
175. Last presacral rib: free (0) or fused to vertebra (1) Yates (2007a).
176. Sacral rib much narrower than the transverse process of the first primordial sacral vertebra (and dorsosacral if present) in dorsal view: absent (0) or present (1) (Yates & Kitching, 2003).
177. Number of dorsosacral vertebrae: none (0), one (1), or two (2) (modified from Gauthier, 1986). Ordered.
178. Caudosacral vertebra: absent (0) or present (1) (Galton & Upchurch, 2004).
179. Shape of the iliac articular facets of the first primordial sacral rib: singular (0) or divided into dorsal and ventral facets separated by a non-articulating gap (1) Yates (2007a).
180. Depth of the iliac articular surface of the primordial sacrals: less than (0), or greater than (1), 0.75 times the depth of the ilium (modified from Novas, 1992).
181. Sacral ribs contributing to the rim of the acetabulum: absent (0) or present (1) (Wilson, 2002).
182. Posterior and anterior expansion of the transverse processes of the first and second primordial sacral vertebrae, respectively, partly roofing the intercostal space: absent (0) or present (1) (Langer, 2004).
183. Length of first caudal centrum: greater than (0), or less than (1), its height (Yates, 2003a).
184. Length of base of the proximal caudal neural spines: less than (0), or greater than (1), half the length of the neural arch (Gauthier, 1986).
185. Position of postzygapophyses in proximal caudal vertebrae: protruding with an interpostzygapophyseal notch visible in dorsal view (0) or placed on either side of the caudal end of the base of the neural spine without any interpostzygapophyseal notch (1) (Yates, 2003a).
186. A hyposphenal ridge on caudal vertebrae: absent (0) or present (1) (Upchurch, 1995).
187. Depth of the bases of the proximal caudal transverse processes: shallow, restricted to the neural arches (0), deep, extending from the centrum to the neural arch (1) (Upchurch, 1998).

188. Position of last caudal vertebra with a protruding transverse process: distal (0), or proximal (1), to caudal 16 (Wilson, 2002).
189. Orientation of posterior margin of proximal caudal neural spines: sloping posterodorsally (0) or vertical (1) (Novas, 1992).
190. Longitudinal ventral sulcus on proximal and middle caudal vertebrae: present (0) or absent (1) (modified from Upchurch, 1995).
191. Length of midcaudal centra: greater than (0), or less than (1), twice the height of their anterior faces (Yates, 2003a).
192. Cross-sectional shape of the distal caudal centra: oval with rounded lateral and ventral sides (0) or square-shaped with flattened lateral and ventral sides (1) Yates (2007a).
193. Length of distal caudal prezygapophyses: short, not overlapping the preceding centrum by more than a quarter (0) or long and overlapping the preceding centrum by more than a quarter (Gauthier, 1986).
