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FIRST ASTRAGALUS OF A TITANOSAUR (DINOSAURIA: SAUROPODA) FROM THE LATEST CRETACEOUS OF INDIA AND THE EVOLUTION OF THE SAUROPOD TARSUS

BY

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Abstract — A sauropod astragalus recovered from latest Cretaceous-aged Lameta Formation (="infratrappean") horizons exposed near the village of Pisdura, central India, represents the first sauropod tarsal element reported from either Indo-Pakistan or Madagascar during that interval. The astragalus is nearly complete and well preserved, lacking only a portion of its proximal articular surface for the tibia. Somewhat surprisingly, the Pisdura astragalus most closely resembles that of Early Cretaceous and early Late Cretaceous-aged titanosaur sauropods from Australia (e.g., *Diamantinasaurus*), South America (e.g., *Ligabuesaurus*), and Asia (e.g., *Erketu*), rather than those of contemporaneous titanosaurs (e.g., *Opisthocoelicaudia*, *Neuquensaurus*). The astragali of these latter latest Cretaceous titanosaurs are distinguished by their highly abbreviated, 'pyramidal' shape, which underlies only the lateral half of the distal tibia and contacts only the middle portion of the pes (metatarsals 2–3). The reduction of the astragalus in titanosaurs is part of a general tendency in sauropods towards reduction of carpal and tarsal elements, associated with the acquisition of the "wide-gauge" limb posture.

INTRODUCTION

The geological and spatial distribution of rocks, differences in collecting practices, and the legacy of colonialism have combined to produce a marked heterogeneity in available fossil data, particularly from countries from the global south (Raja et al., 2021). For example, the record of Cretaceous continental tetrapods is asymmetrically distributed, with most northern landmasses being well represented throughout much of the interval (e.g., Asia, North America) but most Gondwanan landmasses comparably poorly represented and/or restricted to particular intervals. Continental fossil vertebrates from Africa and Australia are best known during the Early Cretaceous and earliest Late Cretaceous, whereas those from India, Madagascar, and Antarctica are known predominantly from the latest Cretaceous. South America is the lone Gondwanan landmass with a well-sampled fossil record from throughout much of the Cretaceous (with most of its record coming from the 'southern cone' of the landmass). The differential distributions of Cretaceous continental tetrapod fossils on southern landmasses have created challenges for paleobiogeographic and evolutionary studies. Publishing paleontological "dark data"—that is, fossil material that has been collected and accessioned but not yet incorporated in scientific litera-

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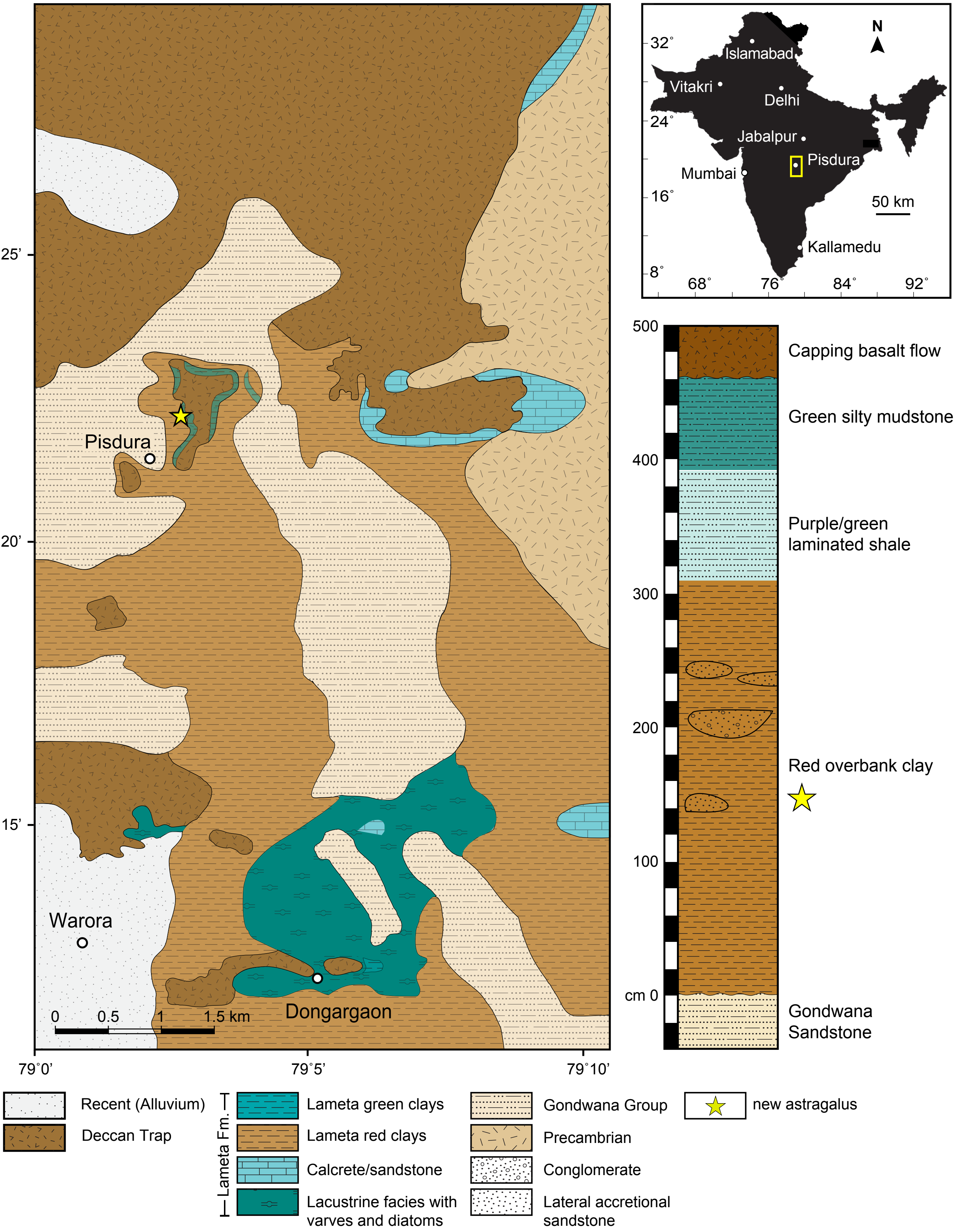
N
32˚
24˚
16˚
8˚
68˚
76˚
84˚
92˚
Islamabad
Vitakri
Delhi
Jabalpur
Pisdura
Mumbai
Kallamedu
50 km
20˚25'
20˚20'
20˚15'
79˚0'
79˚5'
79˚10'
Pisdura
Warora
Dongargaon
0
0.5
1
1.5 km
500
400
300
200
100
cm 0
Capping basalt flow
Green silty mudstone
Purple/green laminated shale
Red overbank clay
Gondwana Sandstone
Recent (Alluvium)
Deccan Trap
Lameta Fm.
Lameta green clays
Lameta red clays
Calcrete/sandstone
Lacustrine facies with varves and diatoms
Gondwana Group
Precambrian
Conglomerate
Lateral accretional sandstone
new astragalus

