**A Giant Dinosaur from the Earliest Jurassic of South Africa and the Transition to Quadrupedality in Early Sauropodomorphs**

**Graphical Abstract**

**Highlights**

- A new species of Early Jurassic South African sauropodomorph weighed 12 metric tons
- Proportional limb robusticity is useful for inferring posture in extinct tetrapods
- Many early-branching sauropodomorphs were quadrupeds with flexed limbs
- Quadrupedal evolution occurs at low body mass but facilitates larger body masses

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**In Brief**

McPhee et al. present a new, gigantic sauropodomorph dinosaur and a quantitative method for inferring postures in extinct tetrapods using proportional limb robusticity. Quadrupedal postures with flexed limbs potentially evolved several times in sauropodomorph dinosaurs before the evolution of derived, columnar-limbed postures of Sauropoda.
A Giant Dinosaur from the Earliest Jurassic of South Africa and the Transition to Quadrupedality in Early Sauropodomorphs

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SUMMARY

Sauropod dinosaurs were dominant, bulk-browsing herbivores for 130 million years of the Mesozoic, attaining gigantic body masses in excess of 60 metric tons [1, 2]. A columnar-limbed, quadrupedal posture enabled these giant body sizes [3], but the nature of the transition from bipedal sauropodomorph ancestors to derived quadrupeds remains contentious [4–6]. We describe a gigantic, new sauropodomorph from the earliest Jurassic of South Africa weighing 12 metric tons and representing a phylogenetically independent origin of sauropod-like body size in a non-sauropod. Osteohistological evidence shows that this specimen was an adult of maximum size and approximately 14 years old at death. *Ledumahadi mafube* gen. et sp. nov. shows that gigantic body sizes were possible in early sauropodomorphs, which were habitual quadrupeds but lacked the derived, columnar limb postures of sauropods. We use data from this new taxon and a discriminant analysis of tetrapod limb measurements to study postural evolution in sauropodomorphs. Our results show that quadrupedality appeared by the mid-Late Triassic (Norian), well outside of Sauropoda. Secondary reversion to bipedality occurred in some lineages phylogenetically close to Sauropoda, indicating early experimentation in locomotory styles. Morphofunctional observations support the hypothesis that partially flexed (rather than columnar) limbs characterized *Ledumahadi* and other early-branching quadrupedal sauropodomorphs. Patterns of locomotory and body-size evolution show that quadrupedality allowed Triassic sauropodomorphs to achieve body sizes of at least 3.8 metric tons. *Ledumahadi*’s Early Jurassic age shows that maximum body mass in sauropodomorph dinosaurs was either unaffected or rapidly rebounded after the end-Triassic extinction event.

RESULTS

Systematic Paleontology

Saurischia Seeley 1888.
Sauropodomorpha von Huene 1932.
Sauropodiformes Sereno 2007.

*Ledumahadi mafube* gen. et sp. nov.

Etymology

Southern Sotho. “Ledumahadi,” a giant thunderclap—in recognition of the tremendous size of this taxon; and “mafube,” dawn—in the sense of the stratigraphically early position of this taxon.

Holotype

BP/1/7120, a disarticulated assemblage of associated postcranial material comprising a partial cervical neural arch; several dorsal vertebrae; partial, conjoined primordial sacral vertebrae; anterior and middle caudal vertebrae; an anterior chevron; a right ulna; a first metacarpal; a left metacarpal, probably III or IV; distal third of the right femur; and a pedal ungual (Figures 1 and 4).

Locality and Horizon

Beginsel farm, 25 km southeast of the town of Clarens, Free State Province, on the border of South Africa and Lesotho (Figures 1 and S1). The *in situ* material was found within mudrocks diagnostic of the upper Elliot Formation, one of the lowermost Jurassic continental successions (Hettangian-Sinemurian, ~200–195 mya; Figures 1 and S1).

Diagnosis

*Ledumahadi mafube* possesses several autapomorphies not observed in any other sauropodomorph: (1) medial edge of the proximal surface of the first metacarpal sharply tapering and curved, giving it a sublacriform outline and differing from the typical “keyhole” shape of the proximal first metacarpals of, e.g., *Aardonyx, Ingentia,* and *Antetonitrus* (Figure 1G); (2) anterior
Articular facet of the anterior caudal vertebra deeply concave, being set back from the anterolateral margin of the centrum 4.5 cm at its deepest; and (3) preserved forelimb elements extremely robust, with the minimum shaft circumference of the ulna 0.57 times the total length of the bone (cf. 0.46 in *Antetonitrus*).

**Anatomy, Osteohistology, and Systematics**

*Ledumahadi* is known from an incomplete postcranial skeleton that preserves several autapomorphies and generally lacks synapomorphies of Sauropoda, indicating a basal (non-sauropodan) phylogenetic position. The postzygapophysis of the single partial cervical neural arch is not elevated relative to the coronal plane, unlike in *Pulanesaura* and more derived sauropods (Figure 1A) [7]. The neural spine of the anteriormost dorsal vertebra is anteroposteriorly short and expands transversely toward its dorsal apex (Figure 1B). The more posterior dorsal neural spines are proportionately tall for non-sauropodan Sauropodomorpha, with the dorsoventral height approximately twice that of the

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**Figure 1. Selected Preserved Elements of *Ledumahadi mafube* and Geography and Stratigraphy of Type Locality**

Preserved bones (A–K) are as follows: (A) middle/posterior cervical vertebra in left lateral view; (B) anterior dorsal vertebra in anterior and right lateral views; (C) middle dorsal vertebra in posterior and right lateral views; (D) first and second “primordial” sacral vertebrae in left lateral view; (E) anterior caudal vertebra in left lateral view; (F) right ulna in proximal and medial views; (G) first metacarpal in proximal and dorsal/ventral views; (H) left third metacarpal in proximal and ventral views; (I) pedal ungual in lateral and proximal views; (J) anterior chevron in posterior view; and (K) distal right femur in distal, lateral, and anterior views.

(L) Simplified geological map of the Elliot Formation in the Republic of South Africa and Lesotho indicating the location of farm Beginsel 346 and aerial extent of the Elliot Formation outcrop area (map modified after the 1:1,000,000 geological map of Republic of South Africa and Lesotho, 1984). (M) Landscape view of the local geology at the Ledumahadi site. Note that the contact of the lower and upper Elliot Formations (LEF and UEF, respectively) has been identified at 1,885 m above sea level; thus the UEF is ~60 m thick. The poorly exposed LEF, which is ~10 m thick here, only contains massive mudstones with very weakly developed pedogenic alteration features, green-gray mottles, and very rare desiccation cracks.

