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AN ASSOCIATED PARTIAL SKELETON OF *JAINOSAURUS* CF. *SEPTENTRIONALIS* (DINOSAURIA: SAUROPODA) FROM THE LATE CRETACEOUS OF CHHOTA SIMLA, CENTRAL INDIA

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Abstract: The Cretaceous dinosaur fauna of Indo-Pakistan has remained poorly understood because of a lack of associated and articulated remains, proliferation of named species, and an incomplete understanding of the dinosaur clades present (e.g. abelisaurid theropods; titanosaur sauropods). Continued work on existing collections, and new discoveries of dinosaur material from India, Pakistan and elsewhere in Gondwana, has begun to resolve the composition and affinities of Indo-Pakistani dinosaurs. Here, we provide archival evidence that documents associations between postcranial remains of a sauropod collected from Chhota Simla, India by C. A. Matley in the 1930s and later described as '*Titanosaurus* sp.' This partial skeleton, which represents only the fifth such documented association from Indo-Pakistan, is referable to *Jainosaurus* cf. *septentrionalis* and provides a fuller understanding of its anatomy and phylogenetic affinities.

Key words: Dinosauria, Sauropoda, Cretaceous, Gondwana, India, palaeobiogeography.

DESPITE the fact that hundreds of dinosaur bones have been collected from the Upper Cretaceous Lameta Formation, Pab Formation and intertrappean deposits of Indo-Pakistan over the past 150 years, very few associations between elements have been documented. This unfortunate circumstance results from a combination of taphonomic, geological and historical factors: some Lameta and Pab formation deposits yield only dissociated elements; many more crop out in a way that only allows surface collection; and other collections were originally obtained without recording detailed quarry or sedimentological data. This situation has contributed to the proliferation of names given to Cretaceous Indo-Pakistani theropod, sauropod and ornithischian dinosaurs, which have received 16, 11 and one species names, respectively (Table 1). More conservative taxonomic reviews recognize only two valid sauropod species, 3–5 theropod species and no ornithischian species (Molnar 1990; Norman 1990; Carrano *et al.* 2002; Wilson and Upchurch 2003; Wilson *et al.* 2003; Novas *et al.* 2004; Carrano and Sampson 2008).

Several of the potentially valid theropod species are based on one or several elements that, while autapomorphic, offer only limited overlap for phylogenetic comparisons with contemporaneous species (i.e. the theropods *Indosaurus matleyi*, *Indosuchus raptorius* and *Laevisuchus indicus*). Thus far, only four dinosaur skeletons collected from the Cretaceous of Indo-Pakistan have been confidently described as associated individuals. Two of these, the holotypes of the sauropod *Isisaurus colberti* and the theropod *Rajasaurus narmadensis*, are partial skeletons whose elements were mapped during collecting, and whose field relationships strongly support the inference that they each pertain to a single individual (Jain and Bandyopadhyay 1997; Wilson *et al.* 2003). The partial skeleton of a hatchling sauropod collected from Dholi Dungri, western India was found in anatomical articulation, and in association with an egg, but is not sufficiently diagnostic to allow species-level identification (Mohabey 1987; Wilson *et al.* 2010). A case has been made for a fourth association, between cranial and postcranial bones of the sauropod *Jainosaurus* (= *Antarctosaurus*) *septentionalis* (Wilson *et al.* 2009). Other partial dinosaur skeletons have been reported as associated, but the evidence supporting these claims is largely anecdotal. These include the holotypes of *Lametasaurus indicus* (Matley 1924), '*Titanosaurus*' sp. (NHMUK R5903, R5931–5933, R5935,

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TABLE 1. Sauropod, theropod and ornithischian species named from Upper Cretaceous horizons of Indo-Pakistan.

	Taxon	Locality	Reference	Valid
SAUROPODA	*Titanosaurus indicus*	Bara Simla (I)	Lydekker (1877)	N
	Titanosaurus blanfordi	Pisdura (I)	Lydekker (1879)	N
	Antarctosaurus septentrionalis	Bara Simla (I)	Huene and Matley (1933)	Y
	Laplatasaurus madagascariensis	Pisdura (I)	Huene and Matley (1933)	N
	Titanosaurus rahioliensis	Rahioli (I)	Mathur and Srivastava (1987)	N
	Titanosaurus colberti	Dongargaon (I)	Jain and Bandyopadhyay (1997)	Y
	Khetranisaurus barkhani	Vitakri (P)	Malkani (2004)	N
	Marisaurus jeffi	Vitakri (P)	Malkani (2004)	N
	Pakisaurus balochistani	Vitakri (P)	Malkani (2004)	N
	Sulaimanisaurus gingerichi	Vitakri (P)	Malkani (2004)	N
	Balochisaurus malkani	Vitakri (P)	Malkani (2004)	N
THEROPODA	*Lametasaurus indicus*	Bara Simla (I)	Matley (1924)	?Y
	Orthogoniosaurus matleyi	Bara Simla (I)	Das-Gupta (1930)	N
	Coeluroides largus	Bara Simla (I)	Huene and Matley (1933)	N
	Compsosuchus solus	Bara Simla (I)	Huene and Matley (1933)	N
	Dryptosauroides grandis	Bara Simla (I)	Huene and Matley (1933)	N
	Indosaurus matleyi	Bara Simla (I)	Huene and Matley (1933)	?Y
	Indosuchus raptorius	Bara Simla (I)	Huene and Matley (1933)	?Y
	Jubbulpuria tenius	Bara Simla (I)	Huene and Matley (1933)	N
	Laevisuchus indicus	Bara Simla (I)	Huene and Matley (1933)	Y
	Ornithomimoides mobilis	Bara Simla (I)	Huene and Matley (1933)	N
	Ornithomimoides barasimlensis	Bara Simla (I)	Huene and Matley (1933)	N
	Brachypodosaurus gravis	Bara Simla (I)	Chakravarti (1934)	N
	Rajasaurus narmadensis	Rahioli (I)	Wilson *et al.* (2003)	Y
	Rahiolisaurus gujaratensis	Rahioli (I)	Novas *et al.* (2010)	?
	Bruhathkayosaurus matleyi	Ariyalur (I)	Yadagiri and Ayyasami (1987)	N
	Vitakridrinda sulaimani	Vitakri (P)	Malkani (2004)	N
ORNITHISCHIA	*Dravidosaurus blanfordi*	Ariyalur (I)	Yadagiri and Ayyasami (1979)	N

The term 'valid' refers to the species: '*Titanosaurus*' *colberti* is now *Isisaurus colberti* (Wilson and Upchurch 2003); '*Antarctosaurus*' septentrionalis is now *Jainosaurus septentrionalis* (Hunt *et al.* 1994). The holotype of *Dravidosaurus blanfordi* is not demonstrably ornithischian; 'I' and 'P' indicate India and Pakistan, respectively.