194. Shape of the terminal caudal vertebrae: unfused, size decreasing toward tip (0) or expanded and fused to form a club-shaped tail (1) (Upchurch, 1995).
195. Length of the longest chevron: is less than (0), or greater than (1), twice the length of the preceding centrum (modified from Yates, 2003a).
196. Anteroventral process on distal chevrons: absent (0) or present (1) (Upchurch, 1995).
197. Midcaudal chevrons with a ventral slit: absent (0) or present (1) (Upchurch, 1995).
205. Length of the humerus: less than 55% (0), 55–65% (1), 65–70% (2), or more than 70% (3), of the length of the femur (modified from Gauthier, 1986). Ordered.
206. Shape of the deltopectoral crest: subtriangular (0) or subrectangular (1) (Gauthier, 1986).
207. Length of the deltopectoral crest of the humerus: less than 30% (0), 30–50% (1), or greater than 50% (2), of the length of the humerus (modified from Sereno *et al.*, 1993). Ordered.
208. Shape of the anterolateral margin of the deltopectoral crest of the humerus: straight (0) or strongly sinuous (1) (Yates, 2003a).
209. Rugose pit centrally located on the lateral surface of the deltopectoral crest: absent (0) or present (1) Yates (2007a).
210. Well-defined fossa on the distal flexor surface of the humerus: present (0) or absent (1) (Yates & Kitching, 2003).
211. Transverse width of the distal humerus: is less than (0), or greater than (1), 33% of the length of the humerus (Langer, 2004).
212. Shape of the entepicondyle of the distal humerus: rounded process (0) or with a flat, distomedially facing surface bounded by a sharp proximal margin (1) Yates (2007a).
213. Length of the radius: greater than (0), or less than (1), 80% of the length of the humerus (Langer, 2004).
214. Deep radial fossa, bounded by an anterolateral process, on proximal ulna: absent (0) or present (1) (Wilson & Sereno, 1998).
215. Olecranon process on proximal ulna: present (0) or absent (1) (Wilson & Sereno, 1998).
216. Maximum linear dimensions of the ulnare and radiale: exceed that of at least one of the first three distal carpals (0) or are less than any of the distal carpals (1) (Yates, 2003a).
217. Transverse width of the first distal carpal: less than (0), or greater than (1), 120% of the transverse width of the second distal carpal (Sereno, 1999).
218. Sulcus across the medial end of the first distal carpal: absent (0) or present (1) Yates (2007a).
219. Lateral end of first distal carpal: abuts (0), or overlaps (1), second distal carpal (Yates, 2003a).
220. Second distal carpal: does (0), or does not (1), completely cover the proximal end of the second metacarpal (Yates & Kitching, 2003).
221. Ossification of the fifth distal carpal: present (0) or absent (1) Yates (2007a).
222. Length of the manus: less than 38% (0), 38–45% (1), or greater than 45% (2), of the humerus + radius (modified from Sereno *et al.*, 1993). Ordered.
223. Shape of metacarpus: flattened to gently curved and spreading (0) or a colonnade of subparallel

