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REASSESSMENT OF THE SAUROPOD DINOSAUR *JAINOSAURUS* (=“*ANTARCTOSAURUS*”) *SEPTENTRIONALIS* FROM THE UPPER CRETACEOUS OF INDIA

BY

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Abstract — Early evaluations of sauropod diversity in the Cretaceous of India recognized three genera, “*Titanosaurus*,” *Antarctosaurus*, and *Laplatasaurus*, each of which was thought to have closely related species on other southern landmasses. Recent systematic work has challenged the validity of the genus “*Titanosaurus*” and the supposed close relationship between its constituent species, particularly those from the Cretaceous of South America and Madagascar. Likewise, *Laplatasaurus* is currently recognized to be restricted to South America, and the Indian species is invalid. Here, we redescribe the anatomy of the Indian sauropod species *Antarctosaurus* (now known as *Jainosaurus*) *septentrionalis* with the goal of examining its validity, constituency, and phylogenetic affinity.

The type series of *Jainosaurus septentrionalis* included a braincase, skull roof, and many postcranial elements that were united on the basis of their large size relative to the other taxon from the same quarry, “*Titanosaurus indicus*”. All postcranial bones were missing until recently, when the type series humerus and a cast of the scapula were rediscovered in the collections of the Indian Museum. We evaluate possible associations between type series elements, bringing to light circumstantial evidence that helps strengthen the case for grouping some of them as a single species. Both the cranial and some postcranial bones are diagnostic, allowing referral of additional materials collected from the same locality and elsewhere in Indo-Pakistan to the species *J. septentrionalis*.

Currently two genera, *Isisaurus* and *Jainosaurus*, are recognized from the Cretaceous of India. Unlike most titanosaurs, both *Isisaurus* and *Jainosaurus* are known from diagnostic cranial and postcranial material recorded from multiple localities. These genera coexist in central and western India, and *Isisaurus* has been reported recently from western Pakistan. The affinities of *Jainosaurus* and *Isisaurus* within Titanosauria are not yet resolved, but a sister-taxon relationship to one another can be ruled out. *Jainosaurus* appears to have close relatives in Madagascar and South America based on the data at hand. Thus far, there is no evidence for an endemic Indian sauropod fauna during the Late Cretaceous.

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INTRODUCTION

Richard Lydekker and Friedrich von Huene made lasting contributions to the study of Indian and South American dinosaurs as a result of their successive surveys of two important collections in the late nineteenth and early twentieth centuries. Their taxonomic decisions, one of which is discussed in detail here, helped to shape the understanding of Indian and South American dinosaur faunas and their relationship to one another. In addition to describing some of the first dinosaurs from these landmasses, Lydekker and Huene independently asserted that India, South America, and Madagascar shared common titanosaur sauropod genera that evidenced a “remarkable community of type which undoubtedly exists between the faunas of southern continents of the world” (Lydekker, 1893: 3). The idea that titanosaurs were Gondwanan in origin and distribution persisted until quite recently (e.g., Bonaparte, 1999), but has given way to the current understanding of titanosaurs as a speciose (50+ genera), globally distributed clade that originated prior to the breakup of Pangea (e.g., Upchurch et al., 2004; Curry Rogers, 2005). Nevertheless, the interrelationships amongst titanosaurs from southern landmasses remains a key issue for Gondwanan paleobiogeography. Resolving the validity, constituency, and affinities of Gondwanan titanosaur genera is the first step in this process.

Lydekker, who specialized in fossil and recent mammals, served on the Geological Survey of India in Calcutta (now Kolkata) from 1874–1882 (Thomas, 1917). During his residence in India, Lydekker produced several volumes in *Palaeontologia Indica* describing “Indian Tertiary and Pre-Tertiary Vertebrata”, continuing a tradition started by Huxley in the 1840s. Among the many fossils he described were the tail vertebrae of India’s first dinosaurs, the sauropods “*Titanosaurus indicus*” and “*T. blanfordi*” from Cretaceous beds of Bara Simla (Lydekker, 1877, 1879; Fig. 1). After returning to England and cataloguing the fossil tetrapods of the British Museum (Natural History), Lydekker was invited to describe the fossil mammal collections in the provincial museum in La Plata, Argentina, visiting twice between 1893 and 1894 (Anonymous, 1896). There, Lydekker described new sauropod dinosaurs as well, including two species of “*Titanosaurus*” (“*T. australis*,” “*T. nanus*”) and the genera and species *Argyrosaurus superbus* and *Microcoelus patagonicus* (Lydekker, 1893).

Huene was a generation younger than Lydekker and specialized in fossil reptiles. Like Lydekker, Huene was invited to describe fossil collections of the Geological Survey of India and of the Museo de La Plata in Argentina. Huene visited Argentina between 1923 and 1926 to study collections in La Plata and Buenos Aires. In La Plata, he revised the collection of bones that Lydekker (1893) studied and divided specimens allocated to “*T. australis*” into the new species “*T. robustus*” and the new genus and species *Laplatasaurus araukanicus* (Huene, 1929: 48, 53). At the Museo Argentino de Ciencias Naturales in Buenos Aires, Huene studied a partial skull and postcranial bones from Patagonia that he named *Antarctosaurus wichmannianus* after their southern provenance and discoverer (Huene, 1929: 66). Although Huene apparently never visited India, he was able to study Charles Matley’s collection of Indian dinosaur bones

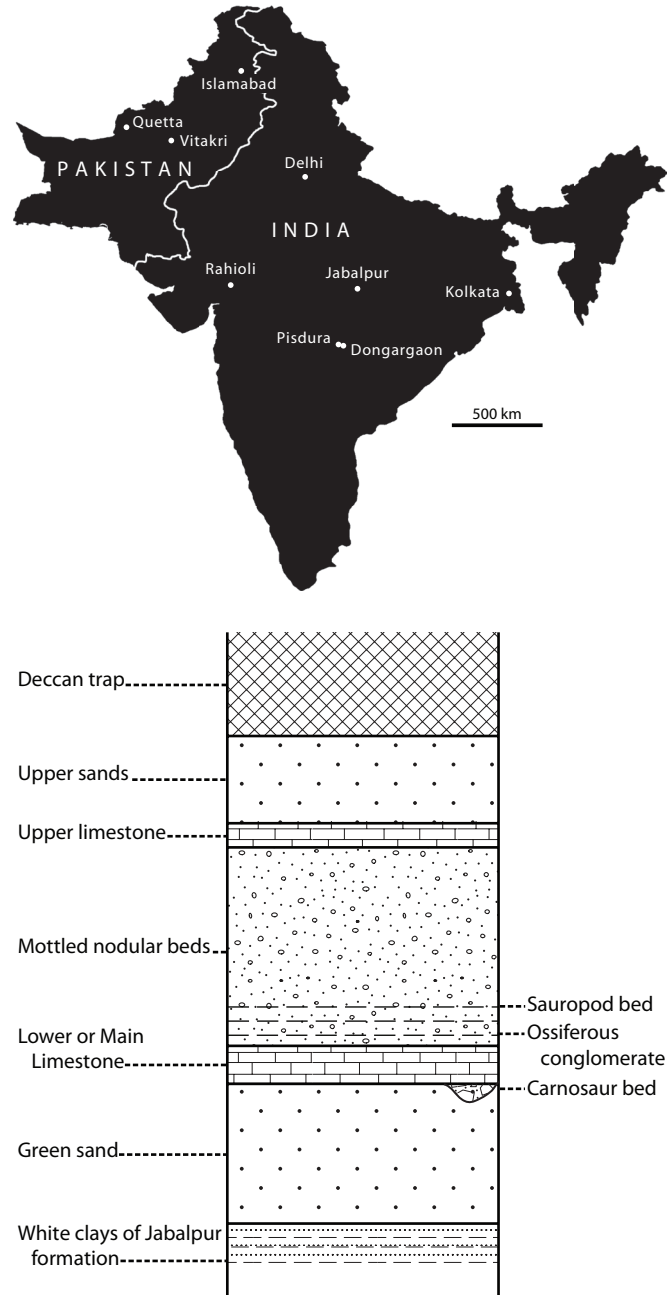


FIGURE 1 — Map of Indo-Pakistan showing the type locality for *Jainosaurus septentrionalis* at Jabalpur, as well as other titanosaur localities. Note that both Bara Simla and Chhota Simla are located at Jabalpur. Schematic stratigraphic section at Bara Simla based on Huene and Matley (1933: fig. 1). Political boundaries are approximate.

whilst they were at the British Museum (Natural History) in the 1930s (Carrano et al., in press). In their monograph describing that collection, Huene and Matley (1933) described new species belonging to genera that Huene described from South America,

including *Laplatasaurus madagascariensis* and *Antarctosaurus septentrionalis*.

Whereas many of the overlapping taxa that Lydekker and Huene named from Argentina and India are fairly fragmentary (e.g., only caudal vertebrae), *Antarctosaurus wichmannianus* and *A. septentrionalis* include partial skulls and postcranial elements that contain numerous characters that can be compared. Huene studied the South American collections before the Indian collections, and consequently *A. wichmannianus* (Huene, 1929) was named prior to *A. septentrionalis* (Huene and Matley, 1933). The latter species epithet, *septentrionalis*, (*septem*, seven; *trio*, plough-ox) is a Latin term referring to the seven stars of Ursa Major (i.e., the big dipper or the plough), which in Roman times was a convenient way to refer to “northern” (e.g., used in Caesar’s “Gallic Wars”; see Hower, 1951). Huene worked within a fixist paleogeographic paradigm and may have chosen the somewhat counterintuitive moniker “Antarctic reptile from the north” to highlight the biogeographic implications of its discovery, which suggested “...a direct land connection from Lemuria [which included India and Madagascar] to South America...via Antarctica, the Australian region, and the Sunda archipelago.” (Huene and Matley, 1933: 72).

Huene defended this distant connection between “northern” and southern *Antarctosaurus* species by the absence of meaningful differences, rather than unique similarities. Consequently, his justification for allocating the South American and Indian specimens to the same genus lacks detail: “This fragment of a titanosaurid skull is very closely comparable with and similar to the posterior part of the skull of *Antarctosaurus wichmannianus* from Patagonia. The Indian specimen is larger than the Patagonian, but is more fragmentary. Apart from the size, the only important difference between these two skulls lies in the fact that the hypophysial fossa in the Indian skull is naturally open below (a so-called ‘pituitary canal’), so that the carotids enter from below, whereas in the Patagonian species the hypophysial fossa is closed below, though very deep, and the carotids enter into the fossa from both sides...In the Indian skull also, the supraoccipital is less hidden by the parietals, and the basiptyergoid processes and the presphenoid are relatively bigger and stronger than in the Patagonian species. But the structure of the skull in general (so far preserved) is very similar in both types; for instance, the angle formed by the axis of the presphenoid and the axis of the condyle is about 115° in both species. In spite of its larger size the Indian skull is less gibbous than the Patagonian.” (Huene and Matley, 1933: 15–16).

More recent comparisons between sauropod braincases and between other elements have revealed that the Indian species, *A. septentrionalis*, is not closely related to the type species, *A. wichmannianus* (McIntosh, 1990). Consequently, Hunt et al. (1994) created the new genus *Jainosaurus* for the Indian taxon, establishing the braincase as the lectotype and suggesting that some of the postcranial bones might belong to the same taxon. Below, the braincase and postcranial remains of *Jainosaurus septentrionalis* are redescribed as a means for evaluating its validity as a diagnostic taxon, similarity to other braincases reported from India, and phylogenetic relationships to other titanosaur taxa.

INSTITUTIONAL ABBREVIATIONS

GSI	— Geological Survey of India, Kolkata (Calcutta), India
GSP	— Geological Survey of Pakistan, Quetta, Pakistan
ISI	— Indian Statistical Institute, Kolkata (Calcutta), India
MML	— Museo Municipal de Lamarque, Río Negro, Argentina
MUCPv	— Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1986

TITANOSAURIA Bonaparte and Coria, 1993

Jainosaurus Hunt et al., 1994

Jainosaurus septentrionalis (Huene and Matley, 1933)

Antarctosaurus septentrionalis Huene and Matley, 1933, p. 11, figs. 5–18; pls. 2–4.

Lectotype.— GSI K27/497, a partial braincase and skull roof (Hunt et al., 1994). Two additional cranial elements, identified as a hyoid and a squamosal, were considered to “belong to the same skull” by Huene and Matley (1933: 15). The element identified as a “left squamosum”, which until recently was missing from collections, is bulky and lacks definitive features of a squamosal (Huene and Matley, 1933: fig. 7). This element cannot be identified, and we exclude it from the lectotype. A small element identified as a hyoid by Huene and Matley (1933: fig. 8), can no longer be located at the GSI collections, and its identity is likewise uncertain.

Postcranial elements found at the same locality and horizon were also attributed to *Jainosaurus* (= *Antarctosaurus*) *septentrionalis* by Huene and Matley (1933: 11–23; Fig. 2). Together with the cranial elements, they form the “type series” or “syn-types” of the species (ICZN Articles 72.1, 73.2). The postcranial elements include dorsal rib shaft fragments (GSI K20/326, K27/425), a caudal vertebra (GSI K20/317), four chevrons (GSI K27/492–494, 496), right and left scapulae (GSI unnumbered), a “sternal plate” (GSI K20/647), a humerus (GSI unnumbered), a radius (GSI K27/490), and an ulna (GSI K27/491). From their description and the discussion that followed, we surmise that Huene and Matley (1933) recognized the presence of at least three individuals. That is, although they considered the cranial and postcranial remains to belong to a single species, they did not consider them to belong to a single individual. Thus, attribution of all remains apart from the first-listed braincase, which Hunt et al. (1994) designated the lectotype, constitutes

a tacit referral, as discussed below (see “*Referred Material*” and “*Comments*”).