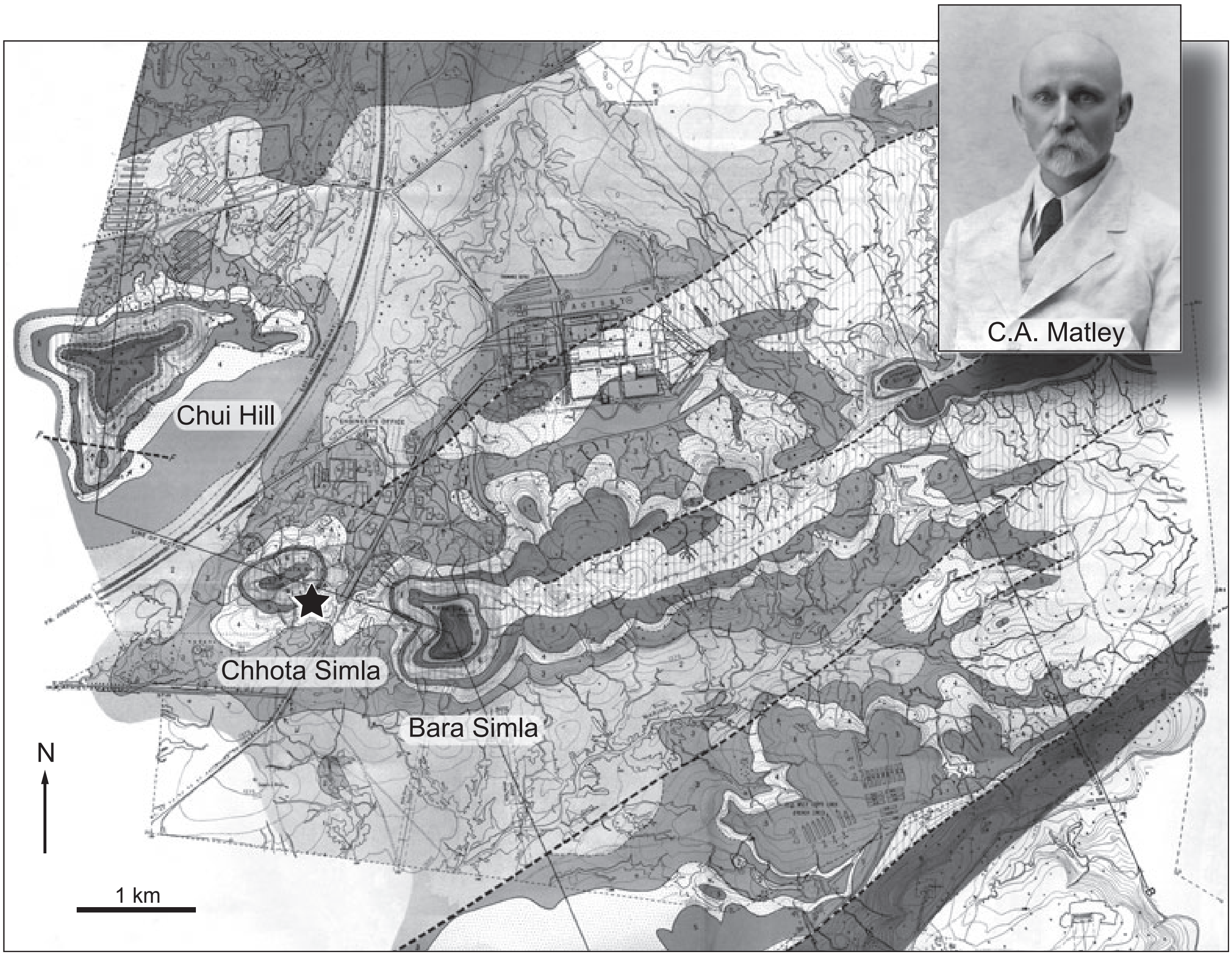
R16481: Swinton 1947) and *Rahiolisaurus gujaratensis* (Chatterjee and Rudra 1996; Novas *et al.* 2010), as well as briefly described sauropod remains (Chatterjee and Rudra 1996). The discovery of new, associated materials, or the introduction of data that might support the association of any of the previously reported remains, would therefore add significantly to the available anatomical and phylogenetic data available for Cretaceous Indian dinosaurs.

Although it can be difficult to identify associations years after the original fieldwork was completed, archival material can sometimes provide convincing evidence for field associations. Here, we report previously unpublished documentation from excavations in the 1930s that sheds light on the original associations of sauropod bones collected from the Lameta Formation of central India in the 1930s. These bones were originally described by Swinton (1947) as '*Titanosaurus* sp.', but we propose that they are instead attributable to *Jainosaurus* cf. *septentrionalis*. This referral provides additional anatomical and phylogenetic information on this once-obscure taxon.

Institutional abbreviations. GSI, Geological Survey of India, Kolkata, India; ISI, Indian Statistical Institute, Kolkata, India; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo La Plata, La Plata, Argentina; NHMUK, Natural History Museum, London, UK.

ARCHIVAL EVIDENCE FOR AN ASSOCIATED PARTIAL TITANOSAUR SKELETON AT CHHOTA SIMLA

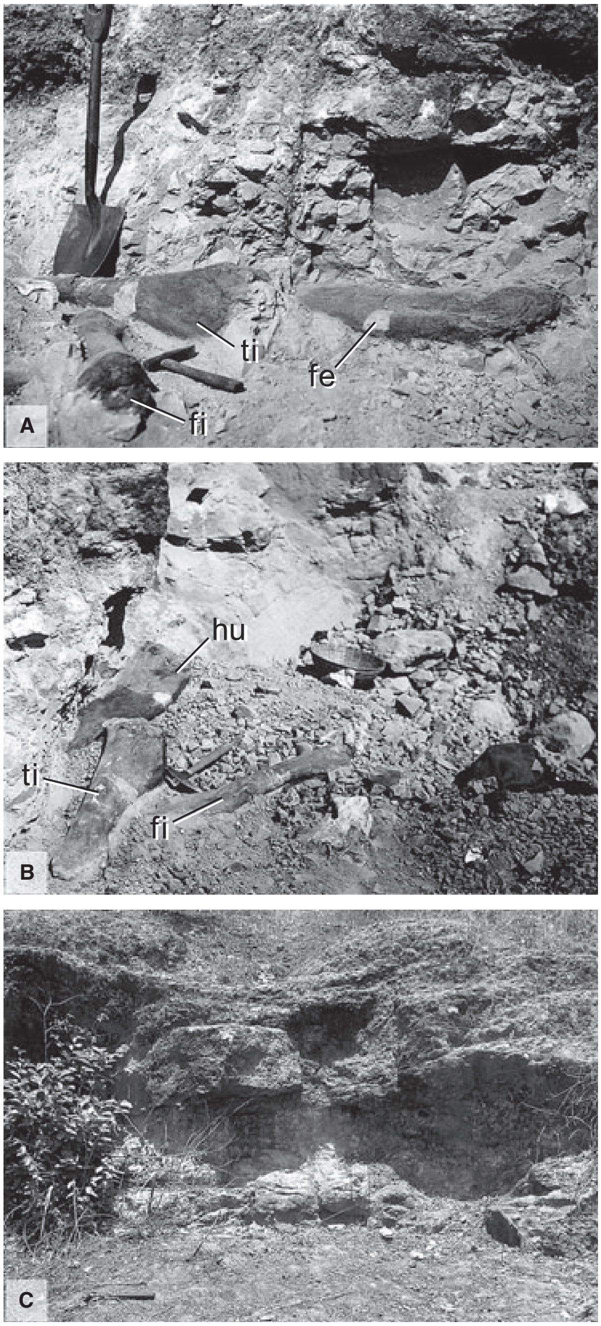
In 1932–1933, Charles Matley collected dinosaur material from central India with the financial support of the Percy Sladen Trust, the Gloyne Fund, the Geological Survey of India and the Natural History Museum (then the British Museum (Natural History)), as well as some of his own personal funds (Text-fig. 1). Extant documentation of his activities consists of two project reports (one for each year's work), shipping manifests, personal letters to the



TEXT-FIG. 1. Geological and topographical map of part of the Jabalpur cantonment, showing positions of Bara Simla, Chhota Simla and Chui Hill. Inset photograph of Charles A. Matley is reproduced by permission of the Geological Society of London. Map is modified from Matley (1921). Star indicates the position of the quarry yielding the referred specimen of *Jainosaurus* cf. *septentrionalis* described herein.

curators at the Natural History Museum who were handling Matley's collections and two photographs of an excavation in progress (NHMUK Archives file number DF100/162/27).

Documentation uncovered in the NHMUK archives provides the first unequivocal evidence that some of the material from Chhota Simla represents the associated remains of a single titanosaur. In a letter to W. D. Lang, the Keeper of Geology at the NHMUK, Matley stated on 9 March 1933 that 'I enclose two photographs of the femur (51″), tibia (32″) and fibula (32″) of a Titanosaur; the femur was at that time only partly excavated. Another femur, possibly the fellow, was found close by; this was crushed and the ends gone, but 46″ was preserved. It lay on a pelvic bone, I think the ilium. We are getting a number of ribs, vertebrae and other parts of probably the same individual…' (Text-fig. 2A–B). A little later, in his Second Report to the Trustees of the Percy Sladen Trust, Matley said of the material that 'most, and possibly all, of the sauropod bones belong to a single individual' and went on to mention that '(t)he sauropod bones are for the most part in excellent preservation and nearly perfect, though some are broken. They belong to a medium-sized Titanosaur, much smaller than the large *Antarctosaurus* bones some of whose bones I discovered previously in the Sauropod Bed of Bara Simla. The new collection contains a nearly complete hind limb, consisting of Femur 51″, Tibia 32″, Fibula 32″, Astragalus, Calcaneum (?), and a few foot-bones; the fellow femur (without ends) 46″; left humerus 36″; right humerus (without lower end) 26″; radius (20″); radius (?) 24″; ilium (?); coracoid; numerous ribs, some complete; several vertebrae, mostly caudal; haemopophyses, &c.' (C. A. Matley, Second Report of the Percy Sladen Trust, January 1933). Finally, in a letter to



TEXT-FIG. 2. Photographs of the titanosaur quarry at Chhota Simla. A and B were photographed by C. A. Matley in 1933 at different points during excavation and at an obtuse angle relative to one another. A, the left femur (fe), tibia (ti), and fibula (fi) in near articulation. B, was taken after the removal of the femur and part of the back wall of the quarry, which exposed the distal end of the right humerus (hu) in posterior view. The distinct colour change on the back wall of the quarry, near the position of the shadow made by the shovel handle in A, marks the contact between the main Lameta limestone (above) and the greensand (below). C, shows the site as it appears today, taken from approximately the same perspective as A but at a slightly larger scale. Geological hammer is 32 cm.