Abbreviations: ap, anterior process; ns, neural spine; op, olecranon process; poz, postzygapophysis; rf, radial fossa; sr, sacral rib; tfc, tibiofibular crest; vt, ventral tubercle. All scale bars represent 5 cm. See also Figures S1 and S2 and Data S1.
Vulcanodon fossa (e.g., a highly reduced olecranon process and much deeper radial fossa, similar to other non-sauropodan sauropodomorph forelimbs) [8–11]. The anterior face is deeply concave, and its posterior face is shallower than that of metacarpal I in Aardonyx and Antetonitrus. However, the proximal outline of metacarpal I is considerably different from those taxa, bearing a subcircular, rather than keyhole, shape, and a proportionally longer shaft. The other preserved metacarpal is similarly stout (Figure 1H). Only the distal third of the femur is preserved (Figure 1K). In cross-section, the shaft is circular, differing from the elliptical (but possibly distorted) cross-section of the femur of Antetonitrus. The distal condyles are anteroposteriorly expansive and strongly concave ventrally, differing from the anteroposteriorly shortened and flatter distal condyles of sauropod femora (e.g., Tazoudasaurus [12]). The single large pedal ungual is most likely from the first or second digit (Figure 1I). It has a subcircular proximal outline, similar to the condition of the first and second digits in other late-branching non-sauropodan sauropodomorph taxa such as Bilikanaaurus.

Osteohistological evidence shows that the holotype of Ledumahadi had reached maximum size and was an adult of approximately 14 years of age at its time of death (Figure S2; STAR Methods). Ledumahadi exhibited high growth rates during early ontogeny, annual temporary decreases in growth from mid-ontogeny, and a gradual transition to parallel-fibered bone and closely spaced growth marks near the periphery representing an external fundamental system (Figure S2; STAR Methods). The closely related sauropodiforms Lessensaurus [13] and Antetonitrus [14] also exhibit rapid, but cyclical, growth throughout ontogeny. Given that Ledumahadi presents growth marks from at least mid-ontogeny (early growth destroyed by secondary remodeling), it is likely that it grew similarly to these other sauropodiforms. It therefore did not exhibit the sustained growth typical of Sauropoda [13], in spite of its sauropod-like adult body size.

Phylogenetic analysis recovers Ledumahadi as a sister taxon of another large-bodied upper Elliot Formation taxon, Antetonitrus ingenipes (Figures 2 and S4; STAR Methods). This is consistent with the general similarities observed between the two taxa. Nevertheless, the presence of several autapomorphies shows that Ledumahadi is distinct from Antetonitrus (see Diagnosis). Together with the South American taxon Lessensaurus (known from very large, but most likely skeletally immature, material [11]), these three genera form a monophyletic Lessensauridae (a fourth member, Ingentia, was too recently described [15] to be included in our analysis). Lessensauridae is within a pectinate grade of non-sauropodan sauropodiforms sensu [8], basal to Leonerasaurus, Gongxianosaurus, Pulanesaura, and the columnar-limbed quadrupeds known as Sauropoda sensu [16] (Figures 2 and S4).

### Body Mass Estimation and Postural Determination

The minimum circumference of limb bone shafts provide information about weight-bearing capacity in tetrapods [17]. Using this relationship for quadrupedal tetrapods [17], the preserved limb elements of BP/1/7120 provide a mass estimate of 12 metric tons for Ledumahadi mafube (Figures 2 and S3; STAR Methods). Furthermore, skeletal dimensions of Ledumahadi mafube are similar to those of geologically younger sauropods, including...
Jainosaurus and Tornieria. This confidently indicates sauropod-like body size in *L. mafube*, unlike the smaller-bodied sauropodomorphs that have hitherto been known from the earliest Jurassic. *Ledumahadi mafube* is thus the largest animal currently known to have lived on Earth at its time. It is more than three times the size of *J. mafube* and considerably larger than the Early Jurassic sauropodomorph *Jainosaurus* (3.8 metric tons; but see [15] for a 7-metric-ton estimate for *Lessemosaurus*) and considerably larger than the Early Jurassic sauropodomorphs *Antetonitrus* (5.6 metric tons; osteologically immature), and *Vulcanodon* (a sauropod; 10.3 metric tons; ?Sinemurian–Pliensbachian). *Ledumahadi* also extends the total known size range for Early Jurassic Sauropodomorpha, which now spans almost two orders of magnitude, down to a minimum of 0.26 metric tons in *Anchisaurus* (STAR Methods).

To quantify quadrupedality, we used a dataset of humeral and femoral circumferences of 81 dinosaur specimens and hundreds of mammals plus several large-bodied reptiles that are confidently known to have been bipedal or quadrupedal. We used a classification of the predominant mode of locomotion during travel, rather than during slow-speed foraging. For example, kangaroos were classified as bipeds, although they can forage as quadrupeds, and non-human apes were classified as terrestrial quadrupeds (they also use four limbs for arboreal locomotion). Linear discriminant analysis of these data demonstrates that the relationship between the forelimb and hindlimb shaft circumferences can be used to make robust inferences of quadrupedality: a linear discriminant function calibrated using femoral circumferences can be used to make robust inferences of quadrupedality (STAR Methods).

We confidently classify *Ledumahadi* and numerous other sauropodomorphs as quadrupeds based on their proportionally robust forelimbs (Figures 1, 2, 3, and S3; STAR Methods). Phylogenetic optimization indicates that the transition to quadrupedality occurred during the origins of the clade unifying *Jinghansanosaurus* and *Xingxuulong* with more derived sauropodomorphs and had evolved at least by the mid-Norian, signaled by the occurrence of *Rojasaurus*. Quadrupedal sauropodomorphs have greater maximum body sizes than those of bipeds (1.5 metric tons in bipeds versus ~4 metric tons, or up to 7 metric tons [15] in Triassic quadrupeds). Nonetheless, *Anchisaurus* (0.26 metric tons) indicates that the smallest quadrupedal sauropodomorphs were similar in mass to the smallest post-Carnian bipeds (*Sarahasaurus*, 0.17 metric tons; see also *Leonerasaurus*). The current phylogenetic position of the inferred bipeds *Mussaurus* and *Yunnanosaurus* suggests the occurrence of at least one reversal back to bipedality. A more detailed understanding of the distribution and evolutionary pattern of quadrupedality is precluded by the lack of reliable appendicular measurements for several taxa, especially some of the closest relatives of Sauropoda (e.g., *Lessemosaurus*, *Ingentia*, *Leonerasaurus*, and *Pulanesaura*), as well as a continued lack of consensus on phylogenetic relationships among non-sauropodan sauropodiforms.

**DISCUSSION**

**Quadrupedality in Sauropodomorph Dinosaurs**

Quadrupedality has been viewed as a key adaptation of Sauropoda, allowing for larger body masses and hence increased gut retention times required for processing low-quality, fibrous vegetable matter (e.g., [18]). Sauropods were unique among quadrupedal dinosaurs in having a columnar stance with erect, parasagittal limbs, allowing efficient, graviportal support of body mass [7, 12, 19], similar to that in large mammals [20]. This is indicated by a set of derived morphological features of sauropod forelimbs, including reduction of the deltopectoral crest; straightening of the humeral and femoral shafts; lengthening of the antebrachium and modification of the proximal ulna to a triradiate shape; modification of the metacarpus into a U-shaped support structure; loss of the lesser trochanter, migration of the fourth trochanter distally and medially, increase in fibular robustness; and many others [16, 18]. These features evolved, at least in incipient forms, by the middle of the Early Jurassic and are exemplified by the early sauropod *Vulcanodon* [19, 21] (see also *Pulanesaura* [16]).

