UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

South Africa's earliest giant: The systematics and palaeobiology of a new species of sauropodomorph

by

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A **Dissertation** submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of **Master of Science** in **Palaeontology**

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Johannesburg March 2023

GENUS DSI-NRF CoE Palaeo

NRF National Research Foundation

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DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

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Signed on the 1st day of March 2023 at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg.

ACKNOWLEDGEMENTS

I get to start my career in this field, a childhood dream and passion for me. My sincerest gratitude goes to Prof. Jonah Choiniere, an encouraging and motivating supervisor and mentor. You have provided guidance and opportunities that I never would have had, and for that I am deeply appreciative of. You have provided me with long-lasting critical skills and an amazing group of colleagues. I look forward to many more years of research alongside you.

To my co-supervisor, Dr. Jennifer Botha. Thank you for your guidance during this interesting time and for teaching me new things. I look forward to many more years together.

To Dr. Kimberley Chapelle, thank you for being a great friend and colleague. I always came to you for advice ever since you were my TA and will continue to do so in the future. To Prof. Roger Benson for assistance with data, analysis, and the many discussions. To Prof. Paul Barrett for all the discussions and advice this year that has assisted me.

To my dear lab mates Chandelé Montgomery, Frederick Tolchard, SoRi La, and Bailey Weiss, thank you for all your support, advice, and a fun-filled time in the lab over the years. Thank you to the rest of the Stormberg Giant members and honorary members, I am privileged to have met all of you and will continue these friendships.

Thank you to the preparators and technicians for their hard work. Thank you to the Evolutionary Studies Institute, Iziko South African Museum, National Museum Bloemfontein, and all the curators for access to the collections.

And finally, to my main pillar of support, love, and motivation throughout all my research, contigo.

This research would not have been possible without the funding from GENUS: DSI-NRF Centre of Excellence in Palaeosciences and the National Research Foundation.

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INTRODUCTION

Elliot Formation

The Stormberg Group is a series of sedimentary rocks representing the early Mesozoic in southern Africa and forming the upper deposits of the Main Karoo Basin. The Elliot Formation (EF) forms the central part of the Stormberg Group, as it overlies the Molteno Formation and underlies the Clarens Formation (Bordy and Eriksson, 2015, Kitching and Raath, 1984). The EF is informally subdivided into the lower and upper EF (lEF and uEF, respectively) based on lithostratigraphic distinctions (Fig. 1; Bordy *et al.*, 2020, Bordy and Eriksson, 2015) that correspond with biostratigraphic changes (Viglietti *et al.*, 2020a, Viglietti *et al.*, 2020b, Kitching and Raath, 1984). Importantly, the EF preserves a diverse faunal assemblage of vertebrates (Kitching and Raath, 1984), representing a temporal range from Late Triassic (Norian) to Early Jurassic (Hettangian-Sinemurian) and encompassing the end-Triassic extinction (Olsen and Galton, 1984, Bordy *et al.*, 2020). The most common members of EF fauna are archosauromorph fossils, particularly those representing members of the dinosaurian clade, Sauropodomorpha (McPhee *et al.*, 2017, Bordy *et al.*, 2020).

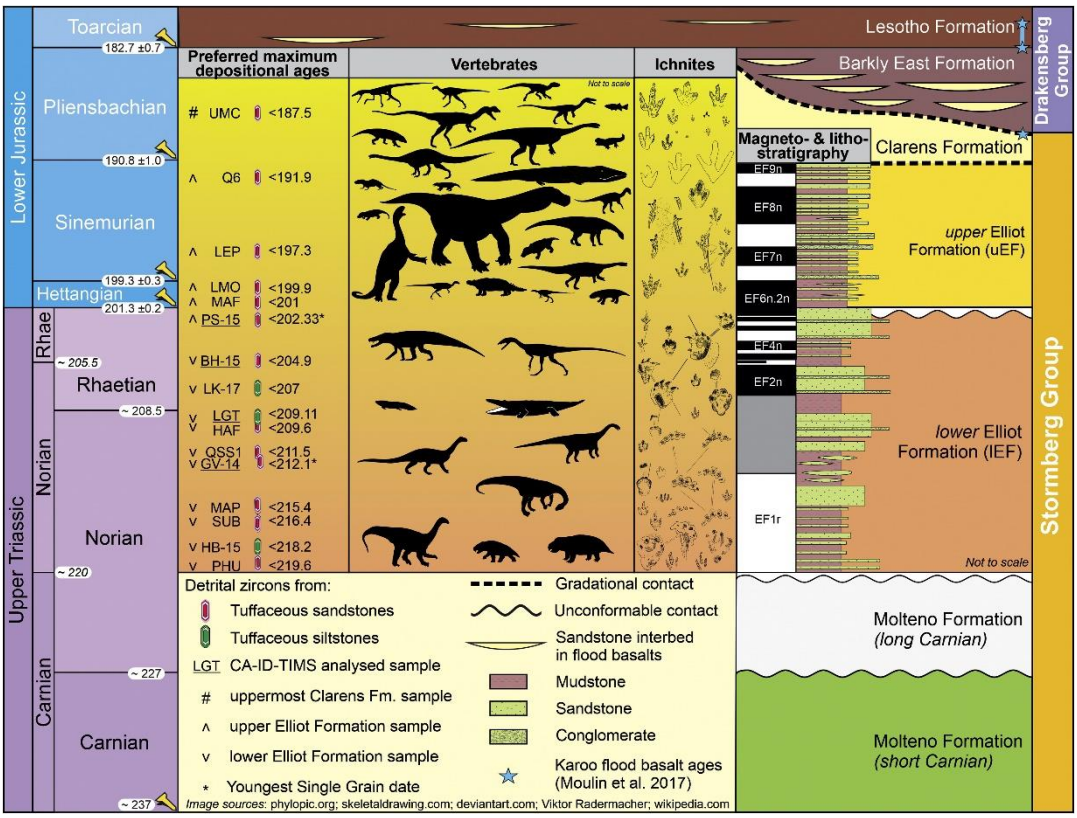

Figure 1: Stratigraphic column illustrating the biostratigraphic changes correlating with the lithostratigraphic distinctions across the Elliot Formation. Modified from Bordy et al. (2020).

Sauropodomorpha

Sauropodomorpha are herbivorous saurischian dinosaurs that are well known for their large body size and range of locomotory styles (e.g., Galton and Upchurch, 2004, McPhee *et al.*, 2018, Benson *et al.*, 2014). Sauropodomorphs were a diverse group of dinosaurs throughout the Mesozoic (Benson, 2018), and they survived the end-Triassic mass extinction but went extinct at the Cretaceous-Palaeogene boundary. Recently, research on non-sauropodan sauropodomorphs has been active (Fig. 2; e.g., McPhee *et al.*, 2015a, McPhee *et al.*, 2017, Apaldetti *et al.*, 2018, Pol *et al.*, 2021b), but insights into their early evolution and macroevolutionary patterns are still hampered by low sample sizes and incomplete specimens.

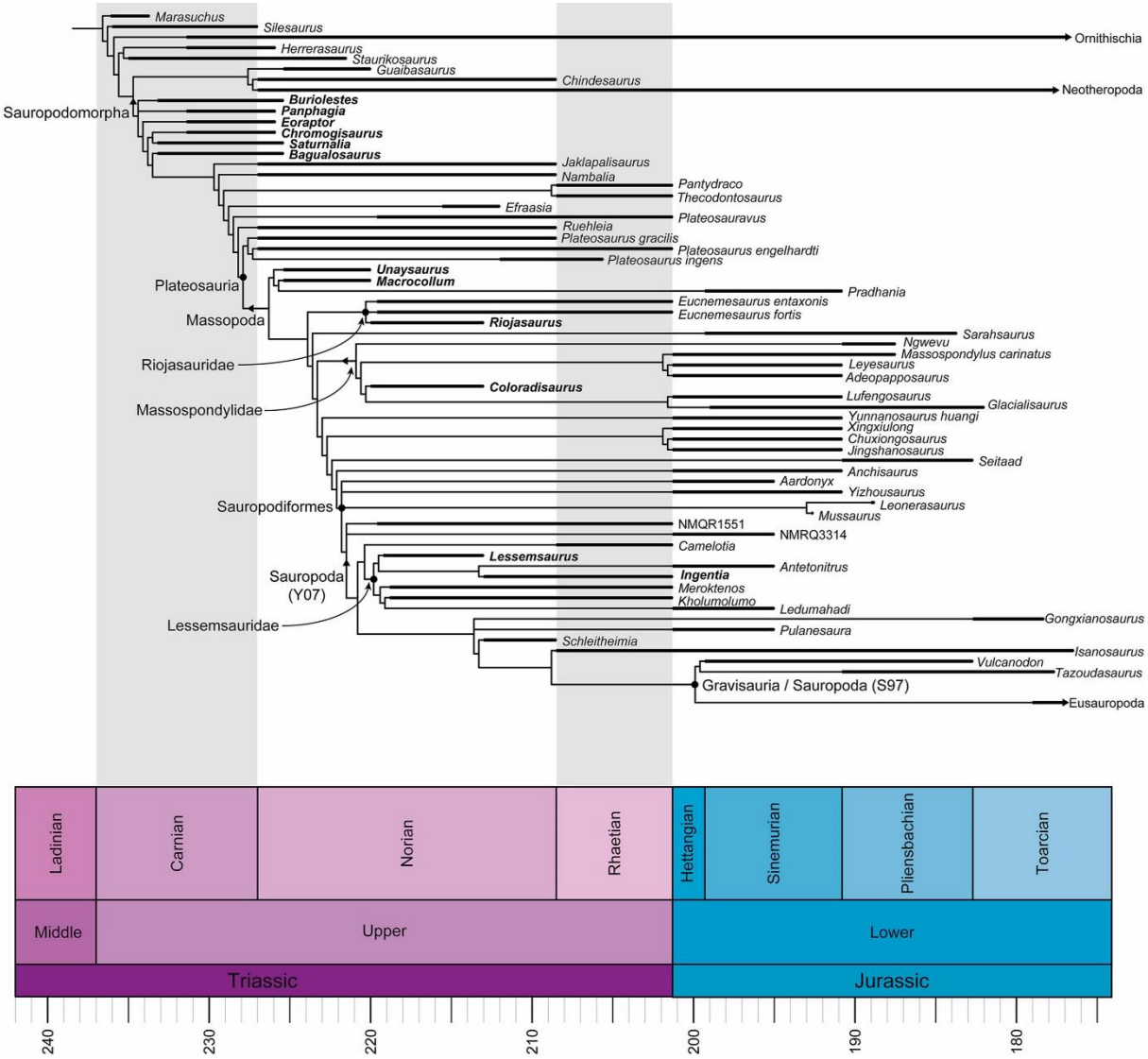

Figure 2: A recent time-calibrated phylogeny illustrating the relationships amongst current sauropodomorph taxa. Modified from Pol et al. (2021b).

The first sauropodomorph named from the EF was *Massospondylus carinatus* by Owen (1854), followed by *Euskelosaurus browni* by Huxley (1866). Haughton (1924) was the first to document the fauna of the Stormberg series including that of sauropodomorphs across the EF and noted the presence of larger-bodied sauropodomorphs in the lower sections with smaller-bodied sauropodomorphs like *Massospondylus* in the upper sections. Kitching and Raath (1984) proposed the first formalized EF biozones, basing them on stratigraphic distributions of sauropodomorph taxa. This scheme biostratigraphically divided the EF into a lower "*Euskelosaurus*" Range Zone, with its middle and upper sections as the *Massospondylus* Range Zone. Recent revision has refined the biozonation of the EF with the *Scalenodontoides* Assemblage Zone (SAZ) replacing the "*Euskelosaurus*" Range Zone and encompassing the lEF, and the *Massospondylus* Assemblage Zone (MAZ) modifying the *Massospondylus* Range Zone and encompassing the uEF and lower Clarens Formation (Viglietti *et al.*, 2020a, Viglietti *et al.*, 2020b).

These biostratigraphic revisions (Viglietti *et al.*, 2020b, McPhee *et al.*, 2017) have left the lEF with only four valid sauropodomorph genera: *Blikanasaurus* (Galton and Van Heerden, 1985), *Eucnemesaurus entaxonis* (McPhee *et al.*, 2015b), *E. fortis* (Van Hoepen, 1920), *Melanorosaurus* (Haughton, 1924), and *Plateosauravus* (Huene, 1932). The holotypes of most of these species are fragmentary partial skeletons, some with questionable provenance, and detailed descriptions are lacking.

Sauropodomorphs are among the most useful dinosaurian global biostratigraphic markers in the Late Triassic (McPhee *et al.*, 2017), however their taxonomy and phylogeny are in a state of flux (Müller, 2019, McPhee *et al.*, 2015a). This is especially problematic in the lEF, which is lacking in well-provenanced, well-represented sauropodomorph specimens (McPhee *et al.*, 2017). This is surprising given the long history of the lEF fossil collection, the relative stratigraphic thickness of the lEF, and the large median body sizes of known lEF sauropodomorph individuals, which makes them easier to find (Haughton, 1924, Bordy *et al.*, 2020). Sampling sauropodomorphs across the lEF will result in well-documented specimens that can be used to build a more reliable biostratigraphy for comparison across contemporaneous formations.

Body Mass & Posture

Sauropodomorphs include the largest land-dwelling tetrapods ever to have evolved on Earth. The earliest branching sauropodomorphs of the Carnian and early Norian in the Late Triassic were omnivorous, small-bodied bipeds that evolved obligate herbivory, large body sizes, and quadrupedal postures during the latest Triassic and Early Jurassic (Benson, 2018, McPhee *et al.*, 2018, Müller and Garcia, 2021). Ongoing research seeks to understand the anatomical changes and evolutionary patterns that occurred during this size and postural transition. Evolutionary experimentation with locomotory styles manifests in non-sauropodan sauropodomorphs as a spectrum between robustness ratios of the forelimb/hindlimb and differences in limb anatomy ranging from flexed limbs in *Ledumahadi* to columnar limbs in sauropods (McPhee *et al.*, 2018, Carrano, 2005, McPhee *et al.*, 2015a, Bonnan and Yates, 2007, Remes, 2008). McPhee *et al.* (2018) showed that quadrupedality and giant body sizes had evolved by at least the Late Triassic (Norian) and likely occurred up to four independent times (McPhee *et al.*, 2018, Chapelle *et al.*, 2020).

As body masses reach higher orders of magnitude, morphological changes in the skeleton are necessary because of the scaling effects (Schmidt-Nielsen and Knut, 1984). Carrano (1999), and other researchers (Benson *et al.*, 2014, Campione and Evans, 2012, Chapelle *et al.*, 2020, Lefebvre *et al.*, 2022, McPhee *et al.*, 2018), elucidated the scaling relationships of body size and features of the long bones such as trochanteric migration as well as the relationships between the individual bones comprising the limb. Other morphological changes that have been observed include: reduction of the deltopectoral crest; columnar limbs; straightening of various limb shafts; the proximal end of the ulna is triradiate; a U-shaped manus and pes; increased limb robusticity (Carrano, 1999, 2005, McPhee *et al.*, 2018, Apaldetti *et al.*, 2018, Rauhut *et al.*, 2011).

These observations accompany a host of more qualitative and pseudo-quantitative approaches to understanding postural transitions, such as those employed by Bonnan and Yates (2007), Barrett and Maidment (2017), and Otero (2018). Other methods for postural determination have been developed but seldom applied to sauropodomorphs, such as centre of mass calculations and volumetric estimations (Otero *et al.*, 2017, Otero, 2018, Gatesy and Biewener, 1991, Hutchinson *et al.*, 2007, Demuth *et al.*, 2020).

When body mass increases, the stresses imposed on the weight-bearing limb elements are increased and the limbs become proportionately more robust. Campione and Evans (2012) investigated the relationship between limb robusticity and body mass within extinct and extant taxa, which builds on pioneering work done by Anderson *et al.* (1985) and Colbert (1962). They show that the stylopodial circumferences have a highly conserved relationship with body mass and that limb robusticity is a strong statistically representative proxy for estimating locomotory styles amongst terrestrial tetrapods (Campione and Evans, 2012, McPhee *et al.*, 2018, Chapelle *et al.*, 2020, Campione *et al.*, 2014). Recent research by McPhee *et al.* (2018) and Chapelle *et al.* (2020) extend this to determining posture using proportional limb scaling.

Osteohistology & Growth

Bone tissue reflects the life history of an animal, which can be observed through the differences in tissue type, rate of deposition, and vascularity. These variables are preserved in fossil bone allowing researchers to study the biology of extinct vertebrates. For example, the ratio between woven bone (WB) and parallel-fibred bone (PFB) or lamellar bone (LB), and the level of vascularization can be used to infer growth rates and patterns; the frequency and type of growth mark paired with the level of bone remodelling can infer individual age or stage of ontogeny (Padian and Lamm, 2013, Klein and Sander, 2007, de Buffrénil *et al.*, 2021, Botha *et al.*, 2022).

Osteohistological methods provide the most information-rich datasets for understanding which growth strategies were present within Sauropodomorpha, and for investigating the physiological means by which they attained gigantic sizes. The osteohistological study of non-sauropodan sauropodomorphs has a deep history, but only a sporadic sample has been examined, which includes: the early branching taxa *Massospondylus*, *Plateosaurus*, *Riojasaurus*, *Coloradisaurus*, *Adeopapposaurus*, and *Leyesaurus*; and the later branching *Lessemsaurus*, *Ingentia*, *Mussaurus*, *Aardonyx*, *Sefapanosaurus*, *Ledumahadi*, *Leonerasaurus*, *Patagosaurus*, and *Volkheimeria* (Chinsamy, 1993, Chapelle *et al.*, 2021, Klein and Sander, 2007, Cerda *et al.*, 2017, Apaldetti *et al.*, 2018, Cerda *et al.*, 2014, McPhee *et al.*, 2018, Botha *et al.*, 2022). In general, the primary bone tissue found in sauropodomorphs consists of a woven-parallel complex (WPC; previously known as fibrolamellar bone; Francillon-

Vieillot *et al.*, 1990, Klein and Sander, 2007, Botha *et al.*, 2022). Non-sauropodan sauropodomorphs have slower, seasonally interrupted growth, with certain earlier branching taxa showing growth plasticity such as *Massospondylus*, *Plateosaurus*, and possibly *Mussaurus* (Chapelle *et al.*, 2021, Klein and Sander, 2007, Cerda *et al.*, 2022). Later branching taxa show relatively higher growth rates with seasonal cessations. In contrast, sauropods were fast growing with uninterrupted growth, with cyclical growth only appearing late in ontogeny (Sander *et al.*, 2011, Sander *et al.*, 2004, Sander and Klein, 2005, Padian and Woodward, 2021, Rogers and Wilson, 2005).

Original hypotheses considered fast growth rates to be a sauropodan trait (Sander *et al.*, 2011, Rogers and Erickson, 2005), whereas more recent research (Apaldetti *et al.*, 2018, Cerda *et al.*, 2017, Botha *et al.*, 2022) suggests that some non-sauropodan sauropodomorphs still showed cyclical cessations, but grew as quickly as giant sauropods. Lessemsauridae, a clade of gigantic taxa often hypothesized as sister to Sauropoda, have rapid growth rates with cyclical cessations, but very recent research shows that some smaller non-sauropodan sauropodomorphs, *Aardonyx* and *Sefapanosaurus*, grew just as quickly indicating that rapid growth preceded giant body sizes (Apaldetti *et al.*, 2018, Botha *et al.*, 2022). Osteohistological sections from more transitional Late Triassic sauropodomorphs will undoubtedly clarify the evolution of their growth strategies.

Phylogenetics, Systematics & Bayesian Inference

Sauropodomorph evolutionary history spans nearly the entire Mesozoic, and they had achieved global distributions by the Jurassic. Continued research on their origins and evolution has dramatically increased the number of sauropodomorph taxa over the years, but there is still little consensus on their phylogenetic relationships, particularly those of early branching groups (McPhee *et al.*, 2015a, Müller, 2019, Sereno, 2007). From Gauthier (1986), the first to present cladistic analyses of Sauropodomorpha, to Pol *et al.* (2021a) the cladistic hypotheses, the size of the character datasets, and the taxa included have drastically changed so that the scope and scale of the analyses have steadily increased (Upchurch *et al.*, 2007, Sereno, 2007).

Maximum parsimony (MP) is a common phylogenetic optimality criterion used to analyse many character datasets, and most dinosaur systematic inquiries use this

method. MP lacks explicit parameters and is agnostic with regards to temporal information (Albert, 2005). Parsimony has traditionally been used for sauropodomorph datasets, and parsimony-inferred relationships remain the status quo for the group. More recently developed techniques such as Bayesian inference with a Fossilized Birth-Death (FBD) model feature explicit parameters of character change and incorporate temporal information (Wright and Lloyd, 2020, Ronquist *et al.*, 2009).

This type of statistical method has been used with many clades such as dipnoans (Cau, 2017), bears (Heath *et al.*, 2014), modern penguins (Gavryushkina *et al.*, 2017), Pterosauromorpha (Foffa *et al.*, 2022), and broad groups such as early amniotes (Ford and Benson, 2020). Bayesian inference has rarely been applied to dinosaurian groups other than Lloyd *et al.* (2016) who focused on overall dinosaurian phylogeny and Felice *et al.* (2020) who focused on cranial evolution along the avian lineage. Griffin *et al.* (2022) recently published on a new early branching non-sauropodan sauropodomorph (EBSM), *Mbiresaurus raathi*, where they were the first to apply this method to sauropodomorphs. Including temporal information in phylogenetic methods provides a perspective on character change. Since temporal information is not represented in MP, then this represents a fundamentally different means of assessing homology.

The Norian sauropodomorph fossil record is primarily limited to South Africa and Argentina, but it is clear that this stage is critically important in the group for the evolution of their many palaeobiological traits (McPhee *et al.*, 2017, Pol *et al.*, 2021b). It is clear that the Norian is the period in which sauropodomorph diversification is most active, in terms of postural and body size variation. During that time, the best global sample comes from Argentina, whereas South Africa has fewer taxa, fewer fossils, and fewer complete specimens. This shortcoming makes it challenging to understand early sauropodomorph evolution.

A bonebed near the village of Qhemegha, Eastern Cape preserves several sauropodomorph specimens that have the potential to provide critical information for the study of Norian sauropodomorphs. The purpose of this research is to describe a large sauropodomorph from this locality, compare it to other early sauropodomorphs, determine its body mass, posture and growth patterns, and assess its phylogenetic position through various optimality criteria and congruency tests.

AIMS & OBJECTIVES

The following are the aims of the research with their corresponding objectives to reach these aims:

1. Describe and identify BP/1/8469
    a. Complete a full anatomical description of all preserved material.
    b. Compare to other sauropodomorph taxa and unidentified material.
    c. Assess whether BP/1/8469 is a new taxon.
2. Determine the body mass and posture of BP/1/8469:
    a. Estimate the body mass based on both locomotory styles.
    b. Assess the posture using a database of extant and dinosaurian taxa.
3. Characterise the ontogenetic age and growth strategy of BP/1/8469:
    a. Osteohistological analysis on the femur.
    b. Determine the presence of growth marks and bone tissue types.
4. Assess the phylogenetic relationships of BP/1/8469:
    a. Produce time-calibrated phylogenies using a recent character dataset.
    b. Test various optimality criteria using a recent character dataset.
    c. Conduct congruency tests to evaluate the significance of the various optimality criteria.

MATERIAL

BP/1/8469 (Fig. 3) consists of associated skeletal elements of a sauropodomorph dinosaur that include: vertebrae from the cervical, dorsal, sacral, and caudal series; forelimb elements including a humerus, radius, metacarpals, and manual elements; hindlimb elements including the ilium, pubis, femur, tibia, fibula, metatarsals, and pedal elements. Other material from the same locality comprises duplicate elements that pertain to a referred individual with identical provenance and similar proportions to BP/1/8469.

The referred material includes: the lateral end of a right astragalus (BP/1/8461); the proximal end of a right tibia (BP/1/8463); and a left astragalus and proximal end of metacarpal IV (BP/1/8472).

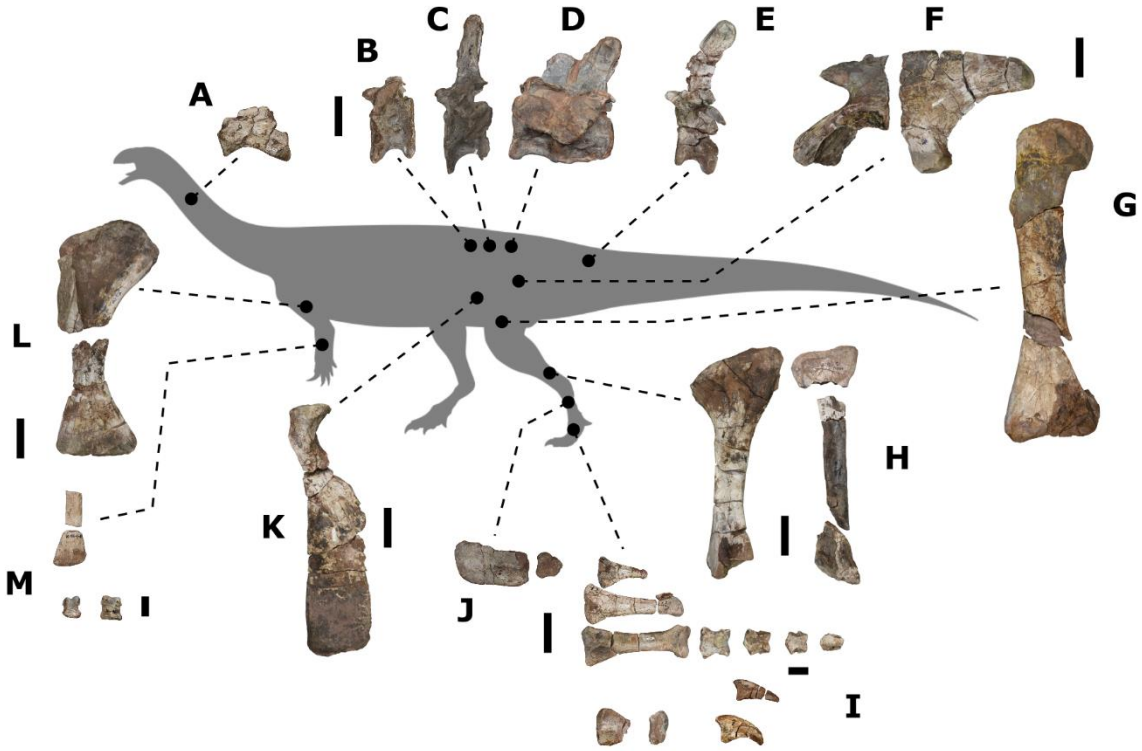

Figure 3: Overview of selected preserved elements of BP/1/8469. (A-E) vertebral series, where (A) cervical, (B) transitional dorsosacral, (C) dorsosacral, (D) sacral, (E) anterior caudal, (F) ilium, (G) femur, (H) tibia and fibula, (I) pedal elements, (J) astragalus, (K) pubis, (L) humerus, (M) radius and manual elements. Scale bar = 10 cm (A - H, J - L) and 5 cm (I and M).

GEOLOGICAL SETTING

The type locality is in the Sterkspruit District, 2 km southwest of the village of Qhemegha (variably spelt “Qimira”, “Qhemira”), Eastern Cape province near the outlet of the Sengu (Orange) river at the border of South Africa and Lesotho (Fig. 4). The material was found in mottled purple/red/yellow silty fine-grained sandstone of the *Scalenodontoides* Assemblage Zone (SAZ) of the lower Elliot Formation (lEF; Viglietti *et al.*, 2020b). BP/1/8469 lies in the lower half of the lEF approximately between 50 and 70 metres above the Molteno – Elliot contact in a region where the lower Elliot is approximately 250 metres thick. By correlation with better-dated strata in the region, it is approximately 216 Ma (Norian; Bordy *et al.*, 2020). The locality likely represents overbank deposits of a meandering river system in the Late Triassic.

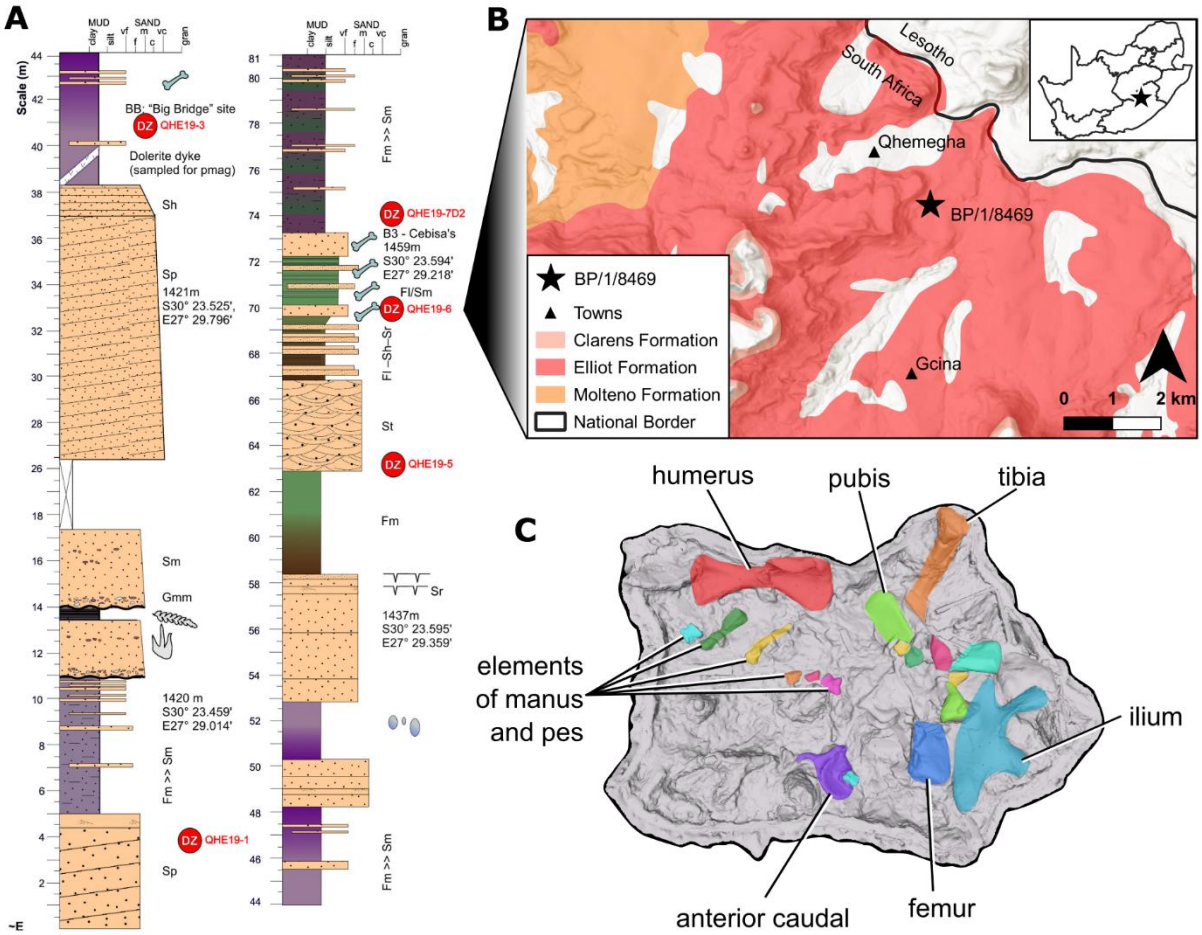

Figure 4: Stratigraphic section of the Qhemegha bone bed site (A). QHE-19-6 represents the bone bed that BP/1/8469 is provenanced. Lithostratigraphy of Qhemegha (B). A model of the plaster jacket (C) that contains BP/1/8469, 8461, 8463, and 8472 at time of quarrying and shows the relationship of some of the preserved elements. Stratigraphic log originally compiled by PA Viglietti, L Sciscio, G Sharmann, and C Suarez and adapted here for illustrative purposes.

METHODS

Descriptions and Comparative Anatomy

Descriptions of BP/1/8469 employ non-standardized Romerian anatomical and directional terms (e.g., “anterior/posterior” rather than “rostral/caudal”). When describing size variation, I use “tall/low” for the dorsoventral axis, “long/short” for the anteroposterior axis, and “wide/narrow” for the mediolateral axis, and exceptions to this are clearly noted. Vertebral laminae and fossae names are based on Wilson’s terminology (Wilson, 1999, Wilson *et al.*, 2011) (see Appendix 1 for full abbreviation list). Some bones of the skeleton were described in non-anatomical positions based on their vertical or horizontal axes for simplicity (e.g., humerus, pubis, manual and pedal elements). Comparative descriptions with other taxa were made through literature or by observations, refer to Table 1 for the list of comparative taxa and their relevant sources.

Table 1: Sources of comparative taxa used in this research

Taxa	Source(s)
Aardonyx celestae	BP/1/5379, 6249, 6316, 6509, 6510, 6512, 6513, 6542, 6542, 6585, 6592, 6593, 6611, 6623, 6641, 6662, 6755, 6893,
Antetonitrus ingenipes	BP/1/4952; McPhee *et al.* (2014)
Blikanasaurus cromptoni	SAM-PK-403; Galton and Heerden (1998)
Eucnemesaurus entaxonis	BP/1/6234; McPhee *et al.* (2015b)
Jaklapallisaurus asymmetrica	Novas *et al.* (2010)
Jingshanosaurus xinwaensis	Zhang and Yang (1994)
Kholumolumo ellenbergerorum	Peyre de Fabrègues and Allain (2020)
Ledumahadi mafube	BP/1/7120; McPhee *et al.* (2018)
Leonerasaurus taquetrensis	Pol *et al.* (2011)
Lessemsaurus sauropoides	Pol and Powell (2007)
Lufengosaurus huenei	IVPP V15
Macrocollum itaquii	Müller *et al.* (2018)
Massospondylus carinatus	BP/1/4934; Barrett *et al.* (2019)
Melanorosaurus readi	NMQR 1551; SAM-PK-3449; Galton *et al.* (2005)
Mussaurus patagonicus	Otero and Pol (2013)
Plateosauravus cullingworthi	SAM-PK-3341, 3342, 3343, 3344, 3345, 3347, 3348, 3350, 3351, 3356, 3602, 3603

Plateosaurus engelhardti	Moser (2003)
Pulanesaura eocollum	BP/1/6186, 6191, 6200, 6210, 6193, 6199, 6646, 6980, 6983, 7366, 7741; McPhee and Choiniere (2017)
Riojasaurus incertus	Bonaparte (1971)
Sarahsaurus aurifontanalis	Marsh and Rowe (2018)
Saturnalia tupiniquim	Langer (2003)
Schleitheimia schutzi	Rauhut *et al.* (2020)
Sefapanosaurus zastronensis	BP/1/386, 7409, 7416, 7420, 7422, 7424, 7425, 7434, 7435, 7438, 7441, 7445, 7447, 7448, 7449; Otero *et al.* (2015)
Spinophorosaurus nigerensis	Remes *et al.* (2009)
Tazoudasaurus naimi	Allain and Aquesbi (2008)
Unaysaurus tolentinoi	McPhee *et al.* (2020)
Xingxiulong chengi	Wang *et al.* (2017)
Yizhousaurus sunae	Zhang *et al.* (2018)
Yunnanosaurus huangi	Young (1942)
Indet. sauropodomorph	SAM-PK-11849
Indet. sauropodomorph	SAM-PK-11851

Body Mass Estimation

Because a humerus and femur are preserved, minimum shaft circumferences can be used to estimate the body mass of BP/1/8469 according to the method proposed by Campione and Evans (2012). The minimum humeral shaft circumference is 237 mm and the minimum femoral shaft circumference is 340 mm. Body mass was estimated using the relationship for quadrupedal tetrapods, the Ordinary Least Squares (OLS) regression, from Campione and Evans (2012):

OLS Regression: $Log_{10}BM = 2.749 \cdot Log_{10}C_{H+F} - 1.104$

I also employed the corrected quadrupedal equation (cQE) from Campione *et al.* (2014) to estimate the mass of bipedal tetrapods:

CQE: $Log_{10}BM = 2.745 \cdot Log_{10}C_{F} - 0.683$

Postural Assessment

A database of limb robusticity measurements (humeral and femoral shaft circumferences) was compiled from the published literature (McPhee *et al.*, 2018, Chapelle *et al.*, 2020, Campione and Evans, 2012) and from personal measurement of specimens, which contains terrestrial taxa with a range of locomotory habits (bipedal to quadrupedal) and analysed following the methods in Chapelle *et al.* (2020). A database of 304 extant taxa with known posture as well as 74 dinosaur taxa where we can estimate their posture with certainty from morphology (e.g., *Velociraptor*) were used as a training dataset (see Appendix 2) in a discriminant function analysis (DFA) using the ratio of Log_{10}HC (humeral shaft circumference) to Log_{10}FC (femoral shaft circumference) as predictors of postural classes “biped” and “quadruped”, as in Chapelle *et al.* (2020). The analysis was conducted in R studio (v.4.2.0) with packages `MASS` (Ripley *et al.*, 2013) and `ggplot2` (Wickham *et al.*, 2016) (see Appendix 3). Because sample sizes between bipeds and quadrupeds were unequal, I performed a bootstrap procedure to obtain class predictions by randomly subsampling 55 taxa from each postural class as a training dataset, generating postural predictions from this training dataset, and repeating the analysis 10 000 times to generate posterior probabilities of being bipedal that were then divided into classes to predict the posture of BP/1/8469 and 76 other sauropodomorph taxa. Log_{10}-transformed and non-log transformed plots between humeral and femoral circumferences of 81 dinosaurian taxa were generated as well as a univariate plot illustrating the ratios between Log_{10}HC and Log_{10}FC of dinosaurian taxa.

Osteohistology

A transverse segment from the right femur was used for osteohistological analysis. The segment was taken from the distal portion of the femoral shaft, approximately 250 mm above the distal condyles. The minimum circumference of the segment is 310 mm. All the osteohistological sections were produced at the National Museum, Bloemfontein following standard methods described in Botha-Brink *et al.* (2018). The sections were then rendered under normal, polarized, and cross-polarized light using a Nikon Eclipse Ci POL polarizing microscope and DS-Fi3 digital camera in NIS-elements D 4.6 (Nikon Corp., Tokyo, Japan). Osteohistological terminology follows that of de Buffrénil *et al.* (2021).

Inferences and analyses of the growth history is based on the posterolateral section of the femoral shaft. An approximate growth curve showing the percentage of growth associated with each growth mark (GM) of BP/1/8469 was generated using the radius of the posterolateral section, similarly done in Chapelle *et al.* (2022).

Phylogenetics & Bayesian Analyses

To assess the relationships of BP/1/8469, phylogenetic analyses were performed using both maximum parsimony (MP) and Bayesian inference as optimality criteria. Both sets of analyses used a recent morphological character matrix by Pol *et al.* (2021a), maintaining the ordered characters with the following minor revisions:

a) Recoding of character 258 so that state 0 represents basal taxa, state 1 represents morphology seen in many non-sauropodan sauropodomorph taxa, and state 2 represents morphology seen in sauropod taxa.
   Character 258: Shape of the caudal margin of the postacetabular process of the ilium: rounded to bluntly jointed (0), square-ended (1), or with a pointed ventral corner and a rounded caudodorsal margin (2).
b) Introduction of character 420 (see Appendix 4).
   Character 420: Paramarginal sulcus on the lateral surface of the deltopectoral crest: absent (0), present (1).
c) Removal of character 353 as it is considered as a size-related feature.
   Character 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 (5).