## APPENDICULAR SKELETON

198. Longitudinal ridge on the dorsal surface of the sternal plate: absent (0) or present (1) (Upchurch, 1998).
199. Craniocaudal length of the acromion process of the scapula: less than (0), or greater than (1), 1.5 times the minimum width of the scapula blade (Wilson & Sereno, 1998).
200. Minimum width of the scapula: less than (0), or greater than (1), 20% of its length (Gauthier, 1986).
201. Caudal margin of the acromion process of the scapula: rises from the blade at angle that is less than (0), or greater than (1), 65° from the long axis of the scapula at its steepest point (modified from Novas, 1992).
202. Width of dorsal expansion of the scapula: less than (0), or equal to (1), the width of the ventral end of the scapula (Pol & Powell, 2007b).
203. Flat, caudoventrally facing surface on the coracoid between glenoid and coracoid tubercle: absent (0) or present (1) (Yates & Kitching, 2003).
204. Coracoid tubercle: present (0) or absent (1) (modified from Pérez-Moreno *et al.* 1994).

- metacarpals tightly curved into a U-shape (1) (Wilson & Sereno, 1998).
224. Proximal width of first metacarpal: less than (0), or greater than (1), the proximal width of the second metacarpal (modified from Gauthier, 1986).
225. Minimum transverse shaft width of first metacarpal: less than (0), or greater than (1), twice the minimum transverse shaft width of second metacarpal Yates (2007a).
226. Proximal end of first metacarpal: flush with other metacarpals (0) or inset into the carpus (1) (Sereno, 1999).
227. Shape of the first metacarpal: proximal width less than 65% (0), 65–80% (1), 80–100% (2), or greater than 100% (3), of its length (modified from Sereno, 1999). Ordered.
228. Strong asymmetry in the lateral and medial distal condyles of the first metacarpal: absent (0) or present (1) (Gauthier, 1986).
229. Deep distal extensor pits on the second and third metacarpals: absent (0) or present (1) (Novas, 1993).
230. Shape of the distal ends of second and third metacarpals: subrectangular in distal view (0) or trapezoidal with flexor rims of distal collateral ligament pits flaring beyond extensor rims (1) Yates (2007a).
231. Shape of the fifth metacarpal: longer than wide at the proximal end with a flat proximal surface (0) or close to as wide as it is long with a strongly convex proximal articulation surface (1) (Yates, 2003a).
232. Length of the fifth metacarpal: less than (0), or greater than (1), 75% of the length of the third metacarpal (Upchurch, 1998).
233. Length of manual digit one: less than (0), or greater than (1), the length of manual digit two (Yates, 2003a).
234. Ventrolateral twisting of the transverse axis of the distal end of the first phalanx of manual digit one relative to its proximal end: absent (0), present but much less than 60° (1), or 60° (2) (Sereno, 1999). Ordered.
235. Length of the first phalanx of manual digit one: less than (0), or greater than (1), the length of the first metacarpal (Gauthier, 1986).
236. Shape of the proximal articular surface of the first phalanx of manual digit one: rounded (0) or with an embayment on the medial side (1) (modified from Sereno, 1999).
237. Shape of the first phalanx of manual digit one: elongate and subcylindrical (0) or strongly proximodistally compressed and wedge-shaped (1) (Wilson, 2002).
238. Length of the penultimate phalanx of manual digit two: less than (0), or greater than (1), the length of the second metacarpal (Rauhut, 2003).
239. Length of the penultimate phalanx of manual digit three: less than (0), or greater than (1), the length of the third metacarpal (Rauhut, 2003).
240. Shape of nonterminal phalanges of manual digits two and three: longer than wide (0) or as long as wide (1) (Yates, 2003a).
241. Shape of the unguals of manual digits two and three: straight (0), or strongly curved with tips projecting well below flexor margin of proximal articular surface (1) (Sereno *et al.*, 1993).
242. Length of the ungual of manual digit two: greater than the length of the ungual of manual digit one (0), 75–100% of the ungual of manual digit one (1), less than 75% of the ungual of manual digit one (2), or the ungual of manual digit two is absent (3) (modified from Gauthier, 1986). Ordered.
243. Phalangeal formula of manual digits two and three: three and four, respectively (0), or with at least one phalanx missing from each digit (1) (modified from Wilson & Sereno, 1998).
244. Phalangeal formula of manual digits four and five: greater than (0), or less than (1), 2–0, respectively (Gauthier, 1986).
245. Strongly convex dorsal margin of the ilium: absent (0) or present (1) (Gauthier, 1986).
246. Cranial extent of preacetabular process of ilium: does not (0), or does (1), project further forward than cranial end of the pubic peduncle (Yates, 2003a).
247. Shape of the preacetabular process: blunt and rectangular (0) or with a pointed, projecting cranioventral corner and a rounded dorsum (1) (modified from Sereno, 1999).
248. Depth of the preacetabular process of the ilium: much less than (0), or subequal to (1), the depth of the ilium above the acetabulum (modified from Gauthier, 1986).
249. Length of preacetabular process of the ilium: less than (0), or greater than (1), twice its depth.
250. Buttress between preacetabular process and the supra-acetabular crest of the ilium: present (0) or absent (1) (Gauthier, 1986).
251. Medial wall of acetabulum: fully closing acetabulum with a triangular ventral process between the pubic and ischial peduncles (0), partially open acetabulum with a straight ventral margin between the peduncles (1), partially open acetabulum with a concave ventral margin between the peduncles (2), or fully open acetabulum with medial ventral margin closely approximating lateral rim of acetabulum (3) (modified from Gauthier, 1986). Ordered.
252. Length of the pubic peduncle of the ilium: less than (0), or greater than (1), twice the craniocaudal width of its distal end (Sereno, 1999).