Unlike sauropods, *Ledumahadi* retains plesiomorphic features of the ulna (i.e., short, robust shaft and a large olecranon process) and femur (i.e., circular shaft and expansive distal condyles). These features are present to some degree in all
most recent common ancestor of Ledumahadi evolved independently to that of sauropods (Figure 2). The metric-ton masses in sauropods [3, 22] contradicts hypotheses that columnar limb posture enabled multi-columnar limbs could attain sauropod-like body sizes. This shows that quadrupedal sauropodomorphs lacking Ledumahadi body mass was most likely much larger [15]) and that a columnar limb posture evolved only later in one sub-lineage, the sauropods. This columnar limb posture led to a major radiation in Sauropodomorpha.

Previous studies of postural evolution in sauropodomorphs have focused on osteological indicators of manual pronation (e.g., [9, 10]). This is thought to be important as it results in a posteriorly facing hand capable of transmitting force to the ground during locomotion. However, non-sauropodan sauropodiforms have intermediate osteologies indicating incomplete development of sauropod-like pronation, preventing firm conclusions based on this evidence alone (e.g., [5, 9]). We also note uncertainties in studies of the reconstructed range of motion of dinosaur forelimbs due to the non-preservation of cartilaginous articular surfaces (e.g., [5]). Furthermore, some previously proposed traits relating to manual pronation (e.g., the ulnar facet on the radius [4]) are of limited utility even across just Dinosauria [23], with recent research suggesting that no dinosaurs could fully pronate the manus [24], unlike mammals. This calls into question the definitiveness of these traits in determining the predominant mode of locomotion during travel, although they clearly do contribute to understanding what a limb is capable of across the range of activities undertaken by an organism. Skeletal correlates of quadrupedality in ornithischian dinosaurs have been more thoroughly explored [23, 25], but even for those, the most reliable inferences depend on the presence of multiple proxy morphologies. Greatest confidence in inferences of quadrupedality should therefore result from indicators that apply universally to independent evolutionary transitions between bipedality and quadrupedality across tetrapods.

Unlike previous approaches, our method is quantitatively validated in a comparative statistical framework and reliably indicates posture across a broad phylogenetic sample of four-limbed tetrapods. Because it uses simple measurements derived from relatively small portions of the skeleton, we can deploy our method on a wider sample of taxa than in previous studies. Many of our assessments match those made from other evidence (e.g., “Melanorosaurus,” NMQR 3314 [10], and Antetonitrus [4]). Temporally, our findings are also supported by evidence from the ichnological record, which clearly shows quadrupedal sauropodomorphs were present and widely distributed in the Late Triassic (e.g., [26–28]). The rich ichnofauna of the lower Elliot Formation of western Lesotho includes many quadrupedal sauropodomorph trackways that predate Ledumahadi. These were assigned a Late Triassic age by Ellenberger [29], which has been upheld by our ongoing bio- and chronostratigraphic work [30, 31]. Interestingly, when first described these tracks were presented as evidence for the early occurrence of sauropods [29].

We confirm the hypothesis that quadrupedality preceded the origin of sauropod-like columnar limbs and was present in sauropodomorphs including NMQR 3314 [10] and Antetonitrus [8]. However, we differ from previous studies in inferring quadrupedality in earlier-diverging taxa such as Anchisaurus and Jing-shansaurus, implying a phylogenetically deeper origin that took place at least 15 million years prior to the earliest skeletal evidence of quadrupedal Sauropoda [7, 21]. This has further

Figure 4. Differences in Forelimb Morphology between Flexed-Limbed and Columnar-Limbed Quadrupedal Sauropodomorphs

Note especially the differences in the size of the deltopectoral crest (dpc), proportional robusticity of the shaft (sh), size of the olecranon process (op), and expansion of the epiphyses (ep).

(A and B) Forelimb elements of flex-limbed sauropodomorphs: (A) left humerus of Riosaurus and (B) right ulna (reversed) of Ledumahadi.

(C and D) Forelimb elements of columnar-limbed sauropodomorphs: (C) left humerus of Tazoudasaurus and (D) right ulna (reversed) of Vulcanodon.

All bones are in anterior view. Silhouettes indicate limb postures and are not to scale. All scale bars represent 5 cm.

Ornithischian dinosaurs evolved quadrupedality in several independent lineages, but their osteology shows that none had fully columnar forelimbs [23]. Our findings suggest that early sauropodiforms followed a similar trajectory in the initial adoption of quadrupedality and that a columnar limb posture evolved only later in one sub-lineage, the sauropods. This columnar limb posture led to a major radiation in Sauropodomorpha.
implications—for example, a previous study suggested that bipedality was primitively retained in *Mussaurus* [3], but we find it instead indicates previously unrecognized homoplasy in the evolution of stance among early sauropodomorphs.

Finally, whereas previous work has implied a gradual transition characterized by intermediate, or "facultative" behaviors [6, 9], we find that most sauropodomorph taxa can be classified unambiguously as either quadrupeds or bipeds, the only exception being *Anchisaurus* (Table S3; 68.9% likelihood of quadrupedality). This suggests that the transition between bipedality and quadrupedality during travel was evolutionarily rapid, with few clear intermediate stages observed in their fossil record so far. This does not preclude a role for the forelimb during foraging or other slow-speed behaviors in otherwise quadrupedal sauropodiforms, and it is possible that *Ledumahadi* represents the maximum size threshold in which a browsing strategy that entailed regular rearing remained viable [7]. Indeed, we find evidence for substantial experimentation in locomotory style among early sauropodomorphs: semi-crouched quadrupedality did not preclude subsequent evolutionary reversals to bipedality (whereas no reversals occur from the columnar-limbed condition of Sauropoda).

**Evolution of Gigantism in Sauropodomorph Dinosaurs**

Based on current knowledge of the fossil record, *Ledumahadi mafube* was the largest land animal to have ever existed at the time it lived in the earliest Jurassic. It is larger than many sauropods and similar in body mass to the largest ornithischians (12–17 metric tons). The occurrence of *Ledumahadi* shows that, as in ornithischians, columnar forelimb postures were not a prerequisite for massive sizes exceeding 10 metric tons in sauropodomorphs. Nevertheless, columnar forelimbs may be a key structural adaptation allowing body masses far in excess of this seen in some younger sauropods [2, 6]. Recently, a body mass of at least 7 metric tons has been postulated for adult specimens of the Norian taxon *Lessemsaurus*, which is sister to *Antetonitrus + Ledumahadi* [15] within the Lessemsauridae. The discovery of *Ledumahadi* indicates a continuous expansion of lessemsaurid body size across the end-Triassic Extinction event (ETE). This indicates that the maximum body size of giant lessemsaurids either was unaffected by the ETE or rebounded rapidly.