These changes resulted in a morphological character matrix of 419 characters and 77 taxa (see Appendix 5). The character matrix was maintained using Mesquite (v.3.70; Maddison and Maddison, 2019).

Parsimony analyses were conducted in TNT (Tree Analysis for New Technology; v.1.5; Goloboff and Catalano, 2016). The heuristic search strategy used 1000 replicates of Wagner trees, TBR (tree-bisection reconnection) branch-swapping, with one tree saved per replication. Bremer support values (Bremer, 1994) were calculated in TNT allowing up to five extra steps as well as absolute Bootstrap

support values with 100 replicates. Consistency and retention indices were calculated using the 'stats.run' TNT script. A representative most-parsimonious tree was imported into R Studio (v.4.2.0) to generate a time-calibrated phylogeny (see Appendix 6) using the `strap` (Bell *et al.*, 2022) and `geiger` (Harmon *et al.*, 2007) packages.

The Fossilized Birth-Death (FBD) model using Bayesian analysis was implemented in MrBayes (v.3.2.7; Ronquist *et al.*, 2012, Heath *et al.*, 2014) and follows the methods of Ford and Benson (2020). As the dataset was of morphological data, the datatype was 'standard' with coding set at 'variable'; the ages of the taxa were specified using a uniform distribution; the rate was set to a gamma distribution. Two runs, each with four chains (three heated and one cold), were analysed for 10 million generations, and sampled every 1000th generation (see Appendix 7).

In addition, other optimality criterion congruency tests were conducted. Implied weighting analyses (Goloboff *et al.*, 2008) were conducted on the parsimony analysis in TNT to examine the effects of down weighting homoplasy at various concavity functions ranging from k=1 to k=12. Stratigraphic fit of each optimal tree topology (under MP, FBD, and IW) was assessed using the function `StratPhyloCongruence` in the `strap` package of R (see Appendix 8). The main metrics of stratigraphic congruency presented here include: Gap Excess Ratio (GER), Stratigraphic Consistency Index (SCI), Relative Consistency Index (RCI), an Manhattan Stratigraphic Measure (MSM; Bell and Lloyd, 2015, Wills, 1999).

A Templeton Test (Templeton, 1983) was conducted in TNT using the code developed by Schmidt-Lebuhn (2016) to compare the phylogenies of MP and FBD, and assess whether the two trees implied significantly different fits to the character matrix. A "sensitivity" analysis (*sensu* Wheeler, 1995) was conducted that assesses and summarizes various phylogenetic statements amongst the phylogenies generated by the different optimality criteria. The scoring was based on two factors and not done in the strictest sense: (1) the taxa included in the clades were relatively consistent based on definition, and (2) the position of selected taxa on the phylogeny relative to their neighbouring taxa. Table 2 includes clade definitions that were used for the "sensitivity" analysis. The scoring was as follows: "observed", same taxa within the clade were grouped together; "to some degree", simple majority of the taxa within the clade were grouped; "not observed", clade not present in any form.

Table 2: Definitions of sauropodomorph clades and their relevant sources that were used in this study.

Clade	Source	Definition
Plateosauria	Sereno (1998)	*Plateosaurus*, *Massospondylus*, their common ancestor and all descendants
Plateosauridae	Beccari *et al.* (2021)	includes species closer to *Plateosaurus trossingensis* than to Sauropoda, most of the time recovered with *Unaysaurus tolentinoi* as sister taxon to *Plateosaurus*
Massopoda	Yates (2007)	most inclusive clade containing *Saltasaurus loricatus* but not *Plateosaurus engelhardti*
Riojasauridae	Yates (2007)	most inclusive clade containing *Riojasaurus incertus* but not *Plateosaurus engelhardti*, *Massospondylus carinatus*, or *Anchisaurus polyzelus*
Massospondylidae	Chapelle *et al.* (2019)	includes *Sarahsaurus aurifontanalis*, *Ignavusaurus rachelis, Leyesaurus marayensis, Adeopapposaurus mognai, Massospondylus carinatus, Coloradisaurus brevis, Massospondylus kaalae* and *Lufengosaurus huenei*
Sauropodiformes	Sereno (2007)	include *Mussaurus patagonicus* and the derived sauropod *Saltasaurus*
Anchisauria	Galton and Upchurch (2004)	include *Anchisaurus*, *Melanorosaurus*, their common ancestor and all their descendants
Melanorosauridae	Galton and Upchurch (2004)	more closely related to *Melanorosaurus* than *Anchisaurus*
Lessemsauridae	Pol *et al.* (2021b)	include *Lessemsaurus*, *Ingentia*, *Antetonitrus*, *Ledumahadi*, *Meroktenos*, *Kholumolumo*
Sauropoda	Salgado *et al.* (1997)	include most common recent ancestor of *Vulcanodon karibaensis* and Eusauropoda and all of its descendants

RESULTS

Systematic Palaeontology

Dinosauria (Owen, 1842)

Saurischia (Seeley, 1888)

Sauropodomorpha (Huene, 1932)

Sauropodiformes (Sereno, 2007)

Anatomical Description of BP/1/8469

Axial skeleton

Cervical vertebra

A single, nearly complete cervical vertebra (Fig. 5) is preserved with missing zygapophyseal articular facets, epipophyses, and a thin portion of the dorsal margin on the neural spine is missing. The cervical lacks spinal lamination. The vertebra is likely from the middle of the cervical series based on the distinction between the diapophyses and parapophyses. It completely lacks any indication of pneumatization. The centrum is slightly distorted so that it deviates laterally to the left. The cervical is 2.5 times longer than it is tall, this is within the range of most non-sauropodan sauropodomorphs (see Appendix 9 for measurements). The neural spine is low and elongated with a ratio of 0.47 of the total anteroposterior length of the vertebra. This is similar to *Massospondylus* (Barrett et al., 2019) but higher than *Aardonyx* (BP/1/6513) and *Sefapanosaurus* (BP/1/7409).

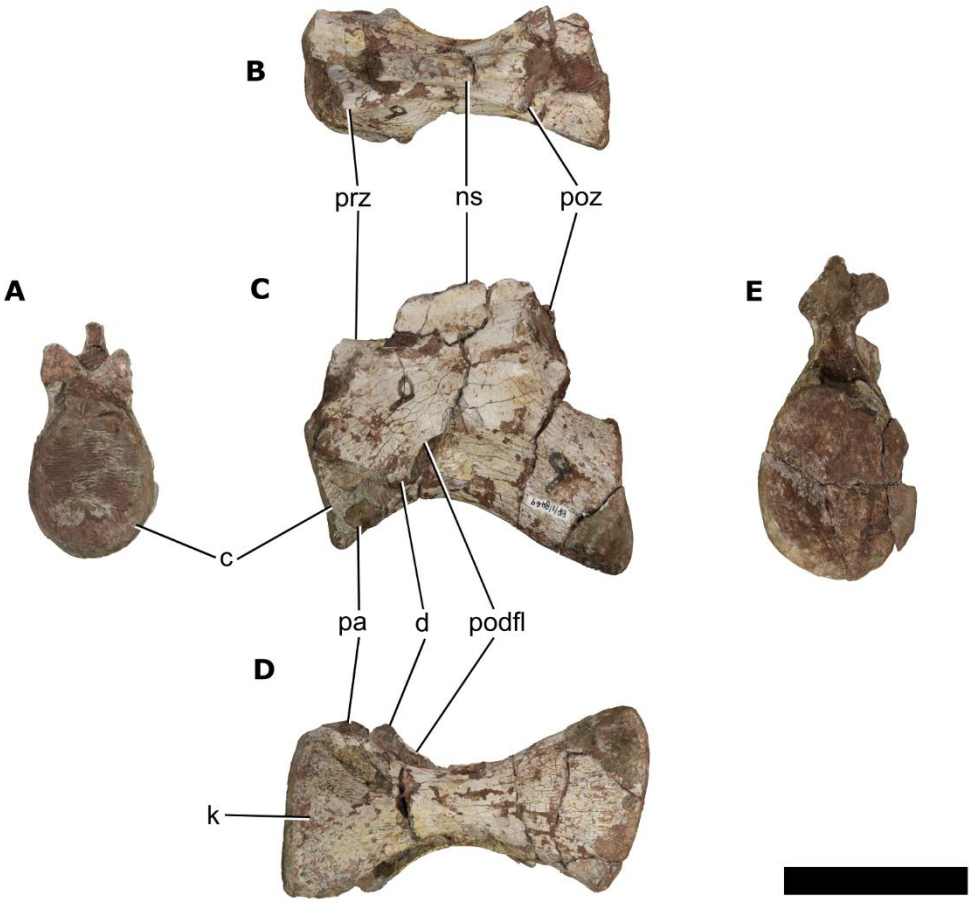

Figure 5: Middle cervical vertebra (BP/1/8469) in (A) anterior, (B) dorsal, (C) left lateral, (D) ventral, (E) posterior views. Abbreviations: c, centrum; d, diapophysis; k, keel; ns, neural spine; pa, parapophysis; podfl, postdiapophyseal flange; poz, postzygapophysis; prz, prezygapophysis. Scale bar = 10 cm.

The prezygapophyses are directed anterolaterally, whereas the postzygapophyses are directed posterolaterally. The postzygapophyses exhibit a dorsal elevation of ~20° from the horizontal plane. This is similar to *Spinophorosaurus* (Remes *et al.*, 2009) but differs markedly when compared to *Ledumahadi* (BP/1/7409), which has little to no elevation, and to *Leonerasaurus* (Pol *et al.*, 2011) where the elevation is 30°.

The lateral surfaces of the centrum bear distinct diapophyses and parapophyses. The diapophysis is situated posterodorsally relative to the parapophysis, projecting laterally at the end of a postdiapophyseal flange (podfl), as in *Spinophorosaurus* (Remes *et al.*, 2009) and in *Sefapanosaurus* (BP/1/7409). The parapophysis is a protuberance situated at the anterior end of the lateral surface of the centrum, immediately posterior to the anterior margin. It projects laterally slightly

beyond the margin of the centrum in anterior view. The parapophysis has an elliptical articular facet that is twice as long as that of the diapophysis.

The amphicoelous centrum has concave anterior and posterior surfaces with raised margins, as in most non-sauropodan sauropodomorphs. The anterior surface is subcircular and the posterior surface is wider than it is tall, and also wider than the anterior surface. The ratio of the articular surfaces is similar to most other non-sauropodan sauropodomorphs, however, in *Massospondylus* (Barrett *et al.*, 2019) the articular surfaces are wider than they are tall, and this is the opposite in *Tazoudasaurus* (Allain and Aquesbi, 2008). The ventral margin of the anterior surface is dorsally offset relative to the level of the ventral margin of the posterior surface, similar to *Antetonitrus* (BP/1/4952), whereas they are approximately the same level in *Plateosaurus* (Moser, 2003). The ventral margin of the centrum is concave with the deepest concavity located just posterior to the parapophyses, similar to *Lufengosaurus* (IVPP V15). In ventral view, the centrum has an hourglass-shaped outline, similar to *Massospondylus* (Barrett *et al.*, 2019). A shallow depression is present on the anterior side of the lateral surface of the centrum located posterior to the diapophyses and parapophyses. This depression is approximately 50% of the anteroposterior length of the centrum. A discrete keel is present on the anterior side of the ventral surface of the centrum.

Transitional dorsal vertebra

An incomplete dorsal vertebra is preserved and is considered as a transitional dorsosacral vertebra (Fig. 6) as it displays morphology of both posterior-most dorsals and the dorsosacral, and appears to be in the early anatomical stages of being incorporated into the sacrum. It lacks a neural spine, postzygapophyses, and the right rib. The anterior surface of the centrum has erosional or depositional damage, it is unclear as to the direct cause.

The neural canal is circular in anterior view and is shorter than the centrum. The posterior neural canal margin is prominent and rounded, extending slightly posteriorly from the rest of the neural arch. The transverse process is almost as long as the centrum and is mediolaterally short and fuses to a dorsoventrally thin rib. The posterior margin of the transverse process has a slight dorsal inclination. A postzygodiapophyseal lamina (podl) on the transverse process projects posteriorly relative to the margin of the centrum adding to the length of the transverse process.

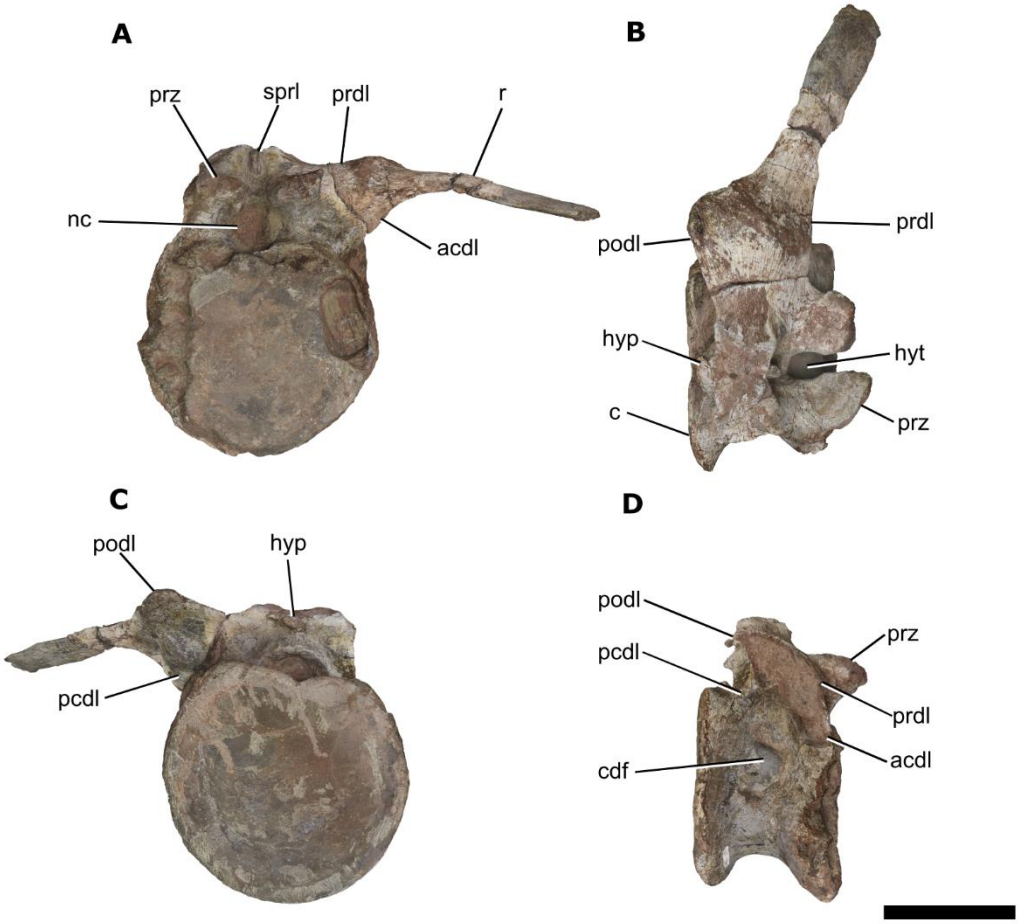

Figure 6: Transitional dorsal (BP/1/8469) in (A) anterior, (B) dorsal, (C) posterior, (D) right lateral views. Abbreviations: acdl, anterior centrodiapophyseal lamina; c, centrum; cdf, centrodiapophyseal fossa; hyp, hyposphene; hyt, hypantrum; nc, neural canal; pcdl, posterior centrodiapophyseal lamina; podl, postzygodiapophyseal lamina; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; r, rib; sprl, spinoprezygapophyseal lamina. Scale bar = 10 cm.

The proximal portion of a single spinoprezygapophyseal lamina (sprl) is present at the base of the neural spine, similar to *Lufengosaurus* (IVPP V15). The prezygapophyses are directed almost dorsally at an approximate angle of 20° with circular articular facets, similar to *Antetonitrus* (BP/1/4952) and *Jingshanosaurus* (Zhang and Yang, 1994). The prezygapophyses extend anteriorly beyond the anterior margin of the centrum, typical of posterior dorsals. The medial margins of the prezygapophyses curve mesially in anterior view. A discrete prezygodiapophyseal lamina (prdl) is present with a slightly thicker anterior centrodiapophyseal lamina (acdl), and a short posterior centrodiapophyseal lamina (pcdl). A hyposphene-hypantrum articulation is present with a deep, rectangular hypantrum in dorsal view and a dorsoventrally thin, small hyposphene in posterior view.

The articular surfaces of the centrum are circular in both anterior and posterior views, with rounded margins along the faces that are thinner than the margins seen in the caudal centra, but similar to the margins in the dorsosacral. The centrum is weakly amphicoelous. The centrum has a medial constriction with a deep ventral margin, similar to *Sefapanosaurus* (BP/1/7416) and *Schleitheimia* (Rauhut *et al.*, 2020). A small centrodiapophyseal fossa (cdf) is visible on the right lateral surface of the centrum.

Dorsosacral vertebrae

A complete, robust dorsosacral vertebra is associated with BP/1/8469 with a damaged posterior surface on the centrum (Fig. 7). The neural spine is 2.9 times taller than it is long, and is proportionately much taller than most EBSMs like

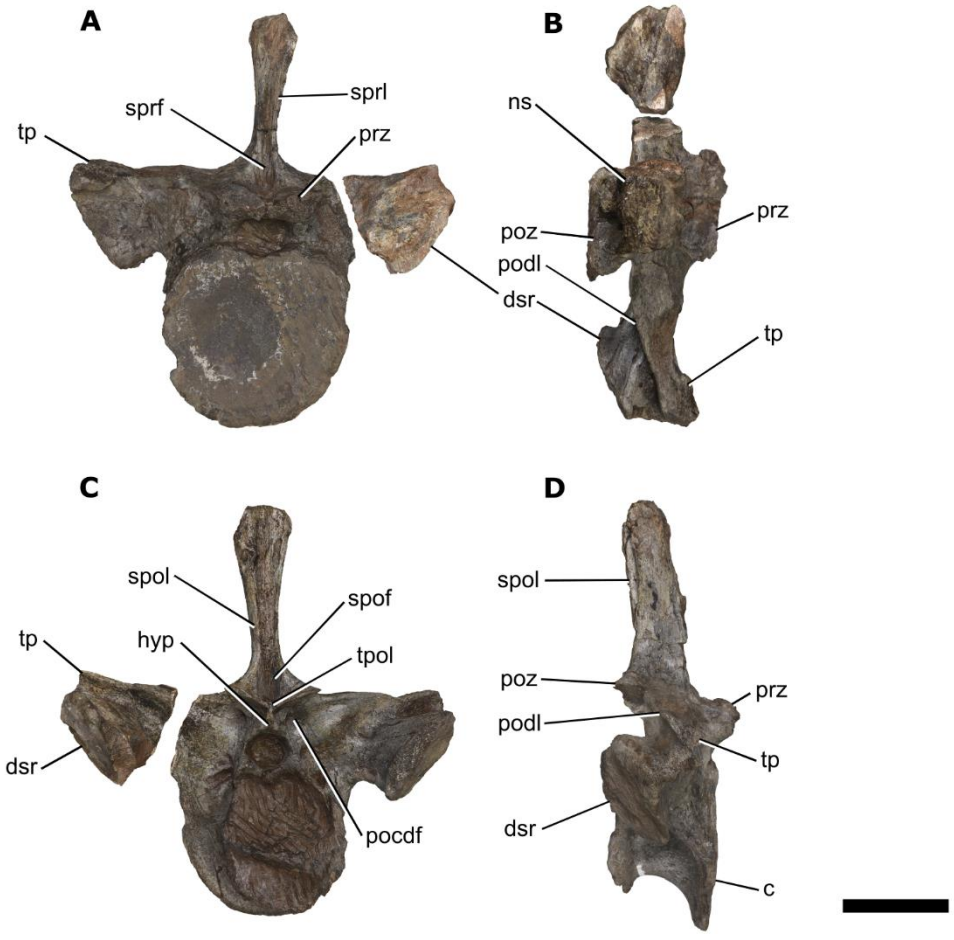

Figure 7: Dorsosacral (BP/1/8469) in (A) anterior, (B) dorsal, (C) posterior, (D) right lateral views. Abbreviations: c, centrum; dsr, dorsosacral rib; hyp, hyposphene; ns, neural spine; pocdf, postzygocentrodiapophyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prz, prezygapophysis; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tp, transverse process; tpol, intrapostzygapophyseal lamina. Scale bar = 10 cm.

Eucnemesaurus (McPhee *et al.*, 2015b) and *Xingxiulong* (Wang *et al.*, 2017). The neural spine is directed dorsally and becomes wider as it extends dorsally with a convex distal margin. This is seen in *Eucnemesaurus* (McPhee *et al.*, 2015b) and *Xingxiulong* (Wang *et al.*, 2017). A sprl is present on the anterior margin of the neural spine. It bifurcates at the ventral end of the neural spine, merges into a single lamina at the midpoint, then possibly bifurcates again close to the dorsal margin of the neural spine. The spinopostzygapophyseal lamina (spol) extends along the posterior surface of the neural spine, and is similar to the sprl because it bifurcates near the base of the neural spine and merges into a single lamina at midpoint. However, the spol differs in that it protrudes posteriorly as a single lamina as it extends dorsally for the rest of the neural spine. Both the sprl and spol form a buttress at the region where they bifurcate resulting in a spinoprezygapophyseal fossa (sprf) and a deep spinopostzygapophyseal fossa (spof) respectively. Dorsosacral neural spines are seldom preserved amongst early branching sauropodomorphs, limiting comparison here. In anterior view, the neural canal is elliptical and wider than tall. In posterior view the margin around the neural canal is a prominent, raised lip of bone.

The transverse processes in the dorsosacral have similar morphology to the first primordial sacral, they are tall with a dorsal horizontal platform connected via a thin vertical lamina to the subrectangular dorsosacral rib that comprises the ventral portion. The dorsosacral rib is angled posteriorly, and is taller than the sacral rib in the first primordial sacral, similar to *Yizhousaurus* (Zhang *et al.*, 2018) and *Yunnanosaurus* (Young, 1942). The dorsosacral rib is taller than it is long. The transverse processes extend laterally with a straight dorsal margin, originating from the neural arch as well as the dorsal half of the centrum, whereas in most sauropodomorphs the transverse process extends from the neural arch only. In dorsal view, the transverse process does not exhibit a constriction at the junction with the rib, as with *Leonerasaurus* (Pol *et al.*, 2011). A prominent podl extends from the base of the postzygapophyses to the dorsolateral end of the transverse processes contributing to the horizontal platform.

The prezygapophyses are dorsoventrally compressed making it difficult to see the articular facets clearly. The prezygapophyses are directed dorsally with flat articular facets that are wider than they are long. This is similar to *Lufengosaurus* (IVPP V15), whereas in referred *Melanorosaurus* (NMQR 1551) they are longer than wide. The prezygapophyses extend anterior to the level of the anterior margin of the

centrum, as in most sauropodomorphs. The postzygapophyses are better preserved and the level of their bases is dorsal to that of the prezygapophyses. Their articular facets are elliptical and ventrolaterally directed at an approximate angle of 30° from the horizontal, similar to *Melanorosaurus* (NMQR 1551). An intrapostzygapophyseal lamina (tpol) is present above a small, thin hyposphene. A small, incipient postzygocentrodiapophyseal fossa (pocdf) is deeply set anteroventrally with respect to the postzygapophyses, it is unclear whether this fossa is present in other EBSM. The anterior surface of the centrum is subcircular in anterior view, and is almost flat, similar to *Jingshanosaurus* (Zhang and Yang, 1994), whereas in *Melanorosaurus* (NMQR 1551) it is elliptical. The margin along the anterior surface is rounded, as in *Yizhousaurus* (Zhang *et al.*, 2018). The ventral margin of the centrum is smooth and deeply concave. The centrum is medially waisted giving it a spool shape in lateral view.

Sacral vertebrae

Two complete, articulated vertebrae with fused transverse processes and sacral ribs are preserved, identified here as primordial sacrals one and two (Fig. 8; *sensu* Wilson and Sereno (1998)). The centra of the sacral vertebrae are co-ossified together. The dorsal half of the neural spine of the first primordial sacral is missing with the ventral portion of the posterior centrum of the second primordial sacral, and the lateral margins of the transverse process and sacral ribs are slightly eroded.

The neural spines are two times taller than they are long. The sacral neural spines of BP/1/8469 are proportionately taller than most EBSM that have short and long neural spines, such as *Massospondylus* (BP/1/4934). The neural spines slope posteriorly as they extend dorsally, with no fusion between them. The anterior margin of the neural spine is suggestive of a sprl in the form of a single lamina on both sacrals, with a spol on the posterior margin that bifurcates ventrally and creates a spof. The neural spine lamination present in BP/1/8469 is similar to *Melanorosaurus* (NMQR 1551). As the neural spine extends dorsally, it widens and has a convex dorsal margin. This is common in most EBSM such as *Sarahsaurus* (Marsh and Rowe, 2018), whereas other sauropodomorphs have a flat dorsal margin as in *Kholumolumo* (Peyre de Fabrègues and Allain, 2020) and *Saturnalia* (Langer, 2003). The neural canal in the first sacral is circular in anterior view, with the margins around the neural canal creating a raised lip of bone. The neural arch appears to be shorter

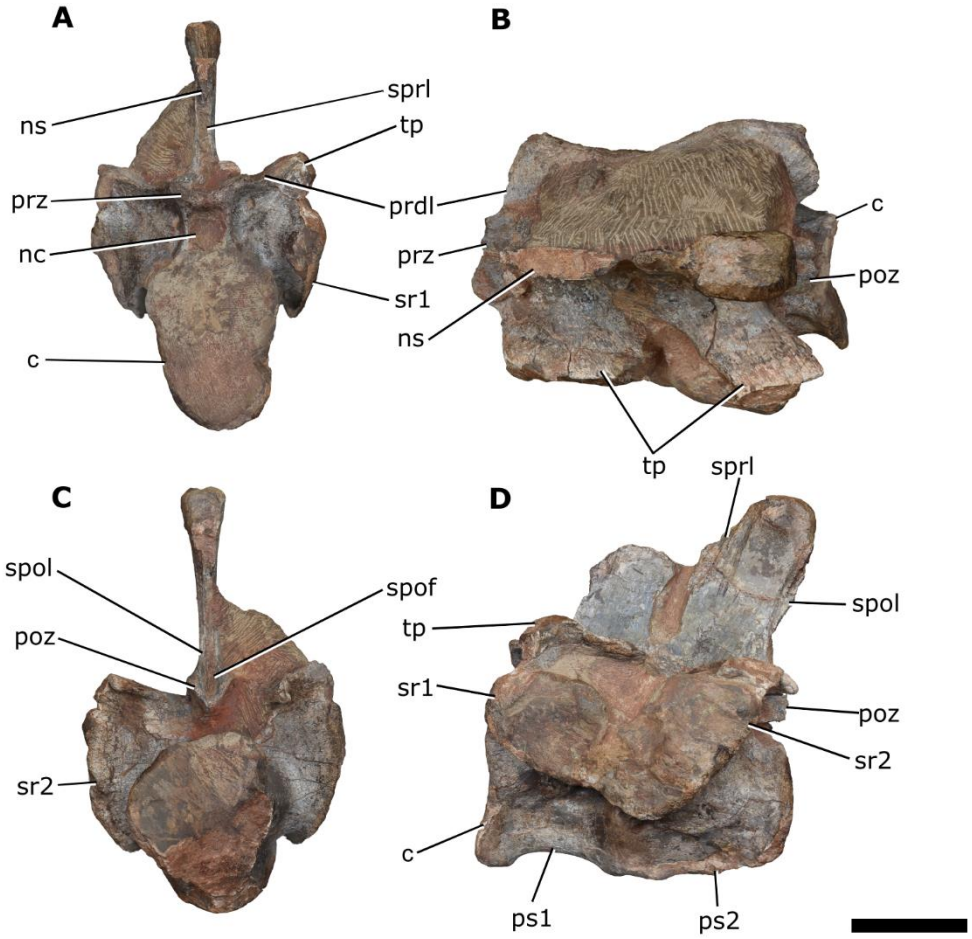

Figure 8: Fused sacral vertebrae (BP/1/8469) in (A) anterior, (B) dorsal, (C) posterior, (D) left lateral views. Abbreviations: c, centrum; nc, neural canal; ns, neural spine; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; ps1, primordial sacral 1; ps2, primordial sacral 2; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; sr1, sacral rib of primordial sacral 1; sr2, sacral rib of primordial sacral 2; tp, transverse process. Scale bar = 10 cm.

than the centrum with the posterior margin of the neural arch set anterior to the posterior margin of the centrum, similar to *Yizhousaurus* (Zhang *et al.*, 2018).

The transverse processes are long and directed posterodorsally. A thin prdl is present on the transverse processes. As the transverse processes extend laterally, they become dorsoventrally thin, and lack a constriction as in *Mussaurus* (Otero and Pol, 2013). The transverse processes of both the first and second primordial sacral vertebrae are fused to each other and with the sacral ribs forming sacrocostal yoke. The sacral ribs are tall, originating from the neural arch in the first primordial sacral and from the dorsal half of the centrum to the neural arch in the second primordial sacral.

The first sacral rib is rectangular in lateral view, with the posterior margin taller than the anterior margin, similar to *Plateosaurus* (Moser, 2003). In contrast, the first sacral rib of *Leonerasaurus* (Pol *et al.*, 2011) is L-shaped in lateral view. In lateral view, the transverse process forms the thin, dorsal horizontal platform, connecting to the first sacral rib via a thin, longitudinal lamina located anteriorly. This creates a C-shape with a long intercostal concavity between the primordial sacrals. This morphology is seen in *Eucnemesaurus* (McPhee *et al.*, 2015b), *Riojasaurus* (Bonaparte, 1971), and *Yunnanosaurus* (Young, 1942). The second sacral rib is rectangular in lateral view, and is taller than the first sacral rib. It is sloping posterodorsally, and situated closer to the anterior half of the centrum. The morphology of the second sacral rib is similar to *Jingshanosaurus* (Zhang and Yang, 1994), whereas it is more vertical in *Ledumahadi* (BP/1/7120). The second sacral rib does not exhibit the sinusoidal morphology as seen in other sauropodomorphs such as *Mussaurus* (Otero and Pol, 2013) or *Yunnanosaurus* (Young, 1942). The transverse process extends laterally and fuses to the dorsal of the second sacral rib creating a complex.

The prezygapophyseal articular facets of the first primordial sacral face dorsally and are held horizontally. Their articular facets are subcircular in dorsal view. The angle of the articular facets in BP/1/8469 is similar to the Lufeng taxa (IVPP V15, Zhang and Yang, 1994, Young, 1942), whereas *Melanorosaurus* (NMQR 1551) has angled articular facets. The bases of the prezygapophyses are immediately anterior to the anterior margin of the centrum. The prezygapophyses of the second primordial sacral are obscured by their tight articulation. It is unclear if any other lamination is present around the prezygapophyses. The postzygapophyses of the second primordial sacral are directed ventrolaterally with elliptical articular facets. The postzygapophyses are at an approximate angle of 50° from the horizontal, similar to *Jingshanosaurus* (Zhang and Yang, 1994), whereas *Ledumahadi* (BP/1/7120) is almost vertical. The postzygapophyses are aligned with the posterior margin of the centrum. A hyposphene-hypantrum articulation appears to be absent in BP/1/8469 as in most early branching sauropodomorph sacra.

The centra of both primordial sacrals are co-ossified with a smooth ventral surface. Both centra are proportionately longer wide with the second primordial sacral longer than first. Both centra have their anterior and posterior margins flared out laterally, as in *Leonerasaurus* (Pol *et al.*, 2011). In lateral view, the ventral margin

of the first primordial sacral centrum is slightly concave, whereas the second primordial sacral centrum is straight. The anterior surface of the first primordial sacral appears to be mediolaterally compressed resulting in a taller centrum with a flat anterior surface, this can be attributed to poor preservation. The margin along the anterior surface is not prominent but is rounded. The dorsal portion of the posterior centrum suggests some concavity with a circular cross-section. The margins along the posterior centrum are pronounced and rounded.

Anterior caudal

A nearly complete anterior caudal is preserved with small fragments from the centrum missing (Fig. 9). This anterior caudal is identified here as the first caudal because it bears no chevron facets. The neural spine is 3.4 times taller than it is long, proportionally taller than that of *Antetonitrus* (McPhee *et al.*, 2014). As the neural spine extends dorsally it becomes wider. The neural spine bows posteriorly, more than it does in *Antetonitrus* (BP/1/4952). This is contrasted by *Tazoudasaurus* (Allain and Aquesbi, 2008) where the neural spines extend strictly dorsally. The neural spine has a convex dorsal margin, similar to *Kholumolumo* (Peyre de Fabrègues and Allain, 2020), whereas some sauropodomorphs have a flat dorsal margin like *Pulanesaura* (BP/1/6646). A single sprl is present on the anterodorsal surface of the neural spine but is missing at the base of the neural spine. Spol are present on the posterior margin of the neural spine and bifurcate towards the postzygapophyses.

The neural arch is low and shorter than the centrum. Its anterior margin is confluent with the anterior margin of the centrum, whereas the posterior margin is set anterior to the posterior margin of the centrum. A short neural arch relative to the centrum is typical in non-sauropodan sauropodomorphs. The neural canal is subcircular and wider than it is tall, in both anterior and posterior views. *Pulanesaura* (BP/1/6646) and *Tazoudasaurus* (Allain and Aquesbi, 2008) have the opposite condition, with taller than wide neural canals.

The transverse processes are very short, projecting posteriorly, and arc ventrally. The arc-like transverse processes of BP/1/8469 (Fig. 7 A, D) have not been documented in other sauropodomorphs and are likely an autapomorphy of the taxon.

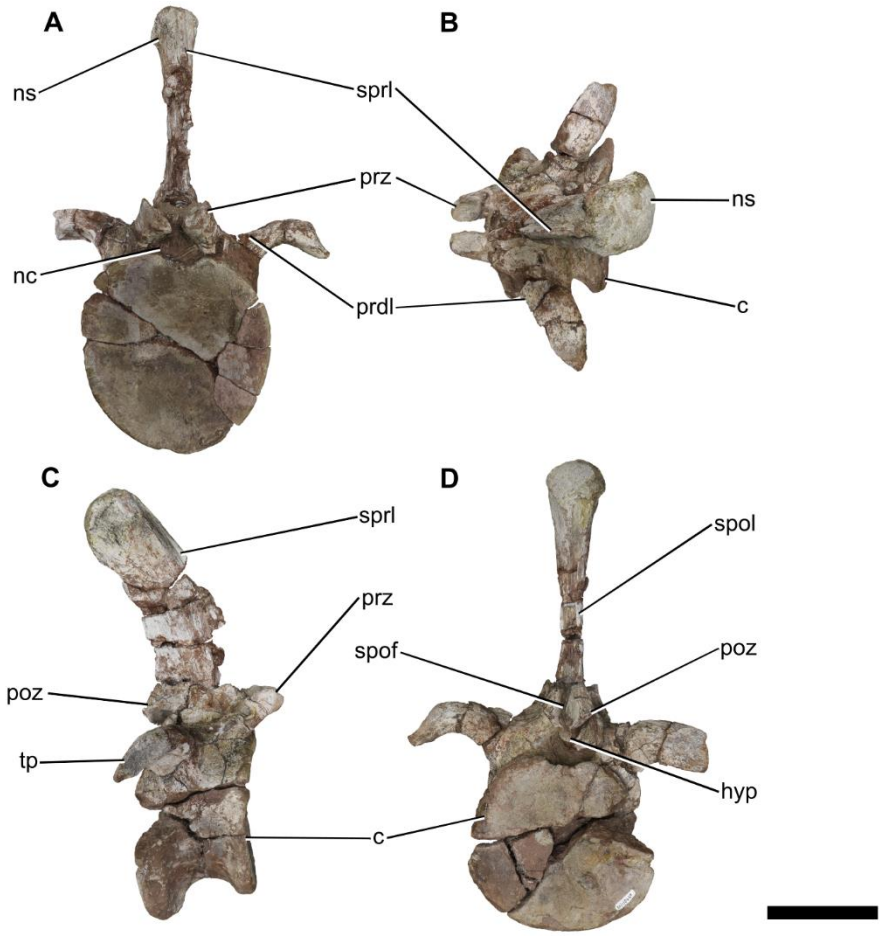

Figure 9: Anterior caudal (BP/1/8469) in (A) anterior, (B) dorsal, (C) left lateral, (D) posterior views. Abbreviations: c, centrum; hyp, hypospene; nc, neural canal; ns, neural spine; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tp, transverse process. Scale bar = 10 cm.

The transverse processes extend from the centrum and are connected to the prezygapophyses by a thin prdl, this is seen in *Xingxiulong* (Wang *et al.*, 2017).

A hypantrum is present between the prezygapophyses and a thin hyposphene is present. A hyposphene-hypantrum articulation is not usually present in non-sauropodan sauropodomorph caudals but has a sporadic distribution and occurs in some taxa such as *Antetonitrus* (BP/1/4952). The prezygapophyseal articular facets are elliptical in dorsal view and are directed dorsomedially. The postzygapophyseal articular facets are directed ventrolaterally with elongated, elliptical facets. The articular facets of both the prezygapophyses and postzygapophyses are at an approximate angle of 45° from the horizontal, differing markedly from *Massospondylus* (Barrett *et al.*, 2019) and *Mussaurus* (Otero and Pol, 2013) that are

much steeper at 70° to almost vertical. Bifurcating spol lead to the postzygapophyses and form a small spof within the buttress. The morphology of the postzygapophyses and associated laminae are similar to *Tazoudasaurus* (Allain and Aquesbi, 2008). In lateral view, the prezygapophyses extend anteriorly beyond the margin of the centrum, and the postzygapophyses are confluent with the posterior margin of the centrum.

The anterior surface of the centrum is concave, whereas the posterior surface is flat to slightly concave, resulting in a weakly amphicoelous centrum typical of non-sauropodan sauropodomorphs. Some taxa, like *Ledumahadi* (BP/1/7120) have procoelous centra. Both the anterior and posterior surfaces of the centrum are subcircular. The centrum is 1.7 times taller than it is long. The posterior surface has a thicker, rounded margin than the anterior surface. In lateral view, the ventral margin of the centrum is concave with an offset between the level of the anterior and posterior surfaces.

Caudals

Two other caudal vertebrae are associated with BP/1/8469: a more complete anterior-to-middle caudal (Fig. 10 A-D); and the neurocentral sutural region of another possible middle caudal (Fig. 10 E-H). The anterior-to-middle caudal lacks most of the neural spine and small fragments along the margins of the anterior and posterior surfaces of the centrum. The middle caudal lacks a neural spine, transverse processes, zygapophyseal articular facets, and majority of the centrum.