253. Caudally projecting 'heel' at the distal end of the ischial peduncle: absent (0) or present (1) (Yates, 2003b).
254. Length of the ischial peduncle of the ilium: similar to pubic peduncle (0), much shorter than pubic peduncle (1), or virtually absent so that the chord connecting the distal end of the pubic peduncle with the ischial articular surface contacts the postacetabular process (2) (Upchurch *et al.* 2004). Ordered.
255. Length of the postacetabular process of the ilium: between 40 and 100% of the distance between the pubic and ischial peduncles (0), less than 40% of this distance (1), or more than 100% of this distance (2) Yates (2007a). Unordered.
256. Well-developed brevis fossa with sharp margins on the ventral surface of the postacetabular process of the ilium: absent (0) or present (1) (Gauthier, 1986).
257. Anterior end of ventrolateral ridge bounding brevis fossa: not connected to (0), or joining (1), supra-acetabular crest (1) Yates (2007a).
258. Shape of the caudal margin of the postacetabular process of the ilium: rounded to bluntly pointed (0), square-ended (1), or with a pointed ventral corner and a rounded caudodorsal margin (2) (Yates, 2003b). Unordered.
259. Width of the conjoined pubes: less than (0), or greater than (1), 75% of their length (Cooper, 1984).
260. Pubic tubercle on the lateral surface of the proximal pubis: present (0) or absent (1) (Yates, 2003a).
261. Proximal anterior profile of pubis: anterior margin of pubic apron smoothly confluent with anterior margin of iliac pedicel (0) or iliac pedicel set anterior to the pubic apron, creating a prominent inflection in the proximal anterior profile of the pubis (1) Yates (2007a).
262. Minimum transverse width of the pubic apron: much more than (0), or less than (1), 40% of the width across the iliac peduncles of the ilium.
263. Position of the obturator foramen of the pubis: at least partially occluded by the iliac pedicel (0), or completely visible (1), in anterior view (Galton & Upchurch, 2004).
264. Lateral margins of the pubic apron in anterior view: straight (0) or concave (1) (Yates & Kitching, 2003).
265. Orientation of distal third of the blades of the pubic apron: confluent with the proximal part of the pubic apron (0) or twisted posterolaterally relative to proximal section so that the anterior surface turns to face laterally (1) (Langer, 2004).
266. Orientation of the entire blades of the pubic apron: transverse (0) or twisted posteromedially (1) (Wilson & Sereno, 1998).
267. Craniocaudal expansion of the distal pubis: absent (0), less than (1), or greater than (2), 15% of the length of the pubis (modified from Gauthier, 1986). Ordered.
268. Notch separating posteroventral end of the ischial obturator plate from the ischial shaft: present (0) or absent (1) (Rauhut, 2003).
269. Elongate interischial fenestra: absent (0) or present (1) (Yates, 2003b).
270. Longitudinal dorsolateral sulcus on proximal ischium: absent (0) or present (1) (Yates, 2003a).
271. Shape of distal ischium: broad and plate-like, not distinct from obturator region (0) or with a discrete, rod-like distal shaft (1) Yates (2007a).
272. Length of ischium: less than (0), or greater than (1), that of the pubis (Salgado, Coria & Calvo, 1997).
273. Ischial component of acetabular rim: larger than (0), or equal to (1), the pubic component (Galton & Upchurch, 2004).
274. Shape of the transverse section of the ischial shaft: ovoid to subrectangular (0) or triangular (1) (Sereno, 1999).
275. Orientation of the long axes of the transverse section of the distal ischia: meet at an angle (0) or are coplanar (1) (Wilson & Sereno, 1998).
276. Depth of the transverse section of the ischial shaft: much less than (0), or at least as great as (1), the transverse width of the section (Wilson & Sereno, 1998).
277. Distal ischial expansion: absent (0) or present (1) (Holtz, 1994).
278. Transverse width of the conjoined distal ischial expansions: greater than (0), or less than (1), their sagittal depth (Yates, 2003a).
279. Length of the hindlimb: greater than (0), or less than (1), the length of the trunk (Gauthier, 1986).
280. Longitudinal axis of the femur in lateral view: strongly bent with an offset between the proximal and distal axes greater than 15° (0), weakly bent with an offset of less than 10° (1), or straight (2) (Cooper, 1984). Ordered.
281. Shape of the cross-section of the midshaft of the femur: subcircular (0) or strongly elliptical with the long axis orientated mediolaterally (1) (Wilson & Sereno, 1998).
282. Angle between the long axis of the femoral head and the transverse axis of the distal femur: about 30° (0) or close to 0° (1) (Carrano, 2000).
283. Shape of femoral head: roughly rectangular in profile with a sharp medial distal corner (0) or roughly hemispherical with no sharp medial distal corner (1) Yates (2007a).
284. Posterior proximal tubercle on femur: well developed (0) or indistinct to absent (1) (Novas, 1996).