W. E. Swinton (then Curator of Fossil Reptiles and Amphibians at the NHMUK), dated 14 June 1939, Matley expressed his disappointment that Swinton wished to confine his description to the hind limb material, stating that '(o)ne of the most important results of the Percy Sladen Trust Expedition was the discovery for the first time, at the type locality, of not only the bones of the hind limb but (associated with them) the two humeri, one or two radii (?an ulna) and a complete rib besides a lot of broken and less important material' (all papers held in NHMUK Archive file DF100/162/27).

Matley mentioned that the excavation had been mapped on gridded paper, which would have provided strong support for associations, but sadly this piece of evidence has not been preserved in the NHMUK Archive. However, the two photographs mentioned in the letter to Lang (see above) do exist and document field associations between hind limb elements (Text-fig. 2). Given Matley's repeated assertions that most of the sauropod material that he excavated at Chhota Simla pertained to a single individual, we follow his interpretation herein. For further details of this expedition, see Carrano *et al.* (2010).

SYSTEMATIC PALAEONTOLOGY

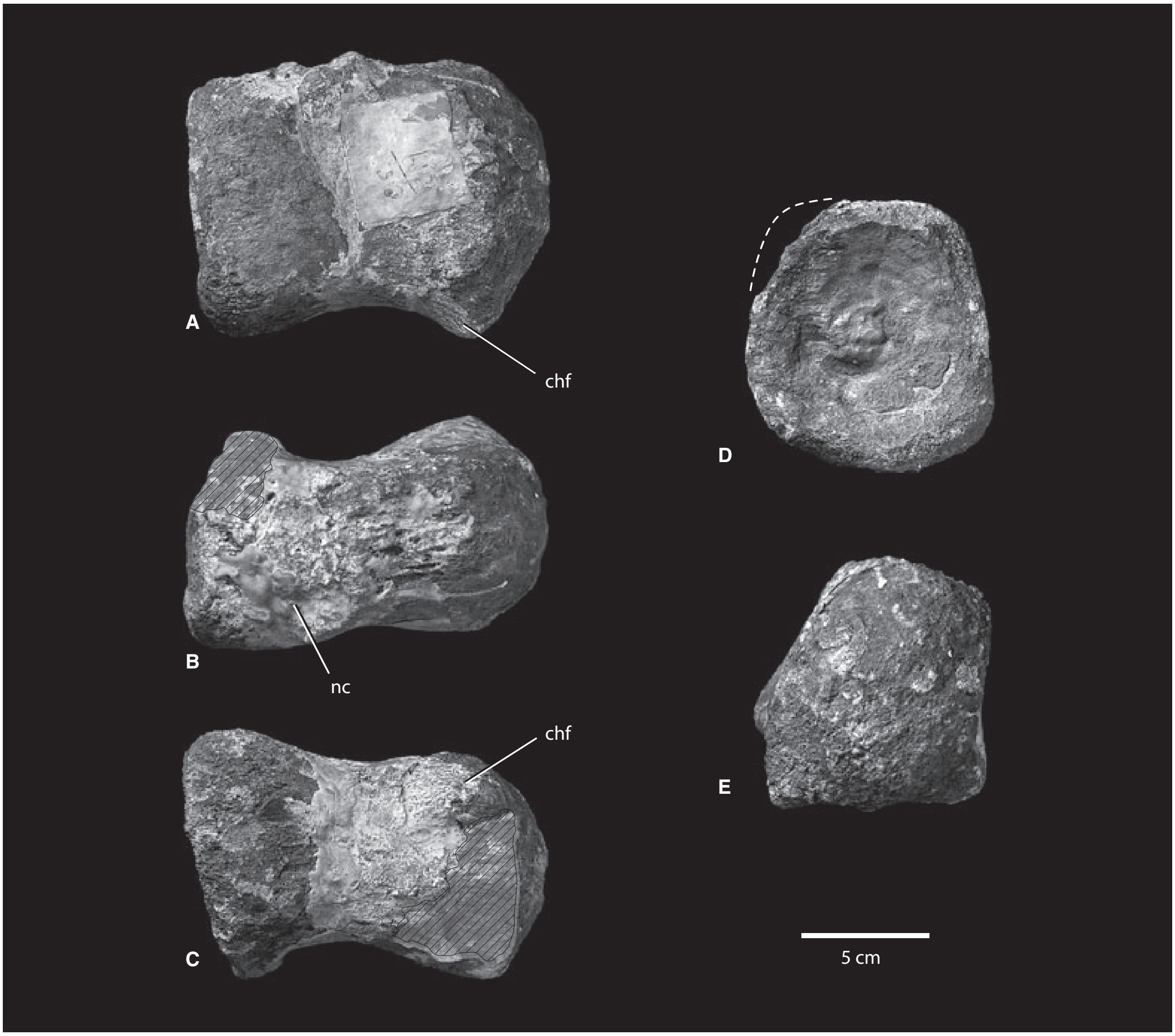
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986
MACRONARIA Wilson and Sereno, 1998
TITANOSAURIA Bonaparte and Coria, 1993

Genus JAINOSAURUS Hunt, Lockley, Lucas and Meyer, 1994

Jainosaurus cf. *septentrionalis* (Huene and Matley, 1933)
Text-figures 3–10

Referred material. A partial skeleton, consisting of a fragment of a dorsal rib (NHMUK R5935), a caudal centrum (NHMUK R16481), a left humerus (NHMUK R5931), the proximal part of a right humerus (NHMUK R5932), a right radius (NHMUK R5933), and an articulated left hind limb including a femur, tibia and fibula (NHMUK R5903).

Locality and horizon. In his second report to the Percy Sladen Trust, Matley provided general locality information for the Chhota Simla titanosaur. He described three drainages (*nullas*), one of which ('*nulla* c') originated at the base of the Chhota Simla blockhouse (Text-fig. 1). For this reason, all of Matley's field numbers begin with 'C' (see below). He stated that the locality was on the south-west slope of Chhota Simla, and that the bone horizon 'lay near the top of the Greensand at a few feet below the Main Lameta Limestone; this is the same horizon as the Carnosaur Bed of Bara Simla hill' (Matley, Percy Sladen Trust Expedition Second Report, p. 3). Recent field reconnaissance (conducted by D. Mohabey, JAW and M. D'Emic) relo-



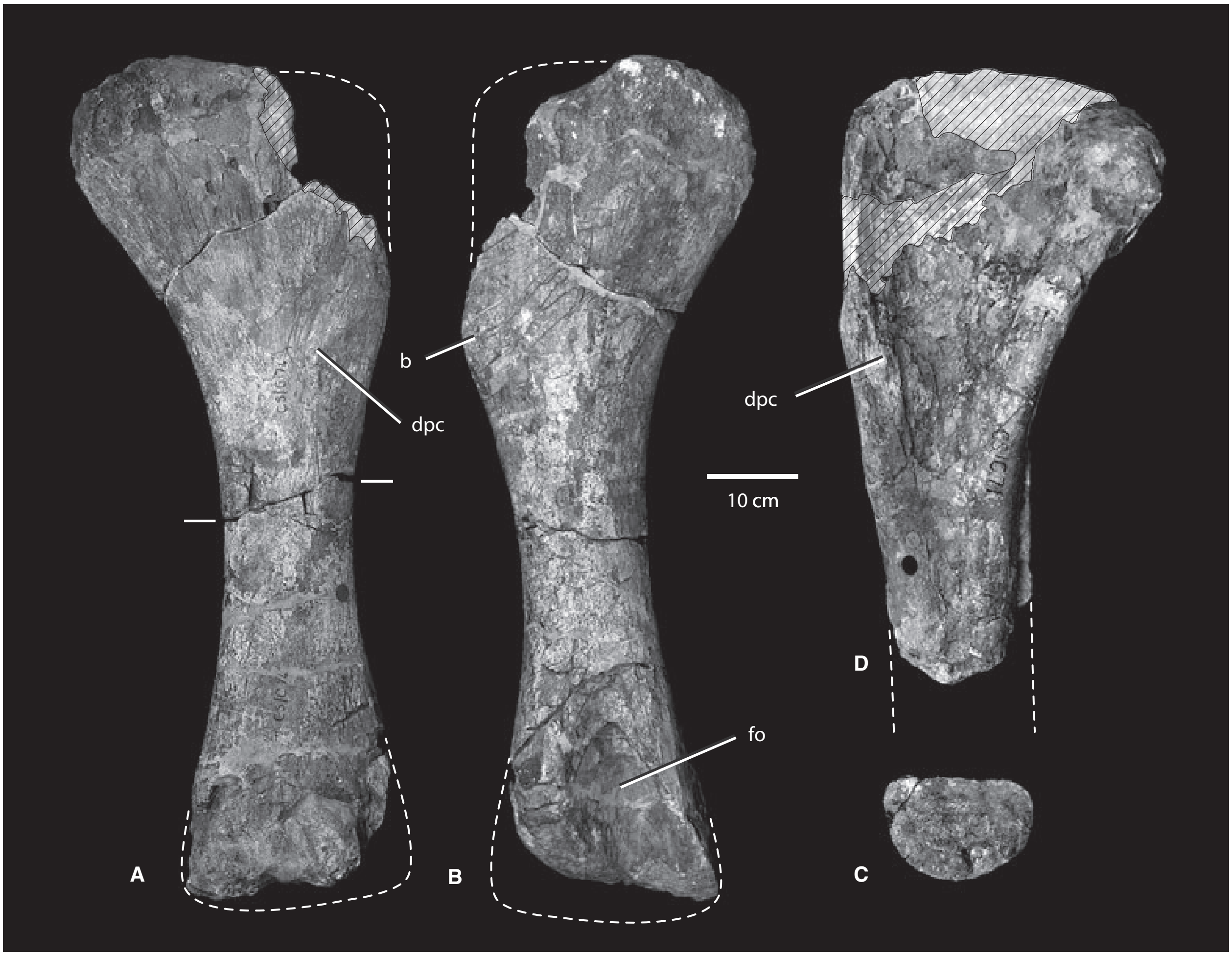
TEXT-FIG. 3. Middle caudal vertebra (NHMUK R16481) in A, left lateral; B, dorsal; C, ventral; D, anterior; and E, posterior views. Scale represents 5 cm. Hatching indicates broken bone. Abbreviations: chf, chevron facet; nc, neurocentral junction.