The more complete anterior-to-middle caudal (Fig. 10 A-D) will be described first. The base of the neural spine suggests that it slopes posterodorsally, common in sauropodomorph caudals. The anterior margin of the neural spine has a sprl in the form of a single lamina, similar to the anterior caudal. The posterior margin is too damaged to determine if a spol is present. The neural canal is small and wider than tall, similar to other vertebrae associated with BP/1/8469. The neural arch is shorter than the centrum and is set mesially on it. The transverse processes are dorsoventrally thin and flat but also long, and directed posteriorly, similar to those of *Melanorosaurus* (SAM-PK-3449).

The single preserved prezygapophysis extends anteriorly beyond the anterior margin of the centrum, whereas the postzygapophyses extend posteriorly slightly beyond the margin of the centrum. The prezygapophyseal and postzygapophyseal

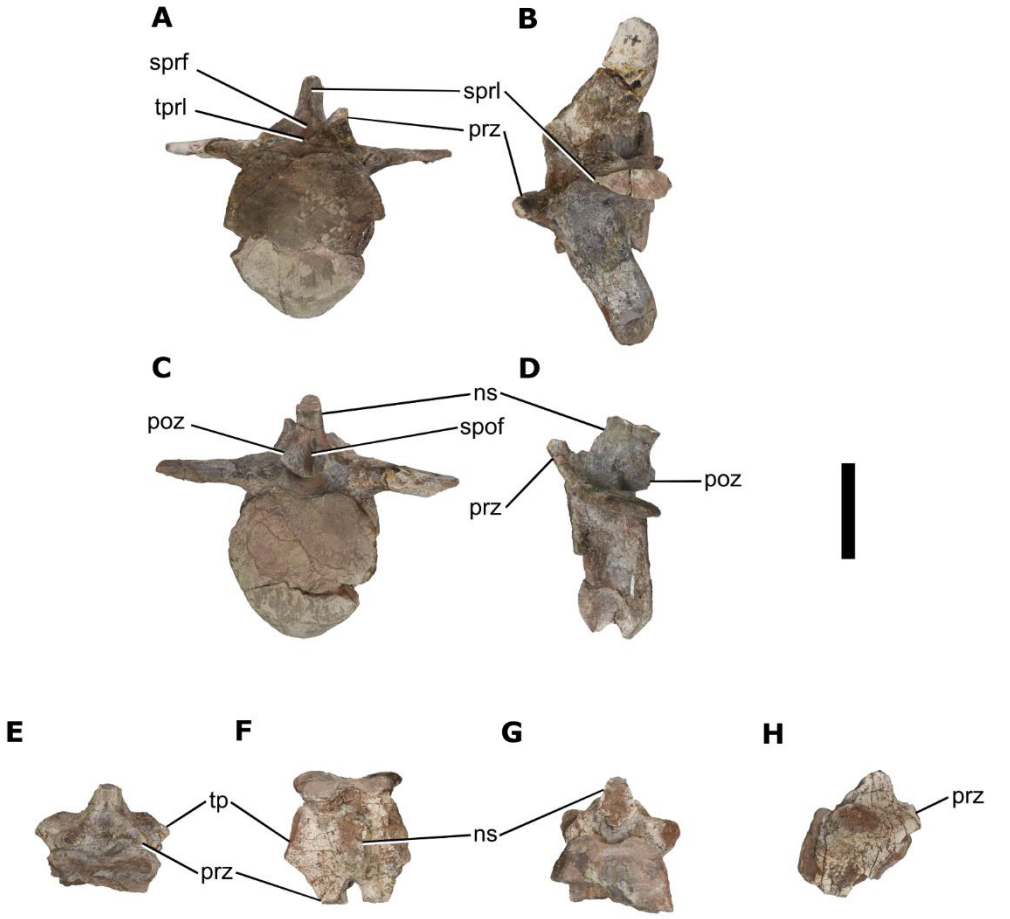

Figure 10: Anterior-to-middle caudal vertebra (A-D) and middle caudal (E-H) of BP/1/8469 in (A, E) anterior, (B, F) dorsal, (C, G) posterior, (D, H) lateral views. Abbreviations: ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; spof, spinopostzygapophyseal fossa; sprf, spinoprezygapophyseal fossa; sprl, spinopostzygapophyseal lamina; tp, transverse process; tprl, intraprezygapophyseal lamina. Scale bar = 10 cm.

facets are elliptical and are directed at an angle of 45° from the horizontal, this is higher than in *Lufengosaurus* (IVPP V15) but similar to *Melanorosaurus* (SAM-PK-3449). A small, deep sprf is created by an intraprezygapophyseal lamina (tprl) with the presence of a thin, deep spof, similar to *Pulanesaura* (BP/1/6646). A hyposphene-hypantrum articulation is not present in this caudal vertebra.

The centrum is short, and amphicoelous with a weakly concave posterior surface. The anterior and posterior surfaces of the centrum are taller than they are wide, giving them a subcircular shape in anterior and posterior view. The margins of the articular surfaces are thick and rounded. The ventral margin of the centrum is shallowly concave, and the ventral end of the anterior and posterior surfaces of the centrum curve mesially, similar to *Ledumahadi* (BP/1/7120) and *Sefapanosaurus* (BP/1/7425).

The preserved neurocentral sutural region of the middle caudal (Fig. 10 E-H) is described here. The dorsal portion of the posterior surface of the centrum is preserved with some distortion along the dorsoventral axis. The base of the neural spine is angled posteriorly. The proximal region of the transverse processes suggests that they are directed posterodorsally. It is unclear whether sprl are present, however, a shallow sprf is present between the base of the prezygapophyses.

Appendicular skeleton

Humerus

The right humerus is preserved in two fragments (Fig. 11), it is nearly complete with approximately 5 cm of the midshaft missing as well as portions of cortical bone along the lateral surface. The humerus has an overall gracile morphology with a distinct humeral shaft, and is widened along the anteroposterior axis at both the proximal and distal ends. The humerus is 69% of the total length of the femur that is associated with BP/1/8469.

The proximal surface of the humerus is convex and is mediolaterally thick with a lightly rugose texture. It is convex both transversely and anteroposteriorly forming a shallow semi-circular arc in medial and lateral views. The proximal surface of the humerus has a sinuous ridge that slopes and transitions onto the deltopectoral crest. The transitional region to the deltopectoral crest is positioned on the anteromedial corner of the proximal surface, and slopes sharply distally and medially without a clear break in slope. The humeral head is mesially positioned and is elliptical in proximal view. It is only slightly expanded on the proximal surface but bulges significantly on the medial margin, where it forms a rugose overhanging lip above the transition to the medial surface. This overhanging lip is not as distinct in other sauropodomorphs, but is present in *Sarahsaurus* (Marsh and Rowe, 2018) and *Antetonitrus* (BP/1/4952). The internal tuberosity is small and subtriangular in medial and lateral views. It projects similarly to SAM-PK-11849 and to *Plateosauravus* (SAM-PK-3342). There is a slight constriction on the mediolateral width of the proximal surface before it transitions to the proximal portion of the internal tuberosity. The lateral surface of the proximal end of the humerus is subtriangular, with the proximal margin forming an arc-like edge with the anterior and posterior margins

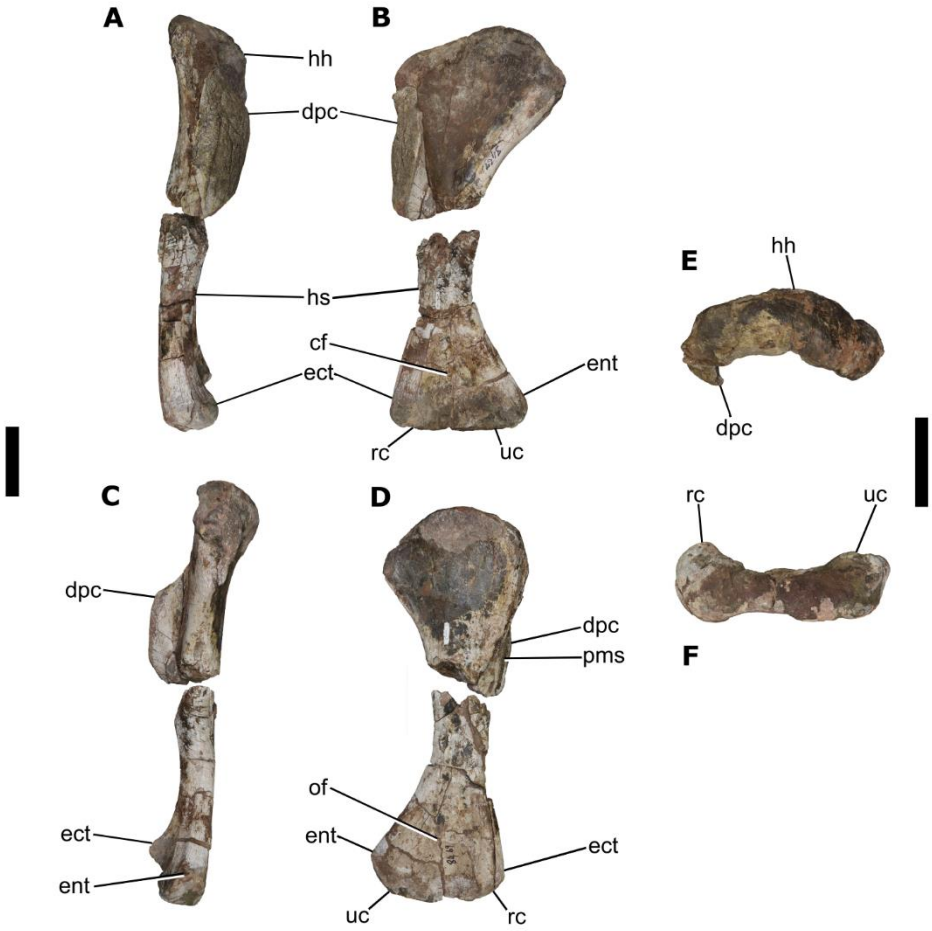

Figure 11: Right humerus (BP/1/8469) in (A) anterior, (B) medial, (C) posterior, (D) lateral, (E) proximal, (F) distal views. Abbreviations: cf, cuboid fossa; dpc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; hh, humeral head; hs, humeral shaft; of, olecranon fossa; pms, paramarginal sulcus; rc, radial condyle; uc, ulnar condyle. Scale bar = 10 cm.

sloping towards each other as they extend distally. Two prominent depressions are located anterior and posterior to the humeral head, these form shallow concave regions that lack clear boundaries. The rest of the lateral surface is convex, a condition usually seen in sauropodomorphs. There is a deep concavity immediately distal to the overhanging lip of the humeral head on the medial surface. A series of longitudinally oriented muscle scars extend into the cavity formed by the deltopectoral crest.

The deltopectoral crest is a proximodistally elongated ridge dominating the anterior surface of the proximal humerus, similar to *Riojasaurus* (Bonaparte, 1971) and *Plateosauravus* (SAM-PK-3342). Its proximal margin rises gradually from the anterior margin and the distal margin forms a sharp step as it joins the humeral shaft. It is subtrapezoidal in anterior view and mediolaterally relatively low. It has a rugose

medial surface. The most salient feature of the deltopectoral crest is a proximodistally oriented sulcus that runs parallel to its medial margin and is slightly offset. This sulcus is defined by a strong overhanging lip on the medial side as it grades into the cortical surface of the bone on the lateral side. This sulcus, identified as the paramarginal sulcus (McPhee *et al.*, 2014), is present in *Antetonitrus* (BP/1/4952) and possibly *Lufengosaurus* (IVPP V15). The deltopectoral crest is perpendicular to the transverse axis of the distal end.

The humeral shaft is considerably thinner than the rest of the humerus and has a clearly defined long region between the deltopectoral crest and the expansion of the distal end. This is similar to *Lufengosaurus* (IVPP V15) but opposite to what is seen in *Massospondylus* (BP/1/4934) with expanded proximal and distal ends with a short humeral shaft. The humeral shaft has a subcircular cross-section that is slightly longer than it is wide. There is much less axial twisting in the humerus relative to other early sauropodomorphs, where the twisting is defined by the angle between the transverse axes of the proximal and distal ends.

The distal end displays an hourglass shape in distal view. The distal end comprises a distinct radial condyle, distinct ulnar condyle, distinct entepicondyle, and an indistinct ectepicondyle. A deep cuboid fossa stretches between the condyles and extends toward the deltopectoral crest as a triangular fossa. A very shallow olecranon fossa is broadly spread over the distal end.

Radius

A right radius is preserved (Fig. 12), missing the proximal end and most of the shaft. The shaft is smooth, circular in cross-section, and narrower than the distal end. The distal end is longer than it is wide, common in most sauropodomorphs. In anterior view, the distal end flares out mediolaterally, as in *Antetonitrus* (BP/1/4952). The distal surface is shallowly convex with the anterolateral corner extending further. A pronounced tubercle is located on the posterolateral corner with a slight depression beside it, likely for the attachment of the ulnar ligament to the radius. The distal end is trapezoidal in distal view, similar to *Unaysaurus* (McPhee *et al.*, 2020).

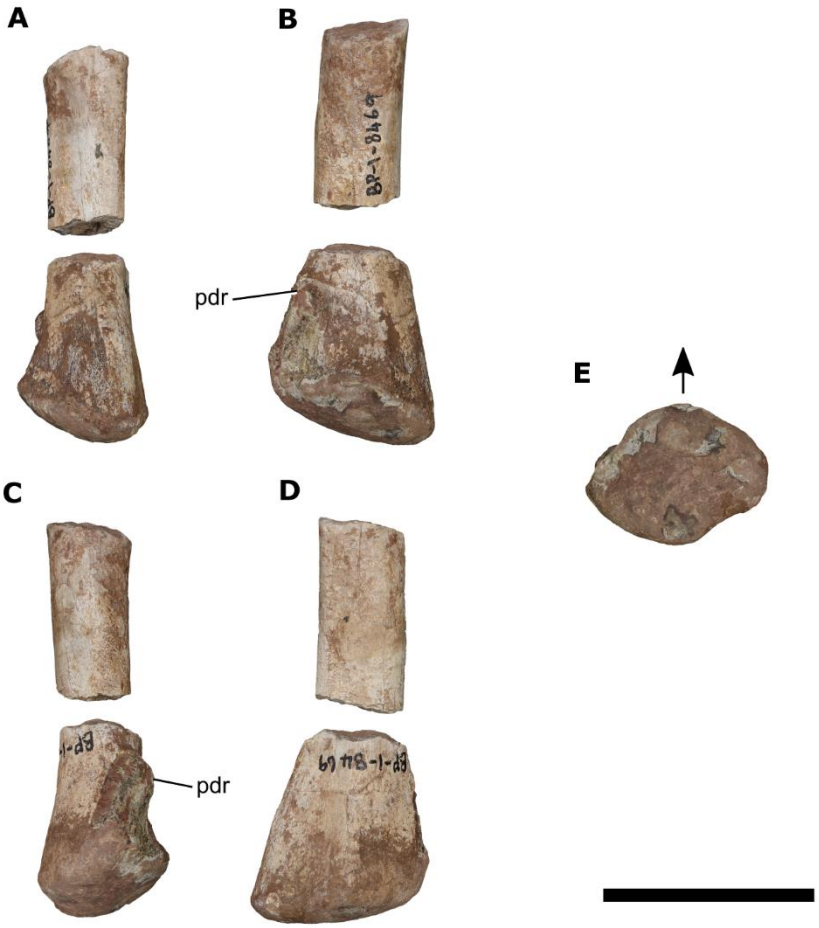

Figure 12: Right distal radius (BP/1/8469) in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) distal views. Abbreviations: pdr, posterodistal ridge. Arrow is directed laterally. Scale bar = 10 cm.

Manus

The few preserved fragments of the manus (Fig. 13-Fig. 15) are restricted to: the proximal end of the left metacarpal II (MCII); the proximal end of the left metacarpal IV (MCIV); the right phalanx 1 of digit I (I-1); right phalanx 1 of digit II (II-1); and the proximal end of two unguals that cannot be assigned to a digit or a side. Another left metacarpal IV (BP/1/8472) is the same size with the same morphology as BP/1/8469 and is referred to a different individual.

MCII (Fig. 13) is trapezoidal in proximal view with a narrower ventral margin than the dorsal margin. The proximal surface is convex, similar to *Ledumahadi* (BP/1/7120). The medial surface has a flat, rounded region near the proximal margin for the articulation of metacarpal I. The proximolateral corner bears a flange-like feature that extends laterally to underlie the adjacent metacarpal III. This prominent flange is not as pointed as in *Antetonitrus* (BP/1/4952).

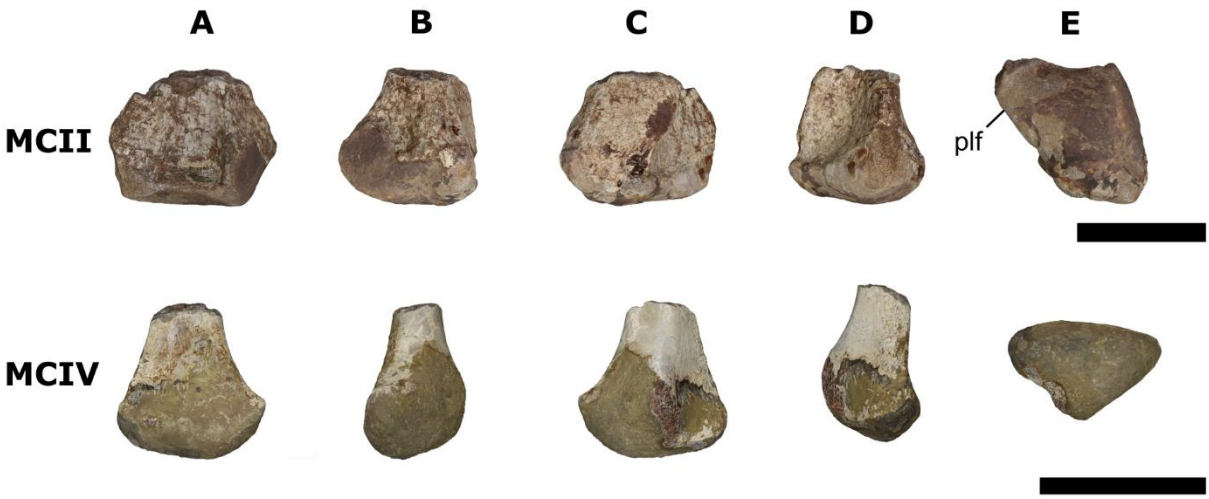

Figure 13: Left metacarpals II and IV of BP/1/8469 in (A) dorsal, (B) medial, (C) ventral, (D) lateral, (E) proximal views. Abbreviations: plf, proximolateral flange. Scale bar = 5 cm.

MCIV (Fig. 13) has a triangular proximal surface with the apex directed ventrolaterally, similar to *Tazoudasaurus* (Allain and Aquesbi, 2008). The proximal surface is convex. In dorsal view, the medial corner has a sharp angle with a rounded lateral corner. The shaft is subtriangular.

Manual phalanx I-1 (Fig. 14) is missing the dorsal portion of the distal condyles and the proximal articular surface is covered by irremovable sediment. The proximal surface is subcircular with the medial margin angled distally. The ventral margin is flat, and the dorsal margin is concave. The ventral portion of the condyles suggest that they were distinct with deep, collateral fossa. The distal end is twisted approximately 20° from the horizontal relative to the proximal end, this is similar to *Aardonyx* (BP/1/6611).

Manual phalanx II-1 (Fig. 14) has a subrectangular proximal surface with distinct proximal margins, and muscle scars present on the ventral surface. The condyles are asymmetrical with the lateral condyle projecting distally. There is a distinct intercondylar groove. There are shallow collateral ligament fossae.

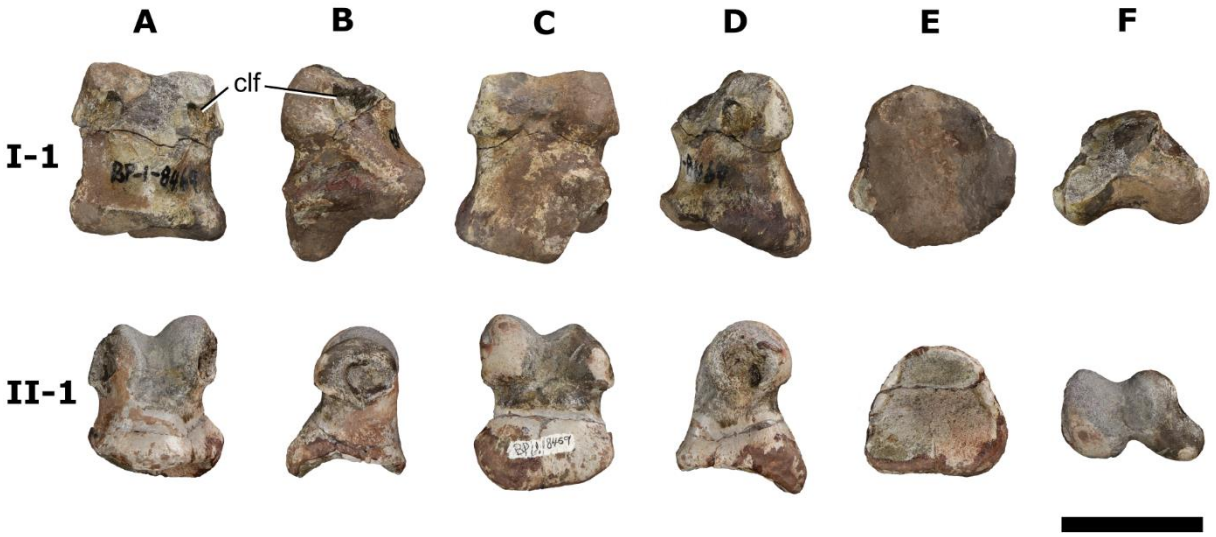

Figure 14: Right manual phalanges of Digits I and II (BP/1/8469) in (A) dorsal, (B) medial, (C) ventral, (D) lateral, (E) proximal, (F) distal views. Abbreviations: clf, collateral ligament fossa. Scale bar = 5 cm.

The first larger ungual (Fig. 15 A) has a flat ventral surface. The proximal surface is subtriangular in cross-section. The right lateral ridge is more distinct than the left lateral ridge. The intercondylar groove is prominent on the dorsal surface. The second smaller ungual (Fig. 15 B) has a weak ventral curve. The proximal surface has a rectangular cross-section with muscle scars along the proximal margin. Both the dorsal and ventral surfaces are relatively flat with ridges on the lateral surfaces.

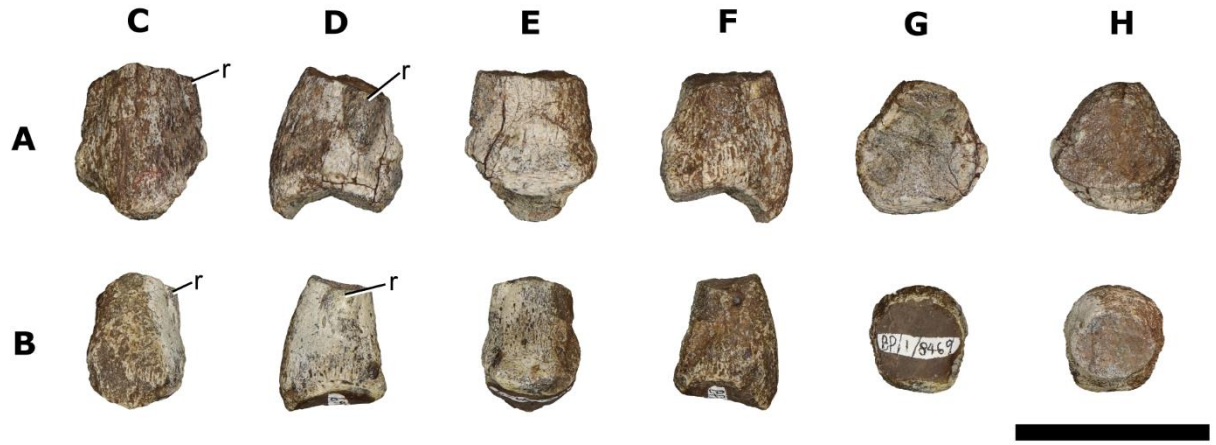

Figure 15: Manual unguals of BP/1/8469 (A & B) with undetermined positions in (C) dorsal, (D) right lateral, (E) ventral, (F) left lateral, (G) proximal, (H) distal views. Abbreviations: r, ridge. Scale bar = 5 cm.

Ilium

A near complete right ilium is preserved (Fig. 16), missing only a thin portion extending dorsoventrally from the iliac blade to the acetabulum. The ilium is large with an elongated iliac blade and an extensive acetabulum. The dorsal margin of the iliac blade is weakly convex and almost parallel to the longitudinal axis of the ilium, similar to *Schleitheimia* (Rauhut *et al.*, 2020) and *Melanorosaurus* (NMQR 1551). On the lateral surface, the region directly above the supracetabular crest is concave and extends to just above the ischial peduncle. Short striations are located along the dorsal margin of the iliac and are oriented dorsoventrally.

The preacetabular process is subtriangular in lateral view, with the apex in line with the dorsal margin of the iliac blade. The preacetabular process is short and taller

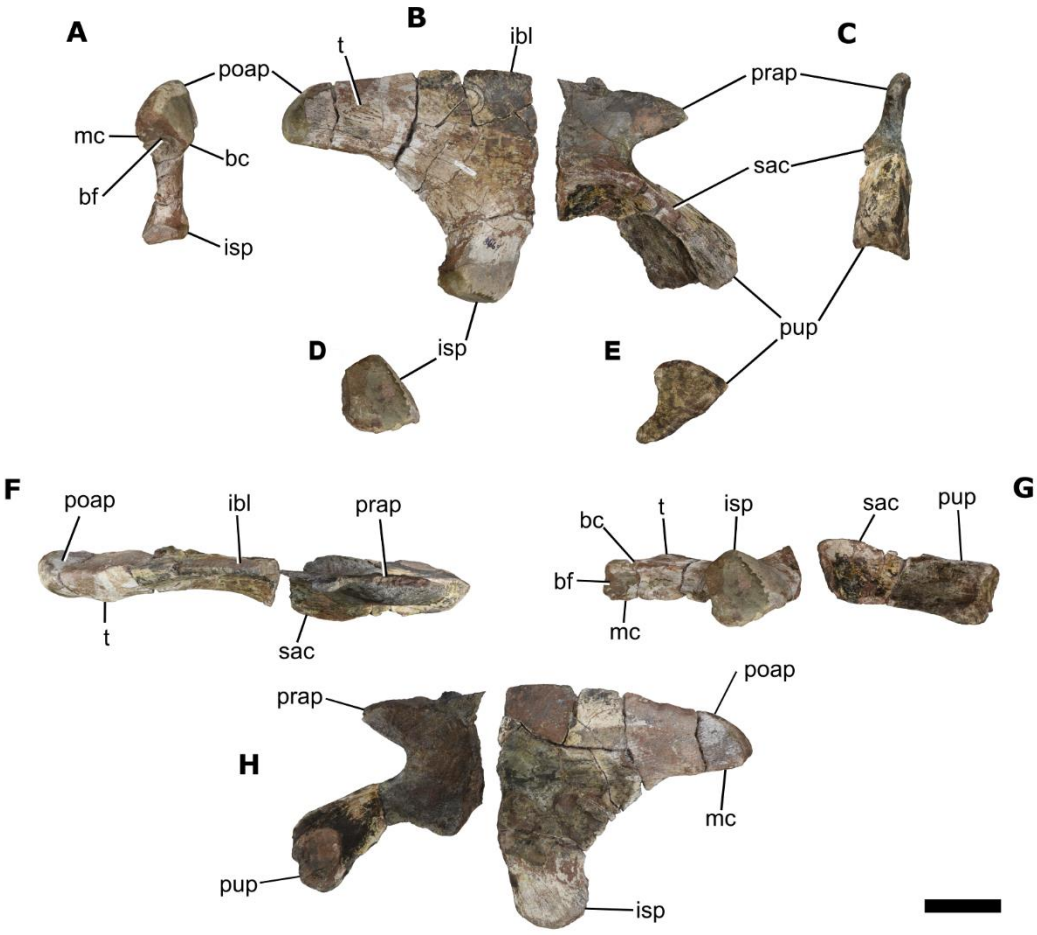

Figure 16: Right ilium (BP/1/8469) in (A) posterior, (B) lateral, (C) anterior, (F) dorsal, (G) ventral, and (H) medial views with distal views of the (D) ischial peduncle and (E) pubic peduncle. Abbreviations: bc, brevis crest; bf, brevis fossa; ibl, iliac blade; isp, ischial peduncle; mc, medial crest; poap, postacetabular process; prap, preacetabular process; pup, pubic peduncle; sac, supracetabular crest; t, tubercle. Scale bar = 10 cm.

than wide. It terminates posterior to the level of the anterior margin of the pubic peduncle, as in most sauropodomorphs. Muscle scars are visible along the dorsal margin of the preacetabular process. They are short striations that are set in the dorsal margin and are angled from anterior to posteroventrally.

The postacetabular process is low and longer than the preacetabular process. The posterior margin of the postacetabular process is subrectangular in lateral view, with a convex dorsal margin and an acute posteroventral corner. A ventrally facing brevis fossa is bordered by a lateral brevis crest and a medial crest. The fossa is longer than it is wide, extending for most of the postacetabular process with uniform width. The brevis fossa is shallow at its anterior end and becomes deeper towards the posterior end. The brevis fossa of BP/1/8469 is wider than in *Melanorosaurus* (NMQR 1551). Short, longitudinal striations representing a muscle origin are located on the lateral surface of the postacetabular process. These striations are raised like a tubercle, similar to *Melanorosaurus* (NMQR 1551).

The supracetabular crest shows typical morphology of EBSM. The crest runs along the lateral margin of the pubic peduncle, originating at the anteroventral corner of the peduncle, bordering the acetabulum, and terminating at the posterior end of the acetabulum just anterior to the ischial peduncle. The supracetabular crest is a prominent ridge that projects laterally slightly. The dorsal roof of the acetabulum is concave to flat. The acetabulum is longer than it is wide.

The pubic peduncle curves anteroventrally, scribing a shallow arc in lateral view, and its cross-section is triangular. The distal surface of the pubic peduncle has a light rugose texture. The pubic peduncle is mediolaterally broader than the preacetabular process with a smooth ventral surface. The medial margin of the pubic peduncle is taller than its lateral margin. The distal end of the pubic peduncle terminates dorsal to the level of the distal end of the ischial peduncle, similar to *Melanorosaurus* (NMQR 1551). The ischial peduncle is dorsoventrally shorter than the pubic peduncle with a smooth distal surface. The posterior margin of the ischial peduncle has a pronounced heel on the posteroventral corner, similar to *Plateosaurus* (Moser, 2003) and *Antetonitrus* (BP/1/4952).

Pubis

A nearly complete right pubis is associated with BP/1/8469, missing only the ischial pedicel and obturator foramen (Fig. 17). The medial margin along the pubic apron is badly fragmented. The pubis is long, slender, and twisted along its length. The iliac pedicel has a flat proximal margin and is anteroposteriorly wide and mediolaterally thick, as observed in *Mussaurus* (Otero and Pol, 2013). The proximal surface has a lightly rugose texture, similar to the ilium. A pronounced, raised, hemispherical tubercle is located on the lateral surface of the iliac pedicel, present in most sauropodomorphs.

The pubic apron extends straight, and is anteroposteriorly thin and wide. The distal surface of the pubic apron is anteroposteriorly expanded and curves slightly posteriorly in lateral view. The distal surface is triangular in distal view with the apex directed posterolaterally. The lateral margin of the pubic apron is thick and rounded,

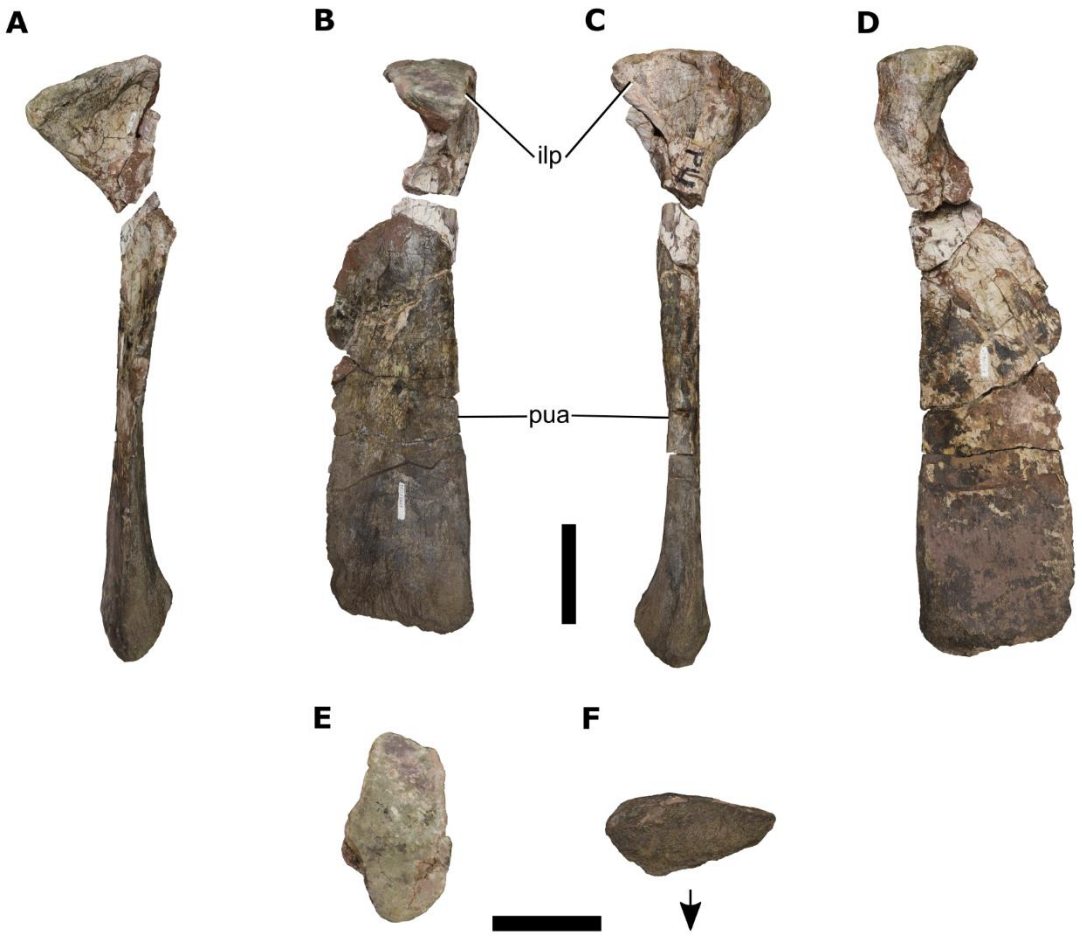

Figure 17: Right pubis (BP/1/8469) in (A) medial, (B) posterior, (C) lateral, (D) anterior, (E) proximal, (F) distal views. Abbreviations: ilp, iliac pedicel; pua, pubic apron. Arrow is directed posteriorly. Scale bar = 10 cm.

whereas the medial margin is much thinner. The pubic apron in BP/1/8469 is much longer and narrower than the shorter and broader pubes of *Antetonitrus* (BP/1/4952) and *Tazoudasaurus* (Allain and Aquesbi, 2008). The proximal margin of the iliac pedicel is perpendicular to the distal margin of the pubic apron, whereas this is 45° in *Melanorosaurus* (NMQR 1551).

Femur

A complete right femur is preserved in four fragments (Fig. 18). Possible traces of indeterminate predatory behaviour (teeth impressions) are located on the anterior surface of the distal end, above the lateral condyle. The femur is large and robust. The femoral head is perpendicular to the longitudinal axis of the femoral shaft, as in most sauropodomorphs. The proximal surface of the femoral head is heavily rugose in comparison to the humerus. The mediolateral axis of the femoral head is directed slightly anteriorly. The proximal surface of the femoral head is convex, with the proximolateral margin sloping posteriorly, resulting in a horizontal proximal surface in anterior view and a laterally sloping proximal surface in posterior view. The femoral head morphology of BP/1/8469 is also seen in *Jingshanosaurus* (Zhang and Yang, 1994). A pronounced posterior tubercle is located proximomedially in posterior view, similar to that of *Eucnemesaurus* (BP/1/6234).

The greater trochanter is a discrete, raised ridge along the lateral margin of the femoral head. The proximal extent of the greater trochanter begins at the same level as the ventral margin of the femoral head, and the distal extent of the greater trochanter grades into the femoral shaft. The lesser trochanter is located on the lateral margin of the femoral shaft and is proximodistally oriented. The lesser trochanter is a well-developed, protruding ridge, similar to SAM-PK-11851 and to a lesser extent *Antetonitrus* (BP/1/4952) as well. The proximal extent of the lesser trochanter is perpendicular to the femoral shaft, and its distal extent grades into the femoral shaft. The lesser trochanter has a prominent lateral projection and is not visible in posterior view, similar to *Melanorosaurus* (NMQR 1551). Short, longitudinal striations occur between the greater and lesser trochanters.