285. Shape of the lesser trochanter: small rounded tubercle (0), proximodistally orientated, elongate ridge (1), or absent (2) (modified from Gauthier, 1986). Unordered.
286. Position of proximal tip of lesser trochanter: level with (0), or distal to (1), the femoral head (Galton & Upchurch, 2004).
287. Projection of the lesser trochanter: just a scar upon the femoral surface (0) or a raised process (1).
288. Transverse ridge extending laterally from the lesser trochanter: absent (0) or present (1) (Rowe, 1989).
289. Height of the lesser trochanter in cross section: less than (0), or at least as high as (1), basal width (modified from Galton, 1990).
290. Position of the lesser trochanter: near the centre of the anterior face (0), or close to the lateral margin (1), of the femoral shaft in anterior view.
291. Visibility of the lesser trochanter in posterior view: not visible (0) or visible (1) (Galton & Upchurch, 2004).
292. Height of the fourth trochanter: tall crest (0) or a low rugose ridge (1) (Gauthier, 1986).
293. Position of the fourth trochanter along the length of the femur: in the proximal half (0) or straddling the midpoint (1) (Galton, 1990).
294. Symmetry of the profile of the fourth trochanter of the femur: subsymmetrical without a sharp distal corner (0) or asymmetrical with a steeper distal slope than the proximal slope and a distinct distal corner (1) (Langer, 2004).
295. Shape of the profile of the fourth trochanter of the femur: rounded (0) or subrectangular (1).
296. Position of fourth trochanter along the mediolateral axis of the femur: centrally located (0) or on the medial margin (1) (Galton, 1990).
297. Extensor depression on anterior surface of the distal end of the femur: absent (0) or present (1) (Molnar, Kurzanov & Dong, 1990).
298. Size of the medial condyle of the distal femur: subequal to (0), or larger than (1), the fibular + lateral condyles (modified from Wilson, 2002).
299. Tibia : femur length ratio: greater than 1.0 (0), between 0.6 and 1.0 (1) or less than 0.6 (2) (modified from Gauthier, 1986). Ordered.
300. Orientation of cnemial crest: projects anteriorly to anterolaterally (0) or projecting laterally (1) (Wilson & Sereno, 1998).
301. Paramarginal ridge on lateral surface of cnemial crest: absent (0) or present (1) Yates (2007a).
302. Position of the tallest point of the cnemial crest: close to the proximal end of the crest (0) or about half-way along the length of the crest, creating an anterodorsally sloping proximal margin of the crest (1) Yates (2007a).
303. Proximal end of tibia with a flange of bone that contacts the fibula: absent (0) or present (1) (Gauthier, 1986).
304. Position of the posterior end of the fibular condyle on the proximal articular surface tibia: anterior to (0) or level with (1), the posterior margin of the proximal articular surface Yates (2007a).
305. Shape of the proximal articular surface of the tibia: ovoid, anteroposteriorly longer than transversely wide (0) or subcircular and as wide transversely as anteroposteriorly long (1) (Wilson & Sereno, 1998).
306. Transverse width of the distal tibia: subequal to (0), or greater than (1), its craniocaudal length (Gauthier, 1986).
307. Anteroposterior width of the lateral side of the distal articular surface of the tibia: as wide (0), or narrower than (1), the anteroposterior width of the medial side Yates (2007a).
308. Relationship of the posterolateral process of the distal end of the tibia with the fibula: not flaring laterally and not making significant contact with the fibula (0) or flaring laterally and backing the fibula (1) Yates (2007a).
309. Shape of the distal articular end of the tibia in distal view: ovoid (0) or subrectangular (1) Yates (2007a).
310. Shape of the anteromedial corner of the distal articular surface of the tibia: forming a right angle (0) or forming an acute angle (1) (Langer, 2004).
311. Position of the lateral margin of descending caudoventral process of the distal end of the tibia: protrudes laterally at least as far as (0), or set well back from (1), the cranio-lateral corner of the distal tibia (Wilson & Sereno, 1998).
312. A triangular rugose area on the medial side of the fibula: absent (0) or present (1) (Wilson & Sereno, 1998).
313. Transverse width of the midshaft of the fibula: greater than 0.75 (0), between 0.5 and 0.75 (1), or less than 0.5 (2), times the transverse width of the midshaft of the tibia (Langer, 2004). Ordered.
314. Position of fibula trochanter: on anterior surface of fibula (0), laterally facing (1), or anteriorly facing but with strong lateral bulge (2) (modified from Wilson & Sereno, 1998).
315. Depth of the medial end of the astragalar body in cranial view: roughly equal to the lateral end (0) or much shallower, creating a wedge-shaped astragalar body (1) (Wilson & Sereno, 1998).
316. Shape of the posteromedial margin of the astragalus in dorsal view: forming a moderately sharp corner of a subrectangular astragalus (0)