Locality and Horizon.— The type series was discovered in the “Sauropod bed” within the lower part of the “Mottled Nodular Limestone” of the Lameta Formation at Bara Simla, Madhya Pradesh State, India (Fig. 1). Other bones recovered from this horizon at Bara Simla include holotypic and referred remains of “*Titanosaurus indicus*” (Lydekker, 1877; Huene and Matley, 1933). The Lameta Formation is capped by the Deccan Trap flood basalts and by virtue of their position are referred to as “infratrappean” sediments. They are considered to be Maastrichtian in age based on coccoliths (Salis and Saxena, 1998), magnetostratigraphy (Hansen et al., 2005), and on the basis of radiometric dates associated with the Deccan Traps (Courtillot et al., 1996; Allègre et al., 1999).

Revised Diagnosis.— *Jainosaurus septentrionalis* is recognized as a derived member of Titanosauria based on the presence of a contact between quadrate and the basal tubera and a pendant, nonarticular ventral flange on the paroccipital processes (Wilson, 2002, 2005). *Jainosaurus* shares general similarities with the South American titanosaur *Antarctosaurus wichmannianus*, such as a tall nuchal crest on the supraoccipital, a sinuous parietal-supraoccipital contact, and broad basal tubera. It shares more specific similarities with “Malagasy Taxon B” (Curry Rogers, unpublished data) and the South American titanosaurs *Pitekunsaurus* (Fillippi and Garrido, 2008), *Muyelensaurus* (Calvo et al., 2007), and an unnamed braincase from Río Negro, Argentina (MML 194; García et al., 2008). These include the presence of a broad, shallow fossa between the basal tubera and basipterygoid processes oriented parallel to the plane of the occiput. Additionally, *Jainosaurus* shares with “Malagasy Taxon B” basal tubera with a small ventrolateral process set off by a notch (Curry Rogers, unpublished data). *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 (shared with other titanosaurs, see below), anteroposteriorly thin bone bounding the deltopectoral fossa on the humerus; and an anteriorly expanded radial condyle on the distal humerus. *Jainosaurus* can be distinguished *Isisaurus* by the orientation of the occipital condyle relative to the occiput, the shape of the basal tubera, differences in shape of the scapula and proximal humerus, and the robustness of the ulnar shaft.

Referred Material.— Referred remains include a partial braincase (ISI R162), dorsal rib shaft fragments (GSI K20/326, K27/425; now lost), right and left scapulae (GSI unnumbered; now represented by a cast of the former), a right humerus (GSI unnumbered), a radius (GSI K27/490; now lost), and an ulna (GSI K27/491; now lost). Other materials from elsewhere in Indo-Pakistan, including humeri collected from

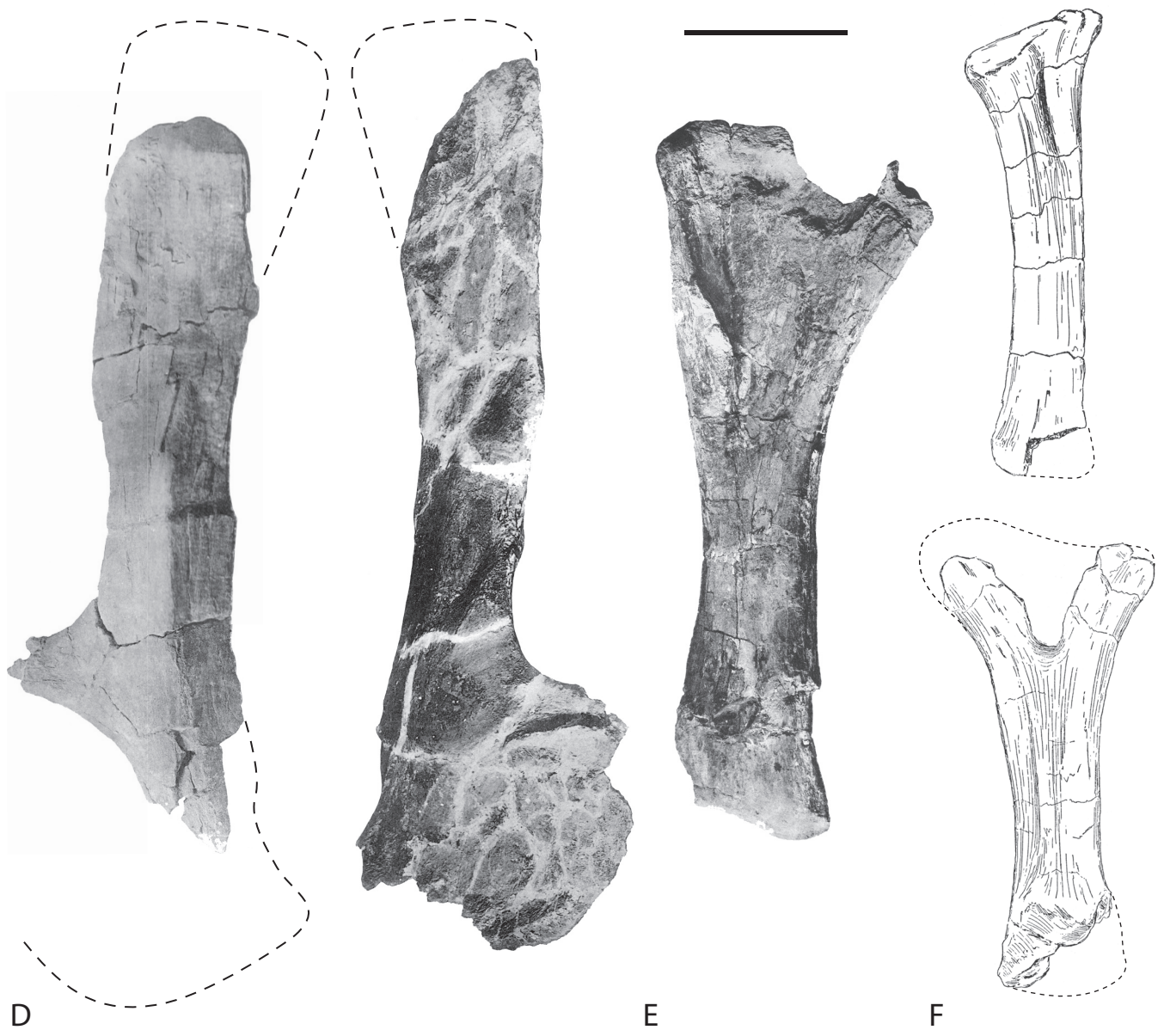
Gujarat, Chhota Simla, and Balochistan share unique features with the humerus (GSI unnumbered) and likely belong to *Jainosaurus septentrionalis*.

We treat the type series postcranial bones listed by Huene and Matley (1933: 34; Fig. 2) as referred elements because those authors clearly did not consider the cranial and postcranial bones to represent a single individual. Of those type series postcranial bones, we regard the ribs, scapulae, humerus, radius, and ulna to represent a single individual that we tentatively refer to *Jainosaurus septentrionalis*. Obviously, there is no overlap between the lectotype and these bones, and our decision relies on circumstantial evidence that is discussed below (see “*Comments*”). Other elements in the type series (i.e., caudal vertebra, chevrons, “sternal plate”) are not included in this referral.

A fragmentary femur (GSI K22/754) and a second humerus (GSI unnumbered) were referred to *Jainosaurus* (= *Antarctosaurus*) sp. by Huene and Matley (1933: 34–35), neither of which can be located in the collections of the GSI. The provenance of the femur is uncertain, and the humerus comes from a horizon below the Sauropod bed. From what can be observed in the figures and plates of Huene and Matley (1933: fig. 24; pl. 5), the humerus is not complete enough to allow evaluation of diagnostic characters of *Jainosaurus septentrionalis*, and the femur does not overlap with type series elements. Neither the femur nor the second humerus can be confidently referred to or excluded from *Jainosaurus septentrionalis*.

A partial braincase from the Lameta Formation of the Bara Simla locality at Jabalpur, Madhya Pradesh State, India (ISI R162, Chatterjee and Rudra, 1996: fig. 11), is also referable to *Jainosaurus* (its provenance was erroneously listed as Rahioli by Wilson et al. [2005: 106–108]). The exact field locality and horizon of ISI R162 were not reported by Chatterjee and Rudra (1996). Thus, its position relative to the type series elements of *Jainosaurus* within the relatively large exposure at Bara Simla Hill (several tens of meters wide) is unknown. ISI R162 was referred to *Jainosaurus septentrionalis* based on similarities “in the construction of the basipterygoid processes and paroccipital processes” (Chatterjee and Rudra, 1996: 514). We support that referral with additional features, including a tall and sinuous suture between the supraoccipital and parietal, a prominent laterosphenoid pillar in the endocranial cavity, and a long spur of the prootic that extends ventrally towards the basipterygoid processes. Minor differences between the lectotype and referred braincases include the shape of the occipital condyle and the otic capsule. Importantly, ISI R162 preserves areas that are absent in the lectotype series braincase (e.g., basipterygoid processes, paroccipital processes) but is less complete in others (e.g., missing laterosphenoid, orbitosphenoid, skull roof). The smaller size and lack of parietal-supraoccipital and prootic-laterosphenoid fusion in ISI R162 suggest that it was younger than the lectotypic individual when it died.

FIGURE 2 (facing page) — *Jainosaurus septentrionalis*, type series elements (GSI K27/497). A, cranial elements (braincase, “squamosal”, “hyoid”); B, dorsal rib fragments; C, caudal elements (caudal vertebra in left lateral, ventral, and anterior views; chevron in two views); D, right and left scapulae in lateral view; E, right humerus in anterior view; F, radius and ulna. The bone fragment identified by Huene and Matley as a sternal plate (1933: pl. 4, fig. 2) was not included. All images are from Huene and Matley (1933). Dashed lines were redrawn from original; dashed line on radius added. Scale equals 30 cm.



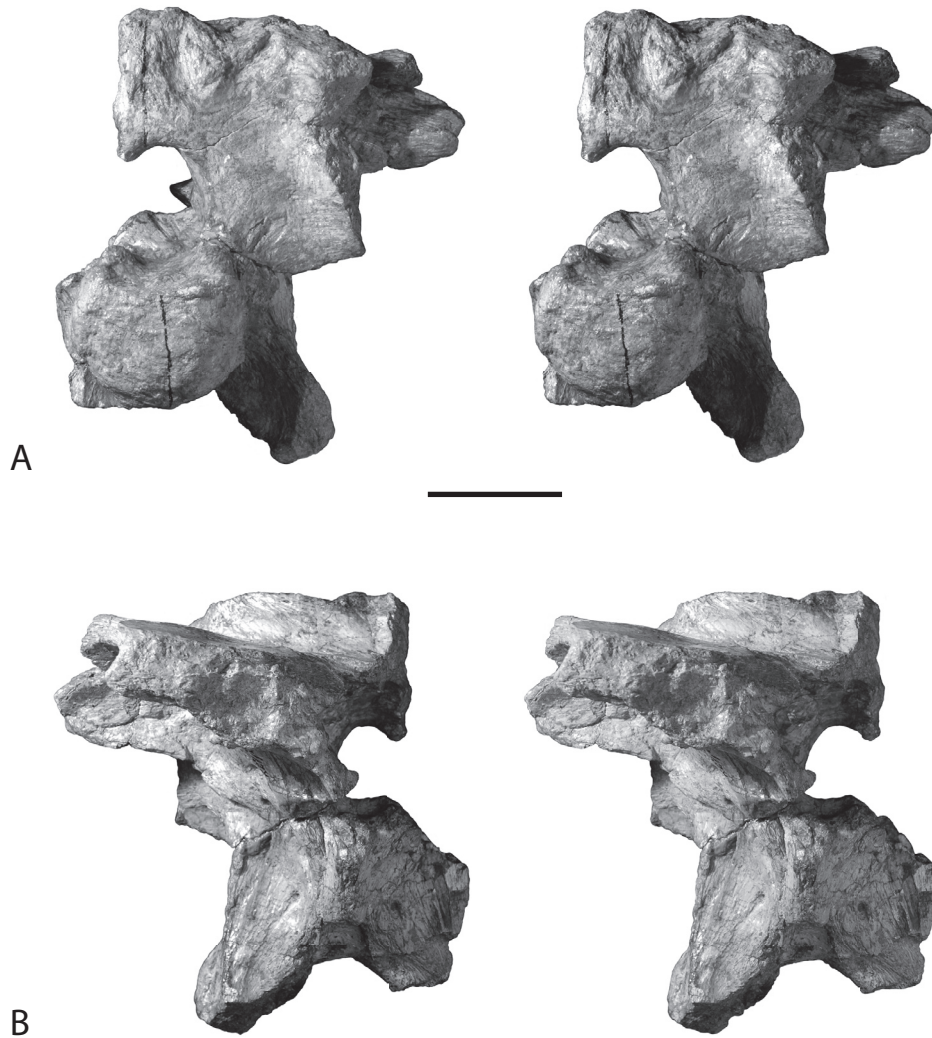
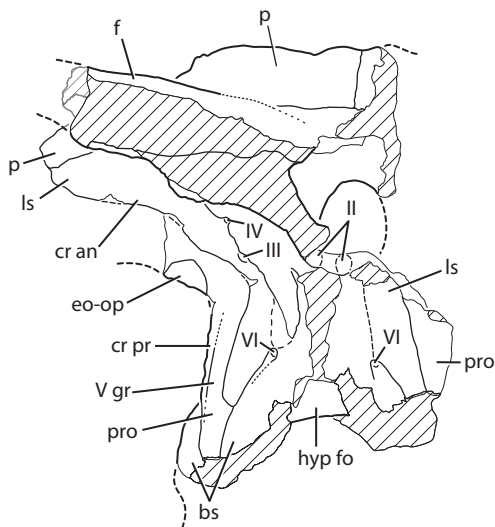
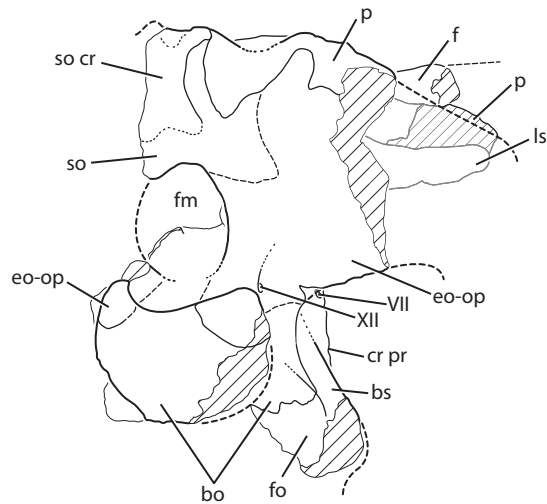


FIGURE 3 — *Jainosaurus septentrionalis*, lectotypic braincase (GSI K27/497). Stereopairs and interpretive line drawings in posterior (A) and anterior (B) views. Scale equals 5 cm. Abbreviations (facing page): *bo*, basioccipital; *bs*, basisphenoid; *bt*, basal tubera; *cr an*, crista antotica; *cr pr*, crista prootica; *eo-op*, exoccipital-opisthotic; *f*, frontal; *fm*, foramen magnum; *fo*, fossa; *gr*, groove; *hyp fo*, hypophyseal fossa; *ica*, internal carotid artery; *ls*, laterosphenoid; *mf*, metotic foramen; *os*, orbitosphenoid; *p*, parietal; *pro*, prootic; *so*, supraoccipital; *so cr*, supraoccipital crest; *stf*, supratemporal fenestra; *II–XII*, cranial nerve openings.