Our findings on *Ledumahadi* provide a striking confirmation of high ecomorphological disparity among earliest Jurassic sauropodomorphs, with a greater disparity of body sizes [2] and postures [31] present than in any other period of sauropodomorph evolution (Figure 2). However, non-sauropodan sauropodomorphs like *Ledumahadi* coexisted for only a short time with columnar-limbed, quadrupedal sauropods like *Vulcanodon*, which by the Toarcian were the only surviving members of the lineage. The reasons for this turnover and the extinction of non-sauropodan sauropodomorphs remain unknown. However, at least among large-bodied quadrupeds such as lessemsaurids, it may reflect competitive replacement, facilitated by energy-saving adaptions of the sauropodan forelimb and feeding apparatus [7, 32].

**STAR+METHODS**

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**SUPPLEMENTAL INFORMATION**

Supplemental Information includes four figures, three tables, and one data file and can be found with this article online at https://doi.org/10.1016/j.cub.2018.07.063.

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**AUTHOR CONTRIBUTIONS**

B.W.M. conducted fieldwork, collected anatomical, phylogenetic, and measurement data, performed analyses, and co-wrote the manuscript. R.B.J.B. collected measurement data, designed experiments, designed and performed analyses, and co-wrote the manuscript. J.B.-B. conducted analyses, and co-wrote the manuscript. Jirah, James Kitching, Adam Yates, Michael Day, and Alex Parkinson. Puseletso Lecheko provided Sesotho translation for the genus and species name.

**DECLARATION OF INTERESTS**

The authors declare no competing interests.

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STAR METHODS

KEY RESOURCES TABLE

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CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Jonah Choiniere (jonah.choiniere@wits.ac.za).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Repository of type specimen
The holotype of Ledumahadi mafube (BP/1/7120) and all osteohistological slides are housed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa.

Geological context for type specimen
The vicinity of the Ledumahadi type locality on Beginsel farm is dominated by the continental sedimentary rocks of the Molteno, Elliot and Clarens formations (Upper Triassic to Lower Jurassic Stormberg Group) as well as the 183 ± 1.0 Ma old intrusive and extrusive mafic rocks of the Drakensberg Group [40] (Figures 1 and S1). The Upper Triassic-Lower Jurassic Elliot Formation is a fluviolacustrine unit and has an unconformable, sharp, regionally traceable contact with the fluviolacustrine and coal-bearing Molteno Formation and a conformable, chiefly gradational contact with the mainly aeolian Clarens Formation [41].

At the Ledumahadi type locality, the lower contact of the host Elliot Formation is not exposed, however <3 km to the west (at 28°32’39.39”S; 28°24’40.97”E), the entire thickness of the Elliot Formation is accessible over a vertical distance of ~200 m. If the lower contact is an even, horizontal surface, the minimum thickness of the Elliot Formation at the Ledumahadi site is ~75 m. Stratigraphically, the in situ Ledumahadi material was recovered ~45 m below the base of the Clarens Formation (Figures 1 and S1). The stratigraphic positioning of the Ledumahadi material within the upper Elliot Formation is not only based on its relative proximity to the base of the Clarens Formation but, more importantly, on the sedimentary facies characteristics of the host silty mudrocks (Figure S1).

Although not all diagnostic features of the upper Elliot Formation (e.g., the unique carbonate nodule conglomerate; laterally persistent, sheet-like sandstone units) are present at the Ledumahadi site, the available sedimentological record is compelling for an upper Elliot Formation stratigraphic positioning of the Ledumahadi material. These features (Figure S1) include the frequent pedogenic alteration of the deep red, maroon to deep pink host rocks (e.g., in situ carbonate nodules, root traces, invertebrate traces), as well as the presence of some typical sedimentary facies of the upper Elliot Formation (e.g., clast-rich sandstones: facies Sc, see Figure S1). Taken together, the sedimentary facies association at the Ledumahadi type locality (Figure S1) suggests that the sediments
were deposited in a vegetated floodplain environment in an overall semi-arid climate. Evidence for increasingly well-drained soils and higher energy depositional conditions (Figures S1G–S1M) toward the upper part of the recorded succession may suggest that the floodplain environment was positioned progressively more proximal to some larger river channels. The earliest Jurassic (Hettangian–Sinemurian) age of the upper Elliot Formation at Ledumahadi site is inferred from regional magneto- and biostratigraphic investigations as summarized by [42] and [31].

Data sources for transitional sauropodomorphs

Anchisaurus polyzelus, based on YPM 1883 [43] for humeral and femoral circumference comparison. The shaft circumferences were estimated from anteroposterior and mediolateral diameters (femur; circumference estimate = 70 mm) and from mediolateral diameter (humerus; estimated to be 60 mm from mediolateral shaft diameter using equation 17 in Benson et al. [2], appendix). The body mass of Anchisaurus was estimated using data from a larger individual (YPM 208; FC = 126 mm; humerus unknown), scaled to the proportional humerus circumference of YPM 1883.

Antetonitrus ingens was measured directly from BP/1/4952.

Jinghsanosaurus xinwaensis, based on LV 003 [44], using anteroposterior and mediolateral shaft diameters to estimate shaft circumferences.

Mussaurus patagonicus based on MLP 68-II-27-1 [45], using anteroposterior and mediolateral shaft diameters to estimate shaft circumferences.

NMQR 3314 is a referred specimen of Melanorosaurus that was measured directly.

Riojasaurus incertus, based on the holotype and largest individual, PVL 3808 using direct measurements of HC and FC from [2, 46].

Yunnanosaurus huangi, based on IVPP V20 [47], using anteroposterior and mediolateral shaft diameters to estimate shaft circumferences.

METHOD DETAILS

The specimen was consolidated in the field using Paraloid B-76 copolymer resin dissolved in acetone. It was excavated using standard field techniques (e.g., plaster and burlap jacket to protect specimen). Removal of rock matrix from fossil bone was done by hand using Palaeotools Mighty Jack and Microjack airscribes. Measurements of all specimens in this analysis were collected using digital sliding calipers and tape measures. Phylogenetic data were assembled in Mesquite v3.40 (and lower versions [33]) and analyzed under the parsimony criterion in TNT [35].

QUANTIFICATION AND STATISTICAL ANALYSIS

Our statistical analyses were conducted in R version 3.1.0 [34] using functions available in the packages nlme 3.1-131 [37], ape 4.1 [38], MASS [36], and paleotree 2.3 [39]. Significance of phylogenetic generalized least-squares regressions was determined using inbuilt t-statistics in nlmef [37].