ture (Marshall et al., 2018)—may help level this asymmetrical distribution of fossil data.

Dinosaur remains from the latest Cretaceous of Indo-Pakistan are recorded in sediments predominantly associated with the Deccan Trap Volcanic Province, though there are important remains from horizons not associated with traps in both India (i.e., Kallamedu Formation) and Pakistan (i.e., Vitakri Formation). Sauropod dinosaurs form the majority of bones collected, which represent perhaps 4–5 species (see Wilson et al., 2011). Although many fewer theropod remains have been collected, and from a subset of the localities preserving sauropods, they too form the basis for 5 species (see Mohabey et al., 2024). As noted elsewhere, apparent collecting bias has led to a predominance of larger, robust elements (e.g., proximal limb bones, caudal centra) and a relative scarcity of small or delicate elements (e.g., cranial bones, presacral vertebrae, manual and pedal elements; see Wilson et al., 2019). To date, for example, there are no sauropod tarsal elements described in the published literature from the Late Cretaceous of either India or Pakistan. Here we describe the first sauropod astragalus known from the Late Cretaceous of Indo-Pakistan or Madagascar. Collected from the Lameta Formation (= "infratrappean") horizons near the village of Pisdura in central India (Fig. 1), this element resembles astragali of earlier appearing titanosaurs from mid-Cretaceous horizons in Australia, South America, and Asia. We provide a description for this element and explore its implications for the evolution of tarsal elements in sauropod history and for locomotor function.

INSTITUTIONAL ABBREVIATIONS

AODF — Australian Age of Dinosaurs Museum of Natural History, Winton, Australia.
GCP — Grupo Cultural Paleontológico de Elche, Museo Paleontológico de Elche, Spain.
IGM — Geological Institute of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia.
MCP — Museu de Ciencias e Tecnologia, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil.
MCS — Museo Cinco Saltos, Río Negro, Argentina.
NGMJ — Nanjing Geological Museum, Nanjing, China.
RTMNU — Rashtrasant Tukadoji Maharaj Nagpur University, Nagpur, India.
SAV — Sant Antoni de la Vespa fossil site Collection of the Museu Temps de Dinosaures-Museus de Morella, Spain.
UMMP — University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.
ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAUROPODA Marsh, 1878
TITANOSAURIA Bonaparte and Coria, 1993
Gen. et sp. indet.
(Fig. 2)

Referred Specimen.— RTMNU/DG/VERT/5/55P/2019, a right astragalus. A cast of the element is available at the University of Michigan Museum of Paleontology (UMMP 119926), and a digital three-dimensional photogrammetric model is available from the University of Michigan's Deep Blue Data (https://doi.org/10.7302/sydq-2469).

Locality and Horizon.— The astragalus (RTMNU/DG/VERT/5/55P/2019) was surface-collected from sediments exposed near the village of Pisdura in the state of Maharashtra, central India in January 2019 (Fig. 1). The locality (20°21′N, 79°2′E) is part of a farmer's field where fossil remains are disinterred by ploughing, which typically results in disassociated specimens (though there are exceptions). First reported by Stephen Hislop (1860:163), "organic remains at Phizdura may be gathered in abundance from the surface of a field, and comprise bones of large Pachyderms, coprolites of various sizes, a Saurian tooth, the vertebra of a large Fish, and fragments of the plastron of a freshwater Tortoise." Bones and bone fragments, coprolites (Matley, 1939; Mohabey, 2001; Prasad et al., 2005), and shells of the gastropod *Physa* are still common occurrences in the overbank red silty clays at the Pisdura locality (Fig. 1), which has produced thus far two distinct turtle species, *Jainemys pisdurensis* (Joyce & Bandyopadhyay 2020) and a larger as yet unnamed species (Wilson et al., in progress), the snake *Madtsoia pisdurensis* (Mohabey et al., 2011), a partial jaw of a noasaurid dinosaur (Mohabey et al., 2024), and remains of titanosaurs including caudal vertebrae that were named *Titanosaurus blanfordi* (Lydekker, 1879). Huene and Matley (1933) later designated those *Titanosaurus blanfordi* centra that possess a squarish cross-section as *Laplatasaurus madagascariensis*.

The deposits at Pisdura were originally considered to be Eocene in age by Hislop (1860), who made the argument that the "pachyderms" (now known to be titanosaurs) at Pisdura are identical to those at Jabalpur, indicating their similarity in geological age. Much later, Matley (1921) concluded that the Lameta beds, including Pisdura, correspond to the upper part of the Lower Cretaceous. Current consensus is that it is latest Cretaceous in age based on coccoliths (Salis & Saxena, 1998), magnetostratigraphy indicating reversed polarity (C29r; Hansen et al., 2005), and palynostratigraphy (Samant & Mohabey, 2005).

FIGURE 1 — (previous page) Geological map and stratigraphic section indicating the position of the Pisdura locality, central India. The astragalus locality is marked by the star. The stratigraphic section at right is based on field reconnaissance by DMM and BS, as published in Mohabey et al. (2024: fig. 1).