The fourth trochanter is a large, pronounced, subrectangular crest. It is located along the medial margin of the femoral shaft, immediately dorsal to its midpoint, whereas in *Plateosauravus* (SAM-PK-3602) the trochanter is more centrally located and projects posteriorly with no deflection. The fourth trochanter is directed

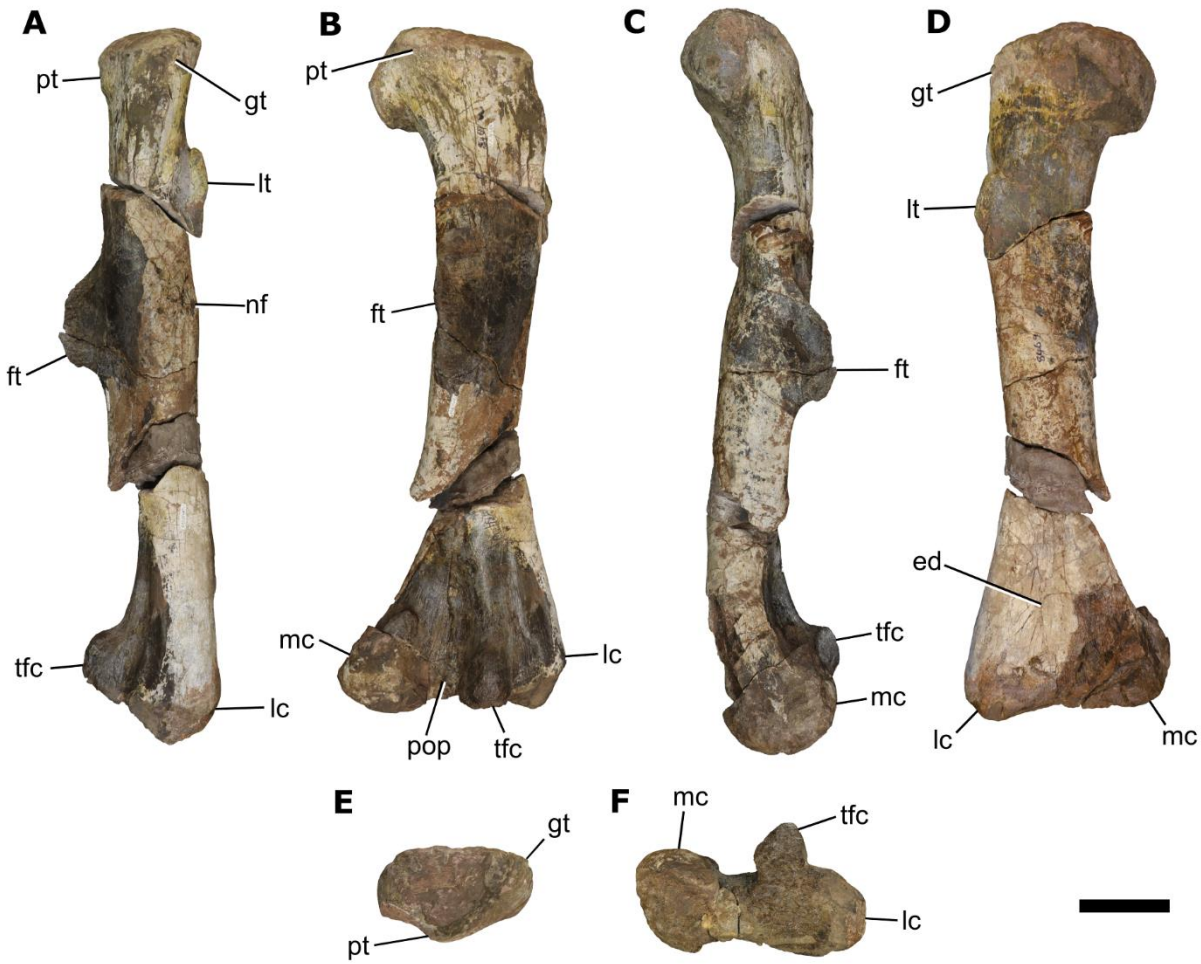

Figure 18: Right femur (BP/1/8469) in (A) lateral, (B) posterior, (C) medial, (D) anterior, (E) proximal, (F) distal views. Abbreviations: ed, extensor depression; fh, femoral head; fs, femoral shaft; ft, fourth trochanter; gt, greater trochanter; lc, lateral condyle; lt, lesser trochanter; mc, medial condyle; nf, nutrient foramen; pop, popliteal fossa; pt, posterior tubercle; tfc, tibiofibular crest. Scale bar = 10 cm.

posteromedially with a sulcus on the medial surface that runs for almost the entire proximodistal length of the trochanter. This sulcus is also present in *Antetonitrus* (BP/1/4952) and *Aardonyx* (BP/1/6510). Muscle striations are present around the fourth trochanter, similar to *Antetonitrus* (BP/1/4952). The proximal extent of the fourth trochanter rises gradually from the femoral shaft, but the distal extent is more abrupt, joining the shaft almost perpendicular to the longitudinal axis of the shaft. The fourth trochanter morphology in BP/1/8469 is seen in many EBSM such as *Plateosaurus* (Moser, 2003) and *Riojasaurus* (Bonaparte, 1971).

The femoral shaft is straight compared to most EBSM that have a sigmoidal shaft. Its cross-section is elliptical being longer than wide, similar to *Mussaurus* (Otero and Pol, 2013). A nutrient foramen is located on the lateral surface of the

femoral shaft opposite the fourth trochanter. The distal end is wider than the femoral shaft and curves slightly posteriorly. A deep, proximodistally elongate popliteal fossa is present between the medial and lateral condyles. The tibiofibular crest is pronounced and posteriorly projecting. It is proximodistally taller than it is wide, similar to *Ledumahadi* (BP/1/7120). The medial condyle is rectangular and the lateral condyle is rounded in distal view. A shallow extensor depression extends for most of the distal end and onto the femoral shaft.

Tibia

A complete, robust right tibia (BP/1/8469; Fig. 19) and the distal end of a referred right tibia (BP/1/8463) are preserved. Both are of similar size with identical morphology to each other. The complete tibia is considered to be part of the

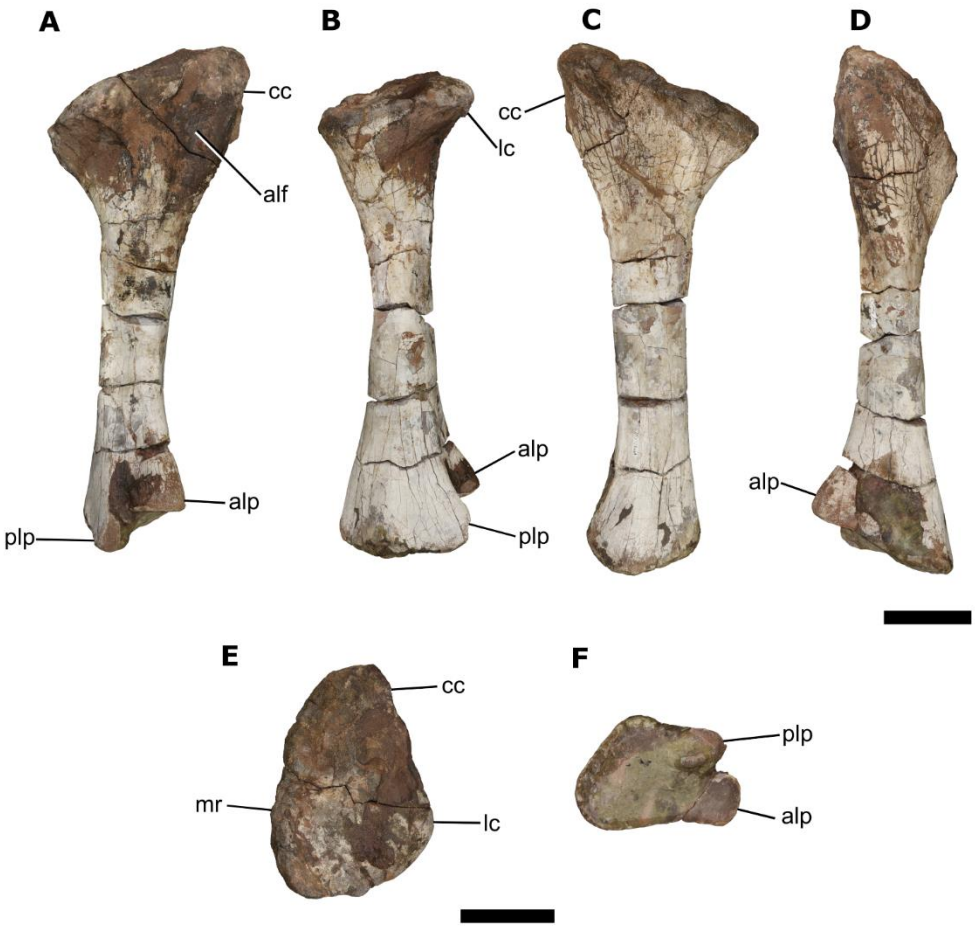

Figure 19: Right tibia (BP/1/8469) in (A) lateral, (B) posterior, (C) medial, (D) anterior, (E) proximal, (F) distal views. Abbreviations: alf, anterolateral fossa; alp, anterolateral process; cc, cnemial crest; lc, lateral condyle; mr, medial ridge; plp, posterolateral process. Scale bar = 10 cm.

individual associated with BP/1/8469 as the size is congruent with the material from the main quarry, and the description will be based on this complete tibia.

The tibia has comparable robustness to *Blikanasaurus* (SAM-PK-403), whereas the tibia of early branching sauropodomorphs like *Saturnalia* (Langer, 2003) are much thinner. The proximal surface is anteroposteriorly expanded relative to the tibial shaft. The proximal surface is subtriangular in proximal view, with the apex directed anteriorly and with the lateral condyle projecting strongly laterally so that it expands beyond the level of the lateral surface of the tibial shaft. The lateral condyle is a semi-circular protuberance. The proximal surface is longer than it is wide, similar to *Lufengosaurus* (IVPP V15).

The most salient feature of the tibia is the hypertrophied proximal end, which bears a prominent cnemial crest. The cnemial crest is rounded rather than angular. The cnemial crest protrudes anteriorly from the anterior surface of the tibia, lacking the anterolateral deflection as in *Plateosauravus* (SAM-PK-3341). Its proximal surface extends further proximally to the level of the posterior end of the proximal tibial surface, so that the proximal margin of the tibia faces posteroproximally in medial and lateral views. This angled proximal margin is also seen in *Blikanasaurus* (SAM-PK-403) but may be exaggerated due to taphonomy or pathology. A slight depression is present posterior to the cnemial crest in lateral view, identified here as the anterolateral fossa.

The shaft of the tibia is smooth and slender with relatively consistent width. The shaft is triangular in cross-section, as is typical of non-sauropodan sauropodomorphs. The distal end of the tibia is wider than it is long, commonly seen in EBSM such as *Mussaurus* (Otero and Pol, 2013) and *Blikanasaurus* (SAM-PK-403). The distal articular surface is subtrapezoidal in distal view, similar to *Melanorosaurus* (SAM-PK-3449) and *Kholumolumo* (Peyre de Fabrègues and Allain, 2020). The anterolateral process gradually slopes to distally join the posterolateral process that gently creates a convex distal surface. A concavity is present between the anterolateral and posterolateral processes for the articulation of the astragalus.

Fibula

A nearly complete right fibula (Fig. 20) that is lacking the proximal and distal ends of the shaft is preserved. The medial surface of the proximal end is concave, and the lateral surface is convex, resulting in a crescentic proximal end in proximal view. This is also seen in *Aardonyx* (BP/1/6316) and *Antetonitrus* (BP/1/4952). The proximal end is longer than it is wide, with the thickest margin located anteriorly and

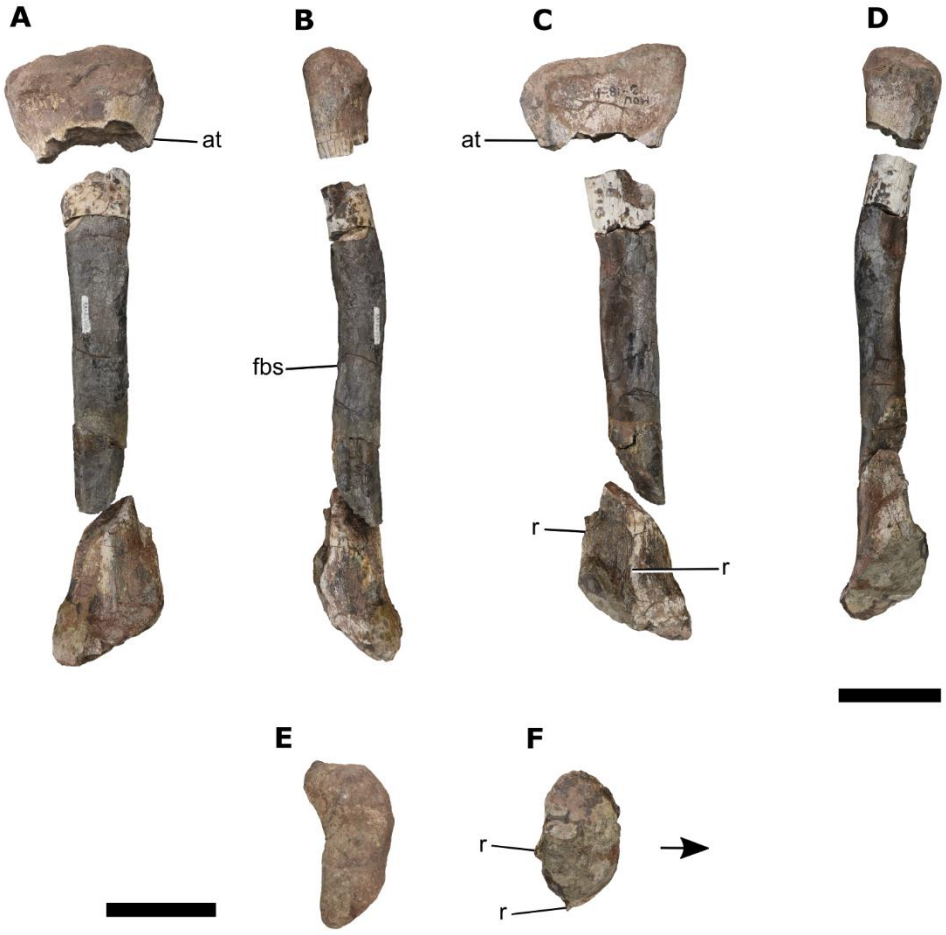

Figure 20: Right fibula (BP/1/8469) in (A) lateral, (B) posterior, (C) medial, (D) anterior, (E) proximal, (F) distal views. Abbreviations: at, anterior trochanter; fbs, fibular shaft; r, ridge. Arrow directed laterally. Scale bar = 10 cm.

becomes narrower towards the posterior margin. The proximal extent of the anterior trochanter projects anteriorly so that it is visible in proximal view, similar to *Tazoudasaurus* (Allain and Aquesbi, 2008), but differs in *Antetonitrus* (BP/1/4952) as the anterior trochanter is not visible in proximal view.

The fibular shaft is elliptical being longer than it is wide. The shaft displays weak lateral bowing. The lateral bowing of the fibula is also present in early sauropodomorphs such as *Riojasaurus* (Bonaparte, 1971) as well as later branching

sauropodomorphs like *Blikanasaurus* (SAM-PK-403). A small ridge is present on the anterior surface of the midshaft alongside a shallow depression. A slight bulge is located on the lateral surface proximal to the midshaft, possibly homologous to the lateral trochanter in *Tazoudasaurus* (Allain and Aquesbi, 2008).

The distal end is longer than it is wide. In lateral view, the distal end is triangular with a flat surface that is sloping posterodistally and the posterodistal corner creating a sharp angle. The medial surface has a thin longitudinal ridge located on the anterior margin, and a second thin longitudinal ridge located mesially, creating a fossa between the ridges. The presence of these two ridges is considered autapomorphic in BP/1/8469.

Astragalus

A complete right astragalus (BP/1/8469; Fig. 21 A-F), the lateral end of a right astragalus (BP/1/8461), and a nearly complete left astragalus (BP/1/8472) with the proximal margin slightly eroded are preserved. The astragali are identical in size and morphology, and probably conspecific. The description is based on the complete astragalus (BP/1/8469) is assigned to the individual from the main quarry as the size matches that of the tibia and it articulates to the distal end of the tibia.

The astragalus (Fig. 21 A-F) is trapezoidal in proximal view with a shorter lateral margin than the medial margin and a narrower posterior margin than the anterior margin. This trapezoidal shape of the astragalus is similar to *Blikanasaurus* (SAM-PK-403), whereas EBSM like *Jaklapallisaurus* (Novas *et al.*, 2010) the astragalus is rectangular. The distal surface is highly convex representing a ‘rolling joint’, similar to *Blikanasaurus* (SAM-PK-403). A constriction along the proximodistal axis is evident near the lateral end and can be seen in both posterior and anterior views. The lateral surface is straight in proximal view and the medial margin is slanted creating a pointed anteromedial corner. The astragalus is subrectangular in lateral view.

The most salient feature of the astragalus is the presence of two vascular foramina, located on the facet for the posterolateral process of the tibia. The other incomplete astragalus (BP/1/8461) also bears two vascular foramina rather than the conventional one foramen and is possibly autapomorphic. The medial side of the proximal surface bears a concavity in its mesial portion, which is bounded anteriorly

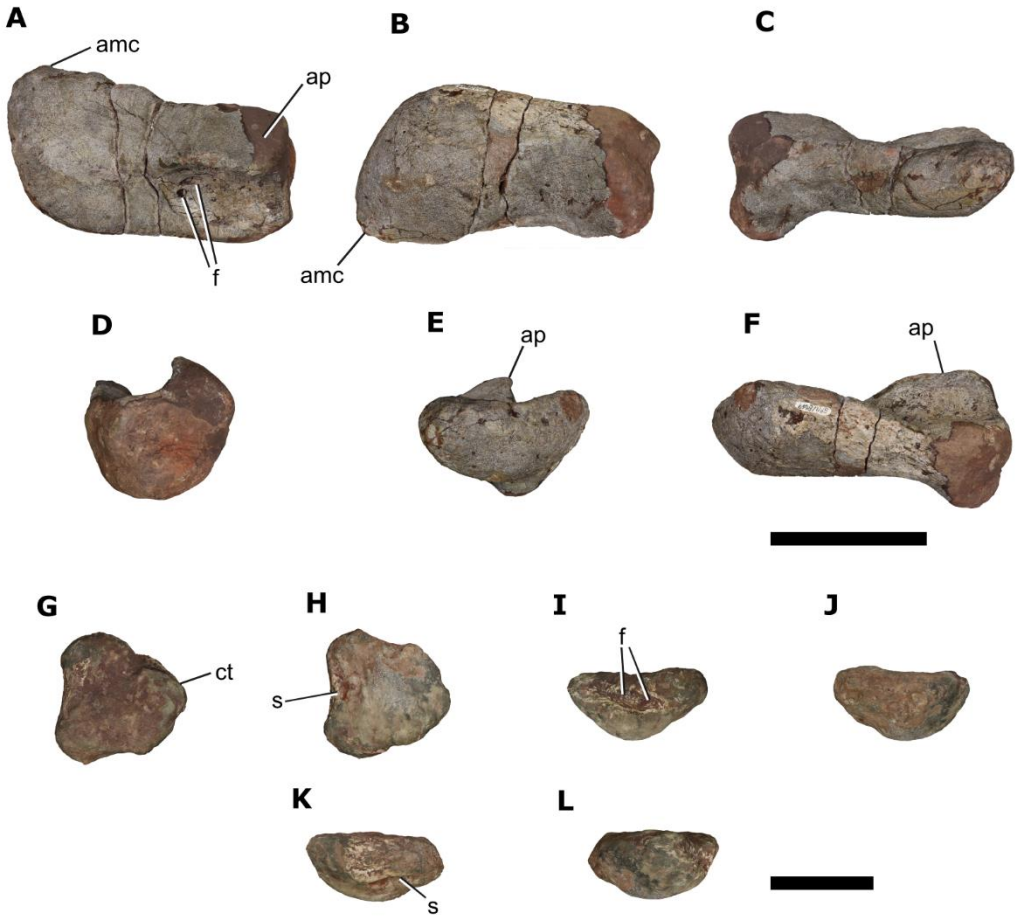

Figure 21: Right astragalus (A-F) and right calcaneum (G-L) of BP/1/8469 in (A) proximal, (B) distal, (C) anterior, (D) medial, (E) lateral, (F) posterior views. Calcaneum in (G) proximal, (H) distal, (I) anterior, (J) posterior, (K) medial, (L) lateral views. Abbreviations: amc, anteromedial corner; ap, ascending process; ct, calcaneal tuber; f, fossa; s, sulcus. Scale bar = 10 cm (A-F), 5 cm (G-L).

and posteriorly by proximally curving margins of the bone. This is in contrast to *Sefapanosaurus* (BP/1/386) where this region is flat.

The ascending process is subrectangular in proximal view and sloping anteriorly with a convex margin. The posterior margin of the ascending process is well-defined. The ascending process in BP/1/8469 is proportionately lower than in *Sefapanosaurus* (BP/1/386). The facet for the posterolateral process of the tibia is concave. The posterior margin forms a lip of bone that articulated with the tibia, similar to many EBSM such as *Plateosaurus* (Moser, 2003), *Lufengosaurus* (IVPP V15), and *Xingxiulong* (Wang *et al.*, 2017).

Calcaneum

A complete right calcaneum is preserved (Fig. 21 G-L). It is a third of the width of the astragalus. The calcaneum is triradiate in proximal and distal views. It is mesially thicker and becomes thinner towards the margins, as in *Sarahsaurus* (Marsh and Rowe, 2018). The proximal surface is flat, and the distal surface is convex. The medial surface of the calcaneum is concave for articulation with the astragalus. The anterior surface has two foramina. The posterior surface has a shallow, transversely oriented concavity. The anteromedial and posteromedial processes are relatively well-developed with a pronounced calcaneal tuber.

Pes

Multiple elements of the pes, including metatarsals, phalanges, and unguals are preserved, and the descriptions below are based on the most complete elements (Fig. 22-Fig. 28). The proximal end of a left metatarsal I (MTI; Fig. 22 A) and the distal end of right MTI (Fig. 22 B) are preserved. The proximal end of the left MTI is wider than it is tall. It has a flat dorsal surface and a concave ventral surface. The lateral corner of the proximal end tapers and slopes ventrally. The distal end of the right MTI is wide with a smaller medial condyle and a larger lateral condyle separated by a distinct ventral groove. The lateral condyle is so large that it occupies the majority of the mediolateral breadth of the distal end. The distinct ventral groove in BP/1/8469 is much wider and deeper than those present in other sauropodomorphs

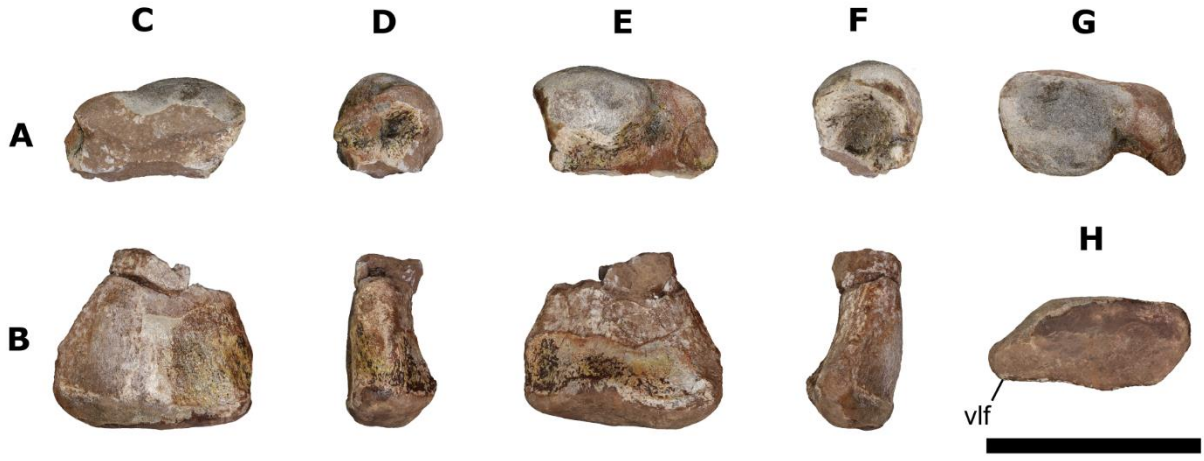

Figure 22: Metatarsals I of BP/1/8469. Distal end of right MTI (A) in (C) dorsal, (D) medial, (E) ventral, (F) lateral, (G) distal views. Proximal end of left MTI (B) in (C) dorsal, (D) medial, (E) ventral, (F) lateral, (H) proximal views. Abbreviations: vlf, ventrolateral flange. Scale bar = 10 cm.

such as *Aardonyx* (BP/1/6893) and *Antetonitrus* (BP/1/4952). The dorsal surface is shallowly convex. Deep collateral ligament fossae are present with the lateral fossa larger than the medial fossa.

A complete left (Fig. 23 A-F) and right metatarsal III (MTIII; Fig. 23 G-L) are preserved. The most salient feature of MTIII is the presence of a notch (indicated by the arrow in Fig. 23 F & L) located at the midpoint of the lateral margin at the proximal end. This notch is present on both MTIII and represents an autapomorphy. The proximal surface is flat and is triangular in proximal view with the apex directed ventromedially. The proximal surface is lightly rugose similar to the other limb

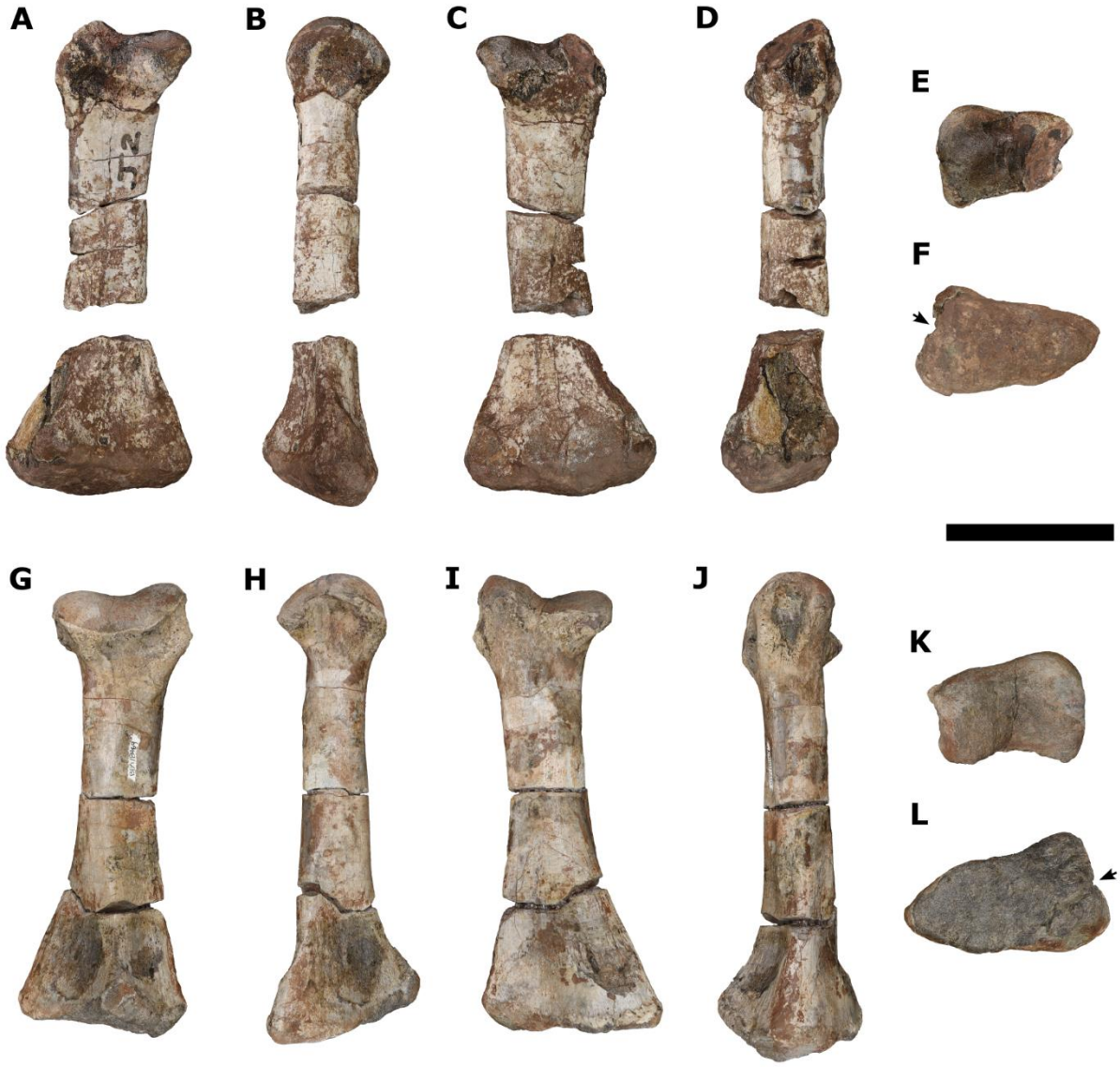

Figure 23: Metatarsals III of BP/1/8469. The left MTIII (A-F) and right MTIII (G-L) in (A, G) dorsal, (B, H) medial, (C, I) ventral, (D, J) lateral, (E, K) distal, (F, L) proximal views. The arrow in the proximal view is indicating the notch on the lateral margin. Scale bar = 10 cm.

elements of BP/1/8469. A ridge originates from the lateral side of dorsal surface and grades into the shaft at just before the midpoint, creating a large, shallow concavity on the lateral surface of the proximal end. This concavity is also seen in *Melanorosaurus* (NMQR 1551). The shaft is smooth and triangular in cross-section. The distal end is twisted laterally relative to the proximal end at 25° from the horizontal. The distal condyles are asymmetrical with the medial condyle wider and taller than the lateral condyle. The distal end is trapezoidal in distal view. The collateral ligament fossa is shallow on the medial side and deep on the lateral side.

A complete left metatarsal IV (MTIV; Fig. 24 A-F) and the distal end of a right MTIV (Fig. 24 G-K) are preserved. The proximal end of MTIV is wide and dorsoventrally thin with the lateral side dorsoventrally thicker than the medial side. A ridge originates from the midpoint of the proximal end on the dorsal surface and grades into the shaft creating a shallow depression on the medial surface, similar to MTIII. The shaft of MTIV is smooth with weak ventral bowing. The distal end is subrectangular in distal view with a ventrolateral flange. Distinct condyles are present with the medial condyle larger than the lateral condyle. The collateral ligament fossa

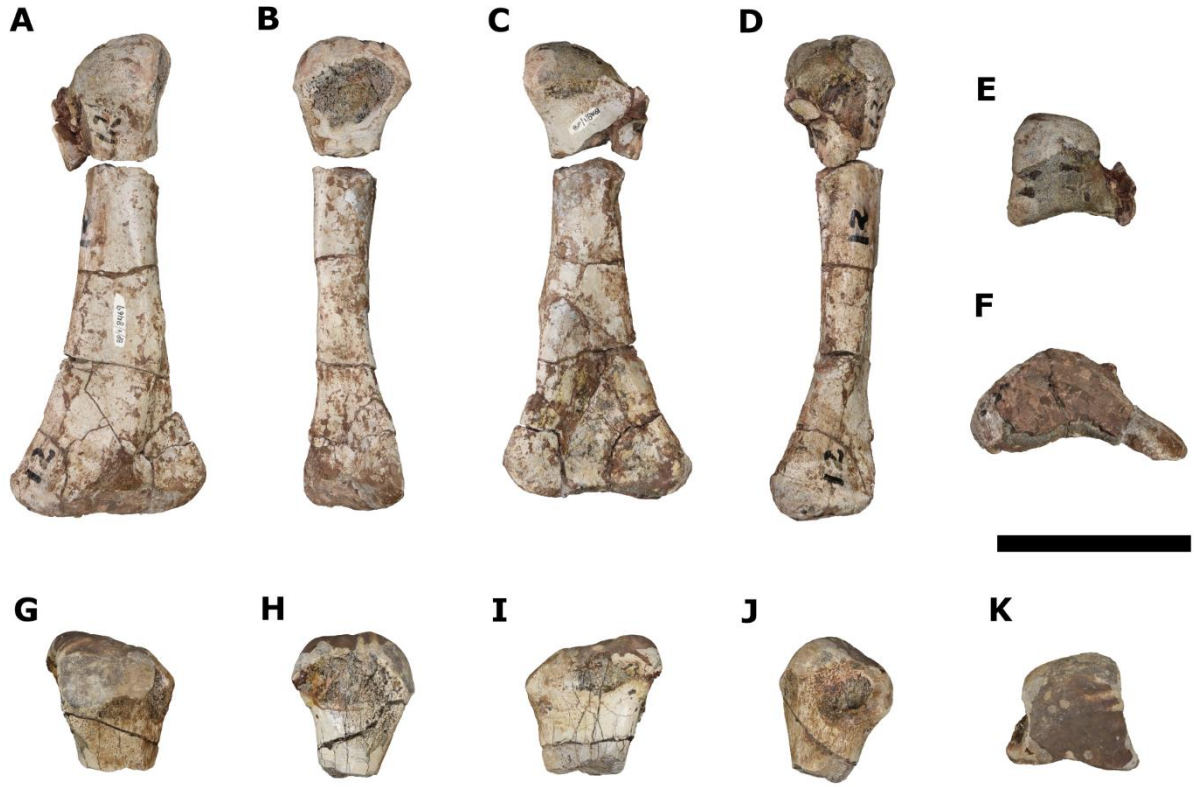

Figure 24: Metatarsals IV of BP/1/8469. The complete left MTIV (A-E) and distal end of right MTIV (H-K) in (A, G) dorsal, (B, H) medial, (C, I) ventral, (D, J) lateral, (E, K) distal, and (F) proximal views. Scale bar = 10 cm.

is similar in size to those of MTIII. The distal surface has a light rugose texture, similar to the other limb elements of BP/1/8469.

A complete left metatarsal V (MTV) is associated with BP/1/8469 (Fig. 25) and displays the plesiomorphic paddle-shaped morphology seen in *Lessemsaurus* (Pol and Powell, 2007). MTV has a slight medial curve in dorsal view and the distal end curves dorsally. The proximal surface is dorsoventrally flat and wide. The medial side of the proximal surface is dorsoventrally thinner than the lateral side. The distal end is rectangular in distal view. The ventral surface has a small tuberosity just proximal to the distal surface.

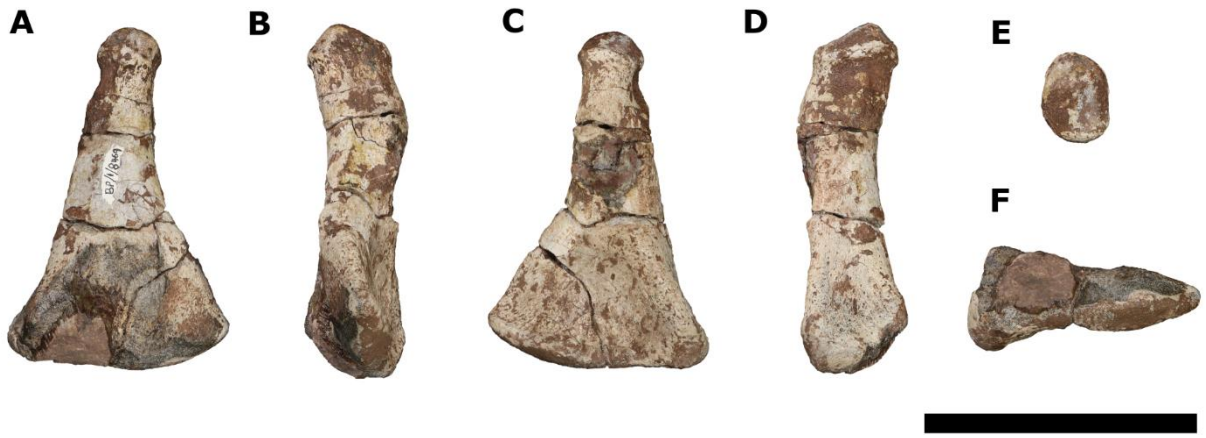

Figure 25: Left metatarsal V (BP/1/8469) in (A) dorsal, (B) medial, (C) ventral, (D) lateral, (E) distal, (F) proximal views. Scale bar = 10 cm.

Unguals of the first (I-2; Fig. 26 A-F) and second (II-3; Fig. 26 G-L) digit of the right pes are preserved and are the largest unguals associated with BP/1/8469. The proximal end of ungual I-2 is taller than wide whereas ungual II-3 is subcircular. The proximal surface of both unguals are triangular with the apex directed dorsolaterally. The ventral surface of ungual I-2 is concave and almost flat in ungual II-3. Distinct medial and lateral ridges are present on both unguals. Short, longitudinal striations are present on the dorsal margin of the proximal end of both unguals. The dorsal margin of the unguals are directed laterally creating an asymmetrical ungual, whereas *Mussaurus* (Otero and Pol, 2013) has vertically oriented unguals that are symmetrical.

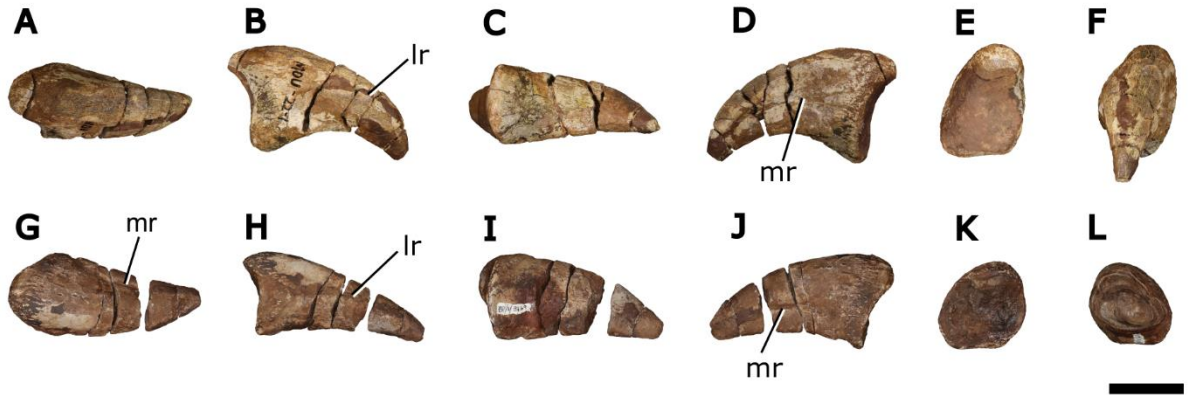

Figure 26: Right pedal digit I (A-F) and digit II (G-L) unguals in (A, G) dorsal, (B, H) medial, (C, I) ventral, (D, J) lateral, (E, K) proximal, (F, L) distal views. Abbreviations: lr, lateral ridge; mr, medial ridge. Scale bar = 5 cm.

The phalanges of digit III of the left pes are associated and can be rearticulated in their life positions (Fig. 27). The third pedal digit has a phalangeal count of four, as is typical of most EBSM such as *Sarahsaurus* (Marsh and Rowe, 2018). In general, the phalanges of BP/1/8469 are proximodistally short and robust with some resemblance to those of *Blikanasaurus* (SAM-PK-403). All pedal phalanges have: similar width to proximodistal lengths; the proximal and distal surfaces are wider than tall; deep collateral ligament fossae on the medial and lateral surfaces of the distal end; distinct intercondylar grooves; and short striations along the margins of the proximal surface. Pedal phalanx III-1 has distinct condyles with the medial condyle slightly wider than the lateral condyle. The shaft has a flat dorsal surface and concave ventral surface. The shaft of pedal phalanx III-2 and III-3 have a concave dorsal margin and a concave ventral margin. The ungual III-4 is missing the margins along the proximal surface and the distal end. Small, circular cavities are present on the medial and lateral surfaces of the proximal end just behind the medial and lateral ridges. These cavities are likely attributable to pathology but is currently indeterminate. The ungual is triangular in cross-section with its apex directed dorsolaterally. Short striations are present along the margin of the proximal surface. It has a convex dorsal surface and a flat ventral surface. The lateral ridge is more distinct than the medial ridge.