cated Matley's locality in '*nulla* c' (Text-fig. 2A, C) at the contact between the 'Main Limestone' and 'Greensand' subdivisions of the Lameta Formation, on the south-east (not the south-west) slope of Chhota Simla (23°10′4.1″N, 79°58′3.2″E).

Lameta Formation sediments are referred to as 'infratrappean' because they are overlain by the Deccan Trap flood basalts, the oldest of which have been radiometrically dated at 65.6 ± 0.3 Ma (Courtillot *et al.* 1996; Allègre *et al.* 1999). Lameta sediments are considered to be Maastrichtian in age based on this stratigraphic position, as well as data from coccoliths (Salis and Saxena 1998) and magnetostratigraphy (Hansen *et al.* 2005).

Diagnosis. Jainosaurus septentrionalis is recognized as a derived member of Titanosauria based on the presence of a contact between the quadrate and basal tubera and a pendant, non-articular ventral flange on the paroccipital processes (Wilson 2002, 2005). *Jainosaurus septentrionalis* is characterized by an elongate spur of the prootic that extends onto the basipterygoid process; a medially inset and obliquely oriented humeral deltopectoral crest; a proximolateral bulge on the deltopectoral crest; anteroposteriorly thin bone bounding the deltopectoral fossa on the humerus; and an anteriorly expanded radial condyle on the distal humerus (Wilson *et al.* 2009, p. 20). Other diagnostic features, furnished by the Chhota Simla specimen of *Jainosaurus* cf. *septentrionalis*, include femur with proximally situated fourth trochanter; tibia and fibula with closely approximated mutual articulation (shared with other titanosauriforms, including *Euhelopus*, *Erketu* and *Epachthosaurus*); and fibula with inset anterior crest set off by ridge.

Remarks. Overlap between the bones of the Chhota Simla skeleton and those of other Cretaceous Indian sauropod



TEXT-FIG. 4. Left humerus (NHMUK R5932) in A, anterior; B, posterior; and C, cross-sectional views. Right humerus (NHMUK R5931) in D, anterior view. Anterior is towards the top of the page in C. Hatching indicates broken bone; tick marks indicate level of cross-section. Scale represents 10 cm. Abbreviations: b, bulge; dpc, deltopectoral crest; fo, fossa.

species are limited. Fortunately, the Chhota Simla material includes a humerus, which is a key element that differentiates *Jainosaurus septentrionalis* from the contemporaneous *Isisaurus colberti* (see below). In addition, the Chhota Simla material includes a caudal centrum, which overlaps with *Isisaurus colberti*, and a radius, which overlaps with *Jainosaurus septentrionalis*. As demonstrated below, the Chhota Simla specimen possesses features of the humerus that are diagnostic of *Jainosaurus septentrionalis*. The difference in size (and probably ontogenetic age), along with certain minor morphological differences, however, lead us to qualify our assignment of this specimen to *Jainosaurus* cf. *septentrionalis* pending further resolution of these issues.

Description

The postcranial skeleton. In his letters to Swinton, the reports sent to the Percy Sladen Trust, and the manifest of specimens that accompanied the shipments of the material, Matley stated that many other elements were associated with this referred individual. Swinton (1947) mentioned associated caudal vertebrae, a dorsal rib (NHMUK R5935) and a partial femur (NHMUK R5934) in his description of the limb bone material. A hand-written note in a catalogue entry for the dorsal rib (NHMUK R5935) states that this specimen was listed as missing in 1956. However, a short fragment of a rib is present in the collection that bears a Matley field number (C55) matching the description given of this element in the specimen manifest ('complete dorsal rib') and probably represents a portion of the large rib described by Matley in his reports and mentioned by Swinton (1947). In addition, a single caudal centrum (NHMUK R16481) has been relocated in the collection that also bears a Matley manifest number (C9) indicating it formed part of the Chhota Simla material. Swinton (1947) stated that a partial femur (NHMUK R5934 (C29)) was associated with NHMUK R5903 and

TEXT-FIG. 5. Right radius (NHMUK R5933) in A, anterior; B, lateral; C, posterior; D, medial; E, proximal; and F, distal views. Anterior is towards the top of the page in E and F. Hatching indicates broken bone. Scale represents 10 cm. Abbreviations: ap, anterolateral process; pp, posteromedial process; r, ridge; ula, ulnar articular facet.

NHMUK R5931–5932. However, Matley did not collect this specimen, and its exact provenance relative to the bones Matley collected at *nulla* c is unknown. According to the specimen manifest, this femur had been collected from Chhota Simla by a Mr Slack several years prior to the Matley expedition, after which it had several owners before being presented to Matley to donate to the NHMUK.

Unfortunately, none of the other elements mentioned in Matley's manifest could be located in the collections of the NHMUK and do not appear in any specimen registers, suggesting that they may have been returned to India along with the bulk of Matley's vertebrate collections (i.e. complete ribs, caudal vertebrae, chevrons, coracoid, astragalus, calcaneum and foot bones). These items were dispatched from London to Kolkata (Calcutta) in June 1936 (NHMUK Archives file number DF 110/4 Geological Department, Boxes Dispatched, Book 4).

Below we provide a description of the axial and appendicular bones that Matley excavated from Chhota Simla in 1932. As discussed above, these remains were associated, with the left femur, tibia and fibula preserved close to one another, so we consider them to represent a single individual. This hypothesis is supported by the absence of duplicated elements, significant size disparity, or reports of other taxa from the same site. All but the caudal vertebra were briefly described by Swinton (1947), although he only illustrated the hind limb bones. Principal dimensions are listed in Table 2.