Comments.— Huene and Matley (1933) did not establish a holotype for *Jainosaurus* (=“*Antarctosaurus*”) *septentrionalis*. Instead, they listed elements in a type series that included the braincase and skull roof, “squamosum”, “hyoid”, dorsal ribs, caudal vertebra, chevrons, scapulae, partial “sternal plate”, humeri, radius, and ulna. They did not associate all the elements as a single individual, but they considered them a single species based on their large size relative to bones of “*Titanosaurus indicus*” found at the same locality. They regarded the limb bones as belonging to different individuals based on limb proportions (Huene and Matley, 1933:32–33), which is surprising for several reasons. First, Matley’s stated first impression (in Huene and Matley, 1933: 4) was “that the majority of them [the appendicular bones] belonged to the same individual...which died elsewhere...

drifted to the locality...and [were] scattered over a limited area”. Second, there is ample information that justifies the association amongst some of the postcranial elements. Huene and Matley (1933: 19–21) remarked that the ribs “were arranged in parallel order side by side”, “right and left scapulae have been found, possibly as a pair”, and that the right humerus was “found near the right scapula and 20 feet from the left scapula”. The radius and ulna are of appropriate size relative to one another and to the humerus to pertain to a single individual (McIntosh, 1990; Wilson and Upchurch, 2003). Thus, there is a moderate level of support for associating some of the postcranial elements as a single individual (i.e., partial rib cage, shoulder, forelimb).

In their discussion and diagnosis, Huene and Matley (1933: 32–33) considered the caudal vertebra, chevrons, braincase,



ribs, and appendicular elements in turn, individually justifying their attribution to “*A.*” *septentrionalis* on the basis of their size. Specifically, they considered each of them to be too large to associate with “*Titanosaurus indicus*” caudal vertebrae, which were collected from the same locality: “...haemopophyses cannot be associated with the smaller type of caudals”, “[t]he skull-fragment is too large for the smaller type of caudals”, “the ribs...probably go with the larger caudal”, and elements of the shoulder and forelimb “all are far too large for the post-medial caudals of *Titanosaurus indicus*”. Subtleties in the original description further illustrate that Huene and Matley (1933) did not consider all the elements in the type series to be a single individual. They distinguished between individual-level and species-level identity between bones in the type series in both the text and the legends to the plates and figures accompanying the paper. For example, the slender element identified as a hyoid was described as being “from the same individual” as the braincase, but postcranial elements in the type series were described as being the same species and from the “same bed and locality”

as the braincase (Huene and Matley, 1933:16–22; fig. 8). The lone caudal vertebra (GSI K20/317) they described, which provides the only potential overlap with “*T. indicus*”, was “probably the same [taxon] as” the braincase and other bones (Huene and Matley, 1933: fig 9).

To summarize, Huene and Matley did not explicitly state that the cranial and postcranial elements of the type series of *Jainosaurus* (=“*Antarctosaurus*”) *septentrionalis* belonged to a single individual, and there is evidence that they considered them to pertain to multiple individuals. Nonetheless, Huene and Matley (1933: 32–33) posited that these elements should form the basis of a new genus and species because of their relatively large size. Unfortunately, there is no supplementary data (e.g., field photographs, maps, personal accounts) that shed light on the original associations, but there is moderate support that at least the ribs, shoulder, and forelimb pertain to one individual (see Wilson and Upchurch, 2003).

The key question, then, is whether circumstantial evidence supports individual associations between the braincase, forequarters, and caudal elements. Presently, five braincases are known from Indo-Pakistan that can be separated into two morphs — the “*Titanosaurus* morph” and the “*Antarctosaurus* morph” (Wilson et al., 2005). Thus far, no definitive associations have been made between any of the five braincases and any postcranial remains. The strongest case for association comes from Dongargaon, central India, where a braincase (ISI R199; Berman and Jain, 1982) and the partial skeleton of *Isisaurus* (=“*Titanosaurus*”) *colberti* (Jain and Bandyopadhyay, 1997) were found at the same quarry, although nearly 20 years apart. No other dinosaur bones have been collected at this locality, and Jain and Bandyopadhyay (1997: 131) considered that “all material [from Dongargaon] belongs to *T. colberti*.” If we accept the association between the “*Titanosaurus* morph” braincase and *Isisaurus* postcranial bones, and if we presume that there are only two common sauropod genera in the Indian Cretaceous, then we have an opportunity to forge associations between the other braincase morph (i.e., the “*Antarctosaurus* morph”) with postcranial bones — so long as those postcranial bones can be distinguished from *Isisaurus* postcranial bones and exhibit similar morphologies when they overlap. As described below, the *Jainosaurus* type series humerus is autapomorphic and can be easily differentiated from that of *Isisaurus*. Thus, on the basis of the probable association between cranial and postcranial remains at Dongargaon, the recognition of only two common sauropod genera in the Cretaceous of India, and the distinctiveness of both the braincase morphs and the postcranial morphs, we can tentatively link each of the braincase morphs to distinctive postcranial elements. Following these associations, we will refer to the “*Isisaurus* morph” and “*Jainosaurus* morph” braincases.

DESCRIPTION

Below is a redescription of the lectotype and referred *Jainosaurus septentrionalis* braincases as well as postcranial remains referred to the species (see above). This redescription is based on observations made at the Geological Survey of India collections

TABLE 1 — Principal dimensions (in millimeters) of the lectotypic and referred braincases of *Jainosaurus septentrionalis*. In the lectotypic braincase, the braincase and skull roof are coossified, and many sutures are fully fused. The referred braincase, in contrast, is from an immature individual. Neither the orbitosphenoid-laterosphenoid nor the skull roof were coossified to the posterior skull elements. In the Malagasy titanosaur *Rapetosaurus*, the laterosphenoid and orbitosphenoid fuse to one another before they coossify with the posterior braincase elements (Curry Rogers and Forster, 2004). Asterisks (*) indicate measurement of an incomplete structure; the “e” indicates an estimate made by doubling.

Region	Dimension	Lectotype (GSI K27/429)	Referred (ISI R162)
Posterior skull	Width	—	148
	Height	—	172
	Supraoccipital to basal tubera	168	118
Lateral skull	Length	58	—
Supraoccipital	Height	48	36
Occipital condyle	Width	60	34
	Height	49	29
	Length	35	29
Foramen magnum	Width	—	24
	Height	41	30
Basal tubera	Width	94e	89
Basipterygoid processes	Length distal to basal tubera	—	47
Supratemporal fenestra	Anteroposterior length	10	—
	Distance to midline	57	—
Hypophyseal fossa	Length	9	—
	Width	20*	—

in Kolkata, Nagpur, and Jaipur, the Indian Museum, Kolkata, the Indian Statistical Institute, Kolkata, Texas Tech University, Lubbock, and the Natural History Museum, London, as well as on information available in the published literature. Principal dimensions of the skulls are given in Table 1.

The lectotypic braincase (GSI K27/497) lacks the paroccipital processes and basipterygoid processes, as well as the anteriormost portions of the basisphenoid and orbitosphenoid (Figs. 3–5). The parietal and frontal are preserved on the right side; the former lacks the squamosal articulation and posterior margin of the supratemporal fenestra, whereas the latter lacks the orbital margin and nasal and prefrontal articulations. The endocranial cavity was cast by Matley (Huene and Matley, 1933: fig. 6), and the floor, roof, and right side wall of the braincase are well preserved. A conspicuous suture separates the skull roof and braincase proper. Other sutures are fused, but their probable courses can be identified by roughened bone texture. A referred braincase (ISI R162) of a younger individual augments the description because it preserves anatomy not present in the lectotype.

Skull Roof

The endocranial cavity is capped by two paired midline elements, the frontal and parietal. These skull roof elements are united to the neurocranial elements that form the back and side

walls of the endocranial cavity via a transversely broad, corrugated suture.

Frontal.— The frontal is mostly complete, but its margins are damaged. Only its posterior margin is completely preserved; its midline contact, anterior articulations with the nasal and prefrontal, as well as its orbital margin are absent. The frontal is broader than long, as in all sauropods except rebbachisaurids (Sereno et al., 1999), and it is thickest dorsoventrally at its lateral extreme (ca. 1.5 cm) and thinnest near the midline (< 0.5 cm). The plane formed by the frontal rises at an angle of 10–15 degrees above horizontal from the midline towards its lateral extreme (Fig. 3B). Ventrally, the frontal contacts two lateral braincase elements, the orbitosphenoid and the laterosphenoid; the latter’s contact is shared with the parietal (see below). The frontal-braincase suture subtends a gentle arc that begins at the posterior margin of the orbit and approaches the midline anteriorly. Although not completely preserved in *Jainosaurus septentrionalis*, this sutural arc would have continued anteriorly as a well marked ridge on the frontal that serves as a division between the olfactory and optic portions of the skull (e.g., *Nemegtosaurus*; Wilson, 2005: 293).

Parietal.— The parietal is a strap-shaped element that has sutural contacts with four neurocranial elements ventrally (supraoccipital, exoccipital-opisthotic, prootic, laterosphenoid), the frontal anteriorly. Its lateral contacts are not preserved. The parietal is abbreviate anteroposteriorly, and its anteroposterior length

probably equaled one-fifth its transverse breadth. The midline parietal suture is sinuous and forms the middle portion of an H-shaped intersection with the frontals anteriorly and the occipital elements posteriorly. The parietal-frontal contact is distinguishable as a coarse, raised scar running transversely across the skull. Within the endocranial cavity, the parietal-frontal suture forms a transversely oriented ridge that, with the laterosphenoid, delimits forebrain from midbrain (see “Endocast” below). Laterally, the parietal separates into anterior and posterior rami, which form the medial border of the supratemporal fenestra. It is not known whether the supratemporal fenestra is completed laterally by the postorbital and the squamosal, as in most sauropods (e.g., *Camarasaurus*; Wilson and Sereno, 1998: fig. 7), or if the squamosal is excluded from its margin, as in some derived titanosaurs (e.g., *Nemegtosaurus*; Upchurch, 1995; Wilson, 2005: fig. 7). The preserved anteromedial portion of the supratemporal fenestra suggests that it was elliptical in dorsal view with its long axis directed nearly transversely (within 15 degrees of orthogonal to the midline). There is no well-defined supratemporal fossa medially on the parietal. The separation between the medial margin of the supratemporal fenestra (i.e., the point at which the parietal splits) and the skull midline is equivalent to half the estimated transverse breadth of the parietal. Based on its preserved medial margin, it appears that the supratemporal fenestra was horizontally oriented in both transverse and sagittal planes. In sauropod genera with laterally canted supratemporal fenestrae, both the parietal and the lateral elements (i.e., postorbital, squamosal) are tipped ventrally, so this condition can be detected from the parietal alone (e.g., *Diplodocus*; Wilson and Sereno, 1998: fig. 6). The anterior and posterior parietal rami of the parietal are floored by the laterosphenoid and prootic, respectively.

The posterior margin of the parietal is raised into a transverse crest on either side of the midline. This parietal crest curls forward slightly in dorsal and lateral views (Figs. 4A, 5A) and has a convex dorsal margin that is highest near the medial margin of the supratemporal fenestra and lowest at the midline. The parietal contact with the posterior neurocranial elements is fused, and the exact course of the suture is difficult to discern. This suture is quite high near the midline and drops down sharply on either side of the supraoccipital crest and then climbs slowly along the dorsal margin of the exoccipital-opisthotic before dipping shortly and flattening out at its lateral extreme.

Braincase

The lectotypic braincase is well preserved, but lacks several critical features, such as the distal ends of the paroccipital processes, the basiptyergoid processes, and the parasphenoid rostrum (Figs. 2–5). The left wall of the braincase is missing, but nearly all lateral elements are present on the right side. The bony enclosure of the brain is formed posteriorly and ventrally by three median elements (supraoccipital, basioccipital, basisphenoid) and laterally by four paramedian elements (exoccipital-opisthotic, prootic, laterosphenoid, orbitosphenoid). These elements are described in order below, with supplementary information from the referred braincase (ISI R162).

Supraoccipital.— The supraoccipital is a median element that forms the posterodorsal portion of the braincase and roofs the foramen magnum. It contacts the exoccipital-opisthotic ventrolaterally and the parietal dorsally. The supraoccipital of *Jainosaurus* is well preserved on its right side, but the left side is mostly missing. The contact between the supraoccipital and parietal is slightly obscured by fusion, but it appears drop sharply as it travels laterally from the nuchal crest, but then rises sharply near the level of the crest of the occipital process of the parietal. This highly sinuous contact is also present in the referred braincase and is shared with *Antarctosaurus wichmannianus*. The suture between the supraoccipital and exoccipital is nearly completely fused in the lectotypic and referred braincases, so the relative contribution of these elements to the foramen magnum is unknown. The height of the supraoccipital is slightly greater than the dorsoventral diameter of the foramen magnum, unlike the condition in *Rapetosaurus* and *Nemegtosaurus* (Wilson, 2002). The nuchal crest is prominent and formed from a single ridge, as in most titanosaurs. Exceptions include *Rapetosaurus*, *Bonattitan*, the Rio Negro taxon (MML 194; García et al., 2008), and *Muyelensaurus*, which have a median groove, and *Pitekunsaurus*, which lacks both the groove and the ridge.