- or evenly rounded without formation of a caudomedial corner (1) (Wilson & Sereno, 1998).
317. Dorsally facing horizontal shelf forming part of the fibular facet of the astragalus: present (0) or absent with a largely vertical fibular facet (1) (Sereno, 1999).
318. Pyramidal dorsal process on the posteromedial corner of the astragalus: absent (0) or present (1).
319. Shape of the ascending process of the astragalus: anteroposteriorly deeper than transversely wide (0) or transversely wider than anteroposteriorly deep (1) Yates (2007a).
320. Posterior extent of ascending process of the astragalus: well anterior to (0), or close to the posterior margin of (1), the astragalus (Wilson & Sereno, 1998).
321. Sharp medial margin around the depression posterior to the ascending process of the astragalus: absent (0) or present (1) (Novas, 1996).
322. Buttress dividing posterior fossa of astragalus and supporting ascending process: absent (0) or present (1) (Wilson & Sereno, 1998).
323. Vascular foramina set in a fossa at the base of the ascending process of the astragalus: present (0) or absent (1) (Wilson & Sereno, 1998).
324. Transverse width of the calcaneum: greater than (0), or less than (1), 30% of the transverse width of the astragalus (Yates & Kitching, 2003).
325. Lateral surface of calcaneum: simple (0) or with a fossa (1) Yates (2007a).
326. Medial peg of calcaneum fitting into astragalus: present, even if rudimentary (0) or absent (1) (Sereno *et al.*, 1993).
327. Calcaneal tuber: large and well developed (0) or highly reduced to absent (1) Yates (2007a).
328. Shape of posteromedial heel of distal tarsal four (lateral distal tarsal): proximodistally deepest part of the bone (0) or no deeper than the rest of the bone (1) (Sereno *et al.*, 1993).
329. Shape of posteromedial process of distal tarsal four in proximal view: rounded (0) or pointed (1) (Langer, 2004).
330. Ossified distal tarsals: present (0) or absent (1) (Gauthier, 1986).
331. Proximal width of the first metatarsal: less than (0), or at least as great as (1), the proximal width of the second metatarsal (modified from Wilson & Sereno, 1998).
332. Orientation of proximal articular surface of metatarsal one: horizontal (0) or sloping proximolaterally relative to the long axis of the bone (1) (Wilson, 2002).
333. Orientation of the transverse axis of the distal end of metatarsal one: horizontal (0) or angled proximomedially (1) (Wilson, 2002).
334. Shape of the medial margin of the proximal surface of the second metatarsal: straight (0) or concave (1) (modified from Sereno, 1999).
335. Shape of the lateral margin of the proximal surface of the second metatarsal: straight (0) or concave (1) (modified from Sereno, 1999).
336. Length of the third metatarsal: greater than (0), or less than (1), 40% of the length of the tibia (Gauthier, 1986).
337. Minimum transverse shaft diameters of third and fourth metatarsals: greater than (0), or less than (1), 60% of the minimum transverse shaft diameter of the second metatarsal (Wilson & Sereno, 1998).
338. Transverse width of the proximal end of the fourth metatarsal: less than (0), or at least (1), twice the anteroposterior depth of the proximal end (modified from Sereno, 1999).
339. Transverse width of the proximal end of the fifth metatarsal: less than 25% (0), between 30 and 49% (1), or greater than 50% (2), of the length of the fifth metatarsal (modified from Sereno, 1999). Ordered.
340. Transverse width of distal articular surface of metatarsal four in distal view: greater (0), or less than (1), anteroposterior depth (Sereno, 1999).
341. Pedal digit five: reduced, nonweight bearing (0) or large (fifth metatarsal at least 70% of fourth metatarsal), robust and weight bearing (1) (Wilson & Sereno, 1998).
342. Length of nonterminal pedal phalanges: all longer than wide (0), proximal-most phalanges longer than wide whereas more distal phalanges are as wide as long (1), or all nonterminal phalanges are as wide, if not wider, than long (2) modified from Wilson & Sereno, 1998). Ordered.
343. Length of the first phalanx of pedal digit one: greater than (0), or less than (1), the length of the ungual of pedal digit one (Yates & Kitching, 2003).
344. Length of the ungual of pedal digit one: less than at least some nonterminal phalanges (0) or longer than all nonterminal phalanges (1) Yates (2007a).
345. Shape of the ungual of pedal digit one: shallow, pointed, with convex sides and a broad ventral surface (0) or deep, abruptly tapering, with flattened sides and a narrow ventral surface (1) (Wilson & Sereno, 1998).
346. Shape of proximal articular surface of pedal unguals: proximally facing, visible on medial and lateral sides (0) or proximomedially facing and visible only in medial view, causing medial deflection of pedal unguals in articulation (1) (Wilson & Sereno, 1998).
347. Penultimate phalanges of pedal digits two and three: well developed (0) or reduced disc-shaped