Osteohistological analysis

The anatomical positions where histological data were collected are shown in Figure S2, and a list of slides with accession numbers is available via the Key Resources Table. The bone tissues of BP/1/7120 show that this individual deposited rapidly forming fibrolamellar bone through much of ontogeny, transitioning to slower growing lamellar-zonal bone later in life (Figures S2A and S2B). Much of the primary bone tissue of the inner half of the cortex of the specimen has been destroyed by secondary remodeling (resorption front, rf in Figure S2A). The middle cortex contains mostly primary fibrolamellar bone with scattered smaller resorption cavities and secondary osteons, thereafter resorption cavities are more restricted (Figure S2C). Some areas in this region have longitudinally-oriented primary osteons and reticular vascular arrangements, but most canals are arranged in a plexiform to laminar network (Figures S2C and S2E). The bands of alternating reticular and plexiform vascular arrangements seen in the closely related sauropodiform Lessemsaurus [48] were not observed, but only part of the anterior region was thin-sectioned, and it is possible that other parts of the midshaft may have exhibited such bands.

The patches of primary bone tissue still present in the inner cortex contain a woven-fibered interstitial matrix with abundant globular osteocyte lacunae (Figures S3D and S3F). In the middle to outer cortex the lamellae surrounding the primary osteons are substantially thicker and frequently contact one another, giving the bone tissue a parallel-fibered appearance with very little interstitial woven-fibered bone between the lamellae [49]. The outermost cortex becomes increasingly lamellar with highly organized flattened osteocyte lacunae. Narrow annuli of avascular lamellar bone, indicating a temporary decrease in growth rate, appear in the outer 40% of the compact cortex (Figures S2A and S2C). It is not known if growth marks only appear during mid-late ontogeny as in the more derived sauropods [13], or if Ledumahadi expressed growth marks from early ontogeny similar to the more basal non-sauropodan Sauropodomorpha [49]. Much of the primary tissues in the innermost cortex have been resorbed by secondary remodeling. Fourteen to fifteen growth marks were counted (Figure S2A), but a large crack in the outer third of the cortex and subsequent fragmentary nature of the bone in this area, as well as the innermost cortical remodeling precludes a definitive count. Lines of Arrested Growth (LAGs), indicating a temporary cessation in growth, begin to appear with numerous annuli within the outermost peripheral lamellar bone. The LAGs are double or triple in places and become increasingly closely spaced indicating a substantial decrease in growth.
rate. Vascular canals separate these outer growth marks and are present at the outermost periphery indicating that the animal was still growing, but the amount of bone deposition between each growth mark is negligible compared to the earlier growth. Thus, we consider the peripheral lamellar-zonal bone to be an External Fundamental System (EFS) where maximum size had essentially been reached, indicating that this individual was an adult at the time of death. The lamellar infilling of the vascular canals, degree of remodeling and abundance of secondary osteones, as well as the presence of an EFS suggest that the bone tissues fall within the Type E to Type F categories of [13] and Histologic Ontogenetic Stage 10 or 11. Extensive Sharpey’s fibers, indicating areas for the probable attachment of the femorotibialis muscles, were found all along the bone periphery, but also extend as thick bundles a third of the way into the cortex. A few remnants are even present in the inner cortex. The Sharpey’s fiber bundles are frequently associated with radially-oriented vascular canals.

Although all sauropodomorph bone tissues studied thus far exhibit rapidly forming woven-fibered bone during early ontogeny, non-sauropodan sauropodomorph bone tissues such as those of Plateosaurus and Massospondylidae tend to exhibit a predominance of the relatively slower forming parallel-fibered bone during mid-late ontogeny [13, 48]. The bone tissues of these taxa are also interrupted by regularly spaced LAGs even during early ontogeny [13, 50]. This differs from more derived Late Jurassic Neosauropoda, which typically exhibit uninterrupted laminar fibrolamellar bone until late ontogeny, when the transition to slowly forming lamellar-zonal bone with clear LAGs indicates a dramatic decrease in overall growth rate [51]. The lack of growth marks throughout much of sauropod ontogeny is thought to be due to the selection for rapid growth rates in order to reach their enormous body sizes [51, 52]. The presence of uninterrupted fibrolamellar bone even in the possibly Late Triassic basal sauropod Isanosaurus suggests that growth acceleration occurred very early in sauropod evolutionary history [52].

Although Isanosaurus shows that the earliest sauropods were capable of sustained growth, late branching non-sauropodan sauropodiforms such as Lessemsaurus [48] and Antetonitrus [53] exhibit growth marks during early ontogeny. Although early cyclical growth cannot be confirmed in Ledumahadi (due to the resorption of the earliest growth), the presence of growth marks from at least 60% through ontogeny suggests that it grew similarly to these other non-sauropodan sauropodiforms. Interestingly, the first few annuli are not associated with LAGs indicating that growth slowed, but did not cease completely, contrary to that observed in other non-sauropodan Sauropodomorpha, including Lessemsaurus [48] and suggests higher growth rates during the unfavorable growing season. Thus, the bone tissues of Ledumahadi contain aspects of non-sauropodan sauropodomorph and more derived sauropod life histories, emphasizing the variability characterizing sauropodiform osteohistology during a period of heightened ecological diversification.

**Phylogenetic analysis**

To assess the relationships of the holotype of Ledumahadi, we scored it using the phylogenetic dataset of [16], which is based on the original dataset of [9]. We added the following two characters:

Ch. 218: Anterior tip of anterior process of proximal ulna: no deflection or continues lateral curvature (0); medially deflected (1).

A medially deflected anterior process of the ulna was originally described as an autopomorphy of Antetonitrus [8]. However, as a similar deflection is observed in Ledumahadi, this feature was added to the dataset as a possible synapomorphy of the two taxa.

Ch. 233: Pronounced tubercle on the ventrolateral corner of the shaft of the non-first metacarps, just below the proximal surface: absent (0); present (1).

This character extends from observations made in [8], in which the presence of a pronounced tubercle on the ventrolateral corner of the shaft was used to side the second metacarpal in Antetonitrus. A large, topographically similar process is observed in the only non-first metacarpal currently known for Ledumahadi (which is possibly a third or fourth based on size comparison with the first metacarpal). Although the lack of well-preserved hands in many sauropodomorph taxa precludes a deeper understanding of the polarity of this character (as well as its manifestation across the metacarpus), current observations suggest that it typifies a group of robust-limbed sauropodiforms, Ledumahadi and Antetonitrus included.

An additional state was also added to ch. 204 (transverse width of the distal condyles of the humerus): (2) 40 percent or more of the length of the humerus (unordored). This was based on the observation that the humerus of some sauropodomorph taxa (e.g., Riojasaurus, Yunnanosaurus, Lessemsaurus) presents apomorphically widened distal condyles.

The following two characters were removed from the dataset:

Sacral rib much narrower than the transverse process of the first primordial sacral vertebra (and dorsosacral if present) in dorsal view: absent (0); present (1).