Basioccipital.— The basioccipital is the posteriormost ventral median braincase element. It is a short, heavy bone that forms the majority of the occipital condyle and part of the basal tubera. It is slightly damaged ventrally and on its left side.

The occipital condyle projects 120 degrees from the vertical, as determined by the angle between the plane of the occiput and the dorsal surface of the occipital condyle (Fig. 4A). The articular surface circumscribing the condyle itself extends far forward at its ventral extreme, suggesting that the skull was held at an angle to the long axis of the anterior cervical vertebrae. The opening for cranial nerve XII passes through the dorsolateral neck of the occipital condyle; it is not clear whether the margin for this opening is partly shared by the exoccipital-opisthotic. A small, poorly defined, ventrally facing, circular depression is positioned between the occipital condyle and the basal tubera, a feature that is present in several neosauropods (Wilson, 2002).

Anteriorly, the basioccipital is expanded into a transversely flat, vertically deep sheet of bone that articulates with the basisphenoid. The basioccipital-basisphenoid suture can be identified traversing the floor of the endocranial cavity between the right and left metotic (= jugular) foramina, though which exit cranial nerves IX–XI and the jugular vein. Consequently, the basioccipital forms the posteroventral margin of the metotic foramen. The basioccipital-basisphenoid suture extends ventrally to the posterior portion of the basal tubera, the bulk of which are made up by the basisphenoid.

The basioccipital is beveled on its lateral extremes for attachment of the paired exoccipital-opisthotic elements. The suture separating the basioccipital from the exoccipital-opisthotic is visible where it undercuts the dorsolateral shoulder of the occipital condyle. The occipital condyle is convex about its circumference except for the middle third of its dorsal margin, where it forms the concave floor of the foramen magnum.

Basisphenoid.— The basisphenoid contacts the basioccipital posteriorly, flooring the endocranial cavity from the level of the

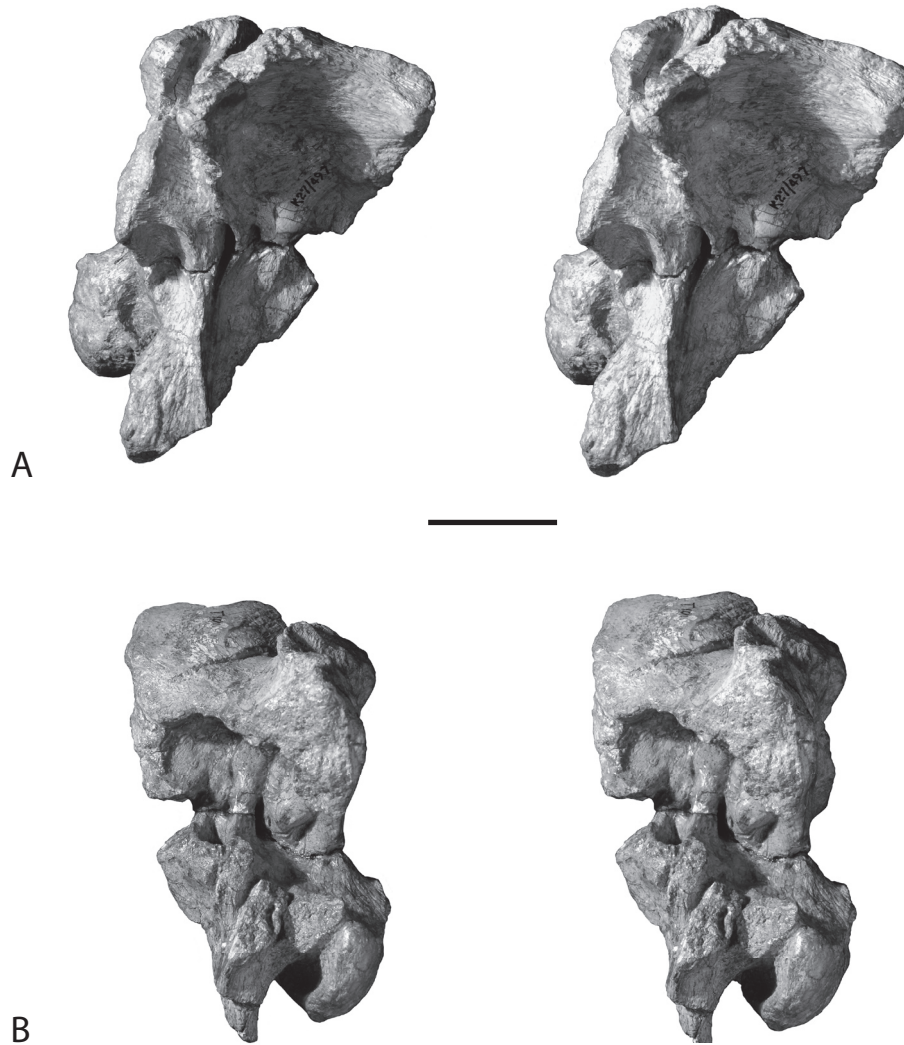


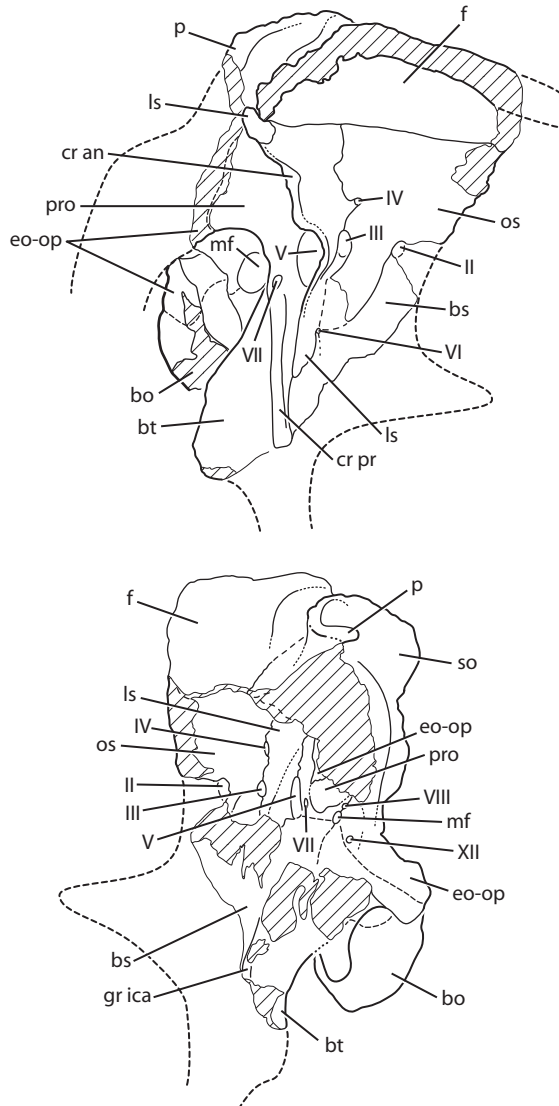
FIGURE 4 — *Jainosaurus septentrionalis*, lectotypic braincase (GSI K27/497). Stereopairs and interpretive line drawings in right lateral (A) and internal (B) views. Scale equals 5 cm. Abbreviations (facing page) as in Figure 3.

metotic foramen forwards. Dorsally, the basisphenoid contacts the prootic, laterosphenoid, and orbitosphenoid, which appear to exclude it from the margin of cranial nerves V and III. The basisphenoid apparently did not border the opening for cranial nerve VIII either, as it is excluded by the prootic and exoccipital-opisethotic. The opening for cranial nerve VI pierces the basisphenoid ventral to the level of these larger cranial nerve openings. The basisphenoid forms at least the posteroventral margin of the opening for cranial nerve II, but because the orbitosphenoid and basisphenoid are broken anteriorly the extent of their contributions is unknown. The basisphenoid forms the bulk of the basal tubera, the basipterygoid processes, a portion of the hypophysial canal, and the parasphenoid.

Neither the parasphenoid nor the basipterygoid processes are preserved in the lectotypic braincase, but the referred *Jainosaurus* braincase (ISI R162) preserves basipterygoid processes.

In ISI R162 the basipterygoid processes are long and directed parallel to the plane of the occiput (Fig. 6B). The distance from the base of the occipital condyle to the basal tubera is subequal to the distance from the basal tubera to the ends of the basipterygoid processes (~4.5 cm). The basipterygoid processes taper transversely towards their distal extreme, but they maintain their anteroposterior dimension along their length. The cross-section of the basipterygoid processes at mid-length is shaped like a quarter-circle, with the posterior face rounded and the anterior and lateral faces flat and oriented about 90 degrees to one another. The long axes of the basipterygoid processes diverge from the midline at an angle of about 50 degrees.

The basal tubera are formed by the basioccipital and basisphenoid. They are sheetlike and quite broad laterally, extending well beyond the lateral margin of the occipital condyle. They do not project far posterior to the occipital plane, and



they grade smoothly into the basipterygoid processes. Although not completely preserved on either side, their breadth and lateral thickening is reminiscent of those of the titanosaurs *Nemegtosaurus* and *Quaesitosaurus*, both of which have a bony connection between the basal tubera and the medial aspect of the quadrate (Wilson, 2005: figs. 9, 16). The basal tubera have a broad, gentle fossa on their posterior surface (Fig. 3A) that is also present in “Malagasy Taxon B” (Curry Rogers, unpublished data) and the South American titanosaurs *Muyelensaurus* (Calvo et al., 2007), *Pitekunsaurus* (Fillipi and Garrido, 2008), and an unnamed taxon from Río Negro (MML 194; García et al., 2008). The posterolateral corner of the basal tubera is not preserved in the lectotype, but it is preserved in the referred braincase (ISI R162). In ISI R162, the posterolateral portion of the basal tubera has a small, pendant process that is divided from the rest of the basal tuber by a sharp notch. This distinctive feature is also present in “Malagasy Taxon B” (Curry Rogers, unpublished data).

Exoccipital-opisthotic.— The paired exoccipital-opisthotic bones form the posterior portion of the endocranial cavity and are exposed on the occiput, where they form the paroccipital processes, the lateral margin of the foramen magnum, and the dorsolateral shoulders of the occipital condyle. Only the right exoccipital-opisthotic is preserved, and it is broken near its base. Consequently, the shape of the paroccipital process as well as its contacts with the parietal, squamosal, and quadrate are not preserved in the lectotype. The broken base of the paroccipital process, however, shows the contact between the exoccipital-opisthotic and prootic in cross-section (Fig. 4A). The latter is sheet like and covers a portion of the anterior face of the paroccipital process. The exoccipital-opisthotic contacts the basioccipital along a nearly horizontal sutural plane extending from metotic foramen posteriorly to the occipital condyle. However, the exoccipital-opisthotic contact with the supraoccipital is not visible, so the relative contributions of these two elements to the border the foramen magnum cannot be determined. A low, transversely elongate prominence on each side of the foramen magnum may represent the proatlantal facets; it cannot be determined whether these are wholly or partly formed by the exoccipital-opisthotic.

The left paroccipital process is completely preserved in the referred braincase from Bara Simla (ISI R162; Fig. 6). This specimen indicates that the paroccipital processes arched ventrally and projected ventral to the occipital condyle. A sharp notch in the dorsal border of the paroccipital process forms the lower margin of the posttemporal foramen. Just distal to this notch is a rounded prominence that articulated with the posterior portion of the quadrate head. This prominence marks the lateral extreme of the paroccipital process, which descends sharply from this point as a tongue-like flange. This flange, which is extremely narrow in lateral view, is probably homologous to the pendant, nonarticular processes present at the distal extreme of the paroccipital processes in other titanosaurs (e.g., *Rapetosaurus*, *Nemegtosaurus*, *Malawisaurus*).

Prootic.— The prootic is a transversely oriented element that forms the posteriormost portion of the braincase side wall. It is preserved only on the right side but is not complete laterally, like the exoccipital-opisthotic. As its name suggests, the prootic is positioned anterior to the ear and shares the perimeter of the metotic foramen with the exoccipital-opisthotic, basioccipital, and basisphenoid. It contacts the laterosphenoid anteriorly, and it has a ventrally-directed spur that overlaps the basisphenoid to the level of the basal tubera. The prootic and laterosphenoid contact one another along a suture that extends from the groove for the exit of cranial nerve V to the medial margin of the supratemporal fenestra, where it intersects the junction between the parietal and the neurocranial elements.