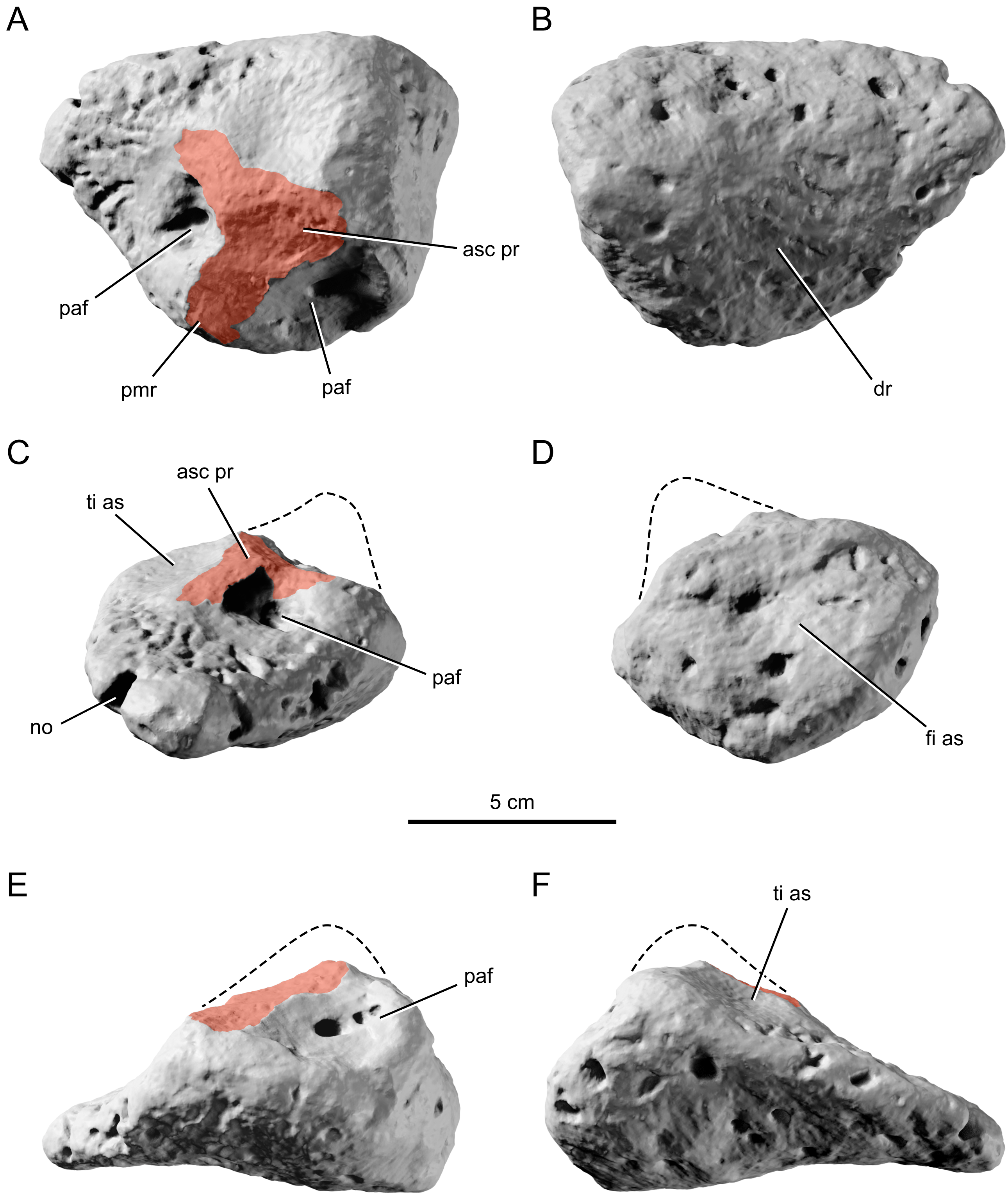

FIGURE 2 — Three-dimensional renders based on photogrammetric models of the right astragalus RTMNU/DG/VERT/5/55P/2019 in proximal (**A**), distal (**B**), medial (**C**), lateral (**D**), posterior (**E**), and anterior (**F**) views. Anterior is towards the top in **A** and **B**. Orange tone indicates broken areas; dashed lines indicate missing bone. Abbreviations: *asc pr*, ascending process; *dr*, distal roller; *f*, foramen; *fi as*,

TABLE 1 — Measurements of the right astragalus RTMNU/DG/VERT/5/55P/2019 from the Late Cretaceous-aged Pisdura locality of central India. Asterisk indicates an incomplete measurement.

measurement	cm	width / measurement
Transverse width	17.1	1.0
Anteroposterior depth	11.3	1.51
Proximodistal height (pres.)	9.1*	1.88*
Proximodistal height (est.)	11.1	1.54

Comments.— The specimen (RTMNU/DG/VERT/5/55P/2019) can be referred to Sauropoda based on its nearly complete encapsulation in cartilage and its wedge shape (see Wilson & Sereno, 1998). The abbreviated proportions of astragalus in the transverse, proximodistal, and anteroposterior planes suggest affinities with Titanosauria. To date, no other lineage of sauropods has been found in the latest Cretaceous of Indo-Pakistan or elsewhere in the world (see Whitlock et al., 2011). Here, we use the definition of Sauropoda as the least inclusive clade containing *Saltasaurus loricatus* but not *Melanorosaurus readi* (Yates, 2006); and the definition of Titanosauria as all somphospondylans closer to *Saltasaurus loricatus* than to *Euhelopus zdanskyi* (Salgado, 2003).

DESCRIPTION

Measurements of the Pisdura astragalus are in Table 1, and scorings for astragalar characters compiled by Carballido et al. (2017) can be found in Table 2. In the description below, we use “proximal” and “distal” to refer to the ends of the astragalus that articulate with the crus and pes, respectively, rather than “dorsal” and “ventral.” We position the astragalus in three-dimensional space with its anterior edge oriented transversely, based on comparisons with specimens that have tarsus and crus preserved in articulation, such as *Erketu* (Ksepka & Norell, 2006). Constraining the rotation about the transverse axis is more challenging, especially in the absence of a complete ascending process or a distal tibia. Here, we refer again to the articulated tarsus and crus of *Erketu* (Ksepka & Norell, 2006) for guidance and orient the Pisdura astragalus so that its articular surface with the tibia is rotated to be nearly parallel with the plane of anterior view and at its greatest height. All figures, measurements, and the description below are based on this orientation.