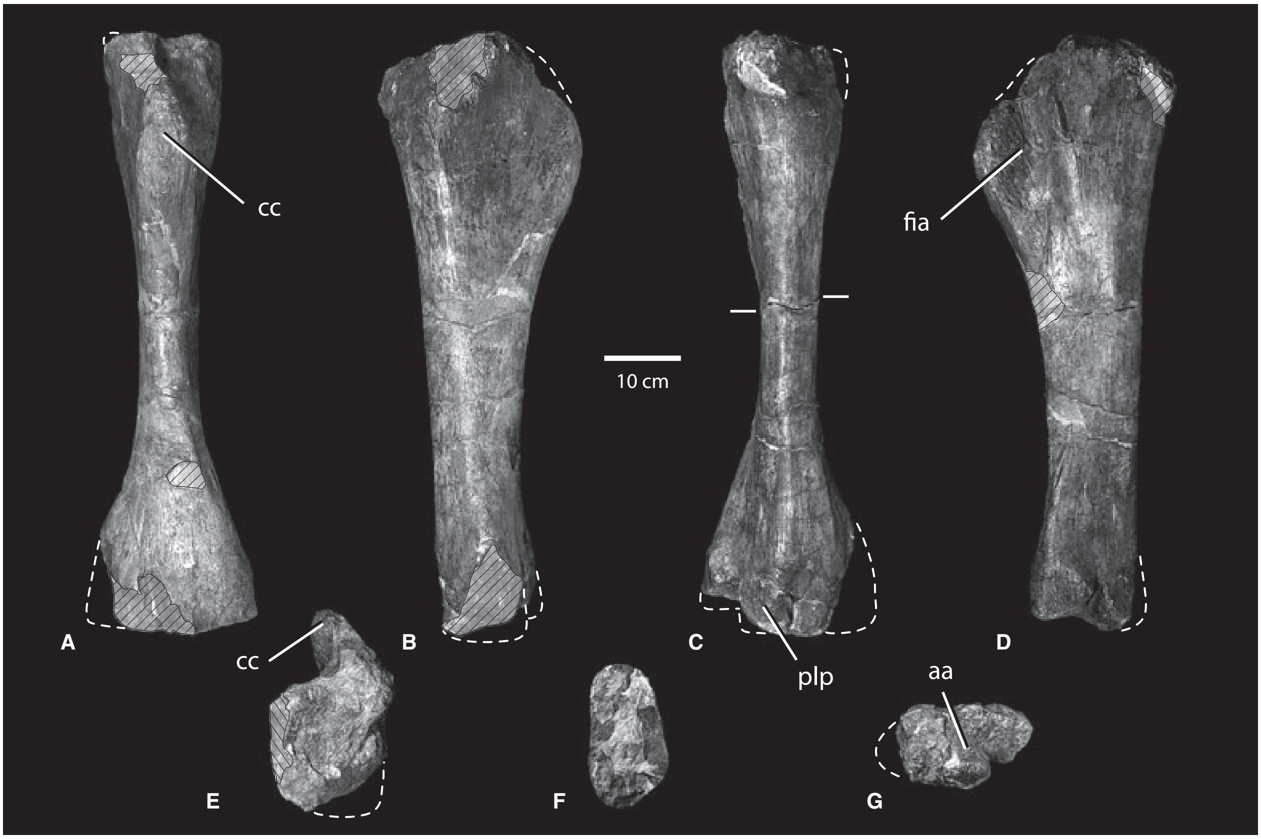
Dorsal rib. A fragment of the shaft probably represents a portion of the complete rib mentioned by Swinton (1947; NHMUK R5935). Both the anterior and posterior surfaces of the rib are mildly convex. Proximally, the shaft exhibits a sub-ovate cross-section, but the central part of the shaft decreases in anteroposterior thickness ventrally, so that the distal cross-section becomes sub-elliptical. The preserved section has a total length of 160 mm, a maximum transverse diameter of 74 mm and a maximum anteroposterior diameter of 38 mm (at the proximal end of the shaft). The rib shaft is solid, as can be expected from a section near mid-length. It is unknown whether the rib

TEXT-FIG. 6. Left femur (NHMUK 5903) in A, anterior; B, medial; C, posterior; D, lateral; E, proximal; and F, distal views. Anterior is towards the top of the page in E and F. Hatching indicates broken bone. Scale represents 10 cm. Abbreviations: ft, fourth trochanter; gt, greater trochanter; h, head; lb, lateral bulge; r, ridge.

was pneumatized more proximally, as occurs in other titanosauriforms (Wilson 2002).

Caudal centrum. Swinton (1947, p. 113) remarked that the limb bones were 'associated with a large number of typical titanosaurian vertebrae'. Of these, only a single caudal centrum (NHMUK R16481) is preserved in the collections of the NHMUK (Text-fig. 3). It bears no transverse processes but exhibits chevron facets, and thus probably pertains to the middle third of the tail. The neural arch was not fused to the centrum, as indicated by the roughened neurocentral junction exposed on the dorsal surface of the centrum. The sacral and middle caudal regions are the earliest to fuse in other sauropods, such as *Camarasaurus* (Ikejiri *et al*. 2005), which suggests that this subadult individual was in the early stages of vertebral fusion. The inferred age of this individual may explain the size difference (recognized by Matley, see above) relative to the holotype of *Jainosaurus* (= *Antarctosaurus*).

The centrum is slightly taller than it is wide, and its length is *c*. 150 per cent its width. The anterior surface of the centrum is concave, and its posterior surface is strongly convex. Although the posterior condyle is not well preserved, it appears to have a rounded, rather than conical, convexity. The lateral surfaces of the centrum are almost planar, but they are gently constricted at midlength. The ventral surface of the centrum is not well



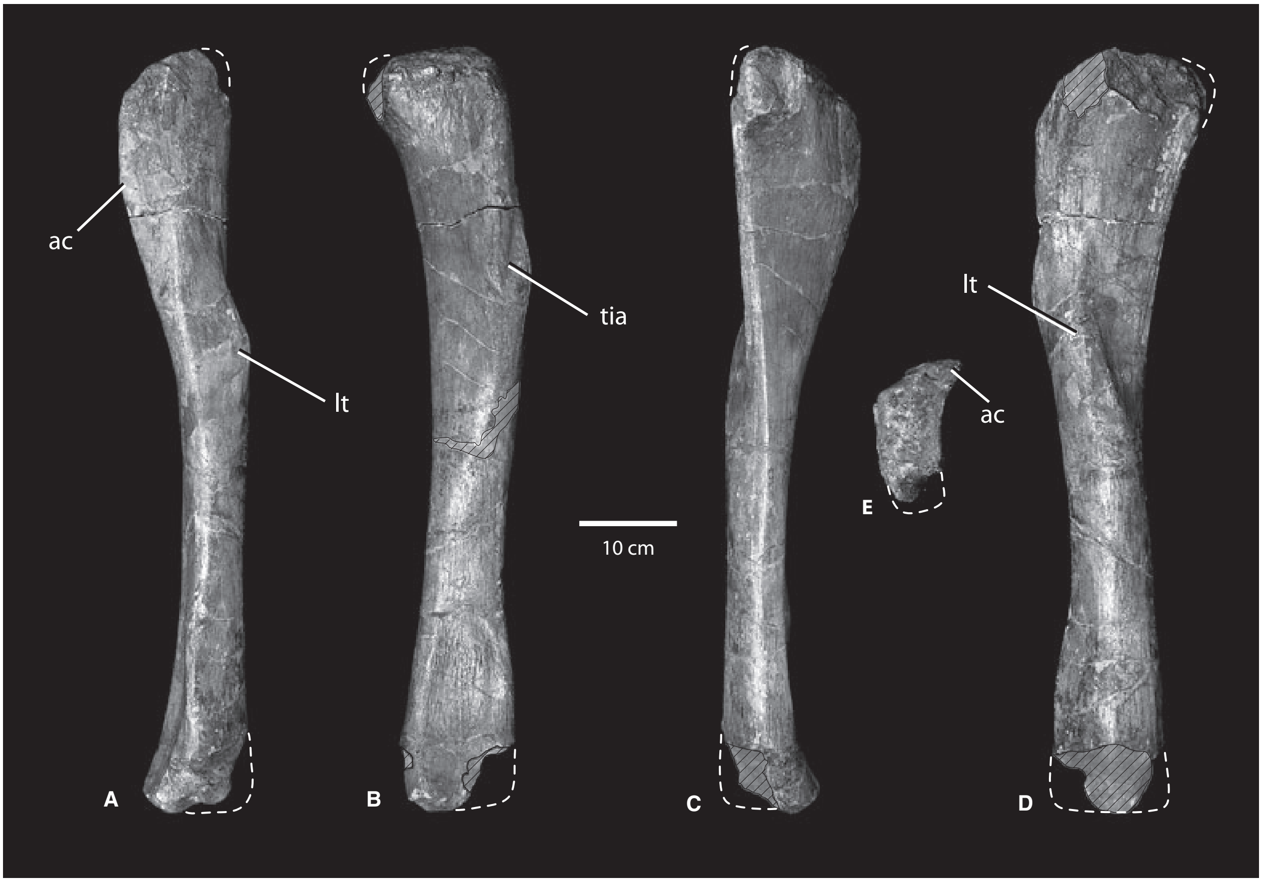
TEXT-FIG. 7. Left tibia (NHMUK 5903) in A, anterior; B, medial; C, posterior; D, lateral; E, proximal; F, cross-sectional; and G, distal views. Anterior is towards the top of the page in E–G. Hatching indicates broken bone; tick marks indicate level of cross-section. Scale represents 10 cm. Abbreviations: aa, astragalar articular facet; cc, cnemial crest; fia, fibular articular facet; plp, posterolateral process.

preserved, but conical prominences near the posterolateral corners of the centrum suggest the presence of posterior chevron facets. Anterior chevron facets were probably present, as implied by the presence of trapezoidal broken areas at the anterolateral corners of the centrum, but their shape is unknown. No ventral hollow is present.