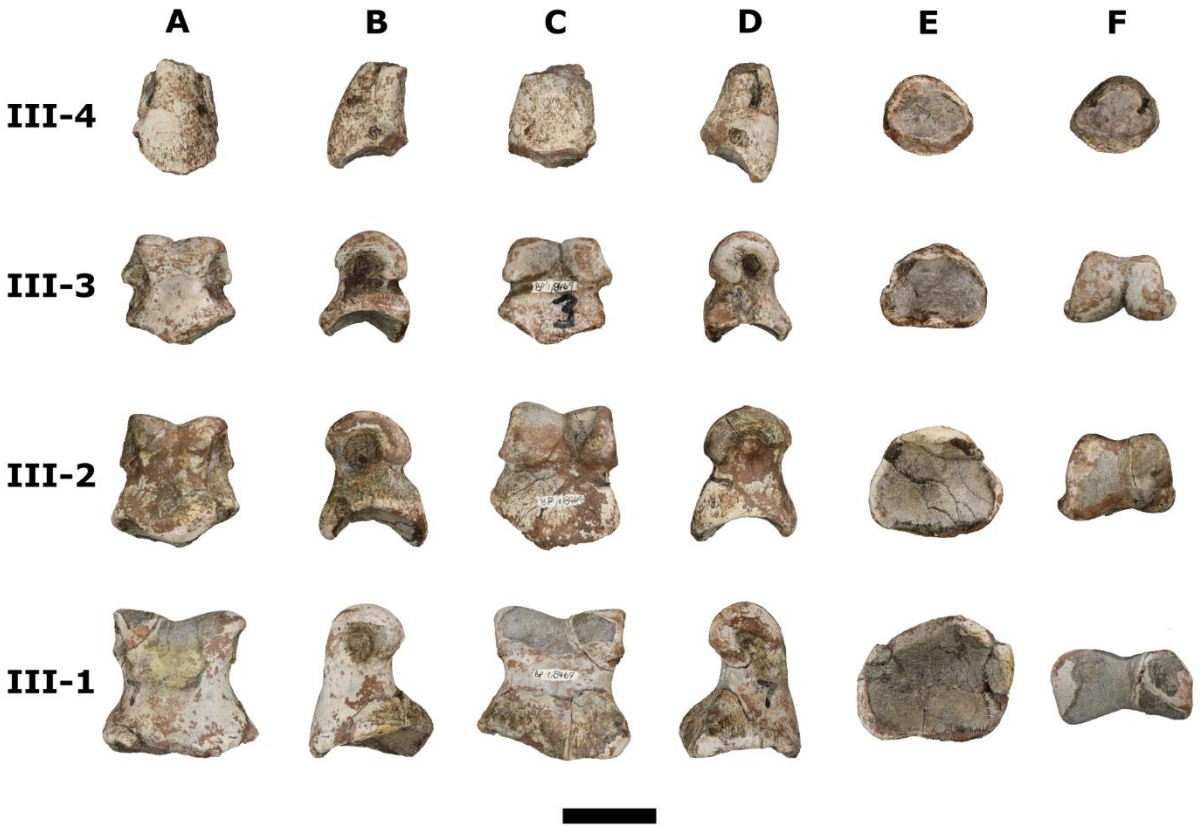

Figure 27: Left pedal digit III (BP/1/8469) with phalanges 1 to 3 and ungual in (A) dorsal, (B) medial, (C) ventral, (D) lateral, (E) proximal, (F) distal views. Scale bar = 5 cm.

Three of the phalanges that are associated with BP/1/8469 are considered pedal, however they cannot be attributed to a digit and are here lettered A – C (Fig. 28). Phalanx A is partially preserved with proximal surface badly damaged and missing the left condyle. This phalanx is relatively large with a distinct right condyle, collateral ligament fossa, and is likely phalanx I-1. Phalanx B and C have proximal and distal ends that are wider and tall, the right condyle is wider than the left condyle, and deep collateral ligament fossae. Both phalanx B and C have a shaft with a concave ventral surface, but the dorsal surface of phalanx B is concave and phalanx C is flat.

Figure 28: Undetermined pedal phalanges, views from left to right. Phalanx A in dorsal, right lateral, ventral, distal views. Phalanx B in dorsal, right lateral, ventral, left lateral, distal and proximal views. Phalanx C in dorsal, right lateral, ventral, left lateral, distal and proximal views. Scale bar = 5 cm.

Body Mass & Postural Assessment

The preserved limb elements of BP/1/8469 provide a mass estimate from the corrected quadrupedal equation (cQE) of 1.8 metric tonnes for a biped and 3.1 metric tonnes for a quadruped from the OLS regression.

The discriminant function analysis (DFA) accurately predicts posture in terrestrial vertebrates with known posture. The DFA correctly classifies many quadrupeds such as elephant, hippo, alligator, and crocodile; but fails with some smaller animals such as an elephant shrew, American beaver, and chinchilla.

A generated mean posterior probability of 0.64_{biped} for BP/1/8469 means that its posture is equivocal according to arbitrary divisions set in Chapelle *et al.* (2020). Of the 77 sauropodomorph taxa, 37 were identified as quadrupeds, 23 as equivocal, and 17 as bipeds (see Appendix 10). 24 out of 77 taxa (31%) are considered to have

been incorrectly predicted. Of the 24 taxa, 19 were classified as equivocal even though they are quadrupedal had 0.35 ≤ pp_{biped} ≤ 0.65, and 4 that were classified as bipedal even though they are quadrupedal had 0.72 ≤ pp_{biped} ≤ 0.91. These taxa are giant sauropods that have morphological affinities with quadrupedalism, are

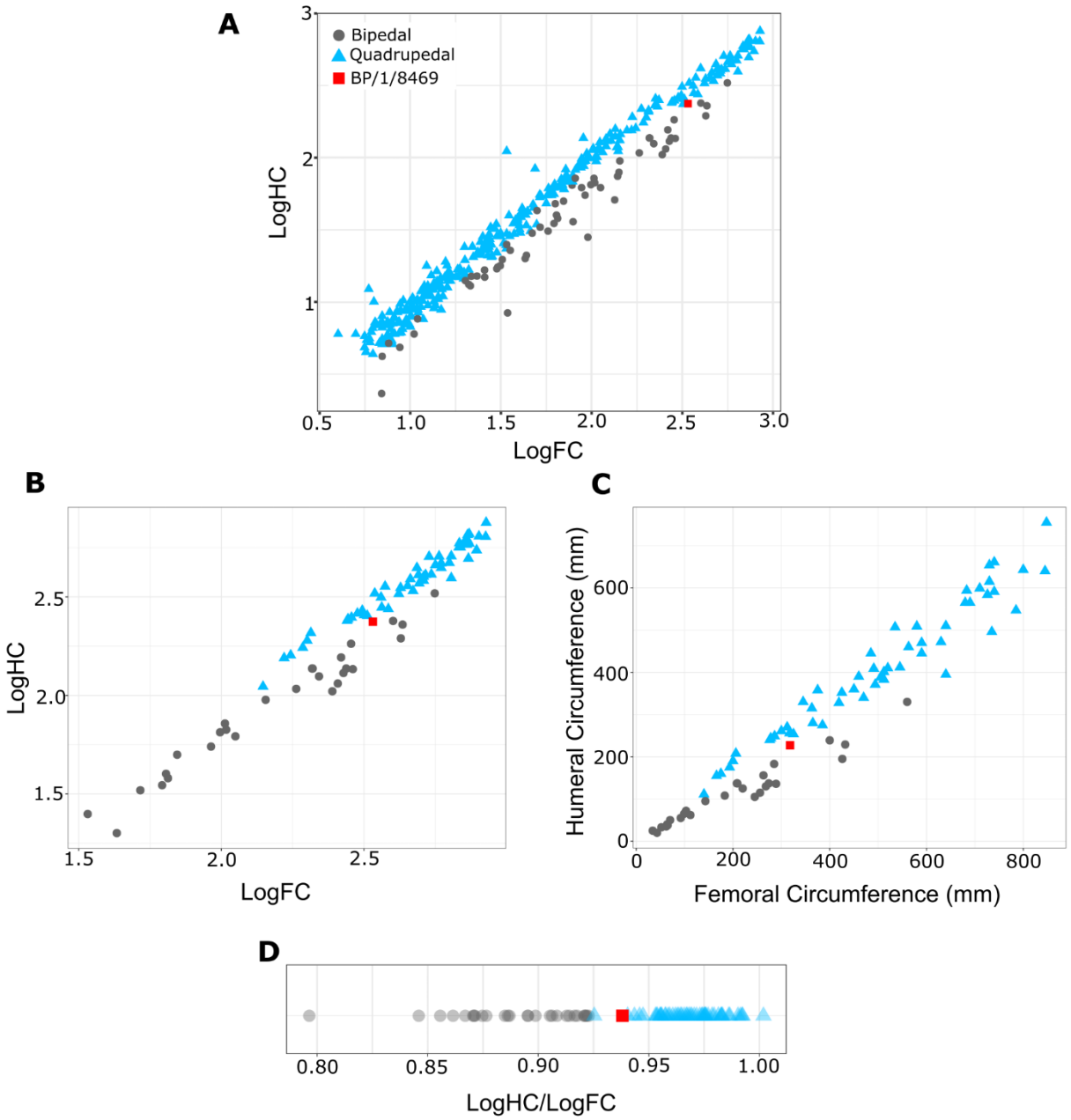

Figure 29: Relationship between humeral and femoral shaft circumferences in tetrapods. (A) Relationship between log-transformed humeral and femoral shaft circumferences of extant and dinosaurian taxa. (B) Relationship between log-transformed humeral and femoral shaft circumferences of dinosaurian taxa. (C) The relationship between humeral and femoral shaft circumferences (mm) of dinosaurian taxa. (D) A spectrum of ratios between log-transformed humeral and femoral circumferences. Gray circles, bipeds; blue triangles, quadrupeds; red square, BP/1/8469.

predicted to be either equivocal or bipedal. In Chapelle *et al.* (2020), *Rapetosaurus krausei* was classified as bipedal to quadrupedal, whereas here *Rapetosaurus* was classified as a quadruped. Many of the predictions of posture here are congruent with the inferred posture in McPhee *et al.* (2018) with the exception of *Jingshanosaurus*. It is inferred to be a quadruped, whereas the DFA predicts it to be a biped (0.69_{biped}). The DFA seems to fail in identifying the posture of giant sauropods.

The relationship between humeral and femoral circumferences is strongly predictive of posture among tetrapods, with quadrupeds having proportionately thicker humeri (Fig. 29). Amongst tetrapods, BP/1/8469 is situated between the locomotory styles amongst the larger-sized taxa. Dinosaurs have a wide distribution of postures from small, bipedal theropods, ornithischians, and sauropodomorphs to giant, quadrupedal sauropodomorphs (Fig. 29 B). Quadrupedal dinosaurs have proportionately thicker humeri than bipedal dinosaurs (Fig. 29 B). Amongst dinosaurs, it is situated in the mid-range of large quadrupeds. Based on stylopodial circumferences (Fig. 29 C), BP/1/8469 is in the low to mid-range in quadrupedal dinosaurs and the mid to upper range for bipedal dinosaurs. Bipedal dinosaurs have a Log_{10}HC to Log_{10}FC ratio (Fig. 29 D) between 0.79 – 0.92, whereas quadrupeds are 0.92 – 1.00. There is no clear distinction between bipeds and quadrupeds, but there is some overlap with bipeds occupying a slightly larger range.

Osteohistology of BP/1/8469

Diagenetic activity is prevalent throughout various areas of the cortex making some interpretations difficult. BP/1/8469 has a relatively thin cortex with a very wide, open medullary cavity. The majority of the inner cortex (Fig. 30 A-B) has been secondarily remodelled with the presence of abundant, non-overlapping secondary osteons. A woven-parallel complex (WPC) is observed in the inner cortex between the secondary osteons (Fig. 30 B).

The mid-cortex (Fig. 30 C-D) also contains WPC and has a circumferentially oriented and elongated laminar vascular arrangement that continues into the outer cortex, with small patches of plexiform vascularity present in the outer cortex (Fig. 31). A few simply longitudinally oriented canals, and some longitudinal primary osteons are present in the mid- to outer cortex (Fig. 30 D). Vascular density is constant throughout the mid-cortex (Fig. 30 F). The bone tissues are interrupted by cyclical growth marks (GM) in the form of annuli (representing temporary decreases

in growth) or as lines or arrested growth (LAGs; representing a temporary cessation in growth; Fig. 31). These occur throughout the mid-cortex. Extensive remodelling of the inner cortex makes it difficult to confirm if growth marks were present in the inner cortex or not (Fig. 31). A minimum of eight mid-cortical cyclical GMs is visible.

The outer cortex consists (Fig. 30 E-F) of parallel-fibred bone (PFB) with laminar and longitudinally oriented vascular canals. Vascularization decreases towards the sub-periosteal surface. Sharpey's fibres (Fig. 31 B) are visible in the outer cortex indicating regions of muscle insertion. LAGs are present in the outer cortex and become closely spaced in comparison to the mid-cortex (Fig. 31 A). An almost avascular region of lamellar/parallel-fibred bone (LB/PFB) with three closely spaced LAGs (Fig. 30 E) may indicate an incipient external fundamental system (EFS; also known as outer circumferential lamellae), which would indicate that substantial growth has ceased. Alternatively, this region may represent a particularly stressful season with multiple interruptions in growth. Growth may have then continued more normally should the individual have continued growing.

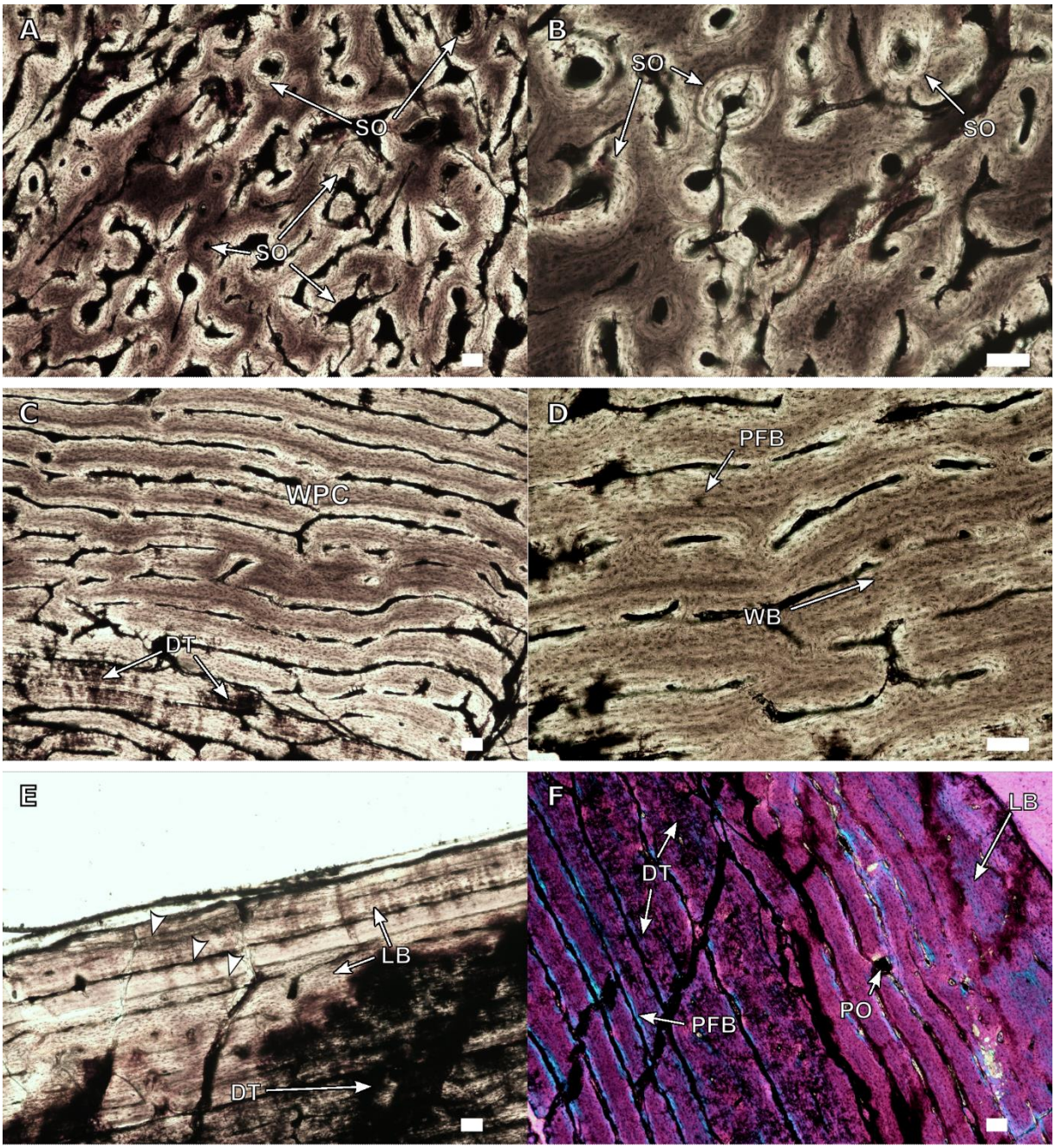

Figure 30: Femoral osteohistology of BP/1/8469. (A, B) High magnification in normal light of the inner cortex showing secondary osteons. (C, D) High magnification in normal light of the mid-cortex showing the mixture of woven and parallel-fibred bone with primary osteons. (E) High magnification in normal light of the outer cortex showing a possible EFS with three closely spaced LAGs in an almost avascular region of lamellar bone. (F) High magnification in cross-polarized light of the outer cortex showing that laminar vascularization continues to the sub-periosteal surface. Arrowheads represent LAGs. Abbreviations: DT, diagenetic tissue; LB, lamellar bone; PFB, parallel-fibred bone; PO, primary osteons; SO, secondary osteons; WB, woven bone; WPC, Woven-Parallel Complex. Scale bars = 100 μm.

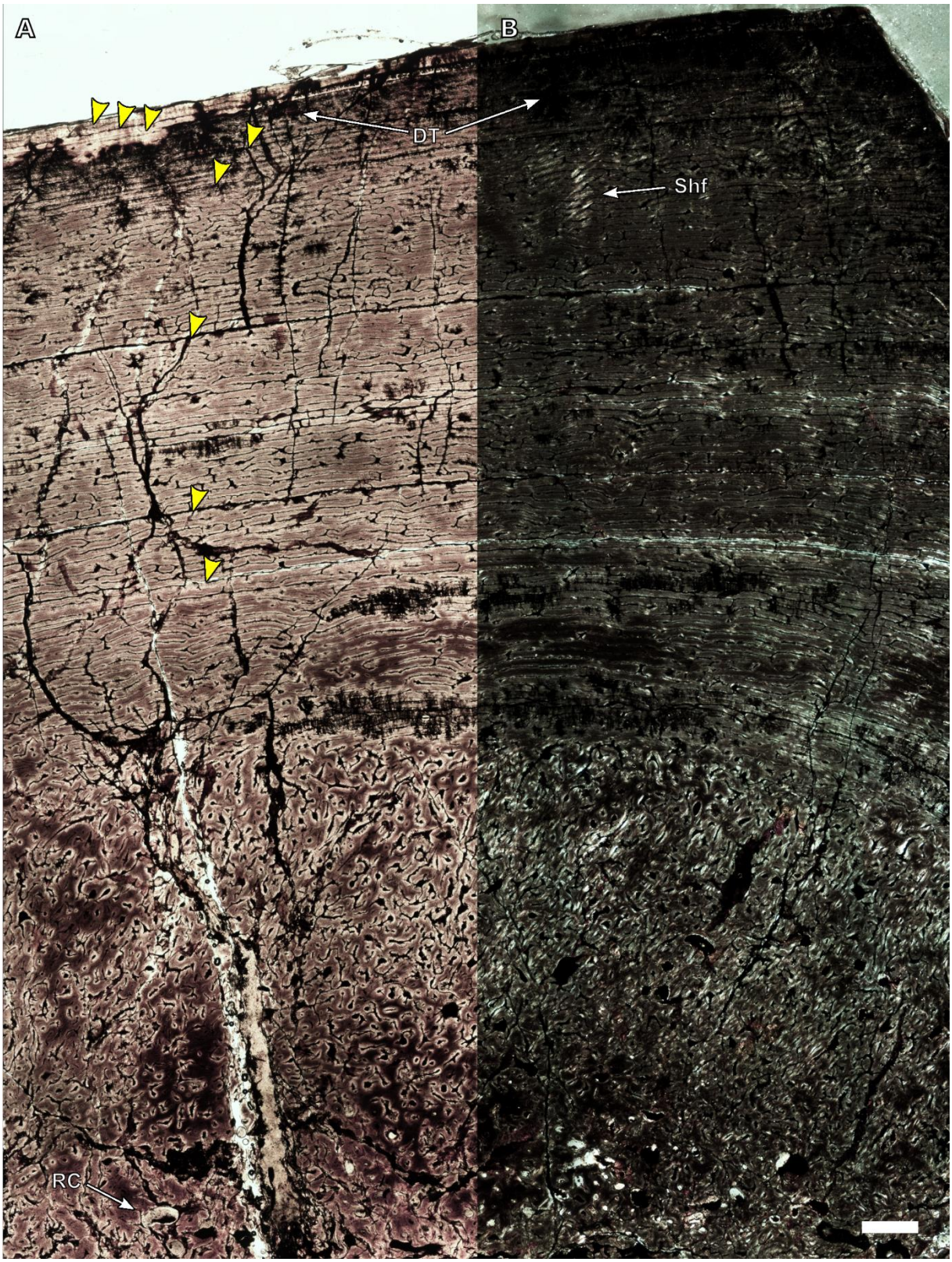

Figure 31: Femoral osteohistology of BP/1/8469. An overall view of the cross-section in (A) normal light and (B) polarized light showing the position of the LAGs throughout the cortex. Yellow arrowheads represent LAGs. Abbreviations: DT, diagenetic tissue; RC, resorption cavities; Shf, Sharpey's fibres. Scale bar = 1000 μm.

The growth curve (Fig. 32) shows the transition between the various tissues into the late ontogenetic stages of BP/1/8469 and that almost 75% of its growth had already occurred. Faster growth occurred within the first four visible GMs of the inner cortex with WPC. From GM 5 to 6, growth began to slow down with the presence of PFB and transitioned to LB from GM 6 to 8 which coincides with a probable EFS.

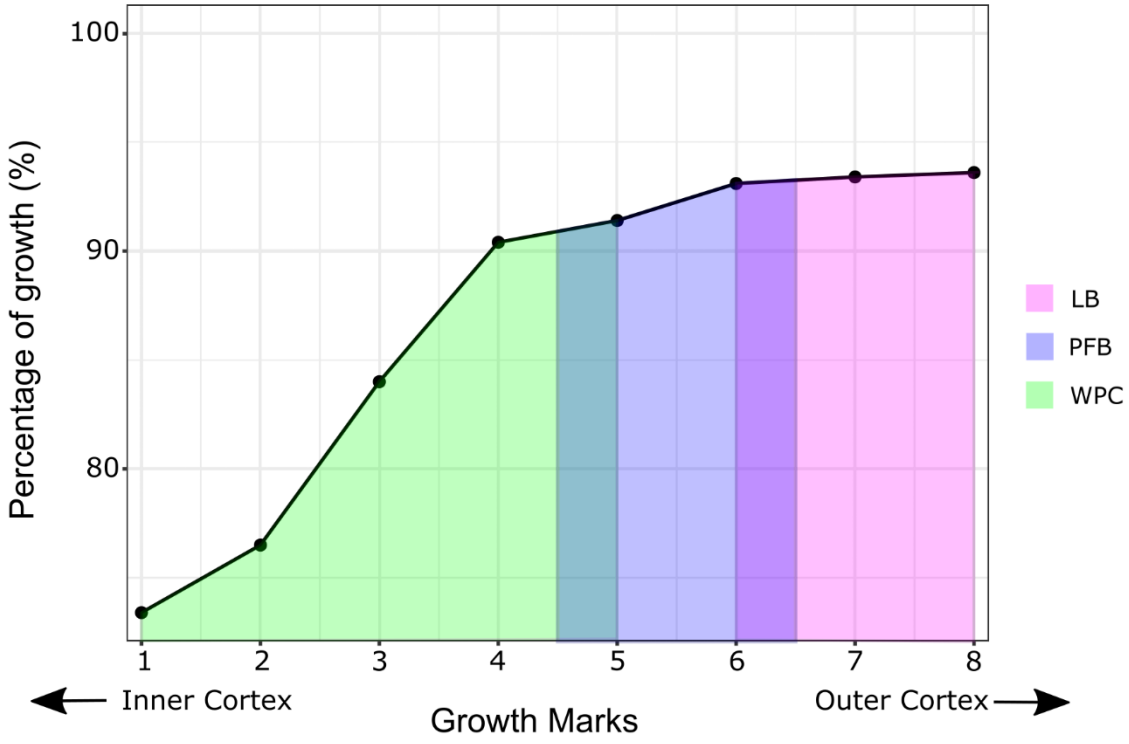

Figure 32: Growth curve of BP/1/8469. The percentage of growth associated with the visible growth marks from the cortex of the femur. The major bone tissue types are optimized relative to growth marks. Growth marks six to nine are associated with the EFS. Abbreviations: WPC, Woven-Parallel Complex; PFB, Parallel-fibred bone; LB, Lamellar Bone.

Optimality Criteria & Congruency Tests

The maximum parsimony (MP) analysis resulted in six most parsimonious trees (MPTs) with a tree length of 1601. These trees have a consistency index of 0,36 and a retention index of 0,61. Bremer and bootstrap supports are relatively low for the majority of the nodes, bremer support ranges from one to two throughout the tree and bootstrap supports are the highest at Riojasauridae with 67. MP places BP/1/8469 as a derived sauropodiform close to the base of Sauropoda (Fig. 33).

The average standard deviation of split frequencies after 10 million generations was 0,022 from the Fossilized Birth-Death (FBD) model indicating that

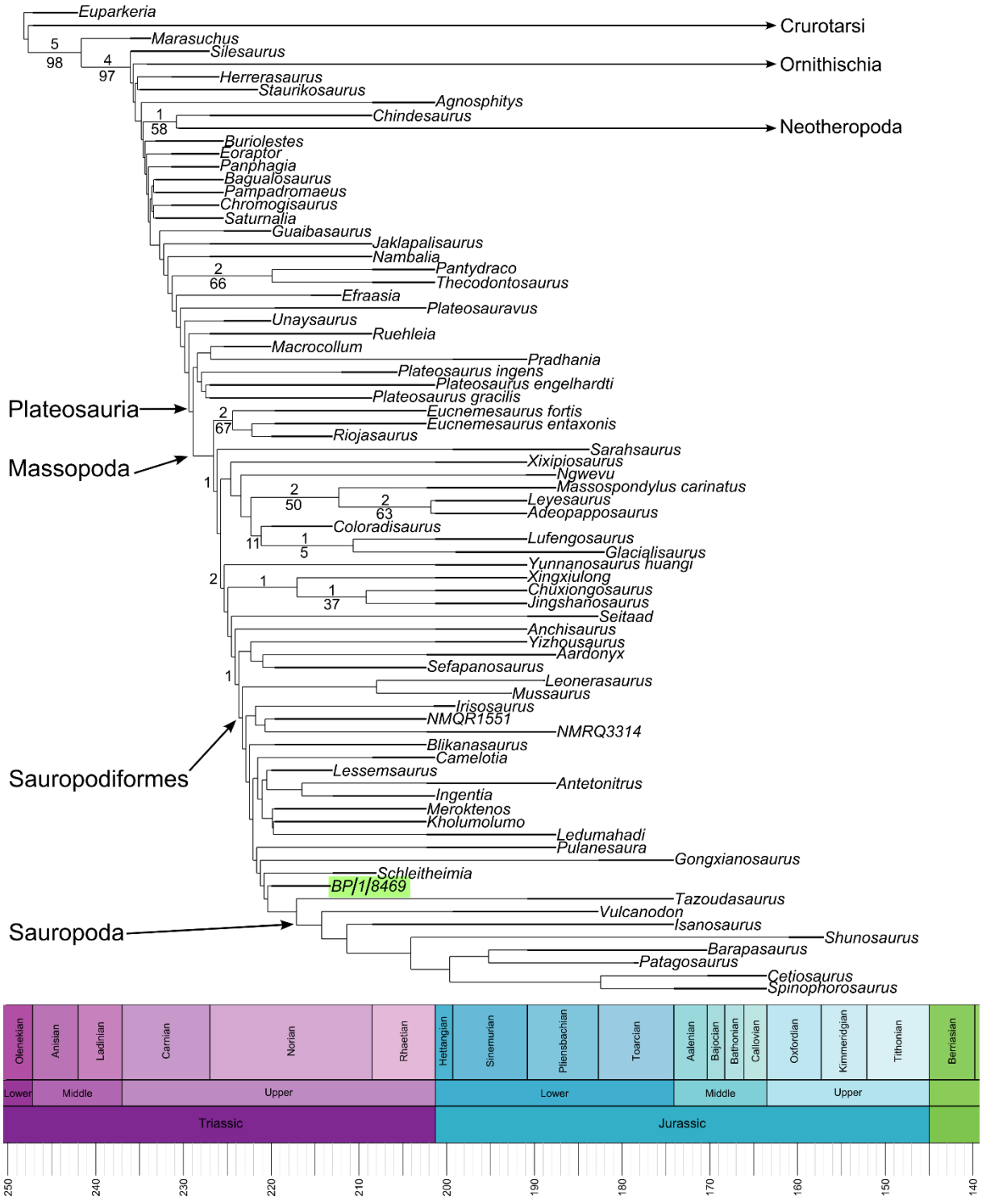

Figure 33: Time-calibrated most parsimonious phylogeny. Numbers above nodes represents Bremer support and numbers below represents Bootstrap support.

the two runs were converging. The posterior probabilities show that the majority of the nodes are weakly supported (Fig. 34) with only a few nodes with a posterior probability above 0,95 that include: *Chindesaurus* + Neotheropoda; *Pantydraco* +

Thecodontosaurus; *Chuxiongosaurus* + *Jingshanosaurus*; and *Leyesaurus* + *Adeopapposaurus*. Nodes with 0,90 to 0,95 posterior probability include: Riojasauridae; and *Tazoudasaurus* + Sauropoda. The FBD model places BP/1/8469 as a basal sauropodomorph near the base of Sauropodiformes.

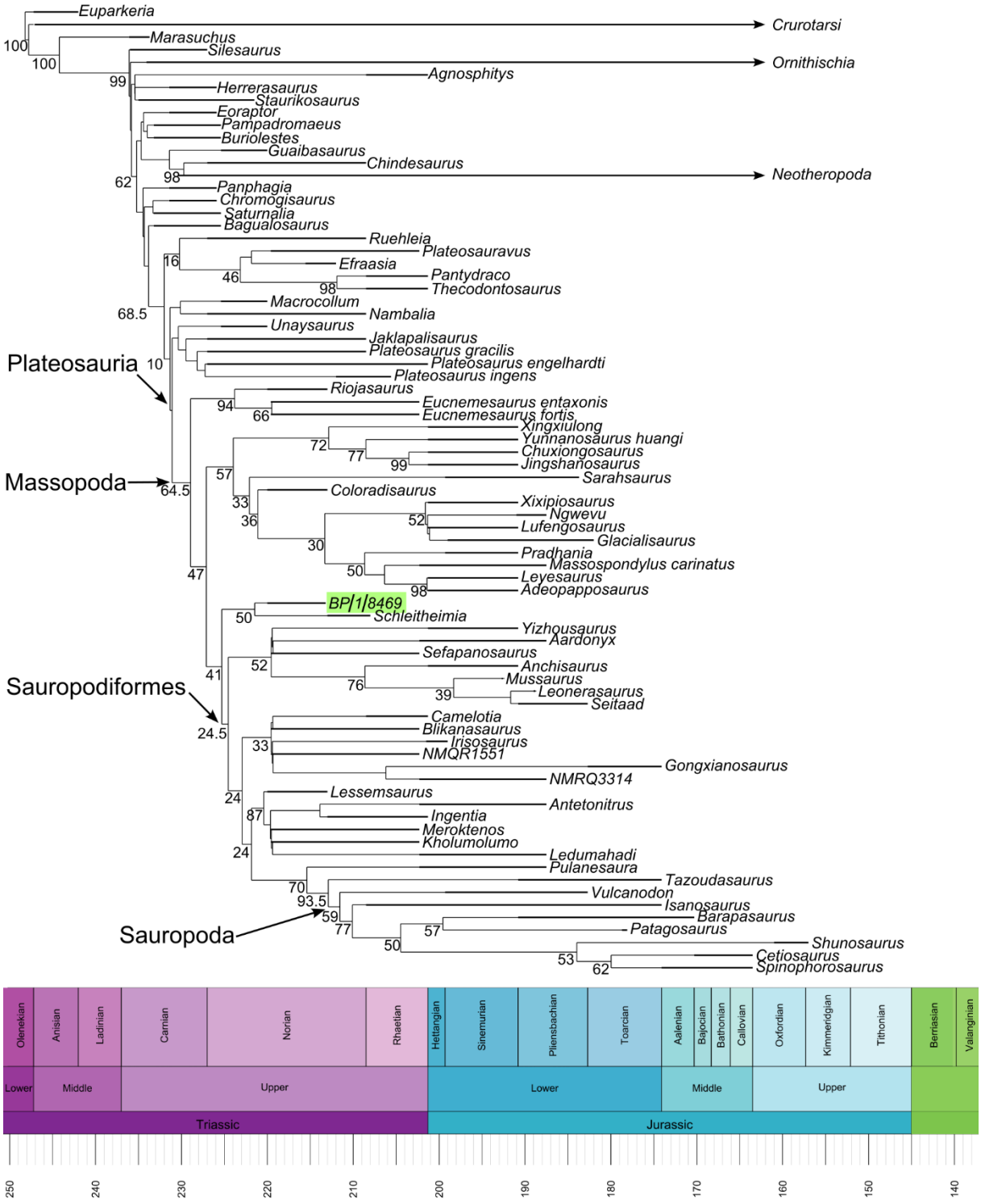

Figure 34: Maximum clade credibility tree recovered from Bayesian time-calibrated FBD model. Numbers at the nodes represents the posterior probability of that node.

The cladograms produced by implied weighting (see Appendix 11) at various weighting functions place BP/1/8469 as a derived sauropodiform, consistent with maximum parsimony. The GER from the stratigraphic congruency test (Table 3) indicates that the FBD model is a better fit to stratigraphy than the other optimality criteria. The Templeton test (Table 3) indicates a significant difference in topological fit, that the FBD model is significantly worse in a parsimony context with a difference of 72 steps in tree length between them.

Table 3: Congruency tests on various optimality criteria. Templeton test compared tree topology between Maximum Parsimony and FBD models of Bayesian analysis. Abbreviations: GER, Gap Excess Ratio; SCI, Stratigraphic Consistency Index; RCI, Relative Consistency Index; MSM, Manhattan Stratigraphic Measure.

Optimality Criteria	**GER**	**SCI**	**RCI**	**MSM**
Maximum Parsimony	0.681	0.720	11.830	0.092
Bayesian FBD	0.765	0.667	32.913	0.121
Implied Weighting (k=1)	0.677	0.653	10.911	0.091
Implied Weighting (k=12)	0.693	0.693	15.052	0.095

Templeton Test

	Sum of Negative Ranks	**No. of non-zero scores**	**Critical Values**		
MP - FBD	3085	144	4395*	4237**	4053***

* 5% ** 2,5% *** 1%

The “sensitivity” analysis (Fig. 35) summarizes the differences and similarities among the various optimality criteria. MP and implied weighting (IW) return relatively similar phylogenetic groups, whereas the FBD model has more differences in comparison. This shows 50% in agreement between MP and FBD and 90% in agreement between MP and the IW phylogenies. Clades that are consistently supported by the various optimality criteria include Riojasauridae, Massospondylidae, Lessemsauridae, and Sauropoda. However, Massospondylidae and

Melanorosauridae appear to be inconsistent in their constituent taxa through the optimality criteria. It is clear from the sensitivity analysis that some clades are monophyletic regardless of the optimality criterion, whereas others only recovered under certain optimality criteria. This implies certain clades should be more stable in other analyses going forward and others will not.

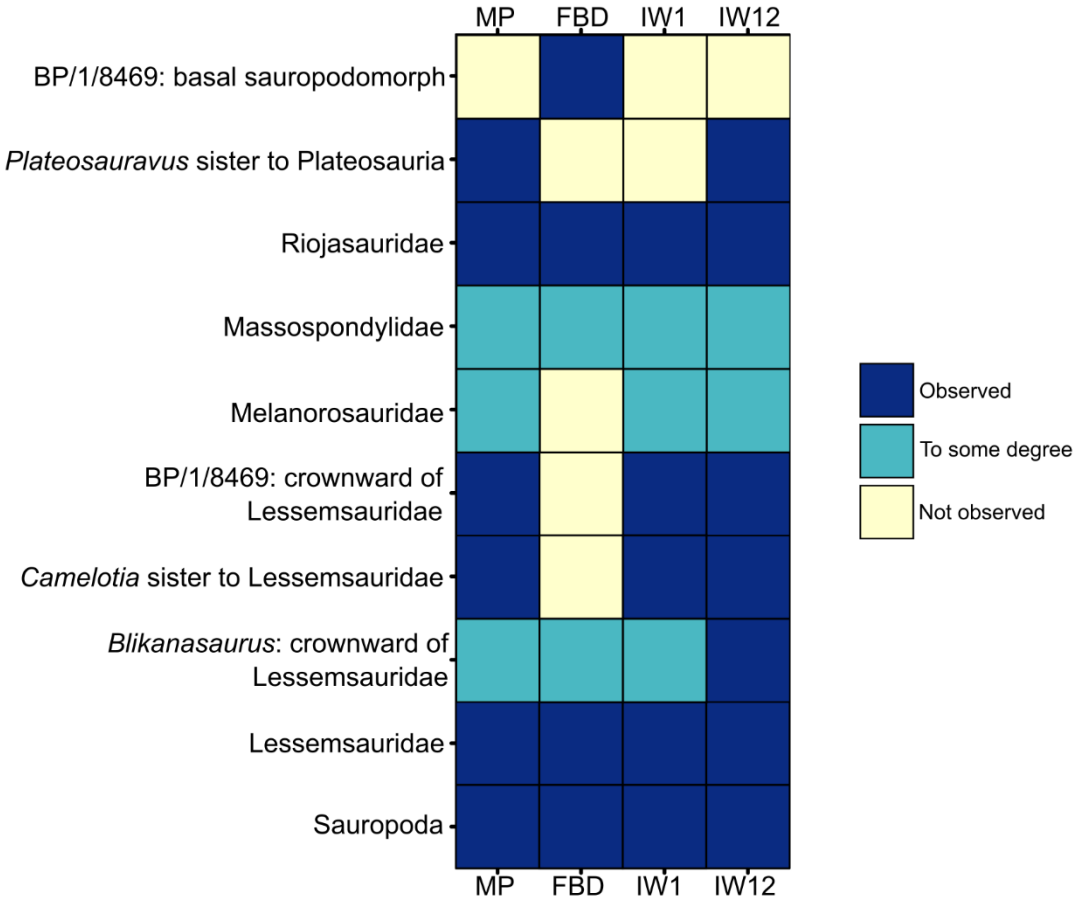

Figure 35: Congruency sensitivity analyses of various phylogenetic optimality criteria. Scoring was based on if the clade was recovered under the optimality criterion.

In Massospondylidae, the MP tree recovers a smaller group of taxa sharing a more common recent ancestor with *Massospondylus* than with other massopodans including: *Xixipiosaurus*, *Ngwevu*, *Massospondylus carinatus*, *Leyesaurus*, *Adeopapposaurus*, *Coloradisaurus*, *Lufengosaurus*, and *Glacialisaurus*. In the FBD tree, this clade includes additional taxa: *Sarahsaurus* and *Pradhania*; and forms an exclusive sister taxon relationship with a Lufeng-dominated group including: *Xingxiulong*, *Yunnanosaurus*, *Chuxiongosaurus*, and *Jingshanosaurus*.