- elements if they are ossified at all (1) (Wilson & Sereno, 1998).
348. Shape of the unguals of pedal digits two and three: dorsoventrally deep with a proximal articulating surface that is at least as deep as it is wide (0) or dorsoventrally flattened with a proximal articulating surface that is wider than deep (1) (Wilson & Sereno, 1998).
349. Length of the ungual of pedal digit two: greater than (0), between 90 and 100% of (1), or less than 90% of (2), the length of the ungual of pedal digit one (modified from Gauthier, 1986). Ordered.
350. Size of the ungual of pedal digit three: greater than (0), or less than (1), 85% of the ungual of pedal digit two in all linear dimensions (Yates, 2003a).
351. Number of phalanges in pedal digit four: four (0) or fewer than four (1) (Gauthier, 1986).
352. Phalanges of pedal digit five: present (0) or absent (1) (Gauthier, 1986).
353. Femoral length: less than 200 mm (0), between 200 and 399 mm (1), between 400 and 599 mm (2), between 600 and 799 mm (3), between 800 and 1000 mm (4), or greater than 1000 mm (modified from Yates, 2004). Ordered.
354. Lateral extent of ventrolateral flange on plantar surface of metatarsal II in proximal aspect: similar in development to ventromedial flange (0) or well developed, extending further laterally than ventromedial flange extends medially (1) (Smith & Pol, 2007).
355. Distal articular surface of astragalus: relatively flat or weakly convex (0) or extremely convex and 'roller-shaped' (1) (Smith & Pol, 2007).
356. Distal surface of tibiofibular crest: as deep anteroposteriorly as wide mediolaterally or deeper (0) or wider mediolaterally than deep anteroposteriorly (1) (Smith & Pol, 2007).
357. Well-developed facet on proximolateral corner of plantar ventrolateral flange of metatarsal II for articulation with medial distal tarsal: absent (0) or present (1) (Smith & Pol, 2007).
358. Proximal outline of metatarsal III: subtriangular with acute or rounded posterior border (0) or subtrapezoidal, with posterior border broadly exposed in plantar view (1) Yates (2007a).
359. Angle formed by the anterior and anteromedial borders of metatarsal IV: obtuse (0), right angle or acute (1) (Smith & Pol, 2007).
360. Well-developed tibiofibular crest on distal femur: absent (0) or present (1) (Smith & Pol, 2007).
361. Shaft of metatarsal I: closely appressed to metatarsal II throughout its length (0) or only closely appressed proximally, with a space between metatarsals I and II distally (1) (Smith & Pol, 2007).
362. Posterior margin of astragalus: straight (0) or convex (1) (Otero & Pol, 2013).
363. Ventromedial ridge of scapula: absent (0) or present (1) (Otero & Pol, 2013).
364. Mediolateral surface of distal astragalus straight (0), concave (1), or convex (0). (Otero & Pol, 2013). Unordered.
365. Anterior fossa on the proximal region of the pubic apron: absent (0) or present (1). (Apaldetti *et al.*, 2012).
366. Proximal end of the tibia with a transverse/ anteroposterior length ratio: narrow (ratio less than 0.7) (0) or broad (more than 0.7) (1) (Apaldetti *et al.*, 2012).
367. Caudodistal tubercle of the radius: absent (0) or present (1). (This contribution).
368. Biceps tubercle of the radius: absent (0) or present (1). (This contribution).
369. Ventromedial margin of first metacarpal: poorly concave (0) or deeply concave (1). (This contribution).
370. Length of first phalanx of manual digit 1: much greater than (0), subequal or equal to (1), or much less than (2), its mediolateral width at proximal end. (This contribution).

CHARACTERS SCORINGS CHANGED FROM  
APALDETTI *ET AL.* (2011)

*Silesaurus*, *Staurikosaurus*, *Marasuchus*, *Herrerasaurus*, *Neotheropoda*, *Ornithischia*, *Aturnalia*, *Chromogisaurus*, *Guaibasaurus*, *Thecodontosaurus*, *Pantydraco*, *Efraasia*, *Plateosaurus engelhardti*, '*Plateosaurus*' *gracilis*, *Adeopapposaurus*, *Coloradisaurus*, *Massospondylus*, *Eucnemoraurus*, *Jingshanosaurus*, *Lessemsaurus*, *Lufengosaurus*, *Plateosauravus*, *Riojasaurus*, *Ruehleia*, *Sarhsaurus*, *Anchisaurus*, *Aardonyx*, *Yunnanosaurus*, *Melanorosaurus*, *Antetonitrus*:

292: 1 → 0

*Vulcanodon*, *Cetiosaurus*, *Patagosaurus*, *Mamenchisaurus*, *Omeisaurus*, *Shunosaurus*, *Neosauropoda*:

292: 0 → 1

CHARACTERS SCORINGS CHANGED FROM OTERO &  
POL (2013)

*Silesaurus*: 362:? → 1, 364:? → 0

*Massospondylus*: 364:? → 1

*Glacialisaurus*: 362:? → 1, 364:? → 0

*Sarhsaurus*: 183: 1 →?, 322: 1 → 0, 363:? → 1

*Mussaurus*: 214: 1 → 0

*Melanorosaurus*: 207: 2 → 1

*Blikanasaurus*: 364:? → 0

*Barapasaurus*: 362:? → 0, 363:? → 0, 364:? → 0

*Cetiosaurus*: 363:? → 1

*Omeisaurus*: 363:? → 0

## SYNAPOMORPHIES OF HIGHER TAXA

Ambiguous character support is indicated by an asterisk.