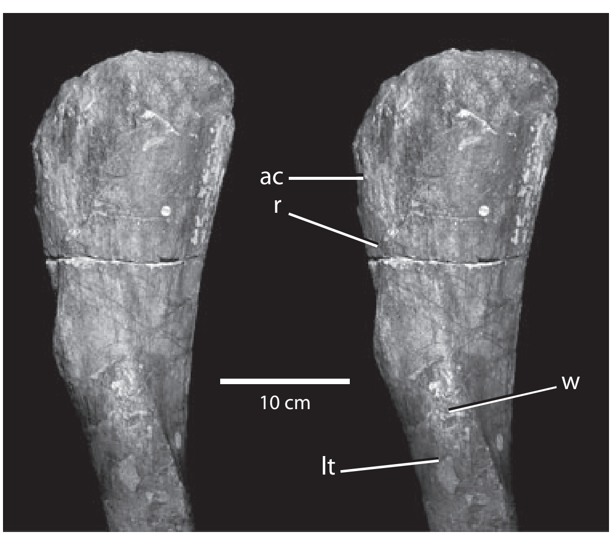
The Chhota Simla caudal centrum has similar proportions to middle caudal vertebrae of *Isisaurus colberti* (centrum length/width *c.* 0.67), and both have procoelous articulations and anteriorly situated neural arches. Apart from these general similarities, however, the Chhota Simla caudal centrum differs strongly from those of *Isisaurus colberti*, which have a conical posterior convexity, a posteroventrally bevelled anterior articular concavity, and a marked ventral hollow (see Jain and Bandyopadhyay 1997, fig. 12).

Humerus. Right and left humeri are preserved (Text-fig. 4, NHMUK R5932 (C72) and R5931 (C74), respectively). The two humeri resemble one another in size and shape and can be considered opposites from the same individual, as suggested by Matley (see discussion above) and Swinton (1947, p. 113). The left is the more complete, lacking only its proximolateral corner and distal end. The right is more complete proximally but lacks its distal half.

The humerus is expanded both proximally and distally, and its midshaft is *c.* 40 and 60 per cent the breadth of these ends, respectively. Viewed anteriorly, both the medial and the lateral sides of the humerus are expanded, the lateral side much less so than the medial side. This contrasts with the condition in *Brachiosaurus*, in which the lateral aspect of the humerus is almost straight in anterior view (Janensch 1961, supp. fig. 186). The lateral expansion is formed by a prominent bulge near the level of the deltopectoral crest, which itself is thickened and obliquely oriented (Text-fig. 4A–B, D). This bulge may indicate the site for attachment of forelimb adductor musculature. In proximal view, the humerus has a crescentic outline, with the humeral head situated at the centre of this crescent. The humeral head is anteroposteriorly expanded with respect to the lateral and medial portions of the proximal end, but its surface is poorly preserved. It appears to slightly overhang the shaft of the humerus posteriorly, with the base of the head merging into the posterior



TEXT-FIG. 8. Left fibula (NHMUK R5903) in A, anterior; B, medial; C, posterior; D, lateral; and E, proximal views. Anterior is towards the top of the page in E. Hatching indicates broken bone. Scale represents 10 cm. Abbreviations: ac, anterior crest; lt, lateral trochanter; r, ridge; tia, tibial articular facet.



TEXT-FIG. 9. Stereopairs of the left fibula (NHMUK R5903) in lateral view. Abbreviations as in Text-figure 8; w, welt.

surface of the proximal humerus. Anteriorly, the proximal humerus bears a marked deltopectoral fossa in the form of an inverted triangle. A low dorsoventrally extending eminence is positioned in the centre of the fossa. The midshaft is a posteriorly flattened oval in cross-section, with a mediolaterally directed long axis, as in most other sauropods (Text-fig. 4C). A small olecranon fossa appears to have been present distally, but the remainder of the distal end is too poorly preserved to make further comment. The proximal articular surface of the humerus is strongly rugose, a feature that also characterizes the other limb bones.

Radius. Swinton (1947, p. 114) referred to this bone as a 'right radius' and identified the complete end as the distal end. We also interpret this bone as a right radius but identify the complete end as proximal based on the shape of the articular surface and presence of an anterolateral process.

The radius is nearly complete, lacking only its distal end (Text-fig. 5; NHMUK R5933 (C140)). We estimate that *c.* 5 per cent of its shaft is missing. The shaft is bowed slightly anteriorly and twisted such that the long axes of the proximal and distal ends are offset by *c.* 45 degrees. The proximal end is elliptical, with its

TEXT-FIG. 10. Articulated left tibia and fibula (NHMUK R5903) in A, anterior; B, posterior; C, proximal; and D, distal views. Anterior is towards the top of the page in C and D. Scale represents 10 cm. Abbreviations as in Text-figures 7–8.

long axis oriented approximately anterolaterally to posteromedially. The proximal radius bears a prominent anterolateral process and a smaller posteromedial process. In proximal view, a slight expansion probably marks the contact with the ulna. This expansion continues down the shaft as a prominent ridge until approximately midshaft. A second, much weaker, parallel ridge arises near midshaft and extends distally. Both ridges probably represent surfaces for the attachment of interosseous ligaments joining the radius and ulna. The distal radius expands markedly, but less so than the proximal end. A prominent flange is present posteriorly that marks a coarsely striated surface for the articulation of the ulna.

The only other nearly complete radius reported from the Cretaceous of India is part of the type series of *Jainosaurus septentrionalis* and was found in association with other forelimb bones in the 'Sauropod Bed' at Bara Simla (GSI K27/490). Although these bones were originally considered to belong to one animal (Matley 1921), Huene believed that the proportions precluded this (Huene and Matley 1933, pp. 4, 32–33). However, the proportions of the forelimb bones do fall within the range observed in other titanosaurs, and they are likely to represent part of a single individual (Wilson and Upchurch 2003; Wilson *et al.* 2009). The Bara Simla radius is no longer present in the collections of the GSI, but it was briefly described and illustrated in one view, which we interpret to be posterior with proximal facing to the left (Huene and Matley 1933, fig. 17). As Matley noted in his Second Report to the Percy Sladen Trust, the Bara Simla radius is longer than the Chhota Simla humerus, which pertains to a subadult (78 cm vs. estimated 52 cm). It is also slightly longer relative to the humerus (58 per cent vs. estimated 54 per cent), but the proportions of the two bones are very similar (proximal width/length 0.33 vs. estimated 0.30). In addition, the two bones are very similar morphologically – both bear an expanded proximal end with a well-developed anteromedial process, a proximal expansion posteromedially that extends as a ridge about to midshaft, and a distal crest for articulation of the ulna. Unfortunately, the radius is not known for *Isisaurus*, so we cannot exclude the possibility that it too shared one or more of the above-mentioned features.

A second limb bone fragment, collected from Pisdura, was identified by Huene and Matley (1933, p. 36 and pl. 6, fig. 2) as a radius of '*Titanosaurus indicus*'. This bone can no longer be found in the collections of the GSI. The

TABLE 2. Measurements (in centimetres) of the partial skeleton of *Jainosaurus* cf. *septentrionalis* collected by Matley at Chhota Simla.

Element	Dimension	Measurement
Caudal centrum	Length	14.9
(NHMUK R16481)	Height, anterior face	11.5
	Width, anterior face	10.3
	Height, posterior face	10.5*
	Width, posterior face	9.5*
Left humerus	Length	95.2
(NHMUK R5931)	Width, proximal	22.8†
	Width, distal	25.6†
	Width, midshaft	14.8
Left radius	Length	52.0*
(NHMUK R5933)	Width, proximal	7.0
	Width, midshaft	5.2
Left femur	Length	128.8
(NHMUK R5903)	Width, proximal	35.8
	Width, distal	35.5
	Width, midshaft	20.6
Left tibia	Length	81.0
(NHMUK R5903)	Width, proximal	16.4
	Width, distal	19.6
	Width, midshaft	7.6
Left fibula	Length	83.0
(NHMUK R5903)	Width, proximal	8.1
	Width, distal	9.1
	Width, midshaft	7.1

*An estimated measurement based on an incomplete specimen.
†A minimum measurement because of breakage.

bone has a triangular articular end and may be more appropriately identified as a metacarpal.

Femur. The left femur is complete (Text-fig. 6, NHMUK R5903 (C1)). The proximal one-third of the femoral shaft is sharply deflected medially, as occurs in other titanosauriforms (Salgado *et al.* 1997; Wilson and Carrano 1999). Aside from this deflection, the shaft of the femur is straight in anterior and lateral views. The proximal end of the femur extends medially into a fairly acute femoral head, whose articular surface does not extend ventrally. The femoral head is elevated relative to the greater trochanter, which forms the proximolateral corner of the element. A conspicuous longitudinal ridge extends along the posterior surface of the femur from the posterolateral corner of its proximal surface. As noted by Swinton (1947), the fourth trochanter is located on the proximal half of the femur, *c.* 35 per cent of the distance down the shaft. The fourth trochanter is medially positioned and situated within a shallow depression bounded by a low ridge posteriorly. It has a welted appearance because of its irregularly wrinkled bone texture. At midshaft, the femur has an elliptical cross-section whose transversely oriented long axis is nearly three times the length of its anteroposteriorly oriented short axis. The distal half of the femur is slightly narrower transversely than is the proximal half. The femur is somewhat gracile, it robustness index is 0.238 (average of the transverse widths of the proximal end, midshaft and distal end/length: Wilson and Upchurch, 2003). This value is very similar to that of *Rapetosaurus* (0.234) and less than those of *Brachiosaurus* (0.252), *Chubutisaurus* (0.25) and *Opisthocoelicaudia* (0.275). The distal condyles appear to have been sheared slightly anterolaterally relative to the shaft of the femur. We interpret this as an artefact of preservation. They are not completely preserved posteriorly, but the preserved portion indicates that the medial condyle was larger but narrower than the medial condyle.