This character was removed on grounds of both difficulty of interpretation, as well as presenting a conflation of two distinct morphologies (the dorsosacral and first primordial sacral vertebrae). In most basal sauropodomorph taxa with three sacral vertebrae (e.g., Adeopapposaurus; Lufengosaurus), the transverse process and sacral rib of the first element combine to form a large ‘C’-shaped attachment with the ilium, with the majority of the anterior and ventral sections of the ‘C’ comprised of the sacral rib. In contrast, the second sacral element often bears a more ‘hourglass’ shaped iliac attachment in which the dorsal transverse process and ventral rib are roughly equivalent in anteroposterior width. Together, the sacral ribs of the conjoined pelvic vertebrae tend to form a continuous shelf that borders the mediodorsal margin of the iliac acetabulum – meaning that, if anything, the sacral ribs are uniformly more expansive than the transverse processes across all sauropodomorph taxa (including sauropods, e.g., Camarasaurus; Figure 44 in [54]). This situation potentially applies to dinosaurs in general (e.g., Figure 7 in [55]).

A further issue pertains to the identity of the first two sacral elements. Whereas the first sacral vertebra in a three-sacral arrangement is often considered to represent a dorsosacral, its anatomy is generally much closer to that of the first primordial sacral vertebra.
in taxa for which only two sacral elements are present (e.g., *Herrerasaurus*, *Efraasia*). In contrast, the middle element (the ‘first primordial sacral’) displays a relatively novel morphology. This was first observed by Nesbitt [56], who interpreted the middle element as a novel insertion between the two primordial sacral vertebrae – rendering the traditional ‘dorsosacral’ of recent sauropodomorph studies the first primordial sacral. It is this interpretation that is considered the most likely here. Further analysis of these morphologies and their distribution across sauropodomorphs (and other dinosaur taxa) is required prior to its re-inclusion in the dataset (see [4, 56, 57] for further comment).

Buttress between preacetabular process and the supraacetabular crest of the ilium: present (0) or absent (1).

This character was scored seemingly randomly across the taxa in the dataset. However, a distinct buttress such as described here is not observable in any dinosuarian taxon. In contrast, some crurotarsan taxa display a pronounced ridge that connects the iliac supraacetabular crest to the anterior portion of the dorsal iliac blade (e.g., *Postosuchus*). If restricted to its actual distribution, the ‘present’ state of this character could only be scored polymorphically for one taxon (Crurotarsi) in the current dataset (i.e., is parimony uninformative). Recently, Baron and Williams [58] noted that a number of dinosauroform taxa have at least a rounded eminence connecting the dorsal surface of the acetabulum to the ventral surface of the preacetabular process – with this feature more pronounced in silesaur and herrerasaurid sauropodomorphs. However, the degree to which this feature can be considered a distinct buttress remains open to interpretation.

We managed the phylogenetic dataset in Mesquite v3.40 [33], and exported character/state information to TNT [35] for analysis under the parsimony criterion. A nexus file containing our matrix is available via the Key Resources Table of this publication. We searched for optimal trees using 1000 Wagner additions, holding 1 tree per replicate and swapping on topologies using Tree Bisection and Reconnection. The final set of trees under this analysis was then subjected to another round of TBR searching, up to a maximum of 10,000 final topologies. The following multistate characters were treated as ordered: 8, 13, 19, 23, 40, 57, 69, 92, 102, 117, 121, 131, 134, 145, 148, 150, 151, 158, 163, 168, 171, 177, 184, 207, 210, 217, 226, 231, 239, 247, 255, 258, 271, 283, 304, 310, 318, 338, 351, 354, 356, 361, 365.

This analysis resulted in 6 MPTs with a shortest length of 1286 steps (CI: 0.338; RI: 0.688). All trees found *Ledumahadi* to be the sister taxon to the upper Elliot taxon *Antetonitrus ingenipes*, a position supported by a Bremer value of 2 and the following unambiguous synapomorphies: dorsoventral height of mid-dorsal neural spines over 1.5 times the anteroposterior length of their base (ch. 168); presence of well-developed spinopostzygapophyseal laminae in posterior dorsal vertebrae (ch. 172); anterior tip of the anterior process of the proximal ulna deflected medially (ch. 218). Overall, the strict consensus topology (Figure S4) is somewhat different from previous topologies (e.g., [7, 45, 59]). Of interest is the non-massospondylid position of *Coloradisaurus* and *Glaciassaurus*, which is undoubtedly a reflection of the numerous paurosaur-like features of the former (especially in regards to the cranial anatomy), a concern treated in detail in [60]. Additionally, restriction of the character scorings for *Riojasaurus* to those observable in the holotype (PVL 3808) appears to have introduced renewed instability to this part of the sauropodomorph tree, with the sauropodiform position of this specimen (based primarily on its derived appendicular proportions) only a marginally better explanation than a position closer to *Plateosaurus*, with which it shares several features (e.g., heel on the posteroventral corner of the iliac ischial peduncle). This is reflected in the bootstrap re-sampling analysis, in which relationships among ‘core prosauropods’ are unresolved at frequencies greater than 50% (Figure S4).

It is clear, therefore, that the major interrelationships of basal sauropodomorph dinosaurs remain far from conclusively settled.

**Body mass estimates of *Ledumahadi mafube***

We used measurements taken from a published database [46] and from personal research by the authors and regression equations taken from [17] to estimate the body mass of *Ledumahadi mafube* from measurements of the preserved limb bones, which include the femur (minimum shaft circumference = 540 mm) and ulna (total length = 490 mm; minimum shaft circumference = 265 mm). Our minimum diameter was taken approximately 10cm proximal to the proximal end of the popliteal fossa, exactly at the same point where the femur of *Antetonitrus* attains its minimum circumference. Therefore, our measurement likely reflects the true minimum circumference of the shaft.

The minimum circumference of the femoral shaft of *Ledumahadi mafube* is only slightly smaller than that of *Tyrannosaurus rex* (RSMP 2523.8; = 570 mm), which is the largest-known bipedal dinosaur with an estimated body mass of 7.69 metric tons. Among quadrupedal sauropodomorphs, it is similar to the dimensions of *Barosaurus lentus* (540 mm; 13.2 metric tons [61]; AMNH 6341), *Tornieria africana* (545 mm; 12.3 metric tons [62]; SMNS 12140, right femur of holotype ‘skeleton A’ of [63]; and *Tastavinsaurus sanzi* (550 mm; 14.0 metric tons [64]) (body masses from [2, 46]). These comparisons demonstrate that *Ledumahadi* is comparable in size to many sauropods, and therefore much larger than the largest other non-sauropodan sauropodomorphs, which have considerably smaller skeletal dimensions. For example, the minimum femoral shaft circumference of *Antetonitrus* is 410 mm, comparable to *Lxodonta africana* in the dataset of [17; minimum femoral shaft circumference = 399 mm].

To estimate the body mass of *Ledumahadi mafube* using the method of [17] we required an estimate of the minimum circumferences of both the humeral and femoral shafts. Although the femur is preserved, and could be measured directly, the humerus is not known. To establish a predictive framework for estimating humeral shaft circumference from ulnar shaft circumference, we used the set of 18 Triassic–Cretaceous sauropodomorphs that were present in our phylogeny, and for which both the ulna and humeral minimum shaft circumferences were known. We compared ordinary and phylogenetic generalized least-squares linear models of the relationship between $\log_{10}$-transformed humeral shaft circumference and ulnar shaft circumference for these taxa. Phylogenetic generalized least-squares (assuming Brownian motion-like evolution of the relationship between variables) is
mathematically analogous to ordinary least-squares regression of independent contrasts [65] and was implemented using the R packages ape version 4.1 and nime version 3.1-131 [37, 38].