## SAUROPODOMORPHA

1. Skull : femur length ratio less than 0.6 (1).
2. Height : length ratio of the dentary greater than 0.2 (98).
3. Long axis of the tooth crowns not distally recurved (116).
4. Postzygodiapophyseal lamina in cervical neural arches 4–8 absent (142).
5. Laminae of the cervical neural arches 4–8 are weakly developed low ridges (143).
6. Prezygodiapophyseal lamina and associated anterior triangular fossa (chonos) absent in mid-dorsals (158).
7. Length of the humerus is less than 55–65% of the length of the femur (205).
8. Transverse width of the distal humerus is greater than 33% of the length of the humerus (211).
9. Length of the pubic peduncle of the ilium is greater than twice the craniocaudal width of its distal end (252).
10. Position of the posterior end of the fibular condyle on the proximal articular surface tibia is anterior to the posterior margin of proximal articular surface (304).

## PLATEOSAURIA

1. Length of the humerus is less than 55–65% of the length of the femur (205).
2. Shape of the caudal margin of the postacetabular process of the ilium with a pointed ventral corner and a rounded caudodorsal margin (258).

## MASSOPODA

1. Rostrocaudal length of the antorbital fossa less than that of the orbit (29)\*.
2. Web of bone spanning junction between anterior and ventral rami of lachrymal absent and antorbital fossa laterally exposed (41)\*.
3. Position of the rostral margin of the infratemporal fenestra extending under the rear half of the orbit (57)\*.
4. Minimum transverse shaft width of first metacarpal greater than twice the minimum transverse shaft width of second metacarpal (225).
5. Shape of the fifth metacarpal close to as wide as it is long with a strongly convex proximal articulation surface (231)\*.
6. Length of the ungual of manual digit two is less than 75% of the ungual of manual digit one (242)\*.

7. Length of the hindlimb is greater than the length of the trunk (279)\*.
8. Fourth trochanter of the femur positioned on the medial margin (296).
9. Length of first phalanx of manual digit one is subequal or equal to its mediolateral width at proximal end (370)\*.

## ANCHISAURIA

1. Lateral margin of descending caudoventral process of the distal end of the tibia set well back from the craniolateral corner of the distal tibia (311).

## SAUROPODIFORMES

1. Shape of posterior margin of middle dorsal neural spines in lateral view concave with a projecting posterodorsal corner (173).
2. Length of manual digit one greater than the length of manual digit two (233).
3. Longitudinal axis of the femur in lateral view weakly bent with an offset of less than 10° (280).
4. Length of the ungual of pedal digit one longer than all nonterminal phalanges (344).
5. Femoral length between 600 and 799 mm (353).
6. Caudodistal tubercle of the radius present (367).

## PLATEOSAURIDAE

1. Medial margin of supratemporal fossa with a projection at the frontal/postorbital–parietal suture producing a scalloped margin (60).
2. Shape of the floor of the braincase in lateral view bent with the basiptyergoid processes and the parasphenoid rostrum below the level of the basioccipital condyle and the basal tuberae (81).
3. Orientation of the symphyseal end of the dentary strongly curved ventrally (99).
4. Longitudinal ventral sulcus on proximal and middle caudal vertebrae present (190)\*.
5. Ventrolateral twisting of the transverse axis of the distal end of the first phalanx of manual digit one relative to its proximal end is 60° (234).
6. Straight lateral margin of the proximal surface of the second metatarsal (335).

## MASSOSPONDYLIDAE

1. Dorsal profile of the snout with a depression behind the naris (20).
2. Web of bone spanning junction between anterior and ventral rami of lachrymal present, obscuring posterodorsal corner of antorbital fossa (41).

3. Position of foramina for midcerebral vein on occiput on the supraoccipital (73).
4. Symphyseal end of the dentary strongly curved ventrally (99).
5. Length of at least cervical 4 or 5 exceeds four times the anterior centrum height (131).
6. Laterally expanded tables at the midlength of the dorsal surface of the neural spines present on the pectoral and cervical vertebrae (149).
7. Asymmetrical profile of the fourth trochanter of the femur with a steeper distal slope than the proximal slope and a distinct distal corner (294).

#### SUPPORTING INFORMATION

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

**File S1.** Phylogenetic information

**Table S1.** Selected measurements of the holotype of *Sefapanosaurus zastronensis* gen. et sp. nov. (BP/1/386).

**Table S2.** Selected measurements of referred elements of *Sefapanosaurus zastronensis* gen. et sp. nov.