In Melanorosauridae, the MP tree also recovers a very small group of taxa that includes referred specimens to *Melanorosaurus readi*: NMQR 1551, NMQR 3314, and *Irisosaurus*. In the FBD tree, Melanorosauridae forms a larger clade distinct from *Anchisaurus* and its closely related taxa; and includes additional taxa: *Camelotia*, *Blikanasaurus*, and *Gongxianosaurus*.

Blikanasaurus does not have a consistent position amongst the various optimality criteria. In MP it is situated as basal to Lessemsauridae, it is situated in Melanorosauridae in the FBD tree, IW at k=1 it places within a clade with *Anchisaurus*, and IW at k=12 it is placed as a basal sauropod.

DISCUSSION

Autapomorphies of BP/1/8469

BP/1/8469 is likely a new sauropodomorph taxon from the lowermost strata of the lower Elliot Formation (lEF) and is Norian in age. It is represented by a very large, associated skeleton and several referred specimens from a multi-taxic bonebed containing at least two other sauropodomorph individuals.

There is abundant morphological evidence that BP/1/8469 represents a new taxon. Support for this assertion comes from the following autapomorphies with the unique autapomorphies indicated by (*): a transitional dorsal vertebra*; at least three sacrals; the anterior caudal has curved transverse processes*; the anterior caudal has a posteriorly curving neural spine*; a hyposphene-hypantrum articulation in the anterior caudal; a relatively straight humerus; the lateral margin of the deltopectoral crest bears a paramarginal sulcus; distinct proximolateral flange on metacarpal II; a sulcus on the medial surface of the fourth trochanter on the femur; a well-developed posterior tubercle on the femoral head; a large cnemial crest with an anteroposteriorly expanded proximal margin; the mediodistal surface of the fibula contains two longitudinal ridges*; two vascular foramina on the proximal surface of the astragalus*; and a notch on the proximolateral margin of metatarsal III*.

BP/1/8469 contains a transitional dorsal vertebra (Fig. 6) that appears to be in the early anatomical stages of being incorporated into the sacrum. It demonstrates a transverse process with a thin, protruding postzygodiapophyseal lamina fused to a dorsoventrally thin, anteriorly projecting rib that does not contact the anterior process of the ilium. The sacrum in non-sauropodan sauropodomorphs typically consists of

three vertebrae with an increase to four to six vertebrae towards sauropods (Wang *et al.*, 2017). This increase in vertebral number has been hypothesized to be due to mechanical changes to facilitate and support larger body size. Notably, sauropodomorphs achieve the increased sacral count by incorporating vertebrae from either the dorsal or the caudal series (Galton, 1999). The homology of the sacral vertebrae clearly shows multiple independent origins of increased sacral count. For example, some non-sauropodan sauropodomorphs have a dorsosacral added into the sacrum, as in *Massospondylus* and *Yunnanosaurus* including BP/1/8469, whereas *Plateosaurus* has added a caudosacral into the sacrum (Wang *et al.*, 2017, Barrett *et al.*, 2019, Young, 1942, Moser, 2003). *Xingxiulong* and *Mussaurus* are of the few non-sauropodan sauropodomorphs that have a four vertebrae sacrum that consist of a dorsosacral, two primordial sacrals, and a caudosacral (Wang *et al.*, 2017, Otero and Pol, 2013). In current literature, the documentation of the anatomical changes that occur during this transition of vertebrae being incorporated into the sacrum is not well-documented, and BP/1/8469 may be the first sauropodomorph to display such morphology.

The anterior caudal (Fig. 9) displays three of the autapomorphies. The neural spine displays a degree posterior curvature that is greater than that of any other described early branching sauropodomorph, which has not been documented to the extent seen in BP/1/8469. The transverse processes are short and arc-like, this morphology is not present in any described sauropodomorphs and is possibly linked to have a closer articulation between the sacrum and the tail. A hyposphene-hypantrum articulation is present in the anterior caudal. This accessory articulation is a complex feature that is widely distributed amongst sauropodomorphs. McPhee *et al.* (2014) discussed the presence of this articulation as a tentative apomorphy in *Antetonitrus* as well as in undescribed and unaccessioned material from the Los Colorados Formation. Sauropodomorph material (BP/1/8489) collected in 2017-2018, provenanced from the lEF that likely belongs to a lessemsaurid also displays a hyposphene-hypantrum articulation (Moopen and Choiniere, 2020).

A paramarginal sulcus is present on the lateral surface of the deltopectoral crest (Fig. 11). This feature is first described in *Antetonitrus* and is likely present in *Lufengosaurus* with BP/1/8469 being the third taxon to display this (McPhee *et al.*, 2014). The functionality of this sulcus is unclear due to the limited taxa that are known to possess this feature. It is likely that this is new morphology that has not

been considered before due to a preservation bias or limited sampling. Ballell *et al.* (2022) described osteological correlates related to the limbs of *Thecodontosaurus*. Based on the various musculature, the paramarginal sulcus likely plays a role for muscle attachment sites related to humeral adduction, abduction, and protraction. The proximolateral flange on metacarpal II (Fig. 13) paired with the distinct ridges likely serves the same function as speculated with *Antetonitrus* related to the mobility of the manus (Otero, 2018, McPhee *et al.*, 2014).

A distinct sulcus on the medial surface of the fourth trochanter (Fig. 18) is likely a size-related feature. This sulcus is also present in *Antetonitrus* and *Aardonyx*, sauropodomorphs not of comparable locomotory styles, i.e., a quadruped and biped, respectively. It is also not present in smaller-bodied sauropodomorphs such as *Massospondylus*. The presence of the sulcus with the size of the fourth trochanter suggest strong musculature associated with hip extension (Ballell *et al.*, 2022). A well-developed posterior tubercle on the femoral head corresponds with that seen in *Eucnemesaurus fortis* and *E. entaxonis*, it is also seen in *Antetonitrus* and BP/1/8489 (McPhee *et al.*, 2015b, Yates, 2007). The posterior tubercle has a similar presence to the sulcus of the fourth trochanter and is likely a size-related feature.

The proximal end of the tibia (Fig. 19) suggests that BP/1/8469 had an autapomorphically large knee joint. The proximal margin of the tibia is large, anteroposteriorly expanded with a laterally protruding cnemial crest. The tibia also has a distinct shaft, whereas other taxa have short and stout tibial shafts such as *Blikanasaurus*. This distinct tibial shaft is also seen in Lufeng taxa, namely *Lufengosaurus* and *Yunnanosaurus* both of which have an estimated body mass below one metric tonne and are considered bipedal. Lefebvre *et al.* (2022) proposed that the change in tibial morphology is related to the trade-off between fast-moving locomotion and efficient weight-bearing properties. The proximal end of the tibia also has important muscle attachment sites associated with knee extension and hip flexion. The robustness of the proximal end of the tibia and the elongated tibial shift of BP/1/8469 could be the intermediate morphology for both locomotion and weight-bearing. That is, it is achieving near-quadrupedal body mass but not yet achieving the associated skeletal adaptations, and the knee is accommodating for the stress.

The mediodistal surface of the fibula (Fig. 20) contains two longitudinal ridges, whereas in other early branching sauropodomorphs (EBSM), usually one longitudinal ridge is observed. The proximal surface of the astragalus (Fig. 21) displays two

vascular foramina instead of the usual one foramen. The distribution of this feature is very poorly documented due to a likely preservation bias as this bone is rarely well preserved, this makes it difficult to determine if it is an autapomorphy. The proximolateral margin of metatarsal III has a notch (Fig. 23) present and this is not documented in other sauropodomorphs as well. The associated function of these three features is currently unknown, until more complete sauropodomorphs are discovered this will remain speculative to body size, posture, ontogeny, or phylogeny.

Derived & Plesiomorphic Features of BP/1/8469

BP/1/8469 not only has some novel autapomorphies but also an interesting combination of derived and plesiomorphic features found in sauropodomorphs. The distal end of the radius becomes more rounded as in sauropodiforms like *Sefapanosaurus* and *Antetonitrus*. The mediodistal shift of the fourth trochanter is considered an Anchisaurian character that also independently evolved in Sauropoda and *Lufengosaurus* (Galton and Upchurch, 2004). The size and asymmetry of pedal ungual of digit I is considered as a derived feature exclusive to sauropods and is present in *Tazoudasaurus* and *Vulcanodon* (Galton and Upchurch, 2004).

As in non-sauropodan sauropodomorphs, but not in sauropods, BP/1/8469 displays a dorsal horizontal shelf connected to a ventral subrectangular sacral rib in the primordial sacrals; a distinct internal tuberosity on the humerus; a thickened humeral head; the proximal and distal axes of manual phalanx 1 of digit I are twisted relative to each other; the preacetabular process terminates anterior to the pubic peduncle; the “heel” at the posterior margin of the ischial peduncle; and the arrangement of the pes is in a mesaxonic structure (Galton and Upchurch, 2004, Carrano, 2005).

Palaeobiology of BP/1/8469

There is an interesting combination of palaeobiological features that can be inferred from BP/1/8469. It was a large, fast-growing individual that was likely experimenting with a postural shift between bipedality and quadrupedality.

Body mass

BP/1/8469 has an estimated body mass of 1.8 metric tonnes (as a biped) to 3.1 metric tonnes (as a quadruped). Along with *Kholumolumo* (estimated at 1.7 to 3.2 metric tonnes), BP/1/8469 is the largest sauropodomorph from the lEF, whereas the upper EF (uEF) has much larger taxa with *Ledumahadi* (12 metric tonnes) and *Antetonitrus* (6 metric tonnes; Peyre de Fabrègues and Allain, 2020). In comparison to other taxa from contemporaneous formations, the body size of BP/1/8469 is similar if not smaller to Argentinian taxa such as *Ingentia* but is larger than the German taxa, *Plateosaurus*. Amongst non-sauropodan sauropodomorphs (Fig. 36), body size is variable from *Saturnalia* (10 kg) to *Ledumahadi* (12 metric tonnes) with some Lufeng taxa reaching two metric tonnes (McPhee *et al.*, 2018, Peyre de Fabrègues and Allain, 2020). However, Lessemsauridae is a clade known for large body sizes and BP/1/8469 is on the lower end in comparison.

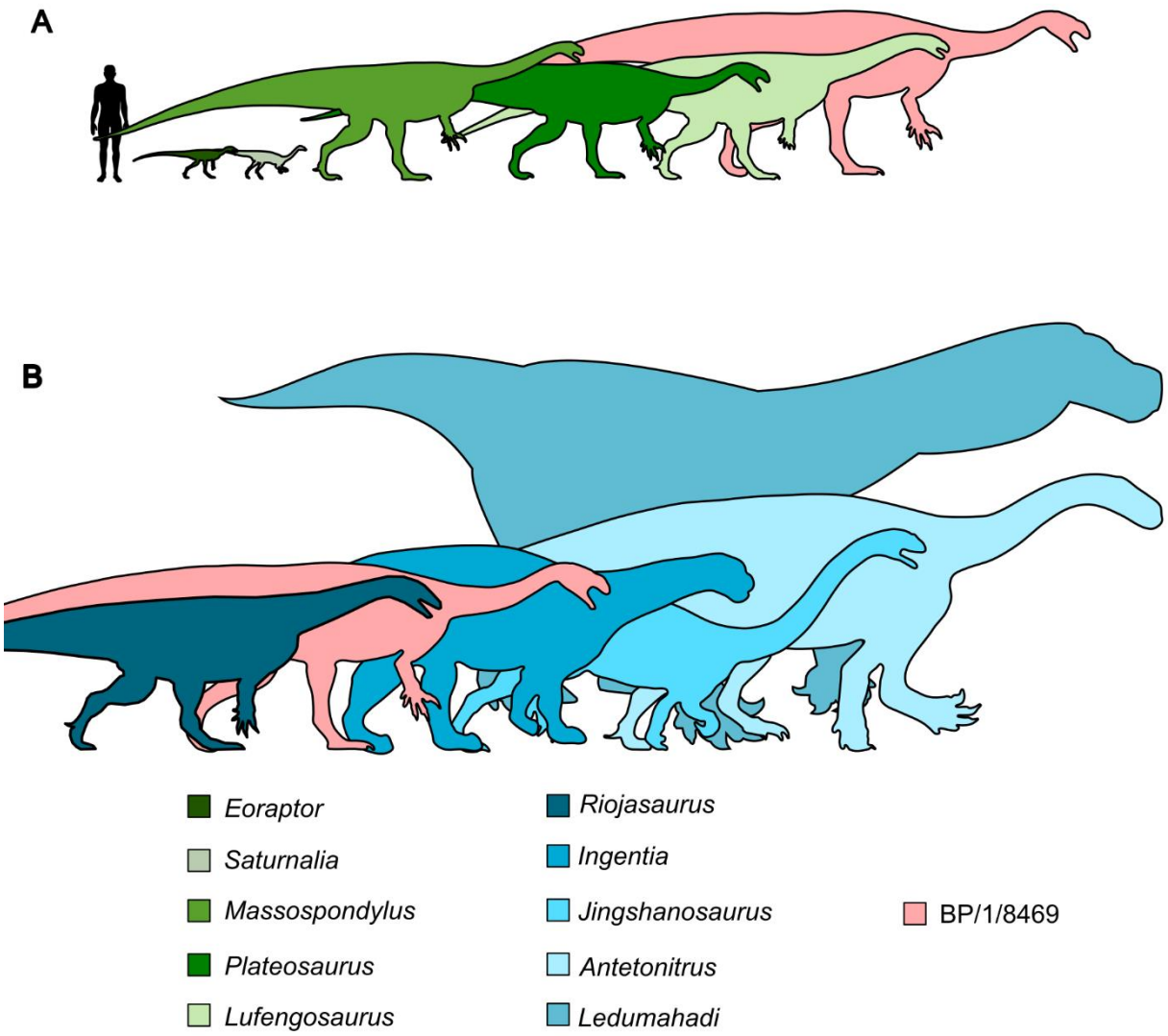

Figure 36: Body mass comparison amongst non-sauropodan sauropodomorphs. (A) Size comparison amongst bipedal sauropodomorphs and BP/1/8469 as a biped. (B) Size comparison amongst quadrupedal sauropodomorphs and BP/1/8469 as a quadruped. Images are adapted from multiple sources and are to scale.

Posture

Amongst dinosaurian taxa, BP/1/8469 is situated between the between the locomotory styles with the next largest bipedal dinosaur as *Suchomimus*, a theropod with much thicker femur. The nearest sauropodomorphs to BP/1/8469 are *Euhelopus zdanskyi* and *Europasaurus holgeri*, both of which have relatively the same thickness in their humeri and femora, are considered as quadrupeds.

In determining the posture of BP/1/8469, it was identified as equivocal, i.e., unclear if it was a biped or quadruped. Based on the phylogenetic position of BP/1/8469 (Fig. 33 & Fig. 34), it could be developing quadrupedal behaviour or it

represents a reversal to bipedality. BP/1/8469 has some anatomical features that are described as being associated with quadrupedal posture that include: a lack of twisting in the humeral shaft; a straight femoral shaft; a medially oriented femoral head; and distal condyles of the femur are perpendicular to the longitudinal axis of the femoral shaft (McPhee *et al.*, 2014, Carrano, 2005, Galton and Upchurch, 2004, Barrett and Maidment, 2017). In addition, a rugose texture is found on the proximal and distal ends of many of the weight-bearing bones suggesting the presence of cartilage caps. It is unclear whether this rugose texture is a result of quadrupedal posture, it is present in *Antetonitrus* (large quadruped) but also in *Sarahsaurus* (small biped) and its presence may be linked to a preservation bias (Bonnan *et al.*, 2010).

BP/1/8469 likely preserves a transition from bipedality to quadrupedality with evidence of experimentation in the hindlimbs. Femoral and tibial morphology are quite robust with a large femoral head, large femoral distal condyles, very pronounced trochanters, and a large tibial proximal end typically seen in many quadrupedal taxa such as *Antetonitrus*, *Tazoudasaurus*, and *Vulcanodon*. The metatarsals have an articulation that is present in EBSMs and are elongated similar to *Lufengosaurus*, whereas sauropods like *Shunosaurus* have shortened metatarsals. The various distinct muscle attachment sites present in the hindlimb elements suggests significant use of a powerful hindlimb. Additionally, the forelimb elements of BP/1/8469 do not display the same level of robusticity as in the hindlimb. Considering the large muscle attachment sites in the limb elements, the quadrupedal affinities and difference in robusticity of the forelimb and hindlimb, it is likely that BP/1/8469 was facultatively quadrupedal. BP/1/8469 adds to the evidence of experimentation in locomotory styles amongst non-sauropodan sauropodomorphs as shown by McPhee *et al.* (2018).

Osteohistology

The bone microstructure of BP/1/8469 is indicative of rapid, interrupted growth with little development plasticity in a near-adult individual and displays a highly vascularized woven-parallel complex (WPC) within the inner cortex to avascular lamellar bone (LB) at the sub-periosteal surface. An inner third of the cortex has been secondarily remodelled with the rest of the cortex regularly interrupted by lines of arrested of growth (LAGs). The LAGs suggest that the individual was at least eight years old at time of death, it was likely older as a LAG in the inner-most cortex

appears to be in the process of being resorbed. Three closely spaced LAGs are present at the sub-periosteal surface and are considered part of an incipient external fundamental system (EFS, also known as outer circumferential lamellae) as they consist of avascular LB. Osteohistological and morphological correlates that indicate skeletal maturity (sub-adult to adult) in BP/1/8469 consist of: an avascular region of LB; an EFS; fused neurocentral sutures in the vertebrae; a partially fused sacrum; and the fusion of long bone epiphyses.

In comparison to other Norian sauropodomorphs, BP/1/8469 displays similar bone microstructure to *Ingentia* with well-vascularized WPC and a cyclical growth pattern (Apaldetti *et al.*, 2018). A more basal sauropodomorph, *Plateosaurus*, displays relatively slower growth with extreme developmental plasticity (Sander and Klein, 2005). BP/1/8469 and *Ingentia* are relatively closely related in the phylogeny, and both occur at temperate south palaeolatitudes, whereas *Plateosaurus* is in the temperate north palaeolatitudes. These taxa occurred contemporaneously and the difference in growth strategy could be attributed to both environmental conditions and phylogenetic variation.

BP/1/8469 presents a valuable additional test of the hypotheses laid out by Cerda *et al.* (2017) and Botha *et al.* (2022), namely that later branching non-sauropodan sauropodomorphs had a rapid, interrupted growth strategy. The osteohistology supports their hypotheses and based on its position in the phylogeny, it indicates that this strategy was present in early Norian sauropodiforms either with *Aardonyx* and *Sefapanosaurus* at the base or BP/1/8469 at the base.

BP/1/8469 & the Norian

BP/1/8469 provides valuable information for understanding the earliest EF dinosaur faunas. As a well-represented, associated individual that is an adult, it presents a wealth of interconnected morphological information that is not available from many other valid lEF taxa, which were historically collected and lacked detailed provenance data or skeletal representation (Bordy *et al.*, 2020, McPhee *et al.*, 2017). We now know that small to medium-sized sauropodomorphs co-existed during the lEF, which developed limb morphologies that facilitated large-bodied sauropodomorphs like *Ledumahadi* in the uEF. The range of associated material and morphological features preserved in the BP/1/8469 has potential to identify previously unidentified material from the EF and to a greater extent, broaden the

sample for understanding the evolution of sauropodomorphs and their ecomorphological disparity. BP/1/8469 is a stepping stone into understanding Norian fauna and advocates for continued sampling of the lEF. Many palaeobiological forms or strategies have been inferred to first appear in the Norian such as quadrupedality or rapid growth strategies (McPhee *et al.*, 2018, Botha *et al.*, 2022). As we find more Norian taxa, the amount of experimentation that sauropodomorphs could facilitate or their process of transitioning should become more evident.

BP/1/8469 not only increases our sample of valid lEF sauropodomorph taxa, but also makes it comparable to other contemporaneous formations such as the Los Colorados Formation of South America and the Trossingen Formation of Germany. South Africa and Argentina now have an overlap of taxa with similar body size ranges as well as growth strategies that could have independently evolved within Gondwanan taxa or suggests that conditions in Gondwana were conducive for a time of experimentation during the Norian (Pol *et al.*, 2021b).

Phylogenetic Affinities of BP/1/8469 & Sauropodomorpha

The position of BP/1/8469 is inconsistent as maximum parsimony (MP) places it as a basal sauropod, whereas the Fossilized Birth-Death model of Bayesian analysis (FBD) places it as a basal sauropodiform. Both analyses are not well supported based on their relative robustness metrics, i.e., one analysis is not more decisive than the other. The phylogeny obtained from the FBD infers more exclusive subclades than the MP, some of which are local such as the Lufeng taxa forming a monophyletic clade, and some are widespread globally like the clade containing *Plateosaurus*, *Jaklapallisaurus*, and *Unaysaurus*. This also demonstrates that some clades are sensitive to optimality criteria such as Massospondylidae and Melanorosauridae, and some are more stable such as Lessemsauridae and Riojasauridae (Fig. 35). The stability of clades may be attributed to the statements of homology that are provided by the character information or the amount of missing data for some taxa.

The MP and FBD models infer very different evolutionary patterns and demonstrates the importance of including temporal information (Zhang *et al.*, 2016). The topology from MP infers fewer clades with few taxa, whereas FBD infers multiple larger, exclusive clades. Different topologies can infer different distribution patterns of certain evolutionary traits. For example, rapid and interrupted growth occurs at the

base of sauropodiforms in both MP and FBD, whereas FBD infers more instances of quadrupedality than in MP.

It appears that by incorporating temporal information in the FBD model, it can differentiate or better assess statements of homology and instances of homoplasy than MP. Particularly, FBD infers many hidden changes in character states that are not clearly evidenced by the data provided by the character state information. Insufficient sampling is likely a contributing factor, in terms of taxa across time as well as in skeletal representation (Sereno, 2009). There are not enough informative characters in the current data sample to falsify statements of homoplasy or to strengthen statements of homology.

This is an existing caveat that needs to be addressed (Sereno, 2009, Upchurch *et al.*, 2007, Peyre de Fabrègues *et al.*, 2015), there is a current lack of evidence for determining the branching structure at deeper nodes in the EBSM tree. Only by a tripartite approach of new homology hypotheses, recoding and rescoring of old characters, and an increase in the sampling can resolve this. In addition, temporal sampling of the Late Triassic will produce taxa that can support inferences of sauropodomorph biology and better understand their early evolution. Informative data into an FBD model is likely to suggest a dynamic period of morphological experimentation within non-sauropodan sauropodomorphs. This is a plausible hypothesis given the short period between Norian sauropodomorphs and sauropods, with their morphological and physiological disparity that they display.

FUTURE RESEARCH

Late Triassic sauropodomorphs are not well-studied as their Jurassic counterparts, especially those from the Elliot Formation of South Africa. This research and others (McPhee *et al.*, 2018, Botha *et al.*, 2022) highlight the Norian as a crucial time for sauropodomorph experimentation from locomotory to physiological adaptations. By expanding the sample of Norian taxa, we can better understand the morphological experimentation and transition from small bipedal taxa to giant quadrupedal taxa, and effectively compare contemporaneous faunal assemblages. This will additionally highlight autapomorphies that may have been poorly documented, undescribed, or previously not preserved in other specimens.

Phylogenetic analyses highlight the importance of including temporal information as this influences the topology produced from the various optimality criteria, which inadvertently affects our hypotheses of macroevolution. A reassessment of the morphological character datasets will address the caveat that has been identified by many other researchers. Together with an updated character dataset and a larger sample of well-represented Late Triassic sauropodomorphs can we develop a more informed branching structure in the early branching sauropodomorph tree.

CONCLUSION

The lower Elliot Formation of South Africa encompasses the Late Triassic and preserves sauropodomorphs with potential to understanding their early evolution. BP/1/8469 is a Norian sauropodomorph that displays autapomorphies and a unique combination of derived and plesiomorphic features, indicating that it is a new taxon. This adult individual represents a relatively large sauropodomorph that displays features typical of a quadrupedal posture, but limb robusticity that is equivocal in that regard, and is considered here as a facultative quadruped. BP/1/8469 demonstrates rapid, interrupted growth that is consistent with the hypothesis of faster growth occurring in Norian-aged sauropodomorph taxa. The addition of new well-preserved sauropodomorph taxa from the Norian of South Africa allows us to compare the lEF with contemporaneous faunal assemblages more effectively.

The phylogenetic analyses including BP/1/8469 have highlighted the importance of sampling characters with informative phylogenetic statements and the inclusion of temporal data. This also emphasises the importance of including Fossilized Birth-Death models of Bayesian analysis to compliment traditional maximum parsimony analysis. A detailed review of sauropodomorph character datasets with more inclusive taxa and temporal information implies that early branching non-sauropodan sauropodomorphs underwent further morphological experimentation than previously thought.

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APPENDICES

Appendix 1

List of Abbreviations:

Vertebrae

acdl	anterior centrodiapophyseal lamina
c	centrum
cdf	centrodiapophyseal fossa
cpol	centropostzygapophyseal lamina
d	diapophysis
dsr	dorsosacral rib
hyp	hyposphene
hyt	hypantrum
k	ventral keel
nc	neural canal
ns	neural spine
pa	parapophysis
pcdl	posterior centrodiapophyseal lamina
pe	pedicle
pocdf	postzygocentrodiapophyseal fossa
podfl	postdiapophyseal flange
podl	postzygodiapophyseal lamina
poz	postzyapophyses
prcdf	prezygocentrodiapophyseal fossa
prdl	prezygodiapophyseal lamina
prsl	prespinal lamina
prz	prezygapophyses
ps1	primordial sacral one
ps2	primordial sacral two
r	rib
spof	spinopostzygapophyseal fossa
spol	spinopostzygapophyseal lamina
sprf	spinoprezygapophyseal fossa
sprl	spinoprezygapophyseal lamina
sr1	sacral rib 1
sr2	sacral rib 2
tp	transverse process
tpol	intrapostzygapophyseal lamina
tprl	intraprezygapohyseal lamina

Humerus

cf	cuboid fossa
dpc	deltopectoral crest
ect	ectepicondyle
ent	entepicondyle
hh	humeral head

Pubis

ilp	iliac pedicel
pa	pubic apron

Femur

ed	extensor depression
fh	femoral head
fs	femoral shaft
ft	fourth trochanter
gt	greater trochanter
lc	lateral condyle
lt	lesser trochanter
mc	medial condyle
nf	nutrient foramen
pop	popliteal fossa
pt	posterior tubercle
tfc	tibiofibular crest

Tibia

alf	anterolateral fossa
alp	anterolateral process
cc	cnemial crest
lc	lateral condyle
mr	medial ridge
plp	posterolateral process

Fibula

at	anterior trochanter
fbs	fibular shaft
r	ridge

Astragalus

amc	anteromedial corner
ap	ascending process
dp	descending process
f	foramen

Calcaneum

ct	calcaneal tuber
s	sulcus

Metacarpals, metatarsals, phalanges, and unguals

hs	humeral shaft
of	olecranon fossa
pms	post
rc	radial condyle
uc	ulnar condyle

Radius

pdr	posterodistal ridge

Ilium

bc	brevis crest
bf	brevis fossa
ibl	iliac blade
isp	ischial peduncle
mc	medial crest
poap	postacetabular process
prap	preacetabular process
pup	pubic peduncle
sac	supracetabular crest
t	tubercle

clf	collateral ligament fossa
icg	intercondylar groove
lc	lateral condyle
lr	lateral ridge
mc	medial condyle
mr	medial ridge
plf	proximolateral flange
r	ridge
vlf	ventrolateral flange

Histology

DT	diagenetic tissue
LB	lamellar bone
PFB	parallel-fibred bone
PO	primary osteon
RC	resorption cavities
Shf	sharpey's fibres
SO	secondary osteons
WB	woven bone
WFB	woven fibred bone
WPC	woven parallel complex

Appendix 2

Table 4: Training dataset used in the discriminant function analysis

	Higher_Clade	Species	HC	FC	Locomotion	LogHC	LogFC
1	Afrotheria	Elephas_maximus	310	315	Quadrupedal	2.491	2.498
2	Afrotheria	Loxodonta_africana	416.3	399	Quadrupedal	2.619	2.601
3	Afrotheria	Petrodromus_tetradactylus	9.5	12.5	Quadrupedal	0.978	1.097
4	Afrotheria	Rhynchocyon_cirnei	9.5	13.75	Quadrupedal	0.978	1.138
5	Afrotheria	Heterohyrax_brucei	21.75	24.25	Quadrupedal	1.337	1.385
6	Carnivora	Alopex_lagopus	23	24.85	Quadrupedal	1.362	1.395
7	Carnivora	Canis_latrans	41	40.6	Quadrupedal	1.613	1.609
8	Carnivora	Canis_lupus	53.25	51.75	Quadrupedal	1.726	1.714
9	Carnivora	Cuon_alpinus	42.35	44.15	Quadrupedal	1.627	1.645
10	Carnivora	Nyctereutes_procyonoides	25.25	25.75	Quadrupedal	1.402	1.411
11	Carnivora	Urocyon_cinereoargentus	24.1	27.15	Quadrupedal	1.382	1.434
12	Carnivora	Vulpes_velox	21.55	23.3	Quadrupedal	1.333	1.367
13	Carnivora	Vulpes_vulpes	26.25	26.95	Quadrupedal	1.419	1.431
14	Carnivora	Vulpes_zerda	16.25	16.25	Quadrupedal	1.211	1.211
15	Carnivora	Acinonyx_jubatus	62.5	67.5	Quadrupedal	1.796	1.829
16	Carnivora	Felis_catus	28.5	30	Quadrupedal	1.455	1.477
17	Carnivora	Leopardus_pardalis	40.5	42	Quadrupedal	1.607	1.623
18	Carnivora	Lynx_canadensis	38.75	40.85	Quadrupedal	1.588	1.611
19	Carnivora	Lynx_lynx	38	39	Quadrupedal	1.580	1.591
20	Carnivora	Lynx_rufus	36.5	38.25	Quadrupedal	1.562	1.583
21	Carnivora	Neofelis_nebulosa	44.7	41.4	Quadrupedal	1.650	1.617
22	Carnivora	Panthera_leo	116	109	Quadrupedal	2.064	2.037
23	Carnivora	Panthera_onca	76	72.5	Quadrupedal	1.881	1.860
24	Carnivora	Panthera_pardus	62	61	Quadrupedal	1.792	1.785
25	Carnivora	Panthera_tigris_altaica	113	102.5	Quadrupedal	2.053	2.011
26	Carnivora	Panthera_tigris_tigris	94	90.5	Quadrupedal	1.973	1.957
27	Carnivora	Panthera_unica	63.5	63	Quadrupedal	1.803	1.799
28	Carnivora	Puma_concolor	65.5	62.5	Quadrupedal	1.816	1.796
29	Carnivora	Crossarchus_obscurus	14.9	15.5	Quadrupedal	1.173	1.190
30	Carnivora	Galerella_sanguinea	14	14.5	Quadrupedal	1.146	1.161
31	Carnivora	Helogale_parvula	11	12	Quadrupedal	1.041	1.079

32	Carnivora	Herpestes_javanicus	11.6	12.5	Quadrupedal	1.064	1.097
33	Carnivora	Ichneumia_albicauda	23.1	27.05	Quadrupedal	1.364	1.432
34	Carnivora	Liberiictis_kuhni	20.5	22.25	Quadrupedal	1.312	1.347
35	Carnivora	Suricata_suricata	13.2	13.65	Quadrupedal	1.121	1.135
36	Carnivora	Arctonyx_collaris	32.1	29.3	Quadrupedal	1.507	1.467
37	Carnivora	Gulo_gulo	39.75	35	Quadrupedal	1.599	1.544
38	Carnivora	Lutra_canadensis	26.1	24.4	Quadrupedal	1.417	1.387
39	Carnivora	Martes_pennanti	22.25	24.5	Quadrupedal	1.347	1.389
40	Carnivora	Mephitis_mephitis	24.05	22.05	Quadrupedal	1.381	1.343
41	Carnivora	Mustela_erminae	7	7.7	Quadrupedal	0.845	0.886
42	Carnivora	Mustela_frenata	9.55	10.2	Quadrupedal	0.980	1.009
43	Carnivora	Mustela_nigripes	12.15	13.05	Quadrupedal	1.085	1.116
44	Carnivora	Mustela_putorius	12.95	12.5	Quadrupedal	1.112	1.097
45	Carnivora	Mustela_vison	14.65	14.7	Quadrupedal	1.166	1.167
46	Carnivora	Taxidae_taxus	33	27.75	Quadrupedal	1.519	1.443
47	Carnivora	Arctocephalus_pusillus	83.95	48.75	Quadrupedal	1.924	1.688
48	Carnivora	Phoca_groenlandica	68.85	70	Quadrupedal	1.838	1.845
49	Carnivora	Procyon lotor	35	37	Quadrupedal	1.544	1.568
50	Carnivora	Ursus_americanus	101.5	96.5	Quadrupedal	2.006	1.985
51	Carnivora	Ursus_arctos	146.25	126.25	Quadrupedal	2.165	2.101
52	Carnivora	Ursus_maritimus	158	135	Quadrupedal	2.199	2.130
53	Carnivora	Viverricula_indica	21.2	24.1	Quadrupedal	1.326	1.382
54	Euarchonta	Aotus_trivirgatus	15	16.85	Quadrupedal	1.176	1.227
55	Euarchonta	Callithrix_jacchus	11.05	11.85	Quadrupedal	1.043	1.074
56	Euarchonta	Cebuella_pygmaea	8.75	8.85	Quadrupedal	0.942	0.947
57	Euarchonta	Saguinus_sp.	12.2	13.35	Quadrupedal	1.086	1.125
58	Euarchonta	Cercopithecus_neglectus	36.95	39.05	Quadrupedal	1.568	1.592
59	Euarchonta	Macaca_fuscata	30	31.5	Quadrupedal	1.477	1.498
60	Euarchonta	Papio_cynocephalus	55	57	Quadrupedal	1.740	1.756
61	Euarchonta	Papio_hamadryas	42.25	44.5	Quadrupedal	1.626	1.648
62	Euarchonta	Euoticus_elegantulus	11.2	12	Quadrupedal	1.049	1.079

63	Euarchonta	Otolemur_crassicaudatus	16	19	Quadrupedal	1.204	1.279
64	Euarchonta	Pongo_Pygmaeus	98.5	88	Quadrupedal	1.993	1.944
65	Euarchonta	Hylobates_lar	28.5	31.45	Quadrupedal	1.455	1.498
66	Euarchonta	Eulemur_fulvus	16.05	19.8	Quadrupedal	1.205	1.297
67	Euarchonta	Lemur_catta	21	26.8	Quadrupedal	1.322	1.428
68	Euarchonta	Tupaia_glis	7	9.35	Quadrupedal	0.845	0.971
69	Eulipotyphla	Atelerix_albiventris	10.95	15.15	Quadrupedal	1.039	1.180
70	Eulipotyphla	Atelerix_algirus	10.2	11.7	Quadrupedal	1.009	1.068
71	Eulipotyphla	Echinosorex_gymnura	11	13.05	Quadrupedal	1.041	1.116
72	Eulipotyphla	Erinaceus_europaeus	15.5	16.75	Quadrupedal	1.190	1.224
73	Eulipotyphla	Condylura_cristata	10.05	6.3	Quadrupedal	1.002	0.799
74	Eulipotyphla	Parascalops_breweri	12.3	5.9	Quadrupedal	1.090	0.771
75	Glires	Aplodontia_rufa	15	15.75	Quadrupedal	1.176	1.197
76	Glires	Castor_canadensis	34.5	49.75	Quadrupedal	1.538	1.697
77	Glires	Cavia_porcellus	12.6	16	Quadrupedal	1.100	1.204
78	Glires	Dolichotis_patagonum	28.6	35.35	Quadrupedal	1.456	1.548
79	Glires	Chinchilla_lanigera	8.85	14.8	Quadrupedal	0.947	1.170
80	Glires	Dicrostonyx_groenlandicus	6.9	7.15	Quadrupedal	0.839	0.854
81	Glires	Dicrostonyx_hudsonius	7.1	8	Quadrupedal	0.851	0.903
82	Glires	Dicrostonyx_richardsoni	5.8	5.6	Quadrupedal	0.763	0.748
83	Glires	Melanomys_caliginosus	6	8.2	Quadrupedal	0.778	0.914
84	Glires	Mesocricetus_auratus	8.85	11	Quadrupedal	0.947	1.041
85	Glires	Microtus_chrotorrhinus	4.85	5.6	Quadrupedal	0.686	0.748
86	Glires	Microtus_pennsylvanicus	4.5	5.7	Quadrupedal	0.653	0.756
87	Glires	Microtus_richardsoni	5.2	6.75	Quadrupedal	0.716	0.829
88	Glires	Nectomys_squamipes	7.6	11.8	Quadrupedal	0.881	1.072
89	Glires	Neotoma_albigula	8.45	11.05	Quadrupedal	0.927	1.043
90	Glires	Oryzomys_albigularis	6	8	Quadrupedal	0.778	0.903
91	Glires	Oryzomys_couesi	7.05	9.85	Quadrupedal	0.848	0.993
92	Glires	Oryzomys_megacephalus	5.75	7.5	Quadrupedal	0.760	0.875

93	Glires	Peromyscus_zarhynchus	5.55	7	Quadrupedal	0.744	0.845
94	Glires	Rhipidomys_leucodactylus	7.9	10	Quadrupedal	0.898	1.000
95	Glires	Sigmodon_hispidus	6.75	10	Quadrupedal	0.829	1.000
96	Glires	Dasyprocta_aguti	20.5	28	Quadrupedal	1.312	1.447
97	Glires	Echimys_didelphoides	10.1	13.5	Quadrupedal	1.004	1.130
98	Glires	Echimys_semivillosus	10.5	14.25	Quadrupedal	1.021	1.154
99	Glires	Proechimys_cuvieri	9.05	13.5	Quadrupedal	0.957	1.130
100	Glires	Erethizon_dorsatum	29.65	37.4	Quadrupedal	1.472	1.573
101	Glires	Geomys_bursarius	10.25	9.15	Quadrupedal	1.011	0.961
102	Glires	Orthogeomys_hispidus	13.95	14.05	Quadrupedal	1.145	1.148
103	Glires	Thomomys_Talpoides	10.7	10.3	Quadrupedal	1.029	1.013
104	Glires	Dipodomys_ordii	5.1	7.35	Quadrupedal	0.708	0.866
105	Glires	Heteromys_desmarestianus	6.15	8.9	Quadrupedal	0.789	0.949
106	Glires	Heteromys_gaumeri	6	8.2	Quadrupedal	0.778	0.914
107	Glires	Heteromys_goldmani	6.1	8.7	Quadrupedal	0.785	0.940
108	Glires	Hydrochaeris_hydrochaeris	60.5	70.5	Quadrupedal	1.782	1.848
109	Glires	Lepus_americanus	14.5	19.65	Quadrupedal	1.161	1.293
110	Glires	Lepus_arcticus	22	30	Quadrupedal	1.342	1.477
111	Glires	Lepus_californicus	17.8	12.3	Quadrupedal	1.250	1.090
112	Glires	Lepus_europaeus	24.75	33.75	Quadrupedal	1.394	1.528
113	Glires	Lepus_townsendii	20.75	28.25	Quadrupedal	1.317	1.451
114	Glires	Oryctolagus_cuniculus	15.5	20	Quadrupedal	1.190	1.301
115	Glires	Sylvilagus_floridanus	14.85	18.35	Quadrupedal	1.172	1.264
116	Glires	Acomys_cahirinus	4.36	6.225	Quadrupedal	0.639	0.794
117	Glires	Arvicanthis_niloticus	6.5	9.05	Quadrupedal	0.813	0.957
118	Glires	Gerbillus_gerbillus	5.1	8	Quadrupedal	0.708	0.903
119	Glires	Gerbillus_pyramidum	5.2	7.3	Quadrupedal	0.716	0.863
120	Glires	Malacomys_cansdalei	5.25	7.1	Quadrupedal	0.720	0.851