The Pisdura astragalus (RTMNU/DG/VERT/5/55P/2019) is well preserved, lacking only a portion of its ascending process and posteromedial ridge, which have been abraded (Fig. 2; Table 1). The surface texture is well preserved, even though it appears coarse and pitted. A small notch on the medial side of the anterior edge of the astragalus appears to be real, and a similar notch is found in *Erketu* (Ksepka & Norell, 2006) and a specimen is referred to *Diamantinasaurus* (Beeston et al., 2024).

The Pisdura astragalus is subtrapezoidal in proximal and distal views (Fig. 2A, B) and subtriangular in anterior and posterior views (Fig. 2C, D). The astragalus is approximately 1.5 times as wide transversely as it is deep anteroposteriorly. The loss of part of the ascending process means a complete height is not preserved (Table 1), but we estimate that approximately 2 cm of its height is missing. This would suggest the astragalus is 1.5 times as wide as tall.

Nearly the entirety of the astragalus bears a coarse texture that consists of bumps, grooves, and pits. This bone texture is identical to that on the articular surface of sauropod limb bones and indicates that the astragalus was nearly completely enveloped in cartilage. Two small patches of smooth bone are present on the posterior side of the proximal astragalus. These posterior astragalar fossae are pierced by several openings that range in size from 4–10 mm in diameter. These represent neurovascular foramina that would have nourished the bone. The coarse texture is uniform apart from a small patch (ca. 4 cm radius) on the distal surface where the pattern is more concentrated, with ridges and grooves more tightly arranged (see Fig. 2B).

The astragalus is trapezoidal in proximal view, with its anterior and posterior bases roughly parallel to one another (Fig. 2A). The longer anterior base is nearly twice as long as the posterior base, and the two are connected to one another by legs that are asymmetrical in length and angulation. The lateral leg is nearly perpendicular to the bases, and the medial leg meets the anterior base at an angle of approximately 53 degrees. The inflection point between the posterior base and medial leg occurs at the point of intersection of the posteromedial ridge, which separates the two posterior astragalar fossae. The fossae are distinguished by smooth bone pierced by 3–5 medium-sized neurovascular foramina (4–10 mm). The more medially positioned of the fossae is larger (4.3 x 5.4 cm) and contains more smooth bone than the smaller, more laterally positioned fossa (ca. 3 cm diameter). The ascending process is not preserved but based on the size and contour of its broken base, we infer that between 1.5 and 2 cm of height is missing.

(continued from previous page) fibular articular surface; *no*, notch; *paf*, posterior astragalar fossa; *pmr*, posteromedial ridge; *ti as*, tibial articular surface.

TABLE 2 — Character scores (bold) for the right astragalus RTMNU/DG/VERT/5/55P/2019 from the Late Cretaceous Pisdura locality of central India. Characters are from various sources, compiled in Carballido et al. (2017).

number	character	score (bold)
372	Astragalus, shape	**(0) at least 1.5x wider than anteroposteriorly long** (1) anteroposterior and transverse dimensions subequal
373	Astragalus, shape	(0) rectangular **(1) wedge-shaped**
374	Astragalus, fibular facet	(0) faces laterally **(1) fibular facet faces posterolaterally**
375	Astragalus, foramina at base of ascending process	**(0) present foramen at base of ascending process** (1) absent
376	Astragalus, ascending process length	**(0) ascending process length limited to anterior 2/3 of astragalus** (1) extending to posterior margin of astragalus
377	Astragalus, posterior fossa shape	(0) undivided posterior fossa **(1) divided by vertical crest**
378	Astragalus, transverse process length	**(0) transverse length 50% more than proximodistal height** (1) or subequal to proximodistal height

The anterior portion of the base of the ascending process bears slightly smoother bone texture than the surrounding bone.

The distal astragalus is sub-trapezoidal in outline (Fig. 2B). It is gently convex, forming a ‘roller’ for articulation with the metatarsus. As mentioned above, the surface texture mostly consists of pits and grooves that are fairly spaced out, but there is a patch where they are concentrated. The small notch near the anteromedial corner of the astragalus is real, created by a deep pit with recessed walls.

The astragalus is subtriangular in anterior and posterior views (Fig. 2C, D). Its ventral base is flat to slightly concave, and its medial vertex is blunted. In articulation, the ascending process would have been hidden by the tibia, and so in anterior view the astragalus would appear as a slightly lower profile triangle. One of the two astragalar fossae is visible in posterior view, the medially positioned fossa can only be seen in medial and proximal views (Fig. 2). The crest dividing the two is broken near its base, which is approximately 2 cm broad.

The astragalus tapers anteroposteriorly and proximodistally towards its medial edge to an unequal extent. The reduction in proximodistal height is greater than the reduction in anteroposterior depth, giving the astragalus a tongue-like medial edge (Fig. 2E). One of the two astragalar fossae is visible in medial view, but the more laterally positioned fossa is blocked from view by the posteromedial ridge.

The astragalus is subrectangular in lateral view (Fig. 2F). The articular surface for the fibula occupies the entirety of the lateral surface, which is flat to slightly concave.

COMPARISONS

The Pisdura astragalus was not associated with a tibia, so assessments of their relative transverse breadths are not possible. However, it is possible to compare proportions of the astragalus itself with those of other sauropods.

In general terms, the Pisdura astragalus resembles those of other sauropods in its pronounced wedge shape, which is created by the reduction in proximodistal height and anteroposterior breadth towards the medial side of the element. It reaches its greatest height and depth on the lateral side, where it would have contacted the fibula and possibly the calcaneum (if ossified). The distal end of the astragalus, sometimes referred to as the “roller,” provides the surface that contacts the metatarsus. The Pisdura astragalus differs from those of Jurassic sauropods in its abbreviated transverse proportions. Whereas the transverse breadth of the astragalus is more than twice its height and depth in most sauropods, in the Pisdura astragalus breadth is reduced to 1.54 times its estimated height and 1.51 times its depth (Table 1). These proportions and the general shape of the Pisdura astragalus are similar to those of a specimen referred to *Diamantinasaurus*, whose proportions are 1.53 and 1.51 (AODF 0666; Beeston et al., 2024: table S15), and to *Erketu*, whose proportions are 1.34 and 1.51 (Ksepka & Norell, 2006). The astragali of *Diamantinasaurus* and *Erketu* differ from that of the Pisdura astragalus in having a more blunted medial end in proximal or distal views. More phylogenetically nested titanosaurs have even more abbreviated proportions in which the transverse breadth is subequal to its height and width (Wilson, 2002).