The prootic forms a vertical crest, the crista prootica, that is visible in both lateral and anterior views. The crista prootica is not expanded laterally into a tab-like structure, as it is in dicraeosaurid sauropods such as *Dicraeosaurus* (Janensch, 1935-6: figs. 94–96) and *Amargasaurus* (Salgado and Calvo, 1992: figs. 1B, 2B). Instead, it is a posteriorly convex crest that forms the posterior margin of the groove for cranial nerve V, which is completely enclosed by the prootic and

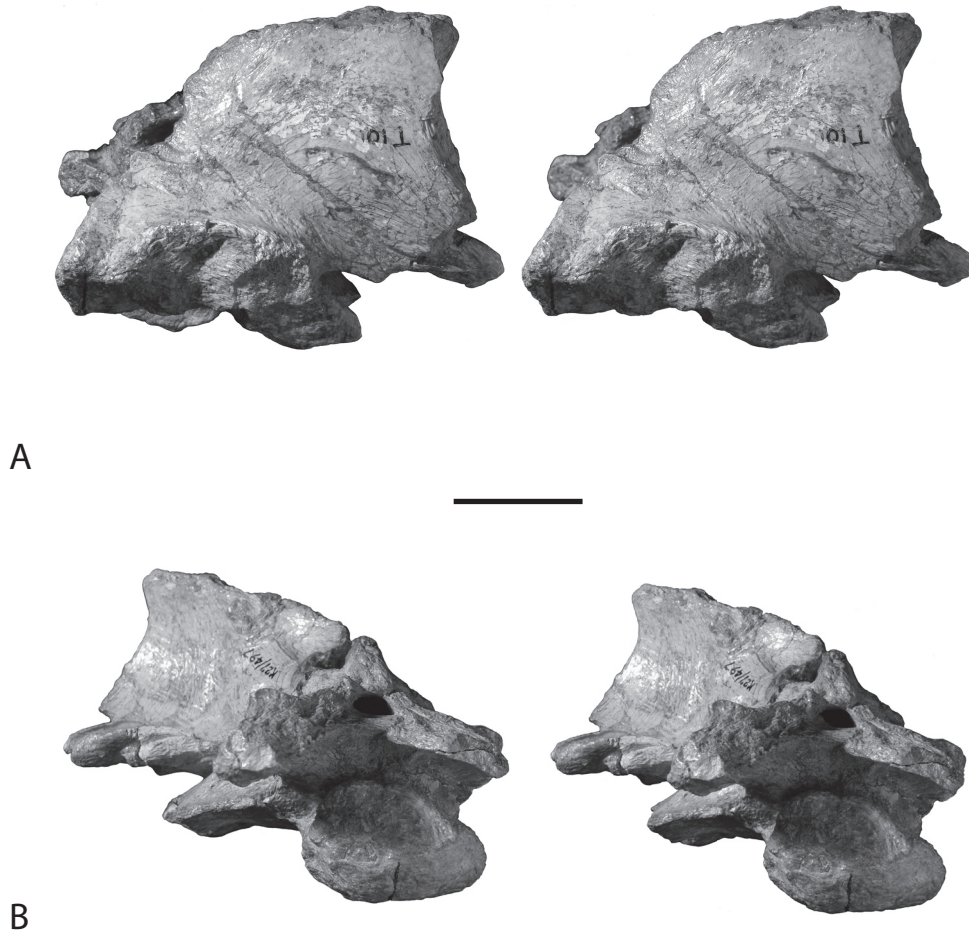


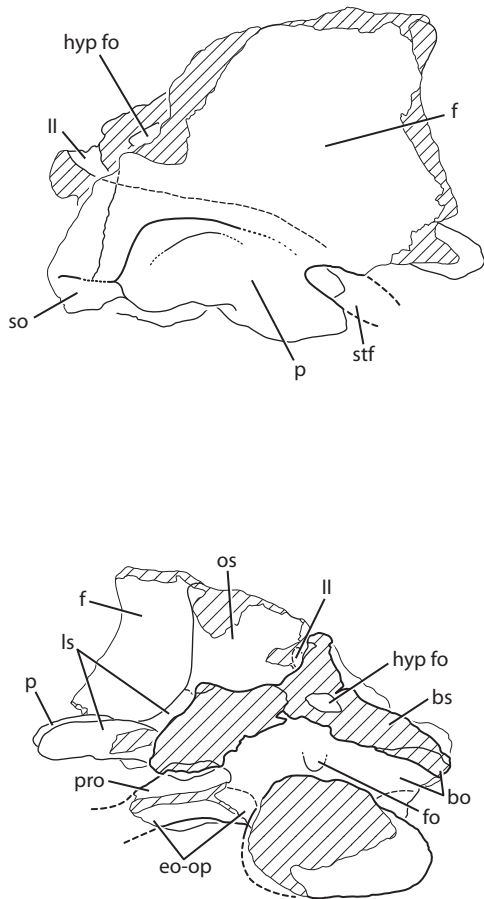
FIGURE 5 — *Jainosaurus septentrionalis*, lectotypic braincase (GSI K27/497). Stereopairs and interpretive line drawings in dorsal (A) and ventral (B) views. Scale equals 5 cm. Abbreviations (facing page) as in Figure 3.

laterosphenoid, continuing ventrally on the basisphenoid as the crest leading to the basiptyergoid processes. Immediately posterior to the crista prootica and slightly ventral to the trigeminal foramen is the opening for cranial nerve VII. The prootic is the neurocranial element that houses the semicircular canals; these elements could not be viewed, but a bulge visible in medial view marks their location. The broken left prootic preserves a small channel that is likely the opening into the vestibule.

Laterosphenoid.— Another transversely oriented element, the laterosphenoid, is important because it marks boundaries within and external to the endocranial cavity. Internally, the pillar of the laterosphenoid divides forebrain from midbrain. The laterosphenoid pillar decreases in diameter dorsally. Externally, its transversely oriented, arched arm (the crista antotica) separates the supratemporal fenestra from the orbit (Figs. 3B, 4A, 5B). The dorsal surface of the laterosphenoid contacts the parietal and frontal and thus marks the course of their suture. Together, the laterosphenoid (ventrally), parietal (posterodorsally), and frontal (anterodorsally) make a three-way contact with the

postorbital. The laterosphenoid is slightly expanded into a condyle distolaterally that represents a synovial contact with the postorbital. The crista antotica continues ventrally as a sharp but low ridge that forms the anterior margin of the groove for cranial nerve V (the posterior margin is formed by the prootic; see above).

The laterosphenoid also has sutural connections to three neurocranial elements, the prootic, orbitosphenoid, and basisphenoid. The anterior and posterior margins of the laterosphenoid contact the orbitosphenoid and prootic, respectively. The laterosphenoid-prootic suture and the laterosphenoid-orbitosphenoid suture are visible on the internal surface of the endocranial cavity. Both are vertical or near-vertical sutures that are interrupted by openings for cranial nerves. Posteriorly, the laterosphenoid and prootic are separated by the opening for cranial nerve V, and their junction passes vertically to the medial margin of the supratemporal fenestra. Anteriorly, the laterosphenoid and orbitosphenoid are separated by the openings for cranial nerves III and IV, and their suture extends dorsally to a position within the posterior portion of the orbital cavity. Medially,



the laterosphenoid bears a narrow pillar that is visible internal view (Fig. 4B). This ridge corresponds to the division of forebrain and midbrain, and it can be seen as a circumferential constriction in the endocast (Huene and Matley 1933: fig. 6).

The contact between the laterosphenoid and the basisphenoid can only be identified internally, where their suture can be viewed on the posterior portion of the hypophyseal fossa. The laterosphenoid extends medially at its base to form the dorsolateral portion of the sella turcica.

Orbitosphenoid.— The orbitosphenoid is the only paired braincase element that forms a midline contact, enclosing the forebrain and forming the anterior portion of the hypophyseal fossa. The orbitosphenoid in *Jainosaurus* is not complete anteriorly, but its contacts with the basisphenoid ventrally, the laterosphenoid posteriorly, and the frontal dorsally are well preserved on the right side. A narrow, ventrally directed process of the orbitosphenoid overlaps the basisphenoid laterally, extending towards the opening for cranial nerve VI, which is near the sella turcica (Fig. 4A). The orbitosphenoid-basisphenoid suture courses anterodorsally to the margin of cranial nerve II. Dorsally, the orbitosphenoid has a long, broad contact with the frontal, with which it forms a portion of the orbit. Although it is not preserved anteriorly, the orbitosphenoid would have formed all but the roof of the openings for cranial nerve I.

Cranial Nerves.— Openings for all but the first cranial nerve are preserved on the lectotypic braincase (GSI 27/497), and all of the posterior cranial nerve openings (V–XII) are preserved on the referred braincase (ISI R162). Openings for cranial nerves II, III, V, and VII–XII fall on a line that extends to the foramen magnum. Openings for cranial nerves I and IV are positioned dorsal to this line, and the opening for cranial nerve VI is positioned ventral to it. This appears to be the general condition for sauropods.

The margins of the opening for cranial nerve I are not preserved, but in most sauropods they are bounded ventrally by the orbitosphenoids and dorsally by the frontals. The anterior end of the braincase preserves approximately half of the margin of the opening for cranial nerve II, which is shared by the orbitosphenoid and basisphenoid. The opening for cranial nerve III is positioned anterior to the crista antotica, and its margin is formed by the orbitosphenoid and laterosphenoid. The opening for cranial nerve IV is also bordered by the orbitosphenoid and laterosphenoid, but it is much smaller than and positioned dorsal to the opening for cranial nerve III.

The trigeminal foramen is formed by the prootic and laterosphenoid. It is large and appears to have accommodated all three branches of the trigeminal nerve exit from a single foramen. In some non-sauropod dinosaurs, branches of the trigeminal nerve (cranial nerve V) have separate exits from the braincase (e.g., *Majungasaurus*; Sampson and Witmer, 2007). The path of the mandibular branch of cranial nerve V is marked by a shallow groove that extends ventrally. In both the lectotypic and referred braincases, this groove is bounded posteriorly by the crista prootica and anteriorly by a narrow spur of the laterosphenoid that represents the continuation of the crista antotica. Just posterior to the crista prootica is a small opening for cranial nerve VII, which is preserved in both braincases. The opening for cranial nerve VI is small and positioned ventrally. As in other sauropods, it faces anterolaterally.

The metotic foramen (cranial nerves IX–XI) and the foramen ovale (cranial nerve VIII) are seated in a large fossa just posterior to the crista prootica. The margin of the metotic foramen is shared by prootic, exoccipital-opisthotic, and the basioccipital, whereas the foramen ovale appears to be bounded by only the prootic and exoccipital-opisthotic. This latter condition is best observed internally, where the foramen ovale is positioned dorsal to the metotic foramen and clearly bordered by only two bones. Externally, however, the foramen ovale appears to be positioned anterodorsal to the metotic foramen, which is typical for sauropods. The foramen ovale is also positioned anterior to the metotic foramen in the referred braincase (ISI R162; Chatterjee and Rudra, 1996: fig. 9B). It appears that the trajectories of these two closely positioned openings are slightly divergent such that their positions relative to one another differ between the inside and outside of the braincase. A single opening for cranial nerve XII is located on the dorsolateral side of the neck of the occipital condyle.

Endocast.— An endocast was prepared by Matley and described and figured by Huene and Matley (1933:fig. 6). Several

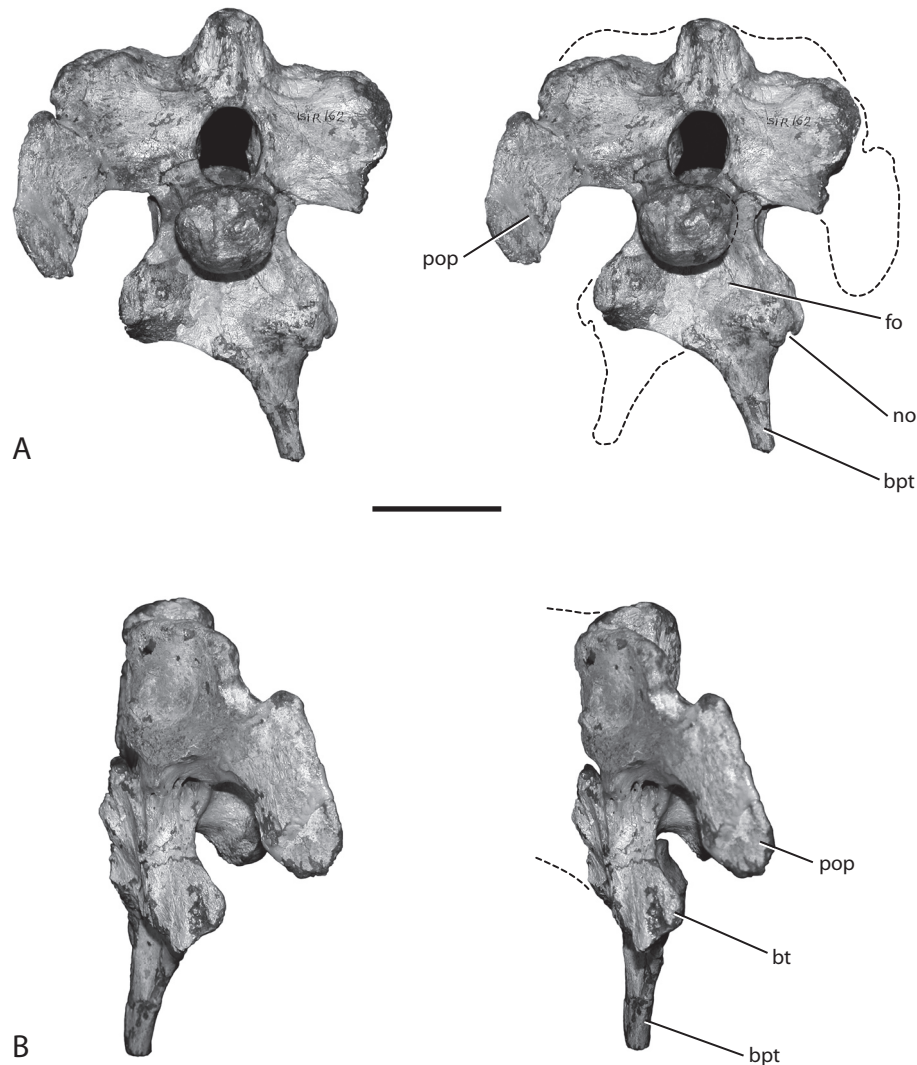


FIGURE 6 — *Jainosaurus septentrionalis*, referred braincase (ISI R162). Stereopairs in (A) posterior and (B) left lateral views. Scale equals 5 cm. Abbreviations as in Figure 3, plus: no, notch; pop, paroccipital process.

general features are observable on the endocast, including the constriction between the forebrain and midbrain by the laterosphenoid pillar, the proximal hypophyseal fossa, and the bases of most cranial nerves (II–V, VII, IX–XI, XII; Fig. 7). The strong circumferential division at the midpoint of the endocast marks the sutural zone between the laterosphenoid (ventrally) and the frontal/parietal (dorsally). The shape of the distal portion of the hypophysis is not preserved in the endocast; its shape and the shape and size of the exit for the internal carotid arteries are unknown.

Postcranial Skeleton

Several postcranial elements were included within the type series of *Jainosaurus* (= *Antarctosaurus*) *septentrionalis* by Huene and Matley (1933: 11–23), some of which appear to represent

a single individual (Fig. 2). These elements, which pertain to the anterior rib cage and forelimb, are redescribed below based on first-hand observations of the two elements that remain in collections. Other elements from the type series are not attributable to this individual (i.e., caudal vertebra, chevrons, “sternal plate”) and not described here; neither are the second humerus and femur referred to the genus by Huene and Matley (1933: 34–35).