121	Glires	Meriones_unguiculatus	5.1	7	Quadrupedal	0.708	0.845
122	Glires	Ondatra_zibethicus	14	16.65	Quadrupedal	1.146	1.221
123	Glires	Rattus_norvegicus	10.9	14.25	Quadrupedal	1.037	1.154
124	Glires	Myocastor_coypus	25.5	32.7	Quadrupedal	1.407	1.515
125	Glires	Cricetomys_emini	12.65	16	Quadrupedal	1.102	1.204
126	Glires	Octodon_degus	7.05	9.45	Quadrupedal	0.848	0.975
127	Glires	Cynomys_leucurus?	13.5	13.5	Quadrupedal	1.130	1.130
128	Glires	Funisciurus_pyrrhopus	9.1	10.25	Quadrupedal	0.959	1.011
129	Glires	Marmota_caligata	28.4	25.1	Quadrupedal	1.453	1.400
130	Glires	Marmota_monax	24.15	22	Quadrupedal	1.383	1.342
131	Glires	Sciurus_carolinensis	13.1	14.6	Quadrupedal	1.117	1.164
132	Glires	Sciurus_niger	16.85	18.25	Quadrupedal	1.227	1.261
133	Glires	Spermophilus_adocetus	8.9	10.05	Quadrupedal	0.949	1.002
134	Glires	Spermophilus_franklinii	11.9	12	Quadrupedal	1.076	1.079
135	Glires	Spermophilus_lateralis	7.3	8.7	Quadrupedal	0.863	0.940
136	Glires	Spermophilus_richardsonii	10.1	10.9	Quadrupedal	1.004	1.037
137	Glires	Spermophilus_tridecemlineatus	9.7	8.8	Quadrupedal	0.987	0.944
138	Glires	Tamias_amoenus	5.25	6	Quadrupedal	0.720	0.778
139	Glires	Tamias_minimus	5.6	5.95	Quadrupedal	0.748	0.775
140	Glires	Tamiasciurus_hudsonicus	10	9.95	Quadrupedal	1.000	0.998
141	Marsupialia	Dasyuroides_byrnei	7.15	8.7	Quadrupedal	0.854	0.940
142	Marsupialia	Sarcophilus_harrisii	27.25	27.45	Quadrupedal	1.435	1.439
143	Marsupialia	Chironectes_minimus	12.25	14.95	Quadrupedal	1.088	1.175
144	Marsupialia	Didelphis_marsupialis	17	18.8	Quadrupedal	1.230	1.274
145	Marsupialia	Didelphis_virginiana	26.5	26.25	Quadrupedal	1.423	1.419
146	Marsupialia	Marmosa_murina	6.2	6.1	Quadrupedal	0.792	0.785
147	Marsupialia	Metachirus_nudicaudatus	9.25	11.45	Quadrupedal	0.966	1.059
148	Marsupialia	Monodelphis_brevicaudata	6.9	6.8	Quadrupedal	0.839	0.833

149	Marsupialia	Philander_opossum	10.95	12.85	Quadrupedal	1.039	1.109
150	Marsupialia	Bettongia_penicillata	12.95	21.45	Bipedal	1.112	1.331
151	Marsupialia	Dendrolagus_inustus	48.25	56.25	Quadrupedal	1.683	1.750
152	Marsupialia	Macropus_fuliginosus	31	57.5	Bipedal	1.491	1.760
153	Mammalia	Macropus rufus	64.5	78	Bipedal	1.810	1.892
154	Marsupialia	Gymnobelideus_leadbeateri	7.75	8.2	Quadrupedal	0.889	0.914
155	Ungulata	Aepyceros_malampus	65	69	Quadrupedal	1.813	1.839
156	Ungulata	Ammotragus_lervia	65.75	67.25	Quadrupedal	1.818	1.828
157	Ungulata	Antilope_cervicapra	47.4	47.55	Quadrupedal	1.676	1.677
158	Ungulata	Bison_bison	191.5	167.5	Quadrupedal	2.282	2.224
159	Ungulata	Bison_bonasus	130	122	Quadrupedal	2.114	2.086
160	Ungulata	Bos_gaurus	154.5	156.5	Quadrupedal	2.189	2.195
161	Ungulata	Capra_aegagrus	58	58.95	Quadrupedal	1.763	1.770
162	Ungulata	Capra_caucasica	89	88	Quadrupedal	1.949	1.944
163	Ungulata	Capra_ibex	54.1	52.65	Quadrupedal	1.733	1.721
164	Ungulata	Connochaetes_gnou	85.5	87	Quadrupedal	1.932	1.940
165	Ungulata	Connochaetes taurinus	116	102	Quadrupedal	2.064	2.009
166	Ungulata	Hemitragus_jemlahicus	61.4	57.8	Quadrupedal	1.788	1.762
167	Ungulata	Oryx_dammah	95	92.5	Quadrupedal	1.978	1.966
168	Ungulata	Ovibos_moschatus	128	111	Quadrupedal	2.107	2.045
169	Ungulata	Ovis_aries	74.5	79	Quadrupedal	1.872	1.898
170	Ungulata	Ovis_dalli	82.5	81.5	Quadrupedal	1.916	1.911
171	Ungulata	Sylvicapra_grimmia	31	46	Quadrupedal	1.491	1.663
172	Ungulata	Tragelaphus_angasii	99	97	Quadrupedal	1.996	1.987
173	Ungulata	Tragelaphus_scriptus	56	62	Quadrupedal	1.748	1.792
174	Ungulata	Tragelaphus_strepsiceros	140	135	Quadrupedal	2.146	2.130
175	Ungulata	Lama_guanicoe	100	95	Quadrupedal	2.000	1.978
176	Ungulata	Alces_alces	145.5	144	Quadrupedal	2.163	2.158
177	Ungulata	Cervus_duvaucelii	101.5	105	Quadrupedal	2.006	2.021
178	Ungulata	Cervus_nippon	70	73	Quadrupedal	1.845	1.863
179	Ungulata	Elaphurus_davidianus	112.5	112	Quadrupedal	2.051	2.049
180	Ungulata	Hydropotes_inermis	33.95	43.65	Quadrupedal	1.531	1.640

181	Ungulata	Odocoileus_virginianus	72	77	Quadrupedal	1.857	1.886
182	Ungulata	Rangifer_tarandus	90.5	85.5	Quadrupedal	1.957	1.932
183	Ungulata	Equus_burchelli?	118	137.5	Quadrupedal	2.072	2.138
184	Ungulata	Equus_caballus	118.25	139.85	Quadrupedal	2.073	2.146
185	Ungulata	Equus_zebra	132	143	Quadrupedal	2.121	2.155
186	Ungulata	Giraffa_camelopardalis	218	188	Quadrupedal	2.338	2.274
187	Ungulata	Okapia_johstoni	131	128	Quadrupedal	2.117	2.107
188	Ungulata	Choeropsis_liberiensis	101	107	Quadrupedal	2.004	2.029
189	Ungulata	Hippopotamus amphibius	226	231	Quadrupedal	2.354	2.364
190	Ungulata	Ceratotherium_simum	257	225	Quadrupedal	2.410	2.352
191	Ungulata	Rhinoceros_sondaicus	213	206	Quadrupedal	2.328	2.314
192	Ungulata	Phacochoerus_africanus	83	72	Quadrupedal	1.919	1.857
193	Ungulata	Tapirus_indicus	109	115	Quadrupedal	2.037	2.061
194	Ungulata	Tapirus_terrestris	94.5	106	Quadrupedal	1.975	2.025
195	Mammalia	Dasypus novemcinctus	23.45	33.86	Quadrupedal	1.370	1.530
196	Xenarthra	Priodontes_maximus	68.25	78.5	Quadrupedal	1.834	1.895
197	Xenarthra	Choloepus_didactylus	40.25	43.25	Quadrupedal	1.605	1.636
198	Xenarthra	Choloepus hoffmanni	34	40	Quadrupedal	1.531	1.602
199	Xenarthra	Tamandua_tetradactyla	34.6	29.8	Quadrupedal	1.539	1.474
200	Reptilia	Alligator_mississippiensis	88.5	86	Quadrupedal	1.947	1.934
201	Reptilia	Caiman crocodilus	55	60	Quadrupedal	1.740	1.778
202	Reptilia	Physignathus_cocincinus	8.05	10.1	Quadrupedal	0.906	1.004
203	Reptilia	Physignathus_leseuri	9.1	10.9	Quadrupedal	0.959	1.037
204	Reptilia	Pogona_vitticeps	9.05	9.5	Quadrupedal	0.957	0.978
205	Reptilia	Uromastyx_aegyptia	14	16.1	Quadrupedal	1.146	1.207
206	Reptilia	Uromastyx_maliensis	9.55	10.2	Quadrupedal	0.980	1.009
207	Reptilia	Chamaeleo_calyptratus	7.05	6.5	Quadrupedal	0.848	0.813
208	Reptilia	Chamaeleo_melleri	8.65	9.5	Quadrupedal	0.937	0.978
209	Reptilia	Furcifer_pardalis	7.3	7.5	Quadrupedal	0.863	0.875

210	Reptilia	Basiliscus_plumifrons	7.55	9.5	Quadrupedal	0.878	0.978
211	Reptilia	Basiliscus_vittatus	5.95	7.5	Quadrupedal	0.775	0.875
212	Reptilia	Gekko_gekko	5.45	5.75	Quadrupedal	0.736	0.760
213	Reptilia	Gerrhosaurus_major	6.5	7.8	Quadrupedal	0.813	0.892
214	Reptilia	Heloderma_suspectum	10.25	10.85	Quadrupedal	1.011	1.035
215	Reptilia	Iguana iguana	23	27	Quadrupedal	1.362	1.431
216	Reptilia	Corucia_zebrata	10.15	10.95	Quadrupedal	1.006	1.039
217	Reptilia	Tiliqua_scincoides	7.75	8.1	Quadrupedal	0.889	0.908
218	Reptilia	Tupinambis_teguixin	15	17.85	Quadrupedal	1.176	1.252
219	Reptilia	Varanus_albigularis	16.8	18.6	Quadrupedal	1.225	1.270
220	Reptilia	Varanus_beccarii	7.25	8.6	Quadrupedal	0.860	0.934
221	Reptilia	Varanus_exanthematicus	25	27.4	Quadrupedal	1.398	1.438
222	Reptilia	Varanus_jobiensis	16.75	21	Quadrupedal	1.224	1.322
223	Reptilia	Varanus_komodoensis	62	67	Quadrupedal	1.792	1.826
224	Reptilia	Varanus_niloticus	29.75	34	Quadrupedal	1.473	1.531
225	Reptilia	Varanus_salvadorii	25.1	25.75	Quadrupedal	1.400	1.411
226	Reptilia	Chelydra_serpentina	29.5	27.25	Quadrupedal	1.470	1.435
227	Reptilia	Chrysemys_picta	10	10	Quadrupedal	1.000	1.000
228	Reptilia	Clemmys_guttata	6.65	7	Quadrupedal	0.823	0.845
229	Reptilia	Cuora_galbinifrons	12.95	11.95	Quadrupedal	1.112	1.077
230	Reptilia	Emydoidea_blandingii	15	16	Quadrupedal	1.176	1.204
231	Reptilia	Glyptemys_insculpta	12.45	13.15	Quadrupedal	1.095	1.119
232	Reptilia	Pseudemys_texana	9.05	10	Quadrupedal	0.957	1.000
233	Reptilia	Terrapene_carolina	11.85	11.45	Quadrupedal	1.074	1.059
234	Reptilia	Trachemys_scripta	13.75	14.2	Quadrupedal	1.138	1.152
235	Reptilia	Kinosternon_baurii	7.25	6.4	Quadrupedal	0.860	0.806
236	Reptilia	Kinosternon_subrubrum	7	6.8	Quadrupedal	0.845	0.833
237	Reptilia	Sternotherus_minor	7.2	7	Quadrupedal	0.857	0.845

238	Reptilia	Sternotherus_odoratus	8	7	Quadrupedal	0.903	0.845
239	Reptilia	Platysternon_megacephalum	12.75	12	Quadrupedal	1.106	1.079
240	Reptilia	Geochelone_carbonaria	19	15.65	Quadrupedal	1.279	1.195
241	Reptilia	Gopherus_polyphemus	24	19.9	Quadrupedal	1.380	1.299
242	Reptilia	Kinixys_homeana	17.9	15.95	Quadrupedal	1.253	1.203
243	Reptilia	Amyda_cartilaginae	16.35	14	Quadrupedal	1.214	1.146
244	Reptilia	Apalone_ferox	22.25	23.6	Quadrupedal	1.347	1.373
245	Reptilia	Apalone_spiniferus	10.3	11	Quadrupedal	1.013	1.041
246	Reptilia	Pelodiscus_sinensis	15.3	13.05	Quadrupedal	1.185	1.116
247	Amphibia	Ambystoma_tigrinum	6	4	Quadrupedal	0.778	0.602
248	Amphibia	Ceratophrys_cranwelli	8.65	8.45	Quadrupedal	0.937	0.927
249	Amphibia	Litoria_caerulea	6	5	Quadrupedal	0.778	0.699
250	Amphibia	Rhinella_schneideri	11.9	12.15	Quadrupedal	1.076	1.085
251	Amphibia	Lepidobatrachus_laevis	8.5	8.5	Quadrupedal	0.929	0.929
252	Amphibia	Osteopilus_septentrionalis	8.5	7.7	Quadrupedal	0.929	0.886
253	Amphibia	Xenopus_laevis	5.4	7.9	Quadrupedal	0.732	0.898
254	Amphibia	Dyscophus_guineti	6.6	6.2	Quadrupedal	0.820	0.792
255	Mammalia	Homo sapiens	62	88	Bipedal	1.792	1.944
256	Mammalia	Felis silvestris	32	34	Quadrupedal	2.046	1.531
257	Mammalia	Antilocapra americana	71	68	Quadrupedal	1.851	1.833
258	Mammalia	Myrmecophaga tridactyla	137	90	Quadrupedal	2.137	1.954
259	Mammalia	Dendrolagus dorianus	45	48	Quadrupedal	1.653	1.681
260	Aves	Struthio camelus	51	134	Bipedal	1.708	2.127
261	Mammalia	Pedetes capensis	17	30	Bipedal	1.230	1.477
262	Mammalia	Macropus agilis	30	47	Bipedal	1.477	1.672
263	Mammalia	Macropus rufogriseus	48	63	Bipedal	1.681	1.799
264	Mammalia	Phascolarctos cinereus	37	38	Quadrupedal	1.568	1.580
265	Aves	Rhea americana	36	79	Bipedal	1.556	1.898
266	Mammalia	Jaculus jaculus	4.2	7	Bipedal	0.623	0.845
267	Mammalia	Jaculus orientalis	6	10.5	Bipedal	0.778	1.021
268	Mammalia	Potorous tridactylus	13.25	21	Bipedal	1.122	1.322

269	Aves	Dromaius novaehollandiae	28.1	95.3	Bipedal	1.449	1.979
270	Aves	Apteryx australis	8.4	34.4	Bipedal	0.924	1.537
271	Mammalia	Smutsia temminckii	43	50	Bipedal	1.633	1.699
272	Mammalia	Phataginus tetradactyla	19.5	20	Quadrupedal	1.290	1.301
273	Mammalia	Phataginus tricuspis	23.5	25.5	Quadrupedal	1.371	1.407
274	Reptilia	Crocodilus niloticus	87.5	90.5	Quadrupedal	1.942	1.957
275		Chlorocebus_pygerythrus	25	28	Quadrupedal	1.398	1.447
276		Ateles_paniscus	32	40	Quadrupedal	1.505	1.602
277		Callithrix_aurita	11	12	Quadrupedal	1.041	1.079
278		Citellus_columbianus_columbianus	12.62	13.94	Quadrupedal	1.101	1.144
279		Zapus_hudsonius_hudsonius	2.32	6.95	Bipedal	0.365	0.842
280		Alactaga_mongolica	4.85	8.76	Bipedal	0.686	0.943
281		Dipodomys_heermani_swarthi	5.18	7.6	Bipedal	0.714	0.881
282		Dipodyms_spectabilis	7.64	10.97	Bipedal	0.883	1.040
283		Aepyprymnus_rufescens	14.87	25.72	Bipedal	1.172	1.410
284		Bettongia_gaimardi_cuniculus	15.06	21.71	Bipedal	1.178	1.337
285		Bettongia_lesueur	15.12	23.32	Bipedal	1.180	1.368
286		Bettongia_penicillata	14.06	20.13	Bipedal	1.148	1.304
287		Dendrolagus_lumholtzi	30.17	40.41	Quadrupedal	1.480	1.606
288		Lagorchestes_conspicillatus	17.85	31.37	Bipedal	1.252	1.497
289		Petrogale_herberti	19.68	32.15	Bipedal	1.294	1.507
290		Onychogalea_fraenata	16.65	25.67	Bipedal	1.221	1.409
291		Setonix_brachyurus	17.48	30.38	Bipedal	1.243	1.483
292		Thylogale_billardierii	22.8	35.58	Bipedal	1.358	1.551
293		Pan_troglodytes	68	72	Quadrupedal	1.833	1.857
294		Gorilla_gorilla	120	120	Quadrupedal	2.079	2.079
295		Wallabia_bicolor	21.06	43.7	Bipedal	1.323	1.640
296		Litocranius_walleri_walleri	55.43	51.8	Quadrupedal	1.744	1.714
297		Glossotherium_myloides	235	319	Quadrupedal	2.371	2.504
298		Sthenurus_sp.	74.36	139	Bipedal	1.871	2.143

299		Sthenurus_sp.	79.18	141.4	Bipedal	1.899	2.150
300		Tylocephalonyx_skinneri	230	223	Quadrupedal	2.362	2.348
301		Moropus_elatus	251	235	Quadrupedal	2.400	2.371
302		Ursus_arctos	107	94	Quadrupedal	2.029	1.973
303		Thalarctos_maritimus	135	120	Quadrupedal	2.130	2.079
304	Macropodidae	Macropus giganteus	72	81.2	Bipedal	1.857	1.910
305	Ornithischa	Lesothosaurus_diagnosticus	20	43	Bipedal	1.301	1.633
306	Ornithischa	Loricatosaurus_priscus	261	300	Quadrupedal	2.417	2.477
307	Ornithischa	Stegosaurus_ungulatus	352	425	Quadrupedal	2.547	2.628
308	Ornithischa	Stegosaurus_mjosi	330	345	Quadrupedal	2.519	2.538
309	Ornithischa	Minmi_paravertebra	111.27	139.9	Quadrupedal	2.046	2.146
310	Ornithischa	Ankylosaurus_magniventris	315	363	Quadrupedal	2.498	2.560
311	Ornithischa	Euoplocephalus_tutus	244	278	Quadrupedal	2.387	2.444
312	Ornithischa	Saichania_chulsanensis	155	166	Quadrupedal	2.190	2.220
313	Ornithischa	Gargoyleosaurus_parkpinorum	175	193	Quadrupedal	2.243	2.286
314	Ornithischa	Hungarosaurus_tormai	160	175	Quadrupedal	2.204	2.243
315	Ornithischa	Sauropelta_edwardsi	256	317	Quadrupedal	2.408	2.501
316	Ornithischa	Niobrarasaurus_coleii	207.54	206.38	Quadrupedal	2.317	2.315
317	Ornithischa	Edmontonia_longiceps	240	276	Quadrupedal	2.380	2.441
318	Ornithischa	Styracosaurus_albertensis	280	365	Quadrupedal	2.447	2.562
319	Ornithischa	Centrosaurus_apertus	249	286	Quadrupedal	2.396	2.456
320	Ornithischa	Pachyrhinosaurus_canadensis	275	385	Quadrupedal	2.439	2.585
321	Ornithischa	Chasmosaurus_russelli	270	312	Quadrupedal	2.431	2.494
322	Ornithischa	Chasmosaurus_belli	254	325	Quadrupedal	2.405	2.512
323	Ornithischa	Pentaceratops_sternbergii	400.5	511.5	Quadrupedal	2.603	2.709
324	Ornithischa	Triceratops_horridus	410	520	Quadrupedal	2.613	2.716
325	Ornithischa	Triceratops_prorsus	444.86	485	Quadrupedal	2.648	2.686
326	Ornithischa	Orodromeus_makelai	38	65	Bipedal	1.580	1.813

327	Ornithischa	Parksosaurus_warreni	72	103	Bipedal	1.857	2.013
328	Ornithischa	Thescelosaurus_neglectus	108	183	Bipedal	2.033	2.262
329	Ornithischa	Hypsilophodon_foxi	50	70	Bipedal	1.699	1.845
330	Sauropodomorpha	Saturnalia	33.23247	52	Bipedal	1.522	1.716
331	Sauropodomorpha	Mamenchisaurus_youngi	328	419	Quadrupedal	2.516	2.622
332	Sauropodomorpha	Mamenchisaurus_constructus	509	580	Quadrupedal	2.707	2.763
333	Sauropodomorpha	Yuanmousaurus_jiangyiensis	360	450	Quadrupedal	2.556	2.653
334	Sauropodomorpha	Cetiosauriscus	507	535	Quadrupedal	2.705	2.728
335	Sauropodomorpha	Omeisaurus_junghsiensis	390	460	Quadrupedal	2.591	2.663
336	Sauropodomorpha	Omeisaurus_maoanus	340	470	Quadrupedal	2.531	2.672
337	Sauropodomorpha	Ferganasaurus	370.9047	494.2514	Quadrupedal	2.569	2.694
338	Sauropodomorpha	Turiasaurus	755	848	Quadrupedal	2.878	2.928
339	Sauropodomorpha	Atlasaurus	565	690	Quadrupedal	2.752	2.839
340	Sauropodomorpha	Amargasaurus	388	505	Quadrupedal	2.589	2.703
341	Sauropodomorpha	Apatosaurus_louisae	640	845	Quadrupedal	2.806	2.927
342	Sauropodomorpha	Apatosaurus_excelsus	591	740	Quadrupedal	2.772	2.869
343	Sauropodomorpha	Apatosaurus_ajax	584	726	Quadrupedal	2.766	2.861
344	Sauropodomorpha	Apatosaurus_parvus	496.1523	734.8208	Quadrupedal	2.696	2.866
345	Sauropodomorpha	Tornieria	411.8543	545	Quadrupedal	2.615	2.736
346	Sauropodomorpha	Diplodocus_hayi	470	590	Quadrupedal	2.672	2.771
347	Sauropodomorpha	Diplodocus_longus	460	563	Quadrupedal	2.663	2.751
348	Sauropodomorpha	Lourinhasaurus	547	785	Quadrupedal	2.738	2.895
349	Sauropodomorpha	Camarasaurus_grandis	472	630	Quadrupedal	2.674	2.799
350	Sauropodomorpha	Tehuelchesaurus	615	730	Quadrupedal	2.789	2.863
351	Sauropodomorpha	Aragosaurus	395.174	640	Quadrupedal	2.597	2.806
352	Sauropodomorpha	Europasaurus	190	200	Quadrupedal	2.279	2.301
353	Sauropodomorpha	Giraffatitan	654	730	Quadrupedal	2.816	2.863

354	Sauropodomorpha	Cedarosaurus	445	590	Quadrupedal	2.648	2.771
355	Sauropodomorpha	Euhelopus	358	375	Quadrupedal	2.554	2.574
356	Sauropodomorpha	Chubutisaurus	599	710	Quadrupedal	2.777	2.851
357	Sauropodomorpha	Ligabuesaurus	510	640	Quadrupedal	2.708	2.806
358	Sauropodomorpha	Futalognkosaurus	643	800	Quadrupedal	2.808	2.903
359	Sauropodomorpha	Epachthosaurus	409	491	Quadrupedal	2.612	2.691
360	Sauropodomorpha	Alamosaurus	661	740	Quadrupedal	2.820	2.869
361	Sauropodomorpha	Opisthocoelicaudia	565	680	Quadrupedal	2.752	2.833
362	Sauropodomorpha	Eoraptor	35	62	Bipedal	1.544	1.792
363	Theropoda	Ceratosaurus	130	268	Bipedal	2.114	2.428
364	Theropoda	Aucasaurus	115	256	Bipedal	2.061	2.408
365	Theropoda	D_sinensis	125	220	Bipedal	2.097	2.342
366	Theropoda	Piatnizkysaurus	105	245	Bipedal	2.021	2.389
367	Theropoda	Suchomimus	239	400	Bipedal	2.378	2.602
368	Theropoda	Chilantaisaurus	229	432	Bipedal	2.360	2.635
369	Theropoda	Acrocanthosaurus	195	426	Bipedal	2.290	2.629
370	Theropoda	Zuolong	62	112.3	Bipedal	1.792	2.050
371	Theropoda	Tanycolagreus	55	92	Bipedal	1.740	1.964
372	Theropoda	Guanlong	67	104	Bipedal	1.826	2.017
373	Theropoda	Dryptosaurus	137	274	Bipedal	2.137	2.438
374	Theropoda	Deinocheirus	330	560	Bipedal	2.519	2.748
375	Theropoda	Nothronychus_graffami	136.1168	289	Bipedal	2.134	2.461
376	Theropoda	Buitreraptor	25	34	Bipedal	1.398	1.531
377	Theropoda	Unenlagia	65	99	Bipedal	1.813	1.996
378	Theropoda	Velociraptor	40	64	Bipedal	1.602	1.806

Appendix 3

R code for DFA:

```
# Set working directory
setwd("~/1 Tash/Wits/MSc/Posture")
list.files("~/1 Tash/Wits/MSc/Posture")
getwd()
# Require packages
require(MASS)
require (plyr)
require(dplyr)
# Load data
extant<-read.csv2("All_extant_format.csv")
MOU<-read.csv("MOU.csv")
Dino.training<-read.csv("Dinosaur_training_set_04October2022.csv")
sauro<-read.csv("sauro_dfa.csv")
# Omit data with NA
sauro1<-na.omit(sauro)
num<-rep(1:77)
sauro2<-rbind.data.frame(sauro1, MOU)
sauro2<-cbind.data.frame(sauro2, num)
# Compile training dataset
trainingset<-rbind.data.frame(extant, Dino.training)
# Filtering by locomotion
bipeds<-trainingset%>%filter(Locomotion=='Bipedal')
quadrupeds<- trainingset%>%filter(Locomotion=='Quadrupedal')
# Running DFA
iter <- 10000
DFA.results.list <- list()
DFA_repeat<-list()
for( i in 1:iter) {
  random<-rbind(sample_n(quadrupeds, 55), sample_n(bipeds, 55))
  DFA.results.list[[ i ]] <- lda(Locomotion ~ LogHC + LogFC, data = random)
  DFA_repeat[[ i ]]<-predict(DFA.results.list[[i]], sauro2)}
#Summarise results
lapply(DFA_repeat, summary)
#Convert results to dataframe, factor 1= Bipedal
Predict_df.sauro <- data.frame(matrix(unlist(DFA_repeat), nrow=10000, byrow=T))
#Summarise all factors for all 77 individuals (out of 10000 repeats)
count.bipeds.per.column.sauro <- ldply(Predict_df.sauro, function(c) sum(c=="1"))
count.bipeds.per.column.sauro$percentage_bipedal<-count.bipeds.per.column.sauro$V1/100
```

```
count.bipeds.per.column.sauro<- count.bipeds.per.column.sauro[-c(78:308), ]
#above is n x 4
row.names(count.bipeds.per.column.sauro)<-sauro2$Species
count.bipeds.per.column.sauro
#get mean post probability bipedal
predict_df_posterior_bipedal<-Predict_df.sauro[,c(78:154)]
#above is n x 2
mean_post_bipedal<-colMeans(predict_df_posterior_bipedal)
mean_post_bipedal<-as.data.frame(mean_post_bipedal)
count.bipeds.per.column.sauro$post<-mean_post_bipedal$mean_post_bipedal
count.bipeds.per.column.sauro$post<-as.numeric(as.character(count.bipeds.per.column.sauro$post))
# Tabulate and view output
count.bipeds.per.column.sauro$post_outcome<-
ifelse(count.bipeds.per.column.sauro$post>0.66,'Bipedal',
                                        ifelse(count.bipeds.per.column.sauro$post<0.66 &
                                               count.bipeds.per.column.sauro$post>0.33,
                                             'Equivocal', 'Quadrupedal'))

count.bipeds.per.column.sauro$post_outcome
```

Appendix 4

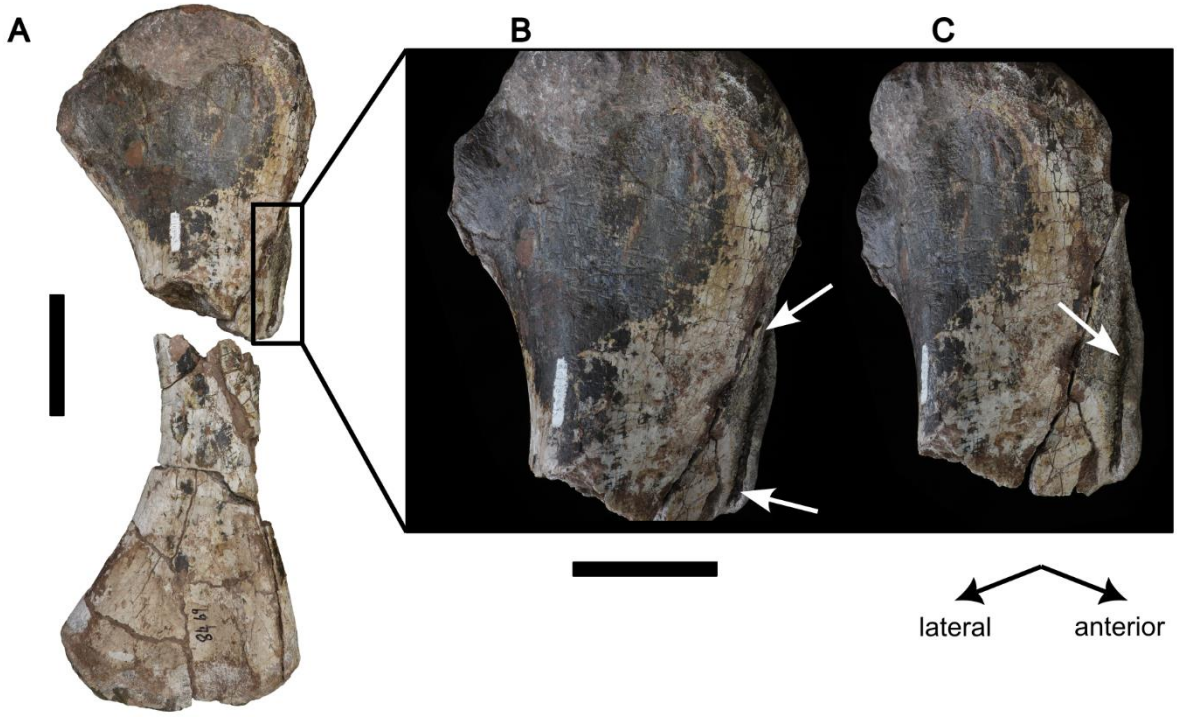

Figure 37: Lateral view of the right humerus of BP/1/8469 (A) with a close up (B) of the paramarginal sulcus and an oblique view (C) of the paramarginal sulcus. Scale bar = 10 cm. .

Appendix 5

Character matrix used in Mesquite:

BEGIN TAXA;

TITLE Taxa;

DIMENSIONS NTAX=77;

TAXLABELS

Euparkeria Crurotarsi Marasuchus Ornithischia Agnosphitys Silesaurus Neotheropoda Staurikosaurus Chindesaurus Herrerasaurus Guaibasaurus Eoraptor Saturnalia Panphagia Chromogisaurus Buriolestes Pampadromaeus Bagualosaurus Thecodontosaurus Pantydraco Efraasia Nambalia Jaklapalisaurus Pradhania Macrocollum Unaysaurus Ruehleia Plateosaurus_ingens Plateosaurus_gracilis Plateosaurus_engelhardti Glacialisaurus Coloradisaurus Lufengosaurus Xixipiosaurus Massospondylus_carinatus Adeopapposaurus Leyesaurus Ngwevu Plateosauravus Riojasaurus Eucnemesaurus_fortis Eucnemesaurus_entaxonis Seitaad Sarahsaurus Yunnanosaurus_huangi Xingxiulong Jingshanosaurus Chuxiongosaurus Yizhousaurus Anchisaurus Mussaurus Leonerasaurus Sefapanosaurus Aardonyx Irisosaurus NMRQ3314 NMQR1551 Meroktenos Ingentia Lessemsaurus Antetonitrus Ledumahadi Kholumolumo Blikanasaurus Camelotia Schleitheimia Pulanesaura Gongxianosaurus Isanosaurus Tazoudasaurus Vulcanodon Shunosaurus Spinophorosaurus Patagosaurus Barapasaurus Cetiosaurus BP_1_8469

;

END;

BEGIN CHARACTERS;

TITLE Character_Matrix;

DIMENSIONS NCHAR=419;

FORMAT DATATYPE = STANDARD RESPECTCASE GAP = - MISSING = ? SYMBOLS = " 0 1 2 3";

MATRIX

Euparkeria

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000010000000010100000?000?00100000000000000??12??000??11111?1100??101?00?0000?0??
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Panphagia

?0??????????????????0?1??????????????????0??1????????1?1?0???????10?0?111????0?
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Chromogisaurus

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Buriolestes

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Pampadromaeus

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Bagualosaurus 10?1?00{1 2}??0?{1
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Thecodontosaurus

?0????????????????????????1??1??1000??????0?0?0?0???000?????????????0???0?1010?10
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100?00121000001???0?000??011??01010?0000111100001011000100000000101100??011010100?
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Pantydraco ?0???0????????????{0
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Efraasia

100?1001?000??1?111?112?1110?100???00100100000??0?10??01?0??1??????10?000?1????10
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Nambalia

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Jaklapalisaurus

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Pradhania

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Macrocollum

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Unaysaurus

?001100?1010??1?111??1??1010??011000????????????0??00?????01???000??0?0??????????
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Ruehleia

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Plateosaurus_ingens

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Plateosaurus_gracilis

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000000000010?1010001010000001000?00????????1200?11100?1011?1010101 0000???10?????0
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Plateosaurus_engelhardti 1001100110002011{0
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1}0000000100000000100111120001 11{0
1}0110111101011100100201000001000010013110010100101000111110010111100001111000010
1100010000101111100100110101000101110001100011100100000100000000011101000000 0{1
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Glacialisaurus

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Coloradisaurus

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00111?????1?1001011010011??000101010001?11?001100200100101?01100?00?001?100110000
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??0?0?131100???011?1100200110010111000001101000010211101000000110110 0??011110?00?
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Lufengosaurus

100???02???0211?1?11?1111?1111101001010110100001011101011000 10?1????0110??01{0
1}0??1001?1001001010010????0111?1100101010001 1?000111001001101 11?0110100020011100
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1}1011110110111101113100101201000102000010013110000101101100210110010110000101101
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Xixipiosaurus

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Massospondylus_carinatus 1001100210002111111111211011111010000101101000110{0
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1}1010100011100?1110020010011111011010002001110011000000000000001011101001{0
1}000000000000 0?01{0 1}011112010111{0
1}0110111101112100101211000002000010013100010101101100100110010111000101101000010
2101010000001101100100111101000111110001110012000100000210 00?011001000001?1000
00????????1???001010011100000000{0 1}10000100000

Adeopapposaurus

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1}011001011000111001010000010 11{0 1}10101011111110{0
1}000111001111002001000111011011002001110011000000000000000100110100100000000010000
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100000011010000102101010000001101100100111101000111010001110012000110000110000000
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Leyesaurus

?001?00?1000211??11?????1010?11010000101101?00?101111111?00100010{0
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Ngwevu

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Plateosauravus

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Riojasaurus

1001?00??0002011?110??001110110110001?10000100?10010?101100010000011101?0?100101?0
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1}10??111100110100101101101000100111001100000000000000010?1101001{0
1}00000011000??0?0100112121011110011111?0101110110010100010 20?001001311001010110
100011011001011001011011101011020110100000011011001001101010 0??011?00011100121011
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Eucnemesaurus_fortis

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Eucnemesaurus_entaxonis

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1}0101??1??0?0?0?11?010110?1011011101001010110?0????110111?1?0??0?????0??????001
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Seitaad

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1}0000010??0???0?10??0??001??????????????????????0???????????????????????????

Sarahsaurus

10?1000?10?11010?11?1?1?0110110100000100001010010?110001100010?0???101000111001??
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Yunnanosaurus_huangi

100?1002??00??10?110?1??111?111????00101111?00??0?1101111?001000?01?01?0?00010???
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1}020?001001310000 0101101{0 1}00{1
2}0?110010111?0010110100001011010101000011011001?0110101000 1111?010111001????1?00
00110??0???11??0??1??010100000?01?1???00??0?10??????????0?000????????1???