EVOLUTION OF THE TARSUS IN SAUROPOD DINOSAURS

Despite the relative abundance of appendicular elements from the region, RTMNU/DG/VERT/5/55P/2019 represents the first astragalus reported from Indo-Pakistan or Madagascar. Below, we discuss evolution of the tarsus within sauropods and their antecedents.

Reptilia.— The tarsus of reptiles differs from that of amphibians in consisting primarily of two rows of ossified elements, as opposed to three (Schaeffer, 1941; Romer, 1956). The middle row of centrales present in amphibians is interpreted to have been either unossified or subsumed within other elements in reptiles. The proximal row of the reptilian tarsus consists of the calcaneum, astragalus, and a centrale. The distal row includes distal tarsals 1–5, each of which is associated with the corresponding metatarsal, for a total of 8 or

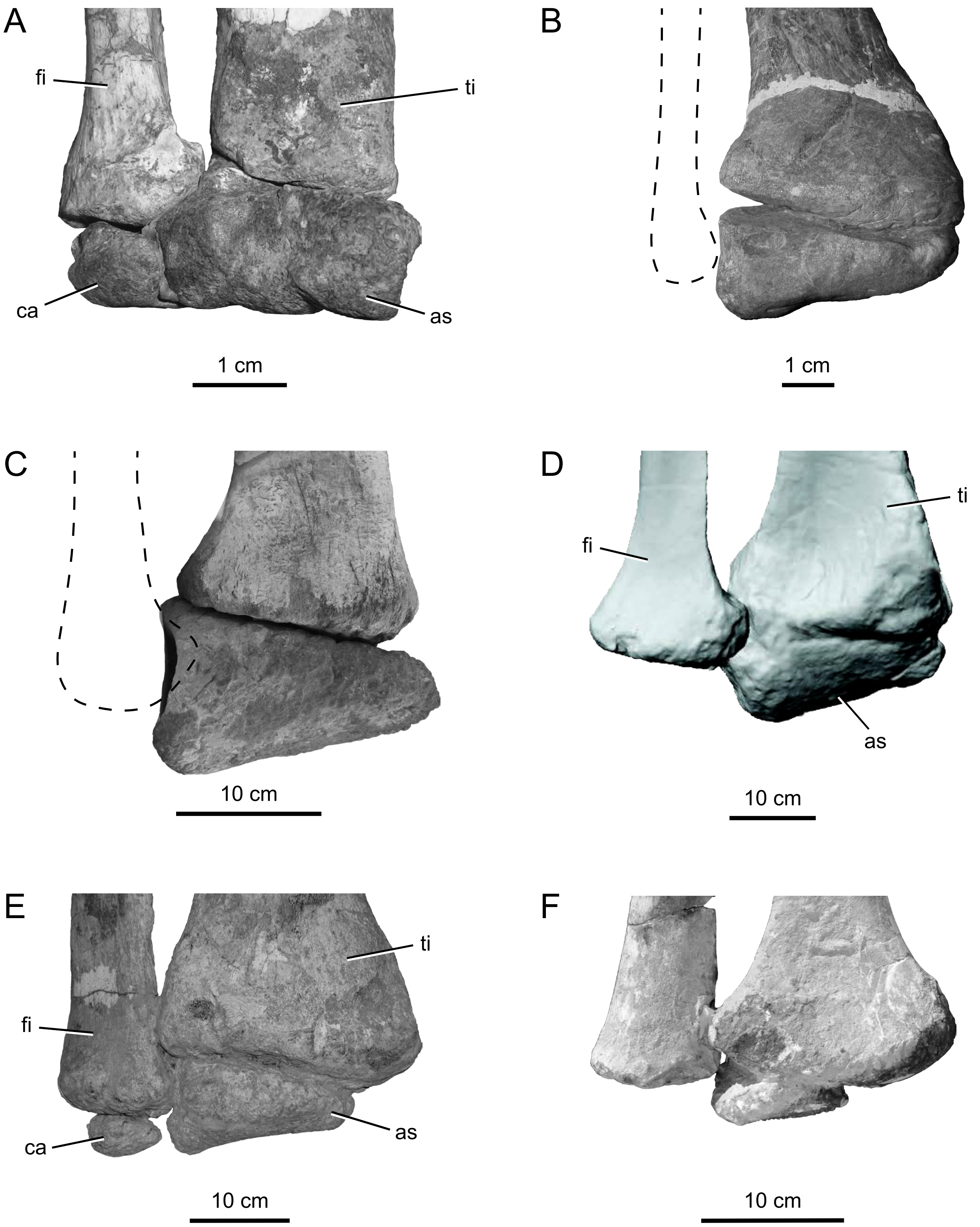

FIGURE 3 — Reduction of the astragalus in sauropodomorphs. **A**–**F**, right crus and tarsus in anterior view, scaled to same distal crural width. **A**, early sauropodomorph *Saturnalia tupiniquim* (MCP-3488-PV); **B**, near-sauropod *Yunnanosaurus huangi* (NGMJ 004546); **C**, basally diverging eusauropod *Spinophorosaurus nigerensis* (GCP-CV-4229, reversed); **D**, titanosauriform *Garumbatitan morellensis* (SAV05-065, 64, 66;

(continued from previous page) modified from Mocho et al., 2024: fig. 13B); **E**, somphospondylan *Erketu ellisoni* (IGM 100/1803); and **F**, saltasaurid titanosaur *Neuquensaurus australis* (MCS 5/25, 5/26, 5/29). Note the reduction in astragalar breadth relative to distal tibia breadth and retention of its contact with the lateral tibia and fibula. It is not yet known whether the absence of an ossified calcaneum in **C**, **D**, and **F** is preservational or a true loss. Abbreviations: *as*, astragalus; *ca*, calcaneum; *fi*, fibula; *ti*, tibia. Photo of *Yunnanosaurus* in **B** courtesy of Diego Pol.

more separate tarsal ossifications. The astragalus is hypothesized to comprise several elements, including the tibiale, the intermedium, and a centrale, whereas the calcaneum corresponds to the fibulare (Schaeffer, 1941). The intermedium, as its name suggests, is in an intermediate position between the tibia and fibula in reptilian development and in amphibians (Schaeffer, 1941), and so the combination of tibiale and intermedium results in an astragalus that is in a position to contact both crural elements (viz., the tibia and fibula).