Ribs.— Huene and Matley (1933: 19) reported that “a large number (about 28) of broken pieces of ribs were found in different parts of the “Sauropod bed”, some of them arranged in parallel order side by side....” The ribs figured by Huene and Matley (1933: figs. 11–15; Fig. 2B) are all broad, but some of the ribs are described by the authors as being triangular in cross-section. Plank-like anterior dorsal ribs with internal pneumaticity would be expected in *Jainosaurus*, as in other titanosauri-

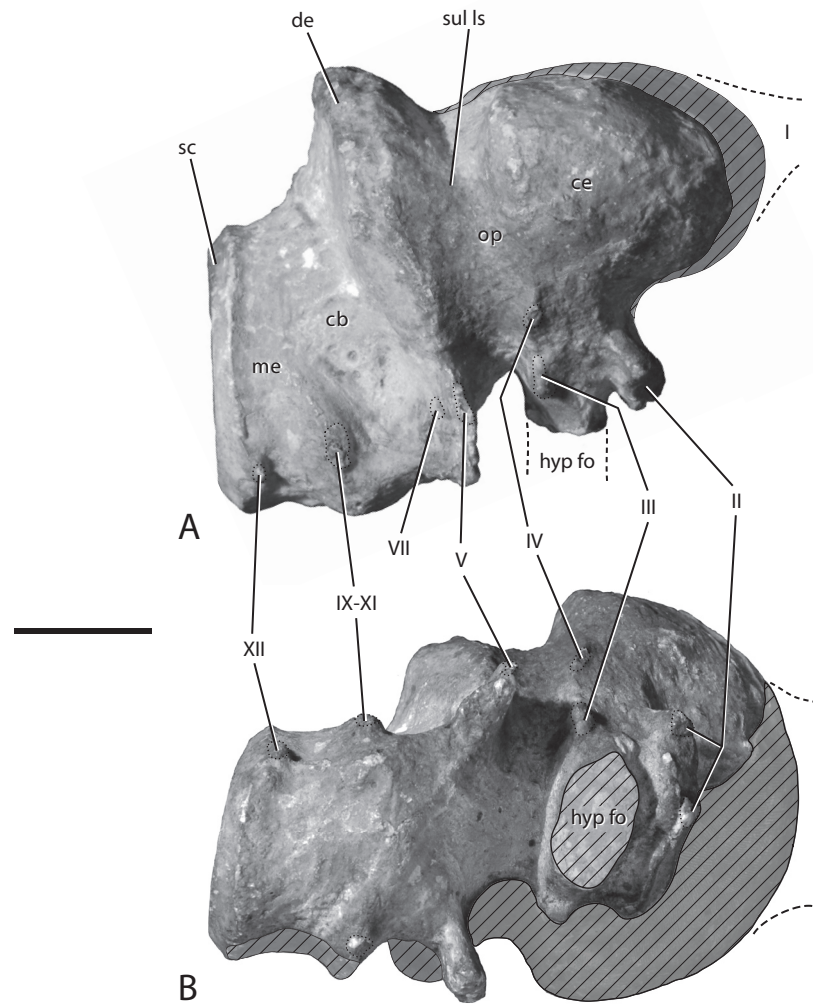


FIGURE 7 — *Jainosaurus septentrionalis*, endocast prepared by C. Matley from the lectotypic braincase (GSI K27/497) in right lateral (A) and ventral (B) views. Positions of brain regions are approximate and based on Witmer et al. (2008). Dotted lines indicate position of cranial nerves. Scale equals 2 cm. Abbreviations as in Figure 3, plus: cb, cerebellum; ce, cerebrum; de, dural expansion; me, medulla; op, optic lobe; sc, spinal cord; sul ls, sulcus for laterosphenoid pillar.

forms (Wilson, 2002), but we cannot confirm these predictions because these elements cannot be located in the collections of the GSI.

Scapula.— A pair of right and left scapulae (GSI unnumbered) were considered by Huene and Matley (1933) to pertain to a single individual due to their similar size and proximity to one another in the “Sauropod bed” (Fig. 2D). Huene and Matley (1933: 20) remarked that the left scapula was found in 1917 and the right scapula in 1919. The latter was complete when it was first found (length = 1.67 m), but it was subsequently broken — presumably prior to photography for the monograph, which clearly shows a broken distal blade (Huene and Matley 1933: pl. 3, fig. 1). The left scapula, in turn, was found incomplete (length = 1.32 m). Despite minor differences, which were enhanced by presentation of the two scapulae in different orientations and at

different scales in Huene and Matley (1933: pl. 3), we consider it likely that these elements pertain to the same individual based on their similar size and shape.

Unfortunately, neither scapula can be located in the collections of the GSI, but a cast of the right scapula sits atop cabinets in the Invertebrate Fossil Gallery of the Indian Museum (Kolkata). There are minor differences between the cast and the published photos of the right scapula (Huene and Matley 1933: pl. 3, fig. 1). Most of these differences are attributable to subtle differences in the orientation of the element, as well as apparent breakage to the base of the scapula between photographs (compare Huene and Matley, 1933: fig. 1a and 1b), but there is nonetheless a minor difference in the dorsal portion of the distal blade resulting from reconstruction to the cast. Based on available photographs of the scapulae, in particular the better-preserved

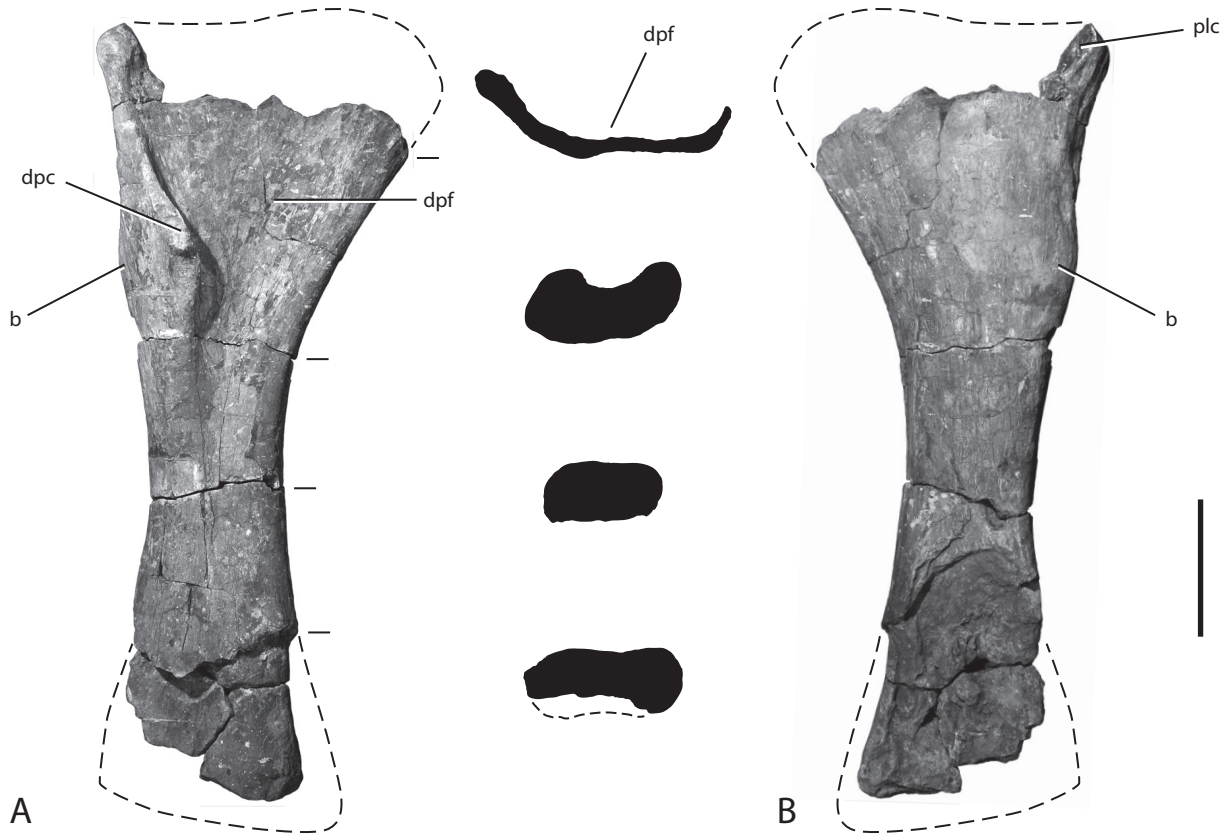


FIGURE 8 — *Jainosaurus septentrionalis*, lectotypic right humerus (GSI unnumbered) in (A) anterior and (B) posterior views. Cross-sections are oriented so that anterior faces up and lateral faces left. The position of each section (black-filled shapes) is indicated by the tick mark adjacent to it. Scale equals 25 cm. Abbreviations: b, bulge; dpc, deltopectoral crest; dpf, deltopectoral fossa; plc, proximolateral corner.

but less complete left scapula, there is a gentle expansion of the dorsal margin of the blade distally. Just proximal to this expansion, the blade is markedly concave and grades into the acromion. The apparent sharp narrowing of the ventral margin of the blade visible in the left scapula (see Huene and Matley, 1933: fig. 16; Fig. 2) is clearly due to breakage; the right scapula shows a continuous, gently concave ventral margin of the scapula. In cross section, the blade appears to have been concave medially and somewhat sharply convex laterally, due to the presence of a strong ridge that extends from the acromial fossa to mid-blade. Neither glenoid is preserved, and the orientation of its articular surface is not known.

Humerus.— The type series humerus (GSI unnumbered) was recently rediscovered atop a case in the Siwalik Gallery of the Indian Museum. Portions of the proximal end and a small piece of the distal end are now missing, but the bone is remarkably well preserved and provides details that were not previously visible in published photographs. Although images of the humerus in two views have been available (Huene and Matley, 1933: pl. 4, fig. 1), inadvertent cropping of the photograph and/or slight

rotation of the humerus resulted in loss of one of the diagnostic features of this bone (see Figs. 2E, 7).

The humerus is not complete, but it would have been somewhat gracile; the breadth of the proximal end is only 30–40% the estimated length of the humerus, and the midshaft transverse diameter (21.5 cm) is only about 15% of the preserved length of the humerus (133 cm). The proximolateral corner of the *Jainosaurus* humerus is pronounced; its lateral margin is very slightly concave and forms a slight but distinct angle with its more gently rounded dorsal margin. This feature has been variously noted as a “squared proximolateral corner” (e.g., Curry Rogers and Forster, 2001: character 119), a “prominent process on the lateral portion of the proximal end of the humerus” (Upchurch, 1998: character C160), or as the enlarged attachment site for the m. supracoracoideus (Borsuk-Bialynicka, 1977). The anterior face of the proximal end of the humerus (i.e., the deltopectoral fossa) is shallowly concave, anteroposteriorly thin, and transversely broad (48 cm). The curvature of the lateral margin of the humeral shaft is less than that of the medial border. The cross-section of the humerus at midshaft is elliptical and measures 21.5 cm by

11.9 cm, with a circumference of 61 cm (Fig. 8). The deltopectoral crest is located proximally, with its apex located only about 25% of the preserved humeral length from the proximolateral corner of the humerus. The transversely thickened deltopectoral crest is medially offset and obliquely oriented with respect to the long axis of the humerus (Fig. 8A). The apex of the deltopectoral crest thickens transversely towards midshaft. Just lateral to its thickest point is a prominent posterolateral bulge, which bears a roughened area indicative of a muscular attachment site. The distal end of the humerus is not preserved.

Several isolated humeri from Indo-Pakistan share diagnostic features with the type series humerus, including the obliquely oriented and medially offset deltopectoral crest, anteroposteriorly thin bone in the deltopectoral fossa, and the prominent posterolateral bulge near the deltopectoral crest, as well as more general features such as its generally gracile profile. Some of these features are present in other titanosaurs (e.g., *Epachthosaurus*, *Opisthocoelicaudia*) and their distribution is not yet well constrained, but they are thought to be derived within Titanosauria rather than primitive for the group. These features are present in sauropod humeri from Indo-Pakistan, such as materials from Raholi, Gujarat (GSI 20008–20010, 20012) described by Mathur and Pant (1986). On the basis of several metrics, Mathur and Pant (1986) linked the Gujarati humeri to the genus *Antarctosaurus*, but not to *A. septentrionalis* due to size differences. Materials from Chhota Simla (near Bara Simla) collected by Matley and described by Swinton (1947) also preserve these features (Wilson et al., in preparation), as do incomplete humeri from the Pab Formation of Pakistan. Although the lengths of the referred Gujarat humeri (70–85 cm) and the Chhota Simla humerus (94 cm) are significantly shorter than the type series humerus (134 cm), their overall shape and diagnostic features justify referral to *Jainosaurus septentrionalis*. The more complete Gujarat humeri can be referred to *Jainosaurus*, and they furnish additional information about humeral morphology, as well as an additional diagnostic feature—the radial condyle of the distal humerus is expanded and exposed anteriorly, whereas the ulnar condyle is not. This feature also appears to be present in the humerus of the recently described Chinese titanosaur *Qingxiusaurus* (Mo et al., 2008) and that of an undescribed large titanosaur from Argentina (MUCPv 1164; J. Calvo, personal communication 2009).

Radius and Ulna.— A radius (GSI K27/490) and ulna (GSI K27/491) were described and figured by Huene and Matley (1933: figs. 17–18; Fig. 2F). These bones cannot be located in the collections of the GSI, so our comments are based on the text and illustrations. The radius appears to be expanded at one end. Most have interpreted that to be the distal end (Huene and Matley, 1933; McIntosh, 1990), but it could reasonably be interpreted as the proximal end. The radius preserves a prominent ridge that likely represents the attachment surface for interosseus ligaments. The ulna is badly eroded proximally and distally, so many of the relevant features cannot be determined (e.g., presence of

olecranon, expansion of distal end). Huene and Matley (1933: 22) described its cross-sectional shape as “stout and somewhat subrectangular”, which distinguishes it from the gracile and triradiate shaft of *Isisaurus* (Wilson and Upchurch, 2003). The humerus:radius ratio reported by Huene and Matley (1933) is 0.58, similar to the value for some derived titanosaurs (Wilson and Upchurch, 2003: table 2). We could not confirm that these bones pertain to the right side, as stated by Huene and Matley (1933). Note that Huene and Matley (1933) incorrectly specified that figures 17 and 18 were scaled to 1/4 natural size. The images are actually scaled to 1/6 natural size, as were other other limb elements, based on the measurements listed in the text.