Xingxiulong

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1}1???00?????????1100111100100110001?0110100020011100110000000001000011001 10??11?
1000001????00?0000???120?011110????1??????1101??????????????0010013110000 10?10110
02??11??000100000011110000101 1010?00000{0
1}10111001001101 0?0?1011000101100012101110000210000000?11????????????????????????
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Jingshanosaurus 1001?002??00211111100???11101{0
1}101100?11?001??1?10?1101111000100 0????0110000010 1?2?1??10?0??1?10110010??111011
00101011001????111??010??????1???10100??0011100?1???000000000000?0??10??0110000000
1000000?0010??11201011110??00??0011?3100100?0100010200001001310000010110010 02??11
0010110?0000110100001011110101000011011 0?12011010?00??????010111101 20011{1
2}0000010?????????????????1?????????????????????0010?????????????????1????1??0
Chuxiongosaurus ?00??002??00??111111?1{0 1}?11101{0
1}10??00?11100???1??0?1101111?0?1000????01?????????????????????101?00?0??111?11
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Yizhousaurus
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1}000011100{1
2}10000000001000010?01000011?000?01???????001001111100011110?????0010?2101101101
000102000010 0?3110000101001100 2?011001011 0?1110111100001011110?????????????????
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Anchisaurus
10???00??0002?1??11?????111011?010?001010?10001100111101 1?0?10??????01?001101?1?2
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2}?0111?0011???1001001111011?10000?010?001100?000??0000000??0100?0??0?01?00?10???
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1}10113100000?01111000100 11?001010000101101000010{0
1}11101000000110111?1?01?010???10111?0?01??0011?001000001001??0????10??0?0?010200
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Mussaurus 10011002?000??111111?11?111011101000010 10{0
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1}0?0?01?0?1?????????????????????????10101111???1?0??0?1?1111001????????00100????0?1
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Leonerasaurus
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Sefapanosaurus

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Aardonyx

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Irisosaurus

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NMRQ3314

1001?10310002111111 01?1110101111???10101011010110111010 11?000000102201101100 10???
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1}10000001??0??100??0?0?10000000??111001??010?0?1??0?????1????{2
3}1100?0?110??????0010?2100101{1 2}0?000102000010 0?31000{0 1}0{0
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NMQR1551

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Meroktenos

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Ingentia

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Lessemsaurus

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Antetonitrus

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2}10001010121001000???1????100?0?01100???0?0011??311000{0
1}0110??????0011?3101???1010???????00100?3???0001011010001????????????11101111001
111111101000000100111010????????????????1111110????{1
2}1200?0????1?100??1?0?00111????????????110??0????2???????????????????????????1

Ledumahadi

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Kholumolumo

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Blikanasaurus

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Camelotia

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Schleitheimia

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Pulanesaura

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01?0001000????????112?11011???0??????????????10??1???????????????????????????????
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Gongxianosaurus

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Isanosaurus

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Tazoudasaurus

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Vulcanodon

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Shunosaurus

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Spinophorosaurus

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Patagosaurus

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Barapasaurus

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Cetiosaurus

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BP_1_8469

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Appendix 6

Time data used:

	FAD	LAD		
Euparkeria	247.2	242		
Crurotarsi	247.2	145.5		
Marasuchus	236.1	233.7		
Ornithischia	231.4	145.5		
Agnosphitys	208.5	201.3		
Silesaurus	236	227		
Neotheropoda	227	145.5		
Staurikosaurus	235	221.5		
Chindesaurus	227	208.5		
Herrerasaurus	231.4	225.9		
Eoraptor	231.4	225.9		
Saturnalia	233.2	225.4		
Panphagia	231.4	225.9		
Chromogisaurus		231.4	225.9	
Buriolestes	233.2	225.4		
Guaibasaurus	225.4	220		
Pampadromaeus		233.2	225.4	
Bagualosaurus	233.2	225.4		
Nambalia	227	208.5		
Thecodontosaurus		208.5	201.3	
Pantydraco	208.5	201.3		
Efraasia	215.5	212		
Ruehleia	227	208.5		
Jaklapalisaurus	227	208.5		
Macrocollum	225.4	220		
Unaysaurus	225.4	220		
Plateosaurus_ingens		212	205.6	
Plateosaurus_gracilis		227	208.5	
Plateosaurus_engelhardti			227	201.3
Pradhania	199.3	190.8		
Glacialisaurus	199	182		
Coloradisaurus	220	213		
Yunnanosaurus_huangi		201.3	190.8	
Lufengosaurus	201.3	190.8		
Xixipiosaurus	201.3	190.8		
Massospondylus_carinatus			202.3	187.5
Adeopapposaurus		201.3	190.8	

Leyesaurus	201.3	190.8		
Ngwevu	191	187.5		
Plateosauravus	219.6	202.3		
Riojasaurus	220	213		
Eucnemesaurus_fortis	219.6	202.3		
Eucnemesaurus_entaxonis	219.6	202.3		
Seitaad	190.8	182.7		
Anchisaurus	201.3	190.8		
Chuxiongosaurus	201.3	190.8		
Jingshanosaurus	201.3	190.8		
Xingxiulong	201.3	190.8		
Sarahsaurus	199.3	183.7		
Yizhousaurus	201.3	190.8		
Kholumolumo	219.6	202.3		
Mussaurus	192.7	192.6		
Leonerasaurus	189	188.8		
Sefapanosaurus	219.6	202.3		
Aardonyx	202.3	187.5		
Irisosaurus	201.5	199		
Meroktenos	219.6	202.3		
NMRQ3314	202.3	187.5		
NMQR1551	219.6	202.3		
Ingentia213	201.3			
Lessemsaurus	220	213		
Antetonitrus	202.3	187.5		
Ledumahadi	202.3	187.5		
Blikanasaurus	219.6	202.3		
Camelotia	208.5	201.3		
Schleitheimia	213	208		
Pulanesaura	202.3	187.5		
Gongxianosaurus	182.7	174.1		
Isanosaurus	208.5	174.1		
Tazoudasaurus	190.8	174.1		
Vulcanodon	199.3	182.7		
Shunosaurus	161	157		
Spinophorosaurus	174.1	163.5		
Patagosaurus	178.7	178.1		
Barapasaurus	190.8	170.3		
Cetiosaurus	170.3	163.5		
BP_1_8469	220	213.2		

Appendix 7

MrBayes code to run FBD model:

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BEGIN DATA;
        DIMENSIONS  NTAX=77 NCHAR=419;
        FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = "  0 1 2 3 4 5";
        MATRIX
        Euparkeria
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Silesaurus

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Herrerasaurus

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Guaibasaurus

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Saturnalia

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Panphagia

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Chromogisaurus

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Buriolestes

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Thecodontosaurus
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Pradhania

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Macrocollum

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Glacialisaurus

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Coloradisaurus

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Lufengosaurus

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Xixipiosaurus
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Adeopapposaurus
1001100210002111011111011011111010000101101000110111111111001000102101(0
1)0110010110001110010100000 1011(0 1)10101011111110(0
1)0001110011110020010001110110110020011100110000000000000001001101001000000000010000
0000000101110001110011011110111210110011100000200001001311001000110110010?1100101
1000000110100001021010100000011011001001111010001110100011100120001100001100000000
011010010000??00000??1?11?11???00101001?100000?010?11100?0000?

Leyesaurus
?001?00?1000211??11?????1010?1101000010110 1?00?1011111111?00100010(0
2)1010?????????00?11???0??1?00?10110??1010?111101000001?1??1111002001000111011???
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Ngwevu
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1011010100???0

Plateosauravus

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2)0011?0011000000000001000000??10??011???0??110????????0???(2
3)1110011110????????????1???????????????0010013110010 1?01????????11??10110?00001
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Riojasaurus

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1)10??11110011010010110110100010011100110000000000000010?1101001(0
1)00000011000??0?0100112121011110011 1111?0101110110010100010 20?0010013110010101 10
100011011001011001011011101011020110100000011011001001101 0100??011?00011100121011
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Eucnemesaurus_fortis

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Eucnemesaurus_entaxonis

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1)0000010??0???0?10??0??001??????????????????????0????????????????????????????

Sarahsaurus

10?1000?10?11010?11?1?1?011011010000010000101001 0?110001100010?0???101000111001??
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000010000010111000011000010010000000100001010210011111110111101102111 1?01110000120
01000013111010110011100111110110111 02?10011000101011100100000 10(0
1)0100010001110100 1?1111011?110011000?100011100??0???11010??000?????????????????
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Yunnanosaurus_huangi
100?1002??00??10?110?1??111?111????00101111?00??0?1101111?001000?01?01?0?00010???
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000000000010?0101101(0 1)0000?00?0??0??000?0??11200?11110??01??0011?2101100201000(0
1)020?001001310000010 1101(0 1)00(1
2)0?110010111?0010110100001011010101000011011001?01101010001111?010111001????1?00
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Xingxiulong
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1)1???00?????????1100111100100110001?0110100020011100110000000001000011001 10??11?
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Jingshanosaurus 1001?002??00211111100??11101(0
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1000000?0010??11201011110??00??0011?3100100?0100010200001001310000001011001002??11
0010110?0000110100001011110101000011011 0?12011010?00??????0101111012 0011(1
2)0000010??????????????????1???????????????????0010??????????????????1????1??0

Chuxiongosaurus ?00??002??00??111111?1(0 1)?11101(0
1)10??00?11100???1??0?1101111?0?1000???01???????????????????????101?00?0??111?11
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Yizhousaurus
1101100210102111111011111111110110000111001000110011111111 00??00???10?100?00101?2
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1)000011100(1
2)1000000000100001 0?01000011?000?01???????0010011111000111 10??????0010?2101101101
00010200001 00?31100001010011002?0110010110?111011110000101 1110??????????????????
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Anchisaurus
10???00??0002?1??11?????111011?010?001010?10001100111111011?0?10??????01?001101?1?2
001110??????10?10?00??100000000101?1(1
2)?0111?0011???10010011111011?10000?010?001100?000??0000000??0100?0??0?01?00?10???
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1)10113100000?01111000100 11?00101000010110 1010000 10(0
1)11101000000110111?1?01?010???10111?0?01??0011?00100000100 1??0????10??0?0?010200
00??01?11?110100?20?10????000??01????1????????
Mussaurus 10011002?000??111111?11?111011101000010 10(0
1)?000?10011?1011000(0
1)0?0?01?0?1?????????????????????????10101111???1?0??0?1?1111001????????00100????0?1
0110??0000?100001000000000?00000010??111?011?1?0001110?????0010?01110011111 0?1?11?
00101210110120100000200???01131000 10?011??1001?011??10110?10101101000010111101000
000110111011011010001??????0101110012001110000110000?00111111?011010(1
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Leonerasaurus
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Sefapanosaurus
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Aardonyx
1101?00210002?11?11?????1110?1011000??????1010??0?11010??10?1????????1?0?????????
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Irisosaurus
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NMRQ3314

1001?1031000211111101?1110101111???1010101101011011101011?00000010220110110010???
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1)10000001??0??100??0?0?10000000??111001??010?0?1??0?????1????(2
3)1100?0?110??????0010?2100101(1 2)0?0001020000100?31000(0 1)0(0
1)????????????1??10110?????????????1???1101000011?011?01?0??0?0???00111001011110
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Meroktenos

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Ingentia

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Lessemsaurus

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Antetonitrus

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Ledumahadi

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Blikanasaurus

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Camelotia

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Schleitheimia

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Pulanesaura

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Gongxianosaurus

1?????0??????????12??
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?0??00000????????????0??0?0?1?0?000?011???2110????1?1????????????????????????????
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2)111?2??????1???1101??????1?0??1???0?1?1????1?11??010???10?2?111200002000???????
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Isanosaurus

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Tazoudasaurus

11???010??1?????????(0
2)011???1???1?????????????????00?00000???0??10?1111012101???000??001010??????0002??1
00001??00200100011020121000????????211?1?111????11?????01?1100100?2????????010?21
0000100?0001?310?1???03101??0?111001002??11??1??1??211001110011010110?0?0010000101
010?1111011111?011?????????????1??10?1????1??0????1?0??1001?????????????????10??
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Vulcanodon

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101012011111O?121?0?1??00?11?00000?????????????1???11?01?21?????????????????????
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Shunosaurus

1100011 3?1102011012000000001011?2010011120101010100110101200001101112101000101 1?1200?????1102001000001201000111111121211 12??01011?1001?1?10010012?1100001011021?000 01?0201210000?11?00?100111011001?111?1?0002110011 00?11000?1011001?000110000??1?31 0111101310110021111 1?01100?111100100211112??0???000?0112101 0?01?0????110?101???11 011??111110100 2?12111?102110???????????0?00020?00000??1?10???0??1121???0??11?12?0 ???1?101??1???

Spinophorosaurus

1????1??????????????????????????????????2????????????0????01?????????0??101111111(1 2)?0???????????1?????????????10011101 2?112?????11?11011?0?01?0002?110??01????(1 2)?11???1?12?1010?0????????(1 2)1??11011?00?1??1110?03?(1 2)0?10??(1 2)?????????????????????????????????????(1 2)????1?1???01(1 2)??011??001??21111111 0?1101??0?020?100???0??11?10??0?0?01????????????????????? ???1???21?0?1?010??1????1????????

Patagosaurus

11?? ?????????????1?00001??????0??0111012111??????1100101100000110020?2001010?00201?01 11112012 1?00?0210011(1 2)00?1?0?100???0?111?00?1100100?(1 2)1????????????????????????????1111013101000211111001100111110010?211112??0???00 11111?101000??0??0?????02??? ????1?11???110????????????????2??????????????11?

Barapasaurus

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Cetiosaurus

1??11?????????????????????? ??2??00111101111101001000 20?2001?10?1020??10 11102010100???(1 2)?????2001??00100???0111101031100100 02????????1?????????????????????1111013?0210 ?2110?1?011??1101?00???211112??0???010?111210100010010111?????????????????????? ??????????????????????????1?000?????????????????????????1?2???????????0?????????????? ?

BP_1_8469

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001????????0?120???11101?????11?001?1?1?01??102???????10111??0001?1????????????1??
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;
END;
begin mrbayes;
outgroup Euparkeria;
constraint ingroup1 = 2 - 77;
constraint ingroup2 = 3 - 77;
log start filename = Mr_Bayes_78taxa_FBD01.log;
        lset rates = gamma coding = variable;
CALIBRATE   Euparkeria        = uniform (242, 247.2);
CALIBRATE   Crurotarsi        = uniform (145.5, 247.2);
CALIBRATE   Marasuchus        = uniform (233.7, 236.1);
CALIBRATE   Ornithischia      = uniform (145.5, 231.4);
CALIBRATE   Agnosphitys       = uniform (201.3, 208.5);
CALIBRATE   Silesaurus        = uniform (227, 236);
CALIBRATE   Neotheropoda      = uniform (145.5, 227);
CALIBRATE   Staurikosaurus    = uniform (221.5, 235);
CALIBRATE   Chindesaurus      = uniform (208.5, 227);
CALIBRATE   Herrerasaurus     = uniform (225.9, 231.4);
CALIBRATE   Eoraptor          = uniform (225.9, 231.4);
CALIBRATE   Saturnalia        = uniform (225.4, 233.2);
CALIBRATE   Panphagia         = uniform (225.9, 231.4);
CALIBRATE   Chromogisaurus          = uniform (225.9, 231.4);
CALIBRATE   Buriolestes       = uniform (225.4, 233.2);
CALIBRATE   Guaibasaurus      = uniform (220, 225.4);
CALIBRATE   Pampadromaeus           = uniform (225.4, 233.2);
CALIBRATE   Bagualosaurus     = uniform (225.4, 233.2);
CALIBRATE   Nambalia          = uniform (208.5, 227);
CALIBRATE   Thecodontosaurus        = uniform (201.3, 208.5);
CALIBRATE   Pantydraco        = uniform (201.3, 208.5);
CALIBRATE   Efraasia          = uniform (212, 215.5);
CALIBRATE   Ruehleia          = uniform (208.5, 227);
CALIBRATE   Jaklapalisaurus   = uniform (208.5, 227);
CALIBRATE   Macrocollum       = uniform (220, 225.4);
CALIBRATE   Unaysaurus        = uniform (220, 225.4);
CALIBRATE   Plateosaurus_ingens     = uniform (205.6, 212);
CALIBRATE   Plateosaurus_gracilis   = uniform (208.5, 227);
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CALIBRATE   Plateosaurus_engelhardti          = uniform (201.3, 227);
CALIBRATE   Pradhania         = uniform (190.8, 199.3);
CALIBRATE   Glacialisaurus = uniform (182, 199);
CALIBRATE   Coloradisaurus = uniform (213, 220);
CALIBRATE   Yunnanosaurus_huangi = uniform (190.8, 201.3);
CALIBRATE   Lufengosaurus = uniform (190.8, 201.3);
CALIBRATE   Xixipiosaurus= uniform (190.8, 201.3);
CALIBRATE   Massospondylus_carinatus = uniform (187.5, 202.3);
CALIBRATE   Adeopapposaurus = uniform (190.8, 201.3);
CALIBRATE   Leyesaurus = uniform (190.8, 201.3);
CALIBRATE   Ngwevu = uniform (187.5, 191);
CALIBRATE   Plateosauravus = uniform (202.3, 219.6);
CALIBRATE   Riojasaurus = uniform (213, 220);
CALIBRATE   Eucnemesaurus_fortis = uniform (202.3, 219.6);
CALIBRATE   Eucnemesaurus_entaxonis = uniform (202.3, 219.6);
CALIBRATE   Seitaad = uniform (182.7, 190.8);
CALIBRATE   Anchisaurus = uniform (190.8, 201.3);
CALIBRATE   Chuxiongosaurus = uniform (190.8, 201.3);
CALIBRATE   Jingshanosaurus = uniform (190.8, 201.3);
CALIBRATE   Xingxiulong = uniform (190.8, 201.3);
CALIBRATE   Sarahsaurus = uniform (183.7, 199.3);
CALIBRATE   Yizhousaurus = uniform (190.8, 201.3);
CALIBRATE   Kholumolumo = uniform (202.3, 219.6);
CALIBRATE   Mussaurus = uniform (192.6, 192.7);
CALIBRATE   Leonerasaurus = uniform (188.8, 189);
CALIBRATE   Sefapanosaurus = uniform (202.3, 219.6);
CALIBRATE   Aardonyx = uniform (187.5, 202.3);
CALIBRATE   Irisosaurus = uniform (199, 201.5);
CALIBRATE   Meroktenos = uniform (202.3, 219.6);
CALIBRATE   NMRQ3314 = uniform (187.5, 202.3);
CALIBRATE   NMQR1551 = uniform (202.3, 219.6);
CALIBRATE   Ingentia = uniform (201.3, 213);
CALIBRATE   Lessemsaurus = uniform (213, 220);
CALIBRATE   Antetonitrus = uniform (187.5, 202.3);
CALIBRATE   Ledumahadi = uniform (187.5, 202.3);
CALIBRATE   Blikanasaurus = uniform (202.3, 219.6);
CALIBRATE   Camelotia = uniform (201.3, 208.5);
CALIBRATE   Schleitheimia = uniform (208, 213);
CALIBRATE   Pulanesaura = uniform (187.5, 202.3);
CALIBRATE   Gongxianosaurus = uniform (174.1, 182.7);
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CALIBRATE    Isanosaurus = uniform (174.1, 208.5);
CALIBRATE    Tazoudasaurus = uniform (174.1, 190.8);
CALIBRATE    Vulcanodon = uniform (182.7, 199.3);
CALIBRATE    Shunosaurus = uniform (157, 161);
CALIBRATE    Spinophorosaurus = uniform (163.5, 174.1);
CALIBRATE    Patagosaurus = uniform (178.1, 178.7);
CALIBRATE    Barapasaurus = uniform (170.3, 190.8);
CALIBRATE    Cetiosaurus = uniform (163.5, 170.3);
CALIBRATE    BP_1_8469 = uniform (213.2, 220);

prset nodeagepr = calibrated;
prset clockvarpr = igr;
prset igrvarpr = exp(10);
prset clockratepr = normal (0.001, 0.01);

prset topologypr = constraints (ingroup1, ingroup2);

prset brlenspr = clock:fossilization;
prset samplestrat = fossilTip;

prset speciationpr = exponential (10);
prset extinctionpr = beta (1,1);
prset fossilizationpr = beta (1,1);

prset treeagepr = uniform (242, 247.2);

mcmcp nrun = 2 nchain = 4 temp = 0.09 ngen= 10000000 diagnfr = 5000 relburnin=yes
burninfrac=0.25 printfreq=1000  samplefreq=1000  savebrlens=yes;
mcmc;

sumt contype = allcompat conformat=simple relburnin = yes burninfrac = 0.25;
sump relburnin = yes burninfrac = 0.25;

end;
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Appendix 8

R code for stratigraphic congruency tests:

```
Require(strap)
MP_stratcong<-StratPhyloCongruence(MP, ages, rlen=1, method = "equal", samp.perm = 1000,
rand.perm = 1000,
                hard=T, randomly.sample.ages = F,
                fix.topology = T, fix.outgroup = T, outgroup.taxon = "Euparkeria")

FBD_stratcon<-StratPhyloCongruence(FBD, ages, rlen=1, method = "equal", samp.perm = 1000,
rand.perm = 1000,
                            hard=T, randomly.sample.ages = F,
                            fix.topology = T, fix.outgroup = T, outgroup.taxon = "Euparkeria")

iw1_stratcon<-StratPhyloCongruence(IW1, ages, rlen=1, method = "equal", samp.perm = 1000,
rand.perm = 1000,
                            hard=T, randomly.sample.ages = F,
                            fix.topology = T, fix.outgroup = T, outgroup.taxon = "Euparkeria")

iw12_stratcon<-StratPhyloCongruence(IW12, ages, rlen=1, method = "equal", samp.perm = 1000,
rand.perm = 1000,
                             hard=T, randomly.sample.ages = F,
                             fix.topology = T, fix.outgroup = T, outgroup.taxon = "Euparkeria")
```

Appendix 9

Table 5: Measurements of postcranial material of BP/1/8469

		Elements	mm
Cervical			
		anteroposterior length (total)	159
		dorsoventral length (total)	92
	centrum	anterior: dorsoventral length	62
		anterior: mediolateral length	64
		posterior: dorsoventral length	61
		posterior: mediolaterial length	75
	neural spine	dorsoventral length (from base)	21
		anteroposterior length	75
Dorsosacral			
		anteroposterior length (total)	116
		dorsoventral height (total)	386
	centrum	anterior: dorsoventral length	160
		anterior: mediolateral length	168
		posterior: dorsoventral length	135
		posterior: mediolaterial length	112
		anteroposterior length	92
	neural spine	dorsoventral length (from base)	155.5
		anteroposterior length	53
	transverse process	mediolateral length	115
		dorsoventral length at distal end	102
		anteroposterior length (at midline)	57
Sacral			
		anteroposterior length (total) of both	283
		dorsoventral height (total)	373
ps1	centrum	anterior: dorsoventral length	144
		anterior: mediolateral length	106
		anteroposterior length	130
	neural spine	dorsoventral length (from base)	~111
		anteroposterior length	85
	transverse process	mediolateral length	77
ps2	centrum	posterior: dorsoventral length	~124
		posterior: mediolaterial length	~116
		anteroposterior length	143
	neural spine	dorsoventral length (from base)	179
		anteroposterior length	90

transverse process	mediolateral length	71
Caudosacral		
	anteroposterior length (total)	121
	min. dorsoventral height (total)	228
centrum	ant: dorsoventral length	145
	ant: mediolateral length	165
	post: dorsoventral length	154.5
	post: mediolaterial length	167
	anteroposterior length	104.5
transverse process	mediolateral length	163
	anteroposterior length (near the neural arch)	34
Anterior Caudal		
	anteroposterior length (total)	121
	dorsoventral height (total)	379
centrum	anterior: dorsoventral length	157
	anterior: mediolateral length	152
	posterior: dorsoventral length	158
	posterior: mediolaterial length	161
	anteroposterior length	93
neural spine	dorsoventral length (from base)	195
	anteroposterior length (at the base)	57
Mid-caudal		
	anteroposterior length (total)	77
	min. dorsoventral height (total)	245
centrum	anterior: dorsoventral length	171
	anterior: mediolateral length	151
	posterior: dorsoventral length	152
	posterior: mediolaterial length	142
	anteroposterior length	77
neural spine	anteroposterior length (at the base)	76.5
transverse process	mediolateral length	85
	anteroposterior length (near the neural arch)	56

Humerus	
Minimum shaft circumference	237
minimum dorsoventral length	569
anteroposterior length (proximal)	242
anteroposterior length (distal)	199
length of dpc from proximal most point of hh	282

	length of dpc	181
	width of crest (at thickest point)	48
Radius		
	total length - dorsoventral	~179
	distal end (antpost length)	78
	distal end (mediolat length)	57
Metcarpal II		
	proximal end: max height	48
	proximal end: max width	51
Metacarpal IV		
	proximal end: max height	43
	proximal end: max width	27
Manual phalanx 1 - I		
	Proximodistal length	55
	proximal end: max height	51
	proximal end: max width	51.5
	distal end: max width	46
Manual phalanx 1 - II		
	Proximodistal length	55
	proximal end: max height	41
	proximal end: max width	43
	distal end: max height	26
	distal end: max width	42
Manual Unguals		
A	Proximodistal length	~36
	proximal end: max height	31
	proximal end: max width	31
B	Proximodistal length	~31
	proximal end: max height	24
	proximal end: max width	21
Ilium		
	minimum anteroposterior length (from prap to poap)	548
	dorsoventral height	305
	length of acetabulum	316
	pubic peduncle length	186
	ischial peduncle length	118
	dorsovent height of iliac blade from sac	138
	supracetabular height	198

anteroposterior length of distal surface of pup	120
anteroposterior length of distal surface of isp	78
length of preacetabular blade	85
length of postacetabular blade	246
Pubis	
length of apron (incomplete)	581
width of the distal end	147
Femur	
minimum anteroposterior length of shaft	85
dorsoventral length	821
Minimum shaft circumference	340
mediolateral length of shaft	108
Tibia	
total dorsoventral length (max)	574
total dorsoventral length (min)	479
anteroposterior length of proximal articular surface	247
transverse width of proximal articular surface	156
transverse width of shaft (middle)	70
anteroposterior length of shaft (middle)	80
mediolateral width of the distal end	169
anteroposterior length of distal articular surface	116
Fibula	
total dorsoventral length	~516
shaft length	323
Astragalus	
anteroposterior length	92
mediolateral width	183
dorsoventral length (max)	82
dorsoventral length (min)	37
Calcaneum	
proximodistal length (max, in middle)	33
mediolateral length (max)	61
anteroposterior length (max)	64
Metatarsal I	
proximal end: max height	40
proximal end: max width	87
distal end: max height	45
distal end: max width	78

Metatarsal III

Proximodistal length	259.5
proximal end: max height	57
proximal end: max width	101
distal end: max height	55
distal end: max width	74

Metatarsal IV

Proximodistal length	240
proximal end: max height	43
proximal end: max width	97
distal end: max height	51
distal end: max width	64

Metatarsal V

Proximodistal length	121
proximal end: max height	32
proximal end: max width	78
distal end: max height	27
distal end: max width	20

Right Pedal Digit I Ungual

Proximodistal length	103
proximal end: max height	69
proximal end: max width	48

Right Pedal Digit II Ungual

Proximodistal length	~116
proximal end: max height	49
proximal end: max width	48.5

Left Pedal Digit III

1 - III

Proximodistal length	75
proximal end: max height	58
proximal end: max width	73
distal end: max height	33
distal end: max width	64

2 - III

Proximodistal length	70
proximal end: max height	51
proximal end: max width	63
distal end: max height	37

	distal end: max width	51.5
3 - III		
	Proximodistal length	52
	proximal end: max height	38
	proximal end: max width	52
	distal end: max height	32
	distal end: max width	52
4 - III		
	Proximodistal length	~60
	proximal end: max height	40
	proximal end: max width	43
Unidentified Pedal phalanges		
A	Proximodistal length	70
	proximal end: max height	47
	proximal end: max width	62
	distal end: max height	41
B	Proximodistal length	60
	proximal end: max height	41
	proximal end: max width	55
	distal end: max height	28
	distal end: max width	56
C	Proximodistal length	67
	proximal end: max height	49
	proximal end: max width	66
	distal end: max height	32
	distal end: max width	55.5

Appendix 10

Table 6: Results from the DFA of sauropodomorph taxa

Species	pp(biped)	post_outcome
NMQR1551	0.718	Bipedal
NMQR3314	0.513	Equivocal
Alamosaurus_sanjuanensis	0.131	Quadrupedal
Amargasaurus_cazaui	0.4	Equivocal
Ampelosaurus_atacis	0.017	Quadrupedal
Anchisaurus_polyzelus	0.793	Bipedal
Antarctosaurus_brasilensis	0.905	Bipedal
Antetonitrus_ingenipes	0.435	Equivocal
Apatosaurus_ajax	0.302	Quadrupedal
Apatosaurus_excelsus	0.318	Quadrupedal
Apatosaurus_louisae	0.447	Equivocal
Apatosaurus_parvus	0.722	Bipedal
Aragosaurus_ischiaticus	0.868	Bipedal
Atlasaurus_imelakei	0.265	Quadrupedal
Barosaurus_lentus	0.269	Quadrupedal
Bonatitan_reigi	0.744	Bipedal
Camarasaurus_grandis	0.468	Equivocal
Camarasaurus_lentus	0.424	Equivocal
Cedarosaurus_weiskopfae	0.45	Equivocal
Cetiosauriscus_stewarti	0.074	Quadrupedal
Cetiosaurus_oxoniensis	0.164	Quadrupedal
Chubutisaurus_insignis	0.211	Quadrupedal
Comahuesaurus_windhauseni	0.552	Equivocal
Dashanpusaurus_dongi	0.138	Quadrupedal
Diamantinasaurus_matildae	0.129	Quadrupedal
Dicraeosaurus_sattleri	0.886	Bipedal
Diplodocus_hayi	0.318	Quadrupedal
Diplodocus_longus	0.264	Quadrupedal
Dreadnoughtus_schrani	0.181	Quadrupedal
Efraasia_minor	0.576	Equivocal
Elaltitan_lilloi	0.483	Equivocal
Eoraptor	0.936	Bipedal
Epachthosaurus_sciuttoi	0.225	Quadrupedal
Euhelopus_zdanskyi	0.065	Quadrupedal
Europasaurus_holgeri	0.063	Quadrupedal
Ferganasaurus_verzilini	0.459	Equivocal
Fukuititan_nipponensis	0.135	Quadrupedal

Futalognkosaurus_dukei	0.306	Quadrupedal
Giraffatitan_brancai	0.128	Quadrupedal
Ledumahadi_mafube	0.443	Equivocal
Jainosaurus_septentrionalis	0.32	Quadrupedal
Janenschia_robusta	0.469	Equivocal
Jingshanosaurus_xinwaensis	0.698	Bipedal
Jobaria_tiguidensis	0.602	Equivocal
Kotasaurus_yamanpalliensis	0.464	Equivocal
Lapparentosaurus_madagascariensis	0.138	Quadrupedal
Ligabuesaurus_leanzai	0.32	Quadrupedal
Lirainosaurus_astibiae	0.047	Quadrupedal
Lourinhasaurus_alenquerensis	0.653	Equivocal
Lufengosaurus_huenei	0.758	Bipedal
Magyarosaurus_dacus	0.087	Quadrupedal
Mamenchisaurus_constructus	0.149	Quadrupedal
Mamenchisaurus_youngi	0.35	Equivocal
Massospondylus_carinatus	0.768	Bipedal
Mussaurus_patagonicus	0.941	Bipedal
Neuquensaurus_australis	0.614	Equivocal
Omeisaurus_junghsiensis	0.194	Quadrupedal
Omeisaurus_maoianus	0.552	Equivocal
Opisthocoelicaudia_skarzynskii	0.237	Quadrupedal
Plateosauravus_cullingworthi	0.652	Equivocal
Plateosaurus_engelhardti	0.906	Bipedal
Rapetosaurus_krausei	0.135	Quadrupedal
Rinconsaurus_caudamirus	0.133	Quadrupedal
Riojasaurus_incertus	0.283	Quadrupedal
Ruehleia_bedheimensis	0.807	Bipedal
Saltasaurus_loricatus	0.131	Quadrupedal
Sarahsaurus_aurifontanalis	0.736	Bipedal
Saturnalia_tupiniquim	0.759	Bipedal
Sauroposeidon_proteles	0.135	Quadrupedal
Tehuelchesaurus_benitezii	0.214	Quadrupedal
Tornieria_africana	0.443	Equivocal
Turiasaurus_riodevensis	0.138	Quadrupedal
Vulcanodon_karibaensis	0.467	Equivocal
Xingxiulong_chengi	0.225	Quadrupedal
Yuanmousaurus_jiangyiensis	0.303	Quadrupedal
Yunnanosaurus_huangi	0.795	Bipedal
BP/1/8469	0.64	Equivocal

Appendix 11

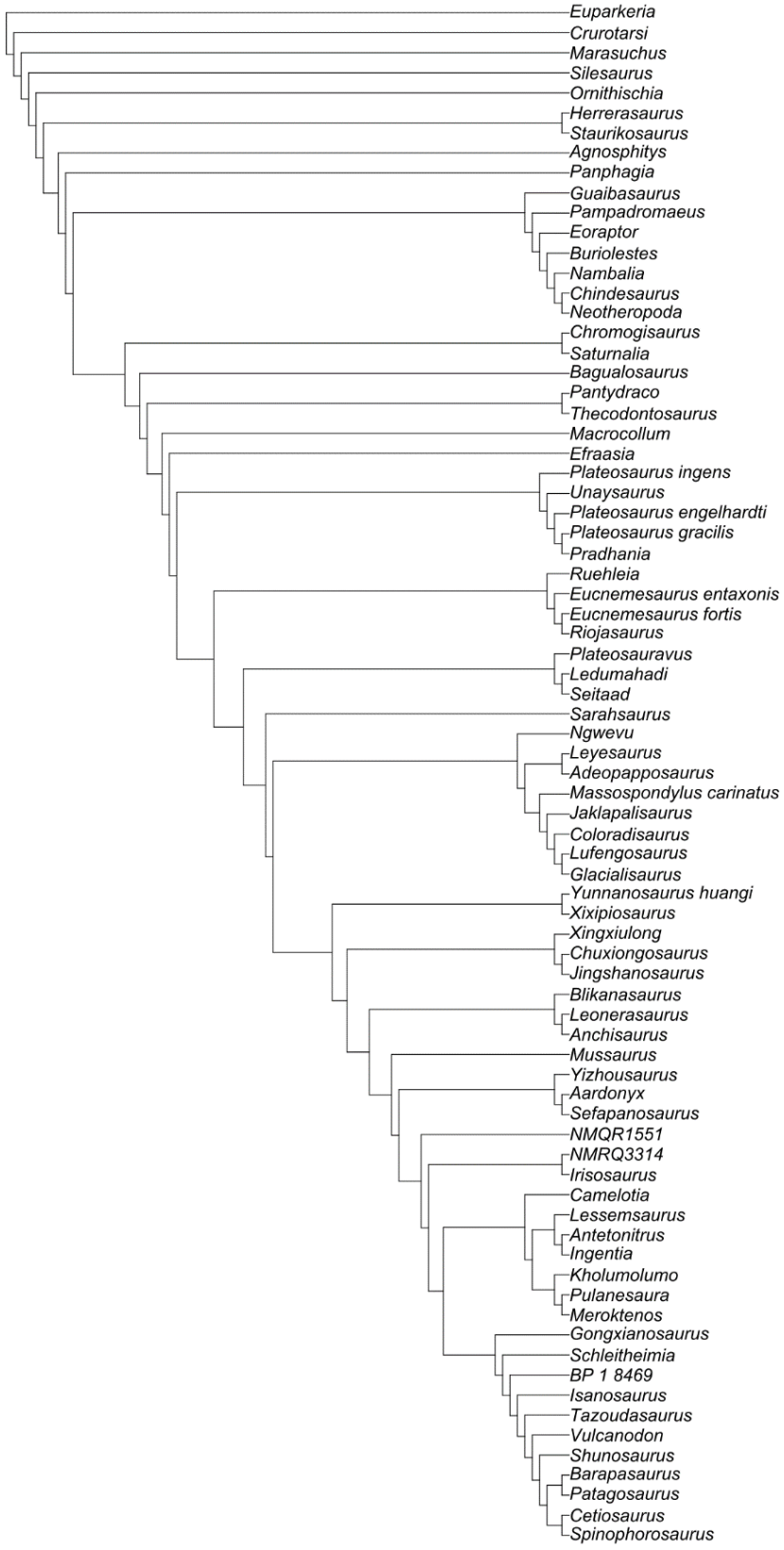

Figure 38: Implied weighting tree at weighting function of one

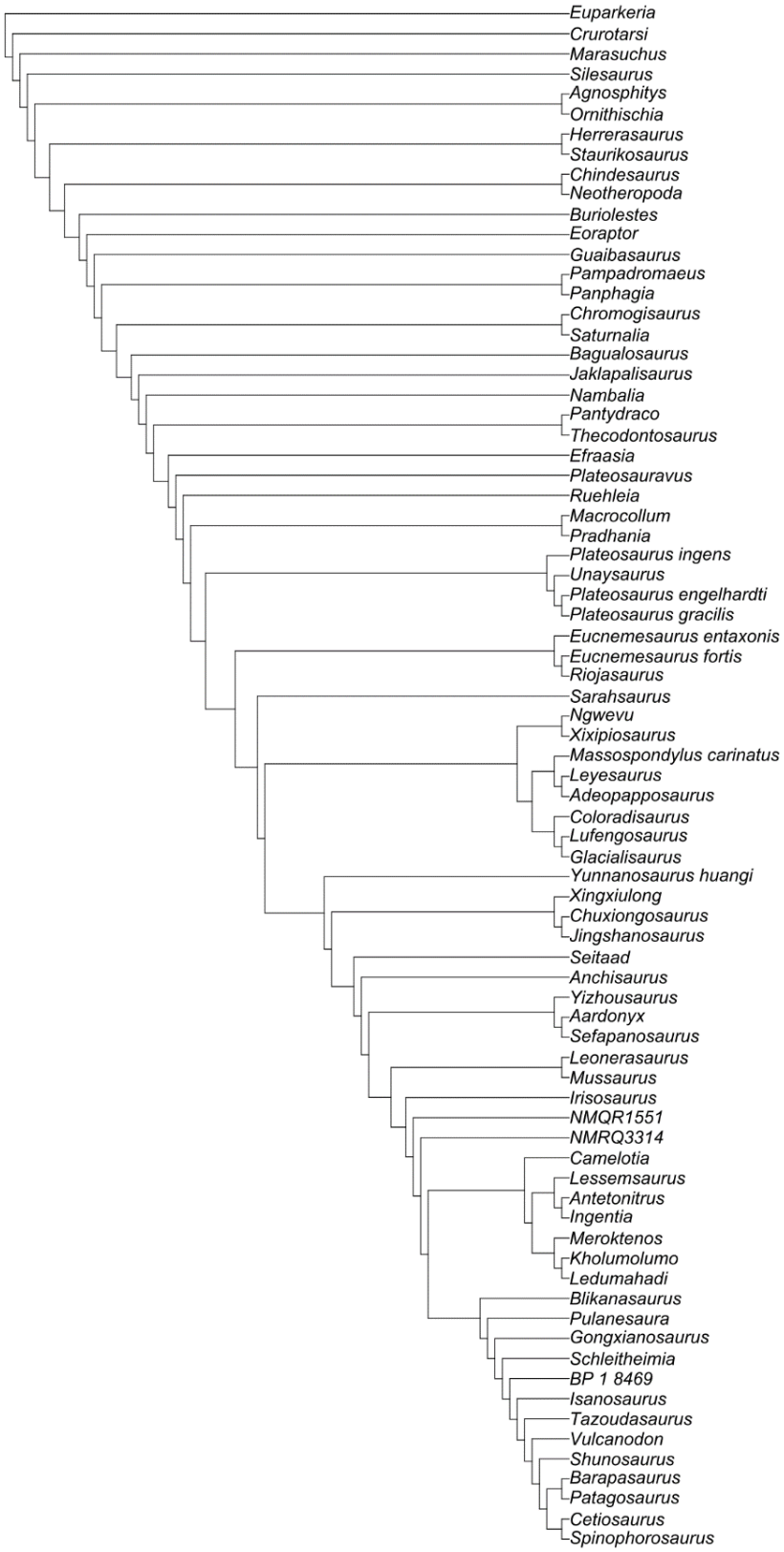

Figure 39: Implied weighting tree at weighting function of 12