Archosauriformes.— Distal tarsals 1 and 2 do not ossify independently in Archosauria and its closest outgroups *Euparkeria* and Proterochampsidae (Sereno, 1991), and distal tarsal 5 is not ossified separately in any of the archosauriforms evaluated in the phylogenetic study by Ezcurra (2016). It has been suggested that distal tarsal 5 was possibly incorporated into the 'hook' of the hooked metatarsal 5 present in many archosauriforms (Gauthier et al., 1988; Joyce et al., 2013; Ossa-Fuentes et al. 2022). In all diapsids examined by Ossa-Fuentes et al. (2022), embryonic cartilages for distal tarsals 1 and 5 do not even form. By contrast, in those same species the distal tarsal 2 anlage does form during development, but it does not ossify independently—and may have been incorporated into the proximal portion of metatarsal 2 (Ossa-Fuentes et al., 2020).

The bird-line archosaurs, including both dinosaurs and pterosaurs, are characterized by a mesotarsal joint, in which movement takes place at a hinge between the proximal and distal ankle elements (Schaeffer, 1941). On one side of the mesotarsal joint, the proximal tarsal bones are tightly associated with the crus, and on the other the distal tarsal bones are tightly associated with the compact metatarsus (Sereno, 1991). Proximal tarsal elements include the astragalus and calcaneum, with the centrale occasionally present distal to them, especially in more basally diverging forms. The distal tarsal elements typically include two or fewer independent ossifications, distal tarsals 3 and 4, which are most closely associated with metatarsals 3 and 4, but also occasionally contact metatarsals 2 and 5, respectively. In dinosaurs and near-dinosaurs, the astragalus is typically broader transversely than the distal tibia and articulates with both the tibia and the fibula; as a consequence the fibular articulation is shared between the astragalus and calcaneum (e.g., *Lagerpeton*, Sereno & Arcucci, 1993; *Marasuchus*, Sereno & Arcucci, 1994; *Pandorvenator*, Rauhut & Pol, 2017).

Sauropodomorpha.— In basally diverging sauropodomorphs and the earliest sauropods, the proximal tarsal elements (viz., astragalus, calcaneum) span the breadth of the distal crus (e.g., *Saturnalia*, Langer et al., 1999; *Blikanasaurus*, Galton & van Heerden, 1985; *Vulcanodon*, Raath, 1972). Two distal tarsals are preserved as individual ossifications in some basal sauropodomorphs (e.g., *Glacialisaurus*, Smith & Pol, 2007) and basally diverging sauropods (e.g., *Blikanasaurus*, Galton & van Heerden, 1985, 1998; *Gongxianosaurus*, He et al., 1998). These are sometimes identified as distal tarsals 3 and 4, implying homology with those bones in more basal reptiles, but sometimes they are referred to agnostically as the "medial distal tarsal" and the "lateral distal tarsal" (Smith & Pol, 2007). However, distal tarsal elements

TABLE 3 — Comparative measurements (cm) of tibia and astragalar breadth in selected sauropod genera. Entries are sorted by geological age (oldest first); standard abbreviations are used for geological stages.

Genus	Geological Epoch	Geological Stage	Distal tibia (breadth)	Astragalus (breadth)	As/Ti Ratio
Blikanasaurus	Late Triassic	Crn/Nor	8.7	9.8	1.13
Spinophorosaurus	Middle Jurassic	?	21.0	24.5	1.16
Garumbatitan	Early Cretaceous	Bar	30.2	28.1	0.93
Euhelopus	Early Cretaceous	Bar/Apt	16.5	15.2	0.92
Tangvayosaurus	Early Cretaceous	Apt/Alb	33.2	27.0	0.81
Gobititan	Early Cretaceous	Alb	27.7	20.3	0.73
Ligabuesaurus	Early Cretaceous	Alb	31.0	22.5	0.73
Erketu	Early–Late Cretaceous	Alb/Cen?	21.8	16.1	0.73
Diamantinasaurus	Late Cretaceous	Cen/Tur	34.9	28.1	0.80
Neuquensaurus	Late Cretaceous	Cmp	16.6	9.4	0.56
Opisthocoelicaudia	Late Cretaceous	Maa	31.5	17.0	0.48