COMPARISONS AND PHYLOGENETIC AFFINITIES

Early assessments of the phylogenetic affinities of *Jainosaurus septentrionalis* linked it to the South American titanosaur *Antarctosaurus wichmannianus* based on features now demonstrated to have a broader distribution within titanosaurs or titanosauriforms (McIntosh 1990; Curry Rogers and Forster, 2004; Wilson, 2005). Although titanosaur phylogeny is still hindered by a lack of significant skull material for the majority of taxa, several comparisons can be made. Below, we make comparisons to titanosaur species that might be expected to share a close relationship with *Jainosaurus septentrionalis* on the basis of original taxonomy (*Antarctosaurus wichmannianus*), sympatry (*Isisaurus colberti*), paleobiogeography (*Rapetosaurus krausei*, “Malagasy Taxon B”), and morphology (various taxa).

Antarctosaurus wichmannianus.— As with *Jainosaurus*, the absence of documented field associations has fostered doubts about the phylogenetic affinities of *Antarctosaurus wichmannianus*. Material originally referred to that genus by Huene (1929) has been suggested to pertain to two or more taxa (Upchurch, 1999; Sereno and Wilson 2005; Wilson, 2005). More recently, others have claimed that the cranial materials pertain to a single individual (e.g., Apestiguía, 2004; Gallina and Apestiguía, 2005; Novas et al., 2005; Salgado and Bonaparte, 2005; Salgado and Coria, 2005). Herein we limit our comparisons to the braincase and skull roof of *A. wichmannianus*, which share with Nemegtosauridae a reduced posterior process of the postorbital and beveled basal tubera, as well as the more widespread condition of paroccipital processes with pendant non-articular distal processes (Wilson, 2005). McIntosh (1990) and Hunt et al. (1994) noted that the braincases of *Jainosaurus septentrionalis* and *A. wichmannianus* were too different to allow their placement into the same genus (both studies also note that the posterania are more similar than the braincases of the two specimens).

The frontals of *A. wichmannianus* are peaked medially and meet in a prominent midline ridge, a feature that may be autapomorphic. In contrast, the frontals of *Jainosaurus* descend slightly towards the midline and lack a midline ridge. In both

A. wichmannianus and *Jainosaurus*, the plane of the frontals rises laterally; but in the latter they are elevated slightly more so than the former. Features of the braincase also distinguish the two taxa. *A. wichmannianus* possesses two openings near the foramen magnum visible in posterior view. Huene (1929: pl. 28) identified the smaller of these as the opening for cranial nerve XII, and the larger as the vestibular foramen, but Powell (2003) regarded the larger as the opening for cranial nerve XII (he did not identify the smaller opening). The identity of these openings remains ambiguous, but the elevated location of cranial nerve XII and the presence of a second opening on the occiput differ from the condition in *Jainosaurus*. In *A. wichmannianus* the occipital condyle is approximately as tall as it is wide, whereas in *Jainosaurus* the condyle is slightly wider than it is tall. The foramen magnum is relatively taller and narrower in *A. wichmannianus* than it is in *Jainosaurus*, but the supraoccipital appears relatively shorter. The basal tubera are broader than is the occipital condyle in both taxa, but other aspects of the basi-crania differ. In *Jainosaurus*, the basal tubera have a broad posterior fossa and grade gently into the basipterygoid processes, whereas *A. wichmannianus* lacks this fossa, and its basal tubera are distinctly offset from the basipterygoid processes. In *Jainosaurus*, the basipterygoid processes have a straight axis, but in *A. wichmannianus*, they are recurved posteriorly. In lateral view, the relative positions of the openings for cranial nerves II–V differ in *A. wichmannianus* and *Jainosaurus*. In *Jainosaurus* the openings for cranial nerves II, III, and V are collinear, but in *A. wichmannianus* this line is inclined such that it also passes through the opening for cranial nerve I. This feature may be autapomorphic. In addition, the braincase of *Jainosaurus* is larger than that of *A. wichmannianus*, but fewer elements are fused, suggesting that the two taxa had substantially different adult body sizes.

Although they do not pertain to the same genus, the braincases of both *Jainosaurus septentrionalis* and *Antarctosaurus wichmannianus* appear to belong to derived titanosaurs, sharing close affinities with Nemegtosauridae. However, the paucity of cranial remains within Titanosauria is such that cranial synapomorphies of Nemegtosauridae are ambiguous (Wilson, 2005); how closely the two genera are related awaits further discoveries and analyses.

Isisaurus colberti.— According to Wilson et al. (2005), Indian sauropod braincases appear to fall into two morphs: a robust and compact *Isisaurus* morph and a wide and flat *Jainosaurus* morph. *Isisaurus* morph braincases include specimens from Dongargaon, central India (ISI R199; Berman and Jain, 1982), Gujarat, western India (ISI R467; Chatterjee and Rudra, 1996), and Balochistan, western Pakistan (GSP-UM 7000; Wilson et al., 2005). *Jainosaurus* morph braincases include the two specimens from Bara Simla, central India, described here (GSI 27/497; ISI R162; Chatterjee and Rudra, 1996).

A salient difference between the *Isisaurus* and *Jainosaurus* morph braincases is the angle of projection of the occipital condyle. Berman and Jain (1982) noted that the occipital condyle is deflected from the plane of the occiput at an angle of about 120 degrees in the *Isisaurus* morph braincase from Dongargaon,



FIGURE 9 — *Isisaurus colberti*, right humerus (ISI R335/59) in anterior view. Scale equals 25 cm. Abbreviations as in Figure 8.

India (ISI R199), a feature that they regarded to be similar to *Diplodocus* and *Apatosaurus*. Wilson et al. (2005) reported a significant downward deflection of the occipital condyle in the *Isisaurus* morph braincase from Pakistan, in which the skull roof and occipital condyle meet at an angle of about 120 degrees. It should be noted that these two metrics measure different angles; the former is in reference to a subvertical plane formed by the plane of the occiput (paroccipital processes and supraoccipital), and the latter is in reference to a subhorizontal plane formed by the frontals and parietals. These two metrics attempt to capture the same feature—the orientation of the occipital condyle relative to a fixed plane in the skull. The long axis of the occipital condyle and the plane of the skull roof are nearly parallel (within 10 degrees) in most sauropods, including *Shunosaurus* (Zheng, 1991), *Camarasaurus* (Madsen et al., 1995), *Brachiosaurus* (Janensch, 1935-36), *Diplocodus* (Osborn, 1912), *Nemegtosaurus* (Wilson, 2005), *Nigersaurus* (Serenio et al., 2007), *Rapetosaurus* (Curry Rogers and Forster, 2004), and the indeterminate titanosauriform from Texas (Tidwell and Carpenter, 2003). In contrast, the long axis of the occipital condyle more closely parallels (within 25 degrees) the plane of the occiput in *Isisaurus* morph braincases from Pakistan, Rahioli, and Dongargaon (GSP-UM 7000, ISI R467, ISI R199, respectively). Wilson et al. (2005) pointed out that the deflection of the skull shared between diplodocids and *Isisaurus* morph braincases is achieved via different structural arrangements of the bones of

the skull: in diplodocids, the occipital condyle and skull roof are subparallel, and the rest of the skull is deflected, and in the *Isisaurus* braincases from Balochistan, Rahioli and Dongargaon, the occipital condyle itself is deflected relative to the skull roof.

Because the skull roof does not directly contact the occipital condyle (i.e., it is separated from the occipital condyle by a potential point of bending between the skull roof and the occiput), it is not as useful a landmark as is the occiput, which directly abuts the occipital condyle. Moreover, the skull roof is often not associated with the braincase (e.g., referred *Jainosaurus* braincase ISI R162), so using the occiput as the reference plane for deflection of the occipital condyle allows scoring of more incomplete specimens. Unlike the condition in *Isisaurus* morph braincases from India and Pakistan, in *Jainosaurus* the occipital condyle and skull roof are subparallel in orientation, and the plane of the occipital condyle forms an angle of 120 degrees with the plane of the occiput.

Like the braincases, titanosaur postcrania from Indo-Pakistan appear to be diagnostic. Unfortunately, there is very little scope for comparison between the known postcrania attributable to *Isisaurus* and *Jainosaurus*. Only the scapula, humerus, and ulna overlap, and the latter is now lost and surviving illustrations are not suitable for detailed comparisons. The scapulae of *Isisaurus* and *Jainosaurus* have strikingly different proportions. Whereas the *Isisaurus* scapula appears to be quite robust (total length = 1.08 m, maximum breadth = 0.60 m, minimum breadth = 0.29 m), that of *Jainosaurus* is more elongate (total length = 1.67 m, maximum breadth = 0.65 m, minimum breadth = 0.28 m). In addition to this proportional difference, the *Isisaurus* scapula also lacks the longitudinal ridge on the dorsal portion of the external blade that is present in *Jainosaurus*. The humeri of *Jainosaurus* and *Isisaurus* are similarly sized but also distinguishable. However, we must caution that the proximal end of the *Isisaurus* humerus is not well preserved (Fig. 9). General differences in the humeri include a much narrower proximal end with a more proximally placed deltopectoral crest in *Isisaurus*. Their overall lengths are similar (*Isisaurus* = 1.48 m; *Jainosaurus* = 1.34 m), but they might have been identical depending on how much of the distal end of *Jainosaurus* humerus is missing. *Isisaurus* lacks the inset and obliquely oriented deltopectoral crest, prominent lateral bulge, and expanded radial condyle that characterize *Jainosaurus*. The ulnae are both approximately 0.8 m long, but apparently had different robustness. Whereas *Isisaurus* has autapomorphically gracile ulnar shaft that is triradiate in midshaft cross-section, Huene and Matley (1933:22) described the shaft as “stout and somewhat subrectangular in section, being bounded by four flattish sides with rounded edges.”

Thus, it appears that there are grounds for establishing *Isisaurus* and *Jainosaurus* postcranial morphs, even if there is not a great deal of overlap between them. Additional features of the postcrania that diagnose *Isisaurus* are ambiguous because comparable material is not preserved of *Jainosaurus* (e.g., vertebral characters listed by Wilson, 2002 and Wilson and Upchurch, 2003). Likewise, diagnostic features in the hindlimb of the partial *Jainosaurus* skeleton from Chhota Simla are currently ambiguous (Wilson et al., in prep.), and definitive *Isisaurus* hindlimb material is not yet known.

Rapetosaurus krausei.— The Late Cretaceous Malagasy titanosaur *Rapetosaurus krausei* is an important taxon for comparisons with more fragmentary titanosaur specimens because multiple individuals are preserved with associated cranial and postcranial remains (Curry Rogers, 2005). As outlined below, the braincase of *Rapetosaurus* shares a few general similarities with that of *Jainosaurus*, but these features are either present in a broader distribution of titanosaurs, or they are dissimilar when viewed in detail. We could not identify unique features shared between *Jainosaurus* and *Rapetosaurus*.

The proportions in the posterior skull are very different between *Rapetosaurus* and *Jainosaurus*. The frontal of *Rapetosaurus* has nearly equal anteroposterior and transverse dimensions (Curry Rogers and Forster, 2004), but that of *Jainosaurus*, which is incompletely preserved, would have been nearly twice as wide as anteroposteriorly long. The frontals of *Rapetosaurus* together form a median dome that is absent in *Jainosaurus* and most other titanosaurs. The parietal of *Rapetosaurus* is more anteroposteriorly elongate than is that of *Jainosaurus*.

The supraoccipital of *Jainosaurus* bears a single nuchal crest that is well developed above the dorsal margin of the rest of the supraoccipital and has subparallel parasagittal sides. In contrast, *Rapetosaurus* possesses a median groove that is flanked by raised parasagittal ridges. *Jainosaurus* also lacks the two anteriorly directed paramedian processes on the supraoccipital that are regarded as autapomorphic for *Rapetosaurus* (Curry Rogers and Forster, 2004).

The occipital condyle of *Rapetosaurus* shares the primitive, parallel orientation relative to the skull roof with *Jainosaurus* and most other sauropods. The occipital condyles of the two taxa are similarly shaped, and both have a small depression on the ventral surface of the basioccipital-basisphenoid suture between the basal tubera. In addition, *Rapetosaurus* possesses a second depression posterior to the first that is located on the basioccipital.

Both *Jainosaurus* and *Rapetosaurus* have broad basal tubera that may have articulated with the quadrate, as in *Nemegtosaurus* and other titanosaurs (Wilson, 2005). Beyond this similarity, however, the morphology of the basal tubera and basiptyergoid processes in the two taxa is quite different. The basal tubera of *Rapetosaurus* are separated along their entire length, and they project at a distinct angle from the basiptyergoid processes, as best seen in lateral view (Curry Rogers and Forster, 2004: fig. 23E). In contrast, the basal tubera of *Jainosaurus* are round in posterior view, connected throughout their length by a web of bone, and are oriented parallel to the basiptyergoid processes in lateral view. Additionally, *Jainosaurus* possesses a small ventrolateral process on its basal tubera, a feature that *Rapetosaurus* and other titanosaurs lack. The basiptyergoid processes of *Rapetosaurus* are oriented parallel to one another and shorter than the basal tubera, whereas those of *Jainosaurus* diverge at an angle of about 50 degrees and are much longer than the basal tubera. This condition in *Rapetosaurus* is similar to that of *Malawisaurus* (Gomani, 2005), whereas the condition in *Jainosaurus* is more similar to *Nemegtosaurus*, *A. wichmannianus*, and *Saltasaurus*.