Akaike’s information criterion for finite sample sizes (AICc; see [66]) favors ordinary least-squares (AICc = −37.4) over pGLS (AICc = −35.0), similar to most scaling relationships between limb bones in other dinosaur groups [2]. This relationship explains an extremely high proportion of the variance in the relationship between the variables ($R^2 = 0.977$), and suggests a constrained relationship between the robustness of the ulna and that of the humerus in sauropodomorph dinosaurs (Figure S3). The OLS model provides an estimate of 408 mm for the minimum shaft circumference of the humerus of *Ledumahadi mafube*, with upper and lower 95% confidence intervals of 381 mm and 436 mm.

Using the OLS scaling relationship of [17] for quadrupedal dinosaurs, the central tendency of our humeral minimum shaft circumference estimate provides a mass estimate of 12.0 metric tons for *Ledumahadi mafube*. If the humeral minimum shaft circumference were confidently known then this would yield narrower confidence intervals (±2 standard deviations: 6.42–22.4 metric tons). However, it is estimated from the ulnar shaft circumference, and propagation of this error through two rounds of regression results in wider confidence intervals (3.46–41.6 metric tons; using scripts provided by [2]). Regardless of how these confidence intervals are interpreted, *Ledumahadi* has skeletal dimensions similar to sauropods with similar femoral shaft circumferences described above, and much greater than those of other sauropodomorphs.

If *Ledumahadi mafube* were assumed to be an habitual biped (an assumption that we strongly reject based on linear discriminant analysis; described below), its body mass would be estimated as 6.63 metric tons (3.55 metric tons – 12.4 metric tons) using the scaling relationship for estimation of the body mass of bipedal tetrapods using femoral shaft circumference provided by [67].

**Analysis of terrestrial vertebrate limb-scaling dynamics**

Quadrupedality evolved from bipedal ancestors at least three times independently among dinosaurs, in sauropods, ceratopsians and thyreophorans (stegosaurs and ankylosaurs) [19, 23, 68, 69]. Further origins of quadrupedality may also be present in iguanodontians [25, 70], although this remains uncertain. Inferring the presence of quadrupedality in some dinosaurs, and especially ‘transitional’ taxa such as non-sauropodan sauropodomorphs is difficult [8, 10, 71, 72], leading to a significant lack of consensus about the locomotory status of key taxa. Previous attempts to infer quadrupedality in dinosaurs have focused on the inference of limb morphology and kinematics, as well as the use of discrete character observations as osteological correlates, and have not yet decisively addressed this question [4, 7–9, 22, 73, 74].

We propose a new method for inferring the number of limbs involved in locomotion that makes use of the robustness of the humeral shaft, captured by a measurement of its minimum circumference, in comparison to that of the femur. Limbs used in locomotion play a critical role in supporting an animal’s body mass against gravity. This has been demonstrated by strength of the relationship between femoral and humeral shaft circumference and body mass in extant quadrupeds (femur and humerus) and bipeds (femur only) [17, 67]. Furthermore, we anticipate that bipeds, which hold the forelimb in aerial suspension, should be under selection to reduce the mass of the forelimb by reducing its cross-sectional diameter. Both considerations should lead to differences in the proportional thickness of forelimb bones of quadrupeds compared to bipeds.

To test this hypothesis, we compiled a database of mammalian, dinosaurian, and other tetrapod limb measurements by expanding existing sources (mammals [17]: [200 mammal species plus 55 reptiles/amphibians], plus measurements of 44 additional mammal species (total = 244 mammal species); dinosaurs [2, 46]). We especially reviewed the data for Triassic and Early Jurassic sauropodomorphs, which are the focus of the current work. Our data contain information on at least four independent transitions from quadrupedality to bipedality in mammals (among macroadiform marsupials, Homo, dipodine rodents, and the spring hare Pedetes [another rodent]). Furthermore, based on examination of natural history videos, we considered *Dendrolagus* (the tree kangaroo) to be a quadruped, capturing a transition from bipedality to quadrupedality among mammals. Our dataset also documents at least three evolutionary transitions from bipedality to quadrupedality in dinosaurs: embodied by the definitively quadrupedal ornithischian clades Thyreophora (Stegosauria + Ankylosauria) and Ceratopsidae (e.g., [23]), and the definitive quadrupedal sauropodomorph clade comprising *Vulcanodon* and all more derived sauropods [7]. Most bipedal taxa in the dataset are relatively small-bodied (smaller than *Homo*). However, larger-bodied definite bipeds are present within all three dinosaur clades, and are shown in Figure S3: Ornithischia (e.g., *Thescelosaurus neglectus*, 340 kg; bipedal according to [25, 75], Sauropodomorpha (e.g., *Plateosaurus*, 920 kg; bipedal according to [76], and especially Theropoda (all theropod dinosaurs are bipeds, and Theropoda includes the largest bipedal animals known [67]: e.g., *Tyrannosaurus rex*, 7.7 metric tons; body mass estimates from [2]). Extinct taxa with uncertain stance (e.g., all iguanodontian ornithischians, including hadrosaurids; non-ceratopsid ceratopsians; ‘transitional’ sauropodomorphs (indicated on Figure S3), and a giant ground sloth (*Glossotherium*) were labeled as uncertain and excluded from use as predictor variables in our analyses.

Examination of the data suggests a clear split in the relationship between humeral shaft minimum circumference and femoral shaft minimum circumference, with quadrupedal mammals, ornithischians and sauropodomorphs having proportionally robust humeri compared to bipedal members of the same clades (Figures 3 and S3). Furthermore, the actual values of these relationships across independent evolutionary transitions from quadrupedality to bipedality (in mammals: apes, rodents, marsupials) and from bipedality to quadrupedality (in ornithischians, sauropodomorphs and *Dendrolagus*) appear consistent (Figure S3). Qualitatively, this suggests that even phylogenetically distant clades of tetrapods achieve quadrupedality by the same proportional increase in humeral shaft robustness, a hypothesis that we test below using regression and discriminant function analysis.
In contrast to the relationship between humeral and femoral shaft circumferences, the relationship of humeral length to femoral length shows little or no apparent distinction between quadrupeds and bipeds among dinosaurs (Table S1; we do not have access to comparable data for other tetrapods). For example, bipedal ornithischians have a similar relationship between humeral and femoral length to that of quadrupedal ornithischians, and theropod dinosaurs (all bipeds) occupy essentially the full range of proportions seen among other dinosaurs of comparable size, regardless of stance. A related metric, forelimb length:hindlimb length, was proposed as a correlate of stance in ornithopods by Galton [76], but was found to be of equivocal use in distinguishing bipeds from quadrupeds among ornithischians by Maidment and Barrett [23, 25]. This contrasts with the apparent distinction between bipeds and quadrupeds shown in the relationship of humeral shaft circumference to femoral shaft circumference (Figure S3), and is consistent with qualitative observations such as the occurrence of proportionally short forelimbs in some ornithischian dinosaurs, especially stegosaurs [77].