Only four other femora have been described from Indo-Pakistan (but others remain undescribed; J. A. Wilson, pers. obs.). A distal portion of a small sauropod femur (NHMUK R 5934), which was collected at or near Chhota Simla before Matley collected there, was described by Swinton (1947). It probably represents an even younger subadult; it is not known whether it pertains to the same species. Lydekker (1877) included an incomplete femur (GSI K22/754) in the original type series of '*Titanosaurus indicus*', but this element was removed by Huene and Matley (1933, pp. 28–29, fig. 23) and referred to *Antarctosaurus* sp. because of its slender proportions, which resemble those of the Patagonian species *A. wichmannianus*. Because the proximal and distal ends are not preserved in GSI K22/754, its proportions are not known with certainty, but its preserved length (116 cm) and minimum breadth (22 cm) were both reported by Lydekker (1877). Based on an estimated total length of 140 cm, the size and proportions of this element are quite close to those of the Chhota Simla femur. Two other femora (GSI K27/619, K27/488) were described by Huene and Matley (1933, figs 22, 25), neither of which remain in collections of the GSI. Both were referred to '*Titanosaurus*' sp. because of their broad proportions, but both femora have suffered anteroposterior compression during preservation. The more complete of these (GSI K27/488) lacks both articular ends but is nonetheless quite large (*c.* 1.54 m) and has broader proportions than does the Chhota Simla femur. However, because these differently sized individuals represent different ontogenetic stages, we refrain from drawing any inferences on their relatedness based on proportional data.

Tibia. The left tibia is complete and well preserved (Text-figs 7, 10; NHMUK R5903 (C2)). Its length is *c.* 63 per cent the length of the femur. In anterior view, with the long axis of the astragalar articular facet oriented transversely, the tibia appears slender at midshaft but expanded at its proximal and distal ends (Text-fig. 7A). At midshaft, the tibia is approximately twice as deep anteroposteriorly as it is transversely, but it twists 90 degrees towards its distal end, where it is much broader transversely than anteroposteriorly (compare Text-fig. 7F–G). Proximally, the prominent cnemial crest projects laterally and overlaps the anterior crest of the fibula when the bones are placed in articulation (Text-fig. 10). The posterolateral surface of the cnemial crest bears a well-demarcated fibular articular facet that is usually poorly preserved in sauropods. Bounded by a low but distinct ridge posterodistally, this concave, triangular surface bears coarsely striated and finer, pockmarked bone indicative of a ligamentous connection to the anterior crest of the fibula (see below). The proximal head of the tibia is expanded anteroposteriorly and transversely and possesses a well-developed fibular condyle that projects laterally and forms the posterior border of the articular surface for the fibula. Although a portion of its posteromedial corner is missing, the femoral articular surface would have been roughly subcircular or subrectangular in proximal view (Text-fig. 7E). The distal end of the tibia is quite robust and bears a well-marked astragalar articular facet. The tibia is nearly rectangular in distal view and bears a sharp notch posterolaterally that represents the articular surface for the astragalar ascending process. In posterior view, this notch is elevated on the tibia and it descends anteriorly. The medial extent of the astragalar articulation is not known, but it is likely that it was transversely abbreviated, as in other titanosaurs (e.g. *Opisthocoelicaudia*: Borsuk-Bialynicka 1977, pl. 14, fig. 2). No other sauropod tibiae have been described from Indo-Pakistan.

Fibula. The left fibula is nearly complete (NHMUK R5903 (C3)), lacking only the posteromedial tip of its proximal end and the anterior corner of its distal end (Text-figs 8–10). It is longer than the tibia, and its shaft bears a slightly sigmoid curvature in lateral view. The proximal third of the fibula extends slightly posteriorly tipped with respect to the rest of the element. The shaft is 'D'-shaped throughout most of its length, with the flat portion facing medially and the convex portion facing laterally. There is considerable variation in the shape of the cross-section along the fibular shaft, especially near its middle third, where two prominent landmarks are located (Text-fig. 9). The first is the anterior crest, which articulates with the anterior half of the proximal tibia. The anterior crest is deflected medially so that it is offset by *c.* 20 degrees relative to the long axis of the distal end; it is directed towards the tibia and nests between the cnemial crest and the body of the tibia (Text-fig. 10). Unlike most other sauropods, the anterior crest is set off from the remainder of the shaft by a raised, roughened ridge of bone that bounds a shallow trough laterally. The trough is finely striated and pockmarked, and it was probably the attachment surface for a ligamentous connection between the fibula and the cnemial crest of the tibia. This feature is also present but more strongly developed in the lectotype of *Laplatasaurus araukanicus* and the holotypes of *Antactosaurus wichmannianus* and *Mendozasaurus neguyelap* (Text-figs 10–11). The second landmark is the lateral trochanter, which is located near midshaft and served as the insertion for the muscles that flex the knee (*m. iliofibularis*, Otero and Vizcaíno 2008). Swinton (1947, p. 120) referred to this as an 'elbow-like process' because of the manner in which it extends from the lateral surface of the fibula. Indeed, the lateral trochanter is conspicuously large and visible in lateral, anterior and posterior views (Text-fig. 8B–D). It is fairly elongate but consists of only a single crest, as in the South American titanosaurs *Neuquensaurus australis*, *Saltasaurus loricatus* and *Laplatasaurus araukanicus* (Powell 2003, pl. 60, fig. 4, pl. 55, fig. 3 and pl. 5, fig. 2; Text-fig. 11A). *Antarctosaurus wichmannianus* has been noted to have a lateral trochanter that consists of two crests (e.g. Huene 1929, pl. 33, fig. 3), but it appears that the second 'crest' is much more subtle than the lateral trochanter and represents the raised boundary of a shallow welt flanking it (Text-fig. 11B). The medial surface of the left fibula bears conspicuous tibial articular surfaces at its proximal and distal ends. Both are marked by a longitudinally striated texture. The proximal tibial articular surface is triangular and expands anteriorly, as it does in other sauropods. This articular surface is much smaller than in other sauropods, which represents a reversal from the primitive condition for sauropods in which this surface occupies one-third the length of the fibula (Wilson and Sereno 1998). It is possible that the additional articulation provided by the anterior crest compensates for this reduced tibial articulation. Distally, the tibial articular surface is extensive. The distal third of the shaft bears a striated bony surface that is bounded anteriorly by a sharp crest. The distalmost portion of the articular surface is set off as a shallow depression that received a lateral projection of the distal tibia.

Only one other fibula has been reported from the Cretaceous of Indo-Pakistan (Huene and Matley 1933, p. 10, fig. 4). It lacks its proximal and distal ends and is no longer available in the collections of the GSI, so only limited comparisons can be made. Like the Chhota Simla fibula, it has a prominent lateral trochanter and is slightly expanded proximally, but no other anatomical details are available.

DISCUSSION

The Chhota Simla specimen shares several features with the holotype humeri of *Jainosaurus septentrionalis*. These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features are currently regarded as autapomorphies for *Jainosaurus septentrionalis* and clearly distinguish it from *Isisaurus colberti*: the presence of an inset, obliquely oriented deltopectoral crest; a small eminence in the deltopectoral fossa; and a small bulge on the posterolateral aspect of the humerus (Wilson *et al.* 2009). Nevertheless, some of these features are present in other titanosaurs and may ultimately prove to be indicative of broader relationships for *Jainosaurus* within Titanosauria rather than autapomorphies: this will only become tractable following additional detailed work on titanosaur interrelationships. Comparisons between the holotypic radius and the Chhota Simla radius are limited because the former element, described by Huene and Matley (1933) from Bara Simla, is now lost. Nevertheless, the general proportions of the Bara Simla and Chhota Simla radii are very similar, and they agree in the shape of the proximal end and the presence of longitudinal ridges on the shaft. The positive aspect of this somewhat limited overlap – which we consider sufficient to defend the referral – is that the Chhota Simla exemplar of *Jainosaurus septentrionalis* adds key morphological information not present in the Bara Simla exemplar (e.g. tail, hindlimb), allowing for a fuller diagnosis of the species.