As in most titanosaurs, *Rapetosaurus* and *Jainosaurus* have pendant paroccipital processes. These processes are peg-like

distally in *Rapetosaurus*, whereas they are broad, flat tabs in *Jainosaurus*. Another difference is that the span across the paroccipital processes in posterior view is proportionately larger in *Rapetosaurus* than it is in *Jainosaurus* and *Antarctosaurus wichmannianus*. In both the latter taxa, the narrow condition is achieved by a sharp ventral bend in the paroccipital processes, which is absent in *Rapetosaurus*. Overall, the paroccipital processes of *Rapetosaurus* more resemble those of *Malawisaurus* and *Saltasaurus* than those of *Jainosaurus* (Curry Rogers and Forster, 2004). The laterosphenoid-orbitosphenoid region is proportionally narrower anteroposteriorly and taller in *Jainosaurus* than in *Rapetosaurus*.

The scapulae of *Jainosaurus* and *Rapetosaurus* are quite different in the proportions of the blades. Whereas the blade of *Rapetosaurus* is relatively short, it is markedly elongate in *Jainosaurus*. Both share the presence of a very moderate dorsal expansion of the scapular blade, but *Rapetosaurus* does not possess the pronounced longitudinal ridge on the external surface of the basal blade that is present in *Jainosaurus*. The humeri of *Jainosaurus* and *Rapetosaurus* are similarly proportioned in the development of their proximal and midshaft breadths relative to their lengths. Both have a bulge on their proximolateral side, but this is most strongly developed proximal to the deltopectoral crest in *Rapetosaurus*, instead of just distal to it as in *Jainosaurus*. Likewise, both taxa have an expanded radial condyle on the humerus, but in *Rapetosaurus* the ulnar condyle is also expanded. The humerus of *Jainosaurus* possesses two features that are absent in *Rapetosaurus*: a medially offset and obliquely oriented deltopectoral crest and thin bone forming the deltopectoral fossa.

“*Malagasy Taxon B*”. — Dissociated bones of a second taxon from the Maevarano Formation of northern Madagascar can be distinguished from *Rapetosaurus*. Differences were first noticed in the caudal centra, which are much more dorsoventrally compressed than *Rapetosaurus*, but other differences are apparent in forelimb elements and a newly discovered braincase of “*Malagasy Taxon B*” (Curry Rogers and Imker, 2007). These bones have not yet been formally described, but they overlap with the lectotypic and referred remains of *Jainosaurus*. In particular, the braincase of “*Malagasy Taxon B*” is strikingly similar to that of *Jainosaurus*, sharing the presence of a broad shallow fossa in the basal tubera, a notch in the ventrolateral corner of the basal tubera, and basiptyergoid processes that are directed nearly vertically (Curry Rogers, unpublished data). These and other similarities in the humerus suggest that *Jainosaurus* and “*Malagasy Taxon B*” are very closely related, a topic that will be developed in future work (Curry Rogers in prep.).

Other sauropod braincases.—Wilson (2002, 2005) noted that *Jainosaurus*, *Nemegtosaurus*, and other titanosaurs possess broad basal tubera, which probably indicate a novel contact between the quadrate and braincase, and a pendant, nonarticular flange on the paroccipital processes. The braincase of *Jainosaurus* shares with *Muyelensaurus* (Calvo et al., 2007), *Pitekunsaurus* (Filippi and Garrido, 2008), and an unnamed taxon from Río Negro (MML 194; Garcia et al., 2008) the

presence of a broad fossa separating the basal tubera and basiptyergoid processes that are directed parallel to the plane of the occiput. These conditions are absent in the *Isisaurus* morph braincases, *A. wichmannianus*, *Bonatitan*, *Rapetosaurus*, and *Nemegtosaurus*. *Pitekunsaurus* and *Muyelensaurus* can be distinguished from *Jainosaurus* by the height of the supraoccipital and the shape of the proximal basiptyergoid process in posterior view. Also, the frontal of *Jainosaurus* is substantially broader transversely, and the postcrania of the two taxa (i.e., scapula, ulna) appear to be significantly different. As in the case of *Antarctosaurus wichmannianus*, more informative comparisons between Indian and Argentine titanosaurs await further discoveries.

Phylogenetic affinities.—The precise phylogenetic relationships of *Jainosaurus* to other titanosaurs must await a full cladistic analysis, but some tentative conclusions can be made here. The only cladistic analysis to consider *Jainosaurus* positioned it in a polytomy including *Euhelopus* and other somphospondylans (Curry Rogers (2005)). Our observations offer additional resolution. Several features noted here, including a quadrate-basal tubera contact and pendant, nonarticular paroccipital processes suggest that *Jainosaurus* is a member of a clade of derived titanosaurs (Wilson, 2002; Wilson et al., 2005). Cranial and postcranial remains of sauropods across Indo-Pakistan separate into two easily distinguishable morphs, regarded here as corresponding to the genera *Isisaurus* and *Jainosaurus*. These morphs are substantially dissimilar cranially and postcranially and are not closely related.

Jainosaurus is more similar to “*Malagasy Taxon B*” and certain South American titanosaurs than it is to *Isisaurus* or the *Malagasy* titanosaur *Rapetosaurus*. Both *Antarctosaurus wichmannianus* and *Jainosaurus* have a tall nuchal crest on the supraoccipital, a sinuous parietal-supraoccipital contact, and broad basal tubera. Significant differences preclude their assignment to the same genus, however, including the orientation and median peak of the frontals, as well as differences in the morphology of the occiput and arrangement of cranial nerve openings. *Jainosaurus* shares additional derived features with the newly reported titanosaurs from the Late Cretaceous of Madagascar (i.e., “*Malagasy Taxon B*”) and South America (i.e., *Pitekunsaurus*, *Muyelensaurus*, the Río Negro taxon) that are not present in *Antarctosaurus*, such as a broad fossa between the basal tubera and basiptyergoid processes oriented in the plane of the occiput. We regard these results as preliminary for several reasons. First, cranial morphology remains unknown for most titanosaur genera, so the distribution of the features shared between *Jainosaurus* and the South American forms is unknown. Second, this hypothesis needs to be tested by a cladistic analysis. Last, there are major gaps in the titanosaur fossil record that result from asymmetric sampling and/or absence of terrestrial sediments in certain parts of the world. As for other terrestrial vertebrates (e.g., abelisaurids, Lamanna et al., 2002) the latest Cretaceous of Africa and Australia and the Early Cretaceous of India and Madagascar remain poorly sampled intervals, which limit our ability to resolve phylogenetic and biogeographic history.

HISTORICAL ASSOCIATIONS AND SYSTEMATIC PALEONTOLOGY

Undocumented field associations abound in early descriptions of dinosaurs. In many cases, the assumption that a collection of bones represented a single individual or a single species was implicit in description of a new taxon, rather than explicitly documented, so assessing the validity of field associations is paramount for revision of key early dinosaur genera. These historical associations can be interpreted across a spectrum that ranges between two extremes. At one extreme, individual or species associations are taken at face value in a “laissez-faire” manner. At the other extreme, associations are rejected out of hand, creating a “tabula rasa” upon which new, carefully documented associations can be established. Each of these extreme interpretations, however, can lead to undesirable taxonomic consequences. The “laissez faire” interpretation (i.e., accept associations and continue) can lead to incorrect assumptions about taxonomic content and propagate continued misassociation, especially when new remains are discovered and incorporated into the existing taxonomic framework. The “tabula rasa” interpretation (i.e., reject associations and start over) can lead to more pernicious problems of proliferating names and a backlog of specimens of uncertain association that play little to no role in furthering our understanding of the fossil record.

The fossil record of Indian dinosaurs has fostered a mix of both “laissez faire” and “tabula rasa” interpretations. Certainly, there has been a proliferation of named dinosaur taxa, which suggests that researchers have favored creating new names rather than incorporating new finds into existing taxa. Of the nearly 30 Late Cretaceous dinosaur species named from India and Pakistan, only 5–9 are valid. This is due in part to the Indian Cretaceous fossil record, from which few associated dinosaur skeletons have been recovered, and exacerbated by the fact that many original specimens, including holotypes, are now lost and comparisons must rely on published descriptions (e.g., “*Titanosaurus*”, *Lametasaurus*, *Indosuchus*). Thus, lack of associated specimens and loss of original materials has led to an implicit shift to the “tabula rasa” extreme. A good example of this approach is the recent discussion of the validity of “*Titanosaurus*”, whose type species was discovered at Bara Simla in 1828 (Sleeman, 1844). Wilson & Upchurch (2003) concluded that the holotypic materials of “*T. indicus*” (whose whereabouts are unknown) are invalid, implying that the genus “*Titanosaurus*” and its coordinated rank-taxa are also invalid. This decision has placed many Indian dinosaur bones formally referred to “*Titanosaurus*” in a more ambiguous—although appropriate—taxonomic position than before. In contrast, a more “laissez-faire” interpretation was presented by Hunt et al. (1994: 266) in their “Taxonomic Case Study” that focused on Indian dinosaurs and *Jainosaurus*: “Isolated, but distinct, postcrania may be considered valid type specimens and disassociated specimens from the same bed should be grouped as much as possible. These usually questionable taxonomic procedures are only tolerated in sauropods because these immense animals are so often represented by such fragmentary or jumbled specimens”. Hunt et al. (1994:266)

did not include the postcranial remains in the *Jainosaurus* lectotype, but instead designated them paralectotypes because “their exact association with the lectotype cannot be determined”. A “paralectotype” refers to specimens of a former type series that remain after the lectotype has been designated (ICZN Article 73.2.2).

Short of recovering additional remains that confirm or refute the claimed associations, relatively few tests can be applied to determine the validity of field associations out of context. As recently outlined by Longrich (2008: 993), testable predictions can be made when fragmentary, dissociated fossils might be referred to a single taxon, including (1) congruent size between elements, (2) similar relative abundances of elements pertaining to the new taxon in question, (3) similar stratigraphic and geographic ranges, and (4) similarity of serially homologous features among dissociated elements. *Jainosaurus septentrionalis* materials were collected from a single locality (the “Sauropod Bed” at Bara Simla) by a single research team (Matley and a field assistant) over a relatively short period of time (field seasons between 1917 and 1920). Apart from the holotypic caudal vertebrae of “*T. indicus*” and remains referred to that species (tibia, fibula, chevron), no other sauropod genera have been reported from the “Sauropod Bed” at Bara Simla. Although Longrich’s (2008) predictions (1)–(3) can be reliable with large sample sizes, these predictions have less power to establish associations for smaller sample sizes, such as for *Jainosaurus*: ontogenetic variation in shape and their ontogenetic size range is unknown, relative abundances are susceptible to taphonomic and other biases, and the spatiotemporal distribution of a fragmentary taxon is subject to expansion. The fourth prediction listed by Longrich (2008) is useful in a general sense, but not for the specific case of *Jainosaurus* due to lack of preservation of serially homologous elements (e.g., teeth, vertebrae, manual or pedal digits).

Our taxonomic decision to refer some postcranial bones to *Jainosaurus septentrionalis* (outlined in “Systematic Paleontology”) attempts to strike a balance between the “laissez faire” and “tabula rasa” approaches. In the latter sense, we agree with Hunt et al. (1994) that none of the paralectotypic postcranial bones can be safely attributed to the same individual as the lectotypic braincase. Likewise we agree with Wilson and Upchurch (2003) that there is a need to ensure the name-bearing materials of a species are definitively associated, and that referrals are based on diagnostic features. In the former sense, we endeavor to enlist as much information as possible about the Indian Cretaceous dinosaur record, stratigraphy, and historical records to establish tentative associations between the braincase morph and the postcranial morph. In the latter sense, our taxonomic decisions are transparent and testable, and they provide a foundation for future work on the Indo-Pakistani Cretaceous dinosaur record.

CONCLUSIONS

Jainosaurus septentrionalis is a Late Cretaceous Indian titanosaur whose taxonomic history has been complicated by several

factors, including its early discovery, which precluded comparisons with more complete taxa (until quite recently; see Curry Rogers, 2005), its discovery in a multi-individual, multi-taxon bonebed from which no records of field associations exist; loss of several of the elements in museum collections over time; and initial comparisons with a South American species that has its own complex taxonomic history (i.e., *Antarctosaurus wichmannianus*). *Jainosaurus septentrionalis* was originally named as the sister species to *Antarctosaurus wichmannianus*, replicating a taxonomic pattern that was common in early descriptions of Indian and South American titanosaurs, but significant differences evident in the braincase preclude its assignment to the Argentine genus.

Historical and taphonomic evidence suggests that most of the elements in the “type series” of *Jainosaurus septentrionalis* by Huene and Matley (1933), including the braincase, scapula, humerus, radius, ulna, and ribs, can be regarded as belonging to a single taxon, and some of them belonged to a single individual. An additional braincase from the same locality (Bara Simla), and humeri from other localities (Chhota Simla, Madhya Pradesh; Rahioli, Gujarat; Vitakri, Balochistan) can also be referred to *Jainosaurus*. The presence of multiple individuals from widespread geographic locations is a rarity within Titanosauria, so that continued excavations in Indo-Pakistan hold promise for bringing to light details of titanosaur paleobiology and paleoecology not available for most single-taxon or single-locality titanosaur genera.

The cranial and postcranial remains of *Jainosaurus* are differentiable from those of the other Indian Cretaceous sauropod, *Isisaurus colberti*, based on many features that include the orientation of the occipital condyle, shape of the basal tubera, and proportional differences in the humerus and scapula. These Cretaceous Indian taxa do not share a sister-taxon relationship within Titanosauria; *Jainosaurus* appears to be more closely related to “Malagasy Taxon B” and the South American titanosaurs *Pitekunsaurus*, *Muyelensaurus*, and *Antarctosaurus wichmannianus* than to *Isisaurus* or to the Malagasy titanosaur *Rapetosaurus krausei*. These phylogenetic conclusions await confirmation via a full cladistic analysis of Titanosauria.

Thus, our current understanding of Indo-Pakistan’s Cretaceous sauropods does not match predictions of faunal endemism following an extended period of isolation as India migrated northwards. Instead, both cranial and postcranial characters indicate close phylogenetic affinities between *Jainosaurus* and titanosaurs from both Madagascar and South America. Future work will aim to better resolve these phylogenetic relationships, as well as those of other titanosaurs.

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