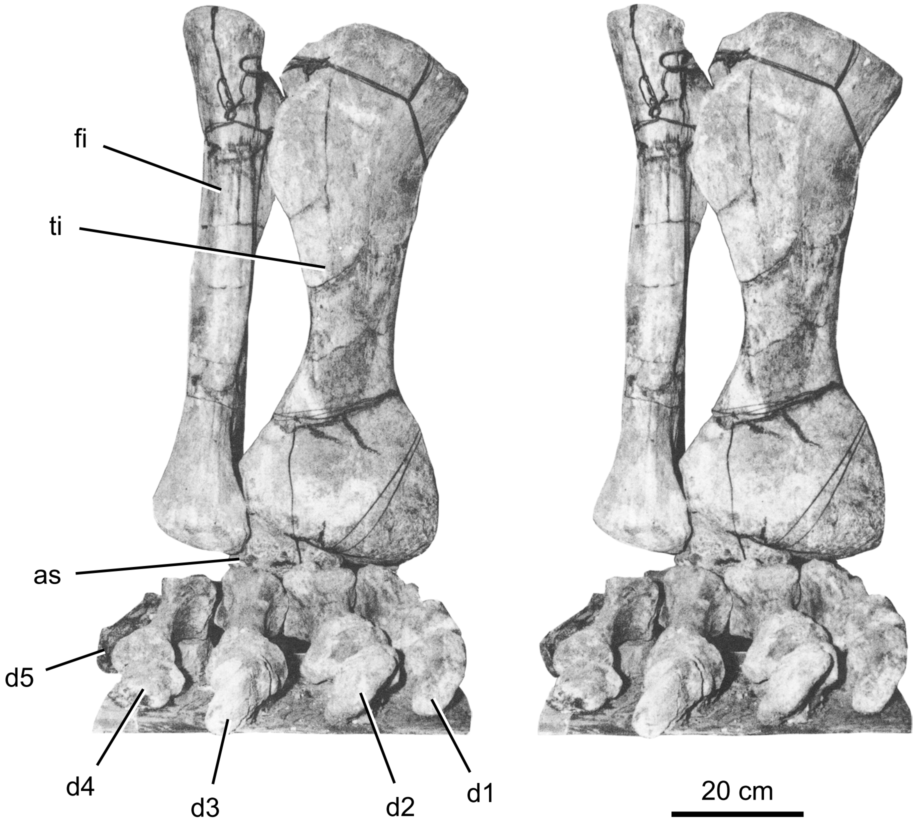

FIGURE 4 — Stereopairs of the right crus and pes of *Opisthocoelicaudia skarzynskii* (ZPAL MgD-J/48) in anterior view. The photographs were published in the original description of the taxon (Borsuk-Białynicka, 1977: pl. 14, fig. 2b), in which it appears the fibula in the mounted specimen is from the left side and has been turned around to fit with the right crus (i.e., the fibula is shown in posterior view). Note that there were some inconsistencies in the cutting of the rubylith matting the original photographs, resulting in a shimmering effect in certain areas (e.g., distal metatarsal 5, proximal tibia). Abbreviations: *as*, astragalus; *d1–5*, digits 1–5; *fi*, fibula; *ti*, tibia.

are not ossified in most sauropods (Raath, 1972; Gauthier, 1986) and represent early stages of the progressive reduction in the ossification of carpal and tarsal elements within the group (Wilson & Sereno, 1998). It is not yet known whether distal tarsals were lost, retained in cartilage, or incorporated into other tarsal or metapodial elements. Determination of the clade characterized by loss of these elements is challenging because accurately recording their absence requires exceptional preservation, collection, and recognition of these small and often nondescript elements. Nevertheless, for the majority of sauropods the tarsus consists solely of two proximal elements, the astragalus and calcaneum.

In most sauropods, the astragalus is wedge-shaped in anterior view, being thickest near its articulation with the fibula and tapering towards its medial edge. The distal articular surface of the tibia is beveled medially to accommodate the wedge of the astragalus, and its posteromedial process accommodates the ascending process of the astragalus. The astragalus also tapers medially in proximal or distal view, with the anteromedial and posteromedial corners reduced. Although these two features were initially hypothesized to be a single feature "wedge-shaped astragalus" and restricted to neosauropods (Wilson & Sereno, 1998: character 85), it is clear that this feature probably characterizes some more basally diverging forms (e.g., *Spinophorosaurus*, Remes et al., 2009: fig. 4N, F. Ortega & P. Mocho pers. comm.; *Barapasaurus*, Bandyopadhyay et al., 2010: text-fig. 15; *Tazoudasaurus*, Allain & Aquesbi, 2008). It is also clear that independent features should code variation in the shape of the astragalus in anterior and proximal views, as in Table 2, because some taxa appear to have one but not the other (e.g., *Vulcanodon*, Raath et al., 1972; *Lamplughsaura*, Kutty et al., 2007; *Lessemsaurus*, Pol & Powell, 2007; see also Lefebvre et al., 2025).

Titanosauriformes.— The ancestral condition for neosauropods and their nearest relatives is that the astragalus is wedge-shaped in anterior and proximal views and extends the breadth of the tibia or slightly more (Table 3), contacting the tibia, fibula, and calcaneum if ossified. This condition is retained in the basally diverging titanosauriforms, including the Late Jurassic brachiosaurid *Giraffatitan* (Janensch, 1961) and the Early Cretaceous somphospondylans *Garumbatitan* (Mocho et al., 2024), *Dongbeititan* (Wang et al., 2008), and *Euhelopus* (Wilson & Upchurch, 2009).

In more phylogenetically nested members of the group, the transverse breadth of the astragalus is reduced progressively. Early Cretaceous and early Late Cretaceous titanosauriforms close to or within Titanosauria reduce the breadth of the astragalus to approximately 70–80% the distal breadth of the tibia (Table 3), including *Ligabuesaurus* (Bonaparte et al., 2006; Bellardini et al., 2022), *Diamantinasaurus* (Hocknull et al., 2009; Beeston et al., 2024), *Ruixinia* (Mo et al., 2023), *Tangvayosaurus* (Allain et al., 1999), *Gobititan* (You et al., 2003), and *Erketu* (Ksepka & Norell, 2006). Notably it is the medial portion of the astragalus that is reduced; the lateral portion retains its contact with the tibia, fibula, and possibly the calcaneum. That is, it is the medial edge of the distal tibia that is not capped by the astragalus, a feature first coded by Ksepka & Norell (2010: character 243) and included in other analyses (e.g., Mannion et al., 2013, 2019). In addition to these changes in the proportions of the tibia, the posterior fossa and the overhanging lip of the ascending process are reduced.