Sauropod fauna of Indo-Pakistan

As shown in Table 1, 11 sauropod species have been named from the Late Cretaceous of Indo-Pakistan, which implies a taxonomic richness for sauropods that would rival that of the much lengthier Late Jurassic Morrison Formation of North America (16 spp., Upchurch *et al.* 2004). While we do not rule out such a possibility *a priori*, the number and quality of specimens supporting the Indo-Pakistani sauropod species are considerably less than those supporting most Morrison sauropod species. Recently, Wilson and Upchurch (2003) re-evaluated the taxonomic validity of '*Titanosaurus*' species and found that of the four species named from India, only '*T.*' *colberti* is valid, which they renamed *Isisaurus colberti*. Wilson *et al.* (2009) re-evaluated the type series of '*Antarctosaurus*' *septentrionalis* and found that although it does not pertain to the South American genus *Antarctosaurus*, it is nonetheless a valid species, which has been renamed *Jainosaurus septentrionalis* (Hunt *et al.* 1994). The Indian species *Laplatasaurus madagascariensis* (Huene and Matley 1933) has not yet received a formal reassessment, in part because the original materials are now missing, but both recent treatments of sauropod taxonomy have regarded it to be an invalid species (McIntosh 1990; Upchurch *et al.* 2004).

The remaining five Indo-Pakistani titanosaur species have been named very recently from the Pab Formation in Pakistan (Table 1). Thus far, no articulated titanosaur remains have been described from this formation, but numerous isolated elements have been recovered, some of which are well preserved and diagnostic. Among these is a nearly complete, relatively undeformed braincase that is referable to *Isisaurus colberti* (Wilson *et al.* 2005), as well as an *Isisaurus*-like ulna (J. A. Wilson, pers. obs.; see Malkani 2006, fig. 20a) and a *Jainosaurus*-like humerus (Wilson *et al.* 2009). The five new species named from the Pab Formation (Table 1) have been separated by Malkani (2004, 2006, 2008) into two groups (i.e. Pakisauridae and Balochisauridae) that are thought to differ in the shape of the caudal centra and the robustness of their limb elements, among other features. This bipartite division of Pakistani titanosaurs mirrors the division of Indian titanosaurs into two genera, and given the presence of both Indian genera in Pakistan, there exists a possibility that the sauropod faunas of the Pab and Lameta formations overlap considerably. Unfortunately, there has not yet been any systematic comparison of the Indian and Pakistani sauropod specimens (see Malkani 2004, 2006, 2008 and references therein), and there remains a strong possibility that more of the remains collected from the Pab Formation will be referable to *Isisaurus* and *Jainosaurus*. Based on the examination of the plates published by Malkani (2006 and references therein) and examination of part of the collection from the Pab Formation (J. A. Wilson, pers. obs.), there does not appear to be a strong case for the validity of any of the five Pakistani titanosaur species.

In summary, while there remains a possibility that there were other titanosaur species in Indo-Pakistan, currently we only have evidence for two, *Jainosaurus septentrionalis* and *Isisaurus colberti*.

The phylogenetic position of Jainosaurus septentrionalis

The sole analysis to examine the phylogenetic position of *Jainosaurus septentrionalis* was not able to resolve it relative to other members of Somphospondyli (Curry Rogers 2005). Features of the braincase place *Jainosaurus* within Titanosauria, including the presence of a nonarticular ventral flange on the paroccipital processes (Wilson 2002, 2005). Still other braincase features link it closely with 'Malagasy Taxon B' (Curry Rogers and Imker 2007; K.

TEXT-FIG. 11. South American titanosaur fibulae. A, stereopairs of the lectotypic right fibula of *Laplatasaurus araukanicus* (MLP-26-306) in lateral view. Abbreviations as in Text-figure 8. B, stereopairs of the proximal portion of the holotypic left fibula of *Antarctosaurus wichmannianus* (MACN 6804) in lateral view. Abbreviations as in Text-figure 9.

Curry Rogers, pers. comm. 2009) and the South American titanosaurs *Pitekunsaurus* (Filippi and Garrido 2008) and *Muyelensaurus* (Calvo *et al*. 2007*a*). These include a broad, shallow fossa between the basal tubera and basipterygoid processes oriented parallel to the plane of the occiput (see discussion in Wilson *et al*. 2009). Of these, *Jainosaurus* appears to be most closely related to 'Malagasy Taxon B' owing to the shared possession of basal tubera with a small ventrolateral process set off by a notch (K. Curry Rogers, pers. comm. 2009). In addition to these cranial characters, the presence of an inset anterior crest of the fibula is a feature shared by *Jainosaurus*, *Laplatasaurus*, *Antarctosaurus* and *Mendozasaurus* (Text-figs 8, 10–11). Somewhat ironically, the shared presence of this and other features in *Laplatasaurus* and the Chhota Simla specimen, which Swinton (1947) referred to as '*Titanosaurus* sp.', led Powell (2003, p. 22) to subsume the genus *Laplatasaurus* within '*Titanosaurus*'. As discussed above, however, the Chhota Simla titanosaur is referable to *Jainosaurus*, not '*Titanosaurus*' – which is a *nomen dubium* (Wilson and Upchurch 2003). The generic name *Laplatasaurus* (Huene 1929) should be retained, as recommended by various authors (McIntosh 1990; Wilson and Upchurch 2003; Upchurch *et al*. 2004).

Unfortunately, the relative phylogenetic proximity of *Jainosaurus* to these South American titanosaurs cannot be assessed yet. Cranial remains are not known for *Laplatasaurus,* and lower hind limb bones are unknown for *Pitekunsaurus* and not yet described for *Muyelensaurus*. Moreover, our observations must be placed in a broader phylogenetic context to demonstrate that the observed similarities are synapomorphies rather than convergences, and to establish the position of these taxa within Titanosauria.

The phylogenetic position of Isisaurus colberti

Isisaurus has been included in several phylogenetic analyses, including Wilson (2002), Upchurch *et al*. (2004) and Curry Rogers (2005). Although its position as an outgroup to Saltasauridae (i.e. *Saltasaurus* and its close relatives) is consistently recovered, its sister-group relationship to other titanosaurs remains unresolved.

Preliminary evidence indicates that *Isisaurus* may be closely related to the South American 'lognkosaurian' titanosaurs, which according to Calvo *et al*. (2007*b*) comprise *Mendozasaurus*, *Futalognkosaurus* and all taxa more closely related to them than to other sauropods. 'Lonkgosaurian' titanosaurs may also include *Ligabuesaurus*, *Puertasaurus*, *Bonitasaura* and other taxa. González-Riga (2005) noted similarities between *Isisaurus* and *Mendozasaurus*, and we augment this with additional data. Features supporting the close relationship between *Isisaurus* and 'lognkosaurian' titanosaurs are thus far restricted to the cervical vertebrae and include a neural arch that is much shorter below the zygapophyseal plane than above it (i.e. infrazygapophyseal portion of neural arch much shorter than the suprazygapophyseal part), a thickened prezygodiapophyseal lamina, a broad and anteroposteriorly compressed neural spine, and a prominent lateral fossa bounded by the prezygodiapophyseal, postzygodiapophyseal, spinoprezygapophyseal and spinopostzygapophyseal laminae. As mentioned for *Jainosaurus*, the distribution of these features within Titanosauria and their weight compared with other character distributions have not yet been tested but will be integral to future considerations of titanosaur systematics.

CONCLUSIONS

Charles Matley's discovery of a titanosaur at Chhota Simla has received relatively little attention as it was described more than 60 years ago (Swinton 1947), in part because of uncertainty about the association of skeletal elements. We uncovered archival evidence that demonstrates that the Chhota Simla titanosaur represents the fifth example of associated dinosaur remains pertaining to a single individual from the Cretaceous of Indo-Pakistan. Based on the morphology of its forelimb bones, we refer the Chhota Simla titanosaur to *Jainosaurus* cf. *septentrionalis* and use the non-overlapping portion of the skeleton to broaden the diagnosis of the species and its distinction from the other valid Cretaceous Indo-Pakistani sauropod, *Isisaurus colberti*. Although both are titanosaurs, *Jainosaurus* and *Isisaurus* do not appear to be closely related. Like the two titanosaurs found in Madagascar (*Rapetosaurus* and 'Malagasy Taxon B'), *Jainosaurus* and *Isisaurus* represent distinct titanosaur lineages. *Jainosaurus* appears to be most closely related to 'Malagasy Taxon B', and slightly more distantly related to the South American titanosaurs *Muyelensaurus*, *Pitekunsaurus*, *Antarctosaurus* and *Laplatasaurus*. In contrast, the interrelationships of *Isisaurus*, which possesses a more complete postcranial skeleton, are less clear. There are no obvious similarities shared between *Isisaurus* and any Malagasy taxa, but preliminary evidence suggests that it may share similarities with the South American 'longkosaurian' titanosaurs *Futalognkosaurus*, *Mendozasaurus*, *Ligabuesaurus* and *Bonitasaura*.

These preliminary phylogenetic results are promising because they suggest that discerning the interrelationships of Indo-Pakistani sauropod fauna is tractable when relatively complete skeletons from associated individuals can be identified. The implications of these patterns for Gondwanan palaeobiogeography must await a fuller understanding of the interrelationships among titanosaurs and improved sampling of latest Cretaceous terrestrial horizons on other Gondwanan landmasses, such as Africa and Australia.

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