Quantitative hypothesis tests

We tested the hypothesis that bipeds and quadrupeds have distinct relationships between the minimum circumference of the humeral shaft and that of the femur by comparison of phylogenetic generalized least-squares [78] linear regression models using information criteria (Akaike’s information criterion for finite sample sizes; AICc [66]). These models capture the relationship between log₁₀-transformed humeral shaft minimum circumference and femoral shaft minimum circumference, optionally including variables describing stance (bipedal|quadrupedal; with taxa having undetermined stances excluded from the analysis) and clade membership (Ornithischia|Sauropodomorpha|Theropoda). For this analysis, sauropods with unequivocal quadrupedal stances and columnar forelimbs were classified as quadrupeds (i.e., Vulcanodon and more apical sauropods), whereas Massospondylus and all more basally-diverging taxa were classified as bipeds (based on evidence in [76] for Plateosaurus and [71, 79] for Massospondylus. Other sauropodomorphs were classified as uncertain and therefore not used in this analysis. Among ornithischians, thyreophorans (stegosaurs + ankylosaurs) and ceratopsids are regarded unequivocally as quadrupeds (reviewed by [23]) and were classified as such. It is also likely that many non-ceratopsid ceratopsians, and many iguanodontians, including hadrosauroids, were quadrupeds. But this is controversial, and they were omitted from our classification. Other ornithischians were classified as bipeds [23]. All theropod dinosaurs were classified as bipeds; only Spinosaurus, for which we do not have limb measurements, was hypothesized as a quadruped [80].

Phylogenetic generalized least-squares (assuming Brownian motion-like evolution of the relationship between variables) is mathematically analogous to ordinary least-squares regression of independent contrasts [65] and was implemented using the R packages ape version 4.1 and nime version 3.1-131 [38]. For these analyses, we used the distribution of time-calibrated dinosaur phylogenies of [37, 46]; minimum branch length = 1), and allowed λ, a phylogenetic signal parameter [81] to be estimated during the model-fitting process using maximum likelihood. We show results from analysis of just one such tree. But these are representative of analyses conducted over multiple trees with different configurations of branch lengths.

This analysis shows that a model explaining humeral shaft minimum circumference in terms of femoral shaft minimum circumference and stance (bipedal|quadrupedal) was overwhelmingly supported, with an AICc weight of 0.998 (Table S1) and intermediate phylogenetic signal (λ = 0.52). Within this model, the coefficient of femoral shaft minimum circumference is 0.958, indicating either very weak negative allometry or isometry of the robustness of the femur with increasing humeral robustness in dinosaurs. The stance covariate has a statistically significant and positive coefficient indicating that evolutionary transitions from bipedality to quadrupedality in dinosaurs are accompanied by an increase in the proportional robustness of the humerus (Table S1).

We also conducted the same pGLS analysis to examine whether the relationship between log₁₀-transformed humeral length and femoral lengths varied between bipeds and quadrupeds among dinosaurs. They do not: the best regression model includes only femoral length (FL) as an explanation of humeral length (HL), and does not include either stance or clade assignment as a covariate (Table S2). Although a model including stance as a covariate has a non-negligible AICc weight of 0.998 (Table S1) and intermediate phylogenetic signal (λ = 0.52). Within this model, the coefficient of femoral shaft minimum circumference is 0.958, indicating either very weak negative allometry or isometry of the robustness of the femur with increasing humeral robustness in dinosaurs. The stance covariate has a statistically significant and positive coefficient indicating that evolutionary transitions from bipedality to quadrupedality in dinosaurs are accompanied by an increase in the proportional robustness of the humerus (Table S1).

Inference of stance in Ledumahadi mafube and other non-sauropodan sauropodomorphs

To provide a predictive framework for inferring the stance in dinosaurs for which this inference cannot otherwise be made unambiguously, we conducted a linear discriminant analysis of our limb measurement dataset. The resulting function is summarized in Tables S2 and S3. This was conducted using the function lda() from the R package MASS [36].

To test the robustness of our initial assignments of taxa to the stance classes (bipedal | quadrupedal), we used ‘leave-out-one’ cross-validation. This returned 100% confirmatory classifications of the taxa included in our analysis (i.e., all taxa were assigned posteriorly to their correct classes). We also tested the classification based on dinosaurs by attempting predictions of the (known) stances of those extant tetrapods from our dataset that were within the size range of our dinosaurs (n = 97, predominantly mammals;
minimum femoral circumference = 34 mm; minimum humeral circumference = 20 mm). The analysis was restricted in this way to avoid extrapolating outside the range of the original data, which would be expected to introduce errors.

In total, the stances of ten extant tetrapods were misclassified (10.3% misclassification) based on our discriminant function for dinosaurs. Confident misclassifications include three rodents, two bovids, one primate, two marsupials and a crocodilian (Table S3), all of which are quadrupeds that were misclassified as bipeds based on the relationship between the minimum shaft circumferences of their femora and humeri (Table S3). This analysis informs our understanding of the performance of our method: quadrupeds can (rarely) have biped-like proportions, but no instances are known in which bipeds have quadruped-like proportions. Therefore, our method can be used to reject the possibility of bipedality in extinct taxa when quadruped-like proportions are present, but cannot be used confidently to reject the possibility of quadrupedality when biped-like proportions are present. This is also consistent with the observation that some large iguanodontian dinosaurs, including hadrosauroids, have slender, biped-like forelimbs and humeri (gray discs at large body size in Figure S3A), but also possess many of the osteological correlates of quadrupedality [25], and show evidence of quadrupedality in fossil trackways [23, 82].

Next, we used the results of the linear discriminant analyses to infer the stances of those sauropodomorphs for which stance was not known, and for which measurements of the humerus and femur were available. Data sources for these specimens are described below, and we believe that this represents the most complete sample of transitional sauropodomorphs that could be obtained after excluding specimens from bonebeds, in which the femora and humeri could have come from individuals of different sizes (e.g., Lessemsaurus [11]), or for which only the femur (e.g., Eucnemesaurus entaxonis [83]), only the humerus (e.g., Seitaad [84]), or neither (e.g., Blikanasaurus [85]), were known. The results of linear discriminant classification of sauropodomorphs are shown in Tables S2 and S3, and in Figure 2.

DATA AND SOFTWARE AVAILABILITY

All data used in this study are available at https://doi.org/10.17605/OSF.IO/HUFYA, including: sauropodomorph measurements, new mammalian measurements, modified data from Campione and Evans [17], modified data from Benson et al. [2], timescaled dinosaur trees, nexus files and tnt files, and estimates of sauropodomorph body masses.