The reduction of astragalar breadth to 70–80% tibial breadth is retained in some early Late Cretaceous titanosaurs such as *Epachthosaurus* (Martínez et al., 2004) and *Elaltitan* (Mannion & Otero, 2012). By contrast, latest Cretaceous titanosaurs further reduce the astragalus to approximately half the width of the tibia (Table 3), attaining a “pyramidal” shape in which its transverse width is subequal to its proximodistal height and anteroposterior depth (Wilson, 2002: character 214). These pyramidal astragali have a nearly square (e.g, *Bonatitan*) to trapezoidal (e.g., *Antarctosaurus*) outline in proximal view. Again, it is the medial portion of the astragalus that is reduced, as shown in articulated specimens where its articulation with the crural elements is preserved (e.g., *Neuquensaurus*, Salgado et al., 2005). The distal tibia is beveled to accommodate the comparably narrow wedge of the astragalus (Fig. 3). The pyramidal astragalus was originally resolved as a saltasaurid synapomorphy (Wilson, 2002: character 214), but a slightly broader distribution of taxa is now known to possess this trait. Pyramidal astragali have been reported in the early Late Cretaceous titanosaur *Bustingorrytitan* (Simón & Salgado, 2023) and the latest Cretaceous titanosaurs *Aeolosaurus* (Salgado et al., 1997; Powell, 2003), *Antarctosaurus* (Huene 1929), *Bonatitan* (Salgado et al, 2015), *Bonitasaura* (Gallina & Apesteguía, 2015), *Dreadnoughtus* (Lacovara et al., 2014; Ullman & Lacovara, 2016), *Kaijutitan* (Filippi et al., 2024), *Neuquensaurus* (Salgado et al., 2005), *Notocolossus* (González Riga et al., 2016), *Opisthocoelicaudia* (Borsuk-Białynicka, 1977), *Uberabatitan* Salgado and Carvalho, 2008), and *Udelartitan* (Soto et al., 2024). A notable exception to this pattern is *Titanomachya*, which is autapomorphically trapezoidal to diamond-shaped in proximal and distal views (Pérez-Moreno et al., 2024).

The astragalus spans metatarsals 1–3 primitively in dinosauriforms (e.g., *Marasuchus*, Sereno & Arcucci, 1994; *Blikanasaurus*, Galton & Van Heerden 1985, 1998), a condition retained in most sauropods. In latest Cretaceous titanosaurs, however, the reduction in breadth of the astragalus to approximately half the tibial breadth results in a narrower articulation with metatarsus. In *Opisthocoelicaudia*, for example, the astragalus is positioned proximal to metatarsals 2 and 3 and equal to their combined width; there is no bony separation between metatarsal 1 and the tibia (Fig. 4).

FUNCTIONAL IMPLICATIONS OF TARSAL REDUCTION

The strength of bones and muscles is proportional to their cross-sectional area (e.g., Galileo, 1638; Thompson, 1917; Smith & Savage, 1956; Alexander, 1991). As animals become larger developmentally or evolutionarily, the load imposed by body mass (L^3) tends to increase faster than does the cross-sectional area (L^2) of the muscles and bone supporting it. Sauropod dinosaurs evolved several features that reduce the dimensional differential associated with large body size, including changes to limb proportions, pneumaticity, and material properties of limb elements.

The most notable material property change is that the articular surfaces of weight-bearing limb bones appear unfinished, bearing a coarse, rugose texture that indicates they were capped by a thick layer of cartilage (Wilson & Sereno, 1998: 56–57; Carrano, 2005). Carpal and tarsal elements consist almost entirely in this rugose bone surface, indicating they were enveloped in cartilage (Wilson & Sereno, 1998: figs. 21, 33). Reduction of the ossified component of the astragalus in titanosaurs is part of this general trend in sauropods of replacement of bone by cartilage, which is excellent at dissipating stress and transmitting it across connections that involve multiple bony elements (see Holliday et al., 2010; Jannel et al., 2022). In fact, tarsal reduction in titanosaurs mirrors that of the carpus within the group, which is completely unossified (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002)—although articulated specimens suggest these elements were retained in cartilage (e.g., *Alamosaurus*, Gilmore, 1946: pl. 4).

The reduction in width of the astragalus is so widespread by the end of the Cretaceous that the Pisdura astragalus stands out for its more primitive proportions, which recall species from the Early to early Late Cretaceous. The reduction in the breadth of the astragalus within titanosauriforms coincides with the evolution of the “wide-gauge” limb posture, which was first recognized in trackways where the manus and pes prints are positioned at a distance from the trackway midline (Farlow, 1992). Titanosauriforms and nested subgroups acquired a series of synapomorphies that are associated with a broader limb posture, including the deflection of the proximal shaft of the femur, increased asymmetry of the femoral shaft, and beveling of its distal condyles (Wilson & Carrano, 1999; Wilson, 2002: characters 198, 199, 201). It is possible that the reduced medial portion of the astragalus was retained as cartilage that extended to the edge of the tibia and metatarsus.

Sauropods had strongly entaxonic hind limbs, in which body mass is most heavily loaded on the medial side, owing to body weight being loaded on the medial projection of the femoral head. Entaxony is reflected in the differential distribution of limb bone minimum cross-sectional areas, which are much greater in the medial elements compared to the lateral (Wilson et al., 2018). Wide-gauge sauropods would have experienced increased compressional loads on the medial aspect of their limbs owing to the combination of axial compression and the compression resulting from the bending moment imposed by the increased distance between the feet and the center of mass (see Wilson & Carrano, 1999; Lieberman et al., 2004). Reduction of the ossified component of the carpus and tarsus in wide-gauge titanosaurs would have placed more cartilage in a position to receive the compressive loads from body weight and from bending and transferred it directly to the feet and ground.

CONCLUSIONS

A sauropod astragalus from the latest Cretaceous of Pisdura, India, represents the first tarsal element recovered from Indo-Pakistan or Madagascar. Its morphology most closely resembles slightly older taxa from the 'mid-Cretaceous' of Asia, South America, and Australia. All other latest Cretaceous sauropods for whom astragali are known possess a highly abbreviated, 'pyramidal' astragalus that is positioned between the tibia and fibula proximally and articulates distally with metatarsals 2 and 3. The stepwise reduction in breadth of the astragalus in titanosauriforms is interpreted as a continuation of a general tendency within Sauropoda to reduce ossification of the articular ends of limb bones, which are inferred to have borne a thick cartilaginous cap. Reduction of the astragalus in titanosauriforms, first to three-quarters and then one-half tibial width, coincides with the appearance of synapomorphies announcing the wide-gauge limb posture. It is possible that the reduced portion of the astragalus was retained as cartilage that provided additional cushion on the medial side of the more broadly spaced hindlimbs.

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AUTHOR CONTRIBUTIONS

JAWM, DMM, and BS designed and conducted the field work. JAWM and PM analyzed the data and generated the photogrammetric images. PM wrote the initial description; JAWM wrote the manuscript. All authors contributed to final manuscript edits. JAWM drafted the figures.

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